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THE SYSTEMATICS AND ECOLOGY
OF THE MANGROVE-DWELLING *LITTORARIA* SPECIES
(GASTROPODA: LITTORINIDAE)
IN THE INDO-PACIFIC

VOLUME II

Thesis submitted by

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PART II: ECOLOGY

CHAPTER 10: COCKLE BAY, THE PRINCIPAL STUDY AREA

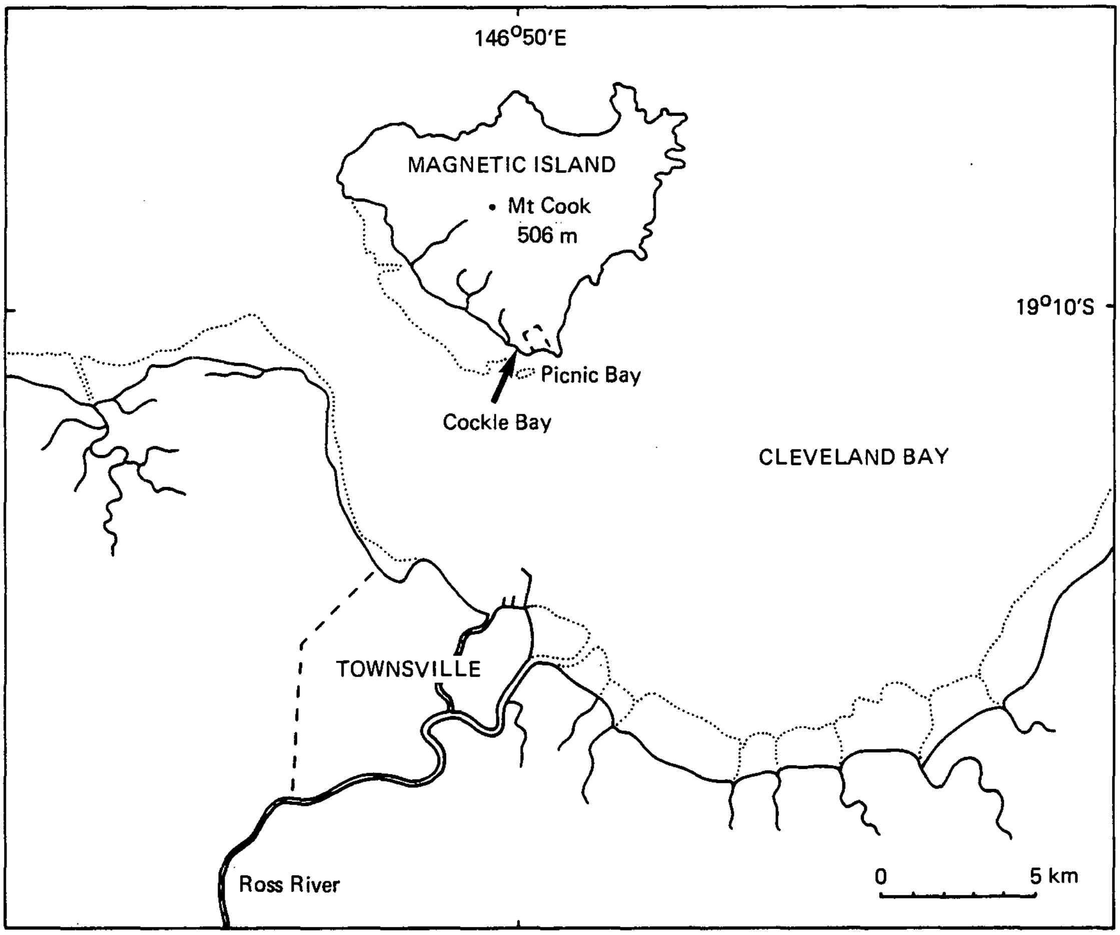
Magnetic Island is situated in Cleveland Bay, 7 km from the city of Townsville (Fig. 10.1). The island is approximately 5000 hectares in area and is mostly mountainous, reaching 506 m at its highest point. The geology of the island is comprised of acid plutonic rocks of late Palaeozoic age, with a narrow coastal plain of Quaternary deposits (Spenceley, 1982). The sheltered landward coast runs for 7 km in a north-westerly direction, separated from the mainland by a channel from 5 to 7 km in width. Along this coast an extensive mangrove forest has developed behind a broad mud flat with beds of sea grass, which extend to a fringing reef 1 to 1.5 km from the edge of the forest.

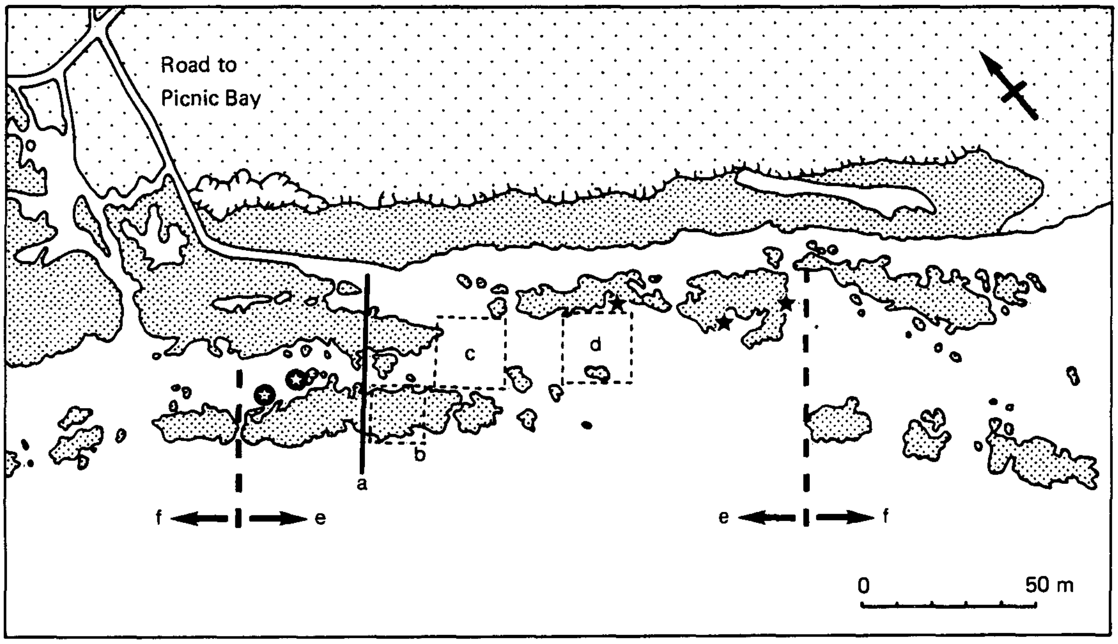
At its widest point, the mangrove forest extends for 500 m, and adjoins a *Melaleuca* swamp or *Eucalyptus* woodland at the level of the highest spring tides. The floristic zones of seaward *Avicennia* fringe, *Rhizophora* forest, *Bruguiera* forest and *Ceriops* thickets are all represented (Section 11.2; Macnae, 1968), but the *Ceriops* zone is in some parts interrupted by a bare salt flat (Fig. 11.2). The vegetation of the island coast has been described in detail by Macnae (1967) and Spenceley (1982).

Climatic and tidal data for the Townsville area are summarized by Spenceley (1982). The rainfall is highly seasonal, 76% of the average annual total falling between January and April. An annual rainfall of 1825 mm (recorded at Picnic Bay, 1 km from the main study site) has permitted a relatively luxuriant development of mangrove vegetation on the landward side of Magnetic Island. In contrast, the mainland coast of Cleveland Bay has a lower rainfall (1163 mm at Townsville, Spenceley, 1982) and mangroves are present

Fig. 10.1 Map of Magnetic Island and Cleveland Bay, Queensland. Dotted line indicates extreme low water of spring tides.

Fig. 10.2 Map of the study area at Cockle Bay, Magnetic Island, Queensland. a, line of transect represented in Fig. 11.1; b, 15 by 15 m study area in *Rhizophora* grove; c and d, study areas (defoliated and normal *Avicennia* bushes respectively) for investigation of frequency-dependent selection on colour forms of *Littoraria filosa* (Section 15.3); e, limits of experimental zone; f, sampling zone; solid asterisks, sites of five *Avicennia* trees for mark and recapture study of *L. philippiana*; open asterisks, sites of two *Avicennia* trees for mark and recapture study of *L. filosa*; light stipple, sclerophyll woodland; heavy stipple, mangrove forest.


146°50′E
MAGNETIC ISLAND
Mt Cook
506 m
19°10′S
Picnic Bay
Cockle Bay
CLEVELAND BAY
TOWNSVILLE
Ross River
0
5 km


Road to
Picnic Bay
a
b
c
d
f
e
e
f
0
50 m

mainly as narrow fringes to extensive bare salt pans (Macnae, 1967). It was for this reason that Magnetic Island was chosen as the main study area. Furthermore, the land behind the mangrove coast is virtually uninhabited, and the area should be less affected by domestic, industrial and agricultural pollution than the mainland coast.

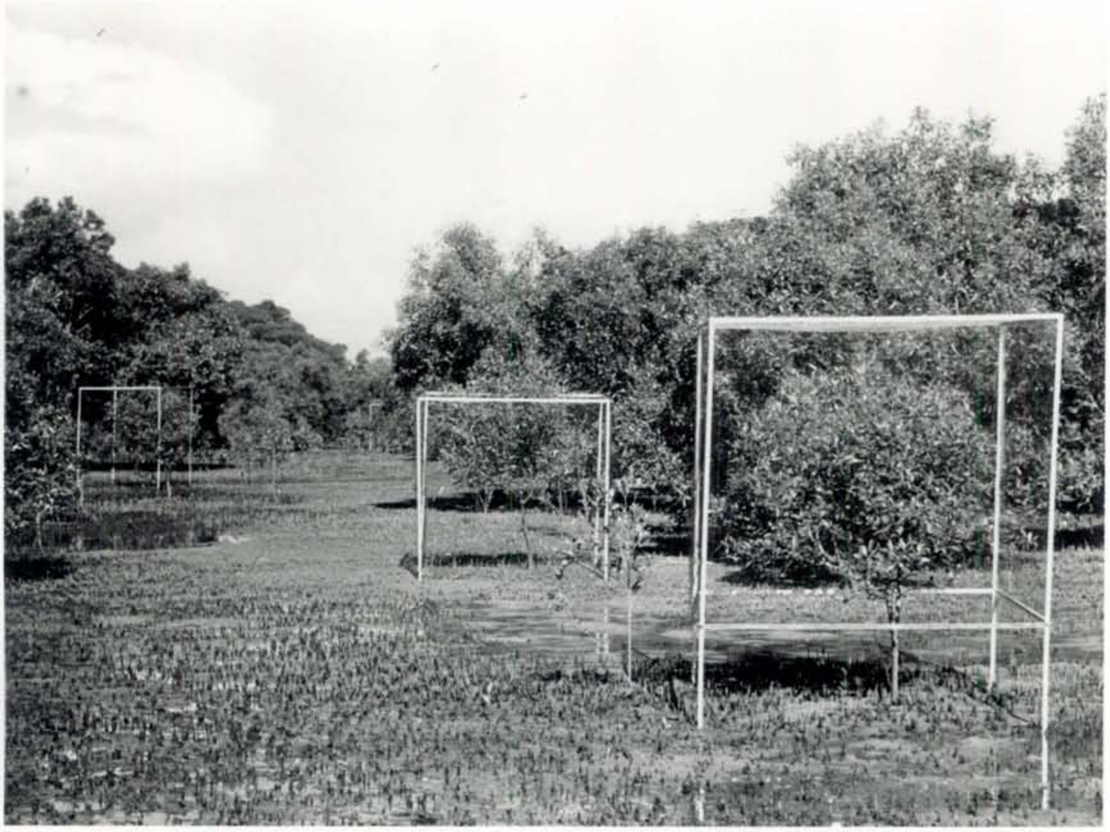
Several *Littoraria* species are scarce or absent on muddy continental coasts, and more common in narrow mangrove fringes and where the coastal water is less turbid (Section 11.4.5). Thus, while only three species were to be found in the broad and muddy forest midway along the mangrove coast of Magnetic Island (as listed, Fig. 11.2), five species were common at Cockle Bay at the southern end of the belt of forest (Fig. 11.1). Cockle Bay was therefore selected as the study site, (19° 10.5'S 146° 49.6'E; Fig. 10.2).

The structure of the forest at Cockle Bay is somewhat atypical, by virtue of a long sand bar which has developed parallel to the coast, within what was once a belt of *Rhizophora* forest. As a result, the typical zonation pattern of the forest has been interrupted. At the present time there are several isolated groves of *Rhizophora stylosa* trees, up to 8 m in height, in front of the dune, and behind them an open area of muddy sand with a few isolated trees of *Avicennia eucalyptifolia* and increasing numbers of colonizing *Avicennia* bushes and saplings (Figs 10.3, 10.4). A transect through this area is represented in Fig. 11.1.

The study area was divided into experimental, sampling and undisturbed zones (Fig. 10.2). Within the experimental zone a number of trees were selected in three areas, on the basis of the abundance of four species of *Littoraria* which were to be studied in detail. The first area comprised all the 64 *Rhizophora* trees in the space of 15 m by 15 m within a *Rhizophora* grove, where *L. scabra*, *L. intermedia* and *L. philippiana* were common. Secondly, two isolated trees of *Avicennia* between the *Rhizophora* grove and sand bar, were chosen because of the abundance of *L. filosa*. Thirdly, five larger

Fig. 10.3 The exclusion cages at Cockle Bay, Magnetic Island, Queensland. See Section 14.2.2 for details. The large *Avicennia* tree behind the foremost cage is one of the two on which the mark and recapture study of *Littoraria filosa* was carried out.

Fig. 10.4 Aerial view of study area at Cockle Bay, Magnetic Island, Queensland. Road to Picnic Bay in background (see map, Fig. 10.2).



Avicennia trees on the edge of the sand bar were selected for study, on each of which *L. philippiana* was common. Details of the dimensions of trees are given in Table 10.1. All trees were identified individually by numbers, and the ground level beneath each was estimated (to the nearest 0.1 m) in relation to tidal datum, by comparison of water depth with predicted tidal heights at recorded times on three occasions.

Within each of these study areas all the snails were individually numbered, for the purposes of recording their location on the trees, their growth and, by employing a mark and recapture technique, to investigate population dynamics. Details of the methods used are given in the appropriate later chapters. Exclusion experiments, to measure loss due to predation and other causes, were carried out on small, isolated *Avicennia* trees in the area between the *Rhizophora* grove and the sand bar (Fig. 10.3). An experiment to investigate frequency-dependent selection was performed in an area with numerous isolated and equally sized *Avicennia* bushes (Fig. 10.2). Specimens for the examination of reproductive condition were collected from the sampling area reserved for the purpose.

Table 10.1 Dimensions of trees in three main study areas at Cockle Bay, Magnetic Island, Queensland.

Littoraria sp. studied	Tree sp.	No. of trees	Height (m)	Lowest foliage (m)	Canopy width (m)	Diameter at breast ht. (cm)
L. scabra, *L. intermedia*, *L. philippiana*	*Rhizophora stylosa*	64	4–8	1–3.5	1–3	5–18
L. filosa	*Avicennia eucalyptifolia*	2	3,4	0.6,0.1	3	5,10
L. philippiana	*Avicennia eucalyptifolia*	5	4–5	0.2–1.4	3–5	10–17

CHAPTER 11: HABITAT AND ZONATION

11.1 Introduction

The association of many members of the genus *Littoraria* with mangrove, salt marsh and drift wood habitats represents a major adaptive shift away from the ancestral habitat of intertidal rocks. That this condition is indeed derived is indicated by the fact that *Littoraria* species typical of rocky substrates occur only in the paraphyletic nominate subgenus (Section 8.1.2 and Fig. 8.2). Outgroup comparison with the sister group *Nodilittorina* leads to the same conclusion, for all but one of the many species of *Nodilittorina* occur only on rocky shores (pers. obs. and museum collections). In littorinid genera other than *Littoraria*, only a few species can be found on vegetation. These include a single species of *Nodilittorina* (a rare, undescribed species from South East Asia), *Bembicium melanostoma* (in eastern Australia), a species of *Peasiella* (in northern Australia) and several members of the genus *Littorina* which are sometimes found on salt marsh vegetation in the northern Atlantic (Raffaelli, 1978b).

At most mangrove localities *Littoraria* species are the only abundant arboreal gastropods. On the trees at the seaward edge of the forest, gastropods typical of rocky shores can sometimes be found, including species of *Patelloida*, *Monodonta*, *Clypeomorus*, *Planaxis*, *Morula* and *Thais*, usually at low densities and at tidal levels below those occupied by *Littoraria*. Within the forest several species of *Nerita* are found, while towards the landward edge of the forest *Cerithidea* and various ellobiid pulmonates climb the mangrove trees, descending to feed at low tide (see Macnae, 1968; Berry, 1972; Frith *et al.*, 1976, for general accounts of the molluscan fauna of Indo-Pacific mangroves). At none of the localities visited during the present study did these other arboreal gastropods occur in large numbers at the same levels as *Littoraria* species, and their respective patterns of distribution did not suggest any evidence of interspecific competitive effects. Other arboreal gastropods have therefore not been considered in the accounts of zonation patterns of *Littoraria* species which follow.

Littorinids are so characteristic of high intertidal levels on both temperate and tropical rocky shores that Stephenson & Stephenson (1949) defined the supralittoral fringe in terms of their occurrence. An extension of their scheme for application to zonation on mangrove trees was suggested by Berry (1963), who defined an upper *Littorina* zone and lower *Nerita* zone in the forest, and at the seaward edge a bivalve zone.

On shores where several littorinid species co-occur, it is well known that they tend to occupy partially separate levels (Underwood, 1973; Vermeij, 1973a; Bandel, 1974; Heller, 1975a; Bandel & Kadolsky, 1982). Such patterns have also been described in the mangrove forests of Indo-Malaya, which is the only region in which more than the one species *Littorina 'scabra'* have previously been recognized (Berry, 1963, 1972; Vermeij, 1973a, b; Sasekumar, 1974; Frith *et al.*, 1976; Murty & Rao, 1977). Other accounts of the habitat and zonation of tree-dwelling littorinids have referred to single species, either *L. melanostoma* (Berry & Chew, 1973) or more commonly to *L. 'scabra'* (Abe, 1942; Stephenson *et al.*, 1958; Macnae & Kalk, 1962; Day, 1974; Nielsen, 1976; Marshall & Medway, 1976; Muggeridge, 1979). These published accounts are sometimes purely qualitative, and in all cases have failed to distinguish correctly between species within the *L. scabra* complex.

The aim of this chapter is to present quantitative descriptions of zonation patterns in a range of representative localities in Australia, South East Asia and Hawaii. The behavioural aspects of zonation, including migratory habits and the distribution of size classes, are examined in Chapter 12. The shell characters of the species are related to their zonation patterns in Chapters 14 and

15.

11.2 The mangrove habitat

As pointed out by Berry (1963, 1972) and Macnae (1968), a mangrove forest provides a three-dimensional substrate, so that the arboreal fauna may show both a vertical zonation pattern up the trees and a horizontal distribution pattern through the swamp from seaward to landward. The most striking example of horizontal zonation in the mangrove environment is that of the tree species themselves. Macnae (1966, 1968) has described the zonation of mangrove vegetation in terms of the dominant tree species in each association, and presented a generalized scheme for the zonation of mangrove forests throughout the Indo-Pacific province. From the seaward edge of the forest he recognized the following zones:

1. *Sonneratia* zone
2. seaward *Avicennia* zone
3. zone of *Rhizophora* forests
4. zone of *Bruguiera* forests
5. zone of *Ceriops* thickets
6. landward fringe

This sequence is only developed fully in the wet tropics.

The seaward limit of mangrove trees is usually at about mean sea level, and the landward limit at the extreme high water mark of spring tides (Macnae, 1968). On many shores the trees at the seaward edge of the forest are species of *Avicennia*, which often form a relatively narrow fringe. *Avicennia* is commonly the pioneering tree species on shores newly colonized by mangroves (Figs 11.7, 11.12) and is the only species to be found at the southern extremes of the geographical range of mangroves (Chapman, 1976; Saenger *et al.*, 1977; Figs 11.5, 11.6). In tropical regions a zone of *Sonneratia* trees may occur to the seaward of the *Avicennia* fringe, but does not usually develop into a dense belt (Macnae, 1968; Figs 11.8, 11.11, 11.13).

Behind the seaward *Avicennia* zone lies the *Rhizophora* forest, usually a dense belt of wide extent. In some circumstances, *Rhizophora* may be the pioneering tree at the seaward edge if no *Avicennia* zone is present (Jones, 1971; Figs 11.3, 11.4, 11.10).

The development of the more landward zones of vegetation depends, to a considerable degree, upon rainfall (Macnae, 1968). Towards the landward side of the *Rhizophora* zone, trees of *Bruguiera* may appear, but only form a definite zone in areas of high rainfall (not clearly visible in any of the transects in the present study, but shown to a small extent in Fig. 11.3). Where rainfall, or freshwater runoff from the land, is lower, the *Bruguiera* zone is compressed or absent, and behind the *Rhizophora* forest a zone of low *Ceriops* thickets is present (Fig. 11.2). *Ceriops* is a genus tolerant of the high levels of soil salinity which occur in these areas, where evaporation is high, rainfall low, and inundation is by spring tides only (Macnae, 1968). Where soil salinity is excessive, bare salt pans appear in this zone, as commonly found in tropical Australia (Spenceley, 1976; Fig. 11.2). Development of the landward fringe is also dependent upon rainfall and freshwater influence. This is the zone of maximum floristic diversity, and is most extensive in the wet tropics (Macnae, 1968; Figs 11.10, 11.11, 11.13). The landward fringe is inundated only by high spring tides, but may receive considerable runoff from the land. In regions of low rainfall, the landward fringe is represented only by a belt of *Avicennia* and by samphires such as *Arthrocnemum* (Saenger *et al.*, 1977).

Mangrove forests occupy a wide variety of coastal landforms, including tidal and alluvial plains, lagoons, drowned bedrock coasts and fringing reefs (Galloway, 1982; Thom, 1982) and their structure and zonation vary accordingly. Although the sites visited during the present work covered a range of conditions, no estuarine or lagoonal sites were investigated.

In some regions mangrove swamps have been considerably influenced by human intervention, often in the form of felling (Fig. 11.10) or drainage (Fig. 11.11). Since *Littoraria* species are dispersed as planktotrophic veligers (Section 7.2), disturbed mangrove areas are soon recolonized (Davis, 1974). No evidence of collection of *Littoraria* species for food or bait was discovered, either at the main study site on Magnetic Island or at the localities in South East Asia.

The structure of the forest can be influenced by many variables, including geographical location, rainfall, landform and human interference, and the few examples presented here can only represent a small proportion of the range of mangrove environments in which *Littoraria* species occur.

11.3 Methods

Observations on the habitats and zonation patterns of *Littoraria* species were made at many sites along the north-eastern coast of Queensland from Proserpine to Cape Tribulation, and elsewhere in Australia in the vicinity of Sydney, New South Wales; at Shark Bay and near Broome in Western Australia; at Darwin and on the Gove Peninsula in the Northern Territory; and in the Torres Strait Islands. Observations were also made at localities in Thailand, peninsular Malaysia, Sarawak, Singapore and in Hawaii. A complete list of the localities visited is given in Table 11.1. Additional information was obtained from data accompanying museum specimens (Section 3.1).

At certain localities (Table 11.1), the distribution of littorinids through the mangrove forest was recorded by sampling at stations along a transect. Descriptions of these localities are given in the captions of Figures 11.1 to 11.14, with rainfall data

Table 11.1 List of mangrove localities visited.

Region	Locality	Figure of transect
Queensland	Shute Harbour, Proserpine	
	Cape Ferguson	
	Long Beach, Cape Cleveland	
	Alligator Creek, Cleveland Bay	
	Rowes Bay, Townsville	
	Three Mile Creek, Pallarenda, Townsville	
	Cockle Bay, Magnetic Island	11.1
	2 km N. of Cockle Bay, Magnetic Island	11.2
	West Point, Magnetic Island	
	Bohle River mouth, 16 km NW. of Townsville	
	Saunders Beach	
	Pioneer Bay, Orpheus Island, Palm Islands	11.3
	Missionary Bay, Hinchinbrook Island	
	Dunk Island	
	Green Island	
	Port Douglas	
	Low Isles	
	Cape Tribulation	
	Thursday Island, Torres Strait	
	St. Paul's Mission, Moa Island, Torres Strait	11.4
New South Wales	Bonna Point, Kurnell Peninsula, Botany Bay	11.5
	Careel Bay, Pittwater	
Western Australia	Little Lagoon, Denham, Shark Bay	11.6
	Red Bluff, 2 km N. of Monkey Mia, Shark Bay	
	Monkey Mia, Shark Bay	
	Mangrove Point, Carnarvon	
	Little Crab Creek, 15 km E. of Broome	
	Lookout Hill, Broome	11.7
	Dampier Creek, Roebuck Bay	
	Willies Creek, 20 km N. of Broome	
Northern Territory	Ludmilla Creek, 6 km N. of Darwin	11.8
	Buffalo Creek, 15 km NE. of Darwin	
	Mindil Beach, Darwin	
	East Arm, 8 km ESE. of Darwin	
	East Point, 7 km N. of Darwin	
	Sadgroves Creek, Frances Bay, Darwin	
	N. side of Inverell Bay, Gove Peninsula	
	Creek opposite East Woody I., Gove Peninsula	11.9
	1 km E. of Nhulunbuy, Gove Peninsula	
Thailand	Ao Nam Bor, Phuket Island	11.10
	Patong, Phuket Island	
	Kanchanadit, 15 km SE. of Surat Thani	11.11
Malaysia	Batu Maung, Penang	11.12
	Pantai Acheh, Penang	
	Pantai Merdeka, Sungei Merbok estuary, Kedah	
	10 km N. of Port Kelang	
Sarawak	Santubong	11.13
Singapore	Jelutong, Pulau Ubin	
Hawaii	Coconut Island, Kaneohe Bay, Oahu	11.14
	Heeia Bay, Oahu	

from the Bureau of Meteorology (1966), Wernstedt (1972), Department of Geography of the University of Hawaii (1973) and Spenceley (1982). The stations were specified by their distance in metres from station 0 at the seaward edge of the forest. Intervals between stations ranged from 5 to 30 m, according to the extent of the forest, and at least one station was sampled in each of the floristic zones present (Section 11.2). At each station the composition of the vegetation was estimated by counting the number of trees (excluding saplings less than 1 m in height) in two 5 m squares, one on each side of the transect line. Maximum tree height and the level of the lowest foliage were recorded for each tree species. Mangrove trees were identified to genus using works by Jones (1971), Percival & Womersley (1975), Lear & Turner (1975) and Semeniuk *et al.* (1978).

Owing to the great range of size and density of mangrove trees, and to differences in shape of their branch and aerial root systems, it was not possible to measure the abundance of *Littoraria* species as the number of individuals occurring per tree, or per unit area of tree surface or of ground area of the forest. Instead, the number of snails seen in a search time of two minutes was employed as an estimate of abundance. Separate two minute searches were made for each *Littoraria* species on each combination of tree species and substrate, so that for each species the search could be concentrated in the zone of maximum abundance. Substrates were classified as leaves (including terminal green twigs) or as bark (including trunks, branches and aerial roots), and searches were made only on the one or two dominant tree species at each station. The snails are conspicuous to a practised eye, and from three to ten trees could be searched in two minutes, so it is thought that the figures obtained for each station were representative. For each species the vertical range was recorded as minimum and maximum heights above the ground, to the nearest 0.1 m.

All transects were run while the area was completely exposed at low tide. Where tidal conditions permitted, ground level at each station was later estimated from water depth and predicted tidal levels. In many cases the most landward station was situated in the middle of the landward zone of the forest, at which the level was taken to be the mean high water mark of spring tides (MHWST) (Macnae, 1968).

The method described provides only an approximate indication of abundance and zonation. When making comparisons of abundance between tree species, the form of the tree needs to be noted: the straight trunks of *Avicennia* are more easily searched than those of *Rhizophora* trees with abundant prop roots; the large leaves of the *Rhizophora* canopy can be scanned more rapidly than the foliage of *Avicennia* with smaller and varicoloured leaves. The abundance of certain *Littoraria* species, particularly those with restricted breeding seasons which occur at the higher tidal levels, may show considerable fluctuations throughout the year (Section 13.3.2). In addition, the vertical distribution of *Littoraria* species is strongly influenced by the phase of the monthly tidal cycle and by rainfall (Chapter 12). For these reasons, abundances and vertical ranges of species at a particular locality should only be regarded as relative, and comparisons between localities should be interpreted with caution.

Generalizations concerning the habitats and zonation patterns of species are based not only upon the transects figured, but upon observations at all localities listed in Table 11.1, and upon data accompanying museum specimens as listed in Chapter 9.

Fig. 11.1 Cockle Bay, Magnetic Island, Queensland.

Tidal levels: MHWS 2.9 m; MHWN 2.0 m; previous high water 2.3 m.

Date: 18 May, 1981.

Description: Rather narrow mangrove fringe at southern end of leeward side of large, high, granite island, 7 km off mainland and 8 km from mouth of the Ross River. Sediment of coarse sand and mud. Water turbid. Extensive mud flat and fringing reef beyond mangrove fringe. Rainfall 1825 mm.

Zonation: *Avicennia* fringe, *Rhizophora* forest, pioneering *Avicennia*, *Rhizophora* forest; double front system caused by relatively recent incursion of sand dune at back of forest. Abbreviations: A, *Avicennia*; Ac, *Aegiceras*; Ae, *Aegialitis*; B, *Bruguiera*; C, *Ceriops*; Ca, *Camptostemon*; DW, dead wood; E, *Excoecaria*; L, *Lumnitzera*; MHWST, mean high water of spring tides; N, *Nypa*; P, *Phoenix*; R, *Rhizophora*; Ra, *Rhizophora apiculata*; Rs, *Rhizophora stylosa*; S, *Sonneratia*; Sc, *Scyphiphora*; X, *Xylocarpus*.

Conventions: Transect diagram (top) shows height of tree species and of lowest foliage; number of trees drawn indicates approximate number that would be seen in a belt 1 m wide along the transect, on the basis of the density of trees estimated at each sampling station (kite diagrams). Histograms of abundance of *Littoraria* species indicate numbers seen in separate two minute searches on bark substrates (black) and on leaves (unshaded); in addition are shown ground level and the range of vertical heights occupied by the species at each station (stippled).

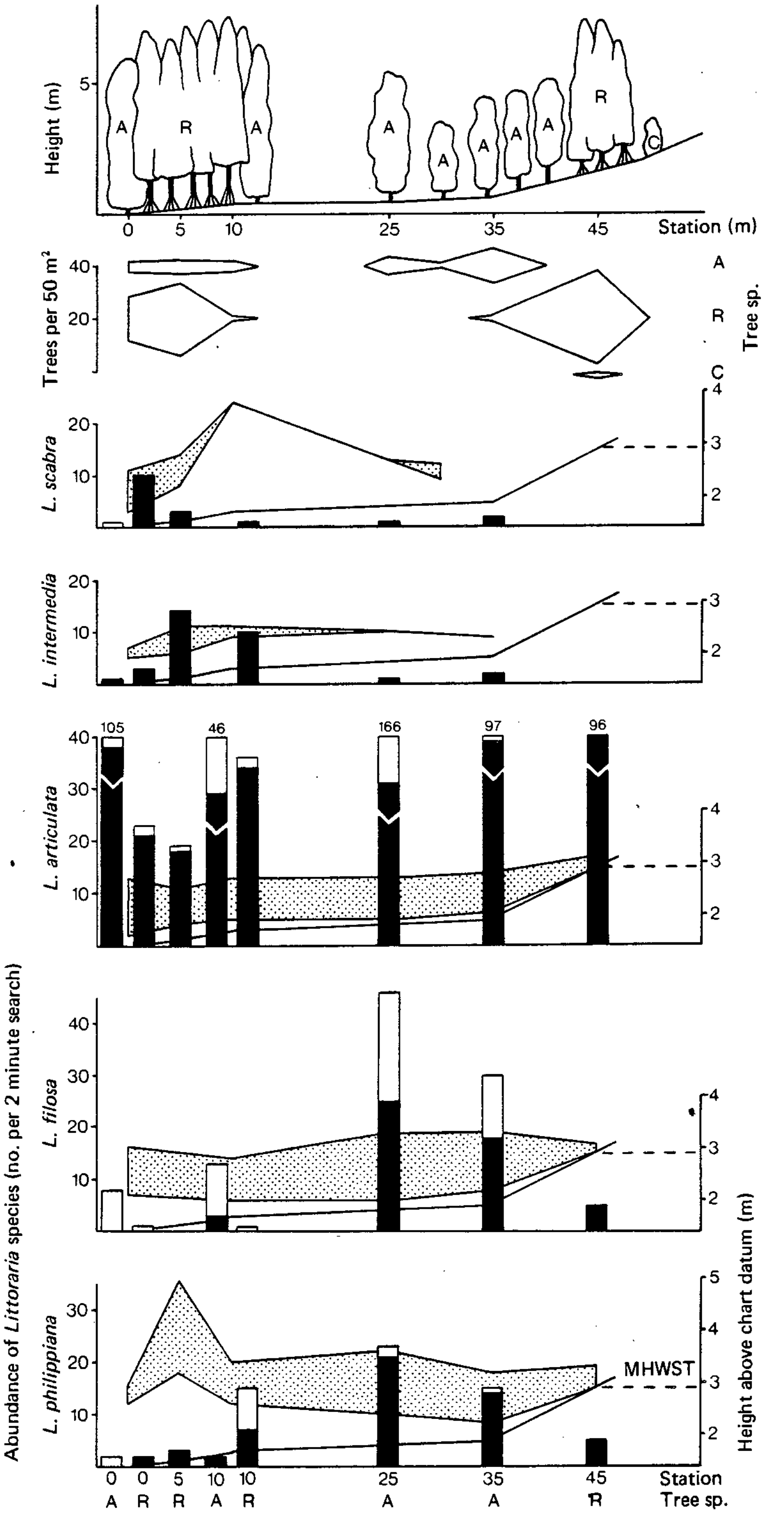

Height (m)
5
A
R
A
A
A
A
A
A
R
C
0
5
10
25
35
45
Station (m)
Trees per 50 m²
40
20
A
R
C
Tree sp.
L. scabra
20
10
4
3
2
L. intermedia
20
10
3
2
L. articulata
105
46
166
97
96
40
30
20
10
4
3
2
L. filosa
40
30
20
10
4
3
2
L. philippiana
30
20
10
5
4
3
2
MHWST
Abundance of Littoraria species (no. per 2 minute search)
Height above chart datum (m)
0 0 5 10 10 25 35 45
Station
A R R A R A A R
Tree sp.

Fig. 11.2 2 km north of Cockle Bay, Magnetic Island, Queensland.

Tidal levels: MHWS 2.9 m, MHWN 2.0 m, previous high water 1.7 m.

Date: 8 September, 1981.

Description: Broad expanse of forest on leeward side of large, high, granite island, 7 km off mainland and 10 km from mouth of the Ross River. Sediment of thick mud. Water turbid. Broad mud flat beyond pioneering fringe of mangroves. Extensive bare salt pan behind *Ceriops* thickets. Rainfall 1825 mm.

Zonation: Pioneering *Avicennia* fringe; *Rhizophora* forest (continuity of this zone interrupted by cyclone damage and subsequent regeneration of *Avicennia*); poorly developed *Bruguiera* zone; *Ceriops* thickets.

Abbreviations and conventions as in Fig. 11.1.

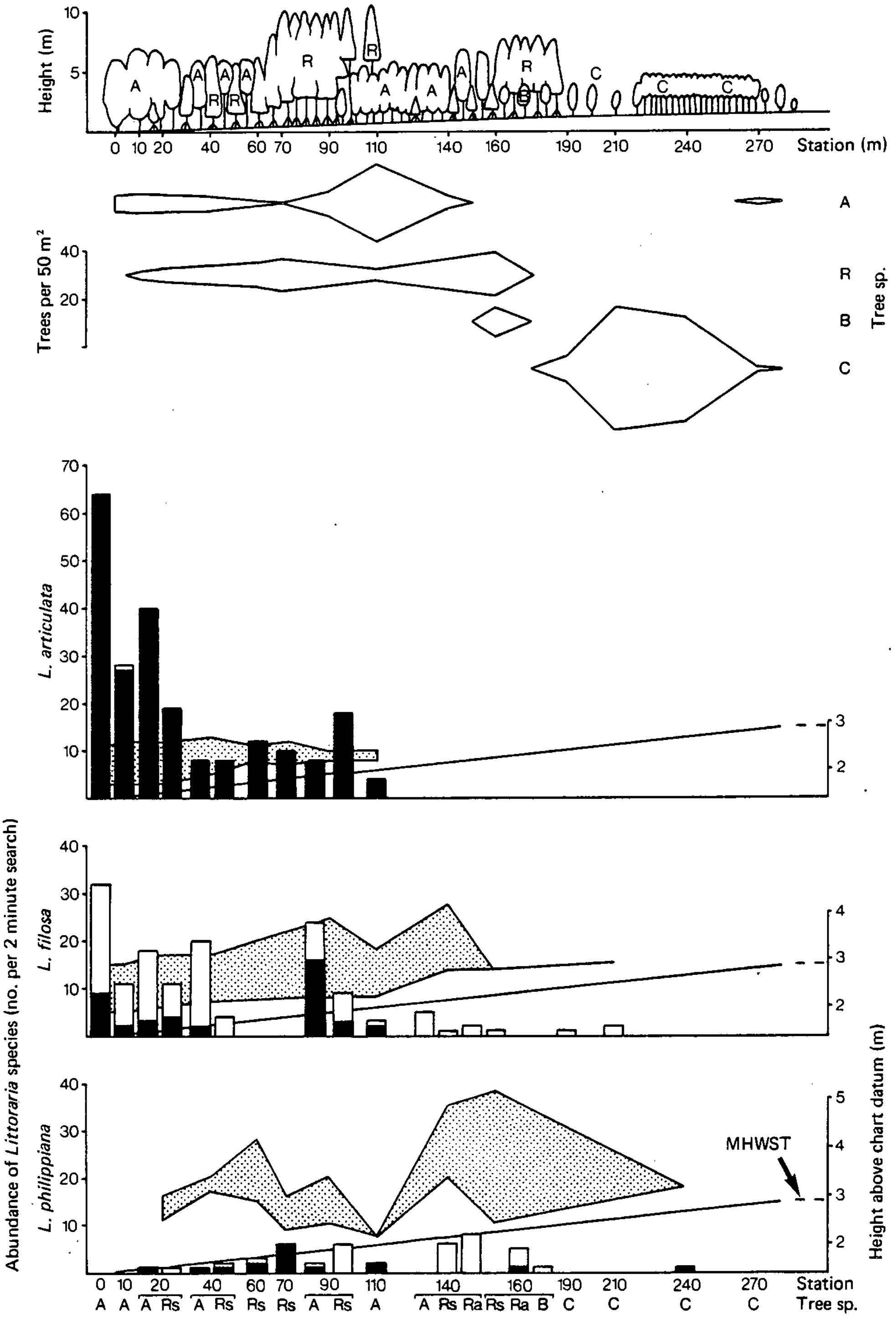

Height (m)
10
5
A
A
A
A
R
R
R
R
A
A
A
R
B
C
C
C
0 10 20 40 60 70 90 110 140 160 190 210 240 270 Station (m)
Trees per 50 m²
40
20
A
R
B
C
Tree sp.
L. articulata
70
60
50
40
30
20
10
3
2
Abundance of Littoraria species (no. per 2 minute search)
L. filosa
40
30
20
10
4
3
2
L. philippiana
40
30
20
10
5
4
3
2
MHWST
Height above chart datum (m)
0 10 20 40 60 70 90 110 140 160 190 210 240 270 Station
A A A Rs A Rs Rs Rs A Rs A A Rs Ra Rs Ra B C C C C Tree sp.

Fig. 11.3 Pioneer Bay, Orpheus Island, Palm Islands, Queensland.

Tidal levels: MHWS 2.7 m, MHWN 1.9 m, previous high water 2.5 m.

Date: 17 September, 1981.

Description: Small bay with fringing reef, on leeward side of small high island 15 km off shore. Narrow mangrove fringe on substrate of coral rubble and sand, with thin silt layer. Clear water. Rainfall 2055 mm (Ingham).

Zonation: *Rhizophora* forest; narrow *Bruguiera* and *Ceriops* zones.

Abbreviations and conventions as in Fig. 11.1.

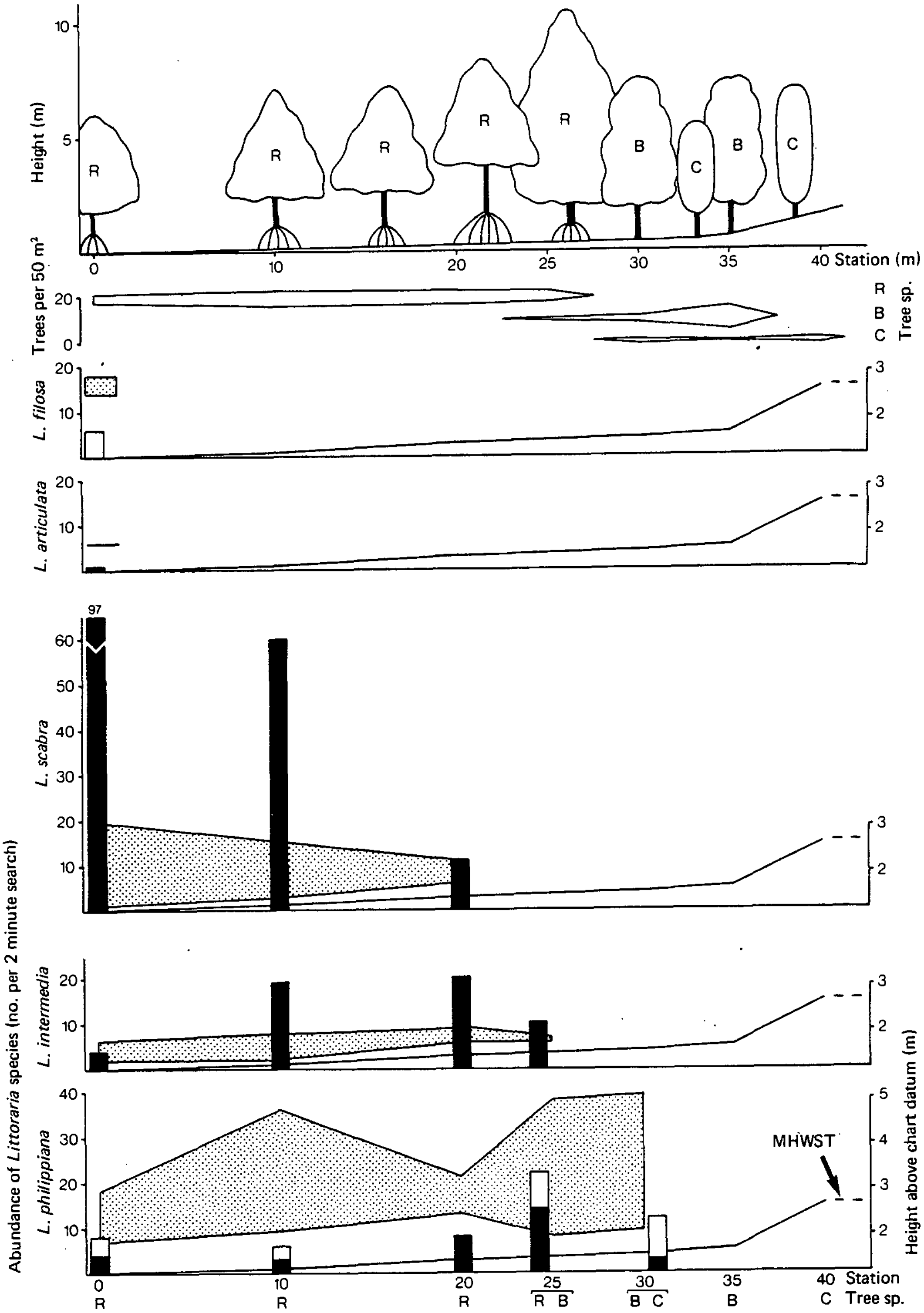

Height (m)
10
5
R
R
R
R
R
B
C
B
C
0
10
20
25
30
35
40 Station (m)
Trees per 50 m²
20
0
R
B
C
Tree sp.
L. filosa
20
10
3
2
L. articulata
20
10
3
2
L. scabra
97
60
50
40
30
20
10
3
2
L. intermedia
20
10
3
2
L. philippiana
40
30
20
10
5
4
3
2
MHWST
Abundance of Littoraria species (no. per 2 minute search)
Height above chart datum (m)
0
10
20
25
30
35
40 Station
R
R
R
R B
B C
B
C Tree sp.

Fig. 11.4 1 km north of St. Paul's Mission, Moa Island, Torres Strait Islands, Queensland.

Tidal levels: MHWS 2.7 m, MHWN 1.8 m, previous high water 1.9m.

Date: 3 October, 1981.

Description: Forest of *Rhizophora* colonizing lagoon behind fringing reef, on windward coast of high island. Substrate of coral rock with peat layer. Clear water. Rainfall 1712 mm (Thursday Island).

Zonation: *Rhizophora* forest; landward fringe.

Abbreviations and conventions as in Fig. 11.1.

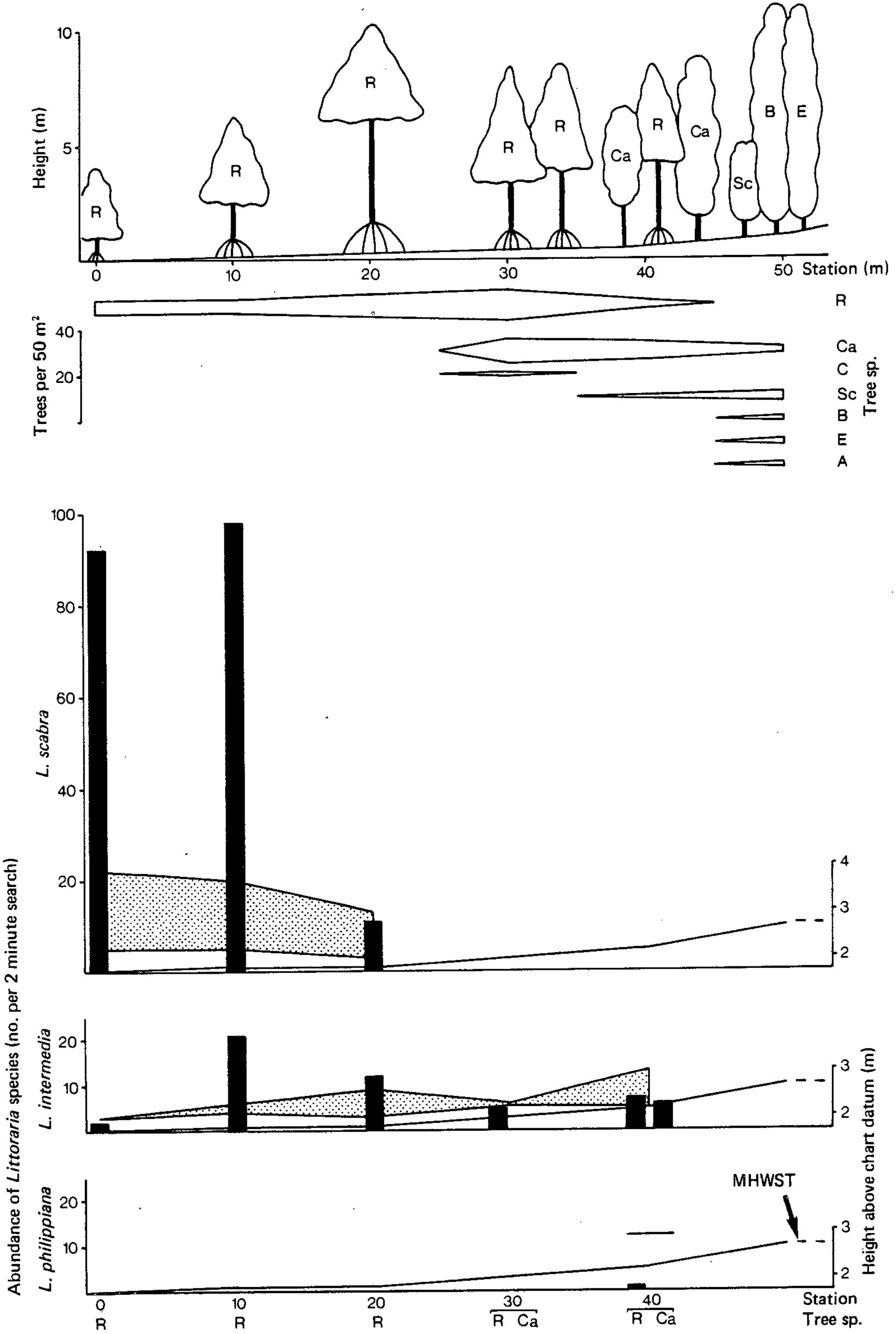

10
Height (m)
5
R
R
R
R
R
Ca
R
Ca
Sc
B
E
0
10
20
30
40
50
Station (m)
R
Trees per 50 m²
40
20
Ca
C
Sc
B
E
A
Tree sp.
100
80
60
L. scabra
40
20
4
3
2
Abundance of Littoraria species (no. per 2 minute search)
L. intermedia
20
10
3
2
Height above chart datum (m)
MHWST
L. philippiana
20
10
3
2
0
R
10
R
20
R
30
R Ca
40
R Ca
Station
Tree sp.

Fig. 11.5 Bonna Point, Kurnell Peninsula, Botany Bay, New South Wales.

Tidal levels: MHWS 1.4 m, MHWN 1.1 m, previous high water 1.1 m.

Date: 21 October, 1981.

Description: Edge of extensive *Avicennia* forest in sheltered bay behind sand spit. Narrow salt marsh behind forest. Rainfall 1142 mm (Sydney).

Zonation: *Avicennia* forest.

Abbreviations and conventions as in Fig. 11.1.

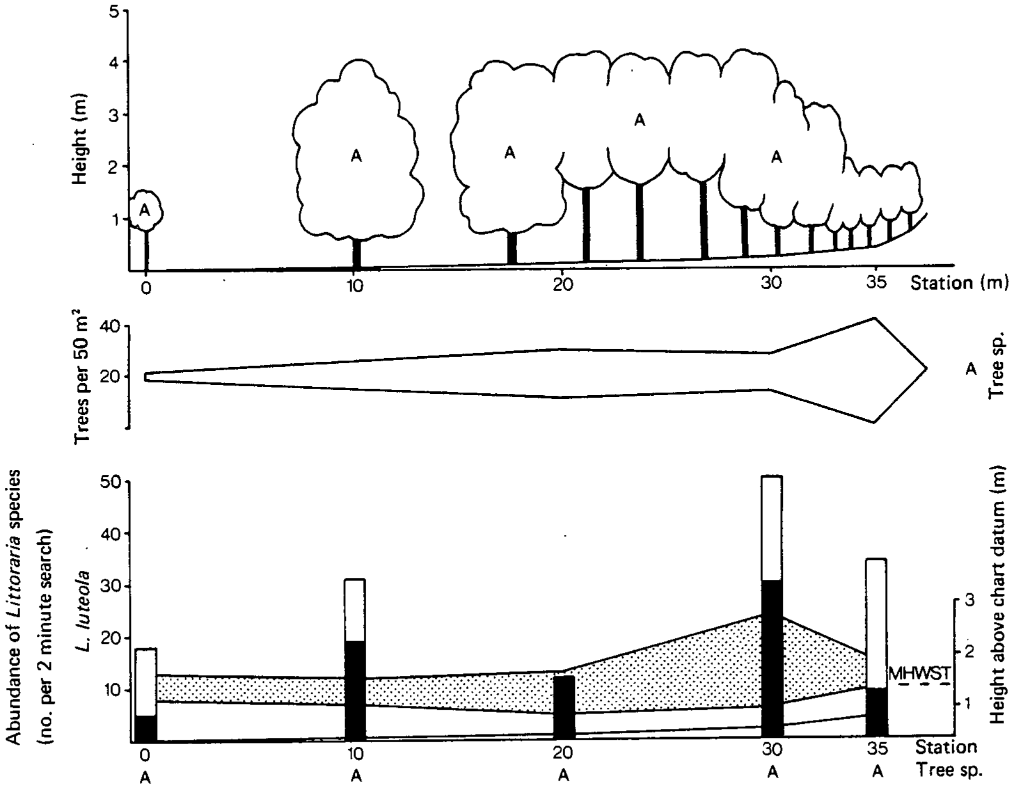

Height (m)
5
4
3
2
1
A
A
A
A
A
0
10
20
30
35
Station (m)
Trees per 50 m²
40
20
A
Tree sp.
Abundance of *Littoraria* species
(no. per 2 minute search)
L. luteola
50
40
30
20
10
Height above chart datum (m)
3
2
1
MHWST
0
10
20
30
35
Station
A
A
A
A
A
Tree sp.

Fig. 11.6 Little Lagoon, Denham, Shark Bay, Western Australia.

Tidal levels: MHWS 1.3 m, MHWN 1.0 m, previous high water 1.1 m (all approximate).

Date: 28 October, 1981.

Description: Narrow belt of *Avicennia* fringing small tidal creek. Sandy substrate with seagrass litter. *Arthrocnemum* scrub and salt pan behind mangrove fringe. Negligible freshwater influence owing to arid climate. Rainfall 200 mm (Hamelin Pool).

Zonation: *Avicennia* fringe.

Abbreviations and conventions as in Fig. 11.1.

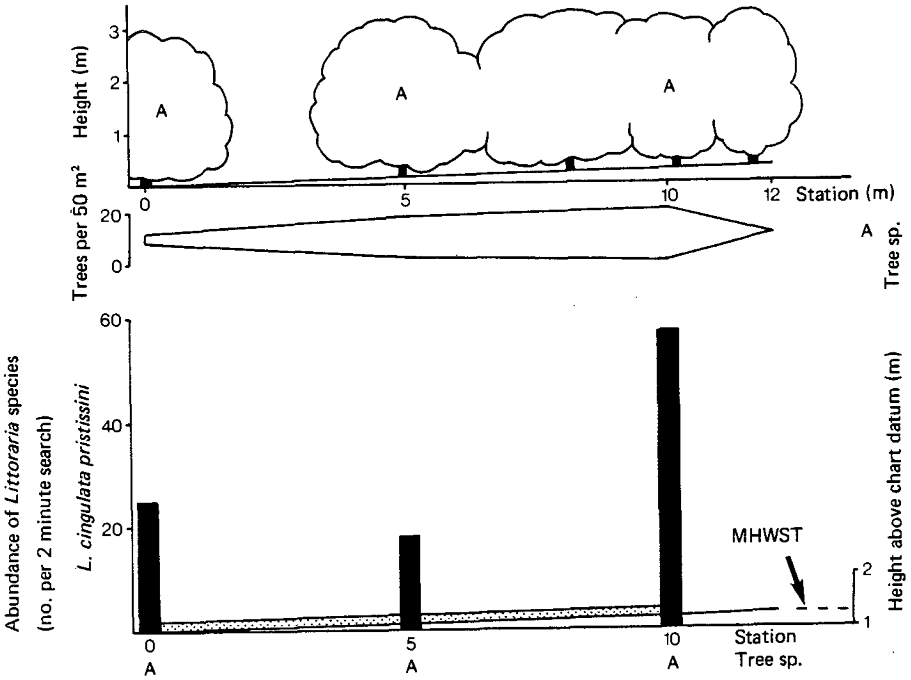

Height (m)
3
2
1
A
A
A
0
5
10
12
Station (m)
Trees per 50 m²
20
0
A
Tree sp.
Abundance of *Littoraria* species
(no. per 2 minute search)
L. cingulata pristissini
60
40
20
MHWST
Height above chart datum (m)
2
1
0
5
10
Station
A
A
A
Tree sp.

Fig. 11.7 Just south of Lookout Hill, Broome, Western Australia.

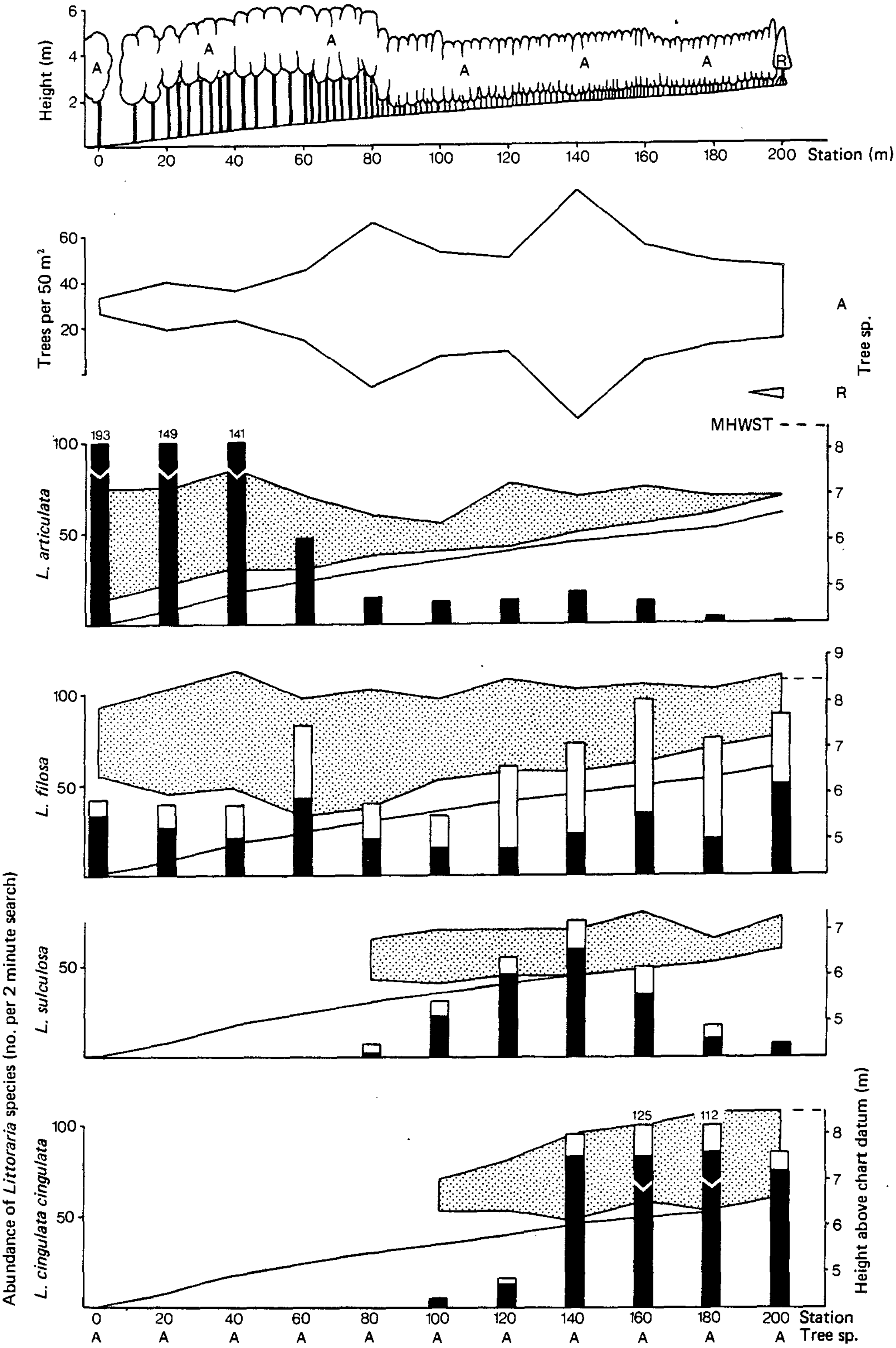
Tidal levels: MHWS 8.5 m, MHWN 5.4 m, previous high water 7.9 m.

Date: 2 November, 1981.

Description: Wide *Avicennia* forest fringing sheltered muddy bay. Substrate of soft, clayey mud. Water turbid. Rainfall 581 mm.

Zonation: Almost entirely *Avicennia* (forest only established for about 50 years), with *Rhizophora* beginning to appear at landward side.

Abbreviations and conventions as in Fig. 11.1.



Height (m)
6
4
2
A
A
A
A
A
A
R
0
20
40
60
80
100
120
140
160
180
200
Station (m)
Trees per 50 m²
60
40
20
A
R
Tree sp.
MHWST
L. articulata
100
50
193
149
141
8
7
6
5
L. filosa
100
50
9
8
7
6
5
L. sulculosa
50
7
6
5
L. cingulata cingulata
100
50
125
112
8
7
6
5
Abundance of Littoraria species (no. per 2 minute search)
Height above chart datum (m)
0
20
40
60
80
100
120
140
160
180
200
Station
A
A
A
A
A
A
A
A
A
A
A
Tree sp.

Fig. 11.8 Ludmilla Creek, 6 km north of Darwin, Northern Territory.

Tidal levels: MHWS 6.9 m, MHWN 5.1 m, previous high water 6.1 m.

Date: 9 November, 1981.

Description: Mouth of small creek entering sheltered, muddy bay. Substrate of soft mud. Water turbid. Rainfall 1489 mm.

Zonation: Seaward fringe of *Sonneratia* and *Avicennia*; *Rhizophora* forest. Zonation disturbed by cyclone damage and subsequent regeneration.

Abbreviations and conventions as in Fig. 11.1.

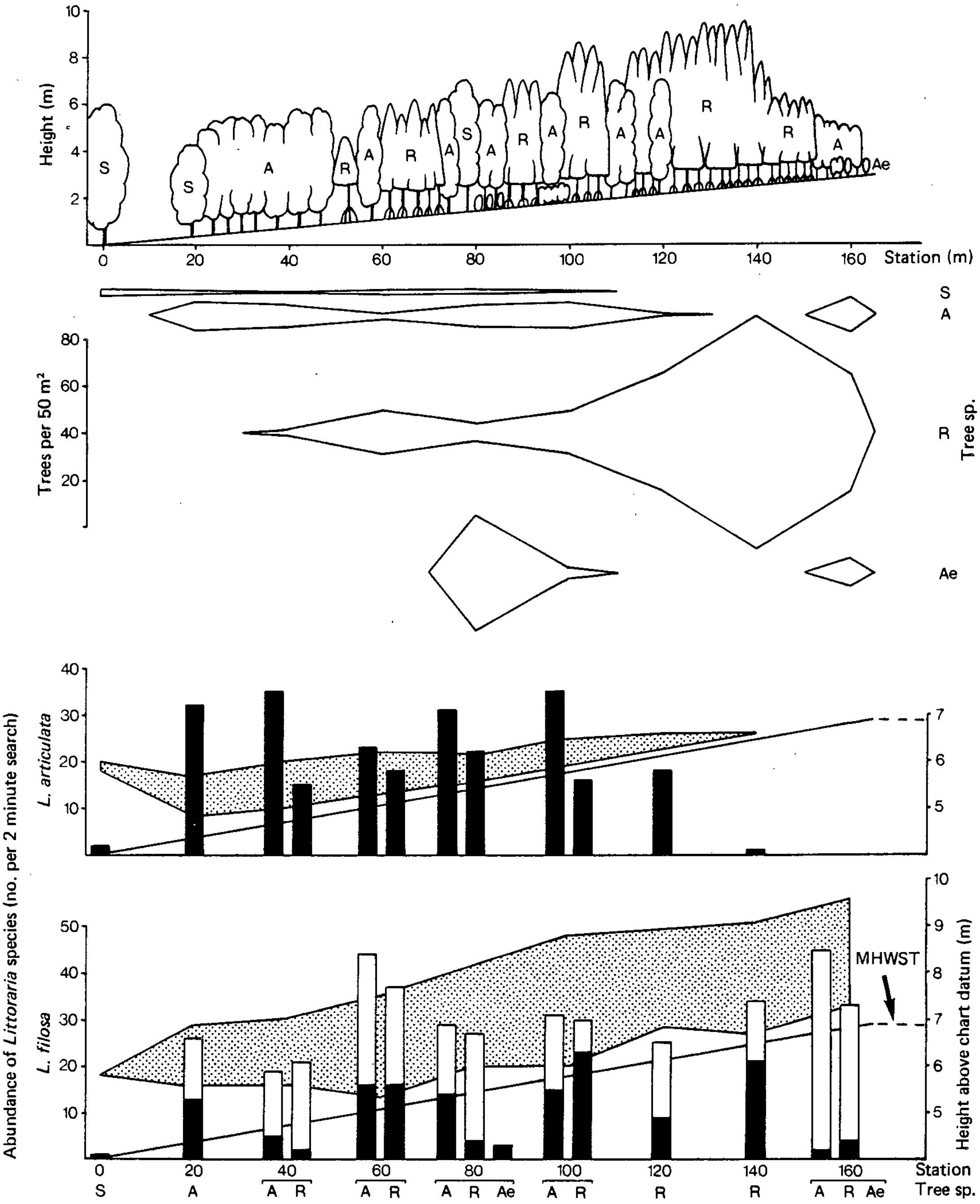

Height (m)
10
8
6
4
2
S
S
A
R
A
R
A
S
A
R
A
R
A
A
R
R
A
Ae
0
20
40
60
80
100
120
140
160
Station (m)
S
A
R
Ae
Tree sp.
Trees per 50 m²
80
60
40
20
Abundance of *Littoraria* species (no. per 2 minute search)
L. articulata
40
30
20
10
7
6
5
L. filosa
50
40
30
20
10
10
9
8
7
6
5
Height above chart datum (m)
MHWST
0
20
40
60
80
100
120
140
160
Station
S
A
A R
A R
A R Ae
A R
R
R
A R Ae
Tree sp.

Fig. 11.9 Creek opposite East Woody Island, Gove Peninsula, Northern Territory.

Tidal levels: MHHW 3.2 m, MLHW 2.2 m, previous high water 3.5 m.

Date: 15 November, 1981.

Description: Small lagoon at mouth of creek behind sandy coastline. Transect crosses small sandbank with trees beyond main mangrove forest. Sandy substrate. Clear water. Rainfall approximately 1294 mm (Cape Don).

Zonation: Pioneering *Rhizophora* and *Aegialitis* on sand bank; *Rhizophora* forest; narrow *Bruguiera* and *Ceriops* zones.

Abbreviations and conventions as in Fig. 11.1.

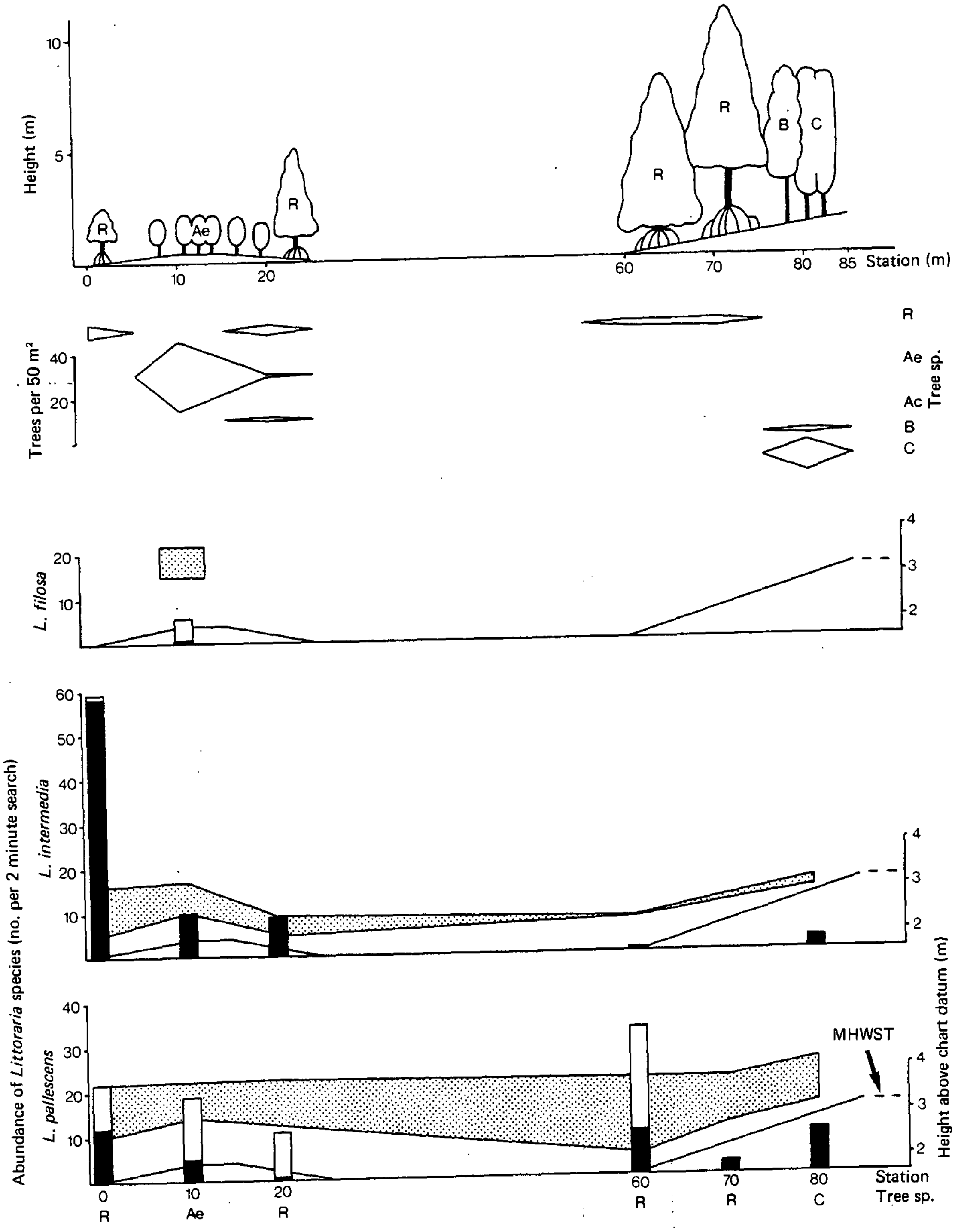

Height (m)
10
5
R
Ae
R
R
R
B
C
0
10
20
60
70
80
85
Station (m)
Trees per 50 m²
40
20
R
Ae
Ac
B
C
Tree sp.
L. filosa
20
10
4
3
2
Abundance of Littoraria species (no. per 2 minute search)
L. intermedia
60
50
40
30
20
10
4
3
2
L. pallescens
40
30
20
10
MHWST
4
3
2
Height above chart datum (m)
0
R
10
Ae
20
R
60
R
70
R
80
C
Station
Tree sp.

Fig. 11.10 Ao Nam-Bor, Phuket Island, south-west Thailand.

Tidal levels: MHWS 3.4 m, MHWN 2.6 m, previous high water 2.8 m.

Date: 31 January, 1982.

Description: Forest fringing sheltered, muddy bay, on eastern side of large continental island. Water turbid. Rainfall 2351 mm.

Zonation: *Rhizophora* forest (small trees; area cut for timber); landward fringe (area periodically cut and burned).

Abbreviations and conventions as in Fig. 11.1.

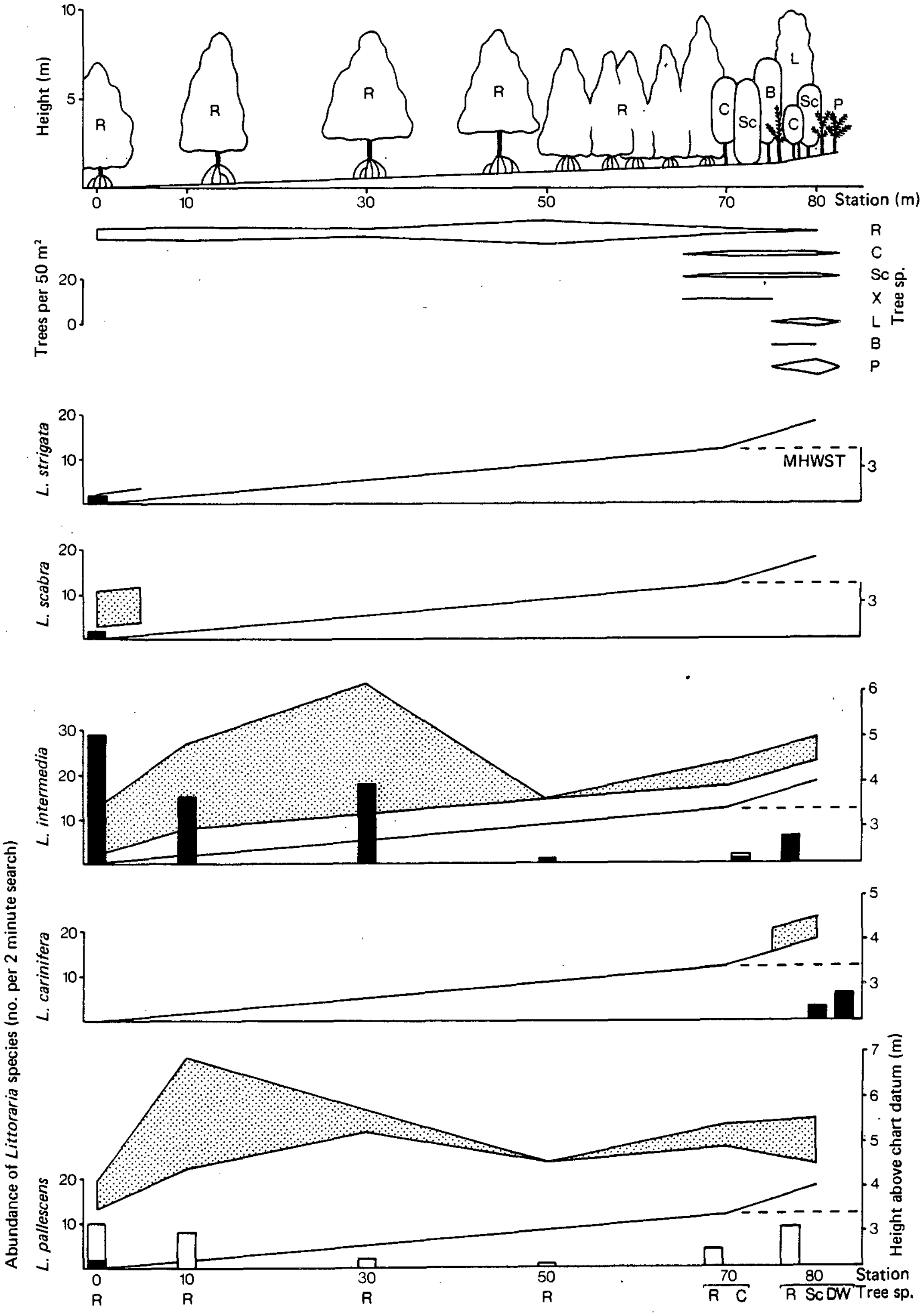

Height (m)
10
5
R
R
R
R
R
C
Sc
B
L
Sc
C
P
0
10
30
50
70
80
Station (m)
Trees per 50 m²
20
0
R
C
Sc
X
L
B
P
Tree sp.
L. strigata
20
10
MHWST
3
L. scabra
20
10
3
L. intermedia
30
20
10
6
5
4
3
L. carinifera
20
10
5
4
3
L. pallescens
20
10
7
6
5
4
3
Height above chart datum (m)
Abundance of Littoraria species (no. per 2 minute search)
0
10
30
50
70
80
Station
R
R
R
R
R C
R Sc DW
Tree sp.

Fig. 11.11 Kanchanadit, 15 km south-east of Surat Thani, south-east Thailand.

Tidal levels: MHWS 1.9 m, MHWN 1.5 m, previous high water 1.5 m.

Date: 3 February, 1982.

Description: Sheltered, muddy coast. Water turbid. Rainfall 2562 mm (Nakhon Si Thammarat).

Zonation: *Sonneratia* and *Avicennia* fringe; *Rhizophora* forest; *Bruguiera* forest; landward fringe (zonation poorly established, area periodically cut for timber and landward fringe partially drained).

Note: *L. articulata* and *L. strigata* could not be distinguished in the field.

Abbreviations and conventions as in Fig. 11.1.

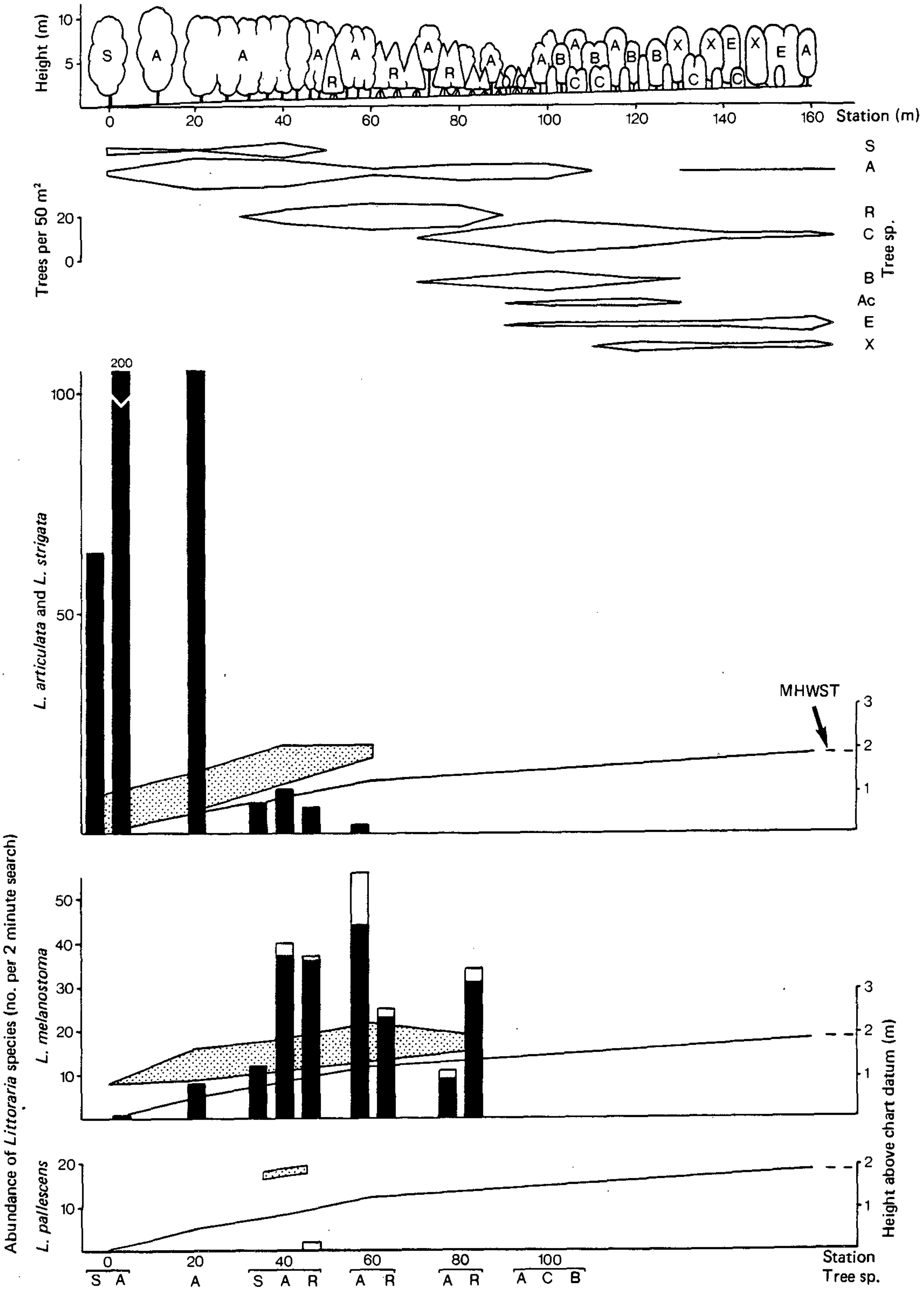

Height (m)
10
5
S
A
A
A
R
A
R
A
R
A
A
B
A
C
B
C
A
B
B
X
C
X
E
C
X
E
A
0
20
40
60
80
100
120
140
160
Station (m)
Trees per 50 m²
20
0
S
A
R
C
B
Ac
E
X
Tree sp.
200
100
50
L. articulata and L. strigata
MHWST
3
2
1
Abundance of Littoraria species (no. per 2 minute search)
L. melanostoma
50
40
30
20
10
3
2
1
Height above chart datum (m)
L. pallescens
20
10
2
1
0
20
40
60
80
100
Station
S A
A
S A R
A R
A R
A C B
Tree sp.

Fig. 11.12 Batu Maung, Penang, Malaysia.

Tidal levels: MHWS 2.5 m, MHWN 1.8 m, previous high water 1.9 m.

Date: 6 February, 1982.

Description: Narrow mangrove fringe on artificial foreshore in sheltered bay. Substrate of soft mud. Water turbid. Rainfall 2689 mm.

Zonation: *Avicennia* fringe.

Abbreviations and conventions as in Fig. 11.1.

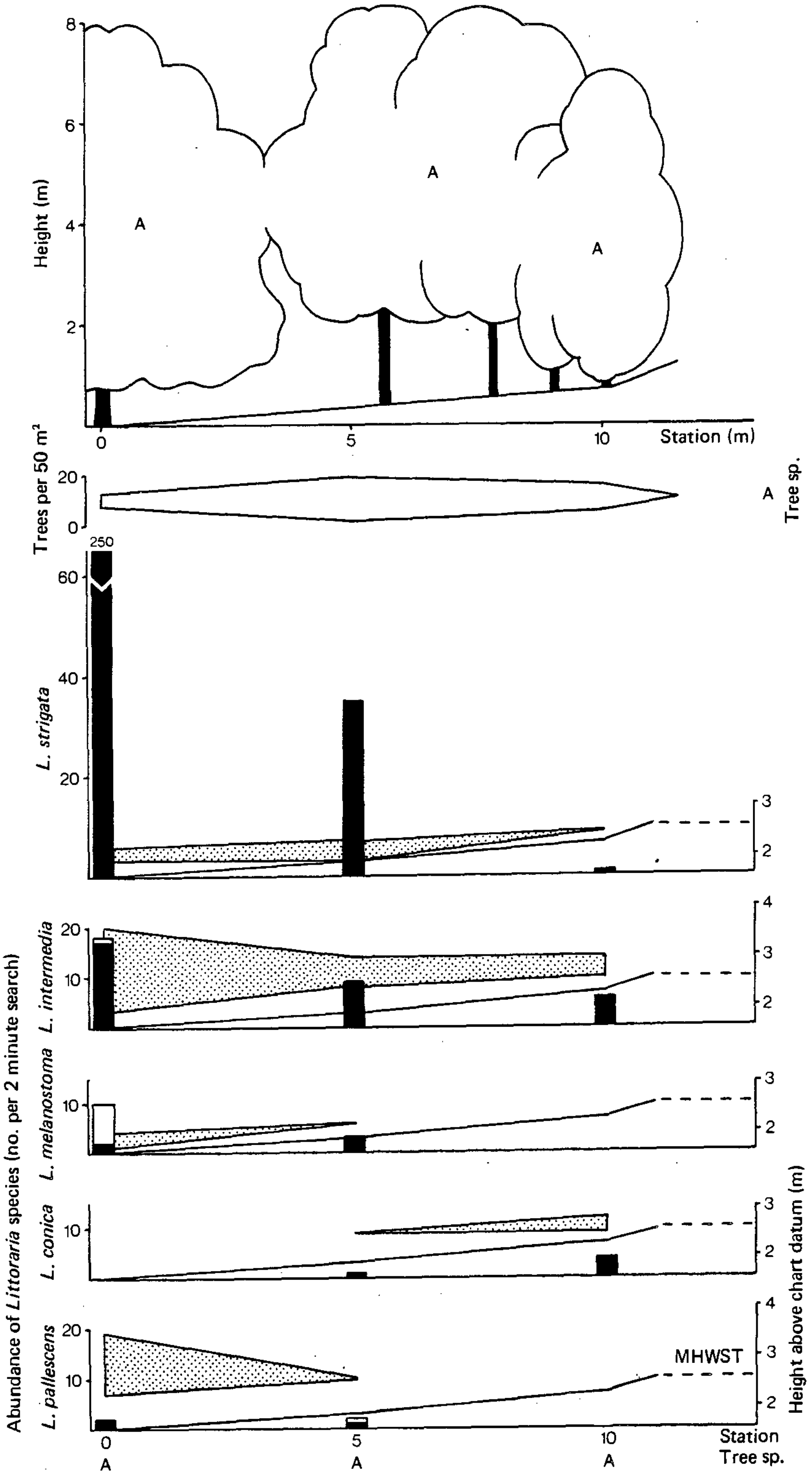

Height (m)
8
6
4
2
A
A
A
0
5
10
Station (m)
Trees per 50 m²
20
0
A
Tree sp.
250
60
40
20
L. strigata
3
2
Abundance of Littoraria species (no. per 2 minute search)
L. intermedia
20
10
4
3
2
L. melanostoma
10
3
2
L. conica
10
3
2
L. pallescens
20
10
4
3
2
MHWST
Height above chart datum (m)
0
5
10
Station
A
A
A
Tree sp.

Fig. 11.13 Santubong, Sarawak, Borneo.

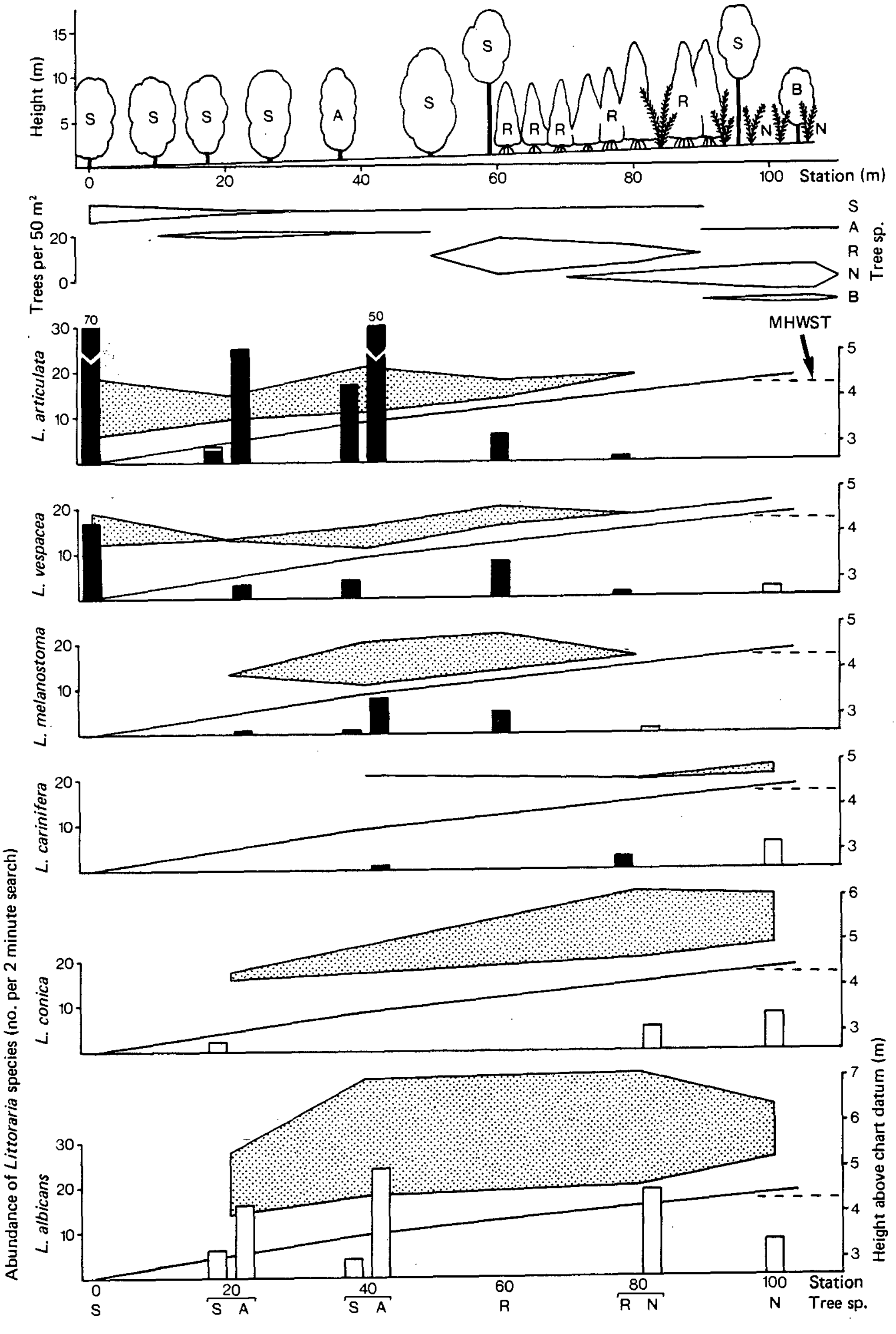
Tidal levels: MHWS 4.3 m, MHWN 4.1 m, previous high water 3.8 m.

Date: 18 February, 1982.

Description: Forest at river mouth. Muddy substrate. Water turbid. Rainfall 4008 mm (Kuching).

Zonation: Wide belt of *Sonneratia* and *Avicennia* at seaward side; *Rhizophora* forest; landward fringe with *Nypa* palms.

Abbreviations and conventions as in Fig. 11.1.



Height (m)
15
10
5
S
A
R
B
N
0
20
40
60
80
100
Station (m)
Trees per 50 m²
20
0
S
A
R
N
B
Tree sp.
70
50
MHWST
L. articulata
L. vespacea
L. melanostoma
L. carinifera
L. conica
L. albicans
30
20
10
3
4
5
6
7
Abundance of Littoraria species (no. per 2 minute search)
Height above chart datum (m)
Station
Tree sp.
S
S A
S A
R
R N
N

Fig. 11.14 Coconut Island, Kaneohe Bay, Oahu, Hawaiian Islands.

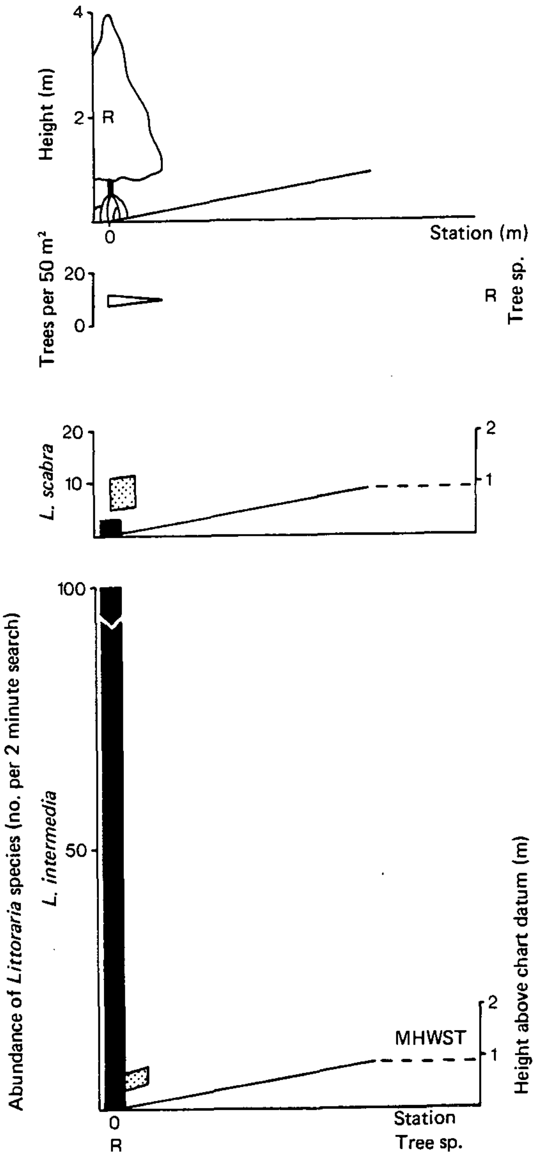
Tidal levels: MHWS 0.9 m, MHWN 0.55 m, previous high water 0.6 m.

Date: 11 November, 1982.

Description: Row of trees around small artificial harbour on leeward side of small island, sheltered by fringing reef. Clear water. Rainfall approximately 1500 mm.

Zonation: *Rhizophora mangle* (introduced into Hawaii this century, Wester, 1981).

Abbreviations and conventions as in Fig. 11.1.


Height (m)
4
2
R
0
Station (m)
Trees per 50 m²
20
0
R
Tree sp.
L. scabra
20
10
2
1
Abundance of Littoraria species (no. per 2 minute search)
L. intermedia
100
50
MHWST
2
1
Height above chart datum (m)
0
R
Station
Tree sp.

11.4 Patterns of zonation and abundance

11.4.1 Horizontal zonation

On 8 of the 14 transects the total number of individuals seen, and therefore the density of the snails, was greatest at the seaward edge of the mangrove forest. Often, this pattern was due to the great abundance of *L. articulata* on the most seaward trees (Figs 11.2, 11.7, 11.11, 11.13), although maximum abundance at the seaward stations was also shown at certain localities where this species did not occur or where it was scarce (Figs 11.3, 11.9, 11.10, 11.12). Among the species represented on the transects, the following showed maximum abundance at the outermost one or two stations: *L. scabra* (Figs 11.1, 11.3, 11.4, 11.10), *L. articulata* (Figs 11.1, 11.2, 11.3, 11.7, 11.11, 11.13), *L. filosa* (Figs 11.1, 11.2, 11.3, 11.9), *L. pallescens* (Figs 11.9, 11.10), *L. intermedia* (Figs 11.9, 11.10, 11.12) and *L. strigata* (Figs 11.10, 11.11, 11.12). It should be noted that the zonation of mangrove trees along the transect at Cockle Bay (Fig. 11.1, Chapter 10) was peculiar, showing a double front, such that both stations 0 and 25 were at the seaward edge of a mangrove belt.

The pattern of horizontal zonation of particular *Littoraria* species showed some variation between localities. At the more exposed localities (Figs 11.7, 11.8) both *L. filosa* and *L. articulata* were relatively less abundant at the seaward edge of the forest and showed a more uniform distribution along the transects than at more sheltered sites. The influence of exposure to wave action was also suggested by the distribution of these two species at Cockle Bay, Magnetic Island (Fig. 11.1); at this locality both species were more abundant at the second front, sheltered behind a more seaward belt of trees, than at the very seaward edge of the transect. *L. intermedia* was often found to be most abundant in the *Rhizophora* zone a little behind the *Avicennia* trees at the seaward edge (Fig. 11.1, and many localities in northern Queensland). In part this may have been due to an association of this species with *Rhizophora* trees (Section 11.4.3), but a similar distribution pattern was shown at some of the more exposed localities where there was no *Avicennia* fringe (Figs 11.3, 11.4). In contrast, at the most sheltered localities (Figs 11.9, 11.10, 11.12) *L. intermedia* was most abundant at the seaward edge, indicating that wave action may influence the distribution of this species.

Some *Littoraria* species were found to be most abundant near the middle of the forest. These included *L. philippiana* (Figs 11.2, 11.3, 11.4), *L. luteola* (Fig. 11.5), *L. sulculosa* and *L. cingulata* (both Fig. 11.7), *L. melanostoma* (Figs 11.11, 11.13), *L. vespacea* (not clearly shown in Fig. 11.13, but found to be the case at Port Kelang and Batu Maung, both Malaysia) and possibly *L. albicans* (Fig. 11.13, not seen at other localities).

Only two species of *Littoraria* were found to become more abundant towards the landward fringe of the mangrove forest. These were *L. carinifera* (Figs 11.10, 11.13) and *L. conica* (Figs 11.12, 11.13). Both are found in Indo-Malaya, where rainfall is often high and the landward fringe of the forest is commonly well developed (Section 11.2). Of the areas visited, only in the monsoonal or ever-wet regions of South East Asia were any littorinids to be found in the landward fringe, and only at the Sarawak locality (Fig. 11.13), with the highest rainfall, were they at all common there. At the Australian localities the rainfall is mostly lower or more seasonal (see rainfall data in captions to Figs 11.1 to 11.14). Here, at localities where the complete mangrove zonation was developed, littorinids were scarce or absent in the *Ceriops* zone, and not found in the landward fringe (Figs 11.2, 11.3, 11.4; and the localities near Broome, Darwin and in the Torres Strait, Table 11.1). Several of the Australian transects appear to be exceptions to this generalization (Figs 11.1, 11.7, 11.8). These were examples of recently established or disturbed mangrove areas, which lacked high tidal flats for the complete development of the mangrove zonation.

At nearby sites at which *Ceriops* and landward zones were present, *Littoraria* species were absent from them. The most southerly localities, in the vicinity of Sydney (Fig. 11.5 and Careel Bay) are another exception, for here *L. luteola* was common through the whole width of well established *Avicennia* forests (only *Avicennia* and *Aegiceras* occur at this latitude, Jones, 1971) and in salt marsh areas behind. These observations suggest that *Littoraria* species may only occur in the landward fringes of well established forests in the wet tropics and in moist temperate climates.

11.4.2 Vertical zonation

From the ranges of vertical distribution indicated on the transect diagrams (Figs 11.1 to 11.14) it is evident that different species of *Littoraria* occupy characteristic vertical zones on the mangrove trees. Where several species are found on the same trees there may be broad overlap between the levels at which they occur.

It is not meaningful to specify the levels occupied by *Littoraria* species in terms of tidal heights, since the zonation patterns are strongly influenced by the cycle of spring and neap tides, and by prevailing weather conditions (Chapter 12). Nevertheless, the observations at the Cockle Bay study site suggest that the relative zonation patterns of species at a locality are maintained. At each locality, species can be described in relative terms as typical of low or high levels. It is not possible to make detailed comparisons of zonation patterns between localities on the basis of the transect records, since observations were made at different stages of the lunar cycle and at different seasons of the year.

Species typical of the lower levels include *L. articulata*, *L. strigata* and *L. sulculosa*. During low tide periods these species were found low on the trees, sometimes even at ground level, although never on the mud between trees. Typical high level species include *L. filosa, L. philippiana, L. pallescens* and *L. albicans*. The maximum heights above the ground recorded for these species were 3.0 m for *L. filosa* (= 1.8 m above MHWST, Magnetic I., Qld.), 5.2 m for *L. philippiana* (= 3.9 m above MHWST, Magnetic I., Qld.), 4.5 m for *L. pallescens* (= 3.5 m above MHWST, Phuket I., Thailand) and 3.5 m for *L. albicans* (= 2.7 m above MHWST, Santubong, Sarawak).

Species did not in general occupy the same vertical range (as defined relative to tidal datum) throughout their horizontal distribution. In most of the figured transects it can be seen that the lower vertical limits of littorinids on trees became closer to the ground at stations further inland from the seaward edge. However, snails were seldom found at ground level, and many species did not occur less than 0.2 to 0.5 m from the ground. The lower vertical levels therefore became higher (relative to tidal datum) towards the landward edge of the forest. This is shown by *L. articulata* and *L. filosa* in Figures 11.2, 11.7, 11.8 and 11.13. Upper levels of vertical distribution sometimes remained similar throughout the forest, but in other cases individual species occupied higher levels in the shade of the *Rhizophora* zone than in the sunnier positions at the seaward edge of the forest. This is shown by some of the species which were most abundant within the *Rhizophora* zone, such as *L. philippiana* and *L. intermedia* (Figs 11.1, 11.2, 11.3, 11.4).

11.4.3 Effect of leaf or bark substrate and of tree species

The transect diagrams show that several *Littoraria* species occurred predominantly on leaf or on bark substrates. In part this may reflect the distribution of foliage and the vertical zonation of the snails; for example, leaves are often not present at low levels on *Rhizophora* trees. However, the distributions of some species suggest that substrate preference may also be involved. For example, at Ao Nam-Bor *L. intermedia* and *L. pallescens* occupied overlapping vertical ranges on the same trees, and while the former was found exclusively on bark, the latter occurred mainly on leaves (Fig. 11.10). At many localities in northern Queensland *L. scabra* was found on bark, but rarely on leaves at the same vertical levels (Figs 11.1, 11.3, 11.4, Table 12.3). At Santubong, Sarawak, *L. albicans* was found exclusively on leaves (Fig. 11.13).

In many cases the horizontal zonation patterns of the snails followed those of the tree species (Section 11.2 and Figs 11.1 to 11.14). It is therefore possible to specify that particular *Littoraria* species are typically to be found in one or two of the floristic zones of the forest (as summarized in the species descriptions, Chapter 9). The question then arises as to whether this observed correlation is the result of dependence of particular *Littoraria* species on particular species of mangrove tree, or whether requirements for the physical factors prevailing in floristic zones are involved.

The snails were abundant only towards the seaward edges of forests, where trees of the genera *Avicennia* and *Rhizophora* are dominant. These trees therefore provide the main habitats. Their respective growth forms show conspicuous differences. *Avicennia* is a slender tree with smooth, greenish brown bark; prop roots are absent; the leaves are thin and lanceolate, with leaf hairs on the lower surface; leaves are borne even close to the ground, forming an open canopy. In *Rhizophora* the bark is dark and fissured; the surface area of the trunk is greatly increased by the numerous prop roots; the leaves are hard, smooth and relatively large, and except on young trees are borne high above the ground, where they form a dense, shady canopy. *Avicennia* grows typically as a pioneering fringe of well spaced trees at the seaward edge of the forest, while *Rhizophora* commonly forms dense stands behind the seaward fringe (Figs 11.2, 11.8, 11.11). There is some evidence that tree-climbing crab predators (*Metopograpsus* species) are more common on *Rhizophora* than on *Avicennia* trees (Section 14.3.1).

In the absence of manipulative experiments it is not possible to make definitive statements concerning associations between *Littoraria* species and species of mangrove trees. Under natural conditions there are too many confounding variables, such as shading by the canopy, shelter from wave action, availability of leaf and bark substrates at low levels on the trees and distribution of predators. Furthermore, direct comparisons of occurrence on *Avicennia* and *Rhizophora* trees, which are so different in architecture, is difficult because of the nature of the technique used to estimate abundance of snails (Section 11.3).

Nevertheless, some trends in distribution can be pointed out which are suggestive of an influence of tree species. Among the species found on bark, *L. articulata* was often more common on *Avicennia* than on *Rhizophora* trees, where both occured at the same transect station (Figs 11.1, 11.2, 11.8). *L. scabra* is a larger shell occupying higher levels, but was likewise found on bark and most abundantly at the seaward edge of the forest; in contrast to *L. articulata*, this species was more frequent on *Rhizophora* (Fig. 11.1, and other localities in northern Queensland). *Sonneratia* trees resemble *Avicennia* in growth form, although the bark is rough and flaky; at several localities *L. articulata* was more common on *Avicennia* than on *Sonneratia* trees at the same transect station (Figs 11.8, 11.11, 11.13).

Of the species found commonly upon both leaves and bark, several were most abundant on *Avicennia* trees. In the case of *L. filosa* this pattern was shown at Magnetic Island (Figs 11.1, 11.2), but less clearly at Ludmilla Creek (Fig. 11.8); at the latter locality *Avicennia* and *Rhizophora* trees were intermingled in close proximity, which may have allowed movement of snails between trees. At Cockle Bay, *L. luteola* was found on *Avicennia* foliage, but was seldom seen on *Rhizophora* trees (this species was not present on the transect illustrated in Fig. 11.1). *L. albicans* was more common on *Avicennia* than on other mangrove trees at the Sarawak locality (Fig. 11.13). In this context it may be significant that both *L. filosa* (Section 12.3.5) and *L. albicans* were seen to graze on the leaf hairs of *Avicennia*. Whether this food source was a major component of the diet is unknown, but it is not available on *Rhizophora* or *Sonneratia* trees, which have smooth, hard leaves. *L. pallescens* and *L. philippiana* were also found on leaves and bark, but were frequent on both *Avicennia* and *Rhizophora* trees (Figs 11.1, 11.2, 11.11, 11.12).

11.4.4 Occurrence in habitats other than mangroves

All the species of the *L. scabra* group are typical of mangrove forests, but some can be found in other habitats also. At several sites in northern Queensland *L. scabra* and *L. articulata* were seen on driftwood and wooden pilings (Cockle Bay; Port Douglas; Green Island). *L. scabra* and *L. intermedia* were found on the trunk of the maritime tree *Hibiscus tiliaceus* growing at the high water mark on the sheltered, sandy shore of Heeia Bay, Hawaii. In temperate regions salt marshes may replace mangrove forests (Saenger *et al.*, 1977). In salt marshes near Sydney, *L. luteola* was common amongst vegetation and on and beneath driftwood in salt marshes (Kurnell Peninsula; Careel Bay). *L. cingulata pristissini* was abundant amongst salt marsh plants fringing sandy lagoons at localities on the arid coast of Shark Bay, Western Australia (Denham; Monkey Mia).

Littoraria species require a hard substrate for effective attachment, locomotion and feeding (Section 12.3.5). Whilst this is generally provided by wood or foliage, a few species survive also on rocks in sheltered situations. *L. scabra, L. subvittata, L. cingulata cingulata, L. cingulata pristissini, L. sulculosa* and *L. strigata* were all found in small numbers on sheltered rocky shores (pers. obs.). Only two species are found regularly and in large numbers on rocks; these are *L. articulata* over most of its extensive central Indo-Pacific range, and *L. intermedia* in such areas as the Red Sea, central Indian Ocean islands and Polynesia (pers. obs. and from data accompanying museum specimens).

11.4.5 Continental and oceanic distributions

The presence of a species at a locality will depend upon the geographical distribution of the species and upon the presence of a suitable habitat. Even when these two criteria are satisfied some anomalies of distribution may be found on a local scale. On the basis of such observations two ecological groupings of *Littoraria* species can be recognized, which will be referred to as continental and oceanic respectively.

Continental species are those which are common in the wide mangrove fringes of large land masses and high islands, in deltaic mangroves, in areas with turbid water and muddy soil, and they occur not only at the seaward edge but also within the forest. In contrast, oceanic species are found in clear water situations, on the trees of narrow mangrove fringes on rocky or coral shores, and on oceanic islands. On continental margins oceanic species may be found on promontories and offshore islands, and if they occur at all in wide mangrove forests they are restricted to the outermost trees at the seaward edge. Only three species, *L. scabra*, *L. intermedia* and *L.pallescens*, are known to belong to the oceanic group. From data accompanying museum specimens it appears that *L. subvittata* may be another oceanic species, while *L. lutea* shows characteristics of both categories. All remaining species are known or suspected to have distributions of the continental type (see distributional data in Chapter 9).

Although the distinction between oceanic and continental species is not absolute, their patterns of distribution can show striking differences even on a small scale. Local distribution patterns are most well known in northern Queensland, where many localities were visited during the present study (Table 11.1). At Magnetic Island, the oceanic species *L. scabra* was common on *Rhizophora* trees at the seaward edge of the narrow mangrove fringe at Cockle Bay (Fig. 11.1), where the sediment was sandy, close to the rocky point at the southern tip of the island. Under similar conditions this species was common at the western point of the island 7 km to the north-west. However, the intervening stretch of coastline was more sheltered, with a much wider mangrove belt and an extensive muddy foreshore, and in this area *L. scabra* was entirely absent (Fig. 11.2). Similarly, in the clear water situation of Orpheus Island (Fig. 11.1), the species was much more abundant than on the mainland coast, or at Magnetic Island. The same pattern was shown by *L. intermedia*, another oceanic species, at these localities. A continental species, *L. articulata*, showed an opposite trend, being rare or absent on offshore islands such as Orpheus Island (Fig. 11.3), Moa Island (Fig. 11.4), Low Isles and Lizard Island, but abundant at localities on the mainland coast of Queensland (e.g. Alligator Creek; Rowes Bay; Port Douglas) and on islands close to the coast (Magnetic Island, Figs 11.1, 11.2; Hinchinbrook Island).

On a larger scale, the contrast between an oceanic and a continental distribution is clearly shown by a comparison of the records of *L. philippiana* and *L. pallescens* from eastern Australia. The former is common both on the mainland coast and on the shores of high islands (Section 9.2.3.4). The latter is rare, and recorded only from Thursday Island, Lizard Island, Port Douglas, Cairns, Dunk Island, Magnetic Island and Moreton Bay (Section 9.2.3.3). The biogeographical implications of these distribution patterns are examined in Chapter 7.

If the transect localities are classified in terms of the *Littoraria* species present and their relative abundance, it can be seen that the transects represented in Figures 11.3, 11.4, 11.9, 11.10 and 11.14 are of the oceanic type, while those in Figures

11.2, 11.5, 11.7, 11.8, 11.11 and 11.13 show a predominantly continental character. The distinction is not absolute, so that on the transects illustrated in Figures 11.1 and 11.2 both continental and oceanic species were well represented. Nevertheless, from a knowledge of the location, sediment type, water quality and extent of the mangrove forest, the assemblages of *Littoraria* species present may be predicted with some certainty. Several exceptions must be mentioned. It was surprising to find the two characteristically oceanic species *L. intermedia* and *L. pallescens* to be common at Batu Maung, Penang (Fig. 11.12), where the sediment was soft mud, the water turbid, and the locality on a high island close to the mainland. The absence of the oceanic species *L. pallescens* from the Torres Strait Islands (pers. obs., but one museum record (QM) from Thursday I.) and of *L. scabra* from the Gove Peninsula (pers. obs., but one museum record (USNM) from Yirrkala) is interesting. Conditions for these species seemed favourable at these localities, and biogeographical explanations for their absence (or sporadic occurrence) should be sought (Chapter 7).

11.5 Discussion

Of the fauna associated with mangroves, species of *Littoraria* are amongst the most characteristic of the habitat, showing a geographical distribution almost as wide as that of mangrove trees, and being found not only in well established forests, but also on isolated trees on rocky and coral shores. Eighteen of the twenty species of the *L. scabra* group show an obligate dependence upon mangrove trees or salt marsh vegetation, not only for shade and shelter as in the case of many animals associated with the habitat (Macnae, 1968), but for the provision of a suitable substrate for feeding and locomotion. Although some of these *Littoraria* species can be found occasionally upon sheltered rocks, only in the cases of *L. intermedia* and *L. articulata* are the rocky shore populations sufficiently large that they could be self-perpetuating, rather than maintained by immigration from nearby mangrove areas.

Since the mangrove forest is a three-dimensional environment, arboreal animals may display zonation patterns in two directions, both vertically on the trees and horizontally through the forest from seaward to landward, as noted by Berry (1963) and Macnae (1968). Mangrove littorinids have been quoted as an example of a vertical zonation pattern in the mangrove environment by both these authors, but this pattern has not hitherto been described accurately. Until recently, ecological workers have accepted Rosewater's (1970) classification of mangrove littorinids, which recognized one species, *Littorina 'scabra'*, throughout the Indo-Pacific province, and two additional species, *Littorina 'carinifera'* and *Littorina melanostoma*, in Indo-Malaya. Reports of differential zonation of species have therefore been limited to the latter area. Working in Singapore, Berry (1963, 1972) briefly described upper limits of zonation in the ascending order *L. 'undulata'*, *L. 'carinifera'*, *L. 'scabra'*, *L. melanostoma*. A similar zonation pattern has been noted, using the same nomenclature, in Singapore and Malaysia by Vermeij (1973a, b) and Sasekumar (1974). These observations are inaccurate both in regard to nomenclature and the zonation implied. *L. 'undulata'* refers to *L. articulata* (and probably also to *L. strigata* and *L. vespacea*); *L. 'carinifera'* may include *L. conica* as well as *L. carinifera s.s.*; while *L. 'scabra'* refers to *L. intermedia* and perhaps also to *L. pallescens* (Chapter 9). Since on stable or accreting shores these species show pronounced horizontal zonation (Section 11.4.1), their vertical distributions cannot be readily compared in descriptive accounts, as given by these authors. Berry (1963, 1972) examined zonation on an eroding mangrove shore, and the other authors may have done likewise; only under these conditions do such a range of species occur together on the outermost trees (pers. obs., Singapore).

Regarding horizontal zonation, previous authors have in general noted only that littorinids become scarce away from the seaward edge of the forest (Berry, 1963, 1972; Macnae, 1968; Berry & Chew, 1973; Murty & Rao, 1977). Only Nielsen (1976) and Frith *et al.* (1976) have observed that *L. carinifera* is in fact typically found in the landward zone of the swamp, as shown here.

The only ecological study in which species previously known as *L. 'scabra'* have been distinguished is that of Cook (1983), who recorded three species (unnamed, but figured) from a swamp in northern Papua New Guinea. Cook noted the segregation between one species (*L. pallescens*) on leaves and another two (*L. scabra* and *L. intermedia*) on bark, as has been found at many localities in the present study.

The observations of habitats and zonation patterns presented here have considerably extended those of previous workers. For the first time detailed accounts of the species hitherto grouped as *L. 'scabra'* have been provided. Despite the limitations of the semi-quantitative technique used in this study, it is clear that the species of *Littoraria* in mangrove forests show characteristic patterns of vertical and horizontal distribution. Where several species occur together, they may show differential zonation patterns, although there is often considerable overlap between them.

Previous studies of the zonation of intertidal gastropods have mostly been carried out on rocky shores. Work in this environment has suggested that zonation patterns are maintained by complex interactions of behavioural responses with components of the physical and biological environments, and that these effects can best be resolved by manipulative experiments (review by Underwood, 1979). Although the present survey has been entirely descriptive, some comparative discussion is pertinent.

The mangrove environment differs in important respects from a rocky shore. Because of the three dimensional structure and often considerable width of the forest, both vertical and horizontal zonation patterns appear, whereas on rocky shores only vertical patterns are obvious. A tropical rocky shore is subject to extremes of insolation and desiccation when emersed, but in a mangrove forest these conditions are ameliorated by the presence of the trees, which provide shade and restrict air movement (Oliver, 1982).

The patterns of zonation commonly described for gastropods on rocky shores differ from those of the mangrove littorinids. Gastropods of rocky shores may occur at high densities (Section 11.5.1), show random feeding excursions (Underwood, 1977) and have seldom been reported to show vertical migrations with the daily tidal cycle (Section 12.4.1). Hypotheses relating to the proximate control of zonation patterns have been derived to a large extent from studies of relatively immobile limpets (review by Underwood, 1979). In these animals, observations of sequential vertical replacement and the results of field manipulations have led to the hypothesis that interspecific competition may determine zonation patterns (Wolcott, 1973; Choat, 1977). In contrast, the *Littoraria* species investigated here occur at low densities, show broadly overlapping distributions and undertake daily tidal migrations (Section 12.3.1), so that their patterns of zonation may be subject to very different controls.

11.5.1 The control of vertical distribution

As summarized by Underwood (1979), the upper limits of vertical distribution of gastropods on rocky shores have been accounted for in terms of physiological tolerance, competition for food and behavioural responses. From a study of limpet zonation, Wolcott (1973) proposed the hypothesis that upper limits of distribution are determined by competition for food with species from higher levels better adapted to emersion; only at the highest level where the distribution of a species adjoins an unexploited food source, will factors such as desiccation become directly limiting.

Such an hypothesis must be modified if it is to apply to mangrove dwelling *Littoraria* species, which show broad overlaps rather than sequential zonation, and usually occur at densities much lower than those at which competitive effects have been recorded in other littorinids (Emson & Faller-Fritsch, 1976; Hylleberg & Christensen, 1978; Stiven & Kuenzler, 1979; Branch & Branch, 1980, 1981; Robertson & Mann, 1982). The highest densities per unit area of surface are found in species of the lower levels, particularly *L. articulata*, and could not therefore prevent upward spread by a co-occurring species. It appears likely that all the snails effectively adjoin an unexploited food source, since densities at upper levels are so low, and competitive effects cannot account for distribution patterns. The mangrove trees provide shade and shelter, and the adult snails are sufficiently mobile to be able to reach the water level at each high tide (Section 12.3.1). It is therefore suggested that desiccation or high temperatures impose upper limits to distribution largely in an indirect manner, by influencing behaviour. Behavioural responses may be the proximate factor controlling upper limits of zonation (Chapter 12), but the ultimate factor which has shaped the behavioural pattern may be the increasingly rigorous microclimatic conditions at higher levels. There is some indirect evidence that microclimatic conditions may contribute to mortality in *Littoraria* species (Section 13.4.4).

Regarding lower limits of distribution, Underwood (1979) emphasized the influences of predation and behavioural responses. There are well documented examples of limitation of sedentary animals such as barnacles (Connell, 1961) and mussels (Paine, 1974) by predators. Since predators are more common at lower levels, it has been assumed that predation may determine lower limits of mobile gastropods also (Underwood, 1979). Amongst *Littoraria* species, those from higher levels possess the thinnest shells and are least resistant to attack by crabs (Chapter 14). There is therefore circumstantial evidence that predation acts either directly to impose a lower limit, or more probably indirectly as a selective force influencing behavioural patterns. Since, in general, *Littoraria* species crawl upwards to avoid submersion by a rising tide, and will not descend from the trees to the ground, it is clear that behaviour is a major determinant of the lower limit of zonation (Chapter 12). Some evidence has been presented for a preference by some species for the surface of leaves rather than bark, and the lower level of foliage may thereby influence the lower limit of distribution in leaf-dwelling species (e.g. *L. albicans, L. filosa, L. luteola, L. pallescens*).

11.5.2 The control of horizontal distribution

When describing zonation, a rocky shore or sandy beach can be considered as a two-dimensional surface, an inclined plane on which patterns of distribution are related to the vertical tidal level of the surface, rather than to the horizontal distance across the width of the shore. In the case of the arboreal fauna of mangrove forests, this is not so, since the occurrence of species is dependent upon both tidal level and horizontal distance. Horizontal patterns have been briefly noted by previous authors as mentioned above, but without any attempt at explanation. Proceeding from seaward to landward through the forest, the physical environment changes; not only does the frequency of tidal inundation decrease, but wave action becomes negligible, while shade and humidity will depend upon the density of the tree canopy. Of the biological features of the environment, the tree species will change according to the zonation of the vegetation, while distribution of predators and potential competitors may also vary.

Although behaviour appears to be an important determinant of vertical zonation, it can have little effect upon horizontal distribution, since the snails do not crawl upon mud or sand and can therefore only move between adjacent trees where roots or branches are in contact (Section 12.3.5). Tidal migrations are in an exclusively vertical plane and there is no evidence for horizontal migration. While competitive effects could conceivably limit spread of a species from middle zones towards the seaward edge of the forest, where high densities sometimes occur, they can have no influence upon landward spread where densities are always extremely low. If competition were significant, complementary patterns of horizontal distribution might be expected at high densities, but in fact the only possible example of such a pattern is provided by *L. articulata* (with *L. strigata*) and *L. melanostoma* at Kanchanadit (Fig. 11.11). Some evidence of associations with particular tree species has been presented, but does not seem to indicate obligate requirements. Even species which are most abundant upon *Avicennia* leaves (of which the leaf hairs form a component of the diet) can also be found upon trees with smooth leaves, although whether growth or survival are then impaired is not known. While association with a particular tree may influence horizontal patterns of abundance, it would not seem to impose limits on distribution. The explanation for such associations is not known, but might involve dietary requirements, distribution of predatory crabs or larval settlement preferences.

The distribution of predatory crabs through the forest has not been examined in detail. Clearly the influence of portunid crabs and other predators which enter the swamp only at high tide will be greatest in the seaward parts where inundation is more frequent. Tree climbing grapsids of the genus *Metopograpsus* are amongst the major predators of *Littoraria* (Chapter 14) and are also more common towards the seaward parts of the forest (pers. obs.; Sasekumar, 1974). Proceeding towards the landward fringe, the predominant decapods are sesarmines and ocypodids (Berry, 1972; Sasekumar, 1974; Frith *et al.*, 1976) which do not in general climb trees and are largely herbivorous or scavenging. The greater intensity of crushing predation towards the seaward parts of the forest might perhaps impose limits on some *Littoraria* species from the middle zones.

Crab predators may also influence distribution on a smaller scale. There is some evidence that the intensity of predation is greater on *Rhizophora* than on *Avicennia* trees, since arboreal crabs are most abundant on the former (Section 14.3.1). This might account for the greater abundance of the low level, bark dwelling species *L. articulata* upon *Avicennia*. At several localities it was noted that on outlying trees beyond the dense *Rhizophora* forest the numbers of individuals of *Littoraria* were greater than on trees on the outer edges of the forest belt (e.g. *L. intermedia*, Fig. 11.9). Isolated mangrove trees on rocky coasts sometimes carried high densities of *Littoraria* (e.g. at Orpheus Island; Moa Island). Since arboreal crabs appeared to be less frequent on outlying and isolated trees, they may have been exerting some influence on patterns of abundance, but this suggestion requires further investigation.

Littoraria species are dispersed as planktotrophic veligers, so that patterns of larval settlement may be partly responsible for the horizontal distribution of adult snails. This possibility has not been examined in the present work. Although there is an extensive literature concerning reproduction of littorinids, several authors have found it impossible to maintain the larvae in aquaria through the period of planktonic development and subsequent metamorphosis (Abe, 1942; Berry & Chew, 1973). Only Struhsaker & Costlow (1968) have reported success (and then with a mean survival through metamorphosis of only 1%), with the rocky shore species *Nodilittorina hawaiiensis* (as *Littorina picta*). These authors found that larvae settled only on surfaces coated with a layer of detritus or algae, but could detect no preferences for particular rock types. Williams (1964) found that the smallest individuals of *Littorina littorea* were most abundant on barnacle covered rocks at low intertidal levels, and explained this distribution in terms of settlement preference. Thus it appears that larval littorinids may not be distributed at random in mangrove forests, but might settle preferentially at certain levels, or on certain substrates (whether leaves or bark, or particular tree species), thereby determining the horizontal distribution of adults. Even were settlement at random, a greater number of juveniles would be expected at the seaward edge of the forest, where inundation is more frequent. Juvenile snails occupy lower vertical levels than adults (Section 12.3.4), where predation is more severe, and it may be that predation upon the smaller size classes effectively limits the horizontal distribution of adults.

From the foregoing discussion it would appear that neither behaviour, competition nor predation are likely to impose the landward limits to the horizontal distribution of *Littoraria* species. At their landward limit it is probable that most of these species are examples of Wolcott's (1973) concept of high level species adjoining an unexploited food supply, in which the limit of distribution is determined by tolerance of physical environmental conditions. One significant adverse condition will be the decreasing frequency of tidal inundation at more landward limits. While the *Ceriops* zone is inundated by all spring tides, the landward fringe may be reached by fewer than 50 tides annually (Macnae, 1968). In the seaward parts of the forest, snails at high vertical levels can migrate down the trees to reach the sea at most high tides, but this option is not available at the landward limits. However, since some *Littoraria* species from high levels may be active during periods of rain (Sections 12.3.1, 12.4.4), it might be expected that landward limits would be extended in wetter climates. That this might be the case is suggested by the presence of *L. carinifera* and *L. conica* in the landward fringe of forests in Malaysia, and the absence of species from this zone in tropical Australia where rainfall is lower. The influence of rainfall on the mangrove vegetation may also be significant, for only in areas with a rainfall exceeding 2000 mm is the landward fringe well developed and densely vegetated (Macnae, 1968). Such a dense forest will provide a more humid microclimate than the narrow landward fringe and open *Ceriops* thickets found on coastlines with lower rainfall.

In summary, although the above discussion of the control of distribution patterns has been highly speculative, some predictions can be made. Vertical distributions up the trees appear to be determined mainly by behavioural responses, of which negative geotaxis to avoid submersion by the tide is the most obvious. Susceptibility to predation at low levels, and to microclimatic extremes at high levels, may be the selective pressures which have set, respectively, the lower and upper limits of distribution. On the other hand the landward limits of horizontal distribution are perhaps directly determined by physiological tolerance. Clearly, no conclusive statements can be based on a purely descriptive account of zonation patterns. As advocated by Underwood (1979), only manipulative field work and experimentation can provide evidence of the control of zonation patterns.

11.5.3 Continental and oceanic distributions

The explanation for the distinction between the two types of distribution here referred to as 'oceanic' and 'continental' is at present obscure. The distinction is evident on both local and geographical scales. On the larger scale, similar observations have been made in other molluscan groups by Abbott (1960, 1968) and Taylor (1971a). Using the example of the prosobranch genus *Bullia*, with a continental distribution around the perimeter of the Indian Ocean, Taylor (1971a) related this pattern to suppression of the free-swimming larval stage in such forms. However, as in the genus *Littoraria* examined here, Abbott (1960) could detect no correlation of the type of distribution with method of development, size, abundance or microhabitat in the genus *Strombus*.

In continental coastal waters nutrient levels may be higher than in the open ocean (Koblentz-Mishke *et al.*, 1970; Haines, 1979). It seems impossible that this could influence adult *Littoraria* directly, since they are rarely submerged. Nutrient levels could, in theory, influence the veliger larvae or their planktonic food supply, or even the algal food of the adults. Nevertheless, since the effect upon distribution can be distinctly local, nutrient levels would seem an unlikely cause. Some of the continental localities visited were close to river or creek mouths, but in such cases freshwater influence was judged to be slight. Intolerance of freshwater influence by oceanic species or their larvae could not explain a pattern of distribution such as that shown by *L. scabra* and *L. intermedia* at Magnetic Island, where they were found only at each end of a belt of forest 7 km in length. The most obvious features of the environment which were correlated with the absence of oceanic species were water turbidity and the associated muddy substrate. Once again it is difficult to envisage a direct effect upon adult snails living above the water level, but an influence upon their food or upon larval settlement is not unlikely. Oceanic species may be less tolerant of the effects of sediment than are continental forms. This suggestion is in agreement with the observation that the three known oceanic species are always most abundant at or close to the outermost edge of the forest, where wave action does not permit the accumulation of layers of silt on the surface of leaves or bark, which may prevent settlement in the inner zones of the forest.

CHAPTER 12: BEHAVIOUR

12.1 Introduction

The patterns of behaviour and behavioural responses of intertidal gastropods have been the subject of numerous investigations. Since littorinids are abundant on most temperate rocky shores, where the majority of studies have been carried out, they have been the most frequently used experimental animals. Investigations of behaviour have mostly been directed towards the explanation of the maintenance of observed patterns of zonation on the shore.

Gowanloch & Hayes (1926) first reported that *Littorina littorea* returned to its original level after displacement up or down the shore. The same result has since been demonstrated many times with various littorinids (Alexander, 1960; Evans, 1961; Bock & Johnson, 1967; Chow, 1975; Gendron, 1977; McQuaid, 1981b), although Petraitis (1982) has found a more complex response in *Littorina littorea*.

Early workers endeavoured to explain their observations in terms of simple behavioural responses to light and gravity, which could be influenced by other aspects of the physical environment. Thus almost all littorinids were found to show negative geotaxis when disturbed and placed in water, but the response was weakened (Gowanloch & Hayes, 1926; Hayes, 1927) or reversed (Newell, 1958b; Bock & Johnson, 1967; Bingham, 1972d) following a period of desiccation, which could account for their return to the level of origin following displacement up the shore. Both high (Bingham, 1972d) and low (Janssen, 1960; Lambert & Farley, 1968) temperatures were found to produce positive geotaxis, perhaps accounting for some cases of seasonal migration down the shore. In laboratory trials, positive phototaxis was shown by open surface species (Gowanloch & Hayes, 1926; Evans, 1965; Bingham, 1972d; Petraitis, 1982) and negative phototaxis by littorinids from macroalgae (Barkman, 1955) and crevices (Bock & Johnson, 1967). In other tests the direction of the phototactic response was found to depend upon temperature (Janssen, 1960) and direction of displacement on the shore (Gendron, 1977). Rheotaxis, a response to a water current, was demonstrated in a littorinid by Neale (1965), and Gendron (1977) accounted for the orientation of *Littorina littorea* by a response to wave movement.

Many authors have attempted to relate tactic responses to the maintenance of zonation patterns on the shore. Newell (1958a, b) explained the maintenance of the position of *Littorina littorea* on flat surfaces by a change from positive to negative phototaxis during feeding excursions, while on vertical surfaces both light and gravity influenced behaviour. The classic study of *Melarhaphe neritoides* by Fraenkel (1927) showed how negative geotaxis combined with a phototactic response, dependent upon immersion and substrate orientation, to produce the observed distribution in crevices above the high water level. This behaviour has been confirmed by Charles (1961) (and in other species by Neale, 1965, and Berry & Hunt, 1980), although some populations are exceptional (Lysaght, 1953). In a laboratory tide model, Evans (1965) found that the natural pattern of zonation of two British littorinids was not achieved in darkness, but Underwood (1972) failed to reproduce this result and suggested that phototaxis was not of great significance in the determination of zonation patterns.

More recently, explanations of behaviour in such simple terms have been criticised as failing to account adequately for the observed maintenance of zonation patterns on the shore (Underwood, 1979). There are indications that the distribution of algal food may influence behaviour. Experiments with littorinids feeding on macroalgae have shown strong food preferences (Bock & Johnson, 1967; Lubchenco, 1978). In the presence of suitable food the almost universal negative geotaxis may be suppressed (Newell, 1958b; Barkman, 1955; Bock & Johnson, 1967; Underwood, 1972), while in some species starved snails show positive geotaxis (Newell, 1958b). So far, little is known of the distribution of microalgal food, and microalgal feeders appear to be nonselective in their diets (Sacchi *et al.*, 1977; Hylleberg & Christensen, 1978).

On the basis of the known behavioural responses of intertidal gastropods, Underwood (1979) has proposed a new hypothesis for the maintenance of their distribution patterns. Displacement to a lower level is believed to stimulate negative geotaxis, while availability of food at the preferred level inhibits upward movement. If snails are displaced to a higher level, desiccation or high temperatures may lead to a reversal of geotaxis, so that the original level is regained.

Even such an hypothesis, taking account of the influence of the biological environment on behaviour, provides only a partial explanation of observed distribution patterns. It appears that the physiology of individuals may also affect behaviour, as in the case of parasitized snails (Lambert & Farley, 1968; Williams & Ellis, 1975). The several cases of breeding migrations to low levels reported in littorinids (Kojima, 1959; Fretter & Graham, 1962, p. 387; Sacchi, 1966) may also be mentioned in this context. Berry & Hunt (1980) have shown experimentally that taxes of *Littorina saxatilis* may change with growth. Newly emerged juveniles were found to show negative geotaxis only while immersed, so that they did not crawl above the high water mark, while adults climbed to higher levels. Phototactic responses were also found to change and together the two effects explained the different distributions of adults and juveniles.

More complex behavioural patterns have been described in littorinids. Evans (1965) and Newell (1965) first suggested the possibility of form vision in *Littorina* species, and Hamilton (1977, 1978b) has provided experimental evidence of visual orientation towards plant stems by *Littoraria irrorata*. It is now well established that littorinids recognize and follow the polarity of mucous trails left by conspecifics, regardless of the sex of the trail-maker (Peters, 1964; Hall, 1973; Gilly & Swenson, 1978; Raftery, 1983). Daguzan (1966) has reported evidence of homing in *Littorina littorea*, but this has not been confirmed in studies of other species (Hall, 1973). Although Stanhope *et al*. (1982) found no evidence of an escape response by *Littoraria irrorata* in the presence of predatory crabs, Hadlock (1980) demonstrated that *Littorina littorea* hides in crevices in response to the juices of crushed conspecifics, thereby reducing the chance of predation.

An activity rhythm with circatidal periodicity has been observed in both *Nodilittorina hawaiiensis* (as *Littorina picta*, Struhsaker, 1968) and *Littorina nigrolineata* (Petpiroon & Morgan, 1983), and a 14 day rhythm in *Littorina saxatilis* (Bohn, 1904). Other authors have failed to detect rhythmicity under constant laboratory conditions (Zann, 1973a; Underwood, 1972; Gallagher & Reid, 1979).

In summary, the picture which emerges from the numerous studies of the behaviour of littorinids (and gastropods in general) on temperate rocky shores is of static zonation patterns, maintained by behavioural responses. The snails make random feeding excursions (Underwood, 1977; McQuaid, 1981b) and only show directional movement following displacement (Petraitis, 1982). The reported cases of fluctuations in zonation levels are mostly on a seasonal or maturational time scale.

Conditions in mangrove forests differ from those on temperate rocky shores in many ways, and the behavioural patterns of their littorinid inhabitants may be expected to differ correspondingly. The trees provide a mainly vertical substrate, on which small migrations can accomplish changes in tidal level that would be impossible on a shelving rocky shore. The shade of the trees ameliorates the extremes of high temperature and low humidity which would be experienced on an exposed rocky shore, and wave action is always slight, thereby modifying the basic environmental restraints on behaviour patterns. The densities of tree-dwelling molluscs are much lower than those at which competitive effects have been reported on rocky shores (Section 11.5.1) and therefore competition may not be a significant factor in the determination of behaviour patterns in the mangrove environment. Perhaps most importantly, mangrove communities are largely tropical. Recent research suggests that in tropical latitudes the incidence of crushing predation upon intertidal molluscs is highest and is reflected in behavioural adaptations (Bertness *et al.*, 1981; Menge & Lubchenco, 1981; Section 12.4.1; Chapter 14).

The records of patterns of zonation, as described in Chapter 11, were all made at low tide, on single occasions. In order to consider gradients of adaptation to predation pressure (Chapter 14), it was necessary to observe zonation patterns throughout a whole tidal cycle. This was achieved by following the movements of individual snails, a technique hitherto applied to littorinids only by Abe (1942). In addition, low tide zonation patterns were followed for a six month period, encompassing wet and dry seasons, and both breeding and nonbreeding periods, to establish whether the species maintained the same order of zonation. Rather few studies have made detailed investigations of zonation patterns of littorinids over long periods (Lambert & Farley, 1968; Underwood, 1973). Not only the tidal level, but also the substrate of the snails, was recorded, to examine the possibilities of cyclic selection and background choice in relation to the maintenance of colour polymorphism (Chapter 15).

12.2 Methods

The behaviour and vertical distribution of five species (*L. scabra*, *L. intermedia*, *L. philippiana*, *L. filosa*, *L. articulata*) were examined at the study site at Cockle Bay, Magnetic Island (Chapter 10).

Daily migration patterns were recorded over one 24 hour period on

26 and 27 December, 1982. Ten adults of each of the five species were selected, in the order in which they were located on the trees. These were numbered individually *in situ* using enamel paint, care being taken not to dislodge or disturb the snails. The ten *L. filosa* were located on a large *Avicennia* tree behind the *Rhizophora* grove in the experimental area of the study site, the individuals of the other four species in the *Rhizophora* grove. On each hour the tidal level, relative humidity and temperature were recorded. Relative humidity was measured in the shade of the *Rhizophora* forest, using a whirling psychrometer; three consecutive readings were taken and averaged. Air temperature was recorded on a thermometer suspended at a height of 2 m above the ground in the *Rhizophora* grove. For each marked snail, the height above ground (to 0.1 m) and means of attachment (by foot or mucus) were recorded every hour for 24 hours. Measurements of the levels for each species were made in turn, so that all ten individuals were recorded in a short space of time. During the night the snails were examined by red light.

In order to investigate the influence of the cycle of spring and neap tides (or synodic cycle, Vannini & Chelazzi, 1978) and of weather conditions upon the distribution of the snails, the study site was visited at one neap tide and at the following spring tide each month, for a period of six months. Individually numbered snails of the four largest species (*L. scabra, L. intermedia, L. philippiana, L. filosa*) were examined on three groups of trees (Table 10.1). These were the same snails used in the mark and recapture experiment, and details of sample sizes and of the marking procedure are given in Section 13.2.2. For each numbered snail located, the height above the ground (to the nearest 0.1 m), the number of the tree and the substrate (aerial roots, trunks (>4 cm diam.), branches (1-4 cm), twigs (<1 cm), morphologically upper or lower leaf surface) were recorded. All records were made during daylight hours at low tide, when the trees were entirely emersed. Weather was defined as wet if rain had fallen in the 24 hours preceding the observations. In the tables of results the total rainfall recorded is that for the date of observation and the previous day (recorded by Bureau of Meteorology, at Townsville airport, 12 km from study site). Only on 13, 18 and 19 January, 1981, was heavy rain falling during the period of observation.

In the case of *L. articulata*, in which shells were too small to number individually, all specimens were removed from seven *Avicennia* trees in a uniform stand, and sorted in the laboratory into size classes of 2 mm increments (smallest class 2-4 mm). Each size class was returned to a separate tree. At each spring or neap tide visit the numbers of snails of each size class present in each 0.2 m vertical zone on the seven trees were recorded. Snails obviously outside the limits of the size class which had been released on a particular tree were ignored. At each visit the snails were collected, resorted into size classes and released at the bases of the trees the following day. At least one week elapsed between visits, and after this time the distributions of the sorted snails did not appear to differ from those of untouched snails on control trees nearby.

During the mark and recapture experiment (Section 13.2.2) the sex and colour of each numbered snail were recorded and measurements of shell height were made each month. These data were used in the analysis of the distribution of the numbered snails (see also Section 15.3). In about 20% of cases, individuals were not recovered for the measurement of shell height at the nearest monthly date on which this was recorded; sizes were then estimated by linear interpolation between measurements on preceding and succeeding occasions. The vertical size gradients of each species on each date were examined by regression of level above chart datum upon shell height. For the four species numbered individually (*L.scabra, L. intermedia, L. philippiana, L. filosa*) an analysis of covariance was carried out to determine the effect of sex upon level, independent of the effect of shell size. This technique was used to avoid the confounding of the effects of sex and size, since most species show pronounced sexual dimorphism (Section 4.2). The analysis was performed using the MANOVA procedure of the SPSS programme, first testing for regression parallelism (Hull & Nie, 1981, p. 15).

12.3 Observations

12.3.1 Daily tidal migrations

During the 24 hour period of observation, the five *Littoraria* species (*L. scabra*, *L. intermedia*, *L. philippiana*, *L. filosa*, *L. articulata*) showed certain similarities of behaviour. All of the individuals observed remained at or above the water level, and those reached by the rising tide climbed upwards to avoid submersion (Figs 12.1 to 12.5). Numerous casual observations on other visits to the study site confirmed that this response to contact with a rising tide was typical. As shown by the figures, the species were found at different vertical levels on the trees. The frequency of contact with a rising tide, and therefore the influence of the tide upon behaviour and distribution, depend upon the vertical zone occupied by the species.

L. articulata and *L. intermedia* occupied the lower levels on the trees, where they were reached by the majority of high tides (Figs 12.7, 12.8). These species followed the rising and falling water level, and at high tide were found in the zone of wave splash within 20 cm of the surface (Figs 12.1, 12.2). Details of the behaviour of these two species differed slightly. Figure 12.1 shows that on the date of observation *L. articulata* followed the descending water level closely in the evening, in many cases almost to ground level, before climbing upwards for 20 to 40 cm and becoming quiescent. In the morning the falling tide was followed for a shorter period, leaving the majority of the snails quiescent at a level higher than that occupied during the night. Although occupying a similar zone and occurring on the same *Rhizophora* trees, *L.*,*intermedia* showed a

Fig. 12.1 24 hour record of the vertical migratory behaviour of ten marked individuals of *Littoraria articulata* on a *Rhizophora* tree at Cockle Bay. Numbered lines are the paths of individual snails. Location of each snail was recorded every hour; attachment by mucus indicated by absence of points on lines; points indicate attachment by foot.

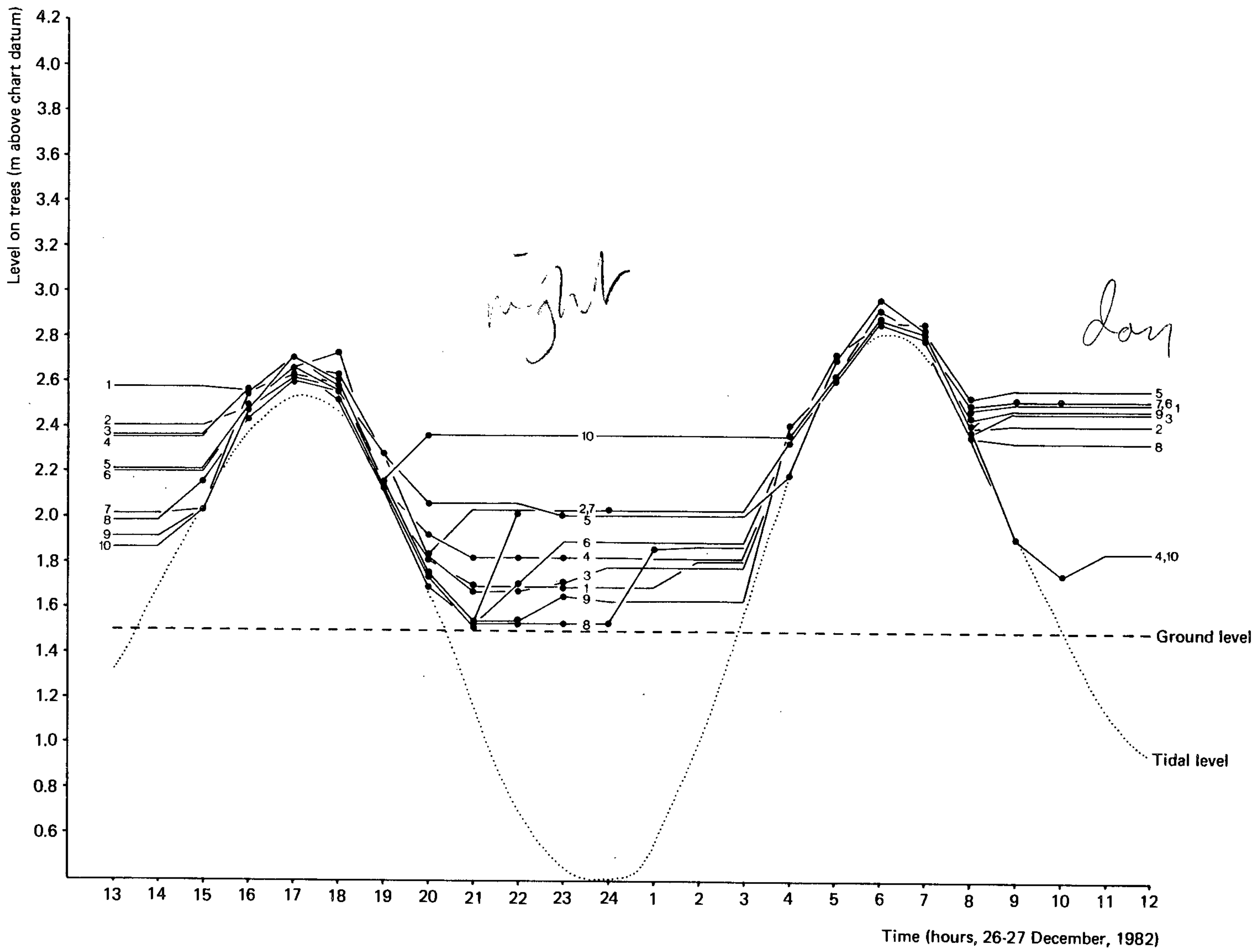

Level on trees (m above chart datum)
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
13
14
15
16
17
18
19
20
21
22
23
24
1
2
3
4
5
6
7
8
9
10
11
12
Time (hours, 26-27 December, 1982)
1
2
3
4
5
6
7
8
9
10
10
2,7
5
6
4
3
1
9
8
5
7,6
1
9
3
2
8
4,10
Ground level
Tidal level
night
day

Fig. 12.2 24 hour record of the vertical migratory behaviour of ten marked individuals of *Littoraria intermedia* on *Rhizophora* trees at Cockle Bay. Symbols as in Fig. 12.1.

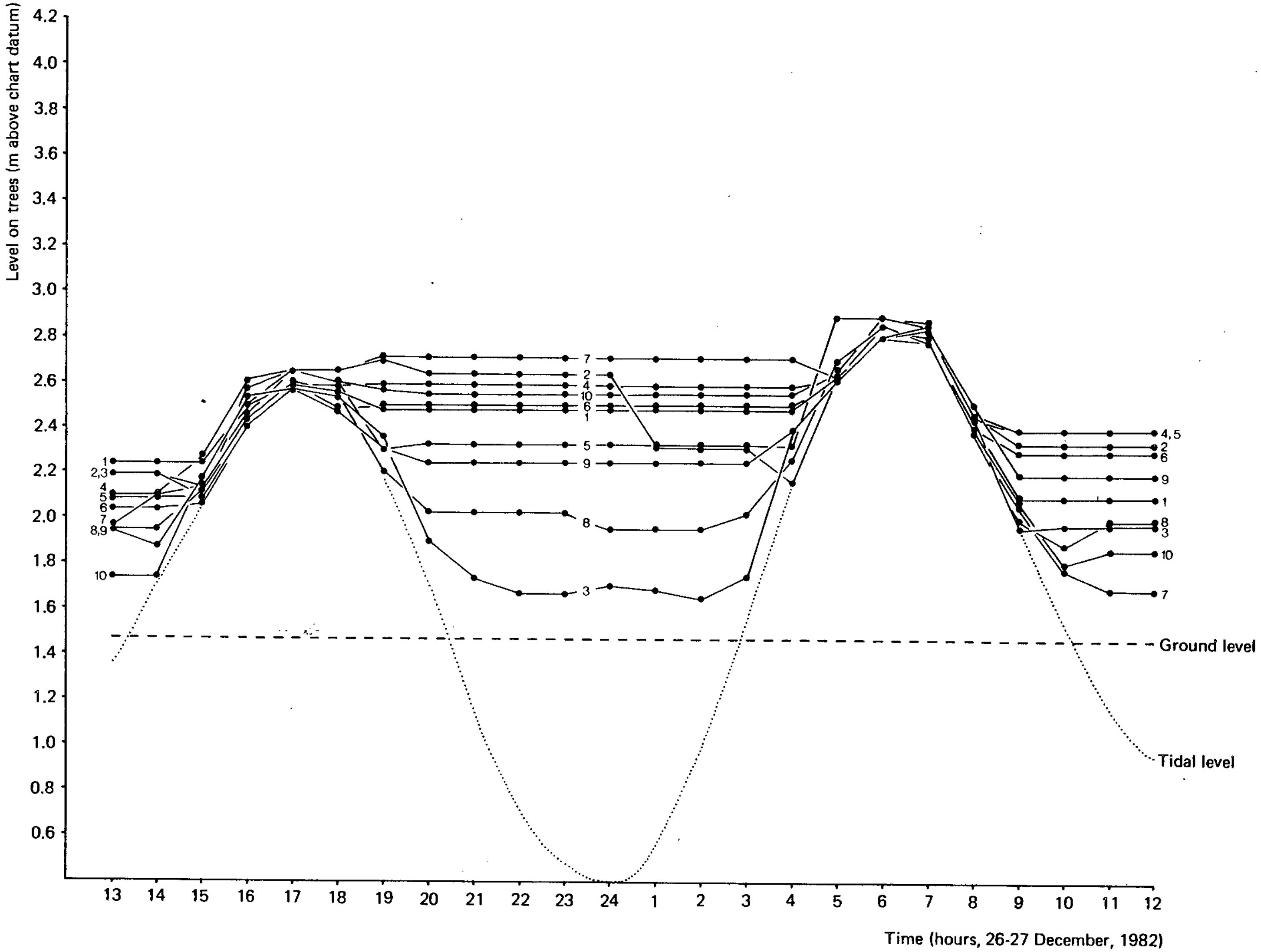

Level on trees (m above chart datum)
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
13
14
15
16
17
18
19
20
21
22
23
24
1
2
3
4
5
6
7
8
9
10
11
12
Time (hours, 26-27 December, 1982)
1
2,3
4
5
6
7
8,9
10
7
2
4
10
6
1
5
9
8
3
4,5
2
6
9
1
8
3
10
7
Ground level
Tidal level

Fig. 12.3 24 hour record of the vertical migratory behaviour of ten marked individuals of *Littoraria scabra* on *Rhizophora* trees at Cockle Bay. Symbols as in Fig. 12.1.

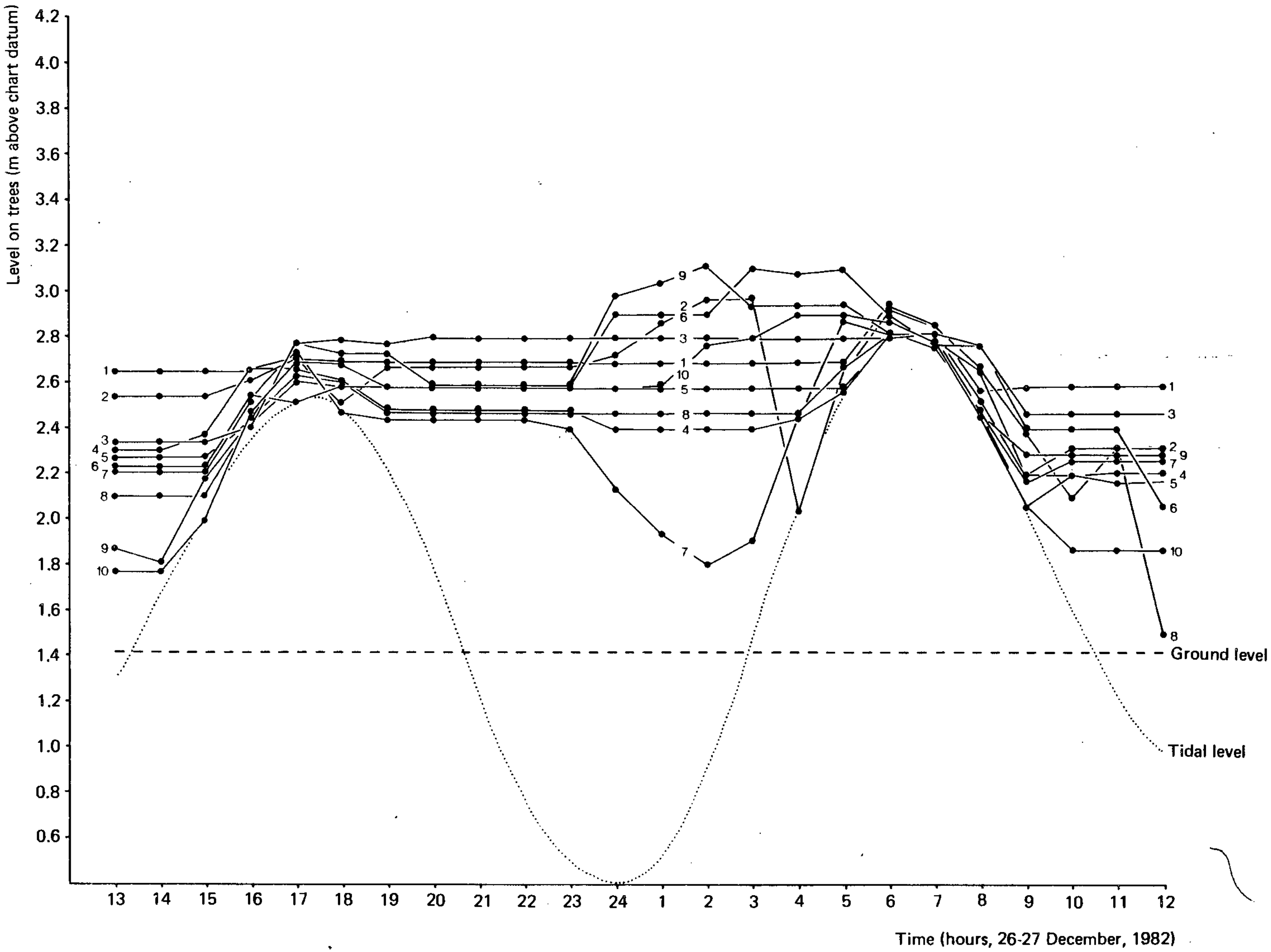

Level on trees (m above chart datum)
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
1
2
3
4
5
6
7
8
9
10
9
2
6
3
1
10
5
8
4
7
1
3
2
9
7
5
4
6
10
8
Ground level
Tidal level
13
14
15
16
17
18
19
20
21
22
23
24
1
2
3
4
5
6
7
8
9
10
11
12
Time (hours, 26-27 December, 1982)

Fig. 12.4 24 hour record of the vertical migratory behaviour of ten marked individuals of *Littoraria filosa* on *Avicennia* trees at Cockle Bay. Symbols as in Fig. 12.1.

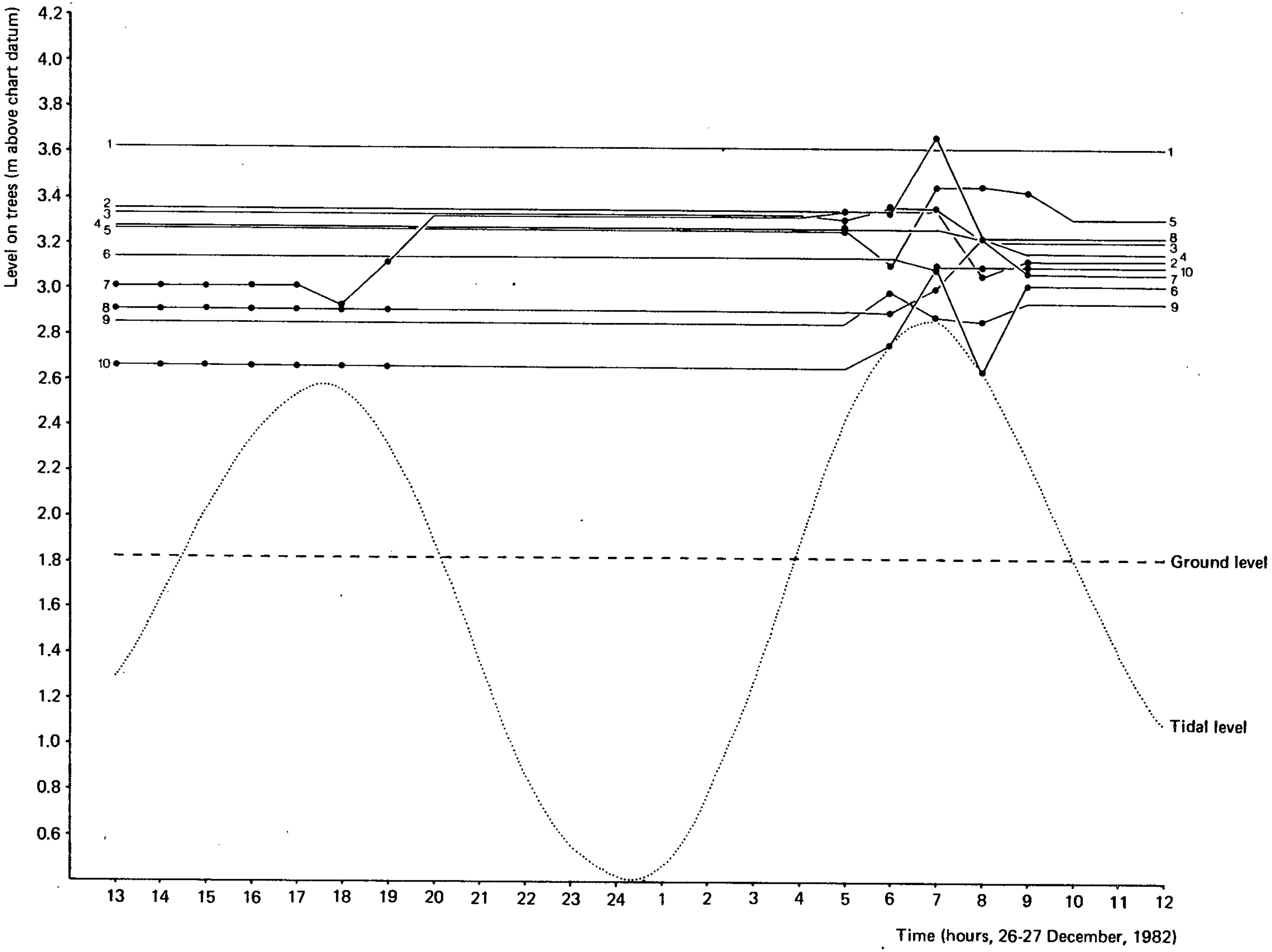
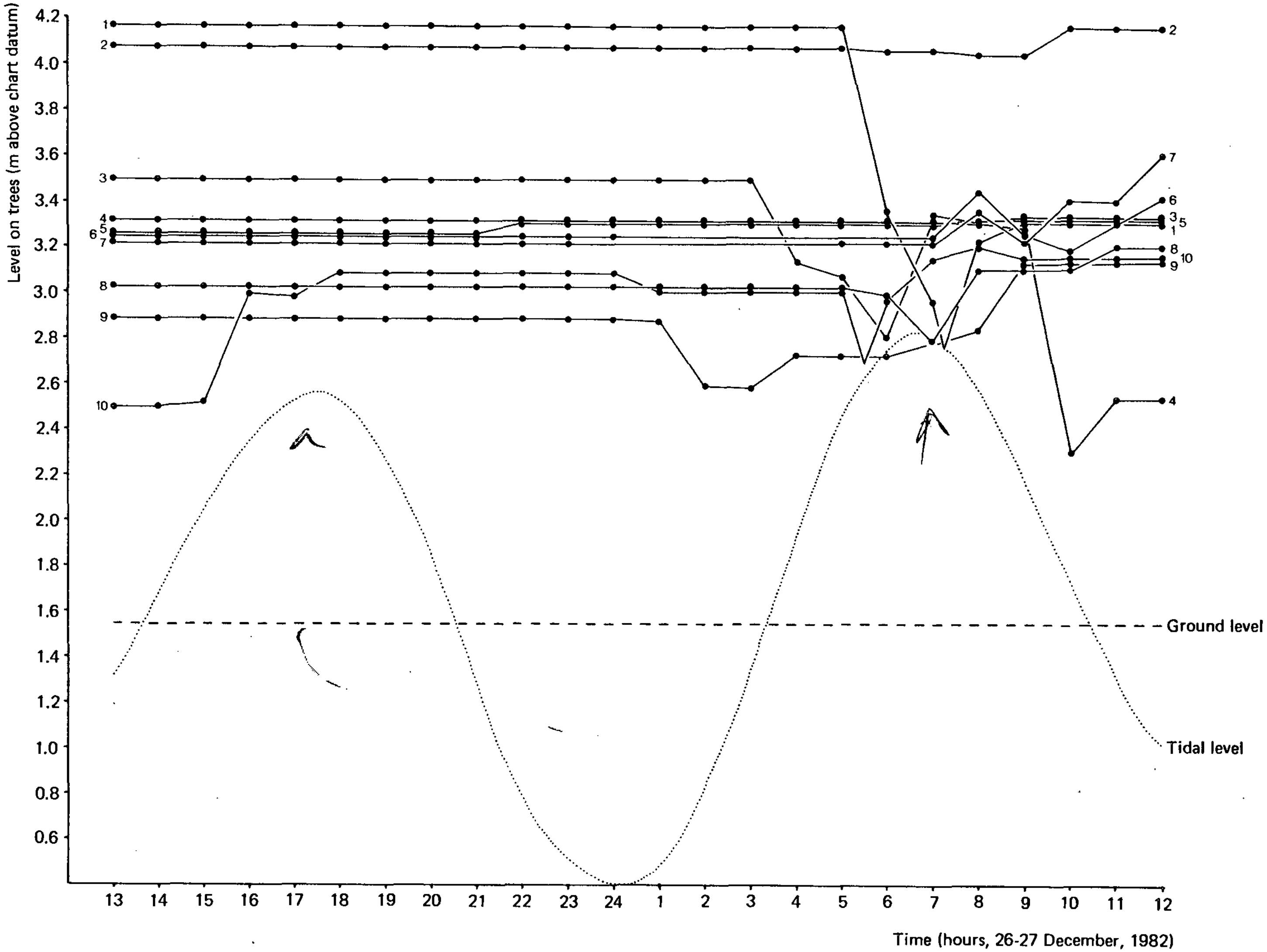

Level on trees (m above chart datum)
4.2
4.0
3.8
3.6
3.4
3.2
3.0
2.8
2.6
2.4
2.2
2.0
1.8
1.6
1.4
1.2
1.0
0.8
0.6
1
2
3
4
5
6
7
8
9
10
1
5
8
3
2
4
10
7
6
9
Ground level
Tidal level
13
14
15
16
17
18
19
20
21
22
23
24
1
2
3
4
5
6
7
8
9
10
11
12
Time (hours, 26-27 December, 1982)

Fig. 12.5 24 hour record of the vertical migratory behaviour of ten marked individuals of *Littoraria philippiana* on *Rhizophora* trees at Cockle Bay. Symbols as in Fig. 12.1.

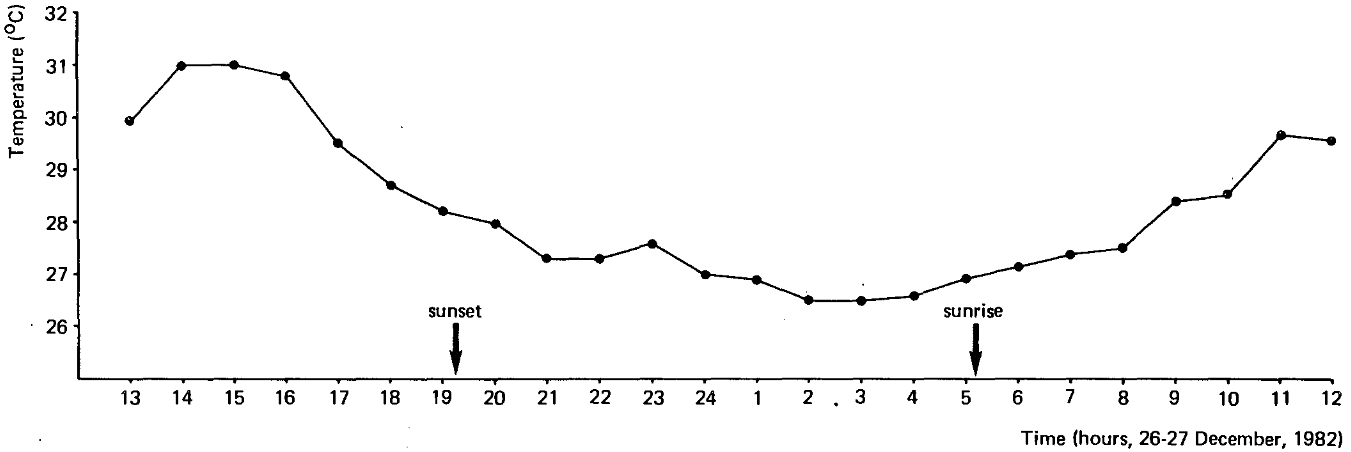


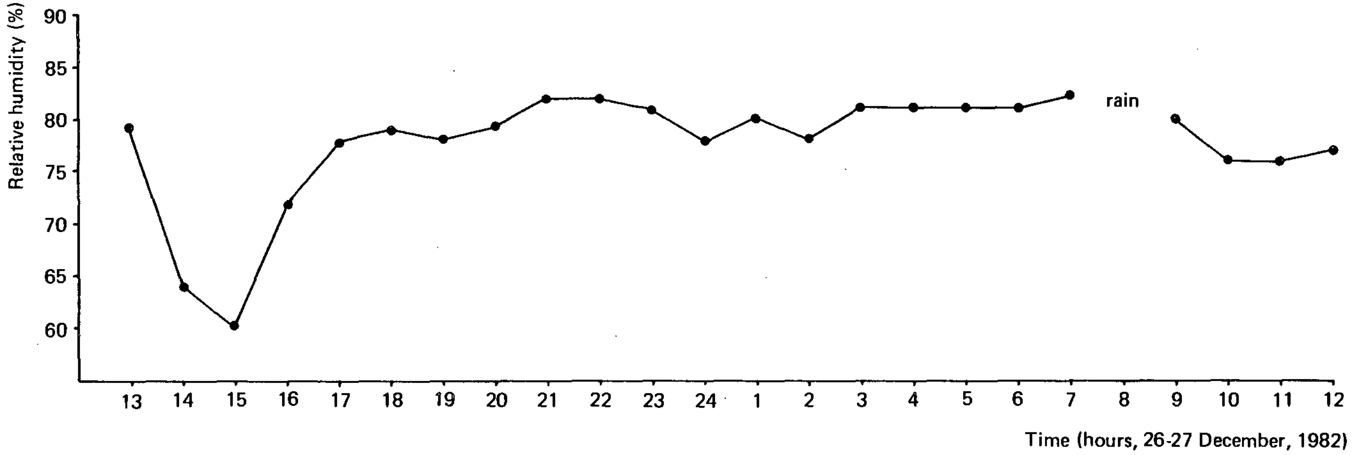
?

Eor spaw
on higher
high tide
[illegible]

little activ
on lesser HT.

Fig. 12.6 Records of temperature and relative humidity during 24 hour observations of vertical migratory behaviour of *Littoraria* species, measured at 2 metres above the ground in the *Rhizophora* forest at Cockle Bay.


Temperature (°C)
32
31
30
29
28
27
26
sunset
sunrise
13 14 15 16 17 18 19 20 21 22 23 24 1 2 3 4 5 6 7 8 9 10 11 12
Time (hours, 26-27 December, 1982)


Relative humidity (%)
90
85
80
75
70
65
60
rain
13 14 15 16 17 18 19 20 21 22 23 24 1 2 3 4 5 6 7 8 9 10 11 12
Time (hours, 26-27 December, 1982)

different behaviour pattern on this occasion, following the descending tide closely only in the morning (Fig. 12.2).

L. scabra occupied a level above that at which *L. intermedia* was found on the same trees (Figs 12.8, 19.9). During the 24 hour observation period, *L. scabra* followed the descending morning tide closely, but did not migrate downwards with the falling tide in the evening (Fig. 12.3). In this respect the pattern of behaviour was similar to that shown by *L. intermedia*. In contrast to *L. intermedia*, however, six of the ten individuals of *L. scabra* observed became active between midnight and the morning tide. Four of the active snails climbed upwards before returning to the water level at high tide (Fig. 12.3).

The three species *L. scabra*, *L. intermedia* and *L. articulata* showed considerable overlap of their respective habitats on the *Rhizophora* trees. This was especially evident during the two high tides, when all the individuals of the three species were concentrated in the zone of wave splash, within 20 cm of the water surface. However, the behaviour of these species differed, so that *L. articulata* followed the descending water surface to the lowest levels, while *L. scabra* was found highest above the water surface.

Of the *Littoraria* species on *Rhizophora* trees, *L. philippiana* occurred at the highest levels (Fig. 12.12), showing little overlap with the three aforementioned species. During the 24 hour observation period (Fig. 12.5), the majority of the ten individuals of *L. philippiana* remained quiescent until the early morning high tide, when all became active. At this time seven snails made a downward and then upward excursion, during which five reached the water level briefly. In one case the downward excursion was of 1.4 m in two hours. This behaviour of descending to the water level at high tide was also seen on other visits to Cockle Bay, but only during the early morning. Observations of mucous trails laid between successive daily visits to the study area suggested that *L. philippiana* made similar excursions during nocturnal high tides.

At Cockle Bay *L. filosa* was abundant only on *Avicennia* trees, on which the 24 hour observations were made (Fig. 11.1). Shade cover, foliage distribution and probably microclimate differ from those in the *Rhizophora* forest (Section 11.4.3), so that direct comparisons of migration patterns between the two environments should be interpreted with caution. All but one of the ten individuals became active in the early morning. This timing coincided with the high tide, but only one animal was reached by the rising tide. Of the others only two made short excursions to the water level and then back upwards (Fig. 12.4). On other occasions also *L. filosa* was observed to be active during early morning, especially after heavy dew or at high tide, but never during the day in hot, clear weather.

Since observations of each individual were made only hourly, it was not possible to ascertain whether, in the three species reached by the high tides, activity was stimulated directly by contact with the water, or whether upward migration began in advance of the rising tide. Since most of the individuals of *L. filosa* and *L. philippiana* occupied levels above the reach of the high tide, the stimulus for activity must have been indirect or endogenous in these species. No marked change in humidity, which could have stimulated activity, was recorded during the rise of the tide (Fig. 12.6) and air temperature showed only small changes throughout the period of observation. It must be noted that at 8 a.m. during the observation period a light shower of rain fell, lasting 5 minutes. This appeared to have no effect upon *L. scabra*, *L. intermedia* and *L. articulata*, clustered near the descending water level. The dampening of the substrate temporarily increased the activity of *L. philippiana* and *L. filosa*, although on this occasion most were already active before the rain began. It was noted on other occasions that light rain during the day initiated activity in *L. filosa* and *L. philippiana*.

Interactions between individuals did not appear to be of significance in the behaviour of these species. Trail following was observed on several occasions, but the snails occurred at low density (Section 11.4.1) and did not usually form aggregations when quiescent. *L. articulata*, the most abundant species at Cockle Bay (Fig. 11.1), was an exception, and formed clusters on those trees where it occurred in large numbers (Fig. 15.2). Reproductive behaviour is briefly considered in Chapter 13; in relation to aggregation it may be noted that during the 24 hour observation period the three species of low levels became concentrated in a narrow band 10 cm in height during the early morning high tide. Copulation was observed only at this time, during which seven of the ten individuals of *L. scabra*, three of *L. intermedia* and seven of *L. articulata* were seen to copulate.

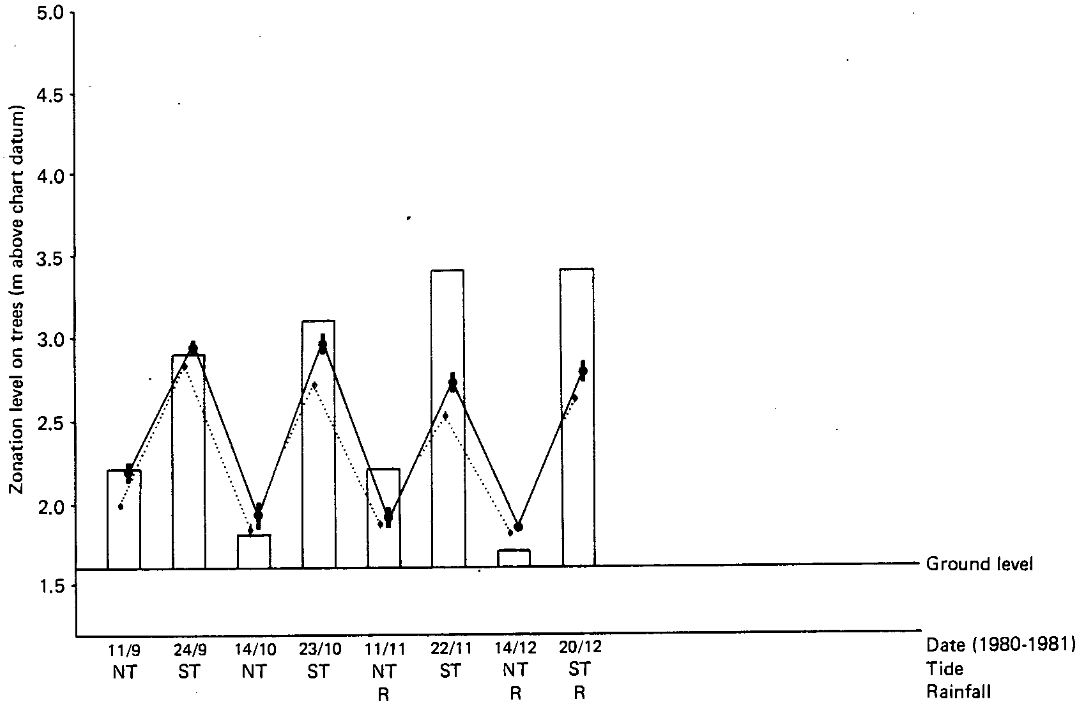
12.3.2 Influence of synodic cycle upon distribution

The measurements of vertical distribution at spring and neap tides were made during daylight at low tide. At such times, if rain was not falling, the majority of the snails were quiescent, as in the corresponding period during the 24 hour study described in Section 12.3.1. The three species from lower levels, *L. articulata*, *L. intermedia* and *L. scabra*, showed pronounced fluctuations of their mean vertical levels with the cycle of spring and neap tides (Figs 12.7, 12.8, 12.9). This may be expected in view of their habits of avoiding submersion and following the descending water surface. However, these figures show that the levels occupied by quiescent snails at either spring or neap tides were rather uniform, bearing no relation to the height of the previous high tide. The difference between levels occupied at spring and neap tides was greatest in the case of *L. articulata*, which as shown by the 24 hour record of migration (Fig. 12.1) followed the descending water level more closely than the other two species.

During dry weather the two species from higher levels, *L. filosa* and *L. philippiana*, also showed fluctuations in level with the synodic cycle (Figs 12.10, 12.11, 12.12). Although most of the

Fig. 12.7 Mean zonation level of *Littoraria articulata* on *Avicennia* trees at Cockle Bay, recorded during low tide at spring and neap tide periods. Solid line connects mean levels of snails of shell height ≥7 mm; dotted line connects mean levels of snails of shell height <7 mm. Error bars are 95% confidence limits. Histogram bars indicate height of preceding high tide. R, significant rainfall during preceding 24 hours (Table 12.1).

Fig. 12.8 Mean zonation level of *Littoraria intermedia* on *Rhizophora* trees at Cockle Bay, recorded during low tide at spring and neap tide periods. Solid line connects mean levels of snails of shell height ≥12 mm; dotted line connects mean levels of snails of shell height <12 mm. Error bars are 95% confidence limits. Histogram bars indicate height of preceding high tide. R, significant rainfall during preceding 24 hours (Table 12.2).


5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
Zonation level on trees (m above chart datum)
Ground level
11/9 NT
24/9 ST
14/10 NT
23/10 ST
11/11 NT R
22/11 ST
14/12 NT R
20/12 ST R
Date (1980-1981)
Tide
Rainfall

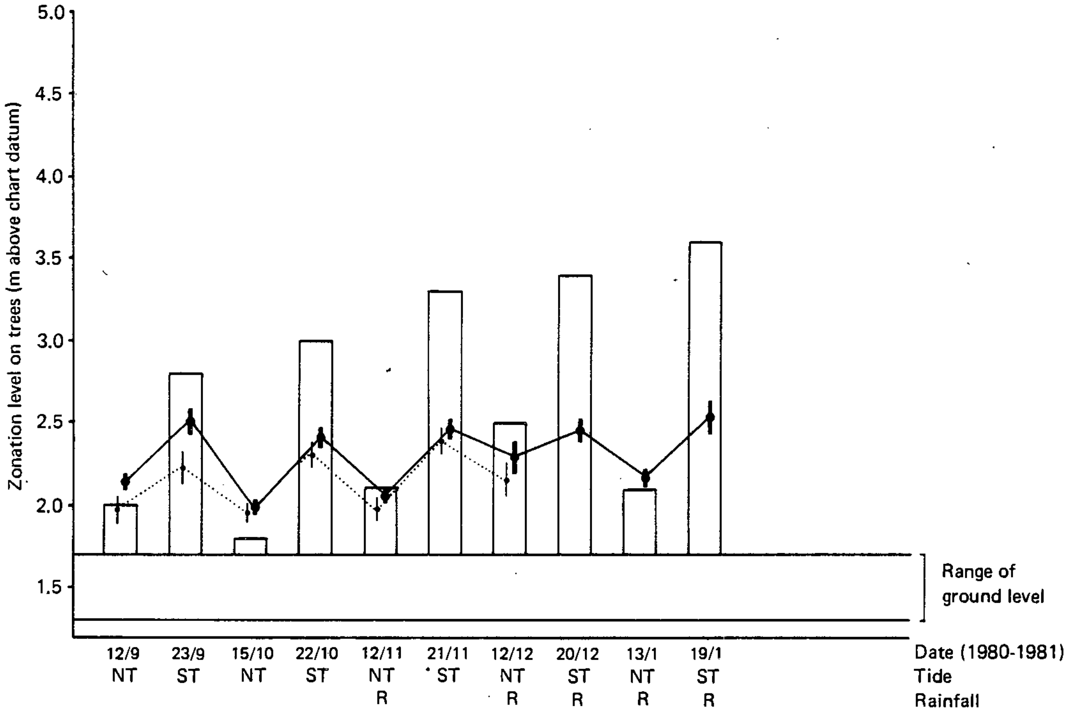
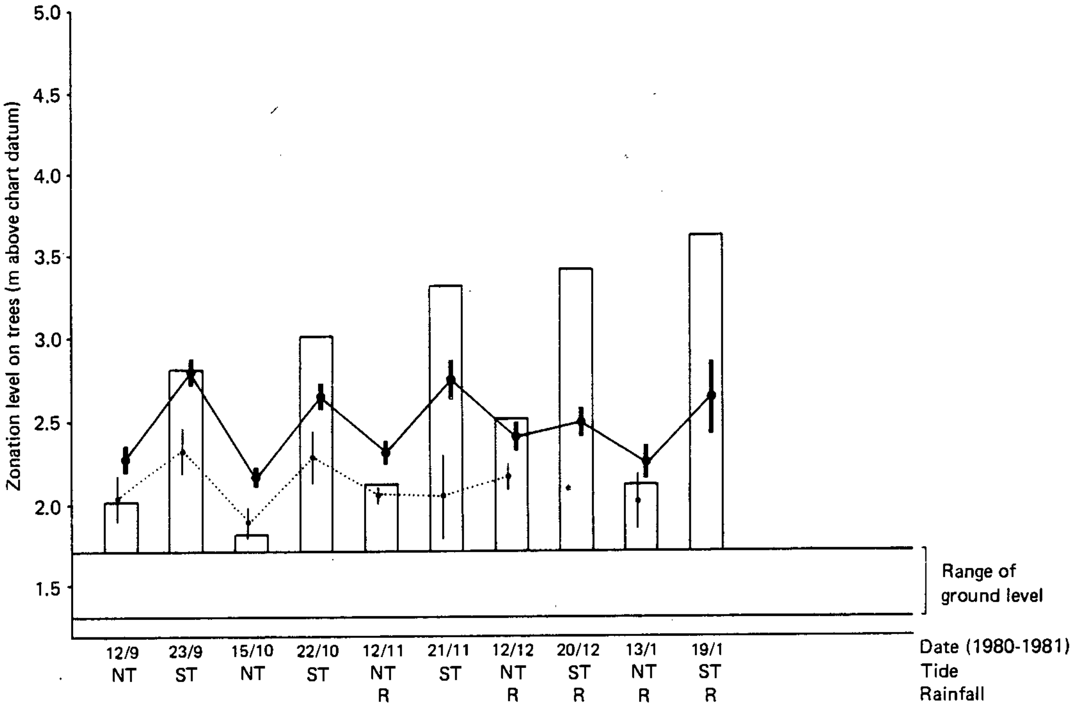

5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
Zonation level on trees (m above chart datum)
Range of ground level
12/9 NT
23/9 ST
15/10 NT
22/10 ST
12/11 NT R
21/11 ST
12/12 NT R
20/12 ST R
13/1 NT R
19/1 ST R
Date (1980-1981)
Tide
Rainfall

Fig. 12.9 Mean zonation level of *Littoraria scabra* on *Rhizophora* trees at Cockle Bay, recorded during low tide at spring and neap tide periods. Solid line connects mean levels of snails of shell height ≥19 mm; dotted line connects mean levels of snails of shell height <19 mm. Error bars are 95% confidence limits. Histogram bars indicate height of preceding high tide. R, significant rainfall during preceding 24 hours (Table 12.3).

Fig. 12.10 Mean zonation level of *Littoraria filosa* on *Avicennia* trees at Cockle Bay, recorded during low tide at spring and neap tide periods. Solid line connects mean levels of snails of shell height ≥14 mm; dotted line connects mean levels of snails of shell height <14 mm. Error bars are 95% confidence limits. Histogram bars indicate height of preceding high tide. R, significant rainfall during preceding 24 hours (Table 12.4).


Zonation level on trees (m above chart datum)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
Range of ground level
12/9 NT
23/9 ST
15/10 NT
22/10 ST
12/11 NT R
21/11 ST
12/12 NT R
20/12 ST R
13/1 NT R
19/1 ST R
Date (1980-1981)
Tide
Rainfall

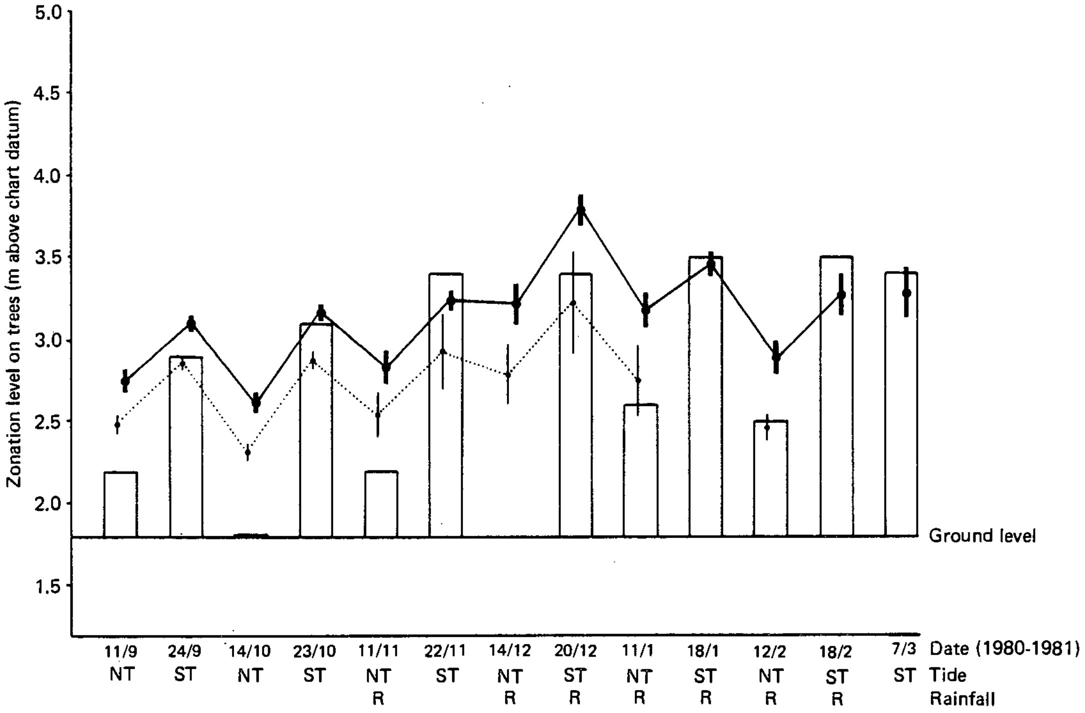
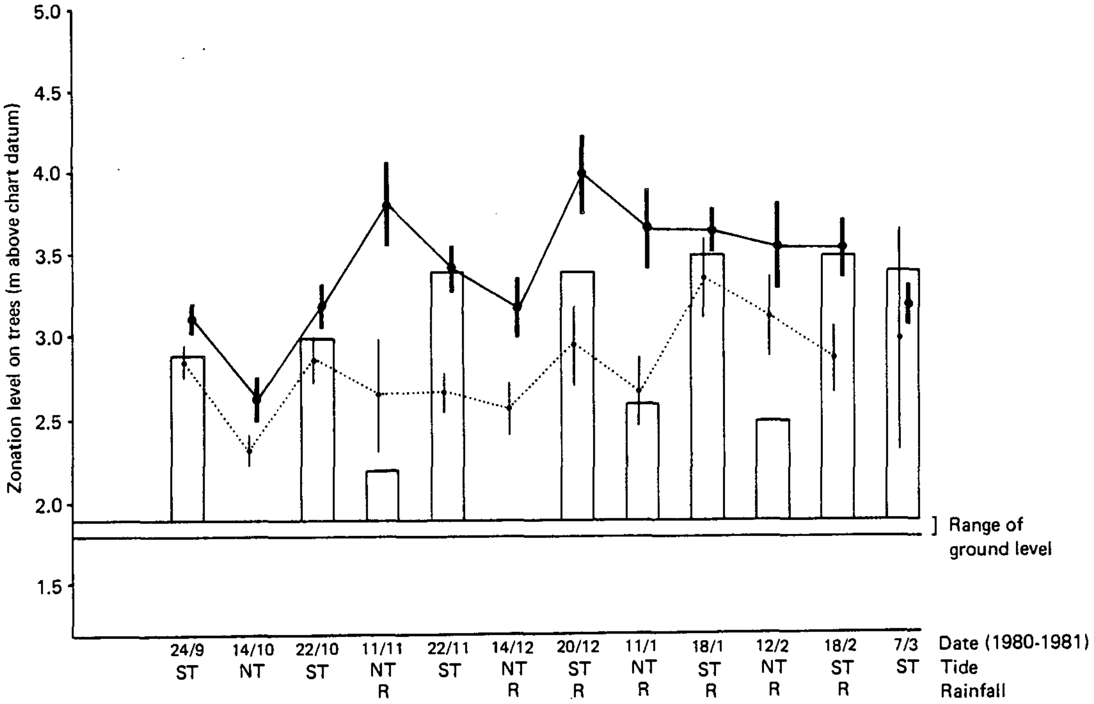
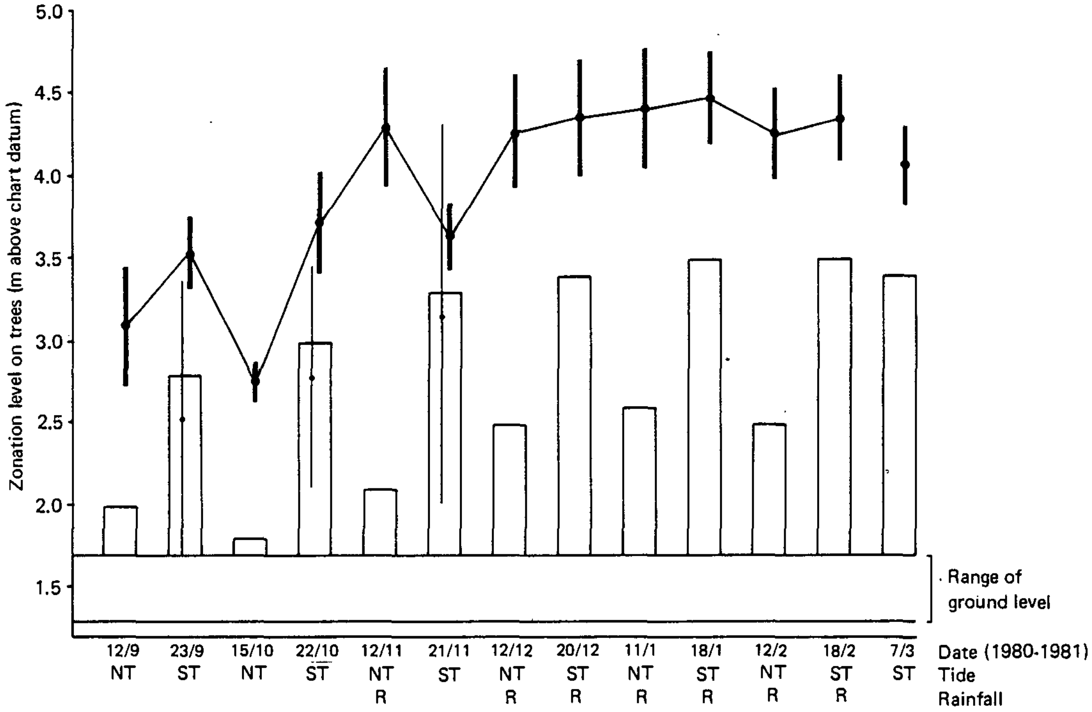

Zonation level on trees (m above chart datum)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
Ground level
11/9 NT
24/9 ST
14/10 NT
23/10 ST
11/11 NT R
22/11 ST
14/12 NT R
20/12 ST R
11/1 NT R
18/1 ST R
12/2 NT R
18/2 ST R
7/3 ST
Date (1980-1981)
Tide
Rainfall

Fig. 12.11 Mean zonation level of *Littoraria philippiana* on *Avicennia* trees at Cockle Bay, recorded during low tide at spring and neap tide periods. Solid line connects mean levels of snails of shell height ≥19 mm; dotted line connects mean levels of snails of shell height <19 mm. Error bars are 95% confidence limits. Histogram bars indicate height of preceding high tide. R, significant rainfall during preceding 24 hours (Table 12.5).

Fig. 12.12 Mean zonation level of *Littoraria philippiana* on *Rhizophora* trees at Cockle Bay, recorded during low tide at spring and neap tide periods. Solid line connects mean levels of snails of shell height ≥19 mm; dotted line connects mean levels of snails of shell height <19 mm. Error bars are 95% confidence limits. Histogram bars indicate height of preceding high tide. R, significant rainfall during preceding 24 hours (Table 12.6).


Zonation level on trees (m above chart datum)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
Range of ground level
24/9 ST
14/10 NT
22/10 ST
11/11 NT R
22/11 ST
14/12 NT R
20/12 ST R
11/1 NT R
18/1 ST R
12/2 NT R
18/2 ST R
7/3 ST
Date (1980-1981)
Tide
Rainfall


Zonation level on trees (m above chart datum)
5.0
4.5
4.0
3.5
3.0
2.5
2.0
1.5
Range of ground level
12/9 NT
23/9 ST
15/10 NT
22/10 ST
12/11 NT R
21/11 ST
12/12 NT R
20/12 ST R
11/1 NT R
18/1 ST R
12/2 NT R
18/2 ST R
7/3 ST
Date (1980-1981)
Tide
Rainfall

adults were found at levels beyond the tidal range, they made periodic excursions to the water level, as shown by the 24 hour records, and their positions may therefore have been constrained by the level of the high tide. Juveniles of these species occupied lower levels (Section 12.3.4), and may have been influenced directly by contact with the rising tide, as in the case of the three species from lower levels (*L. scabra, L. intermedia, L. articulata*). *L. philippiana* was found to occur at higher levels on *Rhizophora* (Fig. 12.12) than on *Avicennia* trees (Fig. 12.11).

If patterns of distribution on the same tree species are compared it can be seen that the order of zonation of the *Littoraria* species was largely maintained over the six month period of observation. From lowest to highest, this order was, on *Avicennia* trees: *L. articulata, L. filosa, L. philippiana* (with considerable overlap between the last two); and on *Rhizophora* trees: *L. intermedia, L. scabra, L. philippiana*. *L. articulata* was of frequent occurrence on both tree species (Fig. 11.1), but the distribution of this snail was recorded on *Avicennia* trees only. It was not possible to apply the technique described in Section 12.2 to this small species on the complex prop root system of *Rhizophora* trees.

12.3.3 Effect of rainfall upon distribution

The fluctuations in mean levels of snails quiescent at low tide were recorded over a six month period extending from the dry spring to the end of the hot, wet summer (for climatic data see Fig. 13.17). Throughout this period the synodic fluctuation of the three species from lower levels (*L. scabra, L. intermedia, L. articulata*) continued with little change (Figs 12.7, 12.8, 12.9). In contrast, the level of *L. philippiana* on *Rhizophora* trees was higher and the fluctuations with spring and neap tides much reduced during wet weather (Fig. 12.12). On *Avicennia* trees this species also occupied higher levels during wet weather (Fig. 12.11), although some synodic periodicity remained. A similar, but less marked, change in level was shown by *L. filosa,* although with synodic periodicity well developed during both the wet season and the dry spring (Fig. 12.10). Both *L. filosa* and *L. philippiana* on *Avicennia* trees showed a progressive lowering of the levels occupied during the course of the wet season. This trend was not found in *L. philippiana* on *Rhizophora* trees.

The movement of *L. filosa* and *L. philippiana* to the undersides of leaves during heavy rain, and the effect of rain on the means of attachment of snails to the substrate, are described in Section 12.3.5.

12.3.4 Effects of shell size, sex and tree species

All five *Littoraria* species showed significant positive relationships between vertical level and shell height on the majority of spring and neap tide visits (analysis of variance of regression, Tables 12.1 to 12.6). However, the proportion of the total variance in level explained by the regression on size (i.e. the coefficient of determination, r^2) was low. This was so because the smaller snails were always found in the lower range of the vertical distribution of each species, while larger snails were found throughout the range, not solely at the upper levels.

In Figs 12.7 to 12.12 each species is shown divided into two arbitrary size classes, greater and less than half of the maximum size at the locality. In all cases the mean level of the smaller size class was below that of the larger. In each species the smaller size class showed fluctuations in mean level with spring and neap tides similar to those of the larger size class. Owing to seasonal recruitment (Section 13.3.2) the smaller size classes were not

Table 12.1 Distribution of *Littoraria articulata* on *Avicennia* trees at Cockle Bay.

Date	Tide[A] (m)	Rainfall[B] (mm)	Level[C] of shells $H<12$ mm (m above CD)			Level of shells $H\geq12$ mm (m above CD)			ANOVA of regression of level on H				Distribution on substrates[D] (%)					
			$\bar{x}$	SE	n	$\bar{x}$	SE	n	r	r^2	F	P	R	TR	BR	TW	LL	LU
11.9.1980	NT 2.2	0	1.98	.01	437	2.18	.03	128	.319	.102	63.7	$<.001$**		100				
24.9.1980	ST 2.9	0	2.83	.01	385	2.94	.02	103	.273	.075	39.2	$<.001$**		100				
14.10.1980	NT 1.8	0	1.83	.02	311	1.91	.04	71	.166	.028	10.8	.001**		100				
23.10.1980	ST 3.1	0	2.71	.01	345	2.96	.03	77	.429	.184	94.9	$<.001$**		100				
11.11.1980	NT 2.2	14	1.86	.01	690	1.90	.03	140	.108	.012	9.8	.001**		100				
22.11.1980	ST 3.4	0	2.51	.01	552	2.72	.03	115	.255	.065	46.3	$<.001$**		100				
14.12.1980	NT 1.7	3	1.80	.01	513	1.84	.01	94	.043	.002	1.1	.295		100				
20.12.1980	ST 3.4	14	2.61	.01	462	2.78	.03	75	.280	.078	45.5	$<.001$**		100				

[A] Height of previous high tide; ST, spring tide; NT, neap tide.

[B] Rainfall on sampling date and previous day (recorded at Townsville Airport, Bureau of Meteorology).

[C] Levels are vertical heights up trees in metres above Chart Datum. MHWN = 2.0 m; MHWS = 2.9 m; ground level = 1.6 m; lowest foliage = 3.0 m above CD; H, shell height (mm).

[D] Figures are % of total sample; R, roots; TR, trunks; BR, branches; TW, twigs; LL, lower leaf surface; LU, upper leaf surface.

Table 12.2 Distribution of *Littoraria intermedia* on *Rhizophora* trees at Cockle Bay.

Date	Tide (m)	Rainfall (mm)	Level^A of shells $H<7$ mm (m above CD)			Level of shells $H\geq7$ mm (m above CD)			ANOVA of regression of level on H				Distribution on substrates (%)						Mucous att.^{B} (%)
			$\bar{x}$	SE	n	$\bar{x}$	SE	n	r	r^2	F	P	R	TR	BR	TW	LL	LU	
12.9.1980	NT 2.0	0	1.97	.05	15	2.14	.03	40	.375	.140	8.7	.005**	96	4					11
23.9.1980	ST 2.8	0	2.23	.05	17	2.51	.04	53	.627	.393	44.1	<.001**	77	23					53
15.10.1980	NT 1.8	0	1.96	.03	19	1.99	.02	60	.300	.090	7.6	.007**	95	5					64
22.10.1980	ST 3.0	0	2.31	.04	13	2.41	.03	70	.472	.223	23.2	<.001**	82	18					66
12.11.1980	NT 2.1	16	1.98	.03	7	2.06	.02	60	.379	.144	10.9	.002**	97	3					34
21.11.1980	ST 3.3	0	2.39	.04	7	2.46	.03	56	.399	.160	11.6	.001**	78	22					83
12.12.1980	NT 2.5	2	2.16	.05	9	2.29	.05	72	.399	.159	15.0	<.001**	90	9		1			0
20.12.1980	ST 3.4	14			0	2.45	.03	80	.171	.029	3.8	.055	78	21	1				64
13.1.1981	NT 2.1	30			0	2.17	.03	70	.110	.012	1.6	.208	91	9					0
19.1.1981	ST 3.6	55	2.35	.25	2	2.53	.05	60	.257	.066	4.2	.044*	87	5	5	3			0

Abbreviations as in Table 12.1.

A MHWN = 2.0 m; MHWS = 2.9 m; ground level = 1.3–1.7 m; lowest foliage = 2.8–4.7 m above CD.

B % of total sample (collected between 10 a.m. and 4 p.m.) attached by mucous holdfast.

Table 12.3 Distribution of *Littoraria scabra* on *Rhizophora* trees at Cockle Bay.

Date	Tide (m)	Rainfall (mm)	Level[A] of shells H<19 mm (m above CD)			Level of shells H≥19 mm (m above CD)			ANOVA of regression of level on H				Distribution on substrates (%)						Mucous att. (%)
			$\bar{x}$	SE	n	$\bar{x}$	SE	n	r	r^2	F	P	R	TR	BR	TW	LL	LU	
12.9.1980	NT 2.0	0	2.02	.07	15	2.26	.04	41	.426	.182	12.0	.001**	82	18					11
23.9.1980	ST 2.8	0	2.31	.07	15	2.79	.04	60	.542	.293	30.3	<.001**	41	45	8		1		3
15.10.1980	NT 1.8	0	1.87	.05	21	2.15	.03	66	.555	.308	37.9	<.001**	82	18					17
22.10.1980	ST 3.0	0	2.27	.08	13	2.64	.04	67	.417	.174	16.5	<.001**	55	39	5		1		8
12.11.1980	NT 2.1	16	2.04	.02	17	2.30	.04	63	.530	.281	30.5	<.001**	78	18	3	1	1		0
21.11.1980	ST 3.3	0	2.03	.11	9	2.74	.06	71	.393	.155	14.3	<.001**	41	41	15	1	1		0
12.12.1980	NT 2.5	2	2.15	.04	10	2.39	.05	49	.497	.247	18.7	<.001**	75	19	5		2		0
20.12.1980	ST 3.4	14	1.90	.10	2	2.48	.05	71	.237	.056	4.3	.042*	60	32	7		1		3
13.1.1981	NT 2.1	30	2.00	.06	4	2.23	.05	57	.388	.150	10.4	.002**	84	10	3	3			–
19.1.1981	ST 3.6	55	1.90		1	2.63	.11	46	.313	.098	4.9	.032*	55	11		15	19		0

Abbreviations as in Tables 12.1 and 12.2.

[A] MHWN = 2.0 m; MHWS = 2.9 m; ground level = 1.3–1.7 m; lowest foliage = 2.8–4.7 m above CD.

Table 12.4 Distribution of *Littoraria filosa* on *Avicennia* trees at Cockle Bay.

Date	Tide (m)		Rainfall (mm)	Level^A of shells H<14 mm (m above CD)			Level of shells H≥14 mm (m above CD)			ANOVA of regression of level on H				Distribution on substrates (%)						Mucous att. (%)
				$\bar{x}$	SE	n	$\bar{x}$	SE	n	r	r^2	F	P	R	TR	BR	TW	LL	LU	
11.9.1980	NT	2.2	0	2.49	.03	75	2.75	.04	147	.606	.367	127.7	<.001**		10	11	18	4	58	53
24.9.1980	ST	2.9	0	2.87	.02	63	3.10	.02	163	.570	.324	107.6	<.001**		20	24	28	3	25	84
14.10.1980	NT	1.8	0	2.32	.03	46	2.62	.03	149	.667	.445	154.7	<.001**		22	15	28	3	33	95
23.10.1980	ST	3.1	0	2.88	.03	37	3.17	.03	168	.606	.367	117.9	<.001**		26	23	28	2	21	61
11.11.1980	NT	2.2	14	2.55	.07	18	2.83	.05	118	.544	.296	56.2	<.001**		11	20	15	6	48	67
22.11.1980	ST	3.4	0	2.93	.12	10	3.24	.03	118	.584	.342	65.4	<.001**		26	23	13	8	30	53
14.12.1980	NT	1.7	3	2.79	.08	7	3.22	.06	82	.553	.306	38.3	<.001**		8	5	6		82	50
20.12.1980	ST	3.4	14	3.23	.13	6	3.79	.05	88	.313	.098	10.0	.002**		3	9	2	10	77	0
11.1.1981	NT	2.6	50	2.75	.09	5	3.18	.05	72	.413	.171	15.5	<.001**		3		18	21	58	3
18.1.1981	ST	3.5	96	3.15	.12	2	3.47	.04	74	.246	.060	4.8	.032*			1	5	41	53	20
12.2.1981	NT	2.5	51	2.46	.03	4	2.89	.05	38	.486	.236	12.4	.001**					10	91	2
18.2.1981	ST	3.5	19	2.68	.05	2	3.27	.06	41	.532	.283	16.2	<.001**		5	9	12	26	49	37
7.3.1981	ST	3.4	0	2.58	.05	2	3.28	.08	23	.662	.438	17.9	<.001**		12	4	16	16	52	24

Abbreviations as in Tables 12.1 and 12.2.

A MHWN = 2.0 m; MHWS = 2.9 m; ground level = 1.8 m; lowest foliage = 1.9–2.4 m above CD.

Table 12.5 Distribution of *Littoraria philippiana* on *Avicennia* trees at Cockle Bay.

Date	Tide (m)	Rainfall (mm)	Level[A] of shells H<19 mm (m above CD)			Level of shells H≥19 mm (m above CD)			ANOVA of regression of level on H				Distribution on substrates (%)						Mucous att. (%)
			$\bar{x}$	SE	n	$\bar{x}$	SE	n	r	r^2	F	P	R	TR	BR	TW	LL	LU	
24.9.1980	ST 2.9	0	2.86	.05	25	3.12	.05	47	.522	.272	26.2	<.001**		76	22	1			1
14.10.1980	NT 1.8	0	2.32	.05	20	2.63	.07	42	.427	.182	13.4	<.001**		89	11				24
22.10.1980	ST 3.0	0	2.87	.07	21	3.19	.07	44	.400	.160	12.0	.001**		80	19	2			3
11.11.1980	NT 2.2	14	2.66	.17	18	3.81	.12	35	.568	.323	24.4	<.001**		64	28	4	2	2	0
22.11.1980	ST 3.4	0	2.67	.06	21	3.42	.07	45	.752	.566	83.4	<.001**		85	15				0
14.12.1980	NT 1.7	3	2.57	.08	23	3.18	.09	38	.618	.382	36.4	<.001**		56	21	3	5	15	0
20.12.1980	ST 3.4	14	2.96	.12	19	3.99	.12	36	.653	.427	39.5	<.001**		46	33	6	6	11	0
11.1.1981	NT 2.6	50	2.67	.10	19	3.66	.12	36	.580	.337	26.9	<.001**		47	9	7	24	13	0
18.1.1981	ST 3.5	96	3.36	.12	16	3.65	.07	38	.296	.087	5.0	.030*		56	11	11	20	2	19
12.2.1981	NT 2.5	51	3.13	.12	16	3.55	.13	20	.441	.194	8.2	.007**		28	28	6	6	33	0
18.2.1981	ST 3.5	19	2.87	.09	8	3.54	.09	33	.659	.434	30.0	<.001**		46	29	7	7	10	0
7.3.1981	ST 3.4	0	2.99	.16	3	3.19	.06	32	.323	.104	3.8	.059		71	20		3	6	0

Abbreviations as in Tables 12.1 and 12.2.

A MHWN = 2.0 m; MHWS = 2.9 m; ground level = 1.8–1.9 m; lowest foliage = 2.1–3.3 m above CD.

Table 12.6 Distribution of *Littoraria philippiana* on *Rhizophora* trees at Cockle Bay.

Date	Tide (m)	Rainfall (mm)	Level[A] of shells H<19 mm (m above CD)			Level of shells H≥19 mm (m above CD)			ANOVA of regression of level on H				Distribution on substrates (%)						Mucous att. (%)
			$\bar{x}$	SE	n	$\bar{x}$	SE	n	r	r^2	F	P	R	TR	BR	TW	LL	LU	
12.9.1980	NT 2.0	0	2.07	.23	2	3.09	.18	21	.311	.097	2.3	.148	39	30	17		4	9	0
23.9.1980	ST 2.8	0	2.53	.20	3	3.54	.11	31	.438	.192	7.6	.010**	18	44	21	3	12	3	9
15.10.1980	NT 1.8	0	1.90		1	2.76	.06	40	.389	.151	6.9	.012*	56	29	2		12		0
22.10.1980	ST 3.0	0	2.79	.16	3	3.73	.15	34	.378	.143	5.8	.021*	19	49	14		19		8
12.11.1980	NT 2.1	16	2.67	.47	2	4.30	.18	28	.454	.206	7.3	.012*	10	27	7	3	50	3	0
21.11.1980	ST 3.3	0	3.16	.27	3	3.64	.10	28	.439	.192	6.9	.014*	10	32	13	3	39	3	0
12.12.1980	NT 2.5	2	3.17	.27	2	4.27	.17	29	.434	.188	6.7	.015*		26	13	13	48		0
20.12.1980	ST 3.4	14			0	4.36	.18	28	.159	.025	0.4	.537	4	21		14	54	7	0
11.1.1981	NT 2.6	50	4.58		1	4.41	.18	27	.149	.022	0.1	.805	7	7	11	11	64		0
18.1.1981	ST 3.5	96			0	4.48	.14	33	.417	.174	6.5	.016*		6	3	9	76	6	6
12.2.1981	NT 2.5	51			0	4.26	.14	24	.043	.002	0	.994	4	25		4	67		0
18.2.1981	ST 3.5	19	3.48		1	4.35	.13	21	.392	.154	3.9	.065		14	5		77	5	0
7.3.1981	ST 3.4	0	3.08		1	4.07	.12	19	.413	.171	2.2	.160		15	15		70		0

Abbreviations as in Tables 12.1 and 12.2.

[A] MHWN = 2.0 m; MHWS = 2.9 m; ground level = 1.3–1.7 m; lowest foliage = 2.8–4.7 m above CD.

represented on all dates, and sample sizes were sometimes small (leading to relatively wide confidence limits on levels). For these reasons the data are insufficient to demonstrate the response of the smaller snails to rainfall.

The smallest numbered specimens used in the study were 9 mm in height in the case of *L. filosa*, 7 mm for *L. philippiana*, and 4 mm for *L. scabra* and *L. intermedia*. The distribution of snails as small as 2 mm in height was examined in *L. articulata*. In all cases snails of these sizes were seen to climb to avoid submersion. Still smaller snails of *L. articulata* were not uncommon in bark crevices, and sometimes in empty barnacle tests on *Avicennia* trees (as described for several rocky shore littorinids, Emson & Faller-Fritsch, 1976; Raffaelli, 1978a). Smaller individuals of *L. scabra* and *L. intermedia* were scarce (Chapter 13), but careful searching revealed small numbers of shells 1 to 2 mm in height in bark crevices (barnacles were not found on *Rhizophora* trees at the study site). Such small snails were not found clustered at the water level and it is presumed that they do not migrate until they have attained a larger size. Observations suggested that for the three species from lower levels (*L. scabra, L. intermedia, L. articulata*), the vertical size gradient may be explained by the more pronounced tendency of smaller snails to follow the descending water surface on the falling tide. It was noticed that the smallest individuals of *L. filosa* (1 to 3 mm) were mostly to be found on the leaves rather than trunks of *Avicennia* trees, and often in the axil at the base of the leaf petiole. Individuals of this species less than 2 mm in length were also observed in the similarly sized chambers of old wasp galls which were numerous on the twigs of *Avicennia*. Once again it is not known at what size tidal migration behaviour begins.

Analyses of covariance of the effect of sex upon vertical distribution level at each of the ten dates of observation, with shell size as the covariate, showed that on no occasion did sex influence the level of the two species from higher zones, *L. filosa* and *L. philippiana*. However, in the case of *L. intermedia*, on every occasion the mean level of females (adjusted for the covariate shell height) was lower than that of males. The difference was significant on only two occasions, 23 September ($F = 4.79$, d.f. = 1,67, $P = 0.032$; adjusted $\bar{x}$ male = 2.51 m; adjusted $\bar{x}$ female = 2.38 m) and 22 October ($F = 4.14$, d.f. = 1,80, $P = 0.045$; adjusted $\bar{x}$ male = 2.45 m; adjusted $\bar{x}$ female = 2.34 m). In another species from lower levels, *L. scabra*, females were found at lower levels on 8 out of 10 visits, with significant differences on 12 November ($F = 4.66$, d.f. = 1,77, $P = 0.034$; adjusted $\bar{x}$ male = 2.29 m; adjusted $\bar{x}$ female = 2.18 m), 21 November ($F = 14.3$, d.f. = 1,78, $P < 0.001$; adjusted $\bar{x}$ male = 2.82 m; adjusted $\bar{x}$ female = 2.47 m) and 12 December ($F = 7.93$, d.f. = 1,56, $P = 0.007$; adjusted $\bar{x}$ male = 2.43 m; adjusted $\bar{x}$ female = 2.25 m). In each of these two species from lower levels the test for regression parallelism (Hull & Nie, 1981) was failed at the 0.05 level on 1 occasion out of 10, a frequency only a little greater than the 1 in 20 expected to arise by chance. On the remaining occasions the slopes of the regressions of level on shell height were the same for each sex (i.e. there was no interaction between the factor sex and the covariate shell height in their influence upon level of distribution on the trees). No data were available for *L. articulata*, because individuals were too small for marking on a large scale.

The distribution of the colour forms of *L. filosa* is considered in detail in Chapter 15, but here it may be noted that no differences in distribution levels were detected.

Data for the comparison of vertical distribution on *Rhizophora* and *Avicennia* trees are available only for *L. philippiana*. On all the dates of observation the mean level of all individuals on *Rhizophora* trees was higher than on *Avicennia* trees. However, the snails on *Rhizophora* attained a larger maximum size than those on *Avicennia* trees (Figs 13.6, 13.7). This might have accounted for the difference in levels, as a result of the effect of shell size upon distribution level evident on each tree species. This possibility was tested by an analysis of covariance of level at each date, with

Table 12.7 Comparison of levels of *Littoraria philippiana* on *Avicennia* and *Rhizophora* trees at Cockle Bay.

Date	Test for interaction between factor 'tree species' and covariate H (test for regression parallelism)		Test for significance of factor 'tree species' adjusted for covariate H (analysis of covariance)[A]		Mean levels (m above CD) adjusted for effect of covariate H	
	F	P	F	P	*Rhizophora*	*Avicennia*
24.9.1980	2.5	.115	3.9	.050*	3.34	3.15
14.10.1980	0.1	.724	0	.931	2.63	2.64
22.10.1980	2.4	.123	4.6	.035*	3.52	3.22
11.11.1980	0	.865	0.9	.339	3.90	3.70
22.11.1980	0.9	.336	0.3	.614	3.41	3.36
14.12.1980	1.4	.234	25.8	<.001**	3.99	3.17
20.12.1980	1.0	.320	0.7	.394	4.08	3.91
11.1.1981	1.4	.240	10.0	.002**	4.18	3.55
18.1.1981	4.4	.040*	-	-	4.35	3.69
12.2.1981	1.1	.308	9.0	.004**	4.11	3.51
18.2.1981	0.5	.466	9.0	.004**	4.08	3.63
7.3.1981	0.9	.338	19.5	<.001**	3.91	3.29

[A] Analysis of covariance not performed if regression coefficients significantly different.

tree species as the factor and shell height as the covariate (Table 12.7). The results show that in only one case out of twelve did the slope of the regression of level on shell height differ between the two habitats. Of the remaining eleven dates, on seven occasions there was a significant difference in mean level after adjustment for the effect of shell height. Therefore on only four out of twelve dates could the difference in levels of *L. philippiana* on *Avicennia* and *Rhizophora* trees be accounted for simply by the larger size of snails on the latter species of tree.

12.3.5 Substrate and attachment

None of the species of mangrove littorinids investigated in this study was ever seen crawling from the roots or trunks of the trees on to the soft substrate beneath. If snails were placed on mud or sand, locomotion was slow. Movement between trees might therefore be expected to occur mainly where roots or branches are in contact. It was noticed that when dislodged from the trees, individuals of the thin-shelled species *L. filosa* were able to float while the mantle cavity was full of air. On one occasion an individual of *L. philippiana* was seen rafting on a floating leaf. These methods may provide alternative means of migration between trees (see Section 13.3.2).

Tables 12.1 to 12.6 indicate the proportions of the five species found upon leaves, twigs, branches, trunks and roots of the trees. These data reinforce the general account of substrate preferences given in Section 11.4.3. It can be seen that the three species from lower levels (*L. scabra, L. intermedia, L. articulata*) were found predominantly on trunks and roots. Snails were not found on the pneumatophores (aerial roots) of *Avicennia*. These were less than 15 cm in height, and none of the *Littoraria* species was found permanently at such low levels. The scarcity of *L. intermedia* and *L.*

articulata on *Rhizophora* leaves (Table 12.2 and Fig. 11.1) can be accounted for by the absence of foliage at the low levels occupied by these species. On *Avicennia* trees, however, foliage was found almost to ground level, yet on these trees the two species were still uncommon on leaves (Fig. 11.1). *L. scabra* was found at higher levels, at which *Rhizophora* foliage was available, but nevertheless was rarely found on leaves (Table 12.3).

L. filosa (Table 12.4) and *L. philippiana* (Tables 12.5, 12.6) were found on both leaf and bark substrates. A two-way analysis of variance of the effects of spring or neap tides and wet or dry weather on the proportion of snails found on leaves (after arcsine transformation, Table 12.8) shows that in each species a significantly greater proportion was found on leaves during wet weather. This effect cannot be attributed solely to the migration to higher levels, where leaves are more abundant, during wet periods (Section 12.3.3). This is suggested by the lack of significant difference between the proportions found on leaves at spring and neap tides (Table 12.8), although the snails occupied higher levels during spring tide periods (Section 12.3.2).

At all times during dry weather, and during wet weather when rain was not actually falling (i.e. all observation dates in Table 12.4, excepting 18 January), greater numbers of *L. filosa* were to be found on the morphologically upper surfaces of the *Avicennia* leaves than on the lower sides (Table 12.4). This was unexpected, since the lower surfaces are shaded and presumably cooler, and in addition feeding is known to take place at least partly on the lower surface, as noted below. The distribution on leaves was recorded on three occasions between 13 and 18 January, 1981, during heavy rain, and the mean proportion on the upper surfaces was then 0.451, significantly less than the mean proportion of 0.881 found when rain was not falling (Table 12.9). The movement to the lower surface was of only short duration in *L. filosa*, for during a brief pause in the downpour on 18 January, snails were seen to crawl quickly on to the upper leaf surfaces once more.

Table 12.8 Analysis of variance of effects of tide (spring or neap) and rain (wet or dry weather) on proportions of *Littoraria filosa* and *L. philippiana* found on leaves at Cockle Bay. (Data in Tables 12.4, 12.5, 12.6; test performed on arcsine transformed proportions, Zar, 1974).

Species	Tree	Source of variation	Degrees of freedom	Sum of squares	F	P
L. filosa	*Avicennia*	tide	1	0.00	0.04	.855
		rain	1	0.64	11.75	.008**
		tide by rain	1	0.01	0.26	.623
		residual	9	0.49		
L. philippiana	*Avicennia*	tide	1	0.00	0.01	.915
		rain	1	0.42	15.65	.004**
		tide by rain	1	0.01	0.33	.580
		residual	8	0.22		
L. philippiana	*Rhizophora*	tide	1	0.16	4.91	.054
		rain	1	0.63	20.06	.002**
		tide by rain	1	0.01	0.18	.679
		residual	9	0.28		

Table 12.9 Comparison of distribution of *Littoraria filosa* on upper and lower surfaces of *Avicennia* leaves during rain and during dry weather at Cockle Bay.

Weather	Date	Proportion of the snails on leaves found on upper surfaces	Sample size n	Mean proportion[A]
rain not falling	11.9.1980	0.941	136	
	24.9.1980	0.903	62	
	14.10.1980	0.928	69	
	23.10.1980	0.935	46	
	11.11.1980	0.890	73	
	22.11.1980	0.792	48	
	14.12.1980	1.000	73	
	20.12.1980	0.889	81	
	11.1.1981	0.738	61	
	12.2.1981	0.905	42	
	18.2.1981	0.656	32	
	7.3.1981	0.765	17	0.881
rain falling	13.1.1981	0.459	61	
	18.1.1981	0.563	71	
	18.1.1981	0.333	30	0.451

Comparison of means by t-test: $t = 4.693$, d.f. = 13, $P < .001$**

[A] calculated from arcsine transformed proportions (Zar, 1974).

In contrast to *L. filosa* on *Avicennia* trees, on *Rhizophora* trees *L. philippiana* was found mainly on the lower leaf surfaces (Table 12.6). On *Avicennia* trees, *L. philippiana* occurred in significant numbers on leaves only during wet weather. Of those found on leaves, the proportion on the upper surface was significantly higher on *Avicennia* than on *Rhizophora* trees (data in Tables 12.5 and 12.6; using data for the five dates when numbers of snails on leaves of *Avicennia* > 7, and excluding 18 January when rain was falling; on *Avicennia* leaves mean proportion on upper surface = 0.648; on *Rhizophora* leaves mean proportion on upper surface = 0.036; t-test on arcsine transformed proportions paired by dates, $t = 7.14$, $P = 0.002$). During heavy rain on 18 January, the proportion of *L. philippiana* on the leaves of *Avicennia* trees which were found on the upper surface was 0.091 (data in Table 12.5). On *Avicennia* trees *L. philippiana* therefore appeared to show a movement to the lower surface similar to that exhibited by *L. filosa*. The preference of both *L. filosa* and *L. philippiana* for the upper surfaces of *Avicennia* leaves, and of the latter species for the lower surfaces of *Rhizophora* leaves, suggests a difference in the respective substrates. One possibility is that the lower surface of *Avicennia* leaves, bearing a fine tomentum of leaf hairs (Semeniuk *et al.*, 1978), provides an unfavourable surface for attachment.

The diet and feeding patterns of *Littoraria* species were not investigated in any detail. The three species from lower levels (*L. scabra, L. intermedia, L. articulata*), found primarily on bark, were observed to graze the damp substrate on the rising and falling tide. No algal layer was visible macroscopically on these surfaces, and these species were presumed to be consuming a film of microscopic algae. Snails of all species were observed grazing on the large brown alga *Turbinaria ornata* which was sometimes stranded amongst roots and branches of the mangrove trees. Radular grazing patterns were frequently seen on the undersides of leaves of *Avicennia* trees on which *L. filosa* was common, suggesting that the leaf hairs are a food source for this species. It was noticed that the lamina of the leaves was sometimes perforated where quiescent individuals of *L.*

filosa were attached. Captive specimens of *L. filosa* were found to continue to graze the substrate while stationary, and this activity appeared to be responsible for the rasping of holes through the leaf lamina. Damage to the lamina of *Avicennia* leaves was slight, even on trees supporting large numbers of *L. filosa*, which suggests that the lamina may not be an important component of the diet. The leaves of *Rhizophora* bear no leaf hairs, are much harder in texture, and showed little sign of grazing damage.

During periods of quiescence the *Littoraria* species may be attached to the substrate by the foot, or alternatively by a mucous holdfast alone, while the operculum is closed. Bingham (1972c) showed that in *Littoraria irrorata* the frequency of holdfast formation increased under conditions of low relative humidity. Casual observations at Cockle Bay suggested that the proportion of snails attached by mucus was highest during the heat of the day. Therefore, to make the results more comparable, the frequencies of attachment by a mucous holdfast given in Tables 12.1 to 12.6 include only those individuals recorded between the hours of 10 a.m. and 4 p.m. The smallest species, *L. articulata*, was mostly attached by mucus while quiescent (Fig. 12.1). *L. intermedia* also showed a high frequency of holdfast formation, except during wet weather (Table 12.2). At a higher level on the same *Rhizophora* trees, a larger species, *L. scabra*, showed a lower frequency of mucous attachment, and almost all snails were attached by the foot during the wet season (Table 12.3). Individuals of another large species, *L. philippiana*, were attached only by the foot on *Rhizophora* trees on the majority of observation dates (Table 12.6). This was also the case on *Avicennia* trees (Table 12.5), although during the wet season a relatively high proportion (19%) of the snails were attached by mucus during the heavy rain on 18 January. It was noticed that many of the individuals thus attached were located in streams of rainwater on the tree trunks. Found at high levels on *Avicennia* trees, *L. filosa* showed a high frequency of holdfast formation on dry dates, and a lower frequency during the wet season (Table 12.4). Again the proportion of mucous attachment was relatively high on 18

January, during heavy rain. In general, holdfast formation was therefore most frequent in smaller species, and was apparently associated with periods of environmental stress, during low tide, the heat of the day, or (in the species from higher levels) heavy rain.

12.4 Discussion

12.4.1 Vertical migration

Vertical migration to avoid submersion by a rising tide has been briefly reported in several other species of mangrove-dwelling *Littoraria*: *L. pallescens* (Abe, 1942, as *Melaraphe scabra*; Nielsen, 1976, as *Littorina scabra*), *L. angulifera* (Lenderking, 1954; Gallagher & Reid, 1979) and *L. melanostoma* (Berry & Chew, 1973). However, in none of these cases have observations been made throughout a 24 hour period, nor have variations in behaviour with climate or the spring and neap tide (synodic) cycle been described. The only species of *Littoraria* for which behaviour patterns have hitherto been described in detail is *L. irrorata*. This species is atypical of the genus in several respects; it occupies a more temperate distribution than any other species (S. Texas to New Jersey, 26°N to 39°N), is typically found in *Spartina* salt marshes, and alone in the genus is known to feed on the mud substrate rather than on the vegetation. At high tide the snails climb the grass stems to avoid submersion (although Stanhope *et al.*, 1982, reported that only about 29% show this response), while during most diurnal and some nocturnal low tides they descend to feed on the substrate (Bingham, 1972d; Hamilton, 1977).

Tidal migration patterns of this type have not been recorded under natural conditions in any other species of the family

Littorinidae, but appear to be characteristic of the genus *Littoraria*. They may be contrasted with the patterns of activity reported in other littorinids. On tropical shores littorinids are virtually restricted to the supralittoral zone (Vermeij, 1973a; Bandel, 1974; Bandel & Kadolsky, 1982), but on temperate shores may be found in the midlittoral and below (Williams, 1964; Underwood, 1973; Heller, 1975a). The majority of studies of the distribution of littorinids on the shore have concerned midlittoral species such as *Littorina littorea*, *Littorina obtusata* and *Littorina saxatilis* on northern Atlantic coasts, and *Bembicium* species in southern Australia. Although few observations have been made in the field, these forms seem active mainly when submerged by the high tide (Alexander, 1960; Underwood, 1972, 1977; Gendron, 1977; but Berry, 1961, reported *Littorina saxatilis* to be active only when damp and emersed). However, a moving water level seems to be necessary to initiate movement, for the animals become inactive when kept in laboratory tanks (Newell, 1958b; Underwood, 1972). Nevertheless, in the field some snails may live completely submerged either subtidally (authors quoted in Williams, 1966) or at high levels in pools (Lysaght, 1953; Evans, 1961). Feeding excursions while submerged are random (Underwood, 1977) or U-shaped (Newell, 1958a, b). At supralittoral levels, littorinids on both temperate and tropical shores are seldom reached by the tide, and therefore are active whenever dampened by wave splash or light rain (Fretter & Graham, 1964, p. 536; Bandel, 1974; Bertness *et al.*, 1981).

It must now be considered why *Littoraria* species differ so conspicuously in their behaviour patterns from other littorinids. Firstly, it is clear that since mangrove trunks provide a narrow, vertical substrate, feeding movements will take place in a predominantly vertical direction. Furthermore, horizontal movements are considerably restricted by the inability of mangrove dwelling *Littoraria* species to crawl on a substrate of soft mud. Amongst other species of the genus, neither *L. melanostoma* (Berry & Chew, 1973) nor *L. angulifera* (Gallagher & Reid, 1979) have been observed to crawl on mud. The exceptional behaviour of *L. irrorata* has been mentioned; Hamilton (1977) records individuals crawling for up to 5 m across sand at low tide. Larger specimens of *Bembicium auratum* are able to feed on mud (Branch & Branch, 1980), while *Littorina littorea* will make feeding excursions from stones on to fine sand (Newell, 1958a). Nevertheless, in general most members of the family seem incapable of survival or prolonged locomotion on a soft substrate (Barkman, 1955; Smith & Newell, 1955; James, 1968). Such considerations of the structure of the habitat fail to explain the upward migration to avoid submersion.

Secondly, it has been considered by some authors that intertidal gastropods may require periodic emersion for adequate respiration (Bannister *et al.*, 1966). When tested in the laboratory, most species have been found to tolerate periods of submersion much longer than those normally experienced, e.g. *Littorina littorea* for at least 57 days (Hayes, 1927), *Littorina scutulata* for at least 10 days (Chow, 1975) and even *Littoraria irrorata*, which frequently avoids submersion, for at least 42 days (Bleil & Gunn, 1978). However, Coomans (1969) found a 50% mortality in *Littoraria angulifera* after 2 days of submersion, so it may be that the tropical mangrove-dwelling forms are less tolerant in this respect. This effect might be connected with the relatively small size of the gill leaflets of *Littoraria* species (Section 5.8), although this also applies to *L. irrorata* (Bleil & Gunn, 1978). As pointed out by Underwood (1979), respiratory requirements do not seem to determine zonation patterns, but should be viewed as adaptations to environments to which species are limited by other factors.

The third and most significant consideration in the comparison of behaviour patterns of *Littoraria* with those of other littorinids concerns the tropical distribution of the genus. Although no similar patterns of natural behaviour are known amongst the well studied temperate littorinids, downshore feeding excursions at low tide, followed by retreat to higher levels, have been recorded in other gastropods from rocky shores. These include *Nerita textilis* in Somalia (Vannini & Chelazzi, 1978), *Nerita scabricosta* in Panama

(Garrity & Levings, 1981) and the chiton *Acanthopleura gemmata* in Somalia (Chelazzi *et al.*, 1983). All are tropical species. Furthermore, while littoral species in warmer climates might be expected to be inactive at low tide to minimize desiccation, various tropical *Nerita* species have been reported to emerge from crevices and feed actively only following exposure by the tide (Safriel, 1969; Hughes, 1971; Zann, 1973b; Levings & Garrity, 1983). Vannini & Chelazzi (1978) related the migratory behaviour of *Nerita textilis* to avoidance of wave action, an explanation which cannot apply in mangrove forests. However, all other authors (including Hamilton, 1976, in the case of *Littoraria irrorata*) have related these behaviour patterns to escape from aquatic predators. Predatory crabs and fish, active at high tide, are believed to be more abundant and more mobile on tropical than on temperate rocky shores, accounting for the types of escape behaviour shown by tropical intertidal gastropods (Bertness *et al.*, 1981; Menge & Lubchenco, 1981). There is now a considerable volume of evidence to suggest that crushing predation on gastropod molluscs is most intense in the tropics (Chapter 14).

A similar explanation of migratory behaviour can be applied to gastropods in mangrove forests. Predation pressure in this environment appears to be at least as severe as in other tropical communities (Chapter 14). In the mangroves of northern Queensland, not only *Littoraria* species, but also *Nerita articulata* and *Cerithidea anticipata*, ascend trees (pers. obs.). The littorinid *Bembicium melanostoma* remains at low levels on the trees during high tide, but is protected by a shell of much greater thickness than those of *Littoraria* species (Section 14.3.5). Mangrove gastropods which remain on the ground in midlittoral regions during high tide are either protected by massive shells (e.g. *Terebralia* and *Telescopium* spp.), return to a hole (*Onchidium* spp., Dakin, 1947), or are abundant, annual forms which rely on high fecundity for survival (e.g. *Cerithidea cingulata*; see Vohra, 1970; Vermeij, 1978, p. 175).

It remains to be considered why the other groups of tropical littorinids do not show tidal migrations. These are mostly species of *Nodilittorina* (*sensu* Bandel & Kadolsky, 1982) which occur at supralittoral levels on rocky shores (Evans, 1961; Struhsaker, 1968; Bandel, 1974). In part, their small size may preclude the long migrations necessary to reach the areas of more abundant food at lower levels on shelving rocky shores, although such migrations can be accomplished by larger animals such as *Nerita* species and chitons. It would be of interest to discover whether the largest littorinids on rocky shores, species of *Tectarius*, perform feeding migrations. More importantly, the small snails are susceptible to dislodgement by wave action (e.g. *Nodilittorina africana*, McQuaid, 1981b) and so cannot migrate close to the water level on exposed coasts, as does the small *L. articulata* on mangrove trees and sheltered rocky shores. Small littorinids on exposed coasts are therefore usually to be found sheltering in crevices (Raffaelli & Hughes, 1978; McQuaid, 1981b) or empty barnacle tests (Emson & Faller-Fritsch, 1976; Raffaelli, 1978a). Of the very few midlittoral littorinids in the tropics, *Bembicium melanostoma* in Queensland has been mentioned. Another is the minute species *Fossarilittorina meleagris* in the Caribbean, which is cryptic amongst and beneath rocks (Bandel, 1974), thereby avoiding predators.

In conclusion, it is apparent that the tidal migration behaviour of the *Littoraria* species dwelling on mangroves in the littoral zone is made possible by the vertical substrate and calm water, and necessitated by the pressure of aquatic predators and the lack of suitable crevices to serve as refuges at low levels.

12.4.2 Rhythms of activity

Tropical intertidal gastropods differ from temperate species in that they are often exclusively nocturnal (Safriel, 1969; Hughes, 1971; Chelazzi *et al.*, 1983; Levings & Garrity, 1983), although exceptions are recorded (Vannini & Chelazzi, 1978). Nocturnal activity is to be expected in view of the more extreme conditions of heat and desiccation experienced during the day in the tropics. None of the well known European or North American littorinids has been described as nocturnal. In the genus *Littoraria*, however, several reports suggest that tropical species may be more active at night (Abe, 1942; Gallagher & Reid, 1979), while the temperate species *L. irrorata* is mostly active during the day (Bingham, 1972d; Hamilton, 1977). In the present study, *L. articulata* and *L. intermedia* at the lowest levels were active whenever reached by the tide. During the 24 hour observation *L. scabra* moved independently of the stimulus of the water level only at night, while the two species from the highest levels, *L. filosa* and *L. philippiana*, moved only in the early morning, at the time of the high tide. These highest species were never seen to be active on sunny days, and it is possible that their periods of activity may coincide with high tides during the night as well as in the early morning, although further observation is needed to establish this.

Since the present approach to the subject of behaviour has been entirely observational, few definite statements can be made regarding the stimuli which initiate and direct movement. For the species from low levels, *L. articulata* and *L. intermedia*, movement appears to be primarily a response to the rising and falling water level. Whether movement is stimulated by contact with the water (Hamilton, 1977; Gallagher & Reid, 1979) or occurs in advance of the tide (Abe, 1942) is not clear from the present work. Abe (1942) suggested that *L. pallescens* moved in response to a change in humidity close to the water surface. It should be noted that the movements described by Abe differ from those recorded here, for he found *L. pallescens*, a high level species, to descend at low tide, though not following the water level. In *Nerita textilis* it is known that return to high levels takes place before flooding (Vannini & Chelazzi, 1978).

Littoraria articulata, *L. intermedia* and *L. scabra* each showed a tendency to follow the descending water surface of the falling tide. A response to a moving water surface has been observed in several midlittoral *Littorina* species. However, this results in tidal migration only in laboratory tide models (Evans, 1965) or on shores from which algal food has been removed (Barkman, 1955). Other authors have failed to find vertical movements with artificial tides in *Littorina* species (Bock & Johnson, 1967; Underwood, 1972). The following of a descending water film has been described in *Littorina obtusata* (Barkman, 1955) and in *Littorina littorea* (Haseman, 1911); in the latter species this habit may lead to small vertical movements in the field, but this has not been observed by subsequent authors working on *Littorina littorea* (Gowanloch & Hayes, 1926; Hayes, 1927; Newell, 1958a, b; Gendron, 1977; Petraitis, 1982).

The two species from upper levels, *L. filosa* and *L. philippiana*, were often found at levels above the reach of the tide, where activity (and in some animals descent to the water) cannot have been stimulated by contact with the rising tide. Since humidity at these levels did not change with the rising tide (Fig. 12.6), an endogenous circa-tidal activity rhythm is suspected. Such a rhythm has been described in *Nodilittorina hawaiiensis* (Struhsaker, 1968, as *Littorina picta*) and in *Littorina nigrolineata* (Petpiroon & Morgan 1983). Circa-tidal rhythmicity is reportedly absent in other littorinids (Haseman, 1911; Underwood, 1972; Zann, 1973a), including *Littoraria angulifera* (Gallagher & Reid, 1979). *L. scabra* showed aspects of behaviour typical of species from both upper and lower levels, some individuals following the water surface while others climbed a little higher at night, later descending to the high tide level.

12.4.3 The maintenance of zonation

In relation to Underwood's (1979) hypothesis of the control of zonation level by a combination of geotaxis and response to food (Section 12.1), the following speculative explanation of the maintenance of zonation in the two high level species, *L. filosa* and *L. philippiana*, may be suggested. Wetting by rain or occasional contact with the tide stimulates negative geotaxis. Feeding movements during periods of activity may be random. After prolonged drying, the geotactic response may be reversed, resulting in the brief descents to the water level for moisture. The evidence for such behaviour patterns in other littorinids has already been reviewed (Section 12.1). Experimental work would be required to test the applicability of this hypothesis to these two *Littoraria* species. The hypothesis would account for the higher levels occupied during rain, the descent to lower levels during neap tides and the lower levels of *L. philippiana* on *Avicennia* trees, in a less shaded (and therefore probably more desiccating) habitat. It would also explain the higher levels of the larger specimens, which may be assumed to be less susceptible to desiccation (Coombs, 1973; Chow, 1975). The progressive lowering of the levels occupied by *L. filosa* and *L. philippiana* on *Avicennia* trees during the course of the wet season (Figs 12.10, 12.11) suggests that exposure to fresh water may also reverse the usual negative geotaxis. The snails may then move down to the tide level to restore their salt balance.

For the species from the lower zones, the response to the descending water level is clearly of importance. This aspect was not considered in Underwood's (1979) model. The three species, *L. scabra*, *L. intermedia* and *L. articulata*, can be found feeding together near the water level at high tide, but their respective levels of zonation at low tide reflect the degree to which each follows the descending water level.

Underwood (1979) considered that the distribution of algal food was of importance in the maintenance of zonation patterns. The influence of food availability on the zonation of *Littoraria* species is not known, but appears unlikely to determine upper limits, since snails survive at levels higher than usual in wet weather, while at least in the case of *L. filosa*, *Avicennia* leaves provide food even at the tops of trees. It remains to be explained what environmental cues prevent the larger individuals of the lower species (and the smaller of the upper species) from descending to the bottom of the trees with the falling water surface.

While migrations of the three species largely confined to trunks and roots could be accomplished simply by negative and positive geotaxis, the movements of *L. filosa* and *L. philippiana*, on the three-dimensional substrate of foliage and branches, must be based on more complex responses. Snails do not often become trapped on low branches by a rising tide, and migrations to higher levels at spring tides must in some cases involve descent of a branch, followed by ascent of the trunk, rather than a simple ascent of a vertical substrate. Abe (1942) observed that an individual of *L. pallescens* was not trapped on an arched root by the rising tide, but that the snail crawled down into the water to reach the trunk and ascend the tree. Evans (1965) showed that British *Littorina* species were not trapped on a 'half tide rock' in a laboratory tide model, and suggested form vision as an explanation. While this suggestion has been verified in *Littoraria irrorata* (Hamilton, 1977, 1978b), other possibilities are that snails may follow mucous trails (Hall, 1973; Gilly & Swenson, 1978; Raftery, 1983) or possess homing ability (Daguzan, 1966). These aspects of complex behaviour would repay further investigation.

12.4.4 Long term changes in zonation patterns

Long term migrations and changes in zonation pattern have been recorded for many intertidal gastropods, including littorinids. Changes in level with a synodic rhythm are apparently unusual, but have been found in *Cerithidea decollata*, a tree-dwelling mangrove species which descends to feed only at neap tides (Brown, 1971) and in *Nerita* species on rocky shores (Taylor, 1971b; Vannini & Chelazzi, 1978). Both Sasekumar (1970) and Berry (1975) have briefly noted that in general arboreal gastropods in mangrove forests are to be found at higher levels at spring tides. Such a response, demonstrated in the present study (and also suggested by Abe, 1942, for *L. pallescens*), is to be expected in view of the reaction to escape submersion by a rising tide. It is, however, curious that the levels occupied by the quiescent snails were independent of the height of the preceding high tide (Figs 12.7, 12.8, 12.9). Clearly the snails did not simply move down for a constant distance after each high tide. It is possible that some feature of the environment such as zonation of microalgal food (Underwood, 1979), might fluctuate with the synodic cycle, and thereby influence the behaviour of the snails. Alternatively, an endogenous rhythm of synodic periodicity could exist. Only Bohn (1904) has reported such a rhythm, in captive littorinids, and the observation has not been confirmed by subsequent authors.

Migrations to lower levels on the shore for spawning have been described in many littorinids from temperate rocky coasts (Kojima, 1959; Sacchi, 1966; James, 1968; Palant & Fischelson, 1968; Pilkington, 1971), although conflicting observations have been made on different populations of *Melarhaphe neritoides* (Fretter & Graham, 1962, p. 387, c.f. Lysaght, 1941). In the present study, no marked change in distribution could be correlated with the onset of the spawning season in the two species with restricted breeding seasons, *L. filosa* and *L. philippiana* (Section 13.3.1). However, in *L. scabra* and *L. intermedia* it was found that females usually occurred at relatively lower levels than males (when their larger size was taken into account), although the difference in mean level was only of the order of 0.1 m, and often not significant. For *L. angulifera*, Lebour (1945) briefly noted a lower zonation pattern in the breeding season, and Lenderking (1954) found females of this species at lower levels when spawning.

The only established case of seasonal migration, unconnected with reproduction, in a littorinid is the downshore movement of *Littorina littorea* in response to low winter temperatures in the more northerly parts of its range (Gowanloch & Hayes, 1926; Lambert & Farley, 1968; Williams & Ellis, 1975; Gendron, 1977; but c.f. Smith & Newell, 1955, and Underwood, 1973, in milder climates). No seasonal changes in distribution have been noted in *Littoraria angulifera* (Gallagher & Reid, 1979) or in *L. irrorata* (Hamilton, 1978a). The upward migrations of *L. filosa* and *L. philippiana* during wet weather are the first documented cases of such a response by intertidal gastropods, although Sasekumar (1970) noted a greater number of gastropods on mangrove trees after rain. Supralittoral littorinids on rocky shores may become active after rain (Fretter & Graham, 1962: 536).

On *Avicennia* trees both *L. filosa* and *L. philippiana* occurred at increased frequencies on the lower leaf surfaces during heavy rain (Section 12.3.5). A similar behaviour pattern has been described in *L. pallescens* on *Rhizophora* trees by Abe (1942, as *Melaraphe scabra*), who interpreted it as a sheltering response to avoid freshwater influence. While this is a likely explanation, it is also possible that rainfall stimulates feeding activity, and *L. filosa* is believed to graze the hairs on the lower surfaces of *Avicennia* leaves.

Whether the greater numbers of *L. filosa* and *L. philippiana* on leaves, compared with bark substrates, during wet weather (when rain was not actually falling) was related to the supposed sheltering response, is not clear. Alternatively, it may be suggested that if feeding in these species occurs mainly on leaves, the wet weather distribution pattern might reflect increased feeding activity, rather than a sheltering reaction to rainfall.

12.4.5 The mucous holdfast

The formation of a mucous holdfast under unfavourable conditions is a response which appears to be characteristic of all littorinids, both temperate and tropical (Wilson, 1929; Berry, 1961; Evans, 1961; Heller, 1976). Vermeij (1971b, 1973a) has stressed the significance of this adaptation in relation to temperature control and conservation of moisture. Bingham (1972c) described the conditions under which *L. irrorata* formed a holdfast, and, as observed in *Littoraria* species in the present study, these included times of osmotic stress and low relative humidity. Holdfast formation was most frequent in the three smallest species (*L. articulata, L. intermedia, L. filosa*; Section 12.3.5), which are likely to be most vulnerable to desiccation and osmotic stress by virtue of their small size (Chow, 1975). The ability of *L. philippiana* to remain attached by the foot for most of the time, although found at high levels, is surprising, but can be accounted for in terms of the sheltered mangrove habitat, the large size of the species and its ability to migrate down to the water level at high tide. This behaviour suggests that *L. philippiana* seldom experiences desiccation stress, in contrast to *L. filosa* from a sunnier habitat on *Avicennia* foliage, which was usually attached by mucus during dry weather.

Under conditions of higher humidity, the mucous holdfast may remain fluid. If the snail is then dislodged, it may remain suspended by a string of mucus, which it subsequently ascends to regain its position. This can be observed most readily in *L. scabra*, in which the mucous secretion is copious. This ability of mangrove littorinids, first recorded by Boschma (1948), has given rise to the misconceptions that 'thread spinning' is a defensive reaction to disturbance (Macnae, 1968) or even assists in climbing from branch to branch (Allan, 1959).

12.4.6 Shell size gradients

Differential distribution of size classes, generally referred to as size gradients, have been described in no fewer than 30 studies of littorinids, embracing 15 species. In a review of size gradients in intertidal gastropods, Vermeij (1972b) proposed that most species from the littoral fringe might be expected to show an upshore increase in size. This was explained by the greater susceptibility of small snails to the more extreme physical conditions at higher levels, and the advantage conferred if the juveniles inhabit the zone of minimum mortality. In contrast, species from the lower littoral were predicted to show an upshore decrease in size, because of more intense predation at lower levels. Many littorinids do indeed show the expected upshore increase in size (Palant & Fishelson, 1968; Fretter & Manly, 1977; Hamilton, 1978), even if found in the lower littoral (Branch & Branch, 1980). The pattern may be confused by the occurrence of large individuals also at the lowest levels, perhaps because growth rates are greater where food is more abundant (Moore, 1940; Williams, 1966; Gendron, 1977; Muggeridge, 1979; Branch & Branch, 1981). Cases of the opposite pattern have also been reported, usually on exposed shores, where juveniles, which are most susceptible to wave action, predominate at levels above the full force of the waves (Bock & Johnson, 1967; McQuaid, 1981b). In exposed habitats the distributions of crevices and barnacle tests, which serve as refuges, are of primary importance in determining the observed size gradient (Emson & Faller-Fritsch, 1976; Raffaelli & Hughes, 1978; McQuaid, 1981b). In very few of these studies have the relative contributions to the size gradient of preferential larval settlement, differential growth or mortality of the newly settled individuals been considered (Fretter & Manly, 1977).

The five *Littoraria* species examined in detail at Magnetic Island all show the common pattern of smaller individuals at lower levels on the trees. This has also been found in studies of other species in the genus: *L. melanostoma* (Berry & Chew, 1973), *L. angulifera* (Gallagher & Reid, 1979) and *L. luteola* (Muggeridge, 1979), although Abe (1942) failed to find a consistent size gradient in *L. pallescens*. In *L. irrorata* there is apparently a horizontal gradient of increasing size up the beach (Hamilton, 1978a), but in contrast to the situation in mangrove-dwelling species, it is said to be the smaller specimens which migrate up the grass stems to avoid submersion, while the larger individuals, less susceptible to aquatic predators, show a greater tendency to remain below the surface (Stanhope *et al.*, 1982).

The ultimate reason for the size gradient in mangrove dwelling *Littoraria* species is presumably, as in rocky shore littorinids, the greater susceptibility of the smaller snails to desiccation during emersion at high levels (Vermeij, 1972b). However, whether the proximate cause is to be found in a different behaviour pattern of juveniles (Berry & Hunt, 1980), or is simply a result of the effect of the greater rate of water loss in smaller snails (Coombs, 1973; Chow, 1975) upon the geotactic response (Newell, 1958b; Bock & Johnson, 1967), remains to be discovered. In the species from the highest levels, in which adults are to be found above the reach of the highest tides, it is clear that juveniles must settle from the plankton at intertidal levels, thereby initiating the size gradient. It must be emphasized that in rocky shore littorinids the size gradients are apparently often produced by gradual upshore migration of the growing snails (Smith & Newell, 1955; Fretter & Manly, 1977) combined with active maintenance of the optimal level (Chow, 1975; McQuaid, 1981b). In contrast, the mangrove *Littoraria* species reproduce the size gradient after each daily or twice daily episode of tidal migration and feeding.

CHAPTER 13: REPRODUCTION, POPULATION DYNAMICS AND GROWTH

13.1 Introduction

Members of the family Littorinidae have attracted considerable attention because of the wide diversity of types of development occurring within the group. As reviewed by Mileikovsky (1975), Underwood (1979) and Underwood & McFadyen (1983), there are four principal methods: pelagic egg capsules and planktotrophic larvae, benthic egg masses from which hatch planktotrophic larvae, benthic egg masses with entirely lecithotrophic development and no planktonic stage, and ovoviviparity. The last mentioned category should be subdivided to recognize the distinction between ovoviviparity with direct lecithotrophic development (as for example in several species of *Littorina s.s.*) and short term brooding of larvae until the early veliger stage (as practised by members of the subgenus *Littorinopsis*). This distinction has important evolutionary and ecological consequences, the former method permitting precise adaptation of populations to local conditions, the latter ensuring wide dispersal. Several authors have suggested the possibility of variation of the developmental type within species (Robertson, 1974; Caugant & Bergerard, 1980; Hughes & Roberts, 1981), but this is considered unlikely, since presumed cases of the phenomenon can be explained by taxonomic confusion or premature spawning under unnatural conditions (Section 5.4).

The earliest work on littorinid reproduction was concerned with anatomy and descriptions of egg capsules, as reviewed in Chapter 5. The first attempts to perceive an ecological pattern in the occurrence of developmental types suggested a correlation with tidal level, pelagic eggs being released at the lowest levels, benthic egg masses produced in the littoral zone and ovoviviparity practised at supralittoral levels (Woodward, 1909; Tattersall, 1920). Subsequent work showed that pelagic egg capsules were commonly released at all levels (Lebour, 1935; Struhsaker, 1966; Borkowski, 1971). The reclassification of the family proposed by Bandel & Kadolsky (1982), which is supported by the anatomical evidence and phylogenetic interpretation of the present study, allows a reinterpretation of developmental patterns in an evolutionary context.

Numerous descriptive ecological studies have demonstrated that reproduction is seasonal in most littorinids from temperate and subtropical regions, with annual regression of the gonads outside the breeding period (Williams, 1964; Palant & Fishelson, 1968; Borkowski, 1971; Underwood, 1974). It has been found that in many species spawning activity is synchronized with the lunar cycle, ensuring release of eggs or larvae at spring tides (Lysaght, 1941; Lenderking, 1954; Berry & Chew, 1973; Gallagher & Reid, 1974; Schmitt, 1979; Alifierakis & Berry, 1980). Spawning is constrained by the need for partial or complete submersion, but under constant laboratory conditions some species have been shown to display a tidal rhythm, spawning at the same time as the high tide in the field (Struhsaker, 1966; Borkowski, 1971; Gallagher & Reid, 1974; Schmitt, 1979). Despite the profusion of work on breeding activity of littorinids, there has been only one report of successful rearing of planktotrophic larvae in the laboratory (Struhsaker & Costlow, 1968), other than which there is no available information on length of larval life, larval dispersal or settlement preferences.

Growth rates have been quite thoroughly investigated in temperate littorinids, particularly in Europe (Moore, 1937; Berry, 1961; Williams, 1964; Moreteau, 1976; Goodwin, 1978; Hughes, 1980; Hughes & Roberts, 1980a; Roberts & Hughes, 1980; Hughes & Answer, 1982; Janson, 1982a), but also in Australia (Underwood, 1975; Muggeridge, 1979; Underwood & McFadyen, 1983) and South Africa (McQuaid, 1981a). Although a few studies have been carried out in subtropical regions (Lenderking, 1954; Bingham, 1972a; Borkowski, 1974; Gallagher & Reid, 1979), the only available information on growth rates of littorinids in the tropics is a report by Whipple (1966) on one species in Hawaii.

An early study of the dynamics of littorinid populations was made by Moore (1937). Only in the past ten years have a number of comprehensive studies of this aspect of littorinid biology been made (Borkowski, 1974; Underwood, 1975; Daguzan, 1976a, b; Gallagher & Reid, 1979; McQuaid, 1981a; Robertson & Mann, 1982; Underwood & McFadyen, 1983). During this time numerous papers have been produced in Britain, covering many aspects of development, growth and population structure (Faller-Fritsch, 1976; Goodwin, 1978; Hughes, 1980; Roberts & Hughes, 1980; Hughes & Roberts, 1980a, b, 1981; Hughes & Answer, 1982; Hart & Begon, 1982; review by Raffaelli, 1982). This interest was stimulated partly by the taxonomic re-evaluation of the European species of *Littorina* (Heller, 1975a; Raffaelli, 1979a; Hannaford Ellis, 1979; Raffaelli, 1982). There was also a desire to test new theories of the evolution of life history strategies (review by Stearns, 1976) in a series of closely related animals with contrasting developmental types. This approach failed to find the predicted correlations between method of development and either reproductive effort (Hughes & Roberts, 1980b) or demography (Hughes & Roberts, 1981). Intraspecific variations in life history traits did not conform to the theoretical expectations (Hart & Begon, 1982).

Since they occupy sequential but overlapping vertical zones on the mangrove trees, the species of *Littoraria* at Magnetic Island provide an opportunity to compare aspects of life history characters in closely related species which are exposed to different intensities of environmental variables such as microclimate and predation pressure. Three basic techniques have been employed in previous studies of growth rate and demography of gastropods. Variations of the mark and recapture technique include unique marking of individuals (e.g. Yamaguchi, 1977; Roberts & Hughes, 1980), notching or painting of the apertural margin and measurement of the subsequent growth increment (e.g. Moreteau, 1976; Janson, 1982a) and marking of size classes (e.g. Hughes, 1980; McQuaid, 1981a). In populations with discrete periods of recruitment and continuous growth, age cohorts appear as modes in the size frequency distribution and changes in density and dimensions of the cohorts can be followed (e.g. Underwood, 1975; Creese, 1981). Although annual growth lines have frequently been used in the age determination of bivalves (Hancock, 1965), they are rather seldom formed in gastropods (Frank, 1969) and have not hitherto been recorded in littorinids. The method of individual marking has the advantage of accuracy, since growth is measured directly (Creese, 1981), although possible deleterious effects of the marking procedure must be considered. This method was successfully used for the four largest species of *Littoraria* at the study site. Recapture efficiency was found to be satisfactorily high in the mangrove habitat. Additional information on maximum longevity of two species was derived from annual varices (Section 4.1) on the shell. Analysis of polymodal size frequency distributions would not have been appropriate, because of the low population densities, slow growth of adults, and pronounced sexual dimorphism.

13.2 Methods

13.2.1 Reproduction

The duration of the breeding season was investigated in the five common species of *Littoraria* occurring at Cockle Bay, over a 13 month period from September 1980 until September 1981. Collections were made at the beginning of each month, ten specimens of each sex being taken for the more abundant species *L. articulata*, *L. intermedia*, *L. philippiana* and *L. filosa*. In the case of *L. scabra*, occurring in low numbers and largely on the outermost trees of the forest, the population in the sampling area was considered to be too small for more than five of each sex to be collected. The sex of individuals was determined in the field by the presence or absence of a penis (Section 5.2), and confirmed by subsequent dissection of the reproductive tract in the laboratory. Samples were restricted to shells of 'adult' morphology, close to the maximum size and with a thickened or flared lip indicating slow growth (Section 4.1). Only one individual, a female of *L. articulata*, was found to contain trematode parasites, and this specimen was excluded from the results.

Various indices of reproductive condition have been employed in studies of prosobranchs, including gross examination of the gonad (e.g. Moore, 1937; Borkowski, 1971), histological resolution of the state of gametogenesis (e.g. Underwood, 1974; Muggeridge, 1979) and, in ovoviviparous species, examination of the contents of the brood pouch (e.g. Berry, 1961; Heller, 1975a). In a study of *Littorina littorea*, Williams (1964) stressed that as many anatomical criteria as possible should be used in order to reduce error, and defined five developmental stages on the basis of the condition of the gonad and degree of development of parts of the reproductive tract. A similar approach was adopted in the present study. For each male examined, shell size, dimensions of the penis and penial glandular disc, extent of the gonad, and size and colour of the vas deferens and prostate were recorded, and a sample of sperm removed from the vas deferens was examined microscopically (Section 3.2.2). For females, a record was made of shell size, dimensions and colouration of the pallial oviduct, size and contents of the seminal receptacle, and presence of larvae in the mantle cavity; in addition a portion of the gonad or eggs from the oviduct was examined microscopically. In contrast to the temperate species examined by Williams, regression of the glands of the pallial gonoducts and of the penis outside the breeding season was found to be slight, so that his classification of developmental stages could not be employed. Only three stages of reproductive development could be distinguished, largely on the basis of the state of the gonad. The three stages used to describe reproductive condition are defined in Tables 13.1 and 13.2.

Table 13.1 Stages of reproductive maturity of male *Littoraria* species.

Stage	Gonad	Vas deferens
Immature or spent	Absent, or minute spots	Thin, dark, hardly coiled; empty of sperm
Maturing or partially spent	Around arteries only	Thin, coiled; containing a little sperm
Mature	Extensive	Swollen, much coiled; full of sperm

Table 13.2 Stages of reproductive maturity of female *Littoraria* species.

Stage	Gonad	Mantle cavity
Immature or spent	Absent	Empty
Maturing or partially spent	Variable extent, immature ova	Embryos or empty
Mature	Extensive, full of mature ova (77–87 μm in *L. filosa*, 59–69 μm in remaining 4 species)	Embryos or empty

Mating activity was recorded over the year, at approximately fortnightly intervals from September until February, and at monthly intervals thereafter. The number of copulating pairs observed on a total of 20 marked *Avicennia* trees and 60 *Rhizophora* trees was recorded, between the hours of 8.30 and 10 a.m., and usually on or immediately following a falling tide (when conditions for copulation were apparently most favourable, Section 12.3.1). All pairs in which the male was attached to the female shell in the copulation position were counted, whether or not the penis was inserted (Section 6.1). The few interspecific pairings were scored for the species of the male of the pair (Section 6.2).

To determine the minimum sizes of mature males and females of each species, samples of shells covering the entire size range were examined during the months of February and March (when all species showed peak reproductive activity, Figs 13.1, 13.2). Maturity was defined by the characteristics indicated in Tables 13.1 and 13.2.

13.2.2 Population dynamics

Estimates of population size, size frequency distribution, survivorship and recruitment were made using a multiple mark and recapture technique. As described in Chapter 10, three study areas of individually marked trees were chosen on the basis of the abundance of the four largest *Littoraria* species. The two trees of *Avicennia* on which *L. filosa* was studied were both isolated from other trees. In the case of the five *Avicennia* trees on which *L. philippiana* was common, direct migration to and from adjacent trees was prevented by pruning of branches. Isolation of the 64 trees comprising the study area in the *Rhizophora* forest was impossible. Only the four larger and relatively common species, *L. scabra*, *L. intermedia*, *L. filosa* and *L. philippiana*, were investigated. *L. articulata* was excluded since its small size made marking and recapture difficult. The study was carried out over a 14 month period, from August 1980 until September 1981, for the three species in the *Rhizophora* forest (*L. intermedia*, *L. scabra*, *L. philippiana*) and for *L. filosa*. For *L. philippiana* on *Avicennia* trees the period was the 13 months from October 1980 until October 1981.

At the beginning of the investigation, all snails above a certain minimum size for each species were collected for individual marking in the laboratory. The minimum sizes were determined by the feasibility of legible marking without damaging the animal, and were 4 mm for *L. scabra* and *L. intermedia*, 7 mm for *L. philippiana* and 9 mm for the very delicate, thin shelled *L. filosa*. The sex of each individual was determined by the presence or absence of a penis; penes were present in all males in these size ranges. Shell colour was recorded (Section 15.2) and shell height measured to the nearest 0.1 mm with vernier calipers (Fig. 3.1). Each shell was cleaned to remove mud and mucus, and the snails left to dry and to become inactive in open petri dishes. The marking technique involved individual numbering on the dorsal side of the body whorl with black or white ink, in figures less than 2 mm high, and final application over the number of a small quantity of 'Discon' polyester resin. The resin was dry to the touch in half an hour and snails were returned to the field 24 hours later. No animals were retained in the laboratory for more than three days, a period which it was hoped would not have had any seriously deleterious effect, in view of the longer intervals of dryness tolerated in the field during neap tides. No mortality occurred during the marking process. Following marking, each snail was returned to the same tree from which it had been removed, at a level normally occupied by the particular species. The release was facilitated by the immediate resumption of activity of all species following wetting in seawater, and by their apparent insensitivity to handling.

Thereafter, the study areas were visited on or near the first of each month and the size of each numbered shell found was measured. Measurement was usually accomplished without the need to remove the snail from the substrate, so that disturbance was minimal. Searching for marked snails was carried out during high or falling tides where possible, when animals were concentrated over a narrow vertical range (Section 12.3.1), thus increasing searching efficiency. All snails found without marks were collected and then recorded, numbered and released as described above. A total of 2204 snails were marked during the study.

Measurements from the samples of snails recorded at each visit were used to construct size frequency histograms for the populations of each of the four species. An estimate of population size was achieved by augmenting the number of captures at each visit by the number of previously marked snails missed, but recovered on subsequent occasions. The probability of capture at each visit was estimated as the number of recaptured marked snails, expressed as a percentage of the number of those previously marked which were recaptured on that or subsequent occasions. The mean probabilities of capture were mostly high, being between 74 and 83% for *L. intermedia, L. scabra, L. philippiana* (on *Avicennia* trees) and *L. filosa*, but only 48% for *L. philippiana*, found at the higher and less accessible levels on *Rhizophora* trees (Table 13.4).

This method of analysis is equivalent to the enumeration (or minimum number known to be alive, MNA) technique which has been used for small mammal populations. Hilborn *et al.* (1976) have demonstrated that the enumeration method gives good estimates of population size which are relatively insensitive to survivorship and probability of capture, when these are greater than 50%. The estimates of population size for the *Littoraria* species may therefore be unreliable in the case of *L. philippiana* on *Rhizophora* trees, but should be only a little below the actual values in the remaining species. The estimates of population size will be least reliable on the first and last dates of collection, when individuals missed but recovered subsequently could not be taken into account.

An attempt was made to measure recruitment directly, by counting the numbers of newly settled snails found in marked areas. However, even with the aid of field magnification it was difficult to search the irregular surfaces of trees thoroughly. The minute snails occurred at very low densities, necessitating examination of large areas, and the shells could only be identified confidently to species level at sizes greater than 2 to 3 mm. This attempt was abandoned. Recruitment was therefore estimated from the number of unmarked snails found at each visit during the mark and recapture experiment. Snails up to 4 mm larger than the minimum size at which each species was marked were defined as 'recruits'. The interval of 4 mm was chosen since growth measurements indicated this to be approximately the maximum increase in size shown by these smallest snails in one month (Section 13.3.3).

In many previous studies of the population dynamics of intertidal prosobranchs, authors have estimated mortality rates by following the decline in numbers or density of cohorts (whether marked in groups or defined by size frequency analysis) over several sampling periods (e.g. Hughes & Roberts, 1981; Creese, 1981). This method was tried in the present study, using the individuals marked on the first sampling occasion. Two cohorts (referred to as juvenile and adult) were defined by inspection of the size frequency distributions, and the subsequent decline of each cohort followed by tracing the survival of the marked individuals therein. Survivorship curves were constructed as the natural logarithm of cohort size (taking account of individuals missed but recaptured subsequently) against time in monthly intervals. These were approximately linear, indicating exponential decay, and instantaneous loss rates (μ) were calculated as the slopes of the regressions. The average survivorship (proportion surviving for time t) was calculated for each cohort as $e^{-\mu t}$. The size of the juvenile cohort of *L. philippiana* on *Rhizophora* trees was too small (Fig. 13.6) to permit analysis.

Small but regular deviations from linearity in the survivorship curves suggested the possibility of variations in survivorship with season, but the effect was confounded with that due to the increasing size (and age) of the individuals. In contrast to many previous studies, individuals were uniquely marked and their sizes precisely known, so that it was possible to separate the effects of size and season upon survivorship. The monthly recapture records for each species were divided into arbitrary size classes (< 12, 12-19, 19-26, > 26 mm) and the survivorship of each class estimated as the proportion surviving until the following month or recaptured thereafter. Survivorship was estimated in this way only for size classes containing ten or more individuals. The resulting data were not suitable for a test of the significance of the effects of size and season by analysis of variance. A two-way analysis of variance without replication requires that main effects should be additive (Underwood, 1981), but this could not be tested owing to empty cells in the data. Inspection suggested that the effects were indeed not additive. Furthermore, variances were heterogeneous owing to the unequal sizes of cohorts from which proportions surviving were calculated. No nonparametric test seemed suitable. Certain trends were, however, evident from inspection of the data.

13.2.3 Growth

Growth rates were estimated from the measurements of shell height made during the mark and recapture study described above. Shell height was considered to be an accurate measure of size, for in these species no erosion of the shell apex occurred and the protoconch was often intact (Section 4.3). From the consecutive monthly measurements, increments in height were calculated and standardized to an interval of 30 days. In many studies (e.g. Moreteau, 1976; Hughes, 1980; Roberts & Hughes, 1980; Perron, 1983), gastropod growth has been modelled using the von Bertalanffy growth equation, which predicts asymptotic increase to the maximum size:

$$L_t = L_\infty (1-e^{-kt})$$

where L_t = length at time t after growth is assumed to begin, L_∞ = asymptotic size and k = instantaneous size-specific growth rate (Yamaguchi, 1975). The instantaneous growth rate is then a linear function of size, with a slope of -k. In practice, growth increments must be measured over a finite time interval, but approximate satisfactorily to instantaneous rates when the interval is short relative to the growth rate of the animal (Yamaguchi, 1975; Hughes, 1980). The value of the growth parameter k can then be estimated as the slope of the regression of growth increment on size at the start of the time interval.

Functions relating monthly growth increment to size for each of the four *Littoraria* species were derived by using a stepwise multiple linear regression technique (New Regression routine of SPSS programme, probability of F-to-enter 0.05, probability of F-to-remove 0.1, tolerance 0.01; Hull & Nie, 1981). By this means, linear or (in cases of significant curvature) quadratic functions were fitted to the data. Since at the time of numbering, the sex of each individual was recorded, it was possible to fit separate functions for the growth increments of males and females. At certain seasons of the year the largest shells showed no growth and, in order to increase the accuracy of prediction of growth increments, these points were excluded from the regression calculation. Inspection of the consecutive monthly increments of non-growing shells showed that measurement was accurate to ±0.2 mm. Therefore, the exclusion of non-growing shells from the calculation was achieved by excluding shell heights greater than that above which monthly growth increments did not exceed 0±0.2 mm. For *L. philippiana* the growth rate was estimated only in the population on *Avicennia* trees; on *Rhizophora* trees the probability of recapture was too low and the sample size too small for reliable calculation.

To examine the possible short-term influence of the marking procedure on the growth rate, the growth increments of individuals in a limited size range, marked at the beginning of the month, were compared with the increments of snails of the same size over the same period, but marked one month earlier. An analysis of covariance technique was employed for the comparison (Hull & Nie, 1981).

Growth curves for each sex were constructed by calculating monthly growth increments from the functions relating increment to initial size (Tables 13.6 to 13.9). The first point on each curve was taken as the mean size of new recruits in the month of maximum recruitment, so that the constructed curve represented growth of the largest cohort in the population. An exception was made in the case of *L. philippiana*, in which consideration of the size frequency structure of the population at the beginning of the observation period, and of the reproductive season, suggested that settlement in 1981 was atypical (Section 13.3.2). In this case the growth curves were constructed for individuals recruited to the population in May, although only a small cohort actually appeared at that time.

The growth curves were constructed for a period of three years, on the assumption of an equivalent pattern of growth in each year. The curves were extrapolated backwards to a point representing settlement of the planktonic veliger at a size of 0.4 mm one month after the period of maximum spawning activity in the population. The basis and validity of this assumption are considered in Section 13.3.3. Such extrapolation is likely to be least reliable for *L. filosa* and *L. philippiana*, in which the minimum size for individual marking was greatest (9 and 7 mm respectively, Section 13.2.2). In these two species the growth increments of smaller snails predicted by the extrapolation were checked by caging experiments. Shells from 3 to 7 mm in height were used as available at different seasons. Groups of up to ten snails in 1 mm size classes were enclosed in sleeves of fine nylon netting (2 mm mesh, sleeve 30 by 20 cm) on *Avicennia* foliage, and the mean sizes of each batch measured after approximately two months. The two batches most closely comparable with the lines of extrapolation of the growth curves comprised ten *L. filosa* of mean size 4.4 mm and four *L. philippiana* of mean size 3.7 mm, caged on 3 May and 12 February, 1981, respectively.

To illustrate the seasonality of growth activity, the growth parameter k was estimated separately for each sex for each month, by calculating the slope of the linear regression of increment on initial size (regardless of significant curvature in certain of the relationships, Tables 13.6 to 13.9, an approximation used by Janson, 1982a).

Inspection of the records of growth increments in the largest individuals of *L. filosa* and *L. philippiana* suggested that at times of negligible growth a proportion of these snails developed thickened or flared apertural lips, which remained as prominent varices when growth was resumed. The seasonality of growth in these large snails was examined by recording the number of marked individuals, with at least one varix, which showed a thickened, non-growing, apertural margin at each monthly visit. Records were restricted to those individuals with at least one varix, since not all large snails showed the tendency to develop such evidence of interruption to growth.

13.3 Results

13.3.1 Reproduction

Although all five species of *Littoraria* showed peak reproductive activity in the summer months (January to March), the duration of the apparent spawning period showed considerable variation between the species (Figs 13.1, 13.2). *L. intermedia* and *L. scabra*, found at low and moderate levels on *Rhizophora* trees, both showed a pattern with mature males and females present at all seasons of the year. The few maturing females with immature gonads, which were present in October and February in *L. scabra*, and from January to March in *L. intermedia*, all contained embryos in their mantle cavities. They

Fig. 13.1 Annual reproductive cycle of adult males of five *Littoraria* species at Cockle Bay. Stages of reproductive maturity as defined in Table 13.1. Heavy cross hatching, mature; light cross hatching, maturing or partially spent; no cross hatching, immature or spent.

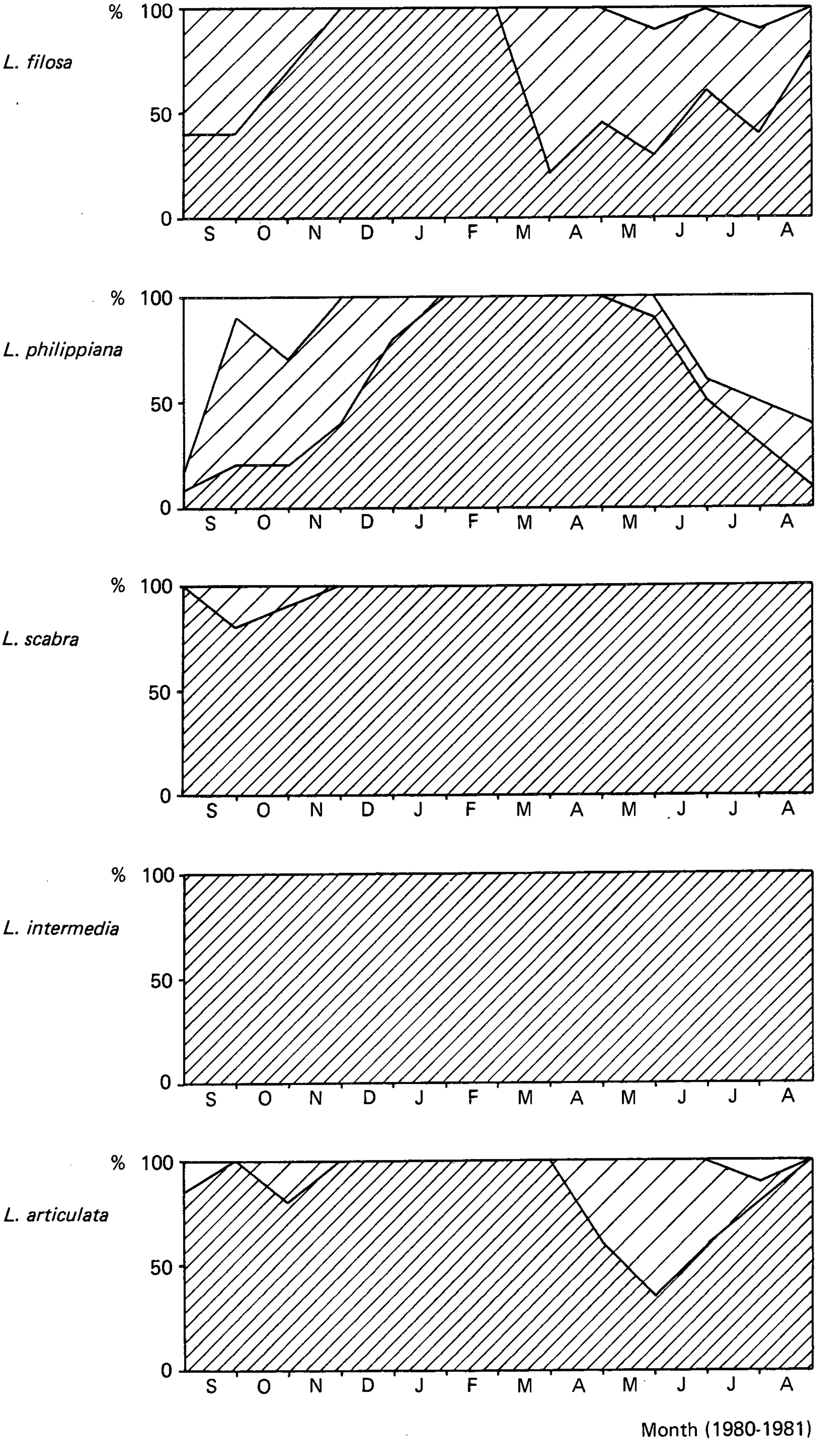
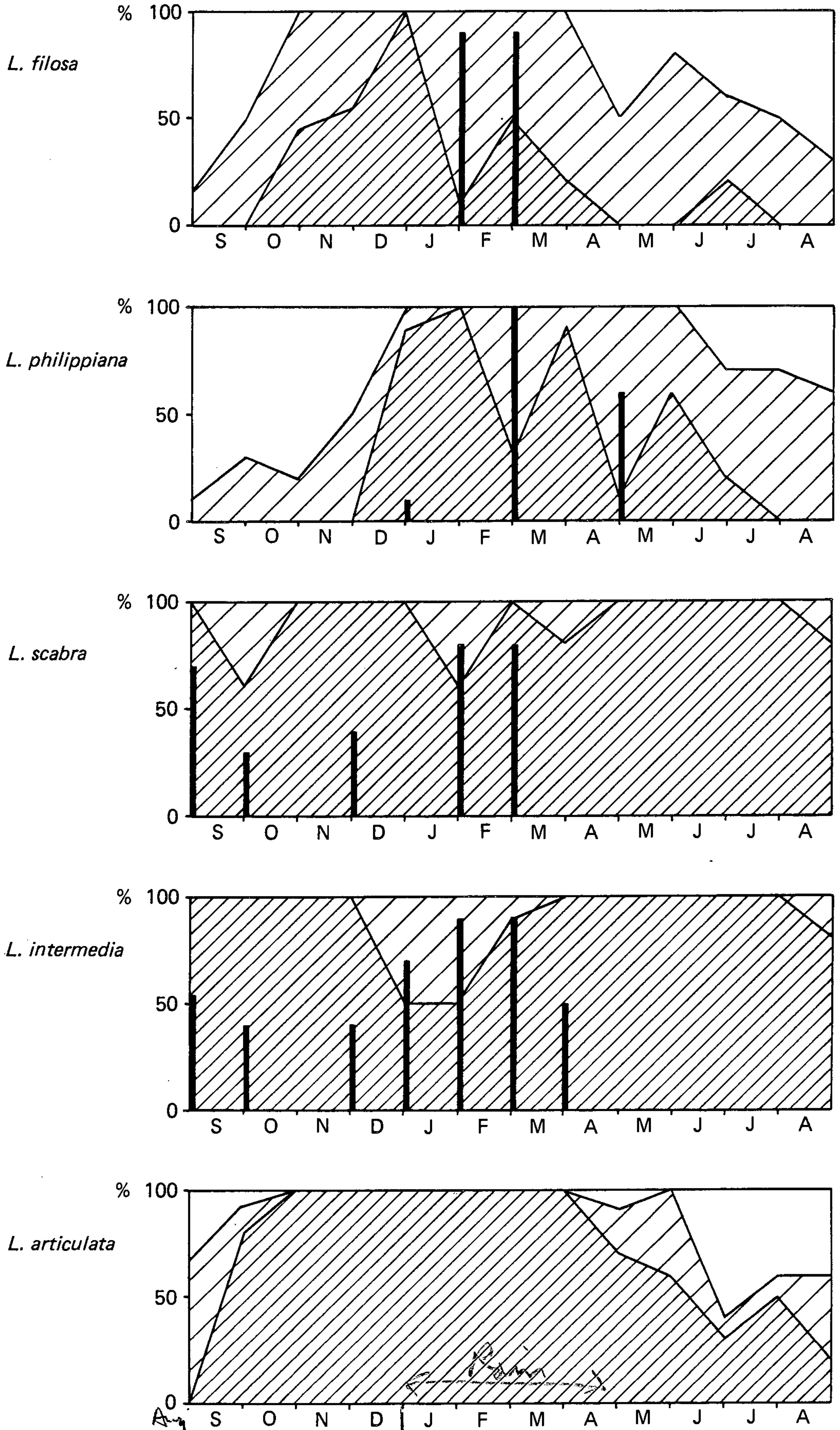

% 100
L. filosa
50
0
S O N D J F M A M J J A
% 100
L. philippiana
50
0
S O N D J F M A M J J A
% 100
L. scabra
50
0
S O N D J F M A M J J A
% 100
L. intermedia
50
0
S O N D J F M A M J J A
% 100
L. articulata
50
0
S O N D J F M A M J J A
Month (1980-1981)

Fig. 13.2 Annual reproductive cycle of adult females of five *Littoraria* species at Cockle Bay. Stages of reproductive maturity as defined in Table 13.2. Heavy cross hatching, mature; light cross hatching, maturing or partially spent; no cross hatching, immature or spent.

What are vertical bars?

Embryos in m.c.?



Aug S O N D J F M A M J J A S O N

dates
spr.
tides

11 9 7 9 9 8 8 6 5 3 2 1

28 26 24 23 23 22 21 21 20 19 18 20 18 16 14 12

31 29 28 27

close after | !! spr | neap | close before spr

So, 1st of M

were therefore individuals which were temporarily spent and recovering from spawning at these times. There was no evidence of synchronized seasonal regression of the gonads in these species. The presence of veligers in the mantle cavity was recorded from September until March in *L. scabra*, and from September until April in *L. intermedia*.

L. articulata is the only oviparous species of the five examined (Section 9.2.4.6), and occupied a habitat similar to that of *L. intermedia*. Females of *L. articulata* were all mature from November until March (Fig. 13.2). Some individuals showed complete regression of the ovary from July to September, but a proportion of the population was mature during this period. Males of this species showed partial regression of the testis from May to August (Fig. 13.1).

L. filosa and *L. philippiana*, both from the highest vertical levels on the mangrove trees, showed a summer reproductive season of shorter duration than those of the species described above. In *L. filosa* the January sample showed complete maturity of the ovary, while the following month the majority of females were depleted of mature oocytes and were brooding embryos in the mantle cavity (Fig. 13.2). A second spawning took place in March, and two females from the sample of ten were mature in July. In *L. philippiana*, maturation of the ovary occurred suddenly in December. One individual from the sample of ten contained embryos in the January sample, but the major spawning episodes were in March and May (Fig. 13.2). In both *L. filosa* and *L. philippiana* the pattern of maturity of the males was similar to that of the females, although a proportion of the males were mature throughout the year.

The sample sizes for the examination of reproductive condition were small (five of each sex for *L. scabra*, ten of each sex for the four other species). However, Figures 13.1 and 13.2 suggest good reproductive synchrony within the populations. In other studies of littorinid reproduction even smaller samples have been found to be satisfactory (Underwood, 1974; Muggeridge, 1979).

Copulation was observed to take place throughout the year in *L. scabra* and *L. intermedia* (Fig. 13.3). Copulating pairs of *L. articulata* were frequent only between September and April. Pairs of *L. filosa* were found from late September until mid February, and of *L. philippiana* only in January and early February. The data did not suggest any correlation of mating activity with the spring tidal cycle or climatic conditions in *L. scabra*, *L. intermedia* or *L. articulata*. *L. filosa* showed greatly increased mating activity during the heavy rainfall in January, while *L. philippiana* was seen to copulate only during rain. Despite the apparent seasonality of copulation in these two species, the majority of females of both showed a seminal receptacle full of active sperm throughout the year.

The length of time for which embryos were brooded in the mantle cavity was not ascertained. Two individuals of *L. philippiana* and one of *L. intermedia* were found in which large numbers of shelled veligers were packed in the alimentary tract.

The sex ratios derived from the total samples of snails used in the mark and recapture experiment are listed in Table 13.3. Significant deviation from equality was shown only by *L. scabra*, with an excess of males.

The minimum sizes of mature snails show that in all species males reached maturity at a smaller size than females (Table 13.3).

Fig. 13.3 Frequency of copulation in five *Littoraria* species over the year of observation at Cockle Bay. The number of copulations is the number of pairs seen at each visit on 20 *Avicennia* and 60 *Rhizophora* trees, between 8.30 and 10 a.m. Note that on no occasion were no pairs of all species found and that visits were at only monthly intervals between February and August.

Relate to tidal regime

on falling tides

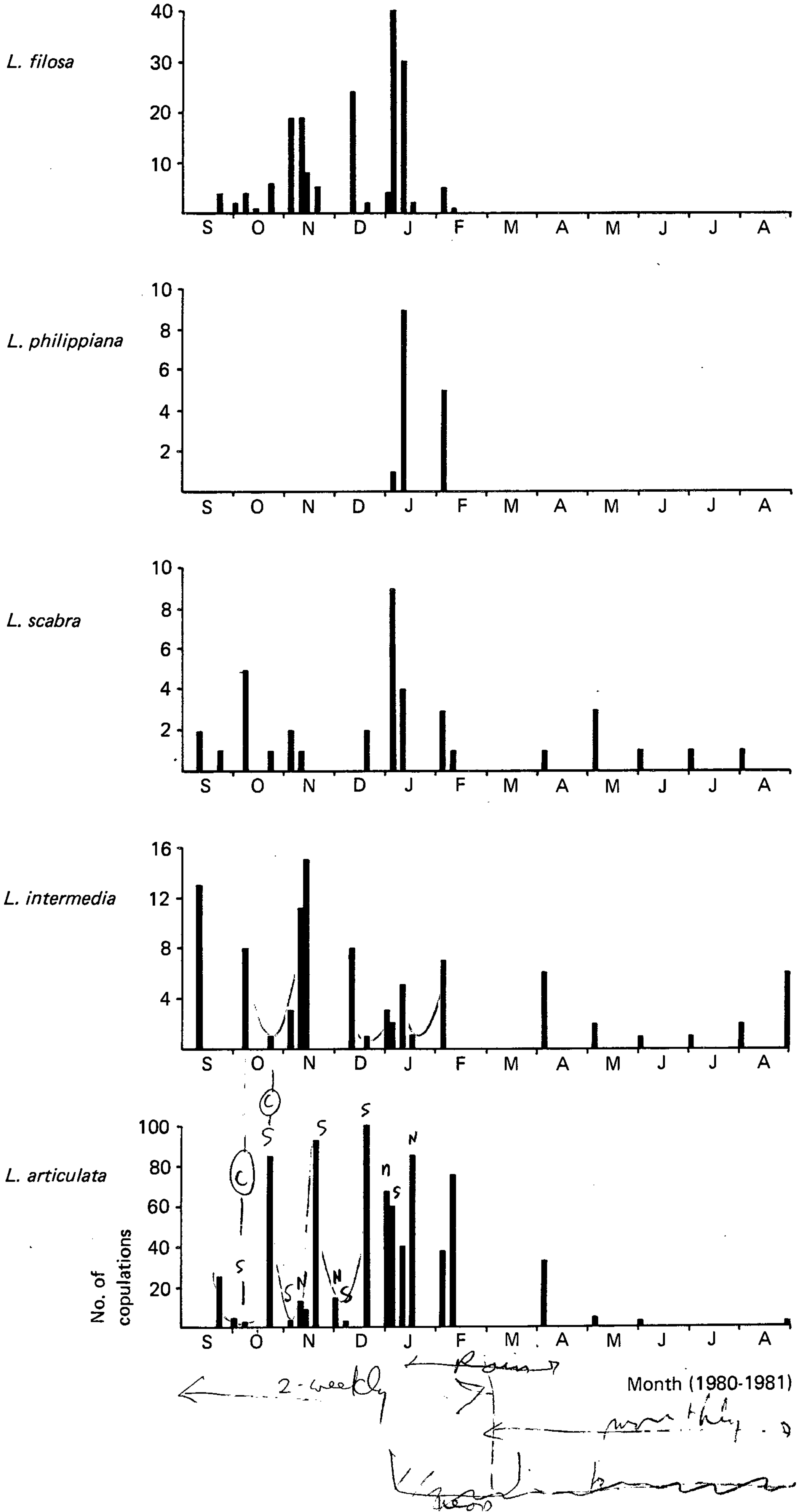

L. filosa
40
30
20
10
L. philippiana
10
8
6
4
2
L. scabra
10
8
6
4
2
L. intermedia
16
12
8
4
L. articulata
100
80
60
40
20
No. of copulations
S O N D J F M A M J J A
Month (1980-1981)
C
C
S
S
S
S
N
N
S
n
S
N
Rains
2-weekly
monthly

Table 13.3 Sex ratios and minimum sizes at maturity for five species of *Littoraria* at Cockle Bay.

Species	Sex ratio ♂:♀	Minimum size of mature male (mm)	Minimum size of mature female (mm)
L. articulata		4.2	4.9
L. intermedia	178:208	9.0	10.6
L. scabra	143:100[A]	15.6	19.7
L. philippiana	112:116	11.1	16.4
L. filosa	600:651	7.6	9.4

[A] significantly different from 1:1, $\chi^2 = 7.26$, $P = 0.007$

Table 13.4 Details of the mark and recapture experiment at Cockle Bay.

Species	Tree	Total number marked	Probability of capture[A] (with 95% confidence interval)	Mean % unmarked larger than 'recruits' (with 95% confidence interval)	% of numbers renewed[B]
L. intermedia	*Rhizophora*	386	74 (68–79)	6.5 (3.3–10.8)	9.8
L. scabra	*Rhizophora*	243	80 (76–85)	7.1 (4.9–9.9)	16.5
L. philippiana	*Rhizophora*	96	48 (36–61)	6.1 (1.4–13.8)	7.3
L. philippiana	*Avicennia*	228	83 (78–87)	9.0 (4.7–14.8)	5.3
L. filosa	*Avicennia*	1251	81 (78–84)	13.9 (8.2–21.0)	3.5

[A] mean % of estimated population size of marked individuals, which were recaptured at each visit; statistics performed on arcsine-transformed proportions

[B] % of total number of marked snails on which numbers were renewed because of flaking of polyester resin

13.3.2 Population dynamics

The size frequency distributions (Figs 13.4 to 13.8) show that the three species *L. intermedia*, *L. scabra* and *L. philippiana* were similar in their population structure, while *L. filosa* stands out as distinct.

Considering the species in turn, *L. intermedia* (Fig. 13.4) showed a clearly bimodal distribution of size classes in August 1980, at the beginning of the observation period. The cohort of smaller snails (shell height H ≤11.9 mm) consisted of juvenile individuals in their first year of growth. This interpretation is based on the subsequent merging of the two cohorts, and the appearance of new recruits in the following year. It is also supported by the observations on growth rates (Section 13.3.3). By October the population showed a unimodal and rather symmetrical size distribution, which persisted until March. Recruits appeared in small numbers from December to February, before the peak period of recruitment during March (Fig. 13.9), which renewed the juvenile cohort. Recruitment continued at a lower level until August. This pattern of recruitment may be compared with the recorded spawning season from September until April, with an apparent peak in February and March (Section 13.3.1). Spawning may, however, have taken place throughout the year (Section 13.4.2). For much of the year (February to June, 1980, August and September, 1981, Fig. 13.4) the adult cohort showed a slight bimodality, with peaks separated by 2 to 4 mm. This reflects the marked sexual dimorphism of the adult snails (Section 4.2, Figs 9.25, 9.26). The juvenile cohort present in August and September of 1981 contained more individuals than that at the same time the previous year, showing that recruitment to the population was more successful in 1981.

The sample sizes for the size frequency distribution of *L. scabra* were smaller, and the peaks therefore less clear (Fig. 13.5). Nevertheless, the general bimodality of the population in August, at

Fig. 13.4 Size frequency histograms for *Littoraria intermedia* on *Rhizophora* trees at Cockle Bay, from August 1980 until September 1981. Broken line indicates minimum size at which individuals were recorded.

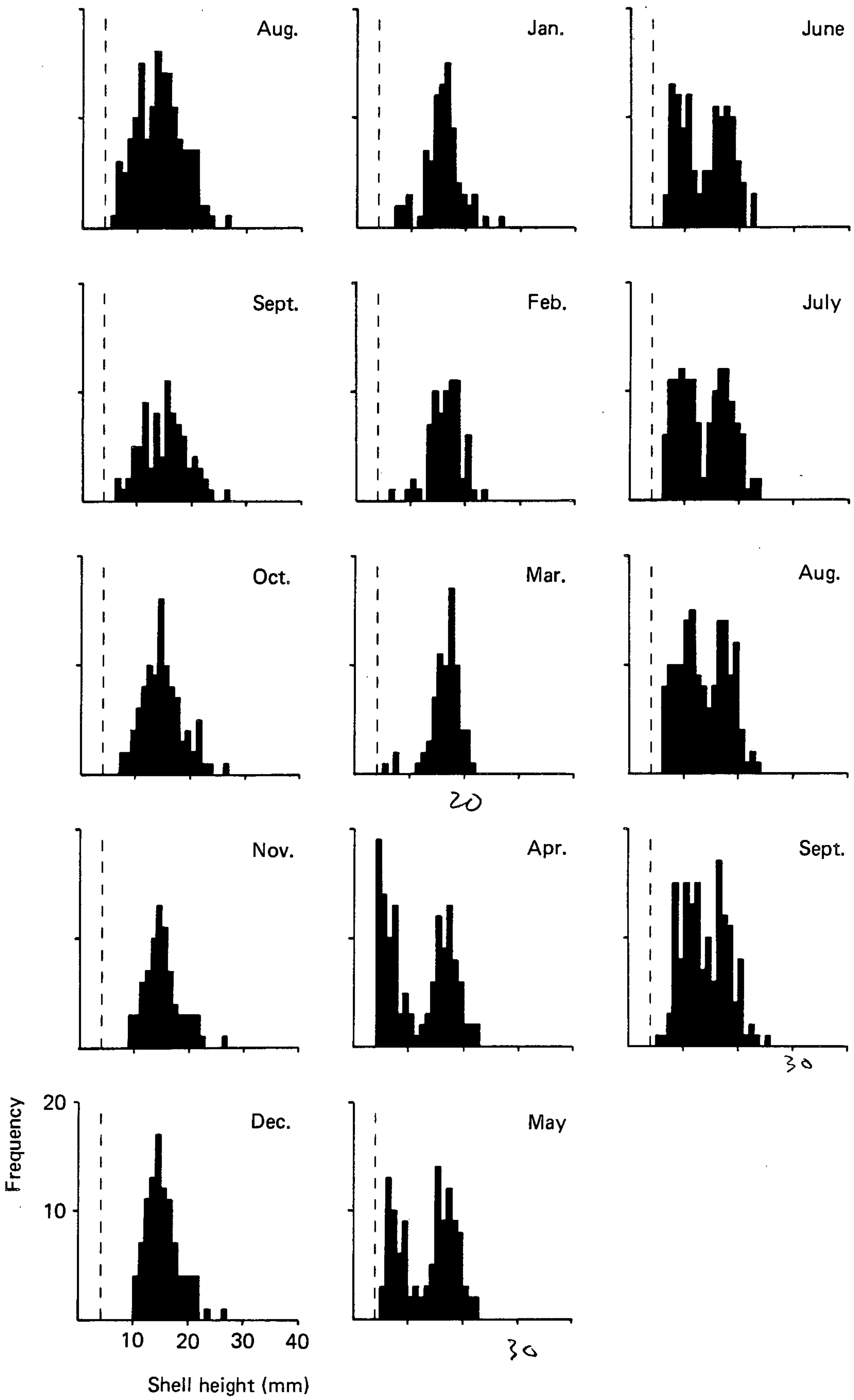

Aug.
Jan.
June
Sept.
Feb.
July
Oct.
Mar.
Aug.
20
Nov.
Apr.
Sept.
30
Frequency
20
10
Dec.
May
10
20
30
40
30
Shell height (mm)

Fig. 13.5 Size frequency histograms for *Littoraria scabra* on *Rhizophora* trees at Cockle Bay, from August 1980 until September 1981. Broken line indicates minimum size at which individuals were recorded.

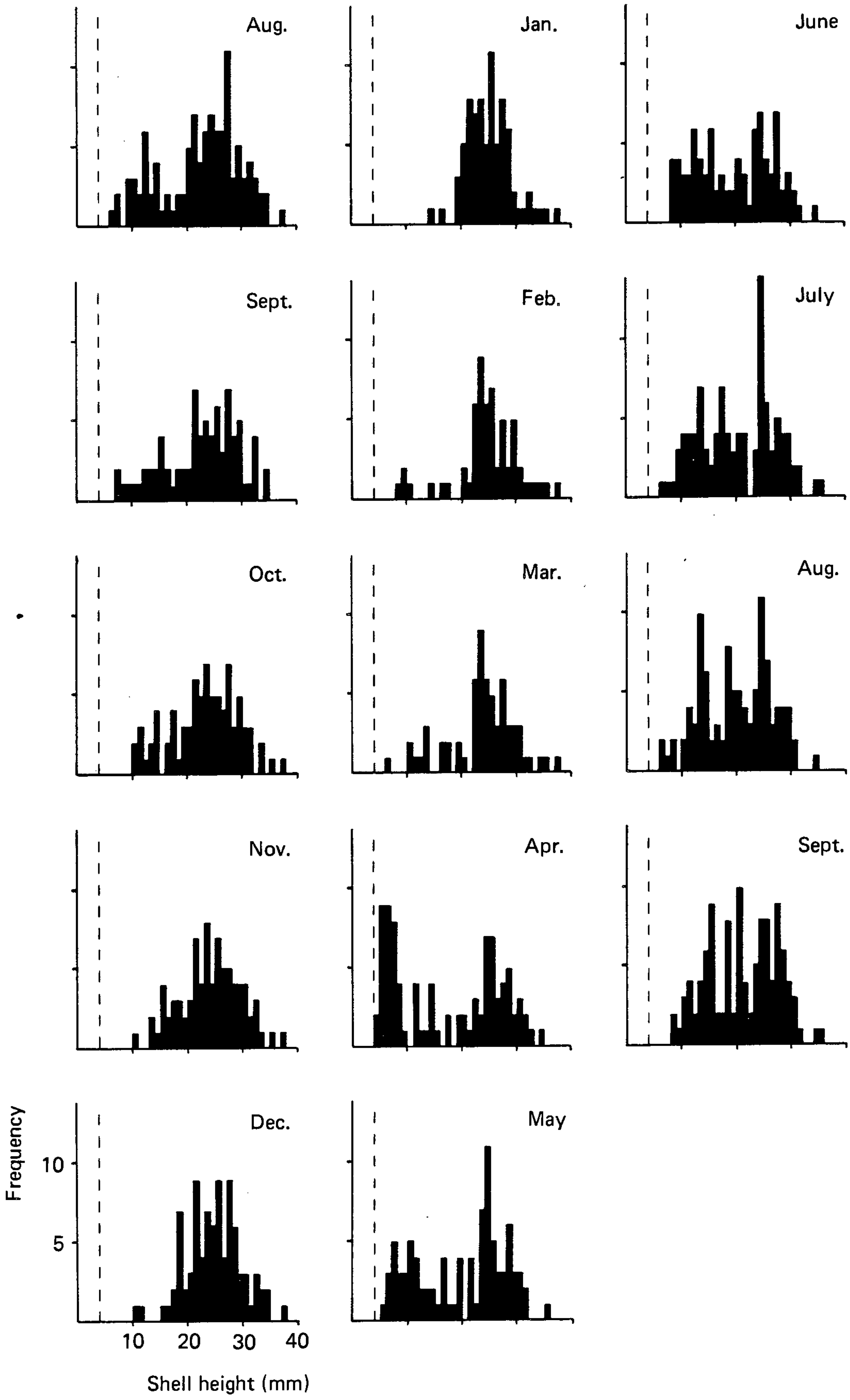

Aug.
Jan.
June
Sept.
Feb.
July
Oct.
Mar.
Aug.
Nov.
Apr.
Sept.
Dec.
May
Frequency
10
5
10
20
30
40
Shell height (mm)

Fig. 13.6 Size frequency histograms for *Littoraria philippiana* on *Rhizophora* trees at Cockle Bay, from August 1980 until September 1981. Broken line indicates minimum size at which individuals were recorded.

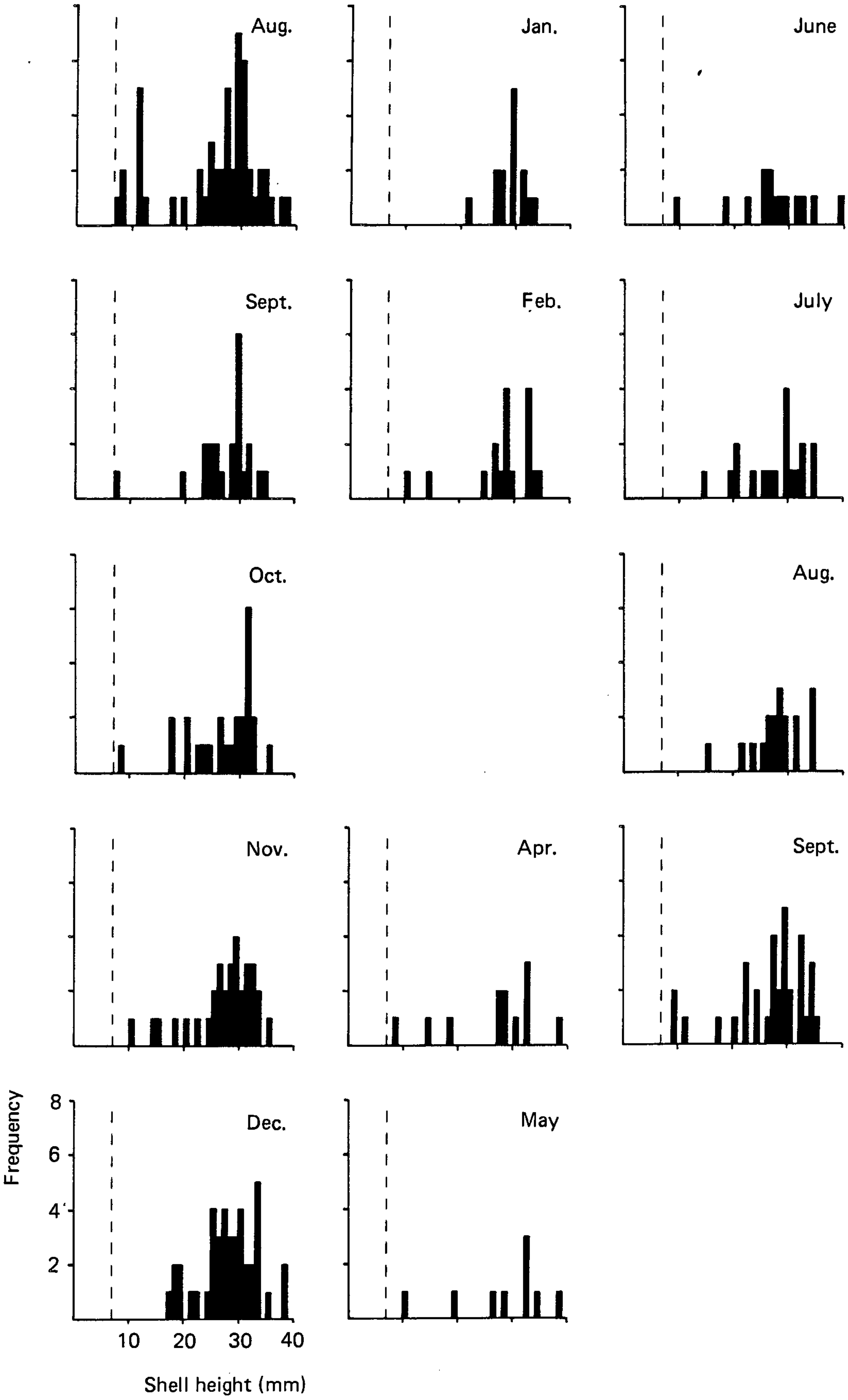

Aug.
Jan.
June
Sept.
Feb.
July
Oct.
Aug.
Nov.
Apr.
Sept.
Dec.
May
Frequency
8
6
4
2
10
20
30
40
Shell height (mm)

Fig. 13.7 Size frequency histograms for *Littoraria philippiana* on *Avicennia* trees at Cockle Bay, from October 1980 until October 1981. Broken line indicates minimum size at which individuals were recorded.

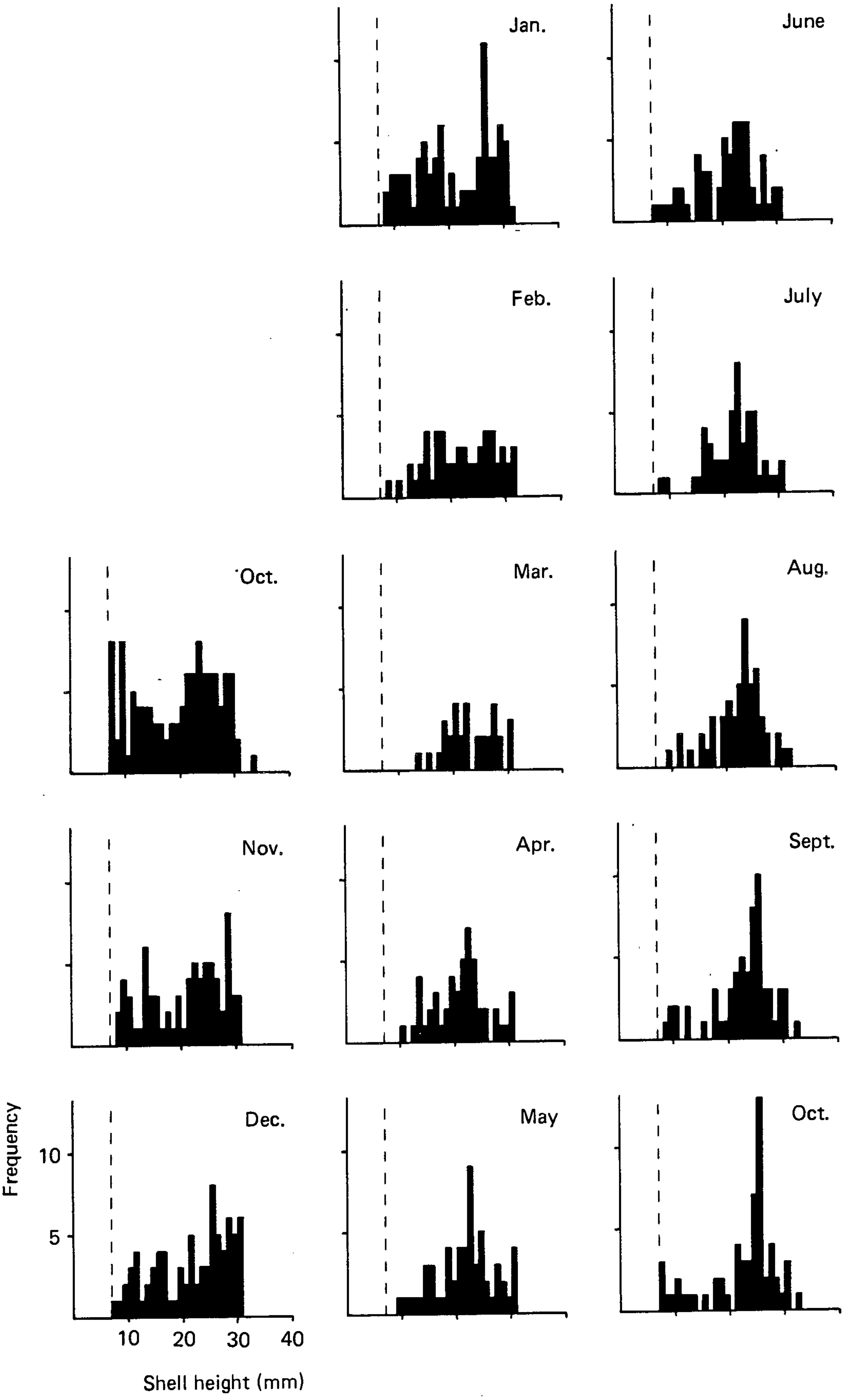
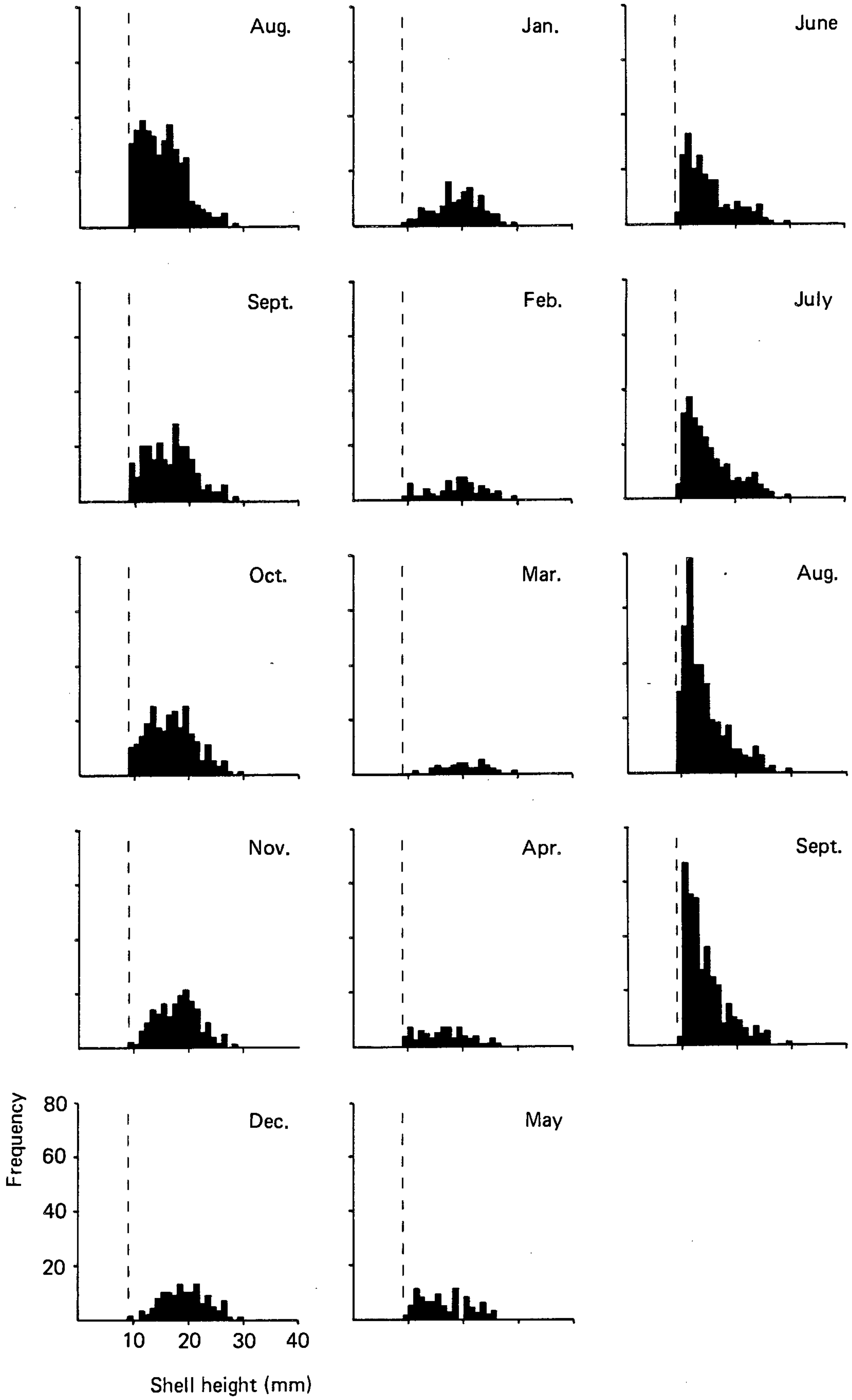

Jan.
June
Feb.
July
Oct.
Mar.
Aug.
Nov.
Apr.
Sept.
Dec.
May
Oct.
Frequency
10
5
10
20
30
40
Shell height (mm)

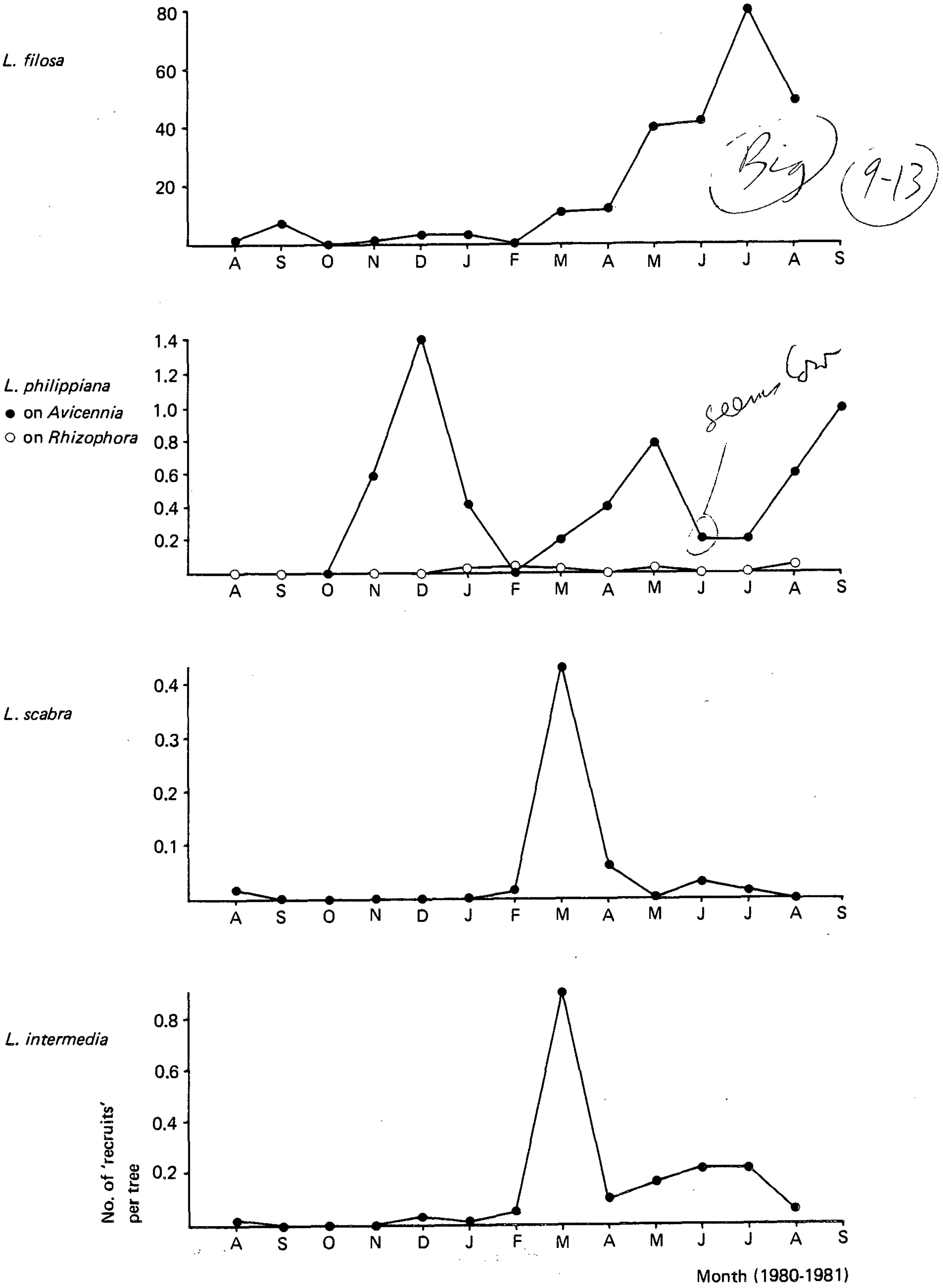
Fig. 13.8 Size frequency histograms for *Littoraria filosa* on *Avicennia* trees at Cockle Bay, from August 1980 until September 1981. Broken line indicates minimum size at which individuals were recorded.


Aug.
Jan.
June
Sept.
Feb.
July
Oct.
Mar.
Aug.
Nov.
Apr.
Sept.
Dec.
May
Frequency
80
60
40
20
10
20
30
40
Shell height (mm)

the beginning of the observation period, is obvious, with the juvenile cohort comprising those individuals less than 17.9 mm in height. The two cohorts had merged by December. Recruitment followed a pattern similar to that of *L. intermedia*, although not commencing until February (Fig. 13.9). Peak recruitment was recorded during March, following the peak spawning period in February and March (Fig. 13.2). As in *L. intermedia*, the bimodality of the adult cohort (especially evident from March until June) corresponds to the sexual dimorphism of *L. scabra*. Comparisons of the size frequency distributions for August and September of 1981 with those for the previous year (Fig. 13.5) show that recruitment to the population was more successful in 1981 than in 1980.

The pattern of the size frequency distributions of *L. philippiana* is less easy to interpret than those of the other species, in part because of the relatively small sample sizes. Size frequency distributions are presented separately for this species from *Avicennia* and *Rhizophora* trees (Figs 13.6, 13.7), because maximum shell size and recruitment patterns differed in the two habitats. Both populations showed overall bimodality on the first sampling occasion, with distinct juvenile and adult cohorts (juvenile cohort ≤22 mm on *Rhizophora* trees in August, ≤17.9 mm on *Avicennia* trees in October). Adults made up the predominant size group at almost all times of the year. Recruitment was negligible in the population on *Rhizophora* trees (Fig. 13.6). In the population on *Avicennia* trees recruitment was low and sporadic, with maxima during December, May and September (Fig. 13.6). By comparison with the size frequency distribution in October 1980, when juveniles were frequent, it appears that 1981 was a year of poor recruitment on the *Avicennia* trees. Since the spawning period of *L. philippiana* was largely confined to March and May (Section 13.3.1), a well defined period of recruitment would have been anticipated. The distinct juvenile cohort present in October 1980 was presumably derived from the spawning period earlier in the year (as supported by the observations on growth rates of juvenile snails, Section 13.3.3). The bimodality of the cohort evident until January perhaps reflects

Fig. 13.9 Seasonal patterns of estimated recruitment of four *Littoraria* species at Cockle Bay. 'Recruits' defined as new arrivals in the following size classes: *L. filosa* 9–13 mm; *L. philippiana* 7–11 mm; *L. scabra* and *L. intermedia* 4–8 mm. *L. filosa* recorded on *Avicennia* trees, *L. scabra* and *L. intermedia* on *Rhizophora* trees, *L. philippiana* on both tree species.



Big

9-13

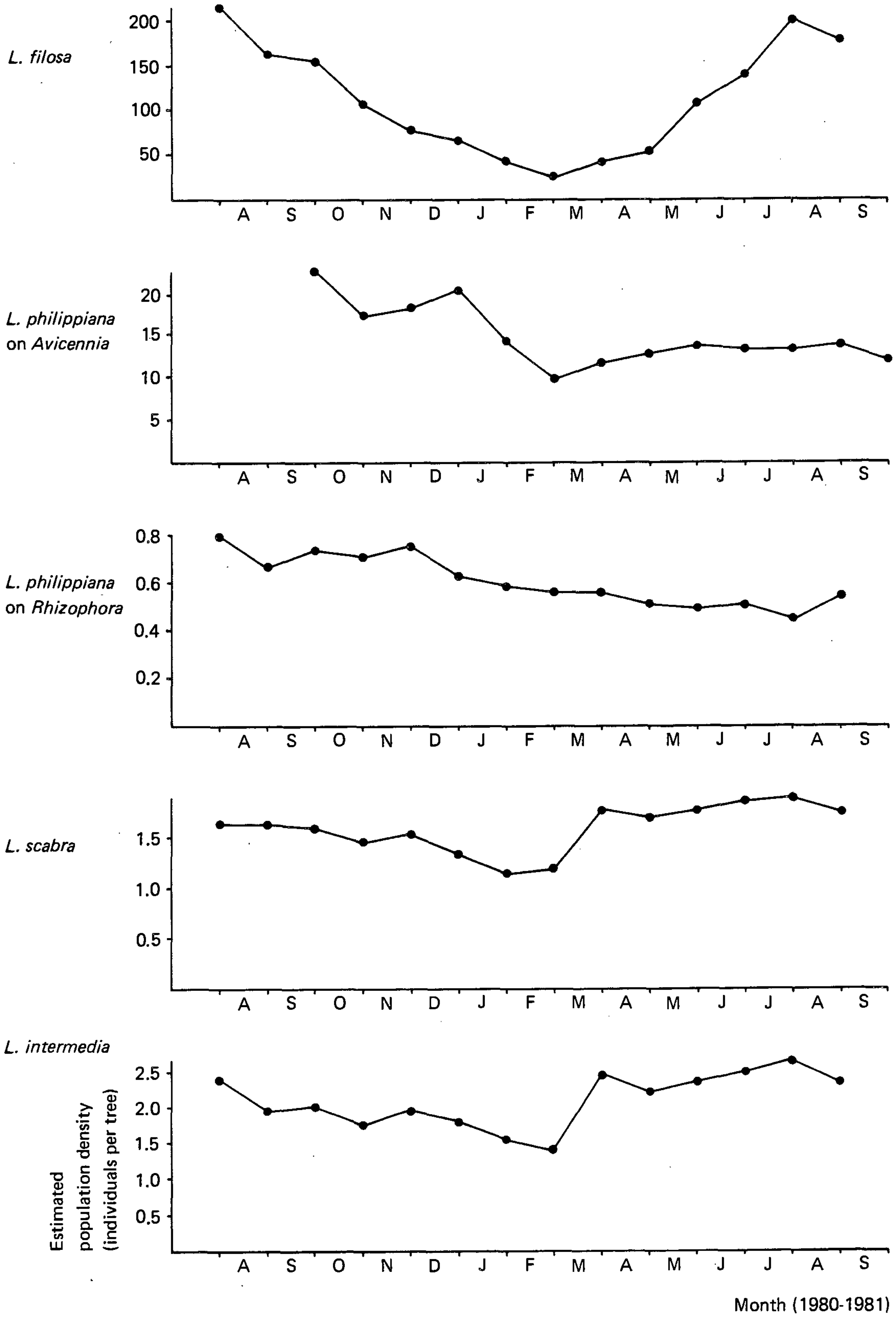
seems low

two episodes of spawning or recruitment. No such pattern was shown in 1981, although the periods of recruitment in May and September may possibly correspond with the spawning episodes in March and May. The greater interval of time between the two recruitment events may be explained by the slow growth rate of snails in the winter months (Section 13.3.3), which could have delayed the appearance of the recruits from the second spawning in the measured size range.

The size frequency distribution for *L. filosa* (Fig. 13.8) is quite different from those described above. As in the other species, the population showed a largely bimodal size distribution when first sampled (August 1980), with a distinct juvenile cohort (≤14.9 mm) and another of adults in their second or later years of life (Section 13.3.3). The two cohorts had merged by December, to produce a symmetrical size distribution, which persisted until May, after which recruits began to appear in large numbers. A small number of recruits were present at most times of the year (Fig. 13.9), with great numbers between May and August. Peak recruitment is believed to correspond with the restricted spawning season in February and March (Section 13.3.1), as supported by the measured growth rate of this species (Section 13.3.3). As in *L. philippiana*, the greater time span of the recruitment period may be explained by the slow winter growth rate (Section 13.3.3), so that snails settling earlier in the year reached the size at which they were measurable as recruits in a shorter time. As in the case of *L. scabra* and *L. intermedia*, 1981 appears to have been a more favourable year for recruitment than 1980.

The major difference noted in a comparison of *L. filosa* with the three other species (*L. intermedia, L. scabra, L. philippiana*) concerns the proportions of juveniles and adults present. At all times of the year the proportion of snails in the juvenile (first year) cohort was equal to or greater than in the adult (second and subsequent year) cohort. In contrast, the other three species showed a preponderance of adult snails for most of the year.

Fig. 13.10 Seasonal variation in estimated population density of four *Littoraria* species at Cockle Bay. Estimates include only those individuals larger than the following minimum sizes: *L. filosa* 9 mm, *L. philippiana* 7 mm, *L. scabra* and *L. intermedia* 4 mm. *L. filosa* recorded on *Avicennia* trees, *L. scabra* and *L. intermedia* on *Rhizophora* trees, *L. philippiana* on both tree species.


L. filosa
200
150
100
50
A S O N D J F M A M J J A S
L. philippiana on Avicennia
20
15
10
5
A S O N D J F M A M J J A S
L. philippiana on Rhizophora
0.8
0.6
0.4
0.2
A S O N D J F M A M J J A S
L. scabra
1.5
1.0
0.5
A S O N D J F M A M J J A S
L. intermedia
2.5
2.0
1.5
1.0
0.5
Estimated population density (individuals per tree)
A S O N D J F M A M J J A S
Month (1980-1981)

A second contrast between *L. filosa* and the other three species concerns the annual fluctuation in population size (Fig. 13.10). Data are presented as numbers of littorinids per tree, to give an indication of population density. *L. scabra* and *L. intermedia* followed an almost identical pattern of gradually declining numbers until recruitment increased the population size in April, the maximum population size exceeding the minimum by factors of 1.67 and 1.92 respectively. The corresponding factor in *L. filosa* was 9.30, the population declining at a very rapid rate following recruitment. Data are presented for 14 months only, but general observations over the following two years indicated that the patterns described were repeated each year. Owing to the low level of recruitment of *L. philippiana* in 1981, populations declined throughout the observation period on both *Avicennia* and *Rhizophora* trees.

The relative rates of decline of the population size in the four species during the period before significant recruitment reflects their respective rates of loss from the study areas. Loss rates were initially examined by following the decline of the two cohorts identified in each population on the first sampling occasion, as defined above. The animals believed to be in their first year of growth will be referred to as the juvenile cohort, and those in their second or subsequent years as the adult cohort. The survivorship curves thus constructed (Fig. 13.11) were approximately linear, permitting the calculation of instantaneous loss rates and average survivorships for the year (Table 13.5).

Comparison of the instantaneous loss rates of the juvenile and adult cohorts within each of the species *L. intermedia*, *L. scabra* and *L. philippiana* (on *Avicennia* trees) showed no significant differences (using t-tests to compare slopes). This suggests that survivorship was independent of age over the size range examined. In contrast, the instantaneous loss rate of the juvenile cohort of *L. filosa* was significantly greater than that of the adult cohort ($t = 0.319$, d.f. = 18, $P = 0.004$), the former with an average survivorship of only 55.8% per month (Table 13.5).

Fig. 13.11 Survivorship curves for 'juvenile' and 'adult' cohorts of four *Littoraria* species at Cockle Bay. Juvenile cohorts defined as those individuals in first year of growth when marked on first sampling date (see Figs 13.4 to 13.8); adult cohorts defined as those in second and subsequent years of growth. *L. filosa* recorded on *Avicennia* trees, *L. scabra* and *L. intermedia* on *Rhizophora* trees, *L. philippiana* on both tree species.

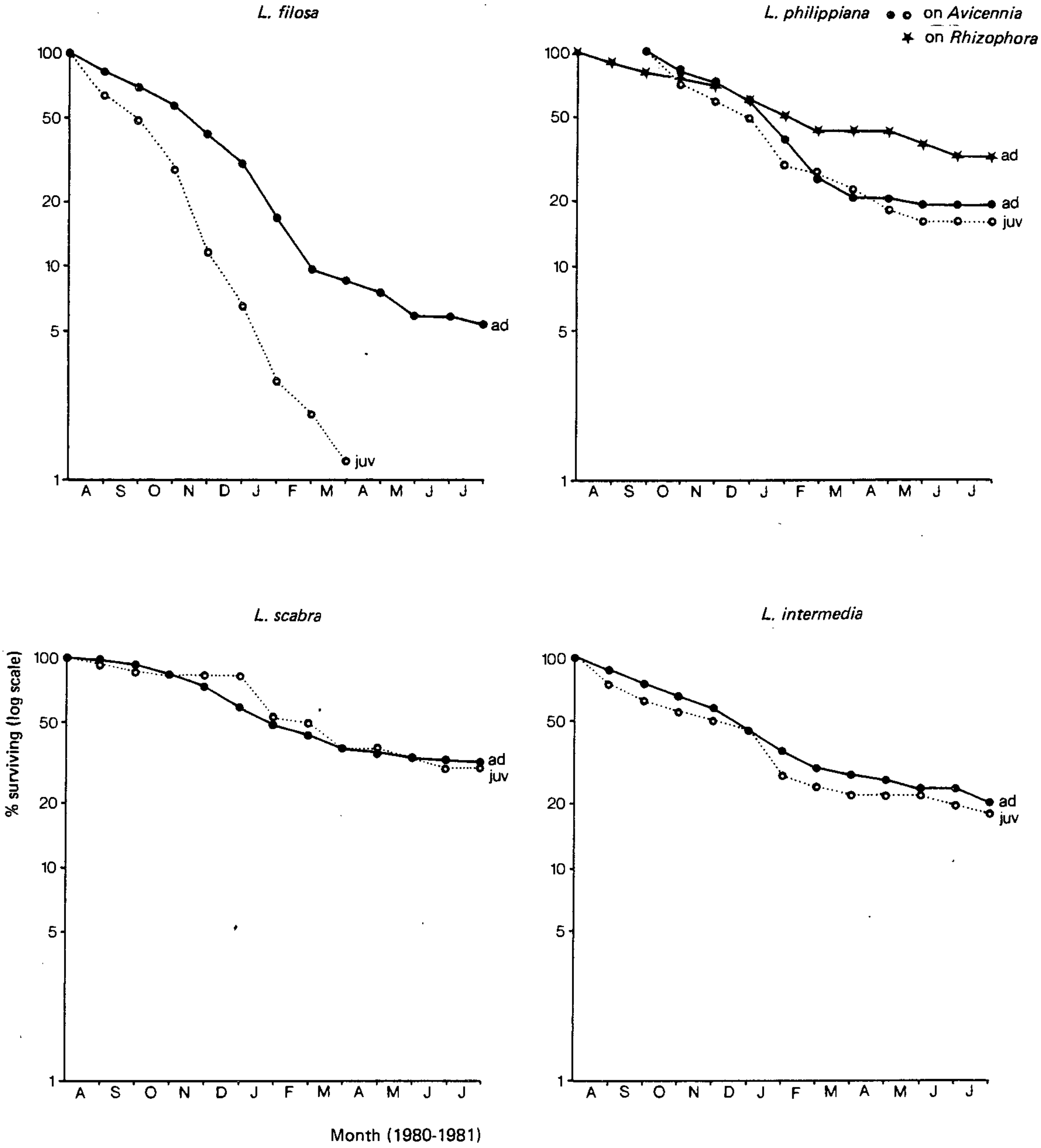

L. filosa
L. philippiana ● ○ on Avicennia
✶ on Rhizophora
L. scabra
L. intermedia
% surviving (log scale)
100
50
20
10
5
1
A S O N D J F M A M J J
ad
juv
Month (1980-1981)

Table 13.5 Survivorships and instantaneous loss rates for cohorts and size classes of four *Littoraria* species, averaged over the year of observations at Cockle Bay.

Species	Tree	Instantaneous loss rate (μ)[A] per month (±95% confidence limits)		Average survivorship per month (= $e^{-\mu t}$) (±95% confidence limits)		Mean survivorships of size classes per month[B] (with 95% confidence limits)			
		Juvenile	Adult	Juvenile	Adult	<12 mm	12-19 mm	19-26 mm	>26 mm
L. intermedia	*Rhizophora*	0.141 (±.026)	0.137 (±.017)	0.868 (±.022)	0.872 (±.015)	0.741 (.607-.853)	0.860 (.809-.902)	0.881 (.802-.942)	
L. scabra	*Rhizophora*	0.117 (±.020)	0.112 (±.016)	0.890 (±.018)	0.894 (±.014)	0.862 (.787-.924)	0.985 (.944-1.00)	0.924 (.861-.969)	0.884 (.812-.940)
L. philippiana	*Rhizophora*		0.098 (±.010)		0.907 (±.009)				0.802 (.678-.902)
L. philippiana	*Avicennia*	0.175 (±.039)	0.166 (±.047)	0.839 (±.032)	0.847 (±.039)	0.761 (.192-1.00)	0.761 (.673-.840)	0.816 (.727-.891)	0.841 (.631-.908)
L. filosa	*Avicennia*	0.583 (±.059)	0.279 (±.039)	0.558 (±.032)	0.757 (±.029)	0.524 (.357-.689)	0.568 (.474-.660)	0.742 (.656-.820)	

[A] slope of survivorship curves (Fig. 13.11); juvenile cohort = individuals in first year of growth on first sampling date; adult cohort = individuals in second or subsequent year of growth on first sampling date

[B] see Figs 13.12 to 13.16; statistics performed on arcsine transformed proportions; survivorships for the last month of observation excluded from calculations (see text)

Making comparisons between species in the same habitat, in the *Rhizophora* forest the adult cohorts of *L. philippiana*, *L. scabra* and *L. intermedia* showed average survivorships of 90.7%, 89.4% and 87.2% per month respectively. There was no overall difference amongst the slopes of their respective survivorship curves (F = 1.128, d.f. = 2,33, P = 0.336). When the two cohorts of *L. scabra* and *L. intermedia* were combined, the difference between the survivorship curves of the two species was shown to be significant (t = 6.383, d.f. = 48, P = 0.015). Of the two species studied on *Avicennia* trees, adults of *L. philippiana* showed an average survivorship of 84.7% per month, significantly greater than the 75.7% of adult *L. filosa* (comparing slopes of survivorship curves, t = 4.120, d.f. = 19, P = 0.0006). Comparison of a species in the two habitats was possible in the case of *L. philippiana*, with an average adult survivorship of 90.7% per month on *Rhizophora* trees, which was significantly greater than the 84.7% on *Avicennia* trees (t = 3.394, d.f. = 19, P = 0.003). Survivorships of both *L. filosa* and *L. philippiana* on *Avicennia* trees were significantly lower than of each of the three species on *Rhizophora* trees, with the exception of the comparison between *L. philippiana* on *Avicennia* and *L. intermedia* on *Rhizophora*, which showed no significant difference.

The loss of marked snails cannot be ascribed entirely to natural mortality. The apparent loss of snails may have included individuals which emigrated from the study area, and those from which the number marks became detached. In an attempt to estimate the significance of these effects, the unmarked snails collected for numbering at each visit which were too large to be defined as 'recruits' were recorded as a percentage of the estimated population size (Table 13.4). These individuals probably included immigrants and those from which the numbers had been lost (as well as individuals present but not found on previous marking occasions). At each visit, snails with loose or flaking marks were collected for renumbering. An indication of the relative permanence of the marks on each species is provided by the percentage of the total number marked on which the numbers were renewed (Table 13.4).

If it can be assumed that the numbers of immigrant and emigrant snails were the same, then the percentage of unmarked snails larger than 'recruits' at each visit will represent the percentage which must be subtracted from the total loss to estimate the mortality rate. Since the percentage of unmarked snails showed considerable fluctuation from month to month, this correction cannot be applied on a monthly basis. A comparison of the monthly percentages of unmarked snails in each of the five populations (Table 13.4) by a one-way analysis of variance, showed that the differences were not quite significant ($F = 2.251$, d.f. $= 4,59$, $P = 0.074$; analysis performed on arcsine transformed percentages), suggesting that the combined effects of emigration and number loss on the apparent rate of loss were similar in all species. When comparisons were made within habitats, the differences were less significant (for 2 species on *Avicennia*: $t = 1.732$, d.f. $= 23$, $P = 0.201$; for 3 species on *Rhizophora*: $F = 0.311$, d.f. $= 2,36$, $P = 0.735$). The proportion of the total apparent loss (= 100% minus the average survivorship, Table 13.5) which can be ascribed to emigration and loss of number marks, can be estimated by expressing the mean percentage of unmarked snails larger than 'recruits' as a percentage of the total apparent loss. For each species, this proportion was close to one half: *L. intermedia* 51%, *L. scabra* 67%, *L. philippiana* on *Rhizophora* 66%, on *Avicennia* 59%, *L. filosa* 57%. The remaining proportion can be ascribed to mortality, which therefore accounted for about one half of the total apparent loss of each species. Since this proportion is similar in each species, their relative loss rates will reflect their relative mortality rates.

Snails were not seen to crawl over the mud substrate between the trees (Section 12.3.5), and might have been expected to migrate between trees only where roots or branches were in contact. It was therefore surprising that the populations of *L. filosa* and *L. philippiana* on the *Avicennia* trees, completely isolated from direct contact with other trees, showed the highest proportions of unmarked snails larger than 'recruits'. In contrast, the study area in the *Rhizophora* forest was in direct contact with adjacent parts of the forest, permitting direct migration to and from the area. The high proportion of unmarked snails on *Avicennia* trees cannot be explained by loss of number marks, since the percentages of renumbered snails were lowest in this habitat (Table 13.4), nor can it be explained by a low probability of capture (Table 13.4). One remaining possibility is the migration of *L. filosa* and *L. philippiana* between trees, by rafting upon leaves or (in the case of the thin shelled *L. filosa*) by direct flotation. These means of transport may be more frequent than might have been supposed (see also Section 14.3.1).

It may be noted that the marking procedure did not appear to have influenced mortality, since the slopes of the survivorship curves for the first monthly interval following marking were not obviously more steep than for subsequent intervals (Fig. 13.11).

Although the survivorship curves (Fig. 13.11) were close to linear, it can be seen that they declined most steeply over the summer months, and especially during January, indicating greater rates of loss at these times. The graphs of monthly survivorship of size groups (Figs 13.12 to 13.16) allow a closer examination of the effects of season and size on loss rates. The distribution of values shows considerable fluctuation, and these data are not suitable for statistical analysis (Section 13.2.2). Nevertheless, some general trends can be distinguished. The mean survivorships of the largest size classes of each species correspond closely with the average figures calculated from the survivorship curves of the adult cohorts over the year (Table 13.5). The lowest values were for *L. filosa*. All species except *L. scabra* showed a pattern of increasing survivorship with increasing shell size, while for *L. scabra* survivorship was greatest at intermediate sizes. (The means summarized in Table 13.5 are not all strictly comparable, since the smaller size classes were absent in some summer months, as indicated in Figs 13.12 to 13.16). The most striking trend is the pattern of reduced survivorship in the summer period, shown by all size classes of each species. This period was of longest duration in *L. filosa* (Fig. 13.16). The majority of size classes showed a large drop in

Fig. 13.12 Seasonal variation in monthly survivorships of size classes of *Littoraria intermedia* on *Rhizophora* trees at Cockle Bay.

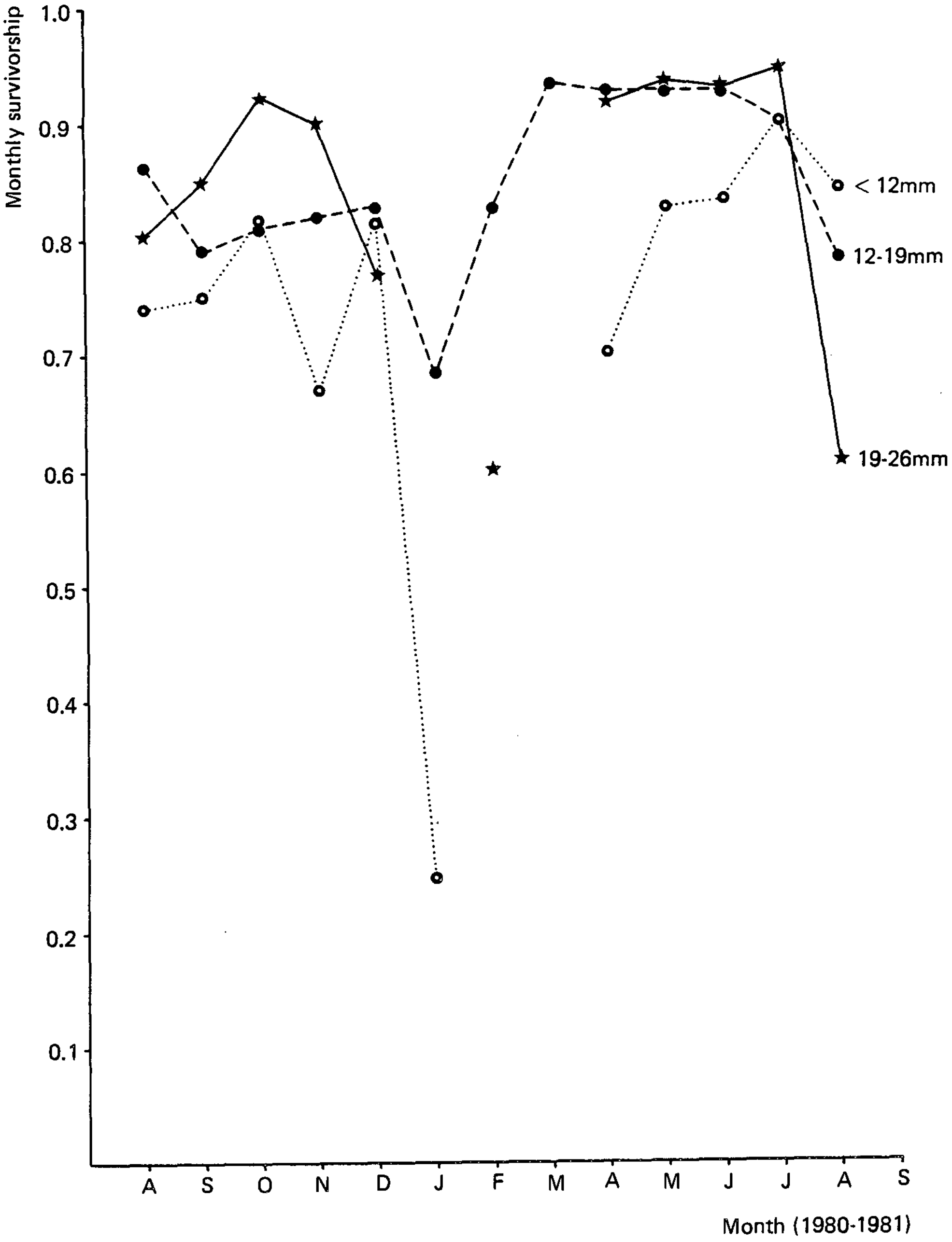

Monthly survivorship
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month (1980-1981)
< 12mm
12-19mm
19-26mm

Fig. 13.13 Seasonal variation in monthly survivorships of size classes of *Littoraria scabra* on *Rhizophora* trees at Cockle Bay.

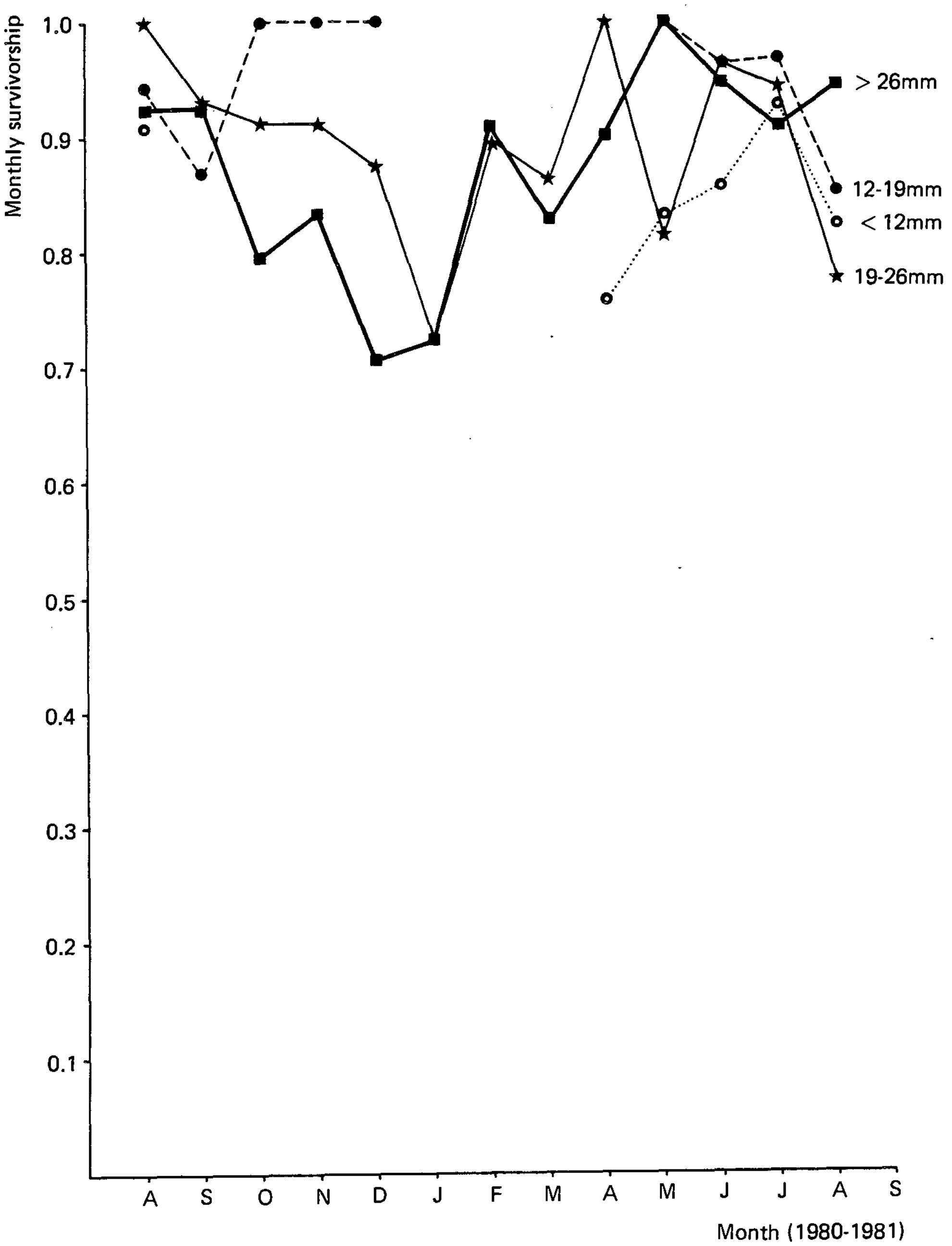

Monthly survivorship
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month (1980-1981)
> 26mm
12-19mm
< 12mm
19-26mm

Fig. 13.14 Seasonal variation in monthly survivorship of one size class of *Littoraria philippiana* on *Rhizophora* trees at Cockle Bay.

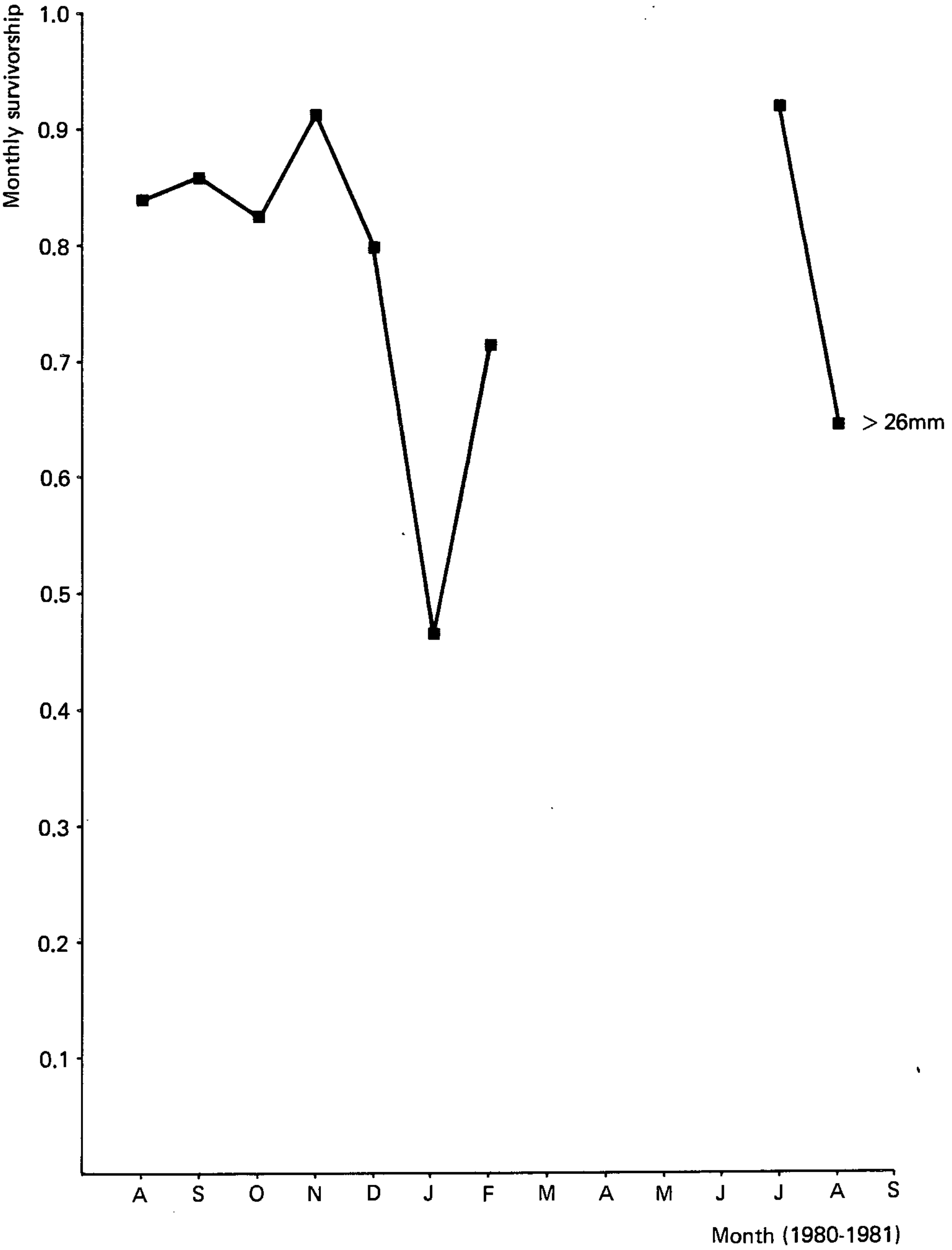

Monthly survivorship
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
> 26mm
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month (1980-1981)

Fig. 13.15 Seasonal variation in monthly survivorships of size classes of *Littoraria philippiana* on *Avicennia* trees at Cockle Bay.

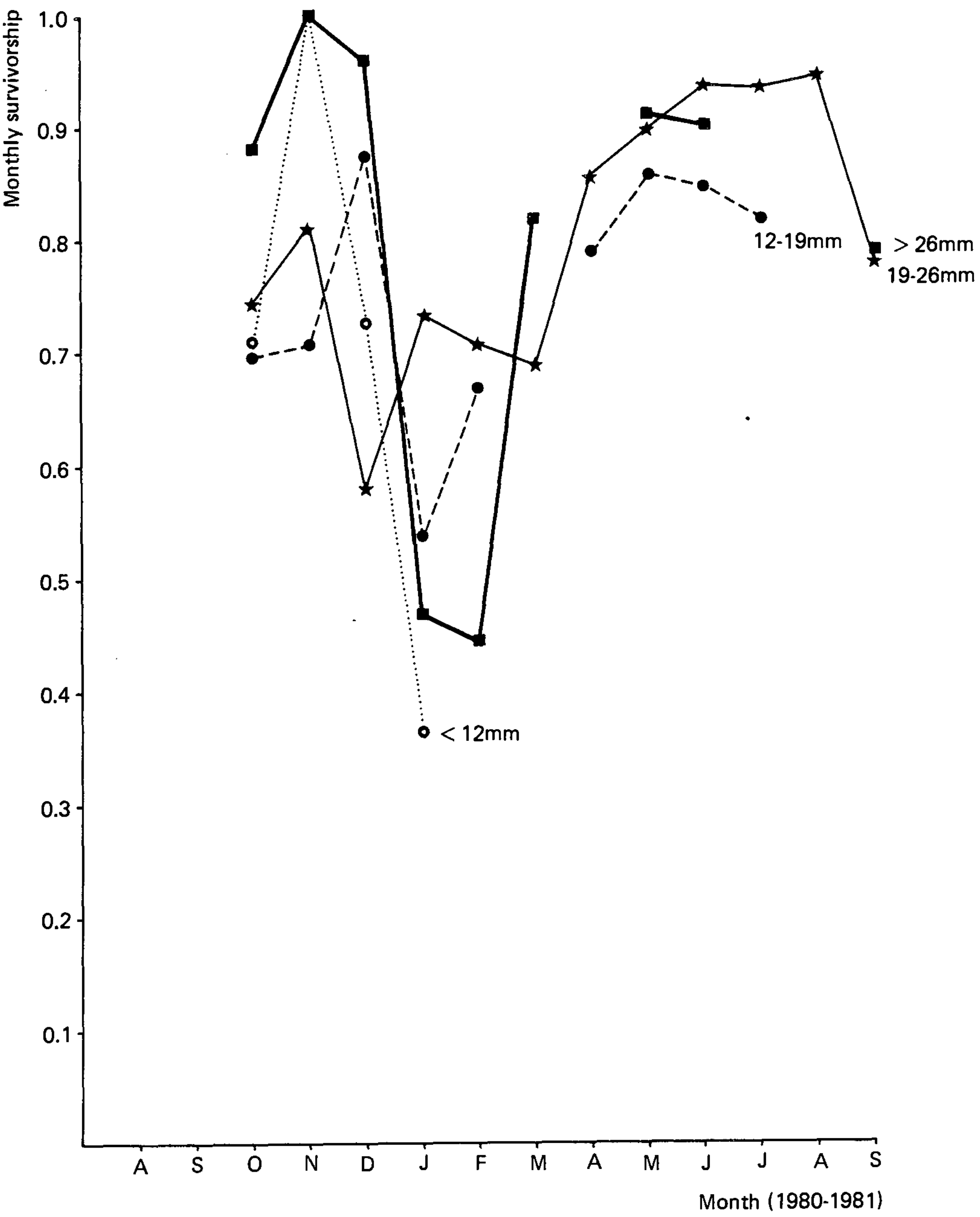

Monthly survivorship
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month (1980-1981)
12-19mm
> 26mm
19-26mm
< 12mm

Fig. 13.16 Seasonal variation in monthly survivorships of size classes of *Littoraria filosa* on *Avicennia* trees at Cockle Bay.

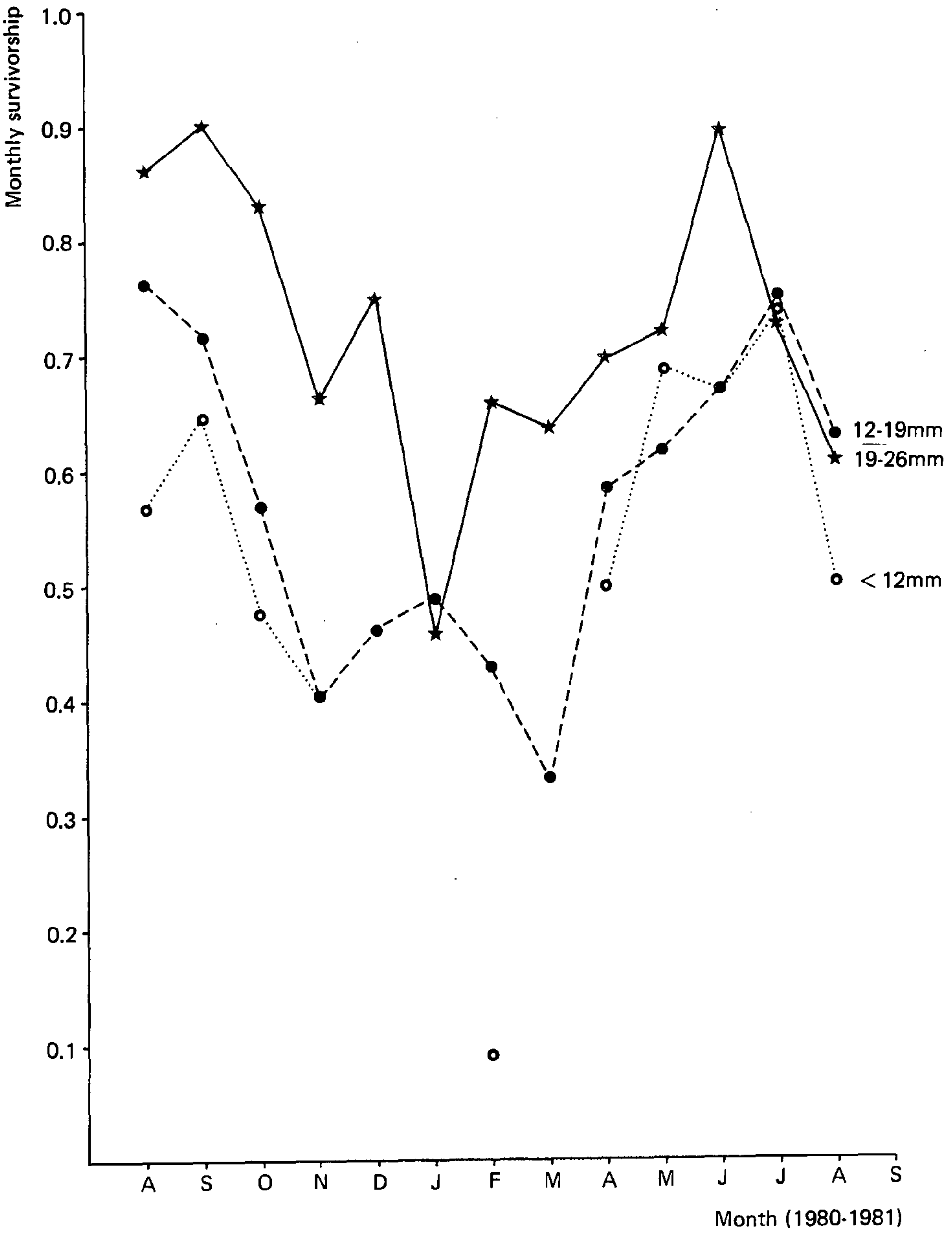
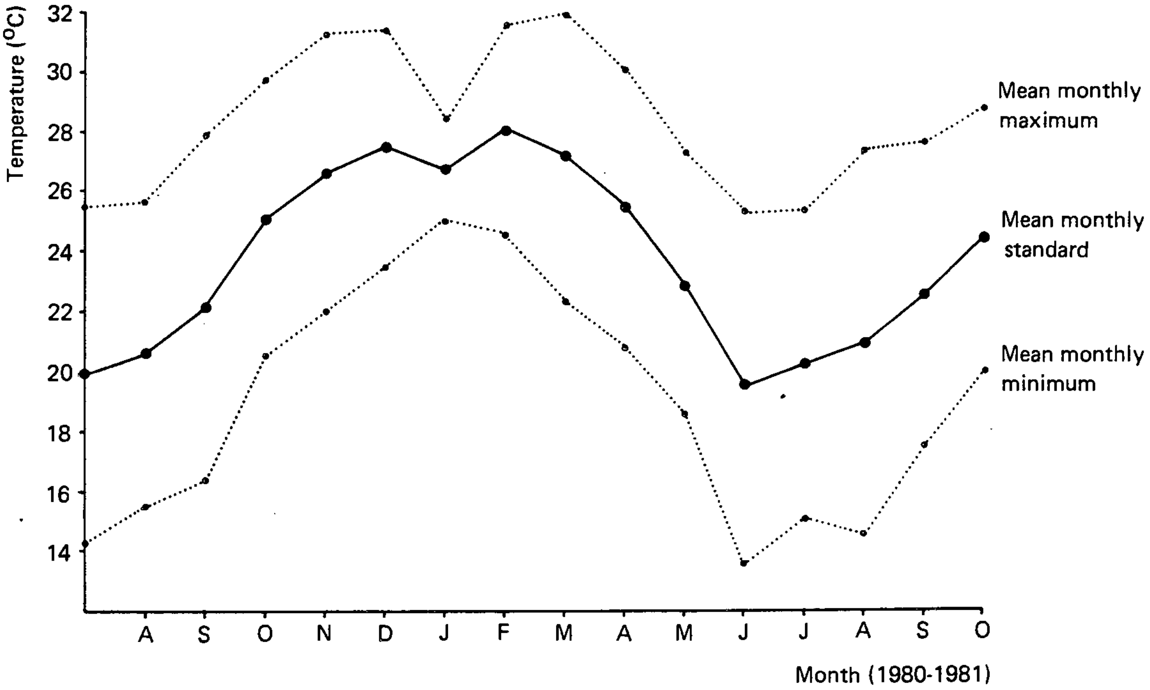
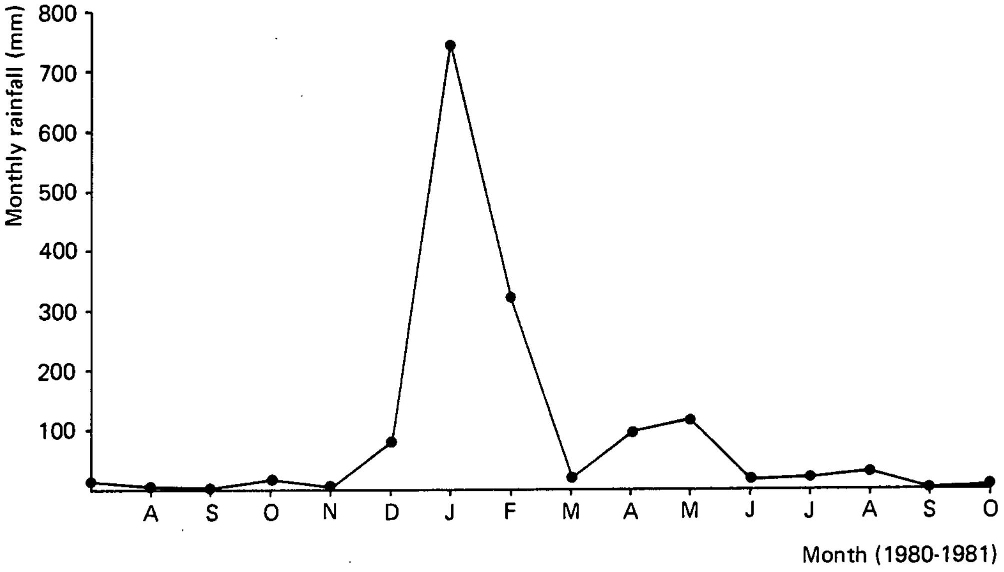

Monthly survivorship
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month (1980-1981)
● 12-19mm
★ 19-26mm
○ < 12mm

Fig. 13.17 Monthly temperature and rainfall for the period July 1980 until October 1981, recorded by Bureau of Meteorology at Townsville airport, 12 km from Cockle Bay.


Temperature (°C)
32
30
28
26
24
22
20
18
16
14
Mean monthly maximum
Mean monthly standard
Mean monthly minimum
A S O N D J F M A M J J A S O
Month (1980-1981)


Monthly rainfall (mm)
800
700
600
500
400
300
200
100
A S O N D J F M A M J J A S O
Month (1980-1981)

survivorship in January 1981, corresponding with a period of exceptionally high rainfall (Fig. 13.17). The drop in survivorship at the end of the study period is believed to be an artefact; since the probability of capture was less than 100% (Table 13.4), some of the missing individuals must have been overlooked and would have been recovered if observations had continued.

13.3.3 Growth

The treatment of the measured growth increments of individually numbered snails, and the derivation of growth curves for the four *Littoraria* species (*L. intermedia*, *L. scabra*, *L. philippiana*, *L. filosa*) are described in Section 13.2.3.

The majority of the curves fitted to the regressions of growth increment on shell height (Tables 13.6 to 13.9) were straight lines or even upward-opening parabolas. However, when the size range included sufficient numbers of the smaller individuals, the fitted curves were shallow downward-opening parabolas, with maxima at between one third and one half of the maximum size attained. The correlation between the shape of the fitted curve and the presence of small snails in the sample is particularly clear in *L. scabra* (Table 13.7) and *L. filosa* (Table 13.9).

To assess the possible short-term effect of the marking procedure upon growth rate, growth increments of newly-marked snails were compared with increments over the same period shown by snails marked one month previously. Adequate samples of snails in a restricted size range, marked in consecutive months, were required for this comparison. Suitable data were available only for *L. intermedia* and *L. filosa*, in each case over the month of July 1981. For *L. intermedia* the size range chosen was 7 to 11 mm. While the slopes of the regressions of increment on initial size were not significantly

Table 13.6 Functions relating monthly growth increment to initial size in *Littoraria intermedia* on *Rhizophora* trees at Cockle Bay, from August 1980 to August 1981. The coefficients tabulated are for the equation $y = aH^2 + bH + c$, where y = monthly increment in shell height; H = shell height at beginning of month.

Sex	Month	Range of H (mm)	Coefficient of H^2 (±S.E.)	Coefficient of H (±S.E.)	Constant (±S.E.)	r^2	F	d.f.	P
Male	Aug.	6-19	+0.0081 (±.0033)	-0.2798 (±.0870)	+2.5936 (±.5517)	0.522	22.4	2,41	<.0001 **
	Sept.	6-19	-0.0053 (±.0010)		+1.3504 (±.1830)	0.598	31.2	1,21	<.0001 **
	Oct.	8-18		-0.1366 (±.0196)	+2.2291 (±.2620)	0.634	48.4	1,28	<.0001 **
	Nov.	9-19		-0.2419 (±.0368)	+3.7230 (±.4843)	0.684	43.2	1,20	<.0001 **
	Dec.	10-18		-0.2605 (±.0608)	+4.3204 (±.8480)	0.433	18.4	1,24	.0003 **
	Jan.	9-18		-0.0393 (±.0380)	+0.9994 (±.6069)	0.082	1.1	1,12	.3211
	Feb.	10-19	+0.0293 (±.0093)	-1.0010 (±.2645)	+8.6014 (±1.873)	0.798	23.7	2,12	.0001 **
	Mar.	6-20	+0.0211 (±.0044)	-0.7176 (±.0999)	+6.1746 (±.5129)	0.969	218.5	2,14	<.0001 **
	Apr.	4-20	-0.0227 (±.0063)	+0.2947 (±.1328)	+0.9367 (±.5874)	0.843	80.7	2,30	<.0001 **
	May	6-19	-0.0078 (±.0008)		+2.1653 (±.1283)	0.743	104.2	1,36	<.0001 **
	June	6-19		-0.1110 (±.0114)	+1.8812 (±.1358)	0.698	94.9	1,41	<.0001 **
	July	6-19		-0.1246 (±.0093)	+2.2051 (±.1137)	0.766	179.7	1,55	<.0001 **
	Aug.	6-19	+0.0073 (±.0027)	-0.3064 (±.0681)	+3.2080 (±.4049)	0.783	111.7	2,62	<.0001 **
Female	Aug.	6-24		-0.0917 (±.0107)	+1.9160 (±.1691)	0.702	73.1	1,31	<.0001 **
	Sept.	9-24		-0.0492 (±.0122)	+1.1711 (±.2210)	0.475	16.3	1,18	.0008 **
	Oct.	8-23		-0.1308 (±.0230	+2.6447 (±.3557)	0.584	32.3	1,23	<.0001 **
	Nov.	9-21		-0.0944 (±.0178)	+1.9109 (±.2975)	0.560	28.0	1,22	<.0001 **
	Dec.	10-23		-0.1811 (±.0307)	+3.8150 (±.4975)	0.572	34.8	1,26	<.0001 **
	Jan.	9-23		-0.1477 (±.0323)	+3.3220 (±.5515)	0.466	21.0	1,24	.0001 **
	Feb.	10-21		-0.1657 (±.0283)	+3.3707 (±.4762)	0.569	34.4	1,26	<.0001 **
	Mar.	14-20		-0.1322 (±.0447)	+2.5564 (±.7484)	0.340	8.8	1,17	.0088 **
	Apr.	4-23		-0.1320 (±.0147)	+2.7189 (±.2198)	0.668	80.4	1,40	<.0001 **
	May	6-23		-0.1441 (±.0125)	+2.9863 (±.1986)	0.783	133.2	1,37	<.0001 **
	June	7-23		-0.0937 (±.0096)	+1.9362 (±.1505)	0.711	95.8	1,39	<.0001 **
	July	6-23	-0.0032 (±.0003)		+1.4309 (±.0849)	0.692	112.5	1,50	<.0001 **
	Aug.	6-23		-0.1128 (±.0091)	+2.3562 (±.1348)	0.744	154.2	1,53	<.0001 **

Table 13.7 Functions relating monthly growth increment to initial size in *Littoraria scabra* on *Rhizophora* trees at Cockle Bay, from August 1980 to August 1981. The coefficients tabulated are for the equation $y = aH^2 + bH + c$, where y = monthly increment in shell height; H = shell height at beginning of month.

Sex	Month	Range of H (mm)	Coefficient of H^2 (±S.E.)	Coefficient of H (±S.E.)	Constant (±S.E.)	r^2	F	d.f.	P
Male	Aug.	9–33	+0.0046 (±.0013)	–0.2556 (±.0549)	+3.6850 (±.5662)	0.513	44.2	2,41	<.0001 **
	Sept.	10–32	+0.0056 (±.0024)	–0.3303 (±.0995)	+4.9102 (±.9947)	0.690	31.1	2,28	<.0001 **
	Oct.	11–34		–0.1878 (±.0193)	+4.7881 (±.3994)	0.812	95.0	1,22	<.0001 **
	Nov.	14–34		–0.1819 (±.0220)	+4.8952 (±.5033)	0.694	68.1	1,30	<.0001 **
	Dec.	11–33		–0.2183 (±.0258)	+5.9728 (±.5979)	0.691	71.6	1,32	<.0001 **
	Jan.	20–33		–0.0477 (±.0218)	+1.4633 (±.5464)	0.167	4.8	1,24	.0382 *
	Feb.	11–32		–0.2406 (±.0284)	+6.1251 (±.6396)	0.782	71.8	1,20	<.0001 **
	Mar.	10–32		–0.2371 (±.0143)	+5.8483 (±.3070)	0.942	274.7	1,17	<.0001 **
	Apr.	4–32	–0.0057 (±.0006)		+3.5100 (±.2494)	0.716	80.5	1,32	<.0001 **
	May	6–31	–0.0045 (±.0005)		+3.0810 (±.2316)	0.721	69.7	1,27	<.0001 **
	June	8–31	–0.0028 (±.0004)		+1.7462 (±.1667)	0.610	43.9	1,28	<.0001 **
	July	7–30	–0.0108 (±.0030)	+0.2759 (±.1039)	–0.2828 (±.8412)	0.688	39.7	2,36	<.0001 **
	Aug.	8–30	–0.0032 (±.0004)		+1.9501 (±.1512)	0.659	79.1	1,41	<.0001 **
Female	Aug.	6–34		–0.0553 (±.0091)	+1.7555 (±.2222)	0.578	37.0	1,27	<.0001 **
	Sept.	8–35		–0.1298 (±.0199)	+3.6968 (±.4549)	0.681	42.6	1,20	<.0001 **
	Oct.	11–38	–0.0036 (±.0007)		+2.9932 (±.3692)	0.562	25.6	1,20	.0001 **
	Nov.	13–38	–0.0048 (±.0009)		+4.2575 (±.4987)	0.588	27.1	1,19	.0001 **
	Dec.	15–38		–0.2461 (±.0353)	+7.5878 (±.8456)	0.698	48.6	1,21	<.0001 **
	Jan.	19–38		–0.1146 (±.0529)	+3.6634 (±1.357)	0.266	4.7	1,13	.0492 *
	Feb.	10–38	+0.0083 (±.0026)	–0.5341 (±.1057)	+8.7810 (±1.018)	0.937	74.7	2,10	<.0001 **
	Mar.	10–35	–0.0055 (±.0010)		+4.8251 (±.7221)	0.768	29.8	1,9	.0004 **
	Apr.	5–35	–0.0047 (±.0007)		+3.9809 (±.3479)	0.676	46.0	1,22	<.0001 **
	May	6–35	–0.0037 (±.0005)		+3.1432 (±.2551)	0.679	48.8	1,23	<.0001 **
	June	9–35	–0.0023 (±.0005)		+1.8830 (±.2333)	0.433	19.8	1,26	.0001 **
	July	6–35	–0.0024 (±.0003)		+2.0787 (±.1754)	0.590	48.9	1,34	<.0001 **
	Aug.	8–35		–0.0919 (±.0129)	+2.7572 (+.2789)	0.585	50.8	1,36	<.0001 **

Table 13.8 Functions relating monthly growth increment to initial size in *Littoraria philippiana* on *Avicennia* trees at Cockle Bay, from October 1980 to September 1981. The coefficients tabulated are for the equation $y = aH^2 + bH + c$, where y = monthly increment in shell height; H = shell height at beginning of month.

Sex	Month	Range of H (mm)	Coefficient of H^2 (±S.E.)	Coefficient of H (±S.E.)	Constant (±S.E.)	r^2	F	d.f.	P
Male	Oct.	7–30	−0.0011 (±.0003)		+0.9834 (±.1356)	0.370	17.6	1,30	.0002 **
	Nov.	8–30		−0.0457 (±.0156)	+1.7485 (±.3568)	0.324	8.6	1,18	.0088 **
	Dec.	9–30		−0.1103 (±.0180)	+3.6259 (±.4508)	0.743	37.5	1,13	<.0001 **
	Jan.	10–31	+0.0152 (±.0025)	−0.7905 (±.1037)	+10.282 (±.9799)	0.943	99.8	2,12	<.0001 **
	Feb.	11–27	−0.0059 (±.0012)		+3.9280 (±.6269)	0.771	23.6	1,7	.0018 **
	Mar.	13–29	+0.0272 (±.0076)	−1.4192 (±.3209)	+18.500 (±3.260)	0.953	30.4	2,3	.0102 *
	Apr.	13–29	−0.0042 (±.0015)		+2.9240 (±.6999)	0.390	7.7	1,12	.0170 *
	May	12–29		−0.2083 (±.0372)	+5.1424 (±.7893)	0.777	31.4	1,9	.0003 **
	June	8–27		−0.1247 (±.0485)	+3.3920 (±1.014)	0.398	6.6	1,10	.0279 *
	July	16–27		−0.0844 (±.0642)	+2.5369 (±1.397)	0.178	1.7	1,8	.2247
	Aug.	13–27	−0.0021 (±.0005)		+1.7315 (±.2598)	0.537	16.2	1,14	.0013 **
	Sept.	8–29		−0.0229 (±.0163)	+0.8999 (±.3378)	0.094	2.0	1,19	.1756
Female	Oct.	7–30		−0.0251 (±.0086)	+1.1601 (±.1776)	0.175	8.5	1,40	.0059 **
	Nov.	8–31	−0.0010 (±.0003)		+1.3046 (±.1672)	0.253	11.2	1,33	.0021 **
	Dec.	7–31	−0.0029 (±.0004)		+2.7178 (±.2052)	0.692	67.6	1,30	<.0001 **
	Jan.	9–31	+0.0113 (±.0043)	−0.6005 (±.1649)	+8.3241 (±1.490)	0.757	28.1	2,18	<.0001 **
	Feb.	13–31		−0.1473 (±.0410)	+4.3135 (±.9344)	0.498	12.9	1,13	.0033 **
	Mar.	16–31		−0.0905 (±.0389)	+2.4941 (±.9251)	0.294	5.4	1,13	.0366 *
	Apr.	13–31	+0.0202 (±.0087)	−1.0204 (±.3479)	+13.069 (±3.388)	0.662	17.6	2,18	.0001 **
	May	10–31		−0.2543 (±.0391)	+6.2540 (±.7998)	0.658	42.3	1,22	<.0001 **
	June	15–31		−0.1455 (±.0283)	+3.8950 (±.6150)	0.535	26.5	1,23	<.0001 **
	July	14–31	−0.0011 (±.0005)		+1.4445 (±.2595)	0.194	6.0	1,25	.0217 *
	Aug.	16–31		−0.0341 (±.0176)	+1.6193 (±.4212)	0.134	3.7	1,24	.0655
	Sept.	12–32	−0.0013 (±.0004)		+1.4011 (±.2914)	0.290	9.0	1,22	.0066 **

Table 13.9 Functions relating monthly growth increment to initial size in *Littoraria filosa* on *Avicennia* trees at Cockle Bay, from August 1980 to August 1981. The coefficients tabulated are for the equation $y = aH^2 + bH + c$, where y = monthly increment in shell height; H = shell height at beginning of month.

Sex	Month	Range of H (mm)	Coefficient of H^2 (±S.E.)	Coefficient of H (±S.E.)	Constant (±S.E.)	r^2	F	d.f.	P
Male	Aug.	7-23	-0.0053 (±.0015)	+0.1456 (±.0440)	-0.4041 (±.3134)	0.111	7.6	2,122	.0007 **
	Sept.	8-24	-0.0014 (±.0003)		+1.0519 (±.0857)	0.193	20.8	1,87	<.0001 **
	Oct.	7-24	-0.0015 (±.0003)		+0.9530 (±.0918)	0.284	29.0	1,73	<.0001 **
	Nov.	13-25		-0.0422 (±.0114)	+0.8749 (±.2164)	0.229	13.6	1,46	.0006 **
	Dec.	11-25	+0.0074 (±.0074)	-0.3467 (±.1343)	+4.1026 (±1.294)	0.430	11.0	2,29	.0003 **
	Jan.	10-25	-0.0012 (±.0004)		+0.7820 (±.1716)	0.244	7.1	1,22	.0142 *
	Feb.	10-25		-0.0678 (±.0207)	+1.6909 (±.4247)	0.519	10.8	1,10	.0082 **
	Mar.	11-25		-0.3051 (±.0841)	+7.4024 (±1.680)	0.814	13.2	1,3	.0360 *
	Apr.	9-25		-0.2078 (±.0398)	+5.4058 (±.7277)	0.695	27.3	1,12	.0002 **
	May	10-25		-0.2847 (±.0358)	+6.8629 (±.6284)	0.725	63.3	1,24	<.0001 **
	June	9-25	-0.0031 (±.0004)		+2.0805 (±.1193)	0.501	61.3	1,61	<.0001 **
	July	9-25	-0.0107 (±.0031)	+0.2985 (±.1048)	-0.8094 (±.8402)	0.331	17.8	2,72	<.0001 **
	Aug.	9-25	-0.0085 (±.0018)	+0.2519 (±.0593)	-0.9523 (±.4536)	0.231	14.7	2,98	<.0001 **
Female	Aug.	7-29	-0.0050 (±.0012)	+0.1430 (±.0415)	-0.1918 (±.3387)	0.279	19.0	2,98	<.0001 **
	Sept.	9-29	-0.0015 (±.0002)		+1.2165 (±.0950)	0.353	34.9	1,64	<.0001 **
	Oct.	9-29	-0.0026 (±.0003)		+1.7314 (±.1092)	0.553	81.6	1,66	<.0001 **
	Nov.	10-29		-0.0564 (±.0115)	+1.3652 (±.2386)	0.414	24.0	1,34	<.0001 **
	Dec.	10-29	+0.0105 (±.0014)	-0.5115 (±.0563)	+6.1297 (±.5534)	0.841	95.1	2,36	<.0001 **
	Jan.	11-29	+0.0102 (±.0044)	-0.4912 (±.1772)	+5.9060 (±1.758)	0.507	11.3	2,22	.0004 **
	Feb.	15-29		-0.0298 (±.0119)	+0.7747 (±.2628)	0.309	6.3	1,14	.0254 *
	Mar.	18-25		-0.1488 (±.0702)	+3.7371 (±1.529)	0.692	4.5	1,2	.1682
	Apr.	10-25	-0.0069 (.0012)		+4.5879 (±.4068)	0.635	33.1	1,19	<.0001 **
	May	10-26		-0.2632 (±.0424)	+6.8226 (±.7321)	0.616	38.5	1,24	<.0001 **
	June	9-29	-0.0030 (±.0004)		+2.3443 (±.1223)	0.484	59.2	1,63	<.0001 **
	July	10-29	-0.0073 (±.0022)	+0.1753 (±.0754)	+0.4605 (±.6171)	0.410	31.2	2,90	<.0001 **
	Aug.	9-29	-0.0088 (±.0019)	+0.2478 (±.0657)	-0.5412 (±.5323)	0.296	24.4	2,116	<.0001 **

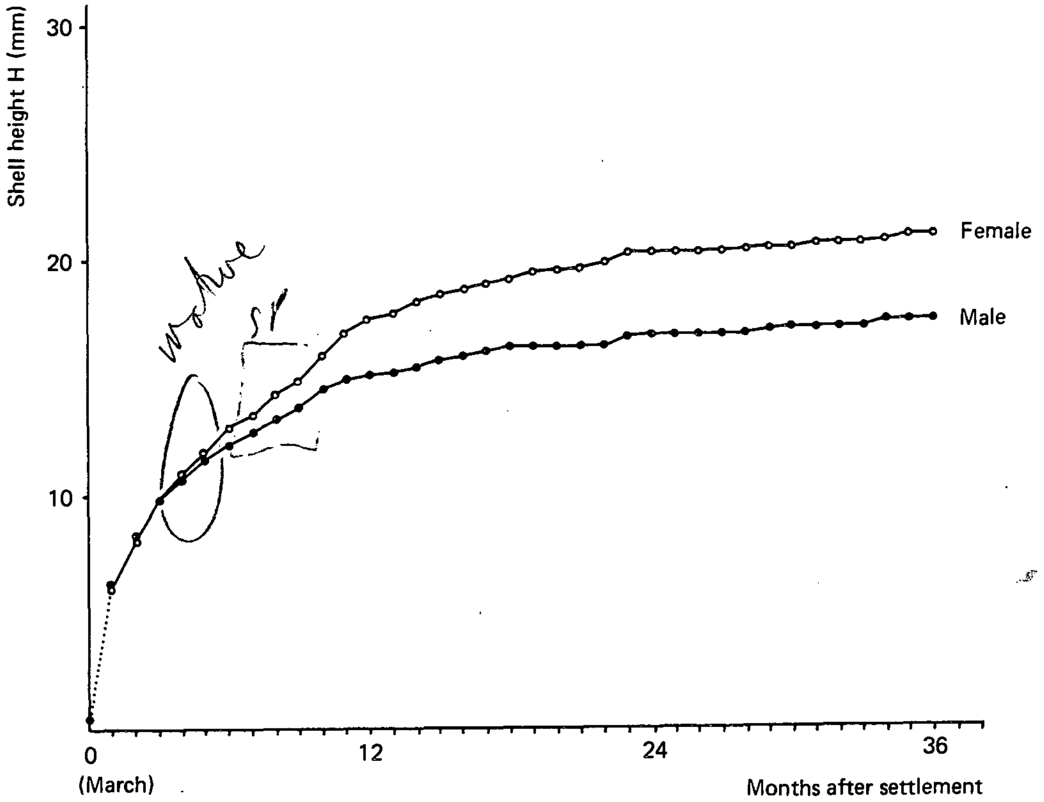
different in the newly and previously marked samples (test for regression parallelism: F = 1.045, d.f. = 1,36, P = 0.314), their elevations were significantly different (analysis of covariance: F = 7.449, d.f. = 1,37, P = 0.010). The adjusted mean increment for the individuals marked at the beginning of July was 0.94 mm, in comparison with 1.23 mm for snails marked one month earlier. The corresponding analysis for *L. filosa* was based on individuals in the size range 11 to 14 mm, and showed the difference in slopes to be not quite significant (F = 3.692, d.f. = 1,65, P = 0.059), while elevations differed significantly (F = 13.56, d.f. = 1,66, P < 0.001), the adjusted means being 1.48 mm for newly marked snails and 1.94 mm for snails marked in June.

It is therefore believed that the marking procedure depressed growth somewhat. This effect presumably accounts for the lower values of the growth parameter k in August 1980, when all individuals were newly marked, in comparison with the value for the same month in 1981 (Figs 13.22, 13.23). Therefore, when constructing growth curves the regression equations for August 1980 were not used. For *L. philippiana* the month of initial marking was October and observations were not repeated in the following year, so that the first regression equations were used for this species. After the initial month of the observation period, newly marked snails made up only a small proportion of the sample, and assuming that marking had no long-term effects on growth, the error introduced is considered small.

The growth curves constructed from the regressions of increment on initial size are shown in Figures 13.18 to 13.21. The relative growth rate was greatest in the two species from the lower and middle levels on the trees, *L. intermedia* and *L. scabra*, which both reached 85% of their maximum size one year after settlement and virtually ceased growth after the second year. In *L. philippiana* 74% of the maximum size was attained after the first year, and 93% after the second year. *L. filosa* displayed the lowest rate of relative growth, reaching 63% of the maximum size after one year, and showing

Fig. 13.18 Growth curves for *Littoraria intermedia* on *Rhizophora* trees at Cockle Bay. Calculated for individuals settling at the time of peak recruitment in March, using functions listed in Table 13.6. Dotted line indicates extrapolation back to protoconch size of 0.4 mm at presumed time of settlement.

Fig. 13.19 Growth curves for *Littoraria scabra* on *Rhizophora* trees at Cockle Bay. Calculated for individuals settling at the time of peak recruitment in March, using functions listed in Table 13.7. Dotted line indicates extrapolation back to protoconch size of 0.4 mm at presumed time of settlement.


Shell height H (mm)
30
20
10
0
(March)
12
24
36
Months after settlement
Female
Male
wahve
sp

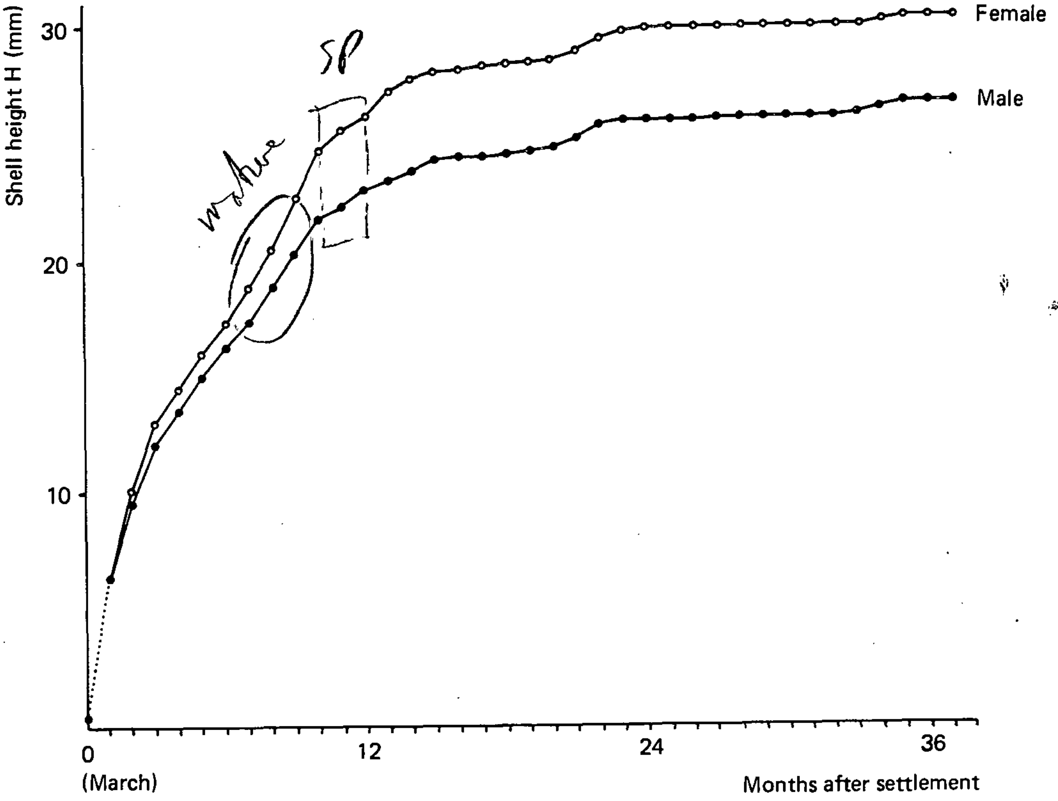
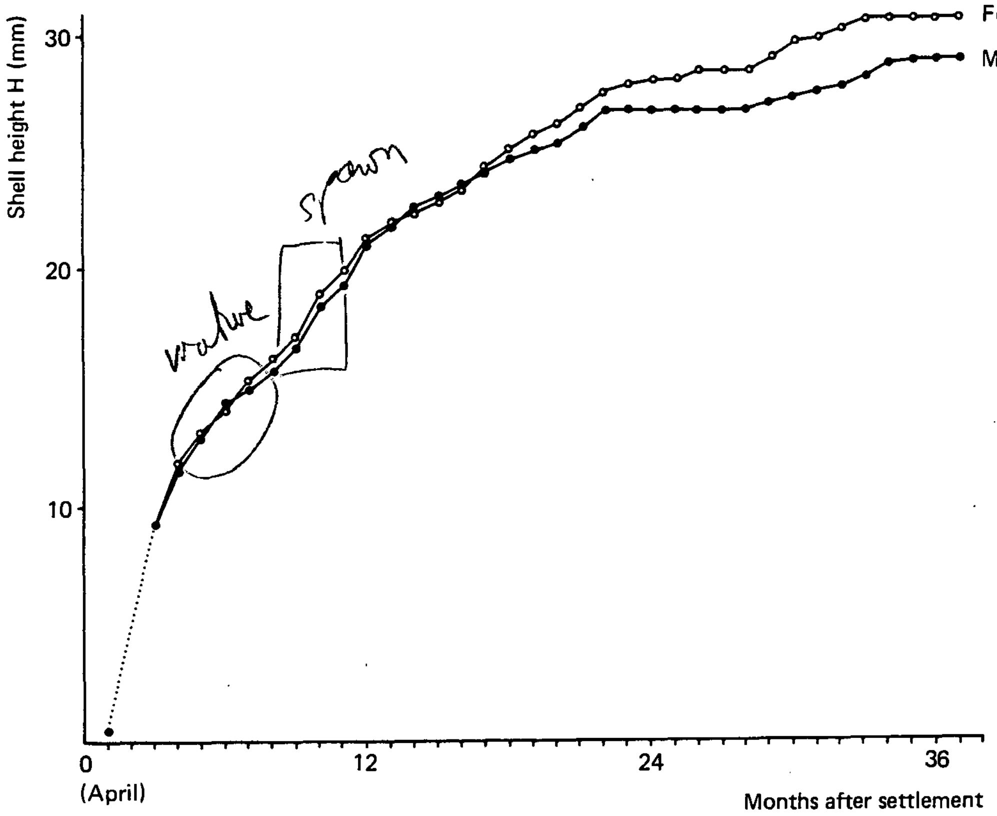
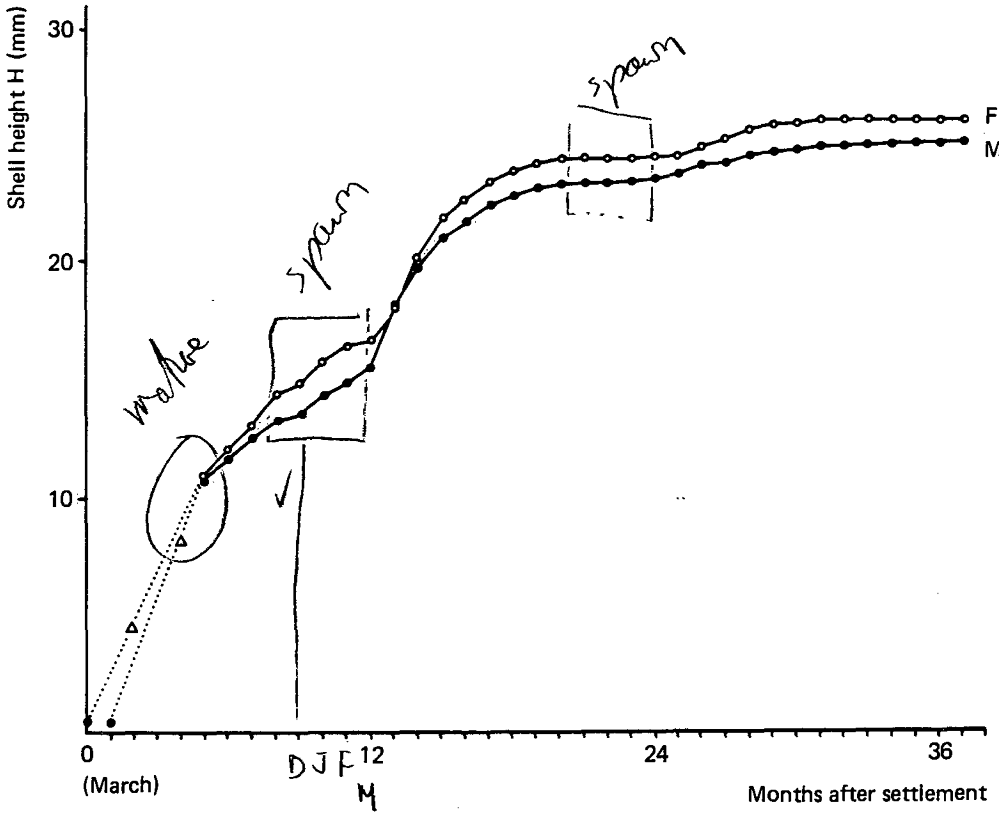

Shell height H (mm)
30
20
10
0
(March)
12
24
36
Months after settlement
Female
Male
wahve
SP

Fig. 13.20 Growth curves for *Littoraria philippiana* on *Avicennia* trees at Cockle Bay. Calculated for individuals settling in April, one month after the peak spawning period, using functions listed in Table 13.8. Dotted line indicates extrapolation back to protoconch size of 0.4 mm at presumed time of settlement.

Fig. 13.21 Growth curves for *Littoraria filosa* on *Avicennia* trees at Cockle Bay. Calculated for individuals settling in March or April, one month after the peak spawning periods, using functions listed in Table 13.9. Dotted lines indicate alternative extrapolations back to protoconch size of 0.4 mm at assumed times of settlement. Triangles show mean growth increment recorded for ten individuals caged for time period indicated.


Shell height H (mm)
30
20
10
0
(April)
12
24
36
Months after settlement
Female
Male
mature
spawn


Shell height H (mm)
30
20
10
0
(March)
12
24
36
Months after settlement
Female
Male
mature
spawn
spawn
D J F M

little further increase after the second year. It should be noted that the growth curves apply only to animals recruited during the period of peak settlement; those settling later in the season grow more slowly, as shown by the variation in the value of the growth parameter k (Figs 13.22, 13.23). The maximum rates of growth measured during the study were high, in the order of 3.8 mm per month in individuals of *L. scabra* at an initial size of 6 mm. In all species the maximum size attained by females was greater than that of males, this dimorphism being due to the faster growth rate of females. Dimorphism was most marked in *L. intermedia* and *L. scabra*. In *L. philippiana* dimorphism was not obvious until the end of the second year of growth, while in *L. filosa* the ultimate size difference between the constructed growth curves for the two sexes was only 1 mm.

The accuracy of the growth curves is difficult to assess, but several lines of evidence suggest that it is good. Firstly, the independently derived curves for males and females of each species show close correspondence in shape, and the degree of sexual dimorphism indicated is close to that measured on small samples of adult shells (Tables 9.3, 9.6, 9.7, 9.9). Comparisons with the size frequency histograms for the populations show that modal classes increased in size as predicted from the growth curves. Finally, the periods of cessation of growth of *L. filosa* and *L. philippiana* were the same as those indicated by examination of the apertural margins of the shell in these species, as shown below.

Extrapolation of the growth curves back to the time of settlement from the plankton, at which the larval shell measures 0.4 mm (Section 4.3), is tentative. It is based upon the assumption that the juvenile snails appearing during the month of maximum recruitment were derived from the preceding period of peak spawning activity in the adult population. There are only two reports of developmental times of the larvae of tropical and subtropical littorinids. *Nodilittorina hawaiiensis* reared in the laboratory underwent metamorphosis and settlement 18 days after hatching

(Struhsaker & Costlow, 1968, as *Littorina picta*), while the planktonic life of *L. angulifera* was estimated as 8 to 10 weeks from the gap between spawning and recruitment (Gallagher & Reid, 1979). On the basis of this slender evidence, the interval between spawning and settlement was taken as one month in the present study.

This assumption leads to the prediction of extremely rapid rates of growth in newly settled snails, for example *L. intermedia* and *L. scabra* attaining a size of 6 mm in the first month of growth (Figs 13.18, 13.19). Such rapid growth is consistent with the size frequency histograms which show the appearance of individuals up to 5 mm larger than the minimum size for marking in the interval between March and April 1981 (Figs 13.4, 13.5). In the case of *L. philippiana*, the pattern of recruitment in 1981 was possibly atypical (Section 13.3.2). Assuming that the recruits appearing during May resulted from the March spawning episode, growth to 9 mm may have occurred in about 2 months from settlement (Fig. 13.20). This is not unlikely, since four snails caged in the field in mid-February increased in mean size from 3.7 to 10.7 mm in 11 weeks. *L. filosa* showed two heavy spawning episodes, at the beginning of February and March (Fig. 13.2), leading to the prediction of the attainment of a size of 10.8 mm in 4 or 5 months from settlement (Fig. 13.21). Ten caged snails increased in mean size from 4.4 to 8.1 mm during a period of 9 weeks from the beginning of May, so that the predicted growth rate of newly settled snails is not improbably high.

For each of the four species, deviations from a smooth increase to maximum size suggest seasonal changes in the growth rate. The effect is most striking in *L. filosa* (Fig. 13.21). In order to visualize the seasonal pattern, values of the instantaneous size-specific growth rate for each month were estimated by linear regression of increment on initial size (Figs 13.22, 13.23). This procedure ignores the curvature of some of the regressions, and fails to take account of the differences between intercepts, caused by the cessation of growth in the largest snails at certain seasons.

Fig. 13.22 Seasonal variation in the instantaneous size-specific growth rate (k) for *Littoraria scabra* and *L. intermedia*, on *Rhizophora* trees at Cockle Bay. Error bars are 95% confidence limits.

Tell some groups on
seen before. Not 1
mean (etc) of all snails!

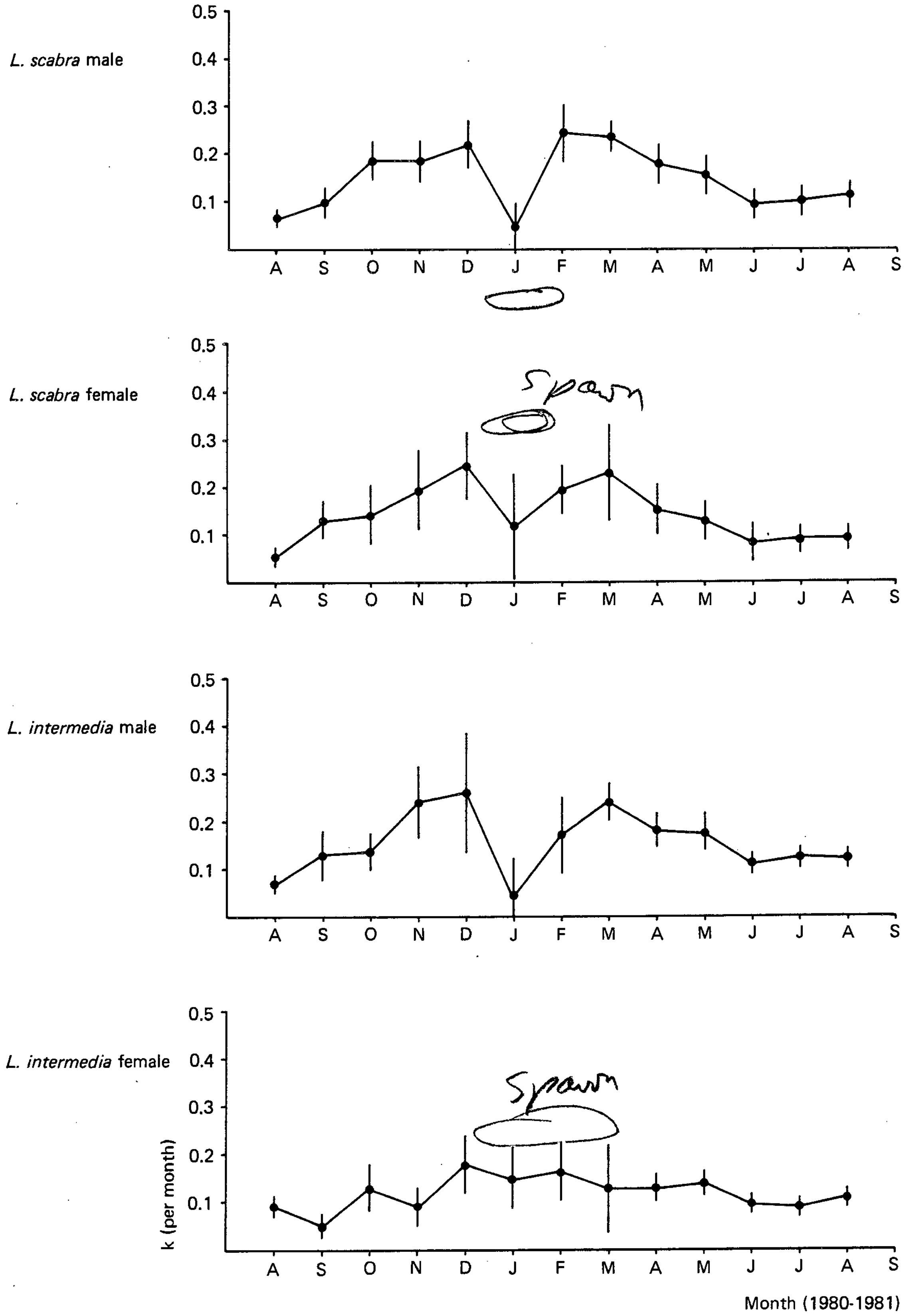
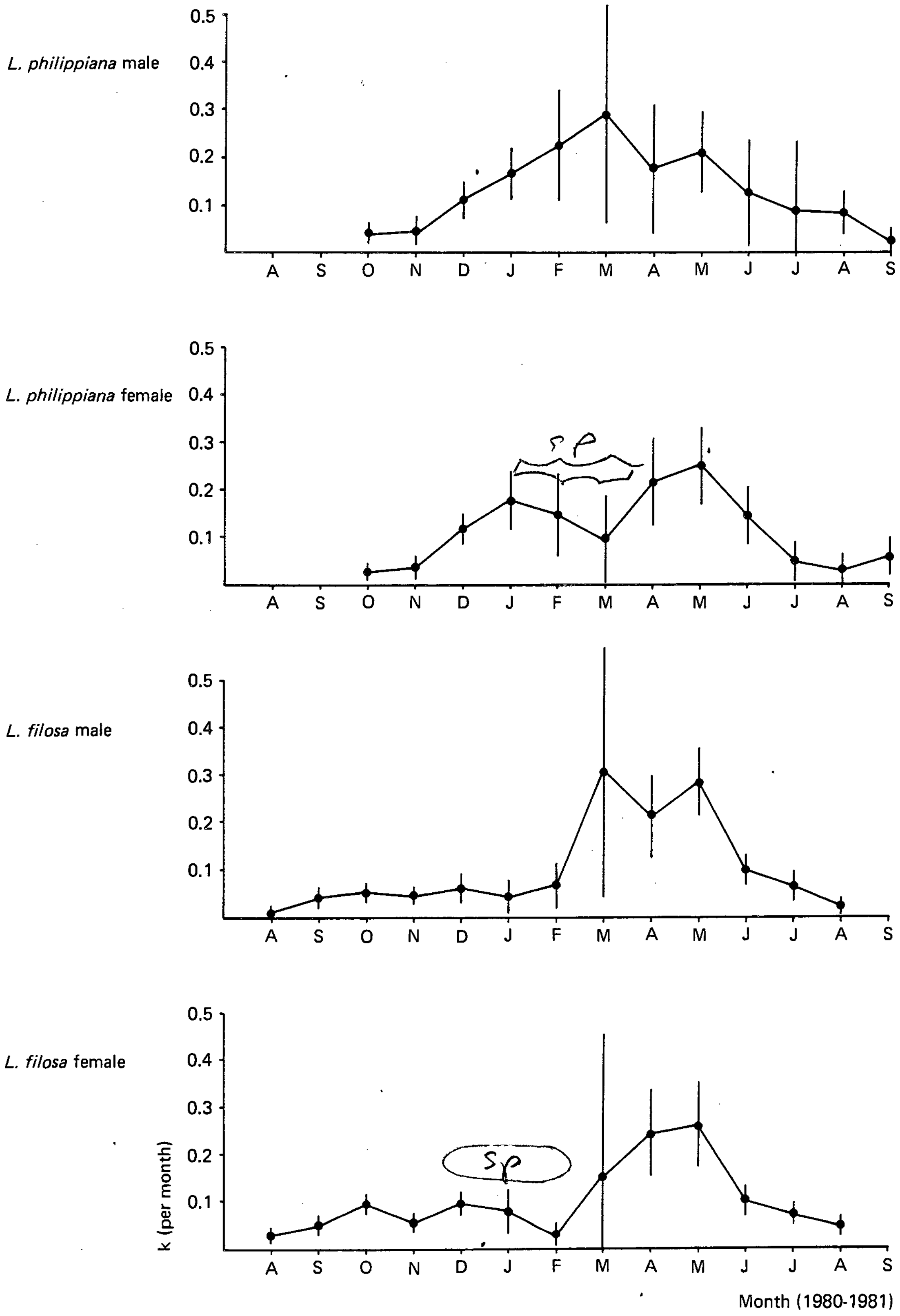

L. scabra male
L. scabra female
Spawn
L. intermedia male
L. intermedia female
Spawn
0.5
0.4
0.3
0.2
0.1
k (per month)
A S O N D J F M A M J J A S
Month (1980-1981)

Fig. 13.23 Seasonal variation in the instantaneous size-specific growth rate (k) for *Littoraria philippiana* and *L. filosa*, on *Avicennia* trees at Cockle Bay. Error bars are 95% confidence limits.


L. philippiana male
L. philippiana female
L. filosa male
L. filosa female
0.5
0.4
0.3
0.2
0.1
A S O N D J F M A M J J A S
sp
sp
k (per month)
Month (1980-1981)

If these errors were significant, high values of k would be associated with cessation of adult growth and low values with appearance of new recruits. This was not found to be the case, the seasonal fluctuations in k being sufficiently great to obscure such effects. The patterns of the values of k therefore closely reflect the predicted growth increments of snails of medium size. This means of comparison of relative growth rates has also been used by previous workers (Hughes & Answer, 1982; Janson, 1982a). Inspection of the monthly values of k showed a similar pattern in *L. scabra* and *L. intermedia*, of increased growth in the summer months (November to May), but with a marked drop in growth rate in January, correlated with the high rainfall in that month (Fig. 13.17). *L. philippiana* also showed faster growth in the summer, but no indication of a drop in growth rate in January. A very different pattern occurred in *L. filosa*, with slow growth at all times except for the 3 months from March to May.

Although all species thicken the apertural margin of the shell from within when increase in shell size slows or stops, the cessation of growth may be more prominently marked in *L. philippiana* and *L. filosa*, by a flaring of the peristome. In samples of snails with at least one flared lip or varix, the proportion in which the current apertural margin was flared and thickened was close to 100% in *L. filosa* from September to March and in *L. philippiana* from January to June (Fig. 13.24). These periods of little or no growth in adult snails correspond closely with the periods of maturity of the gonads (Figs 13.1, 13.2).

The minimum sizes at which sexual maturity was attained are given in Table 13.3. From the growth curves it can be estimated that individuals reached the potential breeding size in 3 to 4 months in *L. intermedia*, 6 to 8 months in *L. scabra*, 3 to 7 months in *L. philippiana* and 4 to 5 months in *L. filosa*. While *L. intermedia* and *L. scabra* may well begin to breed at these ages if breeding is continuous (Section 13.4.2), in *L. philippiana* and *L. filosa* the timing of the reproductive season is such that individuals recruited

Fig. 13.24 Seasonal variation in the percentage of individuals of *Littoraria filosa* and *L. philippiana* with a flared and thickened (non-growing) apertural lip to the shell, in samples of adult snails with at least one varix. Sample sizes between 12 and 69 (mean 24).

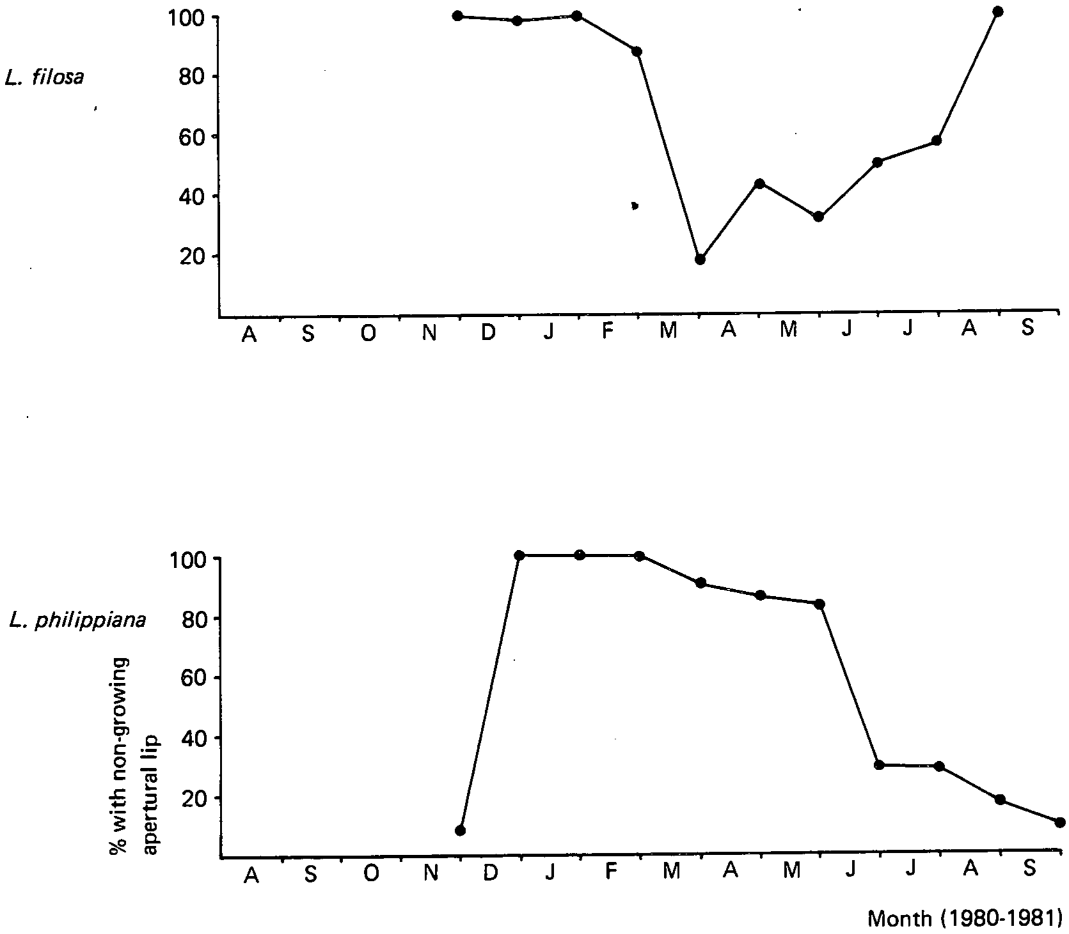

L. filosa
100
80
60
40
20
A
S
O
N
D
J
F
M
A
M
J
J
A
S
L. philippiana
100
80
60
40
20
% with non-growing apertural lip
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month (1980-1981)

Table 13.10 Frequency of varices in *Littoraria* species from Cockle Bay.

Species	Tree	Date	% with given number of varices 0	1	2	3	4	5	6	Sample size
L. filosa	*Avicennia*	24/7/80	96.5	1.1	1.9	0	0.2	0.2	0.2	538
L. philippiana	*Avicennia*	14/9/80	84.4	7.8	6.7	1.1	0	0	0	90
L. philippiana	*Rhizophora*	24/7/80	64.2	5.7	9.4	9.4	7.5	1.9	1.9	53

Table 13.11 Breeding age and longevity of *Littoraria* species at Cockle Bay.

Species	Minimum age at potential breeding size (months)^A	Actual age at first breeding (months)^A	% surviving to age 1 year	% surviving to age 2 years	Maximum longevity (no. of varices)
L. intermedia	3–4	?3–4	18.3	3.5	-
L. scabra	6–8	?6–8	24.7	6.4	-
L. philippiana	3–7	11	12.2	1.7	6
L. filosa	4–5	11	0.09	0.003	6

A minimum for males, maximum for females at the time of peak settlement will not breed until the end of their first year of growth (Table 13.11).

Prediction of age at the largest sizes from the growth curves is not likely to be very reliable, because of their asymptotic form, but the curves suggest that the largest individuals may be 3 or more years old. In *L. filosa* and *L. philippiana* the varices are formed during the annual breeding season, and the occurrence of a very few individuals with six varices suggests a maximum longevity of 6 years in these species. The distribution of varices (Table 13.10) cannot, however, be used as a reliable guide to the age structure of the whole population, since individual records showed that not all non-growing adults developed flared apertural lips. From the average survivorships of first and second year cohorts (Table 13.5), the percentages of individuals surviving to the ages of 1 and 2 years can be calculated (Table 13.11). Very few individuals appear to survive to reach 2 years of age, even in *L. scabra* with a relatively low rate of loss.

13.4 Discussion

13.4.1 Developmental type

In endeavouring to account for the wide range of types of development exhibited by the Littorinidae, most authors have pointed out correlations with the tidal level occupied (Lenderking, 1954; Heller, 1975a; Mileikovsky, 1975; Underwood & McFadyen, 1983). Thus all the species known to produce benthic egg masses are found largely in the littoral zone (*Littorina arcana*, Hannaford Ellis, 1979; *Littorina atkana*, Kojima, 1958a; *Littorina nigrolineata*, Heller, 1975a; *Littorina mariae* and *Littorina obtusata*, Goodwin & Fish, 1977; *Littorina sitkana*, Buckland-Nicks *et al.*, 1973;

Bembicium auratum, Anderson, 1962; *B. melanostoma*, Anderson, 1958; *B. nanum*, Anderson, 1961; *Risellopsis varia*, Pilkington, 1974). Clearly an attached gelatinous egg mass would not survive the periods of prolonged desiccation prevailing in the supralittoral region. In contrast, most of the species previously reported to be ovoviviparous occur in the upper littoral and supralittoral (*Littorina saxatilis*, Berry, 1961; Heller, 1975a; Roberts & Hughes, 1980; *Echininus viviparus*, Rosewater, 1982; *Cenchritis ? muricatus*, an unconfirmed note in Bandel, 1974; *Littoraria angulifera*, Lenderking, 1954; Gallagher & Reid, 1974; *L. 'scabra'*, e.g. Struhsaker, 1966; Muggeridge, 1979); *Littorina neglecta* is an exception, being found at lower levels (Heller, 1975a; Robertson & Mann, 1982). The present re-evaluation of the taxonomy of the *L. scabra* group greatly increases the number of known ovoviviparous species, since at least ten of the species previously confused under that name (i.e. the subgenus *Littorinopsis*, Section 5.4; Fig. 8.2) have been shown to reproduce in this way, and all of these are supralittoral.

Despite these two trends in developmental type, the great majority of the Littorinidae produce planktonic egg capsules, regardless of the tidal level at which they occur (Rosewater, 1970; Mileikovsky, 1975; Section 5.5). Amongst the 36 species of the genus *Littoraria*, all of which are supralittoral, 22 are known to be oviparous on the basis of their anatomy (Section 5.4, Fig. 8.2) and almost certainly all of these produce planktonic egg capsules. Amongst the species of *Littoraria* found in mangrove forests there is no obvious pattern of developmental type in relation to zonation. For example, at the lower supralittoral levels on the trees *L. articulata* and *L. strigata* produce egg capsules, while *L. intermedia* is ovoviviparous, and at the highest levels *L. albicans* and *L. conica* are oviparous, while *L. filosa* and *L. philippiana* brood their larvae. Even in the landward fringe *L. carinifera* and *L. conica* produce egg capsules.

A fact that has not hitherto been noted in the many discussions of littorinid reproduction is that species producing benthic spawn are restricted to temperate and polar latitudes. The genus *Littorina sensu stricto* is found naturally only in the northern Atlantic and Pacific oceans, while the genera *Risellopsis* and *Bembicium* occur respectively in New Zealand and southern Australia (one species extends to Queensland). Furthermore, members of the genus *Lacuna* and other littorinaceans restricted to high latitudes also show a high incidence of this method of development (Fretter & Graham, 1964; Grahame, 1977; Picken, 1979). These distributions conform to the latitudinal gradient of increasing suppression of planktotrophic larval stages towards the poles which was first noted by Thorson (1950), and explained in terms of lack of phytoplanktonic food in polar regions. Other considerations which may account for this trend include the energetic cost of lecithotrophic or planktotrophic development, the effect of adult body size on the number of eggs which can be produced, and the necessity for dispersal of pelagic larvae (review by Underwood, 1979).

Another aspect which has not been considered in previous discussions is the phylogeny of the family. While many distantly related species were classified together in the genus *Littorina sensu lato*, it was impossible to distinguish patterns in the diversity of reproductive types in other than ecological terms. However, in the light of the reclassification of Bandel & Kadolsky (1982) and of the phylogenetic groupings proposed here (Chapter 8), a new interpretation can be made, combining both tidal and latitudinal patterns in an evolutionary framework. It has been argued (Sections 5.4, 5.5) that the ancestral state was the production of planktonic capsules. In northern temperate regions some members of the genus *Littorina* eliminated the planktotrophic larval stage by depositing large eggs in a benthic gelatinous matrix. At supralittoral levels this strategy was modified by the retention of the eggs in the large jelly gland, which formed the brood pouch of ovoviviparous *Littorina* species. The eggs were thus protected from desiccation and hatched, as from benthic egg masses, as crawling juveniles. Other temperate species, and the great majority of tropical species of the family, continued to produce planktonic capsules, even though most inhabit the supralittoral zone. To ensure successful release of the eggs, the supralittoral species exhibit lunar spawning rhythms (Borkowski, 1971; Berry & Chew, 1973), spawn at the time of the high tide (Struhsaker, 1966; Borkowski, 1971; Gallagher & Reid, 1974), release eggs when splashed (Struhsaker, 1966; Pilkington, 1971) or may undertake breeding migrations to lower levels (Fretter & Graham, 1962, p. 387; Palant & Fishelson, 1968).

Tropical littorinids living in the supralittoral zone have evolved ovoviviparity independently in three separate lineages (Section 5.4). In the subgenus *Littorinopsis*, embryos are retained in the mantle cavity for between 4 (*Littoraria angulifera*, Gallagher & Reid, 1974) and 12 days (*L. luteola*, as *Littorina scabra*, Muggeridge, 1979) before release as early veliger larvae. A similar method of development in a species of *Cenchritis* is suggested by a brief note by Bandel (1974; as *Tectarius muricatus*, but subject to confirmation, since Lebour, 1945, and Borkowski, 1971, have described egg capsules in this 'species'). Struhsaker (1966) observed that embryos in the posterior part of the mantle cavity of *L. intermedia* (as *Littorina scabra*) developed in advance of those situated anteriorly, owing to rhythmic egg production over several days. However, in the present study all embryos in the mantle cavity of ovoviviparous species were always found to be at the same stage of development, suggesting a more rapid production of eggs. In ovoviviparous species of *Littoraria* release of the larvae takes place in synchrony with lunar (Lenderking, 1954; Muggeridge, 1979) and tidal (Gallagher & Reid, 1974) cycles, as in the oviparous members of the family discussed above.

The advantage of the retention of embryos in the mantle cavity may be the ability to store the eggs, produced over a period of hours or even days (Struhsaker, 1966), for release in a short space of time at a high spring tide. This is in agreement with the observations of Gallagher & Reid (1974), which showed that the ovoviviparous *L. angulifera* could release up to 246,000 veligers in 30 minutes, while the oviparous *L. irrorata* of similar size released a maximum of 32,000 egg capsules in 2½ hours. If, as argued in Chapter 14, predation on adult snails is most intense at and near the water level in mangrove forests, it will be advantageous for females to spend the shortest time at the water surface before returning to higher levels. If, for any reason, the females are unable to reach the water level to spawn, veligers may be ingested, as found in the present study and also noted by Struhsaker (1966) and Gallagher & Reid (1974). It is difficult to suggest any advantage of this method of development in relation to enhanced survival of the larvae, since retention by the female is for only a few days, in comparison with a probable larval life of at least 18 days (Struhsaker & Costlow, 1968) or perhaps as long as 8 to 10 weeks (Gallagher & Reid, 1979). Furthermore, when released the veligers of *Littorinopsis* species are of the same size (100 to 140 µm, pers. obs.) as those hatching from the egg capsules of oviparous *Littoraria* species (Gallagher & Reid, 1974). Many authors have emphasized the necessity for wide dispersal in high intertidal gastropods (Underwood, 1979; Hughes & Roberts, 1981; Underwood & McFadyen, 1983) in view of the variability of habitats and danger of local extinction in a rigorous environment. These considerations may also apply to *Littoraria* species in mangrove habitats, perhaps accounting for the persistence of a planktotrophic larval stage after initial brooding of the eggs.

Amongst tropical ovoviviparous littorinids, only *Echininus viviparus* has eliminated the planktotrophic stage, brooding larvae in the same manner as temperate *Littorina* species (Rosewater, 1982).

13.4.2 Seasonality of breeding

The monthly samples of L. *scabra* and L. *intermedia* showed that the majority of males and females were mature throughout the year (Figs 13.1, 13.2). However, veligers were found in the mantle cavity only between September and March in L. *scabra* and September and April in L. *intermedia*. The continued presence of mature oocytes in the ovaries and gonadial oviducts during the remaining months suggests that spawning may well have occurred throughout the year. There was no evidence of a period of gonadial regression, as found in littorinids with seasonal breeding (Williams, 1964; Palant & Fishelson, 1968; Borkowski, 1971; Underwood, 1974; Muggeridge, 1979). In other *Littoraria* species, spawning is closely correlated with the lunar cycle (Lenderking, 1954; Berry & Chew, 1973; Gallagher & Reid, 1974; Muggeridge, 1979). If this is also the case for L. *scabra* and L. *intermedia*, the monthly sampling occasions may not always have coincided with the occurrence of embryos in the mantle cavity. A more frequent sampling routine might have resolved this uncertainty.

Both L. *filosa* and L. *philippiana* showed seasonal breeding, with an obvious period of regression of the gonads in both sexes (Figs 13.1, 13.2). The monthly sampling routine again leaves doubts as to the number of spawning episodes. Both species showed a cycle of maturity of the ovary alternating with depletion of oocytes and brooding of embryos, during the course of their respective breeding seasons. These cycles suggest that in L. *filosa* there may have been only two major spawning episodes, and in L. *philippiana* two or possibly three such episodes. This interpretation is supported by the observations of previous authors that in tropical and subtropical littorinids (including members of the genus *Littoraria*) it is usual for one or sometimes two months to elapse between successive spawning episodes of individual females (Struhsaker, 1966; Berry & Chew, 1973; Gallagher & Reid, 1974; Muggeridge, 1979).

The majority of the littorinids for which data are available show a restricted breeding season, with complete or partial regression of the gonads of both sexes at other times of the year. Various authors have attempted to correlate the onset of reproductive maturity or of spawning with either falling (Williams, 1964) or rising (Borkowski, 1971; Muggeridge, 1979) sea temperatures. It has also been found that species with planktotrophic development sometimes synchronize their spawning period with that of maximum abundance of phytoplankton (Underwood, 1974; Muggeridge, 1979). However, at some localities anomalous results have been reported, spawning occurring at different seasons in species with similar methods of development (Kojima, 1960; Lewis, 1960; Palant & Fishelson, 1968). In a review of the literature, data on the breeding seasons of 37 species of Littorinidae have been extracted from 35 papers, and from these some generalizations emerge.

The breeding seasons of only 12 littorinid species have been recorded in tropical latitudes (Lewis, 1960; Struhsaker, 1966; Berry & Chew, 1973; and the 5 species examined in the present study). Of these, 8 species (67%) show continuous breeding throughout the year (including *L. scabra* and *L. intermedia* from the present study, on the basis of their gonadial cycles, and also *L. articulata* with a brief period of regression in some individuals, Figs 13.1, 13.2). Seasonality is more marked in species from subtropical and temperate areas, in which 10 out of 31 (32%) show continuous breeding, and even then usually with marked seasonal peaks (Lysaght, 1941; Lebour, 1945; Lenderking, 1954; Kojima, 1959, 1960; Anderson, 1961; Berry, 1961; Williams, 1964; James, 1968; Lambert & Farley, 1968; Palant & Fishelson, 1968; Borkowski, 1971; Pilkington, 1971; Fish, 1972; Buckland-Nicks *et al.*, 1973; Gallagher & Reid, 1974; Underwood, 1974; Jordan & Ramorino, 1975; Daguzan, 1976a, b; Faller-Fritsch, 1976; Goodwin & Fish, 1977; Goodwin, 1978; Muggeridge, 1979; Schmitt, 1979; Alifierakis & Berry, 1980; Caugant & Bergerard, 1980; Hughes, 1980; Hannaford Ellis, 1983; Underwood & McFadyen, 1983). The trend towards more prolonged breeding seasons at lower latitudes is also apparent within species with wide geographical ranges, such as the Caribbean *Nodilittorina* species (Lewis, 1960; Borkowski, 1971; see Bandel & Kadolsky, 1982, for taxonomy), *Littorina littorea* (reviews by Moore, 1937, Williams, 1964), *Melarhaphe neritoides* (Palant & Fishelson, 1968) and *Littoraria angulifera* (Gallagher & Reid, 1974).

Within temperate latitudes all but 3 of the 10 species with continuous breeding cycles are members of the genus *Littorina* with direct benthic or ovoviviparous development (Buckland-Nicks *et al.*, 1973; Daguzan, 1976a; Faller-Fritsch, 1976; Goodwin & Fish, 1977; Goodwin, 1978; Hughes, 1980; Hannaford Ellis, 1983). The availability of food for planktotrophic larvae may circumscribe breeding seasons outside the tropics (Thorson, 1950; Underwood, 1974), but species with lecithotrophic development should not be subject to this restraint.

There is some suggestion of a phylogenetic pattern to the seasonality of breeding. Thus of the 12 species of *Littorina sensu stricto* for which data are available, 8 spawn in winter or spring, or, if continuous breeders, show a maximum at these times (exceptions have been reported by Buckland-Nicks *et al.*, 1973; Faller-Fritsch, 1976; Hughes, 1980; Hannaford Ellis, 1983). *Fossarilittorina meleagris* breeds in winter (Lewis, 1960) and *Melarhaphe neritoides* in winter and spring (Palant & Fishelson, 1968). Members of the genus *Bembicium*, with benthic egg masses from which planktotrophic veligers are released, have mostly been reported to spawn in winter and spring (Underwood, 1974; Muggeridge, 1979; but Anderson, 1961, reported spring and summer breeding). In contrast, all members of the genera *Nodilittorina* (*sensu* Bandel & Kadolsky, 1982) and *Echininus* which show a seasonal pattern spawn in the summer or show maximum spawning in that season (11 species: Kojima, 1960; Palant & Fishelson, 1968; Borkowski, 1971; Pilkington, 1971; Underwood, 1974; Underwood & McFadyen, 1983). Of the genus *Littoraria*, only 3 species have been examined outside the tropics, and all exhibit summer spawning (*L. angulifera*, Gallagher & Reid, 1974; *L. irrorata*, Bingham, 1972b, Gallagher & Reid, 1974; *L.*

luteola, Muggeridge, 1979, as *Littorina scabra*). To a large extent, these phylogenetic patterns reflect the geographical distributions of the genera, those with tropical and subtropical distributions spawning in summer, and those restricted to more temperate regions in winter and spring. This trend has been noted in molluscan and other invertebrate groups in reviews by Moore (1972) and Underwood (1979). Although more data are required to confirm the phylogenetic trend, it does account for the anomalous cases mentioned above of breeding by species at the same locality at different times of the year.

It remains to be considered why *L. filosa* and *L. philippiana* show restricted spawning seasons, while the other three species at Magnetic Island conform to the general trend of continuous breeding activity in tropical littorinids. As adults, both *L. filosa* and *L. philippiana* occupy the highest supralittoral levels, at which they may be more dependent for their activity upon atmospheric moisture than on tidal stimulation (Section 12.3.1). Rainfall is highly seasonal in this region of northern Queensland (Fig. 13.17), occurring mainly in the summer months, and therefore for much of the year the time available for these species to feed may be limited. In addition, epiphytic algal food might be scarce during the dry season. It is likely that only in the wet summer months is sufficient food assimilated to support reproductive activity, a suggestion strengthened by the highly seasonal growth patterns shown by these species (Fig. 13.23; Section 13.4.7).

There are few comparable studies of the reproductive seasons of littorinid species occupying a range of tidal levels at a single locality. Lewis (1960) found a similar result in Barbados, where *Cenchritis muricatus* from the highest supralittoral level spawned for three months in the summer, while species of *Nodilittorina* at lower levels spawned throughout the year. *Cenchritis muricatus* is one of only two littorinids, other than *L. filosa* and *L. philippiana*, reported to show seasonal breeding in tropical latitudes (the other being the littoral species *Fossarilittorina* *meleagris*, Lewis, 1960). Borkowski (1971) demonstrated a similar, but less striking, trend amongst six species in Florida. In Britain, *Littorina saxatilis* has been reported to show a longer breeding season in microhabitats where food is more abundant and feeding time prolonged (Berry, 1961), while early maturation of an estuarine population of *Littorina littorea* has been explained in terms of improved nutritional status (Fish, 1972). It is interesting that in *Littoraria angulifera*, occurring at supralittoral levels on mangroves in the tropical Atlantic, either spawning activity (Lenderking, 1954) or the duration of the breeding season (Gallagher & Reid, 1974) is correlated with rainfall.

13.4.3 Larval settlement and recruitment to the population

Littoraria intermedia and *L. scabra* spawned over a period of 7 and 8 months respectively, and may perhaps have done so throughout the year (Section 13.4.2). It is therefore surprising that the recruitment period of both these species was so restricted, 51% and 76% respectively of the new recruits appearing during March in 1981 (Fig. 13.9). In both cases these peaks of recruitment appear to have been the result of the period of maximum spawning activity in February and March, while spawning from September until January gave rise to virtually no recruits. Patterns of recruitment in intertidal gastropods are well known to be highly variable from season to season (Underwood, 1975; Gallagher & Reid, 1979; McQuaid, 1981a; Underwood & McFadyen, 1983). However, in the case of *L. intermedia* and *L. scabra* the similarities in shape of the size frequency distributions for August and September of 1980 and 1981 show that the pattern of summer recruitment was repeated in the two successive years. Continuous spawning and restricted recruitment have been reported in a coral reef wrasse by Victor (1983), and explained in terms of the unpredictability of survival of the pelagic larval stage. Long-term data on spawning and settlement would be necessary to test this hypothesis in these mangrove littorinids, but the repetition of the pattern in two successive years suggests that recruitment success may in fact be predictable.

Alternative explanations for the observed pattern of appearance of juveniles are firstly a highly variable length of planktotrophic life, so that larvae spawned at different times might settle together. Although settlement time is known to be variable in some gastropods (Scheltema, 1971), there are no suggestions of this phenomenon in the extensive literature on littorinids. Secondly, it is possible that growth rates of newly settled snails are seasonally variable, so that individuals settling in spring would appear in the size range of snails defined as 'recruits' at the same time as those settling in summer and growing more rapidly. Growth rates of larger snails are indeed more rapid in the summer (Fig. 13.22), but the seasonal difference is too small to account for the apparently restricted recruitment period. A third possibility is that the recruits may suffer heavy mortality for most of the year, as discussed below.

Of the two species from higher levels, *L. filosa* spawned only in February and March, yet recruits appeared in large numbers from May until August. The greater duration of recruitment than spawning may be explained by the highly seasonal growth rate in this species (Fig. 13.23), those snails settling later in the year growing at a slower rate. The appearance of a small number of recruits throughout the rest of the year in this species may have been an artefact of the relatively large size (9-13 mm) at which individuals were defined as 'recruits'. These snails might have been the slowest growing remnant of the previous spawning, or may have been unmarked immigrants from nearby trees. Alternatively, the year-round recruitment may reflect small numbers of larvae which arrived from populations with a more prolonged spawning season, perhaps from areas where rainfall is higher and less seasonal. The size frequency distributions suggest that recruitment of *L. philippiana* was relatively unsuccessful over the year of study, as also indicated by the decline in estimated population sizes of this species. Relative recruitment success did not vary in the same way in all species, since in the remaining three species 1981 was a year of higher recruitment than 1980.

Amongst the three species which recruited successfully in 1981, it is interesting to compare the relative contributions of the recruits to the populations of each. From the size frequency histograms it can be estimated that for *L. intermedia*, individuals recruited in 1980 comprised approximately 34% of the population in August of that year, while in the same month in 1981 new recruits comprised 58% of the population. For *L. scabra* the figures were 25% and 57% respectively. The corresponding figures for *L. filosa* were 57% and 80%. From the monthly recruitment figures (Fig. 13.9), the total number of recruits recorded in 1981 was 112% of the population size in February, at the time of peak spawning, in *L. intermedia*, 51% in *L. scabra* and 612% in *L. filosa*.

No counts were made of the numbers of embryos present in brooding females, but in each of the four ovoviviparous species the mantle cavity was entirely lined with embryos, and sizes of eggs and embryos were similar in each (for *L. filosa*: ova 77-87 µm, veligers 130-140 µm at release; for other 3 species: ova 59-69 µm, veligers 100-115 µm). Furthermore, for *L. filosa* and probably *L. scabra*, and less certainly for *L. intermedia*, the majority of recruits appear to have been derived from two spawning episodes, in February and March. It appears that during the year of study *L. filosa* could not have produced more larvae per unit of population size than the other two species, and probably considerably fewer. Nevertheless, the contribution of recruits to the population was greatest in *L. filosa*. The difference would surely have been even more striking had recruits been recorded at a smaller size in this species; as it was, the 4-8 mm snails defined as 'recruits' in *L. intermedia* and *L. scabra* were only one to two months from settlement, while the 9-13 mm 'recruits' of *L. filosa* were at least four to five months from settlement. Using the survivorships estimated for *L. filosa* from 9 to 12 mm in size for the months May to July (Fig. 13.16), the number of recruits at the same age as those of *L. intermedia* and *L. scabra* would have been three times greater than the number actually recorded for *L. filosa*. The protoconchs of the three species are almost identical in size and shape (Section 4.3), suggesting a similar length of planktotrophic larval life for each.

This speculative interpretation suggests that although the number of larvae spawned per unit of population size in *L. filosa* during February and March was similar to the numbers for *L. intermedia* and *L. scabra* (but over the whole year much less), and although the length of larval life was similar in all three, the success of settlement and recruitment was by far the greatest in *L. filosa*. One flaw in this argument is that it has been assumed that recruits were derived only from the local population (and with a planktotrophic life span of the order of one month, this is unlikely) or from other populations with similar reproductive periods.

The explanation for the relatively lower success of recruitment of *L. intermedia* and *L. scabra* compared with *L. filosa*, and of their lack of recruitment for much of the year despite a prolonged or continuous breeding season, may be found in the respective habitats of the species. As discussed in Chapter 14, predation upon the snails by tree-climbing crabs (*Metopograpsus* species) was more severe in the *Rhizophora* forest than on isolated *Avicennia* trees which supported few such predators. As shown by predation trials (Section 14.3.3) and also reported by other authors (Hylleberg & Christensen, 1978; Hughes & Roberts, 1980b), crabs prey upon small and newly settled snails. It is proposed that the recruitment success of *L. intermedia* and *L. scabra* was low as a result of intense predation by small *Metopograpsus* upon newly settled snails on the roots and trunks of *Rhizophora* trees. Despite prolonged spawning, significant recruitment occurred only after the peak spawning period in February and March, when newly settled snails must have been most abundant. Settling on *Avicennia* foliage, small juveniles of *L. filosa* may largely have escaped predation by

Metopograpsus. Recruitment to the population of *L. philippiana* on *Rhizophora* trees was even less successful than that on *Avicennia* trees, although other factors besides predation intensity, such as settlement preference, could have been involved. The hypothesis of more intense predation on small juveniles on *Rhizophora* trees could be tested by caging experiments in the two habitats, but the difficulty of finding very small individuals of *L. intermedia* and *L. scabra* would make the work laborious.

13.4.4 Mortality

The combination of seasonal recruitment and mortality leads to a seasonal fluctuation of estimated population size, a gradual decline in numbers being followed by a rapid rise at the time of recruitment (Fig. 13.10). Similar annual patterns have been reported in temperate littorinids (Hughes & Roberts, 1981; Robertson & Mann, 1982; Underwood & McFadyen, 1983), and in *L. angulifera* in Florida (Gallagher & Reid, 1979). However, rather than a predictable seasonal pattern, the few published accounts of the population dynamics of littorinids have mostly emphasized large and irregular fluctuations from year to year (Gallagher & Reid, 1979; Hughes, 1980; Hughes & Roberts, 1981). In the present study, *L. intermedia*, *L. scabra* and *L. filosa* showed negligible differences in population size at the beginning and end of the observation period, while *L. philippiana* showed a 46% decline, accounted for by the poor recruitment in that year. Stiven & Hunter (1976) found the population sizes of *L. irrorata* in three North Carolina salt marshes to be relatively stable over a two year period.

The interpretation of the survivorship figures is complicated by the fact that apparent loss from the population is due not only to mortality, but also to emigration and detachment of number marks. The combined effects of emigration and number loss are believed to be similar in all populations, and may amount to about one half of the loss rate (Section 13.3.2). If this is so, the rates of loss of the species (Table 13.5) will reflect their relative mortality rates. Within the *Rhizophora* forest, loss rates were relatively low, being greatest in *L. intermedia*, perhaps reflecting a greater intensity of predation at the lower levels on the trees (Chapter 14). On *Avicennia* trees, *L. philippiana* showed a greater rate of mortality than on *Rhizophora* trees, while the mortality rate for *L. filosa* was the highest of all. The greater loss on *Avicennia* cannot have been the result of more severe predation, since predation is probably more intense on *Rhizophora* trees (Section 14.4.3). Instead it seems possible that some deaths were caused by extremes of heat, desiccation or rainfall, or by factors correlated with microclimate, such as food availability.

Avicennia trees may provide a more rigorous habitat than the *Rhizophora* forest, since the trees are well spaced, the canopies open and the leaves small, while in the *Rhizophora* forest the thick foliage and large leaves provide a dense shade. This suggestion is supported by the relative patterns of vertical zonation of snails on the two tree species (Section 12.4.3). The small *Avicennia* leaves may also afford less effective shelter from rain. Although on *Avicennia* trees *L. philippiana* and *L. filosa* occurred at similarly high levels, the latter was found commonly on the foliage, and usually on the upper leaf surfaces, while *L. philippiana* frequented the trunks and branches (Section 12.3.5). *L. filosa* is therefore more often exposed to direct sunlight, and being smaller should be more susceptible to desiccation (Section 12.4.6), which may account for its higher mortality. It was not uncommon to find dead individuals of *L. filosa* still attached to the leaves of *Avicennia* trees by a mucous seal (Section 15.4.6), although whether such animals had in fact been killed by heat, desiccation, starvation or disease, could not be determined. Mortality caused directly by high temperatures is unlikely, since shading of an *Avicennia* tree produced little change in survivorship of *L. filosa* (Section 14.3.2). In addition no evidence of climatic selection on the colour morphs of *L. filosa* was found, despite small temperature differences between them (Section 15.4.6).

The monthly survivorships of size classes (Figs 13.12 to 13.16) are in agreement with the suggestion that mortality influenced by rigorous microclimatic conditions contributed to the high rates of loss on *Avicennia* trees. All species showed decreased survivorships in the summer months, but this seasonal effect was relatively much greater in the two species on *Avicennia* trees. The summer climate is characterized by high temperatures, high relative humidity and sporadic heavy rainfall. These conditions were less favourable than those prevailing in the winter period, when temperatures are lower, and rainfall negligible (Fig. 13.17). The correlation between lowered survivorship and higher monthly average temperatures is particularly clear for *L. filosa*. The correlation does not necessarily reflect a direct influence of temperature or desiccation upon mortality. Other causes of death, such as predation, could themselves be correlated with climate.

Another feature of the monthly survivorship figures is the severe loss suffered by most size groups of all species during the month of January, when rainfall was exceptionally heavy. While such a correlation may be fortuitous, the behavioural observations (Section 12.3.5) showing that the *Littoraria* species attempt to avoid excessive freshwater influence suggest that heavy rainfall may be deleterious. Furthermore, even surviving individuals of *L. intermedia* and *L. scabra* were adversely affected during the month of January, showing a significantly reduced growth rate (Fig. 13.22). As in the case of the possible influences of desiccation and temperature on mortality, experimental work would be required to determine whether heavy rain is directly harmful because of osmotic effects, or whether the influence is indirect, perhaps restricting activity and feeding, or affecting food supplies.

In all species loss rates of the smallest size classes were generally the highest, but this is to be expected whether loss was caused by climatic extremes or by predation. The significantly lower average survivorship of the first year cohort of *L. filosa* in comparison with adult snails (Fig. 13.11) can be explained by the relatively slow growth rate of this species, so that first year snails remained at small and vulnerable sizes for a longer period. In the remaining three species growth was more rapid, so that while the juvenile cohort initially showed lower survival than the adult group, the difference soon became negligible as growth removed the size difference between the cohorts.

Although the summer was the season of peak spawning activity in all species, the pattern of reduced survivorship did not reflect the respective maturation or spawning periods of the species, so that there was no evidence for a connection between breeding condition and summer mortality. Similarly, increased growth rates were not obviously correlated with seasonal mortality, as has been found in some intertidal gastropods (Creese, 1981). The data showed no suggestion of density-dependent mortality.

It is difficult to make comparisons with other investigations of mortality rates in gastropods, which in general have been carried out on species from temperate rocky shores. Many authors have found higher mortality rates in smaller individuals (Moore, 1937; Hughes, 1980; Creese, 1981), but there are exceptions (Underwood, 1975). Seasonal trends have seldom been examined, but in *Littorina nigrolineata* Hughes (1980) has shown higher survival rates in winter. An investigation directly comparable with the present study is that of Muggeridge (1979), who estimated mortality rates of the littoral species *Bembicium auratum* and the supralittoral *Littoraria luteola* (as *L. scabra*) on *Avicennia* trees near Sydney. From her figures, average monthly survivorships can be calculated as 0.921 and 0.827 respectively, so that *L. luteola*, in the more rigorous microhabitat, showed the higher rate of loss. From data presented by Gallagher & Reid (1979), the average monthly survivorship of *L. angulifera* on a sea wall in Florida was 0.917, rather higher than figures reported here.

There exists an extensive literature concerning the tolerance of extremes of temperature, desiccation and osmotic stress by littoral gastropods, as reviewed by Underwood (1979). In general, it has been found that the animals are tolerant of more extreme environmental conditions than are normally experienced in the field. Littorinids in particular are exceptionally tolerant of microclimatic extremes. Lethal temperatures of between 40 and 50 °C have been reported for temperate and tropical littorinids (Broekhuysen, 1940; Evans, 1948; Fraenkel, 1960, 1961; Whipple, 1966; Markel, 1971; Chow, 1975). Desiccation resistance is correlated with zonation level, and some tropical supralittoral species can survive without water for one to two years (Mattox, 1949; Barkman, 1955; Whipple, 1966). A number of littorinids can tolerate immersion in fresh water for two to five days (Broekhuysen, 1940; Mayes, 1960; Whipple, 1966; Bock & Johnson, 1967; Chow, 1975) and exceptionally up to eight days (Fraenkel, quoted in Barkman, 1955). The suggestion made here of significant mortality caused by climatic conditions is at variance with these findings, so that the apparent influence of at least temperature and desiccation upon mortality may perhaps be indirect. However, Wolcott (1973) has proposed that at the very highest levels on the shore, where the distribution of a species adjoins an unexploited source of food, extreme microclimatic conditions, and especially desiccation, may cause significant mortality, thereby limiting the vertical distribution of the species. As argued previously (Section 11.5.1), this situation might apply to the mangrove littorinids, so that mortality caused by extremes of climate could be expected at the highest levels. Underwood (1979) concluded that rainfall should only be an important cause of mortality of littoral molluscs under unusual circumstances; it seems that the three weeks of continuous monsoonal rain at the study site may have provided just such a circumstance.

The measurement of microclimatic conditions in the field, and experimental investigation of tolerance levels of the *Littoraria* species, would be necessary to test the alternative interpretations of the survivorship data presented here. A more detailed discussion of predation as a source of mortality is presented in Chapter 14.

13.4.5 Longevity

Calculations from the survivorship data show that only a small proportion (6% or less) of the population of each species survives to reach an age of 2 years. The presence of annual varices in *L. filosa* and *L. philippiana* suggests maximum longevities of 6 years in these species. These figures are comparable with estimates of longevity in other littorinids. Species of *Nodilittorina* on subtropical and warm temperate shores survive for 1 to 2 years (Borkowski, 1971; McQuaid, 1981a; Underwood & McFadyen, 1983). In a population of *Littoraria angulifera* in Florida, 30% survived to reach a second spawning season (Gallagher & Reid, 1979), while near Sydney the life span of *L. luteola* was estimated as 3 to 5 years (Muggeridge, 1979, as *Littorina scabra*). Stiven & Hunter (1976) estimated the life span of *L. irrorata* in North Carolina as 13 years, but this is certainly too high, being based upon a falsely low growth rate (see Yamaguchi, 1975; Section 13.4.6). *L. irrorata* may however be more long-lived than other members of the genus so far investigated, since the mortality rate is only 18% per year in large animals (Smalley, 1959, quoted in Borkowski, 1974). The maximum age of *L. pintado* in Hawaii has been recorded as 6 years (Whipple, 1966). Sewell's (1924) estimate of the longevity of *L. 'scabra'* as 5 years was based upon a single size frequency distribution and is unreliable. In temperate *Littorina* species the maximum life span ranges from 2 to 3 years (Goodwin, 1978; Robertson & Mann, 1982) and up to 5 years (Moreteau, 1976; Hughes, 1980), while *Melarhaphe neritoides* is especially slow-growing and long-lived, with a maximum age of 8 years or more (Hughes & Roberts, 1980a).

As pointed out by Underwood (1975), longevity is an aspect of considerable selective importance in populations in which recruitment is so unpredictable as to be absent in some years, as seems to have been the case in *L. philippiana* at Cockle Bay in 1981.

13.4.6 The form of the growth curve

The von Bertalanffy growth equation has often been used to describe the course of growth in invertebrates which show decreasing relative growth as maximum size is approached (Yamaguchi, 1975). The model predicts a smooth asymptotic approach to maximum size and makes the assumption that the instantaneous size-specific growth rate (k) is independent of size. If this assumption is justified, the plot of growth increment against size from which the value of k is estimated should be a straight line of negative slope (Hughes, 1980; Janson, 1982a). As pointed out by Yamaguchi (1975), this function may well appear to be linear if either the time interval for the measurement of the growth increment is relatively long, leading to underestimation of the required instantaneous growth increment (e.g. incorrect methodology applied by Stiven & Hunter, 1976), or if the smaller size classes are not adequately represented in the sample. When the time interval is short and the range of sizes sufficient, it is often found that in small individuals growth increment inceases up to a certain size, then falls in an approximately linear manner (Lenderking, 1954; Yamaguchi, 1977; Hughes, 1980; Janson, 1982a). In this case the value of k is not independent of size, and the growth curve will show an inflexion before rising to the asymptote (Yamaguchi, 1975). The von Bertalanffy model will also be inappropriate if the value of k shows marked seasonal variation. Nevertheless, where the inflexion is not pronounced, and seasonal differences are small, the model has been used successfully to describe the growth of littorinids (Moreteau, 1976; Hughes, 1980; Roberts & Hughes, 1980).

In the present study the relationships between growth increment and size were clearly non-linear when small snails were available for inclusion in the sample. However, since the maxima in the parabolic curves were shallow, and because of monthly changes in the form of the curve, no conspicuous inflexions appear in the constructed growth curves. If the backward extrapolations of the constructed growth curves to sizes at settlement are accurate, there may in fact be no prominent inflexion in the curve, as also found in *Littorina saxatilis* by Roberts & Hughes (1980). The growth rate of newly settled snails may be extremely rapid in littorinids, an increase from 0.4 to 1.0 mm in the first 24 hours having been reported by Fretter & Manly (1977).

The combination of non-linearity of the curves of increment against size, and the pronounced seasonality of growth, indicate that the von Bertalanffy model is not an appropriate one with which to describe the entire course of growth in the *Littoraria* species studied.

13.4.7 Rate of growth

Since there is so little published information on the growth of littorinids in tropical latitudes, it is not surprising that the rates of growth found in the four species (*L. scabra*, *L. intermedia*, *L. philippiana*, *L. filosa*) at Cockle Bay are the highest so far recorded for the family. Relative growth rates can be compared by the value of the instantaneous size-specific growth rate k, which describes the rate at which the maximum size is approached. In the four *Littoraria* species, k ranged from approximately 0.05 per month in seasons of slow growth, to 0.25 per month when growth was most rapid, average values for the year being between 0.1 and 0.15 per month (Figs 13.22, 13.23). For comparison, average values of k reported in European species range from 0.027 per month (*Littorina* *littorea*, Hughes & Answer, 1982) to 0.067 per month (*Littorina saxatilis*, Moreteau, 1976), with an especially low value of 0.006 per month in the supralittoral species *Melarhaphe neritoides* (in Hughes & Roberts, 1980a). Values of k are not available from other studies of *Littoraria* species, but sizes at the end of the first year of growth (with maximum size in parentheses) have been estimated as follows: *L. angulifera* 10 mm (max. 35 mm) (Lenderking, 1954, Florida Keys) and 16 mm (max. 20 mm) (Gallagher & Reid, 1979, Tampa, Florida), *L. luteola* 6 mm (max. approx. 20 mm) (Muggeridge, 1979, Sydney, as *Littorina scabra*), *L. irrorata* 8 mm (max. 20 mm) (Bingham, 1972a, Panama City, Florida), *L. pintado* 3 mm (max. 8 mm) (Whipple, 1966, Hawaii).

If *L. intermedia* does indeed reach potential breeding size in 3 to 4 months from settlement, this is the fastest rate of maturation so far recorded in a littorinid. However, since maturation was not examined in the cohort for which growth rate was estimated, it is not known whether snails do in fact breed at this age. Many littorinids reach maturity towards the end of the first year of growth (Borkowski, 1974; Gallagher & Reid, 1979; Muggeridge, 1979), as do *L. filosa* and *L. philippiana*. Most European *Littorina* species, however, do not breed until their second year (Moore, 1937; Williams, 1964; Moreteau, 1976; Goodwin, 1978).

In all the four *Littoraria* species examined, females showed faster growth rates and reached larger maximum sizes than males, although the time taken to reach maximum size was similar in each sex. This difference in growth rate adequately explains the observed sexual dimorphism in these species (Section 4.2), as found in growth studies of other members of the family (Moore, 1937; Lenderking, 1952, 1954; Borkowski, 1974; Underwood & McFadyen, 1983). There is no evidence of greater longevity of females, which has been said to account for sexual dimorphism in some European *Littorina* species (Pelseneer, 1926; Daguzan, 1977).

Growth rates showed conspicuous seasonal variation in each of the four species studied, but details of the seasonal pattern varied. Trends were similar in *L. intermedia* and *L. scabra*, in which the value of k showed close correlation with the mean monthly temperatures (Figs 13.17, 13.22). Since these species feed largely at the water level (Section 12.3.5), their activity should not be greatly limited by climatic conditions. Probably for this reason, their growth rates did not fall to such low levels in the dry winter season as did the rates of the two species from higher levels. However, the monsoonal rain may have restricted feeding activity in January 1981, when both *L. intermedia* and *L. scabra* showed a drop in growth rate.

The seasonal changes in growth rate of the two species from higher levels, *L. philippiana* and *L. filosa*, appear to reflect the seasonality of rainfall and breeding activity, which obscure the responses of growth rate to temperature change. Thus in *L. philippiana* the season of most rapid growth lasted from December until June, corresponding closely with the months of the year with significant rainfall. No noticeable fall in growth rate occurred in the very wet month of January, despite the fact that loss rates increased at that time (Fig. 13.15). Insufficient data were available to permit the investigation of growth rate of *L. philippiana* in the *Rhizophora* forest, but the size frequency distributions (Figs 13.6, 13.7) show that the species attained larger size in this habitat. This can probably be explained by the higher rate of survival (Table 13.5) and by faster absolute growth in a more favourable habitat, as suggested by the larger sizes of shells at varix formation. For seven months of the year, *L. filosa* showed the lowest growth rates of the four species (Figs 13.22, 13.23), in agreement with the idea that this species occupied the most rigorous habitat. As in *L. philippiana*, activity and therefore feeding of *L. filosa* may be dependent to a considerable degree upon atmospheric moisture (Section 12.3.1). That growth rates remained low from December to February, despite high rainfall during these months, is probably explained by the utilization of assimilated energy for the production of gametes during the maturation and spawning season from November until March (Figs 13.1, 13.2). Only from March to May were growth rates high in *L. filosa*, when conditions of temperature and rainfall were favourable and reproduction completed. In *L. philippiana* the effect of maturation and spawning was not obvious from the monthly values of k, although the small drop recorded for females in March may have been connected with recovery of the gonad for the second spawning episode. Amongst the individuals in their second and subsequent years, the slowing or cessation of growth during the breeding season was clearly shown by the formation of thickened and flared apertural lips.

These results, and the explanations suggested, are comparable with those from other studies of littorinid growth rates. Several authors have accounted for intraspecific variations in growth rates between shores in terms of microclimatic conditions, which determine the time available for feeding (Borkowski, 1974; Roberts & Hughes, 1980; Janson, 1982a) and similar differences have sometimes been found between levels on the same shore (Berry, 1961; Lambert & Farley, 1968). A simple explanation in terms of feeding time may not be adequate, since food quality may vary between habitats, and the rate of feeding may compensate for reduced feeding time (Underwood & McFadyen, 1983). Growth rates generally show seasonal variation, and often a strong dependence upon temperature (Roberts & Hughes, 1980; Hughes & Answer, 1982; Janson, 1982a), as was the case with *L. intermedia* and *L. scabra*. Inhibition of growth during maturation of the gonads has been described in several littorinids (Moore, 1937; Williams, 1964; Borkowski, 1974).

The formation of a thickened apertural lip in adult littorinids during non-growing phases was noted by Moreteau (1976) in *Littorina saxatilis*, but was not related to the breeding cycle. Certain species of the genus *Littoraria* are unique amongst littorinids in the formation of prominent varices on the body whorl of the shell (Section 4.1; Chapter 9). Sewell (1924) supposed that these were formed during adverse seasons when growth was arrested. At least in *L. filosa* and *L. philippiana*, it is clear that varices are formed annually, during the breeding period. In laboratory experiments, Bryan (1969) found that shortage of food, and consequent slow growth, induced apertural thickening in immature *Nucella lapillus*, and in *Littoraria* species diversion of energy from somatic growth into gamete production may have the same physiological effects. As discussed by Palmer (1981), calcification can continue in the absence of feeding, since the process is often not directly limited by its energetic cost. Such varices are not useful for determining the age structure of populations, since they are not formed in all individuals, and males show more prominent development of varices than females.

13.4.8 Summary of life history characteristics

The major features of the population dynamics, reproduction and growth of the four species of *Littoraria* can be summarized. *L. intermedia* and *L. scabra* showed similar characteristics and may be considered together. They inhabited low and middle zones respectively on *Rhizophora* trees, and fed mainly at the water level on most high tides. Significant growth occurred throughout the year and the breeding season was prolonged and probably continuous. The population density was low, and the main source of mortality may have been predation. Mortality of newly settled snails was especially high, and significant recruitment occurred only in late summer. Growth of small snails was rapid, and breeding may have commenced within 3 to 4 months from settlement in *L. intermedia*, or 6 to 8 months in *L. scabra*. Adults from 1 to 2 years of age tended to predominate in the populations at most times of the year, but few survived for more than 2 years.

In contrast, *L. filosa* occurred at high levels in the more rigorous environment provided by *Avicennia* foliage and branches. Periods of feeding activity were restricted by dependence upon atmospheric moisture and the highest tides, and little energy may have been available for either growth or reproduction outside the wet summer months. Consequently, the breeding season was restricted to two spawnings, in February and March, and somatic growth and maturation of the gonads were mutually exclusive. Settlement of larvae was highly successful, perhaps because few small grapsid crab predators (*Metopograpsus* species) inhabited *Avicennia* trees. Population density was high after recruitment. The subsequent mortality of small snails was severe, possibly because as they grew and moved to higher levels they were exposed to unfavourable conditions of insolation and desiccation, and in addition they may have been preyed upon by large swimming crabs (*Thalamita crenata*). Population size therefore declined rapidly following recruitment. The small snails grew relatively slowly through the dry winter months, and reproduced 11 months after settlement. The first year cohort dominated the population throughout the year, and very few individuals survived for more than one year, although maximum longevity may have been as great as 6 years.

L. philippiana exhibited some characteristics in common with each of the other species. It inhabited high levels of both *Rhizophora* and *Avicennia* trees. The habitat may have been less extreme than that of *L. filosa*, since the species was not found on upper leaf surfaces in full sunlight, but frequented trunks, branches and lower leaf surfaces. Activity was stimulated by rain, but *L. philippiana* may have been less dependent upon atmospheric moisture than *L. filosa*, because of its larger size, more shady habitat and the ability of adults to make excursions to the water level at high tides. Growth was greatest in the wet summer months, and spawning was restricted to two or three episodes. The inhibitory effect of reproduction on growth was not conspicuous in the population as a whole (Figs 13.20, 13.23), but was shown in snails in their second and subsequent years (Fig. 13.24). Recruitment was poor overall during the year of observation, but greater on *Avicennia* then on *Rhizophora* trees. Mortality was higher on *Avicennia* trees, though much lower than for *L. filosa*, and population size did not fluctuate greatly. Growth rate was intermediate and breeding began about 11 months after settlement. Adult snails in their second and later years dominated the population during the period of study. Few survived beyond 2 years, but maximum longevity may have been 6 years.

The four species (*L. scabra, L. intermedia, L. philippiana, L. filosa*) exhibited similar methods of development, embryos being brooded in the mantle cavity before release as small veligers. Brood sizes were possibly comparable in each (Section 13.4.3), but eggs and veligers were a little larger in *L. filosa*. Judging by the size of the protoconch, the length of planktotrophic life was similar in all of the species, perhaps of the order of one month.

The data on frequency of spawning and fecundity are incomplete, but the life histories of the four *Littoraria* species may be discussed in terms of the theories of life history strategy. As reviewed by Stearns (1976, 1977), there are two main theoretical approaches. The deterministic concept of r- and K-selection assumes constant mortality and fecundity, while the stochastic view, known as 'bet hedging', considers strategies in terms of fluctuations in these parameters. The former approach predicts the association of life history traits into two groups at the extremes of a continuum. In unstable environments, favouring rapid population growth, 'r-selection' should favour large reproductive effort, small and numerous offspring, early maturation, short generation time and low assimilation efficiency. In stable environments, where competition and predation are significant, 'K-selection' should favour the converse of these traits. The stochastic approach predicts the same combination of traits, but for different reasons (Stearns, 1977). Typically 'r-selected' traits are predicted in fluctuating environments where adult survival is more variable than that of offspring, and 'K-selected' traits where adult survival is the more predictable.

Littoraria filosa inhabits an environment that seems to be 'r-selecting', in which rigorous microclimatic conditions may produce density-independent mortality and corresponding fluctuations in population size. Since settlement of *L. filosa* appears to be successful, and subsequent mortality high, it could be argued that early juvenile survival is more predictable than survival later in life. Both stochastic and deterministic theories would predict traits associated with r-selection for this species. *L. intermedia* and *L. scabra* occupy a less rigorous environment. This could be considered more 'K-selecting', since although competitive effects are unlikely to be significant (Section 11.5.1), predation may well be the major source of mortality of both adults and juveniles, and population size is relatively constant. In both these species recruitment is unsuccessful for most of the year, while adults suffer relatively low mortality, so that the stochastic theory would also predict the occurrence of the traits associated with K-selection. From both theoretical points of view, it is unexpected that *L. filosa* produces fewer offspring during the year, that these are somewhat larger, and that individuals breed at a later age. This anomaly might be partially explained if an estimate could be made of reproductive effort, the proportion of assimilated energy allocated to reproduction (Hughes & Roberts, 1980b). Since the growth rate of *L. filosa* was lower and feeding time more restricted than in the other species, it is possible that reproductive effort was in fact higher, as expected on theoretical grounds.

It may, however, be a mistake to attempt to fit life history strategies into a rigid theoretical framework. Investigations of reproductive effort in prosobranchs with contrasting habitats and types of development have sometimes been adequately explained by existing theories (Grahame, 1977), but a recent report on the life histories of British littorinids concluded that strategies can best be interpreted by consideration of the physiology and natural history of each species (Hughes & Roberts, 1980b). Similar conclusions have been drawn from comparisons of reproductive strategies in populations of *Littorina saxatilis* in contrasting habitats (Faller-Fritsch, 1976; Hart & Begon, 1982). In the same way, in the present study the later maturity and brief reproductive season of *L. filosa* are dictated by the seasonality of the climate, while the prolonged breeding periods of *L. intermedia* and *L. scabra* may be necessitated by the intense predation upon small snails, despite the relative stability of the environment.

CHAPTER 14: PREDATION AND SHELL MORPHOLOGY

14.1 Introduction

The subjects of predation and gastropod shell form are intimately connected for two reasons: firstly, because predation has been one of the significant selective forces acting on shell morphology, and secondly, since during the past dozen years the synthesis of ideas concerning the adaptive significance of shell form, especially in relation to crushing predation, has largely been the work of G.J. Vermeij (review by Vermeij, 1978). Drawing on worldwide experience, Vermeij has demonstrated consistent morphological patterns along latitudinal and shore level gradients, and between marine zoogeographical provinces, and has interpreted these in terms of both antipredatory devices (Vermeij, 1979a, b) and as adaptations to desiccation and temperature stress in the intertidal zone (Vermeij, 1973a).

The potential predators of gastropods have been reviewed by Vermeij (1978), and Pettitt (1975) has gathered literature records of predation upon the genus *Littorina* in the north Atlantic. Predation by fish on gastropods has been reviewed by Palmer (1979), but most attention has been concentrated upon crabs as predators (Vermeij, 1977a, 1982a; Zipser & Vermeij, 1978; Bertness & Cunningham, 1981; and others). Predation by birds is also a possibility in the intertidal zone (Pettitt, 1975) and will be considered further in Chapter 15.

The methods of attack used by crab predators have been described in detail for many species, and fall into two main categories: crushing of the whole shell or spire, if the prey is relatively vulnerable, or a rather specialized 'peeling' of the body whorl beginning at the aperture, if the prey is large and strong (Rossi &

Parisi, 1973; Hamilton, 1976; Vermeij, 1978, 1982a; Zipser & Vermeij, 1978; Hughes & Elner, 1979). In the most specialized molluscivorous crabs, the chelae are usually conspicuously dimorphic, one a massive master claw with proximal teeth, the other a more slender cutter claw (Shoup, 1968; Vermeij, 1977a; Bertness & Cunningham, 1981). The predation strategy of the shore crab, *Carcinus maenas*, has been shown to conform to the expectations of optimal foraging theory when feeding upon mussels, an abundant prey item (Elner & Hughes, 1978; Jubb *et al.*, 1983). When feeding upon sparsely distributed snails of relatively unpredictable energy value, this crab attacks all prey encountered, rejecting resistant shells after a set persistence time (Hughes & Elner, 1979; Elner & Raffaelli, 1980).

The proximate result of predation by crabs on gastropods may be mortality, but if a proportion of attacks are unsuccessful, the ultimate effect may be selection for improved antipredatory defence (Vermeij, 1982c). As agents of mortality, predators may influence population and community structure. Although these effects are understood in the cases of some sessile intertidal forms, such as barnacles and mussels preyed upon by crabs, starfish and thaids (Connell, 1970; Paine, 1974; Menge, 1983), there is relatively little corresponding information for gastropods. The influence of crushing predators, and particularly of crabs, upon gastropods has largely been considered in an evolutionary context, as a force of selection. The possibility of behavioural adaptation to predation pressure is discussed in Section 12.4.1. Structural adaptation is better understood, and may involve such features as narrow or toothed apertures, strong sculpture, large size and increased shell thickness (review by Vermeij, 1978). The adaptive significance of such properties has been shown by laboratory predation trials (Reynolds & Reynolds, 1977; Zipser & Vermeij, 1978; Palmer, 1979; Bertness & Cunningham, 1981; Vermeij, 1982a), and is supported by estimations of mortality caused by crushing (Vermeij, 1979b, 1982a). In addition, indirect evidence is available from correlations between shell form and crab abundance amongst populations of some species with direct development (Ebling *et al.*, 1964; Kitching & Lockwood, 1974; Heller, 1976; Raffaelli, 1978b; Vermeij, 1982b), and from the simultaneous appearance of powerful predators and armoured prey in the fossil record (Vermeij, 1977b). Selection by predators may also influence aspects of the life history of the prey, especially when, as in gastropods, there is a fundamental interrelationship between size, growth rate and skeletal thickness (Vermeij, 1978; Palmer, 1981).

The geographical patterns in the incidence of antipredatory architecture in gastropods are in agreement with the widespread belief that predation pressure increases towards the tropics (Vermeij, 1978, 1979a; Vermeij & Currey, 1980). The diversities of both molluscivorous crabs (Vermeij, 1977a) and of shell-crushing fish (Palmer, 1979) increase at lower latitudes. Tropical crabs may be more specialized for crushing (Zipser & Vermeij, 1978), although whether they are relatively more powerful is disputed (Abele *et al.*, 1981). It has been shown that, within certain tropical habitats, snails from the Indo-Pacific province bear the most heavily armoured shells, suggesting that crushing predation may be most intense in that region (Vermeij, 1974, 1976, 1979a; Vermeij *et al.*, 1980), although this trend is not evident in assemblages from mangroves (Vermeij, 1974, 1978). The present study does not address large scale geographical patterns, but they must be considered when making comparisons with studies in other parts of the world.

It is unfortunate that much of the evidence for the importance of predators as agents of mortality and selection is indirect. This is to some extent unavoidable, since predation is rarely observed and difficult to study in the field. Exclusion cages have yielded useful results in studies of abundant sessile animals in the intertidal zone (Connell, 1970; Menge, 1983), but the low density of gastropods often renders the use of such cages impracticable. Samples of dead shells can be collected in some subtidal habitats and the incidence of lethal predation assessed (Vermeij, 1979b, 1982a), although in the intertidal zone dead shells are rapidly washed away. Laboratory predation trials have demonstrated the crushing capabilities and foraging strategies of predators, but may be criticised for their artificiality. A new and potentially useful technique is the estimation of the intensity of sublethal damage from the frequency of repaired injuries in samples of shells (Vermeij, 1982a; Vermeij *et al.*, 1980). The data must, however, be interpreted carefully, and this technique is considered in detail in Section 14.4.3.

The majority of previous work on predation and shell form has been carried out on rocky shores or reefs. Hitherto, there has been no detailed study of predation upon gastropods in mangrove swamps, and very few in any tropical marine habitats. The species of *Littoraria* associated with mangroves provide an interesting case for study, since four or more congeneric species can commonly be found together, with different assemblages in various regions of the tropics. The species are rather distinctly zoned (Chapter 11) and each assemblage can be examined in relation to shore level gradients in predation pressure and microclimatic conditions, to search for consistent trends in shell morphology.

14.2 Methods

14.2.1 Occurrence and distribution of potential predators

Records were kept of all potential predators observed in the mangrove habitat during the course of field work at Cockle Bay.

The distribution of tree-climbing crabs of the genus *Metopograpsus* was recorded in detail during the 24 hour study of the behaviour of *Littoraria* species (Section 12.2). Ten *Rhizophora* trees were chosen in the seaward half of the *Rhizophora* grove, and ten *Avicennia* trees in the open area behind (see Chapter 10 for description of study site). Every hour the numbers of crabs visible in successive 0.5 m vertical zones above the ground were recorded.

14.2.2 Caging experiments using *L. filosa*

The relative importance of predation as a source of mortality was examined in *L. filosa* by setting up a series of exclusion cages. Five isolated *Avicennia* bushes, each about 1.5 m tall and with a canopy diameter of 1.2 m, were selected on the basis of similarity of size, shape and situation. Initially, all *L. filosa* present on each experimental tree were collected, down to a minimum size of 4 mm, sorted in the laboratory into size classes (≤7.0, 7.1-12.0, 12.1-17.0, ≥17.1 mm) and scored for shell colour (YO or otherwise, see Section 15.2). Identical populations were then released on each tree, at densities and colour proportions equivalent to those of the pooled natural populations of the experimental trees.

Snails of two size classes were released, 7.1 to 12.0 mm, and larger than 17.1 mm. The numbers in the smaller size class were equal to the average number in the same size class in the natural populations. The larger size class was released in numbers equal to those of snails larger than 12.1 mm in the natural population. Since no snails in the size range 12.1 to 17.0 mm were released, the overall density of snails larger than 7.0 mm in the artificial populations was the same as that occurring naturally. This design was adopted to ensure that growth of snails during the experiment did not affect the distinction between the two size classes. In the smaller size class 21 yellow (colour code YO, Section 15.2) and 44 brown (colour codes Y3, B4 and B5) snails were released on each tree, and in the larger size class 10 yellow and 15 brown. Each snail was marked with a small spot of white ink (about 0.5 mm in diameter), using the method described in Section 13.2.2, so that immigrant snails could be distinguished.

The cage specifications and inferred sources of mortality are shown in Figure 14.2. Nylon netting of mesh size 10 mm was used to exclude crabs and birds, and 50% black nylon shade cloth used to shade tree number 5 from direct sunlight. The netting was supported on a square aluminium framework, and care was taken to ensure that the foliage did not touch the sides of the exclosure. The artificial populations were released on 14 July 1981 and every 30 days for 4 months thereafter the surviving snails were collected. All snails lost, and any of the smaller size class which had grown too large, were replaced at each visit. Unmarked snails were recorded as immigrants. For trees 4 and 5 the numbers of fallen leaves within the cages were counted, and numbers of leaves on the trees estimated, in order to assess leaf fall as a possible source of loss of snails.

To examine the possible effects of submergence on survival, on two occasions 13 *L. filosa* were released on an *Avicennia* seedling at ground level, confined in a sleeve of fine (2 mm mesh) nylon netting. An equivalent number were released on an unprotected seedling close by. Survival was determined after one month.

For comparison with an experiment designed to investigate apostatic selection (Section 15.3), an additional *Avicennia* bush was stripped of about 80% of its leaves and maintained in this condition by regular defoliation. The bush was enclosed in a complete cage of nylon netting, and the survival of an artificial population of snails was monitored as described above.

No comparable exclusion experiments could be performed for the several species on *Rhizophora* trees, because of the large size and complex root systems of these trees, and the low natural density of the snails.

14.2.3 Laboratory predation trials

Laboratory predation trials were conducted to determine whether the three most common crab species in the mangrove habitat at Cockle Bay were able to prey upon *Littoraria* species. Eight specimens of *Metopograpsus latifrons*, and two each of *Thalamita crenata* and a *Clibanarius* species, were kept individually in tanks 30 by 15 and 25 cm high. The tanks were filled to a depth of 5 cm with recirculating sea water and each contained a tripod of *Rhizophora* roots on which the crabs could climb. In the preliminary trials crabs were supplied on alternate days with five prey, covering a range of snail sizes and species.

Using the eight *Metopograpsus*, selected to cover a wide range of size, the relationship between size of the predator and maximum size of the prey was investigated. Two prey species, *L. articulata* and *L. filosa*, were used in the trials, since these were respectively the species with the thickest and thinnest shells at Cockle Bay, and both were abundant, making a wide size range of each readily obtainable. Crabs were fed individually by placing the prey within reach, and were supplied with prey at the rate of one snail per day, considerably below the level of satiation. The two snail species were supplied on alternate days. Maximum prey sizes were determined by gradually increasing the size of the snails offered.

14.2.4 Analysis of repaired shell breakages

Unsuccessful predation attempts by crabs often result in a V-shaped or jagged breakage of the outer apertural lip of the shell. With further growth of the shell such breakages remain as conspicuous scars, which are distinct from the regular axial growth lines. The shell therefore preserves a record of damages sustained throughout the life of the snail. While the incidence of repaired breakages may not be proportional to the occurrence of successful predation, it does provide a measure of the intensity of sublethal shell damage (Vermeij, 1982a, b).

Previous authors have used as an index of repair the proportion of shells bearing scars in a sample (Raffaelli, 1978b; Elner & Raffaelli, 1980), or have calculated the mean number of scars per shell (Vermeij, 1982a, b). In the present study the method was refined by recording the number of repaired breakages on each whorl of the shell. Whorl number was defined as the number of revolutions beyond the sinusigera ridge marking the end of the protoconch (Section 4.3). On the last whorl, scars were counted only on complete half-revolutions. Samples used for the analysis comprised only adult shells with thickened apertural lips, and were collected at Cockle Bay during January and February 1981. The mean numbers of repairs per shell were compared by means of t-tests, in samples of each species from *Avicennia* and *Rhizophora* trees.

It is difficult to make comparisons between species when data are in the form of repair frequency per whorl, owing to differences in the geometry of shell coiling and in the rate of growth (Section 14.4.3). Samples of approximately 40 snails, covering the complete size range of each species, were used to estimate the relationship between shell height and whorl number. From the resulting regressions, sizes at the start of each whorl were calculated, and the measured growth rates (Figs 13.18 to 13.21) used to predict the time in months for the addition of each whorl to the shell. The number of repairs per whorl was divided by the time span represented by each revolution, to obtain a measure of the rate of sublethal damage per unit time.

14.2.5 Shell morphology and the zonation of species

Morphological characters of the shell were examined in relation to zonation patterns along each of the transects described in Chapter 11. At each locality random samples of all *Littoraria* species present were taken, by collecting individuals along the length of the transect. The animals were removed completely from the shells after boiling. From these collections, ten adult shells (i.e. with thickened or flared apertural lip) of each sex of each species were chosen at random. For the uncommon species, sample sizes were sometimes smaller. For each specimen, shell height (H), breadth (B), aperture length and width (LA and WA) were measured to 0.1 mm with vernier calipers (Fig. 3.1). The mass (M) of each clean, dry shell was measured to 0.001 g. The volume (V) of each was measured by filling the shell with small ball bearings, plugging the aperture with plasticine level with the peristome, and submerging the specimen in a dilute detergent solution in the reservoir of an apparatus designed to measure volume by displacement of fluid. The meniscus level in the reservoir was adjusted to its previous level, through a graduated eyepiece, by drawing fluid into a graduated capillary using a syringe. An accuracy of 0.01 cm^3 was obtained, as established by adding measured volumes of water to the displacement reservoir. The following indices of shell shape were calculated:

Shell proportion	PR = H/B
Apertural circularity	S = WA/LA
Relative spire height	SH = H/LA
Thickness index	TI = M/V

Several measures of shell thickness have been employed by previous authors, including direct measurement of lip thickness (Raffaelli, 1978b; Vermeij, 1982d) and mass divided by shell volume (Kitching & Lockwood, 1974; Hughes, 1979b; Vermeij & Currey, 1980; Naylor & Begon, 1982). Direct measurement is only accurate in species lacking prominent external sculpture, and suffers from the serious difficulty that lip thickness varies considerably with growth activity (Section 13.3.3). For these reasons, direct measurement was unsuitable in the present study, and the index of thickness used was mass divided by volume. The index was not converted to a relative measure of thickness by division by shell height, since shell strength is proportional to the square of absolute thickness (Vermeij & Currey, 1980). Shell volume has in the past been estimated as the product of shell length and breadth squared (Vermeij & Currey, 1980; Naylor & Begon, 1982), as internal shell capacity (Kitching & Lockwood, 1974) or by displacement (Hughes, 1979b). Clearly the displacement method, as employed here, will provide the most precise measure.

The species at each locality were subjectively ranked in order of increasing prominence of external shell sculpture.

The order of zonation of species at each locality was quantified in three ways, as height above the ground, height above chart datum, and as horizontal distance from the seaward edge of the forest (transect station 0). The vertical level of a species at each station on a transect was taken as the mid point of the vertical range, and the overall level calculated as the mean of these levels, weighted by the relative abundance of the species at each station. Where data were available for several tree species at a station, only those from the tree with the greatest abundance of the snail species were used. Horizontal distribution was quantified in a similar way, as the mean distance from the seaward edge of all stations, weighted by the abundance of the species at each.

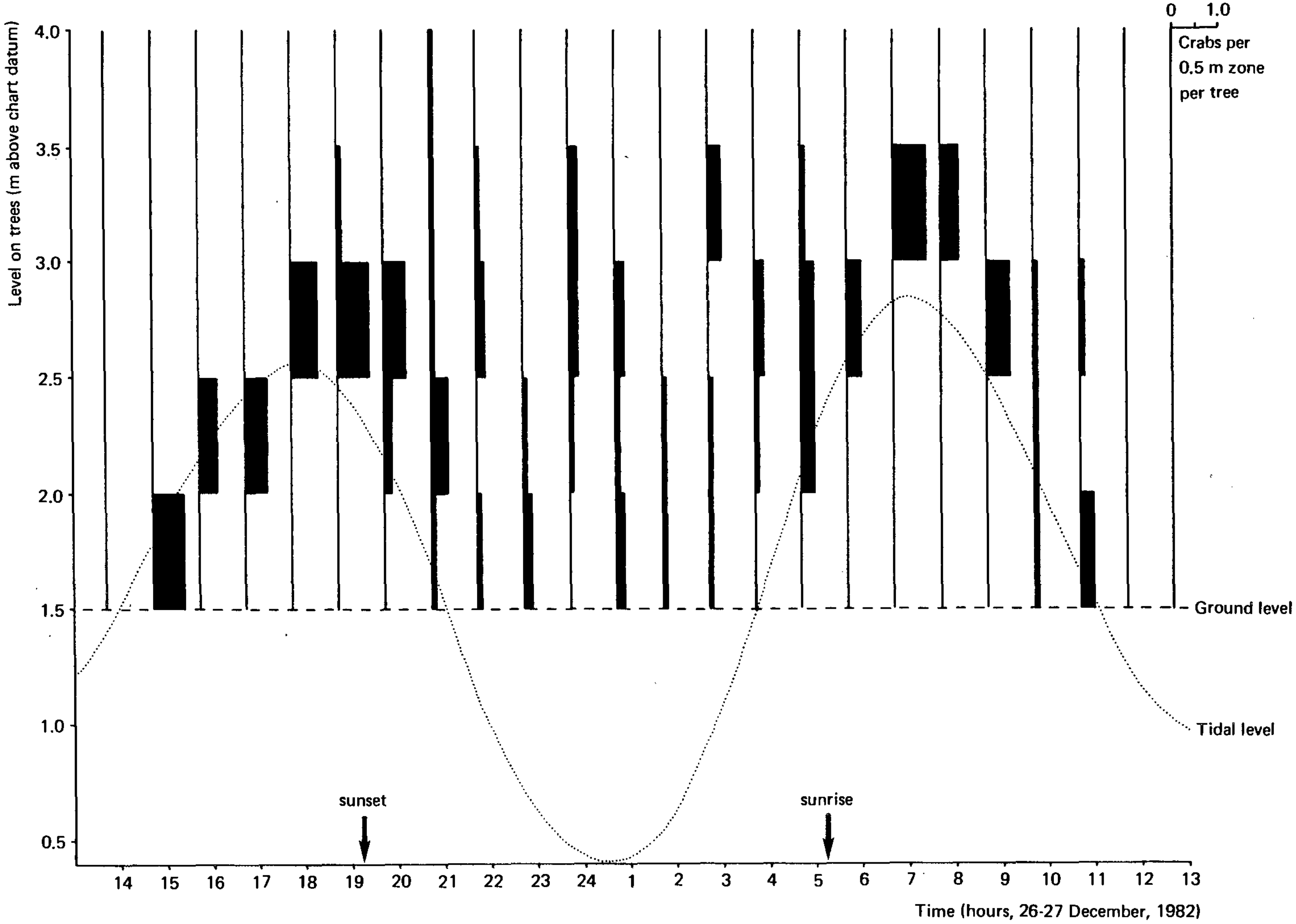
Associations between shell characters and zonation patterns were investigated by the computation of Spearman rank correlation coefficients, using all the individual measurements of the shape indices (Zar, 1974). Multiple correlation was not attempted, because the three potential independent variables (the zonation parameters) were all related to the tidal level on the transect, and were therefore highly correlated. The measures of zonation employed provide only a ranking of the species at each locality on the date of observation. As shown in Chapter 12, zonation levels are considerably affected by the spring tide cycle, by rainfall and by shell size, although the relative zonation patterns are usually maintained. Thus while rank correlation within localities was justified, it was not possible to standardize measures of zonation in terms of the tidal range in order to combine or compare data from different localities.

14.3 Results

14.3.1 Field observations of potential predators at Cockle Bay

Of the crab species occurring amongst the mangrove trees at Cockle Bay, the species seen most frequently was *Metopograpsus latifrons* (White). This is a species typically associated with mangroves (Macnae, 1968) and was abundant on the prop roots and trunks of trees in the *Rhizophora* grove at the study site. The species seldom had a carapace width exceeding 35 mm. Although probably the most important crustacean predator of the *Littoraria* species, predation by *M. latifrons* was only seen in the field on one occasion, when an individual of carapace width 25 mm was observed on a *Rhizophora* trunk 1.2 m above the ground, where it was consuming a 25 mm *L. filosa*, having chipped away half of the body whorl to reach the snail within. *Metopograpsus frontalis* Miers, a similar species only distinguishable from *M. latifrons* by close examination (Bannerjee, 1960), was occasionally found on the mangrove trees, but was much more common on sheltered rocky shores. As an indication of the abundance of these two species, up to eight unidentified individuals were seen on ten *Rhizophora* trees in an area of 20 m^2 near the outer edge of the *Rhizophora* grove during the 24 hour observation period on 26 and 27 December, 1982 (Fig. 14.1). The two species were uncommon on the isolated *Avicennia* trees behind the

Fig. 14.1 Vertical distribution of *Metopograpsus* species in *Rhizophora* forest at Cockle Bay over 24 hours, 26 to 27 December, 1982.



Level on trees (m above chart datum)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0
1.0
Crabs per 0.5 m zone per tree
Ground level
Tidal level
sunset
sunrise
14 15 16 17 18 19 20 21 22 23 24 1 2 3 4 5 6 7 8 9 10 11 12 13
Time (hours, 26-27 December, 1982)

Rhizophora grove, and during the observation period none was seen on ten *Avicennia* trees in this area. Observation of the ten *Rhizophora* trees throughout the 24 hour period showed that the crabs were not visible during the low tide at midday, were found just above the water level during the remaining daylight hours, and were distributed from ground level to a height of 2.5 m during the nocturnal low tide (Fig. 14.1). An additional species, *Metopograpsus thukuhar* (Owen), was recognizable by its characteristic colouration. It was rarely seen on trees at the seaward edge of the forest, but was more common inside rotten logs at ground level within the forest.

The portunid *Thalamita crenata* (Latreille) was commonly seen foraging at ground level while the area was submerged. This swimming crab may, however, be a significant predator of *Littoraria* species. This was suggested by the observation of a specimen clinging to a *Rhizophora* sapling at the water surface when the water depth was 1 m; the crab moved around the trunk several times, reaching up repeatedly with the chelae, and clambered to 10 cm above the surface, although no snails were within reach. *Thalamita crenata* reached a carapace diameter of 50 to 80 mm, and successfully attacked *Littoraria* species in laboratory trials. Another portunid crab occasionally seen in the study area was the very large *Scylla serrata* (Forskål). No attempts at predation on *Littoraria* species were observed. Remains of shells of the large potamidid *Telescopium telescopium* were common beside a burrow, 30 cm in diameter, of *S. serrata* near the study site, and many of these showed broken spires.

Several individuals of an unidentified xanthid crab, up to 50 mm in carapace diameter, were found in holes in trees and inside logs near ground level. Whilst dimorphic chelae suggested a molluscivorous habit (Vermeij, 1977a), the short legs and heavy carapace were ill adapted for tree climbing. The only remaining potential crustacean predators seen at the study site were large pagurids of the genus *Clibanarius*, which inhabited *Terebralia* and *Telescopium* shells. These pagurids were common and able to climb up

Table 14.1 Birds seen in mangrove forest at Cockle Bay. Records from casual observations on 39 days from April 1980 until October 1981.

Species[A]		Number seen	Habitat[B]		
			A	R	G
Little Pied Cormorant	(*Phalacrocorax melanoleucos*)	1		+	
Eastern Reef Egret	(*Egretta sacra*)	3		+	+
Striated Heron	(*Butorides striatus*)	1		+	
Sacred Ibis	(*Threskiornis aethiopica*)	5		+	+
Brahminy Kite	(*Haliastur indus*)	1		+	
Grey-tailed Tattler	(*Tringa brevipes*)	1		+	
Peaceful Dove	(*Geopelia placida*)	9	+	+	
Torresian Imperial-Pigeon	(*Ducula spilorrhoa*)	1		+	
Gould's Bronze-Cuckoo	(*Chrysococcyx russatus*)	4	+	+	
Sacred Kingfisher	(*Halcyon sancta*)	3		+	
Collared Kingfisher	(*Halcyon chloris*)	6		+	
Little Kingfisher	(*Ceyx pusilla*)	2		+	
Black-faced Cuckoo-shrike	(*Coracina novaehollandiae*)	2		+	
Varied Triller	(*Lalage leucomela*)	20	+	+	
Rufous Whistler	(*Pachycephala rufiventris*)	1		+	
Little Shrike-thrush	(*Colluricincla megarhyncha*)	2		+	
Leaden Flycatcher	(*Myiagra rubecula*)	14	+	+	
Shining Flycatcher	(*Myiagra alecto*)	2		+	
Grey Fantail	(*Rhipidura fuliginosa*)	4	+	+	
Willie Wagtail	(*Rhipidura leucophrys*)	1		+	
Mangrove Gerygone	(*Gerygone levigaster*)	2		+	
Helmeted Friarbird	(*Philemon buceroides*)	36	+	+	
Dusky Honeyeater	(*Myzomela obscura*)	2		+	
Yellow-bellied Sunbird	(*Nectarinia jugularis*)	8	+	+	
Mistletoebird	(*Dicaeum hirundinaceum*)	1	+		
Figbird	(*Sphecotheres viridis*)	2	+		
Spangled Drongo	(*Dicrurus hottentottus*)	2		+	
Pied Currawong	(*Strepera graculina*)	6	+	+	
Torresian Crow	(*Corvus orru*)	2	+		+

[A] nomenclature after Royal Australian Ornithologists' Union (1978); identifications from Pizzey (1980).

[B] A, observed in *Avicennia* trees; R, in *Rhizophora* trees; G, on ground.

to 1 m above the ground. In laboratory trials they manipulated, but did not crush, shells of the fragile *L. filosa* 5 mm in length, although they consumed snails removed from their shells.

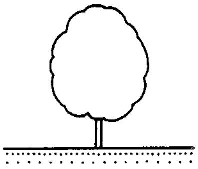
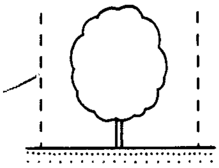
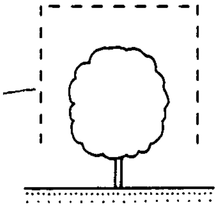
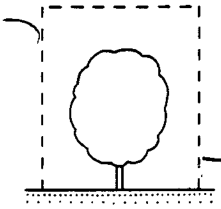
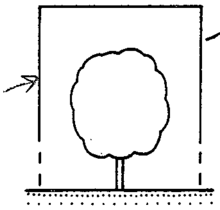
Birds were observed infrequently at the study site, but over an 18 month period of casual observations 31 species were recorded (Table 14.1). During this time only one predation attempt was observed, when a Figbird hammered a yellow *L. filosa* (approximately 25 mm in length) on an *Avicennia* branch, but did not succeed in breaking the shell. Of the commoner species at Cockle Bay, the most likely predators were Helmeted Friarbirds and Varied Trillers, both of which foraged amongst the foliage of *Avicennia* and *Rhizophora* trees even at low levels, and were seen to catch large mantis, spiders, crickets, cockroaches and small crabs, which were hammered on branches before being eaten.

Brushtail possums were occasionally seen in the mangroves, and the tracks of water rats were found. Fish entering the forest at high tide included molluscivorous rays. The only carnivorous mollusc present on the mangrove trees at Cockle Bay was *Morula granulata* (Duclos), but this species was only observed to feed upon oysters (*Saccostrea* and *Isognomon* spp.).

14.3.2 Sources of mortality of *L. filosa*

The survivorships of small (7-12 mm) and large (≥17 mm) individuals of *L. filosa* under the different caging regimes are shown in Figure 14.2. For the small snails, a two-way analysis of variance of the arcsine-transformed survivorships recorded each month on each tree showed significant differences between trees, but not between months ($F = 0.74$, d.f. = 3,19, $P = 0.551$). The survivorships for each of the four successive months were therefore used as replicates of the caging regimes. The subsequent one-way

Fig. 14.2 Design and results of the exclusion cage experiment at Cockle Bay, to determine sources of mortality of *Littoraria filosa* on *Avicennia* trees. A: broken line indicates 10 mm nylon mesh, solid line 50% shade cloth. B: components of survivorship from sources of mortality: B, birds; C, crabs; D, death from other sources including desiccation; E, loss by emigration; H, loss ascribed to direct insolation and prevented by shading.

Cage design[A]	Tree number	Components of survivorship[B]	Mean survivorship per month of snails in size class 7-12 mm (with 95% confidence limits)	Mean survivorship per month of snails in size class 17 mm (with 95% confidence limits) ⓒ	
			Small	big	
	1	C x B x H x D x E	0.687 (0.531 – 0.825) ④	0.940 (0.756 – 1.000)	③
good 	2	B x H x D x E	① 0.861 (0.666 – 0.979) best	0.985 (0.881 – 1.000)	②
worst 	3	C x H x D x E	⑤ 0.656 (0.484 – 0.809) worst	worst 0.892 (0.825 – 0.944)	⑤
= to no cover!  1 cm mesh	4	H x D x E	③ 0.794 (0.628 – 0.920)	0.932 (0.724 – 1.000)	4
shade cloth good 	5	D x E	0.827 (0.703 – 0.923) ②	0.995 (0.913 – 1.000) best	①

1 m

analysis of variance again showed significant differences between trees (F = 3.374, d.f. = 4,19, P = 0.037), but a Student Newman Keul's multiple range comparison test did not distinguish between the treatments. This latter result is not surprising in view of the variability in survivorship, as indicated by the 95% confidence ranges (Fig. 14.2).

The variability of the data precludes rigorous statistical treatment, but the mean survivorships of snails in the exclosures show a consistent pattern from which inferences can be drawn. The close similarity in survivorship on trees 2, 4 and 5 on one hand, and on trees 1 and 3 on the other, suggests that exclusion of birds and shading of the tree had little effect on snail survival, but that predation by crabs was significant. Assuming that survivorships from crabs and other sources are multiplicative, then dividing the mean survivorship on trees 1 and 3 (0.673, mean of arcsine transformed values) by that on trees 2, 4 and 5 (0.828) gives a figure of 0.813 for the component of survivorship which can be ascribed to crabs (Fig. 14.2). The corresponding proportional loss caused by crabs (1 minus 0.813) can be expressed as a percentage of the total loss (1 minus mean survivorship on trees 1 and 3). Thus it can be estimated that the loss due to predation by crabs comprised 57% of the total loss, equal to 19% of the artificial population per month. This treatment assumes that all snails present on the trees were found at each visit. Although this may not have been the case, the probability of recapture of snails on the small experimental trees was probably higher than that on the larger trees used for the mark and recapture experiment (Tables 10.1, 13.4).

The sources of the remaining 43% of the loss are unclear. Bird predation was apparently insignificant; in fact access by birds appeared to enhance survival by between 5 and 8 % (survivorship on tree 1 divided by that on tree 2 = 105%; for trees 2 and 4 = 108%). Shading of tree 5 produced a negligible enhancement of survival, so that there is little evidence that direct insolation caused death under natural conditions. Partial defoliation of a completely caged tree produced the lowest survivorship of 7 to 12 mm snails (mean 0.568, 95% confidence range 0.331–0.790; of snails ≥12 mm 0.970, 95% confidence range 0.961–0.978). Emigration was probably a significant source of loss. If immigration and emigration rates are assumed to be equal, the rate of appearance of unmarked immigrant snails of the same size class can be used as an estimate of emigration. Based upon this assumption, the loss by emigration accounted for 34% of the total loss. In making this estimate, the immigration rate was averaged over all the experimental trees, because inspection of the data did not reveal any correlation between caging regime and immigration rate. Counts of leaf fall for trees 4 and 5 showed that only 10% of the leaves were lost each month, too few to account for the high level of emigration. Assuming a 34% loss by emigration, and therefore total mortality amounting to 66% of the total loss, crab predation accounted for 86% of the mortality in the 7 to 12 mm size class.

The loss rates of snails in the larger size class (≥17 mm) were too low for analysis, for out of a possible total of 500 snails, only 33 (or 7%) were lost.

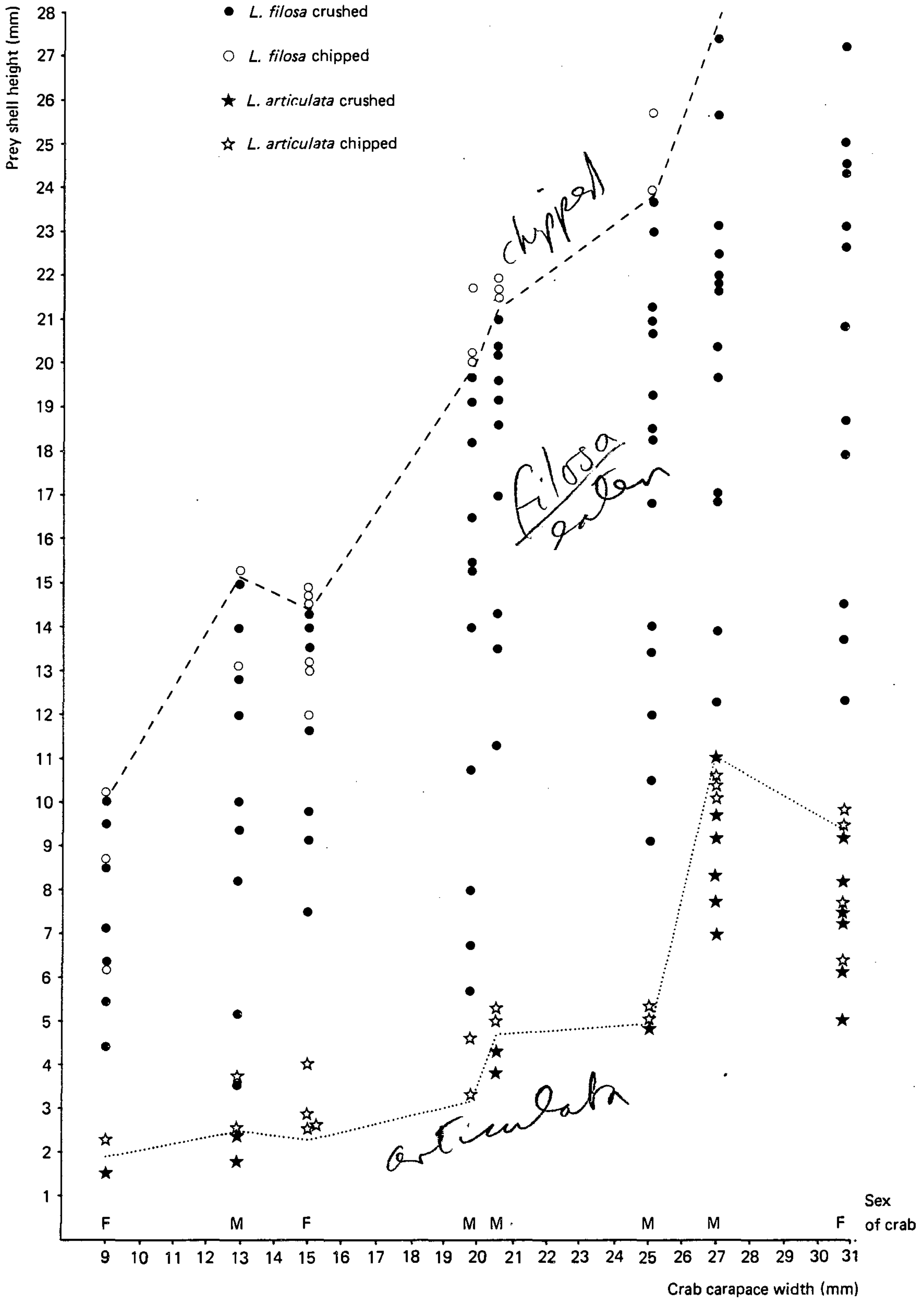
Of the *L. filosa* confined in sleeves at ground level, no mortality occurred, although on seedlings unprotected by netting all snails disappeared.

14.3.3 Laboratory predation trials

The two *Thalamita crenata* used in the predation trials were of average size for the species (55 and 57 mm carapace width) and both successfully attacked and ate all snails that were offered, including the largest *L. scabra* and *L. philippiana* (30 mm). The chelae were large and dimorphic, the larger right chela of the crab of carapace width 57.5 mm measuring 41.2 mm in length and 17.6 mm in maximum depth. During attacks shells were manipulated by the mouthparts and the more slender left chela, and crushed across the aperture by the master chela, in such a way that the massive molar of the dactyl broke away pieces of the outer apertural lip. Sometimes the *T. crenata* were seen to crush shells across the spire whorls in order to extract the last pieces of flesh. These crabs were voracious, one consuming 16 *L. articulata* and *L. filosa* from 10 to 20 mm in length in the space of 30 minutes.

Predation by *Metopograpsus latifrons* was investigated in more detail, since this crab was probably the major predator of *Littoraria* species. The chelae were squat, relatively smaller and less obviously dimorphic than in the portunid, the larger claw measuring 16.1 by 8.7 mm in a crab of carapace width 30.7 mm. The opposing surfaces of the chela lacked the specialized arrangement of proximal crushing molars, but bore only small serrations along their entire length. In the laboratory, crabs were seen to attack snails crawling on the tripods of mangrove roots in the experimental tanks, and were also quick to seize snails floating on the surface. Peeling by crushing across the aperture, as described above, was only practised on relatively small and weak prey. By far the most common method of attack was a gradual nibbling away of the body whorl from the outer lip of the aperture, sometimes through one entire revolution of the shell, until the animal within could be extracted. The process was slow, the largest crabs taking as long as 4 hours to consume the largest *L. filosa*. In the early stages of attack, peeling as practised by either *Thalamita* or *Metopograpsus* resulted in similar jagged V-shaped gashes on the shell lip. It was noted that when a shell was close to the maximum size successfully attacked by a particular *Metopograpsus*, the presence of a thickened and flared aperture was sometimes an effective protection against lip peeling. Not uncommonly the apical whorls of the spire were crushed in addition to peeling from the aperture. The maximum size of the *L. filosa* successfully attacked showed a close correlation with crab carapace width (Fig. 14.3); the crabs successfully manipulated and attacked snails equal in length to their own

Fig. 14.3 Results of laboratory predation trials in which *Littoraria filosa* and *L. articulata* were preyed upon by eight *Metopograpsu latifrons* of various sizes. Symbols: closed circles, *L. filosa* successfully crushed; open circles, *L. filosa* chipped (sublethal damage); closed asterisks, *L. articulata* successfully crushed; open asterisks, *L. articulata* chipped; broken line, approximate maximum size of *L. filosa* successfully crushed; dotted line, approximate maximum size of *L. articulata* successfully crushed; prey offered but not damaged are not shown.


● L. filosa crushed
○ L. filosa chipped
★ L. articulata crushed
☆ L. articulata chipped
Prey shell height (mm)
28
27
26
25
24
23
22
21
20
19
18
17
16
15
14
13
12
11
10
9
8
7
6
5
4
3
2
1
F
M
F
M
M
M
M
F
Sex of crab
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
Crab carapace width (mm)
chipped
filosa
eaten
articulata

carapace width, and twice the size of their chelae. The attack success rate was high, 93% of attacks on snails smaller than the maximum size being successfully completed.

Specimens of *L. articulata* (with a thicker shell than *L. filosa*, Section 14.3.5) were immune from successful attack by *Metopograpsus* at a much smaller size than *L. filosa* (Fig. 14.3). Several of the crabs were unable to crush the *L. articulata* which they manipulated, and ignored snails of smaller size. However, all consumed animals of *L. articulata* which had been removed from their shells.

14.3.4 Incidence of repaired shell breakages

All *Littoraria* species at Cockle Bay showed very high frequencies of repaired shell injuries, indicating unsuccessful predation attempts (Tables 14.2, 14.3). The mean numbers of repairs per adult shell ranged from 0.661 to 3.476. In the four species (*L. filosa*, *L. articulata*, *L. scabra*, *L. philippiana*) of which at least a few specimens could be found on both *Rhizophora* and *Avicennia* trees, the mean number of repairs per shell was highest on the former, the difference being significant in three cases (Table 14.2). The frequencies of repair of these four species fell into the same ranking order on both tree species (from lowest to highest, as listed above). When scored on each whorl of the shell, it was found that the frequency of repair often increased with whorl number, although *L. scabra* and *L. philippiana* showed a more complex bimodal pattern on *Rhizophora* trees (Fig. 14.4).

There are many confounding variables to be considered in the interpretation and comparison of the incidence of repair per whorl (Section 14.4.3). Two difficulties may be overcome by recasting the data. Since whorl number does not correspond to the same shell height in each species, the regressions given in Table 14.4 were

Table 14.2 Comparison of mean numbers of repaired breakages per shell in *Littoraria* species on *Avicennia* and *Rhizophora* trees at Cockle Bay. Samples as in Figure 14.4.

Species	Mean number of repairs per shell (±95% confidence limits)		t	d.f.	P
	Avicennia	*Rhizophora*			
L. filosa	0.661 (±.170)	1.273 (±.367)	3.44	152	0.001 **
L. philippiana	2.500 (±.525)	3.476 (±.495)	2.68	150	0.008 **
L. scabra	2.385 (±.536)	2.980 (±.614)	1.47	99	0.146
L. intermedia	-	3.221 (±.330)	-	-	-
L. articulata	0.949 (±.276)	1.364 (±.304)	2.03	112	0.045 *

Table 14.3 Proportions of shells of *Littoraria* species at Cockle Bay showing one or more repaired breakages on the last two whorls. (For comparison with records in the literature, see Section 14.4.2). Samples as in Figure 14.4.

Species	Proportion of shells with repairs	
	on *Avicennia*	on *Rhizophora*
L. filosa	0.339	0.643
L. philippiana	0.588	0.571
L. scabra	0.500	0.592
L. intermedia	-	0.800
L. articulata	0.458	0.709

Table 14.4 Regressions of shell height on whorl number for *Littoraria* species at Cockle Bay.

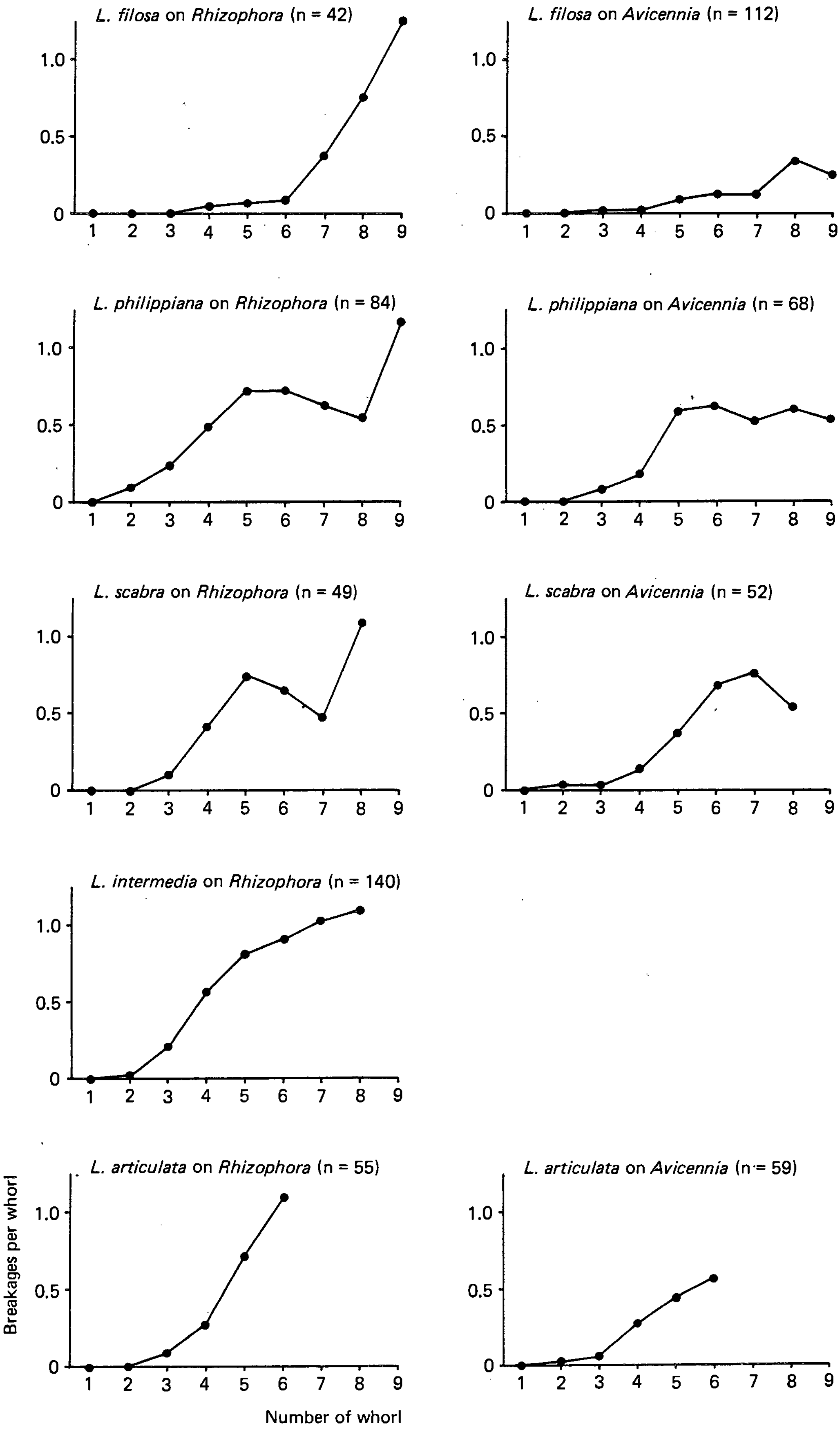
Species	Regression[A]	r^2	n	Range of W[B]	Sizes at whorl numbers[C]				
					0	1	2	3	4
L. filosa	$\ln H = 2.966 \ln W - 3.129$	0.953	38	4–8.5	0.4	0.6	1.1	1.8	
L. philippiana	$\ln H = 3.412 \ln W - 3.822$	0.955	41	5–8.5	0.4	0.7	1.1	1.9	3.2
L. scabra	$\ln H = 3.170 \ln W - 3.216$	0.978	36	4–8	0.4	0.7	1.2	1.9	
L. intermedia	$\ln H = 2.966 \ln W - 2.927$	0.976	33	4–8	0.4	0.7	1.2	1.9	
L. articulata	$\ln H = 2.378 \ln W - 1.639$	0.966	37	3–6	0.4	0.7	1.3		

[A] H = shell height (mm); W = whorl number (revolutions of teleoconch); for each analysis of variance of regression, $P < 0.0001$.

[B] range of whorl number over which relationship between ln H and ln W is linear.

[C] shell heights at whorl numbers smaller than specified range.

Fig. 14.4 Distribution of repaired shell breakages per whorl on five species of *Littoraria* from *Rhizophora* and *Avicennia* trees at Cockle Bay. Sample sizes in parentheses.



L. filosa on *Rhizophora* (n = 42)

L. filosa on *Avicennia* (n = 112)

L. philippiana on *Rhizophora* (n = 84)

L. philippiana on *Avicennia* (n = 68)

L. scabra on *Rhizophora* (n = 49)

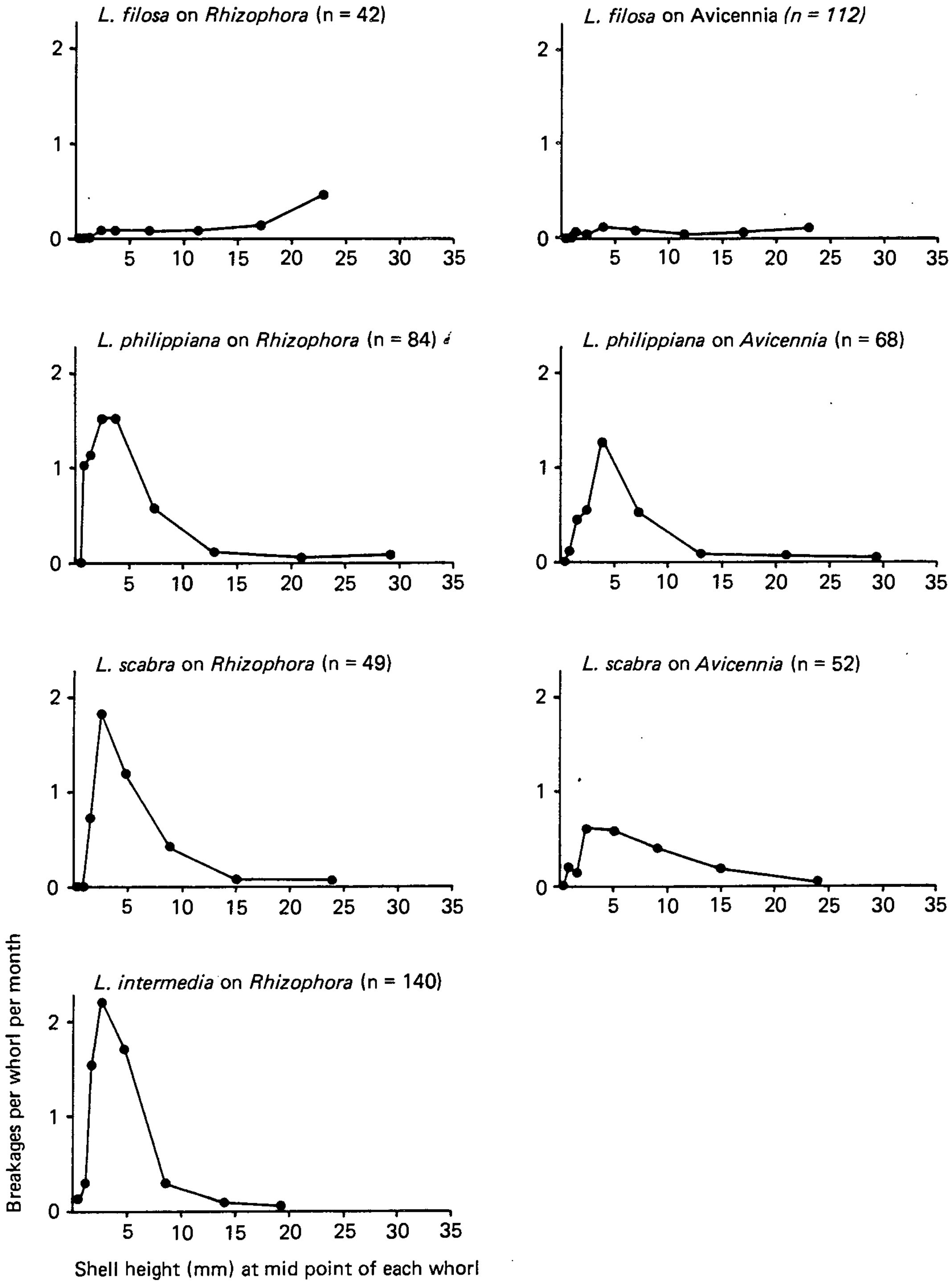
L. scabra on *Avicennia* (n = 52)

L. intermedia on *Rhizophora* (n = 140)

L. articulata on *Rhizophora* (n = 55)

L. articulata on *Avicennia* (n = 59)

Fig. 14.5 Rate of sublethal damage (repaired breakages per whorl per month) plotted against shell size, for four species of *Littoraria* from *Rhizophora* and *Avicennia* trees at Cockle Bay. Sample size in parentheses.


L. filosa on Rhizophora (n = 42)
L. filosa on Avicennia (n = 112)
L. philippiana on Rhizophora (n = 84)
L. philippiana on Avicennia (n = 68)
L. scabra on Rhizophora (n = 49)
L. scabra on Avicennia (n = 52)
L. intermedia on Rhizophora (n = 140)
0
1
2
5
10
15
20
25
30
35
Breakages per whorl per month
Shell height (mm) at mid point of each whorl

used to transform the horizontal axis from whorl number to shell height. Secondly, the frequency of repair on each whorl was converted to a rate of repair by dividing by the time taken for the species to add the whorl to the shell. When thus transformed, the data show that for *L. philippiana*, *L. scabra* and *L. intermedia* the rate of sublethal injury reached a peak at around 2.5 mm and declined to a low level in larger snails (Fig. 14.5). In *L. filosa* the rate of injury appeared uniformly low, rising slightly in the largest snails from *Rhizophora* trees. This result shows that the pattern of an increasing number of repairs on successive whorls was caused not by a greater rate of attack on larger shells, but by the accumulation of scars from the relatively rare attacks on large and slow growing animals. The transformed data also show that the rates of sublethal injury on the two tree species differed most conspicuously in the smaller size range.

14.3.5 Shell morphology and the zonation of species

Shell parameters for the species on each of the transects described in Chapter 11 are summarized in Table 14.5. Spearman rank correlation coefficients between each shell parameter and the three measures of zonation, on those transects with two or more species, are given in Table 14.6. It can be seen that because of the large sample sizes even quite low correlation coefficients were statistically significant. Although some localities were exceptional, in general the trends revealed by correlation with height above chart datum and height above the ground were closely similar.

The height of the shell, and therefore also the volume, were highly correlated with one or both measures of vertical zonation at all but one of the ten localities. A more striking trend was shown by the index of shell thickness (Fig. 14.6), negatively correlated

Table 14.5 Shell shape parameters for species of *Littoraria* on mangrove transects.

Locality	Species	Zonation[A]			Shell shape parameters[B]						SR[C]	Col. var. E[D]	Sample sizes[E]
		›CD	›GR	HZ	H	PR	S	SH	V	TI			
Cockle Bay, Qld.	*L. articulata*	2.28	0.51	23	11.19 (.35)	1.373 (.012)	0.744 (.007)	1.655 (.014)	0.186 (.017)	0.841 (.022)	1	2.19	20,58
	L. intermedia	2.28	0.70	7.7	18.52 (.38)	1.509 (.009)	0.795 (.006)	1.830 (.019)	0.655 (.041)	0.829 (.024)	2	1.25	20,55
	L. scabra	2.38	0.92	7.1	27.33 (.69)	1.441 (.011)	0.768 (.008)	1.769 (.013)	2.456 (.182)	0.504 (.024)	3	1.69	20,34
	L. filosa	2.64	0.83	25	22.76 (.53)	1.666 (.014)	0.747 (.005)	2.018 (.014)	1.011 (.066)	0.257 (.012)	5	4.63	20,129
	L. philippiana	2.97	1.12	24	28.10 (.68)	1.674 (.022)	0.799 (.005)	1.975 (.017)	1.989 (.115)	0.428 (.016)	4	2.86	20,191
Moa I., Qld.	*L. intermedia*	2.20	0.38	19	16.54 (.43)	1.459 (.021)	0.812 (.007)	1.799 (.031)	0.474 (.032)	0.599 (.024)	1	1.00	14,18
	L. scabra	2.97	1.22	6.0	34.98 (.69)	1.464 (.011)	0.757 (.006)	1.797 (.012)	4.808 (.258)	0.351 (.009)	2	1.54	20,73
Kurnell, NSW	*L. luteola*	1.62	1.05	22	15.21 (.76)	1.680 (.026)	0.755 (.006)	1.975 (.037)	0.311 (.041)	0.388 (.009)	–	4.98	20,95
Denham, W.A.	*L. pristissini*	1.2	0.1	8.3	22.09 (.46)	1.566 (.025)	0.760 (.004)	1.995 (.022)	1.086 (.069)	0.559 (.023)	–	5.77	19,113
Gove, N.T.	*L. intermedia*	2.66	0.94	7.1	17.23 (.67)	1.534 (.011)	0.810 (.005)	1.896 (.020)	0.523 (.076)	0.664 (.028)	1	3.09	20,66
	L. pallescens	3.22	1.37	35	20.72 (.47)	1.520 (.014)	0.822 (.007)	1.885 (.016)	0.948 (.061)	0.663 (.018)	2	3.01	20,63
	L. filosa	3.45	1.45	10	26.98 (.56)	1.660 (.017)	0.766 (.004)	2.021 (.021)	1.658 (.101)	0.353 (.018)	3	4.96	20,26
Darwin, N.T.	*L. articulata*	5.78	0.60	60	11.52 (.33)	1.422 (.010)	0.763 (.006)	1.706 (.013)	0.188 (.017)	0.738 (.025)	1	2.13	20,108
	L. filosa	7.26	1.57	95	24.90 (.26)	1.597 (.011)	0.760 (.005)	1.959 (.014)	1.382 (.047)	0.353 (.016)	2	6.35	20,115
Broome, W.A.	*L. articulata*	6.20	1.49	34	13.85 (.30)	1.424 (.005)	0.762 (.006)	1.696 (.010)	0.318 (.020)	0.743 (.020)	1	3.44	20,127
	L. sulculosa	6.54	0.60	137	15.88 (.55)	1.546 (.008)	0.724 (.007)	1.856 (.013)	0.421 (.039)	1.225 (.022)	3.5	2.36	20,138
	L. cingulata	7.28	1.07	166	17.53 (.18)	1.594 (.016)	0.742 (.005)	1.979 (.021)	0.495 (.014)	0.732 (.020)	3.5	2.23	20,181
	L. filosa	7.38	1.69	116	21.84 (.53)	1.696 (.013)	0.720 (.006)	1.992 (.016)	0.889 (.063)	0.291 (.008)	2	4.43	20,94
Santubong, Sarawak	*L. articulata*	3.96	0.89	19	11.29 (.35)	1.425 (.011)	0.752 (.008)	1.676 (.016)	0.177 (.014)	0.716 (.027)	2.5	1.00	20,70
	L. vespacea	4.20	1.04	28	12.48 (.66)	1.334 (.008)	0.800 (.006)	1.678 (.015)	0.291 (.044)	0.820 (.031)	4	1.00	20,100
	L. melanostoma	4.32	0.72	48	23.83 (.42)	1.769 (.031)	0.681 (.006)	1.998 (.013)	1.005 (.056)	0.902 (.039)	2.5	1.00	4,8
	L. carinifera	4.73	0.51	88	19.02 (.35)	1.339 (.012)	0.795 (.006)	1.738 (.017)	0.841 (.046)	0.809 (.023)	5	1.78	18,40
	L. conica	5.26	1.14	89	19.36 (.49)	1.430 (.008)	0.747 (.004)	1.708 (.009)	0.892 (.075)	0.481 (.022)	1	2.63	18,28
	L. albicans	5.46	1.84	54	15.59 (.74)	1.601 (.017)	0.769 (.006)	1.873 (.016)	0.382 (.051)	0.355 (.032)	6	5.31	20,67
Batu Maung, Penang	*L. melanostoma*	1.93	0.26	1.2	20.47 (.85)	1.689 (.032)	0.690 (.007)	1.872 (.039)	0.683 (.069)	0.743 (.051)	2	1.00	6,7
	L. strigata	2.06	0.42	0.7	12.07 (.42)	1.420 (.015)	0.755 (.007)	1.668 (.019)	0.222 (.025)	0.713 (.016)	3	1.77	20,50
	L. conica	2.62	0.40	9.0	17.69 (.88)	1.383 (.024)	0.779 (.009)	1.703 (.032)	0.731 (.093)	0.471 (.028)	1	2.86	8,14
	L. intermedia	2.75	0.94	3.2	23.38 (.65)	1.536 (.016)	0.783 (.005)	1.815 (.029)	1.285 (.103)	0.404 (.022)	4	1.98	17,24
	L. pallescens	2.75	1.00	2.5	22.62 (.83)	1.512 (.019)	0.821 (.008)	1.883 (.038)	1.231 (.135)	0.458 (.028)	5	3.11	13,13
Ao Nam-Bor, Thailand	*L. strigata*	2.40	0.20	0	11.55 (.75)	1.491 (.009)	0.706 (.008)	1.736 (.021)	0.185 (.035)	0.893 (.093)	2	1.00	2,4
	L. scabra	2.90	0.70	0	21.71 (1.8)	1.405 (.028)	0.764 (.010)	1.713 (.033)	1.350 (.291)	0.551 (.037)	4	2.00	7,9
	L. intermedia	3.85	1.24	19	14.82 (.39)	1.514 (.016)	0.772 (.005)	1.815 (.020)	0.350 (.029)	0.633 (.042)	2	1.34	20,50
	L. carinifera	4.16	0.16	80	16.21 (.40)	1.375 (.010)	0.780 (.010)	1.775 (.019)	0.480 (.041)	0.738 (.028)	5	1.00	7,11
	L. pallescens	4.83	1.91	35	14.02 (.23)	1.501 (.009)	0.799 (.005)	1.840 (.017)	0.295 (.018)	0.479 (.031)	2	3.16	20,93
Kanchanadit, Thailand	*L. art.+str.*[F]	0.76	0.46	8.3	12.79 (.49)	1.428 (.014)	0.770 (.008)	1.721 (.018)	0.268 (.032)	0.769 (.019)	2	1.85	20,64
	L. melanostoma	1.66	0.49	56	24.33 (.44)	1.782 (.014)	0.642 (.005)	1.972 (.016)	1.083 (.068)	0.735 (.015)	1	1.32	19,55
	L. pallescens	1.90	1.00	40	31.3 –	1.729 –	0.781 –	2.019 –	2.400 –	0.487 –	3	–	1
Coconut I., Hawaii	*L. intermedia*	0.60	0.60	–	19.78 (.50)	1.524 (.013)	0.807 (.005)	1.899 (.024)	0.801 (.074)	0.682 (.031)	1	1.69	20,43
	L. scabra	0.80	0.80	–	31.73 (2.2)	1.490 (.022)	0.761 (.009)	1.793 (.038)	3.769 (.650)	0.423 (.037)	2	1.83	8,12

[A] ›CD, weighted mean height above chart datum (m); ›GR, weighted mean height above ground (m); HZ, weighted mean distance from seaward edge of forest.

[B] as defined in Section 14.2.5; H in mm; V in cm^3; values are means with standard errors in parentheses.

[C] sculptural rank of species at each locality.

[D] index of colour variation E (Section 15.3).

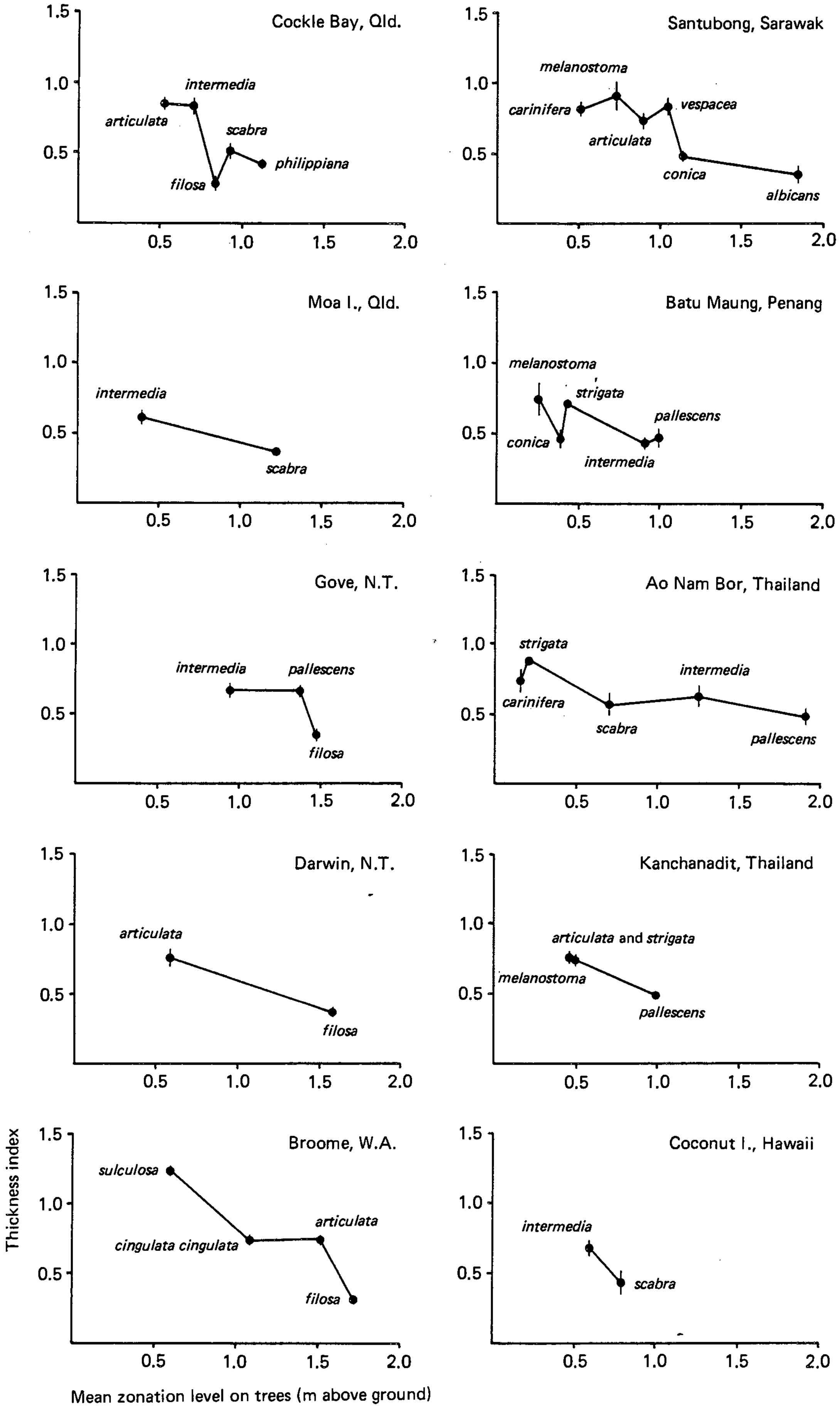
[E] sample sizes for, respectively, calculation of shell shape parameters and index of colour variation.

[F] *L. articulata* and *L. strigata* (indistinguishable in the field).

Table 14.6 Spearman rank correlation coefficients between shell shape parameters and three measures of zonation level on mangrove transects with two or more *Littoraria* species. Abbreviations as in Table 14.5.

Zonation level	Locality	Correlation coefficients of shell parameters with zonation level H	PR	S	SH	V	TI	SR	Sample size n	Number of species
>GR	Cockle Bay, Qld.	0.907 **	0.544 **	0.361 **	0.545 **	0.890 **	-0.618 **	0.700	100	5
	Moa I., Qld.	0.853 **	0.116	-0.670 **	0	0.853 **	-0.853 **	1.000	34	2
	Gove, N.T.	0.844 **	0.569 **	-0.558 **	0.489 **	0.813 **	-0.684 **	1.000	60	3
	Darwin, N.T.	0.867 **	0.866 **	-0.091	0.866 **	0.867 **	-0.866 **	1.000	40	2
	Broome, W.A.	0.416 **	0.264 *	0.013	0.140	0.406 **	-0.862 **	-0.738	80	4
	Santubong, Sarawak	-0.065	0.525 **	-0.156	0.286 **	-0.132	-0.737 **	0.058	100	6
	Batu Maung, Penang	0.522 **	0.197	0.657 **	0.339 **	0.555 **	-0.523 **	0.700	64	5
	Ao Nam-Bor, Thailand	-0.523 **	0.518 **	0.457 **	0.388 **	-0.514 **	-0.508 **	-0.671	56	5
	Kanchanadit, Thailand	0.877 **	0.840 **	-0.735 **	0.839 **	0.877 **	-0.263	0.500	40	3
	Coconut I., Hawaii	0.764 **	-0.255	-0.622 **	-0.401 **	0.764 **	-0.666 **	1.000	28	2
>CD	Cockle Bay, Qld.	0.757 **	0.727 **	0.166	0.722 **	0.681 **	-0.800 **	0.872	100	5
	Moa I., Qld.	0.853 **	0.116	-0.670 **	0	0.853 **	-0.853 **	1.000	34	2
	Gove, N.T.	0.844 **	0.569 **	-0.558 **	0.489 **	0.813 **	-0.684 **	1.000	60	3
	Darwin, N.T.	0.867 **	0.866 **	-0.091	0.866 **	0.867 **	-0.866 **	1.000	40	2
	Broome, W.A.	0.851 **	0.876 **	-0.385 **	0.823 **	0.788 **	-0.600 **	0.316	80	4
	Santubong, Sarawak	0.494 **	0.442 **	-0.048	0.536 **	0.426 **	-0.623 **	0.319	100	6
	Batu Maung, Penang	0.692 **	0.179	0.666 **	0.360 **	0.754 **	-0.792 **	0.821	64	5
	Ao Nam-Bor, Thailand	-0.386 **	0.145	0.541 **	0.351 **	-0.353 **	-0.347 **	0.112	56	5
	Kanchanadit, Thailand	0.877 **	0.840 **	-0.735 **	0.839 **	0.877 **	-0.263	0.500	40	3
	Coconut I., Hawaii	0.764 **	-0.255	-0.622 **	-0.401 **	0.764 **	-0.666 **	1.000	28	2
HZ	Cockle Bay, Qld.	0.006	0.646 **	-0.171	0.623 **	-0.130	-0.546 **	0.600	100	5
	Moa I., Qld.	-0.853 **	-0.116	0.670 **	0	-0.853 **	0.853 **	-1.000	34	2
	Gove, N.T.	0.341 **	-0.074	0.101	-0.054	0.386 **	0.030	0.500	60	3
	Darwin, N.T.	0.867 **	0.866 **	-0.091	0.866 **	0.867 **	-0.866 **	1.000	40	2
	Broome, W.A.	0.230 *	0.388 **	-0.182	0.555 **	0.189	0.261 *	0.949	80	4
	Santubong, Sarawak	0.730 **	0.033	-0.032	0.213 *	0.739 **	-0.312 **	-0.029	100	6
	Batu Maung, Penang	0.595 **	0.116	0.316 *	0.261 *	0.654 **	-0.732 **	0.600	64	5
	Ao Nam-Bor, Thailand	-0.163	-0.149	0.389 **	0.215	-0.134	-0.065	0.344	56	5
	Kanchanadit, Thailand	0.836 **	0.872 **	-0.841 **	0.814 **	0.836 **	-0.191	-0.500	40	3
	Coconut I., Hawaii	-	-	-	-	-	-	-	40	2

Fig. 14.6 Relationships between index of shell thickness and vertical zonation above the ground of *Littoraria* species, at localities in Australia, South-east Asia and Hawaii. See Chapter 11 for descriptions of transects through mangrove forests at these localities. Error bars are 95% confidence limits.


Cockle Bay, Qld.
intermedia
articulata
scabra
filosa
philippiana
Santubong, Sarawak
melanostoma
carinifera
vespacea
articulata
conica
albicans
Moa I., Qld.
intermedia
scabra
Batu Maung, Penang
melanostoma
strigata
pallescens
conica
intermedia
Gove, N.T.
intermedia
pallescens
filosa
Ao Nam Bor, Thailand
strigata
intermedia
carinifera
scabra
pallescens
Darwin, N.T.
articulata
filosa
Kanchanadit, Thailand
articulata and strigata
melanostoma
pallescens
Broome, W.A.
sulculosa
articulata
cingulata cingulata
filosa
Coconut I., Hawaii
intermedia
scabra
1.5
1.0
0.5
0.5
1.0
1.5
2.0
Thickness index
Mean zonation level on trees (m above ground)

with vertical level at all localities, and highly significantly so at all but one. The two shell parameters relative spire height and shell proportion tend to covary, since if the spire becomes taller, the shell becomes relatively narrower and the aperture smaller relative to the total height. Both parameters showed similar patterns of correlation with the measures of vertical level, demonstrating that at eight of the ten localities the species at higher levels were narrower and more high-spired. Apertural circularity showed no consistent trends. For the correlations of sculptural rank and vertical level, the number of cases, equal to the number of species at each locality, was so small that even the highest correlations were not significant. The values of the correlation coefficient have nevertheless been included to show the directions of the associations, demonstrating that in most cases the degree of sculpture increased at higher levels.

Shell morphology did not appear to vary in a consistent manner with horizontal zonation patterns (Table 14.6). The relatively few large and significant correlations reflected the tendency of some species from higher vertical levels to extend further back from the seaward edge of the forest.

No attempt was made to examine intraspecific variation along transects, for shell form is rather constant within species (Section 4.1). One case of intraspecific variation deserves mention. At Penang, *L. intermedia* was found to occupy an unusually high position on the trees (Fig. 11.12) and the shells were larger and thinner than the typical forms, in agreement with the interspecific trend; this variety appears to be a regional form characteristic of the Bay of Bengal (Section 9.2.3.5).

14.4 Discussion

14.4.1 Potential predators and other sources of mortality of *Littoraria* species

In the mangrove habitat studied at Cockle Bay, crabs were the major predators of the larger postlarval stages of *Littoraria* species. Two species of crabs are believed to be of particular importance. The most common crab on the *Rhizophora* trees was *Metopograpsus latifrons*, a small, agile grapsid with relatively weak and unspecialized chelae. Although hidden amongst roots or found just above the tide level during the day, the wider vertical distribution observed on the trees at night suggests that this may have been the time of most active foraging (Fig. 14.1).

The second important crab predator is the portunid *Thalamita crenata*. This swimming crab is a powerful predator with large chelae, specialized for crushing gastropod shells. Although no predation attempts were observed in the field, the observation of a crab clinging to a *Rhizophora* root at the water surface suggests that *T. crenata* may reach snails at low levels on the trees. A similar foraging behaviour has been recorded by Hamilton (1976) for the portunid *Callinectes sapidus*, feeding on *Littoraria irrorata* in a Florida salt marsh.

Of the other crustaceans seen at the study site, only large pagurids (*Clibanarius* species) were sufficiently common to be considered as significant predators. However, the laboratory trials showed that they were unable to crush small specimens of the fragile *L. filosa*. It is possible that *Clibanarius* species may prey upon the smallest, newly settled snails. The large portunid *Scylla serrata* was occasionally seen in the study area. During the study 12 empty shells of *L. scabra* were found with the spire broken away and the aperture undamaged. This method of attack was uncharacteristic of *Thalamita crenata*, but reminiscent of the broken shells of potamidids attacked by *S. serrata*. Of the potential predators, only *S. serrata* may have the strength to break large *Littoraria* species in this way.

Other aquatic predators, such as fish, cannot be significant, since all but the smallest snails migrate in order to remain above the water level at all stages of the tide (Section 12.3.1). No gastropods preyed upon the *Littoraria* species at Cockle Bay. However, the muricid *Naquetia capucina* (Lamarck) is found in mangroves in Indo-Malaya (Radwin & d'Attilio, 1976). This species was common in mangroves near Darwin, and one drilled and ate a *Littoraria articulata* with which it was confined in a bag. Under natural conditions this muricid may normally attack sessile prey such as oysters and barnacles (Nielsen, 1976).

Birds must be considered as potential predators, in particular of the *Littoraria* species inhabiting higher levels amongst the foliage of the mangrove trees. In view of its habitat on leaves and its thin and conspicuous shell, *L. filosa* would seem to be a likely prey for birds. However, the caging experiment showed no enhancement of survival in this species when protected from birds, so birds are evidently not major predators on the size classes of *L. filosa* used in the experiment. The possibility remains that birds may feed on the smallest snails, swallowing them whole. Shells of *L. 'scabra'* 4 mm in length have been found in the faeces of Lewin's Honeyeaters (*Meliphaga lewinii*) in south-east Queensland (Liddy, in press), and various birds consume entire small individuals of *Littorina* species on rocky shores in Britain (review by Pettitt, 1975). Indirect evidence for bird predation and its possible evolutionary significance will be examined in Chapter 15.

As a result of the caging experiment it was estimated that 57% of the total loss (or 86% of the total mortality) of 7 to 12 mm individuals of *L. filosa* could be ascribed to crab predation. The sources of the remaining 43% are a matter for speculation. Exclusion of bird predators actually appeared to reduce survival. Whilst birds were seen to eat crabs at the study site, this interaction seems unlikely to explain the result. Error and variability between trees were probably responsible (see Section 15.4.7 for further evidence of variability of loss rates between trees). The experimental design would have been improved by applying each caging regime successively to each tree, but the labour involved in erecting cages was prohibitive.

Other sources of mortality might include insolation, desiccation and food shortage, and also rainfall (Section 13.3.2). Since shading produced a negligible enhancement of survival, it may be concluded that direct insolation was not a significant cause of death. This result may appear to be at variance with the suggestion that microclimatic extremes contribute significantly to the mortality of *L. filosa* (Section 13.4.4). However, the caging experiment was carried out from July to November, before climatic conditions were at their most severe. If microclimatic extremes cause death by desiccation rather than by heat stress, shading of the tree may not have enhanced survival greatly. Although occurring mainly on the upper leaf surfaces, only 24% of individuals of *L. filosa* were found in direct sunlight (Table 15.10). It is unfortunate that it was not possible to continue the experiment during the summer months. The low survival on the partially defoliated tree is consistent with death resulting from reduced shading by foliage or to lower food availability.

If the immigration rate can be used as an estimate of the rate of emigration from the trees, emigration accounted for 34% of the total loss. This may be an underestimate, since the susceptibility of snails to predation is likely to be increased while they are floating or crawling between trees. The mark and recapture experiment also suggested that emigration was a significant source of loss from trees (Section 13.3.2). Differences in the number of immigrants recorded on the experimental trees appeared to be correlated with the proximity of other trees rather than with the caging regime. Since the mesh size of the cages precluded the passage of floating vegetation, this observation suggests that floating or crawling of snails may be a more important means of transfer between trees than rafting on vegetation (Section 13.3.2). This is in agreement with the percentage of leaf fall each month, which was only about one third as great as the estimated percentage of snails lost by emigration. Since for much of the time individuals of *L. filosa* are attached only by mucus, they may be susceptible to mechanical dislodgement when the branches are buffeted by the wind.

The observations on snails released on *Avicennia* seedlings at ground level suggested that regular submergence by the tide had no deleterious effect. Loss from mortality and or emigration was total when snails had no refuge above the water level at high tide (Section 12.4.1).

The survivorships of the two size classes of *L. filosa* on trees 1 and 3 (Fig. 14.2), with all significant sources of loss operating, agreed closely with the values recorded for similar size classes and in the same season during the mark and recapture experiment conducted during the previous year (Fig. 13.16).

14.4.2 The intensity of predation by crabs

It is generally agreed that crabs are significant predators of intertidal gastropods in a wide range of habitats, but the available evidence is almost entirely indirect, the impact of the predators being inferred from the presumed consequences of their predation. For example, predators are believed to exert a potent force of selection upon prey populations. The most well documented example amongst intertidal gastropods is provided by *Nucella lapillus*, which in exposed localities shows a thin shell, with low spire and large aperture, well adapted for clinging to rocks; in sheltered areas, where crabs are more frequent, the shell is thick, with tall spire and narrow aperture, and demonstrably more resistant to attack (Ebling *et al.*, 1964; Hughes & Elner, 1979; Vermeij, 1982b). *Littorina saxatilis* exhibits a similar variation in shell shape between exposed and sheltered localities, and again selection imposed by predatory crabs may account for the modification of shape on sheltered shores (Heller, 1976; Raffaelli, 1979a; Elner & Raffaelli, 1980; Janson, 1982b). Such localized intraspecific responses are found only in species with nonplanktotrophic development (Vermeij, 1982b, d), but comparisons between species, assemblages and even faunas of biogeographical provinces, reveal comparable trends of increasing development of antipredatory shell architecture in areas where crab predation and consequent selection are presumed to be more intense (Vermeij, 1976, 1978, 1979a, b). Although the evolutionary effects of crab predators are striking, they are not necessarily an indication of the contribution of crabs to the total mortality of gastropods (Vermeij, 1982c).

The importance of crab predation on *Littoraria* species is suggested by several lines of indirect evidence. In the *Rhizophora* grove at the study site the density of *Metopograpsus* was estimated as 0.6 crabs per tree, which may be compared with the maximum density of newly recruited *L. intermedia* and *L. scabra*, 0.88 and 0.44 individuals per tree respectively (Fig. 13.9). Since these species are both more thin shelled than *L. articulata*, as used in the laboratory predation trials, individuals in the size range defined as 'recruits' (4-8 mm) must be susceptible to attack by at least the larger *Metopograpsus*. At the seaward edge of the forest *L. articulata* are more sbundant than this and may provide an additional prey item, but within the forest all three species occur at comparable densities (Fig. 11.1). The crabs are highly mobile, and the snails are concentrated above the water level at high tide, so that at comparable levels of abundance of predator and prey, the latter could be expected to suffer heavy losses. Newly settled snails must be more abundant than 'recruits', and heavy predation at this stage could perhaps explain the failure of recruitment for most of the year, despite an extended and possibly continuous breeding season (Section 13.4.3). The rates of sublethal shell damage derived from the distribution of scars on the shells must be interpreted with caution (Section 14.4.3), but are consistent with the suggestion of intense predation on the smallest size classes.

In terms of the number of snails consumed each day, predation is an uncommon event. For example, assuming that all mortality of *L. intermedia* in the marked size range (≥4 mm) at the study site was caused by crabs, it can be calculated that one snail was consumed every 3 days, over the area occupied by 64 *Rhizophora* trees (average survivorship = 87% per month, hence monthly loss = 13%, of which 51% may be due to emigration, the rest to mortality, average population size = 134; see Section 13.3.2). It is therefore not unexpected that so few predation attempts were observed in the field. Furthermore, the observations of *Metopograpsus* suggest that foraging may have occurred chiefly at night. The two predation attempts that were observed are nevertheless of some significance, showing that *Metopograpsus* is capable of feeding on *L. filosa* as large as its own carapace width in the field, as in the laboratory, and that snails at and near the water level are not immune from attack by the powerful *Thalamita crenata*.

Direct evidence of the contribution of crabs to overall mortality is available only for *L. filosa* (Sections 14.3.2, 14.4.1). The predators responsible are not known, but since *Metopograpsus* species were uncommon on isolated *Avicennia* trees, it is possible that the swimming crab *Thalamita crenata* caused many of the deaths. It may seem surprising that *L. filosa* should experience intense crab predation, when it is a species of relatively high vertical levels. However, the smaller snails (as used in the experiment) are found closer to the water level than adults, and a proportion are reached by high tides (Figs 12.4, 12.10), or may perhaps be trapped on low foliage and submerged by a rising tide. To produce the estimated rate of predation, one snail should have been eaten on each experimental tree every 2½ days. It can only be guessed that predation accounts for a similar, or possibly higher, proportion of the total mortality of the *Littoraria* species on *Rhizophora* trees, where *Metopograpsus* species were much more common than on *Avicennia* trees, and *T. crenata* appeared no less so.

There are few comparable investigations of the intensity of crab predation on littoral gastropods in the temperate zones, although precise data are available on the impact of crab predators on sessile mussels on rocky shores in New England (Menge, 1983). Spight (1976) estimated that *Cancer productus* was responsible for 10% of the mortality of *Nucella lamellosa* larger than 15 mm at a locality in Washington. The complementary distributions of crabs and their vulnerable prey at certain localities have been explained in terms of severe predation, although other causes cannot be ruled out (Ebling *et al.*, 1964; Muntz *et al.*, 1965). Some investigators have found crushed gastropod shells in the field, as evidence of crab predation (Feare, 1970), but usually such evidence is removed by waves (Pettitt, 1975). In the tropics, the contribution of crushing predation to overall mortality has been measured as the proportion of collections of dead shells judged to have suffered lethal damage (Vermeij, 1979b, 1982a). Although this may be a conservative estimate, the frequencies of lethal damage are commonly 50% or greater in the more vulnerable species on reef flats (Vermeij, 1979b) and in shallow soft bottom habitats (Vermeij, 1982a).

There is little available evidence of the importance of crab predation on gastropods in salt marsh or mangrove habitats. In Wales, adult *Carcinus maenas* are scarce in salt marshes, and shells of *Littorina saxatilis* show a very low frequency of sublethal injury (Raffaelli, 1978b). However, shells are as thick as those from populations exposed to heavy crab predation, perhaps because juvenile crabs, which are common in salt marshes, prey heavily on the smallest snails, thereby imposing selection for thick shells (Hughes & Roberts, 1980b; Raffaelli, 1982). In the salt marshes of the south-eastern United States the portinid *Callinectes sapidus* is a common predator of the abundant *Littoraria irrorata*, taking snails less than 17 mm in height (Hamilton, 1976; Stanhope *et al.*, 1982). Dimorphic chelae are characteristic of molluscivorous crabs, and have been noted in two xanthid genera from mangrove swamps (Vermeij, 1977a). The large portunid *Scylla serrata*, commonly found in mangrove habitats, is known to feed on molluscs (Hill, 1976). The genus *Metopograpsus* is common and widely distributed in Indo-Pacific mangrove swamps (Macnae, 1968), but has not previously been reported to feed on molluscs. In apparent agreement with the small number of molluscivorous crab species known from mangrove habitats, Vermeij (1974, 1978) has commented on the low incidence in mangrove gastropods of modifications of the aperture (such as a narrow opening, internal teeth and an inflexible operculum) which confer resistance to attack by crabs.

In the light of the present results, it is clear that crab predation is both an important component of mortality and an agent of selection (Section 14.4.4) on the genus *Littoraria* in the mangrove habitat. The lack of apertural defensive structures amongst mangrove gastropods in general is at least partly accounted for by the poor representation of neogastropods in the fauna, which as a group show the highest diversity of apertural form (Vermeij, 1971a). Furthermore, many mangrove gastropods show behavioural patterns such as ascent of trees, burrowing or concealment in logs, during high tide, which can be interpreted as methods of avoidance of aquatic crab and fish predators (Section 12.4.1). Those few that are exposed to aquatic predators at high tide (e.g. *Telescopium telescopium*, *Terebralia* spp., *Nerita planospira* and *Bembicium* sp. at the study site) are in fact well protected by shells of considerable thickness, which bear evidence of their effectiveness in the form of high frequencies of repaired sublethal injuries. The evidence suggests that crushing predation is likely to prove as significant a source of mortality and selection in mangrove gastropods as it is recognized to be in those from other shallow water tropical habitats.

14.4.3 The interpretation of repaired shell breakage data

The examination of repaired shell breakages would appear to be an elegant method for the investigation of predation on snail populations, but there are a number of difficulties to be considered if the data are to be interpreted correctly.

On exposed rocky shores, damage may be caused not only by predation attempts, but also by crushing between moving rocks. Breakages from these two sources cannot be distinguished and their respective likelihoods tend to covary (Raffaelli, 1978b), although crushing by boulders is probably of lesser significance (Reimchen, 1982). In some habitats the repaired breakages are obscured by erosion of the shell, so that complete records of predation attempts cannot be read on adult shells (Stanhope *et al.*, 1982). *Littoraria* species in mangrove forests suffer from neither of these disadvantages, since their habitats are always so sheltered that substantial damage can only be caused by predators, and because the snails remain above the water level their shells are not eroded. The scars on the shell of *Littoraria* species are therefore a record of unsuccessful predation attempts.

The observed frequency of shell repair in a population (the average number of scars per individual) will be influenced by three main factors, of which the first two have been pointed out by Vermeij (1982a) in his evaluation of the technique. Firstly, the frequency depends upon the abundance of the predator and the likelihood of attack. Secondly, it depends upon the probability of an attack being successful, as determined by the strength of the shell (related to shape, size and thickness) relative to the strength of the predator. If the shell is weak, all attacks may be successful, so that no record of attacks is found on intact shells. In relatively stronger prey the likelihood of unsuccessful attack increases and repairs will be common, although if shells are completely impregnible, unsuccessful attempts at predation may not even damage the lip, and again no repairs will be evident. Thirdly, the record of scars will be influenced by the longevity of the gastropod, for they will accumulate with time. The presence of repaired injuries does not significantly reduce the strength of the shell (Blundon & Vermeij, 1983).

The relationship between sublethal and lethal damage, or in other words between repair and mortality caused by the predator, is complex and depends upon the relative strengths and abundances of predator and prey (Vermeij, 1982a, c). Assuming that shells are not so strong that unsuccessful predation seldom results in damage, then the relatively weaker the prey (or more powerful the predator), the higher will be the proportion of successful attacks and the lower the frequency of shell repair. Vermeij (1982a) has demonstrated just such an inverse correlation between lethal and sublethal breakage; when making comparisons between species of gastropods on a reef flat in Guam, he found that repair frequency in the field was highly correlated with the failure rate of the crab *Calappa*, so that the more resistant species exhibited the highest frequencies of repair. Conversely, when making intraspecific comparisons between populations, and if the only variable is relative abundance of the predator, frequencies of lethal and sublethal damage will show a positive correlation, as has again been demonstrated by Vermeij (1982a) within some groups. However, even if repair and mortality are positively correlated, there may not be a linear relationship between them (Vermeij, 1982a).

While a high frequency of repair may not necessarily be an indication of the contribution of crushing predators to overall mortality, it demonstrates that the shell may function as a protection against such mortality (Vermeij, 1982a). In addition, Vermeij (1982c, d) has argued that repair frequency is a measure of the potential for selection in favour of traits which confer resistance to crushing. This was said to be so because a high repair frequency indicates that a large proportion of the population has been exposed to selection for resistance, and such selection is then less likely to be counterbalanced by selection from other agents than when the frequency of repair is low. A degree of unsuccessful predation, enabling some prey to survive attack, is clearly a necessary condition for selection in favour of antipredatory traits, but Vermeij's argument is difficult to accept because the potential strength of a selective force must depend upon the intensity of mortality which it produces, rather than the frequency with which the animals survive the test. The opportunity for selection for resistance to crushing should therefore be correlated with lethal, rather than sublethal, breakage. Although sublethal breakage may not impair survival (Zipser & Vermeij, 1980), it may nevertheless have an associated cost in terms of reduction of fitness, since repair of the shell may divert energy from growth or reproduction. Even if lethal breakage is infrequent, sublethal damage alone may impose a small selective force for improved shell resistance.

Vermeij (1982a) has questioned why predators so often attack unsuitable or oversized prey, leading to a low attack success rate. For crabs foraging for sparsely distributed snails, the most productive technique appears to be to attack all prey encountered, rejecting those shells which remain unbroken after a set giving-up time (Hughes & Elner, 1979; Elner & Raffaelli, 1980). This strategy is dictated by both the sparse distribution and the relatively unpredictable value of the prey, and may be contrasted with the selection of optimally sized items, as predicted by the theory of optimal foraging, when crabs feed on an abundant prey such as mussels (Elner & Hughes, 1978; Jubb *et al.*, 1983).

Data on the frequency of repaired shell injuries are available from several studies of temperate littorinid species for comparison with the present results. Previous workers have often expressed their results in the form of the proportion of shells in a population showing evidence of repair. To enable comparisons to be made, the data for mangrove littorinids has been recalculated as the proportion of shells showing one or more repairs on the last two whorls (Table 14.3); this conservative estimate of the frequency of damaged shells makes allowance for the usually eroded state of the apical whorls of temperate species (Stanhope *et al.*, 1982). In *Littorina saxatilis* from Britain, Raffaelli (1978b) found the median proportion of repaired shells to be 0.06, and the maximum 0.48, out of 24 populations. From the data of Reimchen (1982), the mean and maximum proportions for *Littorina mariae* and *Littorina obtusata* in Britain were 0.07 to 0.13 and 0.50. Vermeij (1982d) measured the average number of scars on the last whorl in numerous populations of *Littorina littorea* throughout its range in the north Atlantic, and recorded maximum values between about 0.3 and 0.4, with most figures being much lower; these data are directly comparable with those shown in Figure 14.4. In a population of the warm temperate species *Littoraria irrorata* from Virginia, the maximum proportion of damaged shells was given as 0.6 by Stanhope *et al.* (1982). Figures for the populations of *Littoraria* species at Cockle Bay are comparable with or exceed the highest reported by these previous workers, and the species clearly support a relatively high incidence of sublethal damage by crushing predators. Although the data for the family Littorinidae are limited, they are in agreement with the geographical trend of increasing incidence of repair towards the tropics, as shown in the Thaidae (Vermeij, 1978), Terebridae (Vermeij *et al.*, 1980) and in *Littorina littorea* over part of its range (Vermeij, 1982d).

In the light of the earlier discussion, the interpretation of this geographical trend is uncertain. If longevity and relative effectiveness of defence of the prey from local predators are assumed to be constant, the increased frequency of repair at lower latitudes could reflect the increasing abundance of crushing predators, for which there is indeed some evidence, in terms of species richness (Vermeij, 1978, 1982d; Vermeij *et al.*, 1980). However, for many gastropod groups the absolute strength of the shell (Vermeij & Currey, 1980) and the incidence of antipredatory shape and sculpture (Vermeij, 1978, 1979a; Palmer, 1979) increase towards the tropics. Whether the shells are also stronger relative to local predators, as inferred by Vermeij *et al.* (1980) from the increased incidence of repair, requires assumptions about the abundance and strength of temperate and tropical crabs which cannot yet be justified. Vermeij (1977a; also Zipser & Vermeij, 1978) has in fact suggested that tropical crabs are relatively stronger and more specialized than temperate species (although reanalysis of the data has cast doubt on the interpretation, Abele *et al.*, 1981).

The shells of the largely tropical and subtropical genus *Littoraria* are, contrary to the trend in some other families, thinner than those of temperate *Littorina* species, but some of their principal predators (*Metopograpsus* species) are relatively weak and unspecialized molluscivorous crabs. It should also be considered that the success rate of crabs in the mangrove habitat may be lower than on a rocky shore (thereby increasing the frequency of sublethal damage), owing to the high relief of the substrate and consequent chance of losing the prey if it is dropped. The success rate was almost total in the laboratory, but this was clearly unnatural since predator and prey were confined together in small tanks. Amongst the Littorinidae, longevity appears comparable in temperate and tropical species (Section 13.4.5), so that this should not be a confounding variable in the interpretation of repair frequencies. Although it cannot as yet be said whether the observed trends in shell repair frequencies reflect increasing abundance of crushing predators or relatively more well defended prey towards the tropics, in either case the trend is in agreement with the frequent assertion that crushing predation is potentially a more potent force of selection at lower latitudes (Vermeij, 1977a, 1978, 1979a, 1982c, d; Palmer, 1979; Vermeij & Currey, 1980; Vermeij *et al.*, 1980; Bertness *et al.*, 1981).

When comparisons are made between the species of *Littoraria* at Cockle Bay, similar difficulties of interpretation arise, because relative strength of the prey and abundance of predators are confounded. The high frequency of sublethal damage found in *L. intermedia* is consistent with its occupancy of low levels on the trees, where the intensity of predation is likely to be stronger, and also with its thick shell which decreases the likelihood of lethal breakage. At the opposite extreme, the frequency of repair in *L. filosa* was relatively low, but whether because of its thin and susceptible shell, its high level habitat, its shorter life span, or a combination of these, is not known. *L. philippiana* occupies an even higher zone (although making periodic excursions to the water level, Section 12.3.1), yet had the highest frequency of sublethal injury, and a thicker and larger shell than *L. filosa,* implying that the susceptibility of the latter may be the chief reason for its low frequency of repair. Neither repair frequencies nor shell thicknesses were significantly different in *L. scabra* and *L. philippiana,* although the latter occupies a higher zone. The lower frequency of sublethal damage in *L. articulata* in comparison with *L. intermedia,* with which it shares a thick shell and low level habitat, could be accounted for by the smaller size and therefore greater susceptibility of the former.

When making intraspecific comparisons of the *Littoraria* species from *Rhizophora* and *Avicennia* trees, the major variable to be considered is the abundance of predators. The greater abundance of *Metopograpsus* in the *Rhizophora* forest could account for the higher level of sublethal damage in this habitat.

The distribution of repaired breakages over the whorls of a shell is also dependent upon the three principal factors discussed above, namely, the likelihood of attack, strength of the shell relative to that of the predator, and the time over which damage accumulates. Viewed from an ontogenetic perspective, these factors will be influenced by differing patterns of juvenile and adult distribution, ability of the crabs to crush only a particular size range of prey, and the size-specific growth rate. Of these three confounded variables, the effect of the changing growth rate can be removed by calculating a rate of sublethal damage during the formation of each whorl of the shell. Comparison of the figures of repairs per whorl (Fig. 14.4) and of rate of repair per whorl (Fig. 14.5) clearly shows that the increasing number of scars on the larger whorls is to a considerable degree an artefact of the longer time taken to add the larger whorls to the shell. The likelihood of encounter with a crab may be higher in smaller snails, since these are distributed at lower levels on the trees (Section 12.3.4), so that, other factors being equal, the rate of sublethal breakage should be higher in juveniles. However, other factors are not equal, and the overriding effect is the increasing strength of the shell (relative to the strength of the predator) which is attained with growth. Although here considering rates of attack, the argument is similar to that given in relation to interspecific comparisons of repair frequencies. When the shell is extremely vulnerable the attack success rate will be high, and the rate of repair low. As size increases, a greater proportion of attacks will be unsuccessful, increasing the rate of repair. When the shell reaches the maximum size that the predator is capable of crushing successfully, the rate of unsuccessful attack will be at a maximum. Beyond this point the rate of repair is expected to decline gradually, because predators may be unable to inflict even sublethal damage on the strongest shells.

In the field this theoretical pattern of rate of repair with increasing prey size is likely to be modified if individual predators vary in size and strength, or if the gastropods are prey to several predators of differing capability. The major predators of juvenile *Littoraria* species are believed to be crabs of the genus *Metopograpsus*, which by virtue of small size, mobility and unmodified chelae, are well equipped to search the trees for small prey. Crabs of a wide size range are found on the trees, but most are between 15 and 25 mm in carapace width. From the laboratory predation trials, it can be estimated that *L. articulata* achieves immunity from the majority of crabs at a shell height of 2.5 to 5 mm (Fig. 14.3). The growth rate of this species was not measured, so the rate of repair is not known, but *L. intermedia* occupies a similar zone and is almost identical in shell thickness as an adult (Fig. 14.6). The pattern of rate of repair for *L. intermedia* (Fig. 14.5) reveals a marked peak between 1.5 and 4.5 mm, as would be predicted if it achieves immunity in the same size range as *L. articulata*. A similar pattern is shown by *L. philippiana* and *L. scabra* on *Rhizophora* trees; although these species have somewhat thinner shells than *L. articulata* as adults (Fig. 14.6), this result suggests that as juveniles they could be of comparable thickness.

Comparison of the rates of repair on *Rhizophora* and *Avicennia* trees is in agreement with this interpretation, since *Metopograpsus* were less common on the latter, and observed rates of repair lower, especially at smaller shell sizes. At large shell sizes, *Thalamita crenata* may be the only significant crushing predator. Since this crab is so powerful as to be able to crush all sizes of *Littoraria* shells (Section 14.3.3), the rate of sublethal damage caused should be low. In addition, this crab is less common than the *Metopograpsus* species, and can only reach prey close to the water level. The low rates of repair observed at large shell sizes in *L. intermedia*, *L. scabra* and *L. philippiana* (Fig. 14.5) are consistent with this interpretation.

The pattern of the rate of sublethal damage in *L. filosa* is completely different (Fig. 14.5). Since the shell is so fragile, the success rate of attacks must be high, and the rate of repair correspondingly low. The laboratory predation trials showed that only at a size of 14 to 24 mm does this species achieve immunity from *Metopograpsus* in the size range 15 to 25 mm (Fig. 14.3), which may explain the increased rate of repair on the final whorl of the shells from *Rhizophora* trees. As in the case of the other *Littoraria* species, the peak is less marked, in fact virtually absent, on *Avicennia* trees, where *Metopograpsus* species are scarce.

The distribution of repaired shell breakages over the whorls of the shell, and the inferred rates of sublethal damage during the course of shell growth, are therefore in agreement with the results of the laboratory predation trials. This technique, by which scars are recorded on successive whorls of the shell, is a useful refinement of the analysis of shell repair frequency. If data are available on the growth rate of the shell, the shell size at which the rate of repair is highest may indicate the size above which the species is immune from successful attack by most of its predators.

14.4.4 Microenvironmental gradients and trends in shell morphology

The intertidal zone is a region of abrupt transition between marine and terrestrial environments, across which there are steep gradients in microenvironmental conditions. Proceeding from low to high tidal levels there are gradients of increasingly severe desiccation and heat stress (Vermeij, 1971b, 1973a), of greater variation in osmotic conditions (Mayes, 1962), of decreasing time available for feeding during submergence or wetting (Janson, 1982a; Underwood & McFadyen, 1983) and of decreasing intensity of wave action (McQuaid, 1981b). In mangrove forests these gradients in the physical environment are less steep than on rocky shores, because of the ameliorating influence of the trees (Chapter 11). Various biological interactions may increase in intensity at lower levels on the shore, but from the viewpoint of the present discussion it is significant that predation is believed to be more severe, as has been concluded from studies on rocky shores (Feare, 1970; Vermeij, 1974, 1978; Hughes & Elner, 1979; Reimchen, 1982; Menge, 1983). The distribution and habits of the crab predators at Cockle Bay (Section 14.3.1) suggest that in this mangrove habitat there is a similar gradient of increasing predation intensity at lower levels on the trees. In many environments there appears to be a general inverse correlation between the intensity of predation and environmental rigour (Paine, 1976).

Many authors have commented on supposed trends in shell morphology with shore level, but in most cases have generalized from observations on a small number of species in a limited geographical area. More convincing are those trends which are consistently shown by different assemblages of species in comparable habitats over a wide geographical area. Such data were assembled by Vermeij (1973a) for gastropods of the high intertidal zone, and are paralleled by the data presented here for assemblages of mangrove littorinids. Even when consistent patterns are identified, they cannot be accepted uncritically as adaptive trends produced by selection. The physical environment may have a direct influence on form, particularly through constraints on growth rate, and allometric relationships may produce morphological trends for which an adaptive explanation is unnecessary.

Some of the best documented examples of the adaptive significance of shell morphology concern intraspecific variation in *Littorina saxatilis* (Newkirk & Doyle, 1975; Heller, 1976; Raffaelli, 1979a; Smith, 1981; Janson, 1982b) and *Nucella lapillus* (Kitching *et al.*, 1966; Hughes & Elner, 1979; Vermeij, 1982b). These two species show ovoviviparity and nonplanktotrophic development in benthic egg capsules respectively; dispersal is therefore limited and as a consequence of restricted gene flow populations are able to maintain precise morphological adaptation to local conditions (Gaillard, 1972; Berger, 1973; Snyder & Gooch, 1973; Heller, 1975a; Currey & Hughes, 1982; although Wilkins & O'Regan, 1980, have shown that the correlation between genetic variability and method of development in littorinids is less clear than has been supposed). In *Littoraria* species, as in most other littorinids with planktotrophic development, morphological differences between populations are less marked, so that adaptive significance must be deduced from interspecific comparisons. Even in littorinids with planktotrophic larvae, localized adaptation is possible when selection is sufficiently strong (Struhsaker, 1968).

Intraspecific variation in adult size is common in gastropods (Vermeij, 1980) and has sometimes been explained by faster growth in more favourable habitats, where there may be a higher productivity of food (Vermeij, 1980; McQuaid, 1981b) or a longer time available for feeding (Berry, 1961; Roberts & Hughes, 1980; Janson, 1982a).

Littoraria species are no exception, most showing variation in adult size by a factor of two or more in different habitats (Chapter 9). If this direct environmental effect were the principal determinant of size differences between *Littoraria* species, the larger littorinids would be expected at lower levels, whereas in fact the reverse trend is generally observed (Table 14.6). Studies of the growth rates of four species at Cockle Bay revealed no clear correlation with adult size (Section 13.3.3).

On rocky shores in temperate regions there is some evidence that size and growth rate of littorinids are partly determined genetically (Janson, 1982a). Strong wave action is believed to impose selection for small size (Palant & Fishelson, 1968; Heller, 1976; Janson, 1983). This may be because small snails are able to shelter in crevices (Emson & Faller-Fritsch, 1976; Raffaelli & Hughes, 1978), or because they are better able to withstand the mechanical force of waves (North, 1954; Struhsaker, 1968; Behrens, 1972). However, some authors have shown experimentally that adherence capability is actually greater in larger snails, and have found a positive association between shell size and exposure on open rock surfaces (Chow, 1975; Hylleberg & Christensen, 1978; McQuaid, 1981b). Since *Littoraria* species remain above the water level and because mangrove environments are always sheltered, neither wave action nor crevice availability should influence shell size.

Amongst the *Littorina* species of Britain, size is greater in species from lower levels. This may be related to the danger of dislodgement and consequent advantage of small size in supralittoral species which are frequently attached by mucus (Heller, 1976). Alternatively, the trend could represent an adaptation to predation by crabs upon littoral forms (Reimchen, 1982). Immunity of shells above a critical size from predation has been shown here for *Littoraria articulata* and the crab *Metopograpsus latifrons*, and there are numerous similar reports in the literature (Ebling *et al.*, 1964; Zipser & Vermeij, 1978; Elner & Raffaelli, 1980; Bertness & Cunningham, 1981; Reimchen, 1982). This explanation cannot apply to species of *Littoraria* in mangroves, in which shell size and presumed intensity of crushing predation are negatively correlated.

Intraspecific patterns of upshore size increase have been described for many species of gastropods typical of the high intertidal zone. This is believed to reflect the greater tolerance of larger individuals of rigorous physical conditions (review by Vermeij, 1972b; Section 12.4.6). With increase in size the surface to volume ratio of the body is reduced, so that larger snails are more tolerant of desiccation (Behrens, 1972; Coombs, 1973) and osmotic extremes (Chow, 1975). These effects may account for the larger adult size of *Littoraria* species from higher levels. This suggestion has also been made by Vermeij (1973b) who noted an upshore increase in size amongst the Littorinidae, Neritidae and Potamididae from mangroves in Singapore. Conservation of moisture must be important for mangrove littorinids at high levels, to permit activity independent of wetting by the tide.

Amongst littorinids and other groups from the high intertidal zone of tropical rocky shores, there are no consistent trends in adult size with zonation level (Vermeij, 1973a). Although the advantages of larger size at higher tidal levels must still apply, they may be counteracted by the fact that temperature regulation in the full sun is more effective in smaller gastropods, in which the surface to volume ratio is more favourable for convective heat loss (Vermeij, 1973a). In support of this idea it is noteworthy that the few large littorinids from the highest supralittoral levels on tropical rocky shores (*Tectarius*, *Echininus* and *Cenchritis* spp.) possess strongly sculptured shells, which achieve a combination of large volume for water storage and high surface area for heat loss. In the shaded habitat of mangrove forests, dissipation of heat may be less important, so that the upshore increase in size is freely expressed.

In view of the correlation between size and vertical level amongst mangrove *Littoraria* species, the corresponding trends in shell shape (Section 14.3.5) must be interpreted in the light of possible allometric effects. Some authors have been unable to detect significant allometry of shell shape indices in relation to shell height in littorinids (Raffaelli, 1979a; Smith, 1981), but even so the angles describing the geometrical coiling of the shell may show changes during the course of growth (Borkowski, 1974). In species of *Littorina* in which allometry has been described, the relative spire height increases, and the aperture becomes more circular, with increasing shell size (Daguzan, 1977; Marion, 1981; see Section 14.2.5 for definitions). The spire outline of *Littoraria* species is somewhat convex (Chapter 9). The apical angle (half the angle subtended at the apex by the periphery of the last whorl) therefore decreases with growth, this decrease being in the order of 10 to 15°. The relative spire height therefore increases with size. The parallel trends of increasing size and increasing relative spire height at higher tidal levels could therefore be at least partially explained as an allometric effect. As noted by Vermeij (1980), a decrease in the apical angle during ontogeny is common in gastropods, and may be geometrically tied to the declining growth rate. This effect may also contribute to the relatively taller spires and narrower shells of the high level species, of which growth rates are slower than in species which feed near the water level (Section 13.3.3).

If the pattern of shell shape with tidal level amongst *Littoraria* species is a product of allometric and growth rate effects, it cannot be taken as evidence of an adaptive trend. Nevertheless, it should not be assumed that allometry is not adaptive (Gould, 1968; Vermeij, 1978). As in mangrove forests, the littorinids of the high intertidal zone on tropical rocky shores show a pattern of relatively higher spires and smaller apertures at higher levels. This has been interpreted as an adaptive response, reducing the relative area of the foot for conduction of heat from the substrate and for evaporative water loss (Vermeij, 1973a). Similar advantages could apply in mangrove littorinids (Vermeij, 1973b). However, the ability of the snails to attach to the substrate by a mucous seal and thus to survive inactive for long periods with negligible water loss is likely to be of greater significance than small modifications of shell shape. Vermeij (1973b) reported that littorinids in the mangroves of Singapore showed a pattern of increasingly elongate apertures at higher levels, but from the present results this is not a general trend.

On temperate shores, gradients in shell shape are less distinct, perhaps because exposure to wave action is of more significance (Vermeij, 1973a). In the ovoviviparous species *Littorina saxatilis* there is a genetic component of shell shape (Newkirk & Doyle, 1975), and populations from more exposed localities show lower spires and larger apertures, to accomodate a larger area of foot for adherence to the substrate (James, 1968; Raffaelli, 1979a; Smith, 1981; Janson, 1982b). Wave action is not likely to be a selective force in the sheltered mangrove environment.

Another consideration is resistance to crushing predation, since attributes such as narrow or toothed apertures and strengthened apertural margins are known to improve resistance to attack by crabs (Zipser & Vermeij, 1978; Vermeij, 1979b, 1982a, b; Bertness & Cunningham, 1981). A low spire may also be adaptive, but only if in combination with a narrow or toothed aperture (Vermeij, 1979a), otherwise a very tall spire may confer resistance against peeling crabs (Vermeij *et al.*, 1980; Vermeij, 1982a). The observed trends in shell shape in *Littoraria* species do not suggest that adaptation to crushing predation has been important. While the thickened or flared apertural lip undoubtedly does reduce the vulnerability of some *Littoraria* species to attack, flaring is most well developed in the species found at high levels on foliage, and may be of more significance in relation to other factors, such as increasing the area for adhesion by a mucous seal (McNair *et al.*, 1981). A toothed or narrowed aperture appears to be denied to the Littorinidae by phylogenetic constraints, and possibly by the necessity for effective adhesion to a hard substrate (McNair *et al.*, 1981).

Strong shell sculpture is believed to have been developed as an antipredatory device in some gastropods, enhancing protection from crabs (Kitching & Lockwood, 1974; Vermeij, 1979a; Bertness & Cunningham, 1981) and fish (Palmer, 1979). Raffaelli (1982) has suggested that spiral sculpture in juvenile *Littorina littorea* may increase the strength of the shell. Shell sculpture may also be adaptive on exposed coasts, dissipating the force of impinging waves (Vermeij, 1978), and on temperate shores some *Littorina* species are indeed more strongly sculptured where wave action is heavy (James, 1968; Heller, 1975a; Smith, 1981). However, in the variable species *Nodilittorina hawaiiensis* smooth shells occur on the more exposed shores (Struhsaker, 1968, as *Littorina picta*). Interspecific gradients in the degree of sculpture of littorinids are only conspicuous on tropical shores. The stronger sculpture at high levels is believed to increase the surface area for heat loss by re-radiation and convection (Vermeij, 1973a), although this has not been investigated experimentally.

Amongst mangrove littorinids, the sculptural trend is not particularly clear and the species of the lower and middle supralittoral levels are mostly rather feebly sculptured. It is nevertheless striking that all of the species found at the highest levels (*L. filosa*, *L. philippiana*, *L. pallescens*, *L. cingulata cingulata*, *L. albicans*; see Chapter 9) show relatively strong sculpture. Temperature control may be important in these species found amongst foliage. It is interesting that in *L. albicans* the strong sculpture is achieved by axial varices, while in all other species spiral carinae are developed. The two low level species *L. sulculosa* and *L. carinifera* show anomalously strong spiral ribs, and protection from predators could be significant in these cases.

Neither the shape nor sculpture of mangrove littorinids from low levels are conspicuously adapted to withstand crushing predation, but a degree of protection is afforded by a thick shell. The greater thickness of the shell at lower levels is a consistent trend in *Littoraria* species (Table 14.6), but nevertheless possible nonadaptive explanations must be considered. The species of high levels are in some respects analogous to terrestrial and freshwater pulmonates, in which low availability of calcium carbonate may limit shell thickness (Graus, 1974). However, calcium carbonate is unlikely to be in short supply even in a supralittoral marine habitat; *L. carinifera* at the landward edge of the forest may be reached only by the highest spring tides, and yet develops a thick shell. During periods of inactivity when anaerobic respiration takes place, some molluscs redissolve the shell to buffer the pH of the body fluids (Crenshaw & Neff, 1969), but since the respiratory rate of inactive littorinids must be extremely low (Vermeij, 1973b), this effect is unlikely to account for the thinner shells at higher levels.

The attainment of immunity from crushing predators at a smaller size by species with thicker shells has been demonstrated here in two *Littoraria* species, and similar experiments have been reported by previous authors (Ebling *et al.*, 1964; Reynolds & Reynolds, 1977; Bertness & Cunningham, 1981; Reimchen, 1982). Differences in shell thickness between populations of thaid species (Ebling *et al.*, 1964; Kitching & Lockwood, 1974; Hughes & Elner, 1979) and of *Littorina saxatilis* (Raffaelli, 1978b, 1982; Janson, 1982b) have therefore commonly been explained in terms of selection for thicker shells where crab predation is more intense (although in the latter case crushing by boulders may also be significant). Vermeij (1982b) has shown that populations of *Nucella lapillus* north of Cape Cod developed thicker shells following the establishment of the crab *Carcinus maenas* in the area early this century. Amongst British *Littorina* species the greater thickness of species at lower levels is believed to reflect a similarly adaptive response (Heller, 1976; Elner & Raffaelli, 1980; Reimchen, 1982), and in view of the intensity of crab predation in mangrove swamps the same explanation may apply.

The pattern of shell thickness can also be interpreted as a trend towards thinner shells at higher levels on the shore. Heller (1976) suggested that the weight of the shell represented an energetic cost if not supported by upthrust during submersion, but such a consideration cannot apply to *Littoraria* species which all remain above the water level. Heller (1976) also noted that lighter shells would be less susceptible to dislodgement while attached to the substrate by mucus. This advantage of a thin shell may be important in *Littoraria* species from the highest levels, which remain attached by mucus for long periods. The danger of dislodgement must be greatest in species habitually found amongst the foliage; in *L. filosa*, for example, the rate of emigration from *Avicennia* trees was high (Section 14.3.2), and may be accounted for by accidental dislodgement (Section 14.4.1). Other species commonly found on leaves include *L. luteola*, *L. conica*, *L. pallescens* and *L. albicans*, and in each case the shell is thin. Dislodgement may carry a severe penalty, for the thin-shelled snails will be highly susceptible to attack by crabs at ground level. Even if dislodged, a thin shell might be an advantage; individuals of *L. filosa* float for several minutes while air remains in the mantle cavity.

It may, however, be unnecessary to propose a selective advantage for thin shells at high levels, since, if energy is required for shell production, in the absence of selection for thickened shells species should maintain shells as thin as possible (Elner & Raffaelli, 1980). It is noteworthy that thin shells are also characteristic of the tree-dwelling members of the families Neritidae (e.g. *Nerita articulata*) and Potamididae (e.g. *Cerithidea* spp.) in mangrove forests (pers. obs.).

Both a thick shell and large size can confer resistance to crushing predation, but there appears to be a fundamental inverse relationship between thickness and rate of growth, dictated by the rate at which calcification can be achieved (Palmer, 1981). Many gastropods with determinate growth, well protected as adults, solve this conflict by growing rapidly to large size as thin-shelled juveniles, which avoid predators by means of cryptic habits (Vermeij, 1978). This option is not available to mangrove littorinids, which are always accessible to crabs. The inverse correlation between size and thickness in these species (all species in Table 14.5 combined, Spearman rank correlation coefficient r_s = -0.500, n = 642, P <0.0001), with small thick shells at low levels and large thin ones above, could therefore represent differing evolutionary solutions to the conflict of size and thickness, according to the intensity of predation at successive levels. As in most gastropods, *Littoraria* species thicken the shell marginally and internally when adult size is reached and growth is slow, providing a further advantage of rapid attainment of the slow-growing adult stage in species subject to heavy predation, even if this is achieved at the cost of small size. Reimchen (1982) has proposed a similar explanation in relation to *Littorina obtusata* and the smaller, thicker *Littorina mariae* in Britain.

It is not at present possible to decide between these several explanations for the observed trends in shell size, shape, sculpture and thickness amongst the *Littoraria* species in mangrove forests, and indeed they are not mutually exclusive. Further work will be necessary to clarify the allometric relationships between shell parameters, and their dependence upon growth rates, and also to test the selective advantages which have been suggested. Even if selective advantages can be shown experimentally, populations may not prove to be optimally adapted to particular selective agents, whether because of counterbalancing selection by other forces, gene flow, or other unrecognized constraints (Vermeij, 1982d; Gould & Lewontin, 1979).

CHAPTER 15: SHELL COLOUR POLYMORPHISM

15.1 Introduction

In the family Littorinidae most species show some variability in shell colouration, but only in the genera *Littorina* and *Littoraria* can true polymorphism be found, in which colour variation is discrete (Ford, 1945). The seven European species of *Littorina sensu stricto* are each polymorphic to some degree (reviews by Sacchi, 1974; Raffaelli, 1982), but most strikingly so in the species with nonplanktotrophic development. This has led to the suggestion that restricted dispersal encourages localized adaptation and variability within species (James, 1968; Gaillard, 1972; Heller, 1975a). However, in the genus *Littoraria* all known species (with the probable exception of *L. aberrans*, Section 4.3) have planktotrophic development (Section 5.4). Other polymorphic groups on temperate shores include members of the genera *Lacuna* (Smith, 1973), *Crepidula* (Hoagland, 1977) and *Nucella* (Berry & Crothers, 1974; Spight, 1976). Polymorphism within species becomes more frequent in tropical latitudes, well known examples including members of the families Neritidae (Safriel, 1969; Grüneberg, 1976) and Donacidae (Smith, 1971, 1975), although striking colour variation is present in other groups also (A.H. Clarke, 1978).

The best known and most intensively studied of molluscan colour polymorphisms are those of pulmonates, especially of two species of the genus *Cepaea* in Europe (reviews by Jones *et al.*, 1977; Clarke *et al.*, 1978). Many of the genetic processes discovered in *Cepaea* populations may operate in polymorphic intertidal molluscs.

The study of polymorphic *Littorina* species began with attempts to classify the colour forms by bestowing subspecific and varietal names (Dautzenberg & Fischer, 1912, 1914). Detailed work on the local distribution of colour forms attempted to correlate their occurrence with environmental conditions, as in the long series of papers by Fischer-Piette and others on *Littorina 'saxatilis'* (Fischer-Piette & Gaillard, 1971, and references therein). However, this approach failed to detect consistent patterns of distribution, no doubt in part due to the confusion of the four distinct species in the *saxatilis* complex (see Chapter 2 and Raffaelli, 1982, for reviews). Based on an understanding of the taxonomy of the genus, more recent studies have reported some correlations between the frequencies of colour morphs and the visual properties of the background, suggesting that visual selection by predators may occur (Heller, 1975b; Smith, 1976; Naylor & Begon, 1982). However, only the work of Reimchen (1979) has demonstrated experimentally that a visually hunting predator, in this case the fish *Blennius pholis*, can indeed exert selection for crypsis on littorinid shells. A criticism of several studies of correlations between shell and background colouration (Giesel, 1970; Heller, 1975b, 1979) is their failure to consider adequately the possibility of a direct environmental influence upon shell colour, in favour of explanations involving visual selection by predators (Underwood, 1979). Several authors have found correlations between colour frequencies and the exposure of the habitat to wave action, but not with its visual properties, and have therefore suggested that selection acts on pleiotropic characters unrelated to shell colour (Sacchi, 1969; Raffaelli, 1979b).

In *Littoraria* species a number of colour forms were given varietal names by Philippi (1847-48). Since then the conspicuous colour variation within the *scabra* group has been noted by many authors. Until recently, only Abe (1942) had recorded proportions of colour forms in different populations, in *L. pallescens* (as *Melaraphe scabra*) at Palao, finding differences between samples from several localities. Working in Papua New Guinea, Cook (1983) noted that two unnamed species (*L. scabra* and *L. intermedia*) on *Rhizophora* trunks were monomorphic and cryptic, while a third species (*L. pallescens*) on the leaves was polymorphic. He discussed briefly the possible selective forces which could maintain such a polymorphism, by analogy with the studies on *Cepaea*.

In the present study the distribution of colour forms in the genus *Littoraria* was examined at several levels: between species, within species on a geographical scale, and within populations on a fine environmental scale. At the interspecific level, the phylogenetic distribution of colour forms is discussed in Section 4.5, and detailed descriptions of colour patterns are given in the systematic section (Chapter 9). In this chapter correlations of colour variation with habitat are examined, both within and between species. On the basis of studies of the five common species of *Littoraria* at Cockle Bay, and in particular of *L. filosa*, some suggestions are made concerning the basis and possible maintenance of the variation. It has been necessary to discuss the extensive and scattered literature at some length, in the absence of comprehensive reviews of the subject by previous authors.

The present work is necessarily of a preliminary nature, and it is believed that these species have potential for further research. Their tree-dwelling habit permits manipulation and isolation of sub-populations in a way impossible with the largely ground-dwelling *Cepaea* and with other intertidal gastropods. Such a preliminary investigation cannot aspire to the provision of definitive answers to questions concerning the evolution and maintenance of shell colour polymorphism. The literature from 30 years of research upon the subject in *Cepaea* indicates the complexity of the problem, and shows that several evolutionary processes may act singly or in combination, and in different ways upon different populations (Jones *et al.*, 1977).

15.2 Description and classification of the colour polymorphism

The colour patterns of *Littoraria* species are described in detail in Section 4.5 and in Chapter 9. To summarize, in those species showing the widest range of variation, the ground colour of the shell may be white to yellow, or sometimes orange pink. Some shells may lack further pigmentation, but in most a pattern of more or less discrete brown to black spiral dashes is superimposed (see Frontispiece). This variability can be described as a polymorphism in the strict sense of Ford (1945), since there are clear discontinuities between yellow and pink ground colours, and between patterned and nonpatterned shells. However, within the patterned category there is a continuous range of variation from faint to dark pigmentation. It should be noted that the degree of pigmentation of the body is usually correlated with that of the shell (Section 5.1, Chapter 9).

Ford's (1945) definition stipulates that in a polymorphism the discrete morphs should be present in proportions which are too large to be maintained simply by recurrent mutation. In practice, mutation rates are seldom known, and by convention the term is restricted to cases in which the frequency of the commonest morph is less than 99% (Clarke *et al.*, 1978). The frequency of yellow patterned shells is less than this value in the polymorphic *Littoraria* species. The truly polymorphic species found in the Indo-Pacific province are *L.* (*Lamellilitorina*) *albicans*, and, in the subgenus *Littorinopsis*, *L. lutea*, *L. pallescens*, *L. philippiana*, *L. filosa*, *L. cingulata pristissini*, *L. luteola*, *L. ardouiniana* and *L. delicatula*. To these may be added *L.* (*Littorinopsis*) *angulifera* from the tropical Atlantic, and possibly *L. aberrans* (of which few specimens are known) from the eastern Pacific. In the less colourful species, only the degree of patterning varies, and these are here termed 'variable', as opposed to 'polymorphic'. *L. articulata* and *L. melanostoma* are not considered polymorphic, since although pink shells have been found, they occur at frequencies of much less than

1%. *L. intermedia* is peculiar, being polymorphic in only parts of its range (Section 9.2.3.5).

In previous investigations of polymorphic gastropods, the colour polymorphism has sometimes been described in terms of a background colour with superimposed dark patterning. Genera in which this method of classification has been used include *Clithon* (Grüneberg, 1976), *Littorina* (Pettitt, 1973a; Naylor & Begon, 1982) and *Nucella* (Berry & Crothers, 1974), besides the well known case of *Cepaea* (review by Jones *et al.*, 1977). By analogy with the genetically determined colour polymorphism of *Cepaea*, Pettitt (1973a) devised a detailed classification of the morphs of *Littorina 'saxatilis'*, based on seven shades of ground colour, four banding types and three other distinct patterns (although Heller (1975a, b) could not distinguish discrete colour morphs in *Littorina saxatilis s.s.*, as *Littorina rudis*).

Amongst *Littoraria* species the patterns are not discrete and there are essentially only two distinct ground colours, so a simpler scheme was developed. Yellow or pink ground colours were denoted as Y and P respectively. Approximately 1 shell in 1000 of the most polymorphic species, *L. filosa*, showed a ground colour intermediate between pink and yellow, here scored as pink, although this may represent an additional, rare, colour class. The degree of patterning was estimated on a six point scale: 0 (absent), 1 (faint spots at periphery and suture only), 2 or 3 (diffuse patterning), 4 (dark patterning) and 5 (dark pigment covering entire surface). Since in pattern classes 4 and 5 the ground colour was obscured, these shells were denoted as brown (B). In fact these shells were linked to those with yellow ground colour by a continuous range of intermediates. As in *Cepaea* (Jones *et al.*, 1977), pink shells with heavy patterning were rare. In the 'polymorphic' *Littoraria* species the possible range of colour and pattern combinations was therefore Y0 to Y3, B4, B5, P0 to P3 (see Frontispiece), and in the 'variable' species Y1 to Y3, B4 and B5. This scheme was applicable to all *Littoraria* species, although because of differences in the distribution of the pigment forming the pattern, the pattern classes were not strictly comparable between species. In order to ensure consistency of scoring of colour patterns in *L. filosa*, the species investigated in most detail, a reference series of shells was used. The intensity of the shell pattern fades somewhat with time, but since pattern distribution rather than intensity was the criterion, little difficulty was experienced in scoring old shells.

When calculating the 'index of colour variation' (Section 15.3), the complete detailed classification of colour morphs was used, since an estimate of diversity of colour was required. When making comparisons of samples scored for colour on different occasions, when sample sizes were small, or when samples included small juvenile snails, a coarser classification was employed to guard against possible inconsistencies of scoring amongst the more detailed categories. The coarser scheme combined classes as follows: yellow (Y = Y0 + Y1), yellow-brown (YB = Y2 + Y3), brown and pink (BP = B4 + B5 + P0 to P3).

15.3 Methods

Interspecific trends in the diversity of colour variation with zonation level were examined on the mangrove transects described in Chapter 11. Trends were quantified by correlation between an index of colour variation and each of three measures of zonation (above the ground, above chart datum and from the seaward edge of the forest; Section 14.2.5). Samples were collected by denuding trees along the transects of their snails.

The index of variation used was derived from the Shannon-Wiener function for diversity (Pielou, 1966):

$$H' = -\Sigma_{i=1}^{m} p_i \ln p_i$$

where p_i is the proportion of the 'i'th colour form in the population and m the total number of forms. An estimate, H", is obtained by using the proportion of the 'i'th form in the sample as p_i. This is a biased estimate which may be corrected by the function:

$$H''_{corrected} = H'' - \frac{(S - 1)}{2N}$$

where S is the total number of possible forms in the species concerned, and N is the sample size (Pielou, 1966). H is measured in bits per individual, but a more useful index can be derived by the function:

$$E = e^{H''corrected}$$

where E is measured in forms, and is equal to the number of equally common forms which would have the same diversity as that of the sample (Smith, 1976). This index was used as a measure of colour variation in both polymorphic and variable species. It is not an index of polymorphism, since the forms are arbitrarily defined in a continuum of variation and are not morphs in the strict sense of Ford (1945).

As a result of personal collections and from material available in museums (BMNH, AMS, WAM, RNHL, USNM, ANSP, MCZ), reasonably large samples of *L. filosa* and *L. pallescens* were available from the entire geographical ranges of these species. These samples were examined for possible trends in colour frequencies on a geographical scale.

The association between sex and shell colour was investigated in *L. filosa* at Cockle Bay (where this species was studied in detail) and in a population from Ludmilla Creek, near Darwin, N.T. This association was also examined in *L. luteola* from Kurnell, Botany Bay, N.S.W.

At four localities, samples of adult shells of a total of six species were collected from *Avicennia* and *Rhizophora* trees. At Ao Nam-Bor, Phuket Island, Thailand, samples of *L. pallescens* were collected from the leaves of *Sonneratia* trees in an open, sunny position at the seaward edge of the forest, and also from the leaves of *Rhizophora apiculata* in a similar position (adjacent to, but not in direct contact with, the *Sonneratia* trees), and from the foliage of *Rhizophora apiculata* in a dense, shady forest 200 metres from the first site. At Kurnell, N.S.W., samples of *L. luteola* were collected from leaves and from trunks of *Avicennia* trees. For each species at each locality, the distributions of colour forms in the two or three microhabitats were compared by means of chi-squared contingency tables. These tests were performed using the raw data, although results are presented as proportions to facilitate comparison.

At Cockle Bay the possibility of a direct influence of substrate upon the phenotypic expression of shell colour was investigated by confining small juveniles (mostly <5 mm) of *L. filosa*, *L. philippiana* and *L. scabra* on either the foliage or bark of both *Avicennia* and *Rhizophora* trees, in sleeves of fine nylon netting (see Section 13.2.3 for description of caging procedure). Transfer between tree species of larger juveniles (individually numbered as described in Section 13.2.2) was also attempted. Transfers of individuals originating from each tree species were performed, and some snails returned to their tree of origin to act as controls. Before release, the shell height and colour of each individual were recorded. The snails were measured at monthly intervals and examined for signs of colour change on the shell increment added since the initial marking. Totals of 12 *L. scabra*, 48 *L. philippiana* and 200 *L. filosa* were used in the transfer experiments.

To investigate the possibility of differential selection acting upon the colour forms of *L. filosa*, a large scale survey of the snails on *Avicennia* trees at Cockle Bay was carried out in February 1981. Twenty trees were selected, representing a range of microenvironmental conditions. As an indication of the relative area of foliage and bark, a 'leaf : bark index' was estimated for each tree. This was done by envisaging the foliage of the tree below a level of 2 metres above the ground (the maximum level occupied by most of the snails) to be projected on to a circle equal in diameter to that of the tree canopy. The proportion of the circle occupied was estimated in eighths, giving a value ranging from 0 for trees with no foliage at the levels occupied by snails, to 8 for those with abundant foliage at these levels. Trees with an index between 0 and 3 were classed as 'bare', and from 4 to 8 as 'leafy'. In each category, half the trees were in open sunny situations, and half shaded by a dense canopy or by the foliage of adjacent *Avicennia* trees. All specimens of *L. filosa* were collected from each of the twenty trees and shell height and colour recorded. Chi-squared tests were used to compare colour proportions in sun and shade, on bare and leafy trees, and within and between size classes. The survey was repeated in July 1981, when snails were more abundant, using seven leafy and three bare trees, all in sunny positions.

In order to follow the changing colour proportions of a cohort of *L. filosa* over time, five leafy and ten bare trees were denuded of snails in May 1982, and after scoring for colour, those snails in the size range 3 to 6 mm were released on the trees from which they had been removed. After four months it was estimated (from the growth curve, Section 13.3.3) that the snails would have grown to at least 15 mm, so all those larger than 15 mm were collected and scored for colour.

The individually numbered specimens of *L. filosa*, used for the investigation of behaviour (Chapter 12), population dynamics and growth rate (Chapter 13), were all scored for colour at the time of numbering, so that these aspects could be compared in different colour classes (yellow, yellow-brown, brown and pink). Distribution of colours on leaf and bark substrates was examined by combining data for the six dates on which weather was dry (Table 12.4), after using a chi-squared test to check for homogeneity between dates. During wet weather the majority of snails occurred on leaves (Table

12.4), so these dates were excluded. On four dates sufficient numbers of *L. filosa* were recorded in direct sunlight, to allow comparison of colour distribution in sunlit and shaded positions on the trees; data for these dates were combined after testing for homogeneity. The vertical distribution of colour forms was examined on each date, by analysis of covariance, with shell size as the covariate and sex and colour as the factors (Hull & Nie, 1981). Rates of loss of yellow (Y) and brown (BP) shells were compared in two ways, firstly by calculating instantaneous loss rates for each (see Section 13.2.2 for details; comparison of slopes by t-test) and secondly by comparing monthly survivorships (arcsine transformed figures compared by t-test). Growth rates of colour classes were compared by analysis of covariance of monthly growth increments, with initial height as the covariate and colour class as the factor (see Section 13.2.3).

In some gastropods, shell colour is believed to be of adaptive significance in temperature regulation (Jones *et al.*, 1977). Ten empty adult shells of each of six colour classes (yellow, faded yellow, yellow-brown, brown, faded brown, pink) of *L. filosa* were placed in similar orientation on a white plastic tray and exposed to direct sunlight at midday on a cloudless summer day. Shell surface temperatures were recorded with a telethermometer after two hours. A limited number of measurements of shell and body temperature were taken in the field under similar conditions, using the same instrument.

One of several possible mechanisms by which visible polymorphism may be maintained in natural populations involves frequency dependent selection of the morphs by predators. This possibility was investigated in *L. filosa* at Cockle Bay, by altering the colour proportions on a series of *Avicennia* bushes and recording the numbers present after an interval of two weeks. Eight *Avicennia* bushes were selected for similarity of size, shape and position, in an open, sparsely treed area of 20 by 20 metres (Fig. 10.2). The branches were pruned as necessary to make the bushes more closely comparable, and to prevent contact between them. Each measured approximately 2 m in height, with a leafy canopy 1.5 m in diameter. On 29 July 1981 all snails were removed from the bushes and artificial populations of 60 snails, in the size range 7 to 10 mm, were released on each (that is, at an approximately natural density for this size class). The ratios of yellow (Y0) to brown (in this case Y3, B4 and B5 snails, since B4 and B5 together were too scarce to provide the large numbers necessary for the experiment) on the eight trees were 0, 0.1, 0.2, 0.3, 0.5, 0.7, 0.9 and 1.0. Since all snails released were unmarked, three further bushes of similar size and shape were denuded of snails, in order to measure immigration of snails in the 7 to 10 mm size range. Effectively there was an extra tree for measuring immigration, since on the bushes with ratios 0 and 1.0 the immigration of brown and yellow snails respectively could be recorded. After two weeks the numbers of yellow and brown snails on each bush in the range 7 to 11 mm (allowing for growth) were counted. The experiment was repeated for five successive two week periods, the proportions released being rotated between bushes to overcome any variability between them. Another experiment was run concurrently, similar in all respects except that the bushes were situated in an area 20 m from the first, and were pruned severely at each visit, to reduce their natural leaf area by about 80%. The populations released on these relatively bare bushes numbered 40 snails, but the colour proportions were the same. In each experiment the average number of immigrants found on the bushes denuded of snails after each time interval was used to correct the numbers of snails present on the experimental bushes for the effect of immigration.

The data from these experiments were analysed as recommended by Greenwood & Elton (1979). These authors have developed a model of frequency dependent selection by a predator which relates the ratio of two prey types eaten (e_1/e_2) to the ratio of these prey types available (A_1/A_2), by the function:

$$e_1/e_2 = V\,(A_1/A_2)^b$$

The value of b is a measure of the frequency dependence of the selection, being greater than 1 if predation is disproportionately heavy on the more common prey type. A measure of frequency independent selection, or in other words a preference for one prey type irrespective of its frequency, is provided by the departure of V from unity. Logarithmic transformation of this function yields the expression:

$$\log e = b \log V + b \log A$$

(where $e = e_1/e_2$, $A = A_1/A_2$), from which estimates of b and V can be derived from a series of values of log e and log A by normal linear regression methods. If no individuals of either prey type are lost in any trial, this method cannot be used, since the corresponding value of log e will be plus or minus infinity. In this case, Greenwood & Elton (1979) recommend the combination of replicates at each relative prey density, which yields results closely comparable with the complex alternative of the non-linear least squares method (see also Willis *et al.*, 1980). This recommendation was followed in the present study, to obtain estimates and confidence limits of b and V, which were tested for departure from unity (details of tests in Greenwood & Elton, 1979). The results are presented as plots of the proportion of yellow shells amongst the snails lost during the two week intervals (equivalent to $e_1/(e_1 + e_2)$) against the proportion available at the start of the period (equivalent to $A_1/(A_1 + A_2)$), as described by the relationship:

$$\underbrace{\frac{e_1}{(e_1 + e_2)}}_{\text{propn yellows lost}} = \frac{(VA_1/(A_1 + A_2))^b}{(VA_1/(A_1 + A_2))^b + (1 - \underbrace{(A_1/(A_1 + A_2)))^b}_{\text{propn yellows available at start}}} \quad ✓$$

It should be noted that the ratio A_1/A_2 may change during the 2 week interval, since lost snails were not replaced until the following trial. As discussed by Greenwood & Elton (1979), the analysis is still applicable, but the test for frequency dependence is less sensitive.

The proportions of snails lost at each combination of yellow and brown shells were compared (after arcsine transformation) by a one-way analysis of variance. In addition, loss rates from individual trees were compared in the same way. The experimental design was too non-orthogonal to permit two-way analysis of these factors together.

From the results of the mark and recapture experiment with *L. filosa* (Section 13.2.2), it was possible to compare the colour proportions in the samples recorded on 14 successive monthly visits. To examine the possibility of an association between the diversity of colour forms and the population density, the index of colour variation (E) for each monthly sample was correlated with the estimate of population density per tree (Section 13.3.2).

During the course of the mark and recapture experiment a total of 34 shells of *L. filosa* were found dead and attached to the trees. The colour proportions in this combined sample were compared with the averaged colour proportions of the living snails throughout the year.

In any investigation of colour polymorphism in natural habitats there is the danger that the results obtained may reflect the searching behaviour of the experimenter. During the studies described here, trees were searched in a systematic fashion, branch by branch, each examined from upper and lower surfaces, in an effort to avoid bias towards the more conspicuous colours. In the mark and recapture experiment (Section 13.2.2) the mean probability of capture of *L. filosa* on the two large and leafy *Avicennia* trees was 81% (Table 13.4). On several monthly visits, the number of snails missed, but recaptured on a subsequent visit, was sufficiently great to permit comparison, by chi-squared test, of the colour proportions of the snails overlooked with those of the sample recaptured. Although not an ideal test for bias, the comparisons showed no significant differences ($P > 0.22$ in each of six tests).

15.4 Results

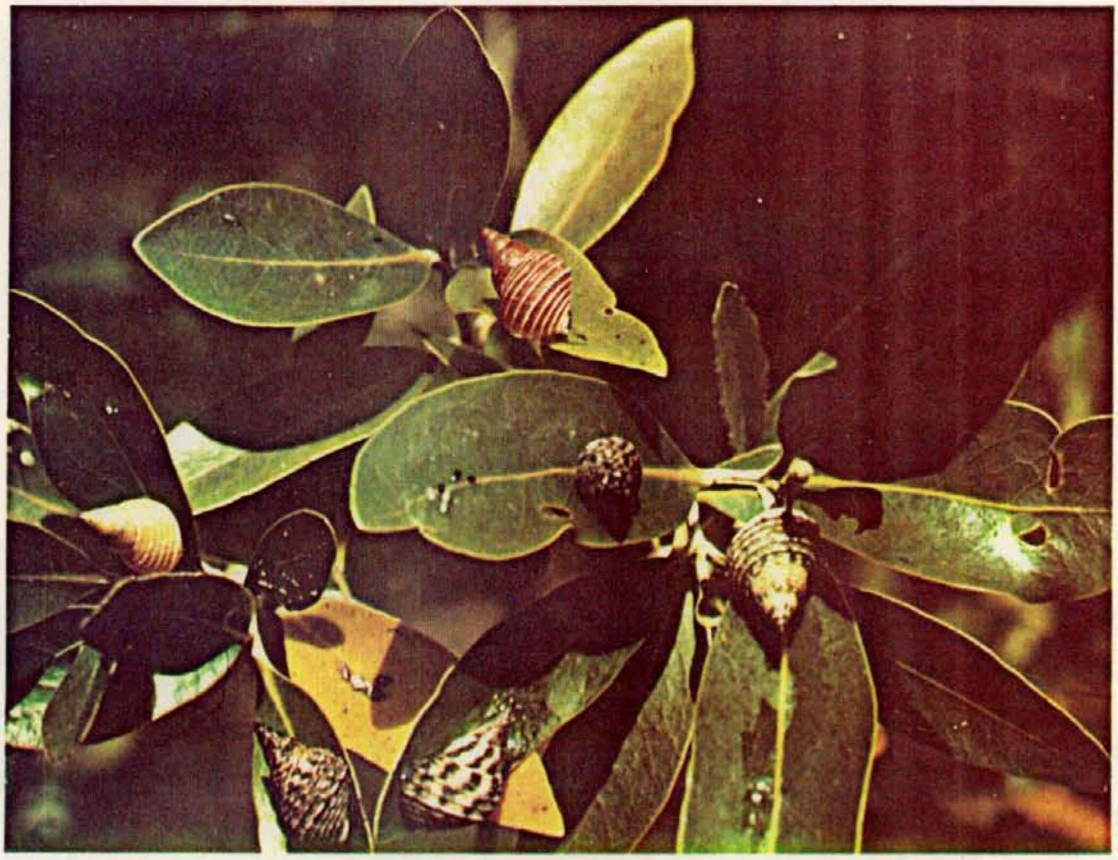
15.4.1 Polymorphism and habitat

Of the *Littoraria* species collected in the field during the present study, the most highly polymorphic were the species typically found on foliage at the higher levels above the ground. These included *L. filosa* (Fig. 15.1), *L. luteola*, *L. pallescens* and *L. albicans* (Table 14.5). *L. philippiana* was usually less polymorphic than these four, and was found on both bark and leaves at high levels. Both *L. luteola* and *L. cingulata pristissini* were sometimes found in salt marshes (Section 11.4.4), and while the former was usually drab in this habitat, the latter was brightly coloured and highly polymorphic. The habitats of the polymorphic species *L. lutea* and *L. ardouiniana* are less well known, but both were found amongst foliage and on branches at moderate levels on mangrove trees in Singapore. The variable (non-polymorphic) species of the genus were found at lower levels, largely or exclusively on bark substrates, and were mostly drab coloured. Figure 15.2 illustrates the three common bark-dwelling species (*L. scabra*, *L. intermedia*, *L. articulata*) found at low and moderate levels on the trees at Cockle Bay.

The association between a high level habitat and variability of shell colour and pattern is quantified by the correlation between zonation level and the index of variability E (Table 15.1, Fig. 15.3). Only one of the correlations is statistically significant, since the number of points is equal to the number of species occurring on each transect, which does not exceed six. Nevertheless, the correlation coefficients indicate the direction and relative magnitude of the associations. No consistent trend is apparent in the relationship between horizontal zonation and colour variation (Table 15.1).

Fig. 15.1 *Littoraria filosa* arranged on foliage of *Avicennia eucalyptifolia* at Cockle Bay, showing range of colour forms. Natural size.

Fig. 15.2 The three common bark-dwelling species of *Littoraria* at Cockle Bay, on trunk of *Rhizophora stylosa*. From left, copulating pair of *L. intermedia*, clusters of *L. articulata*, single *L. scabra*. Natural size.



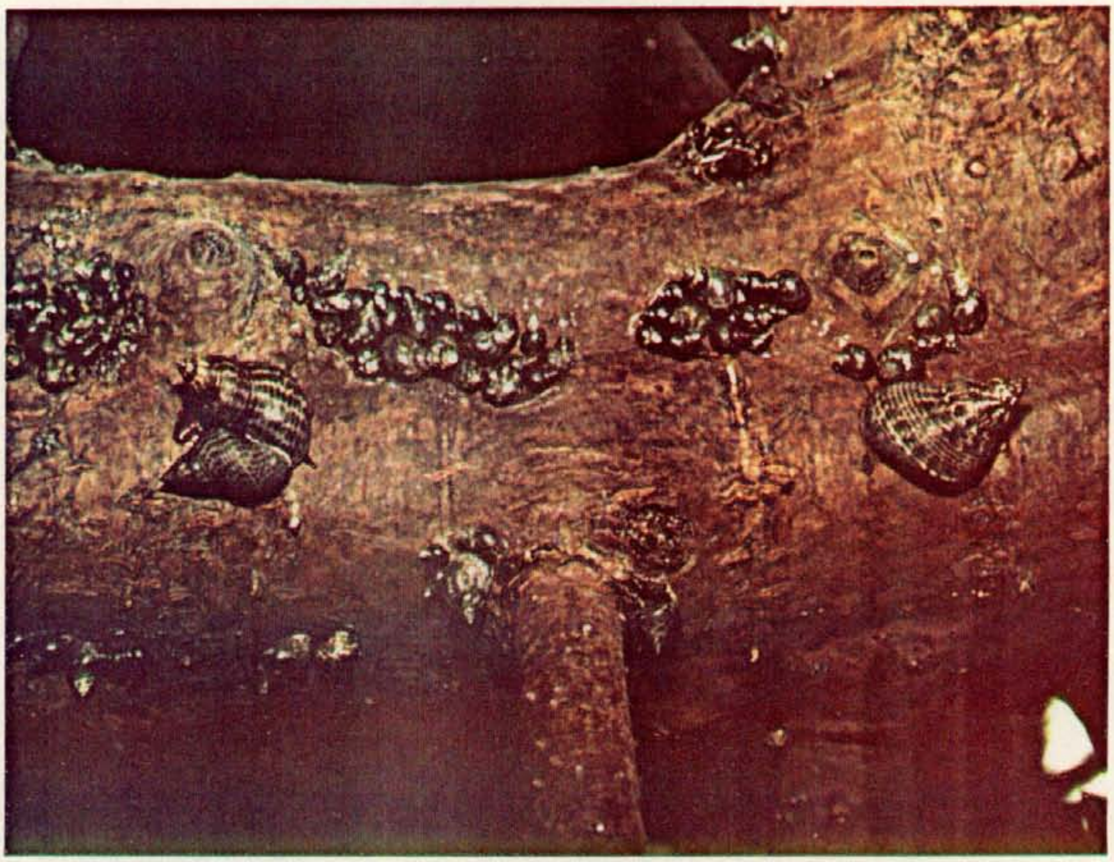
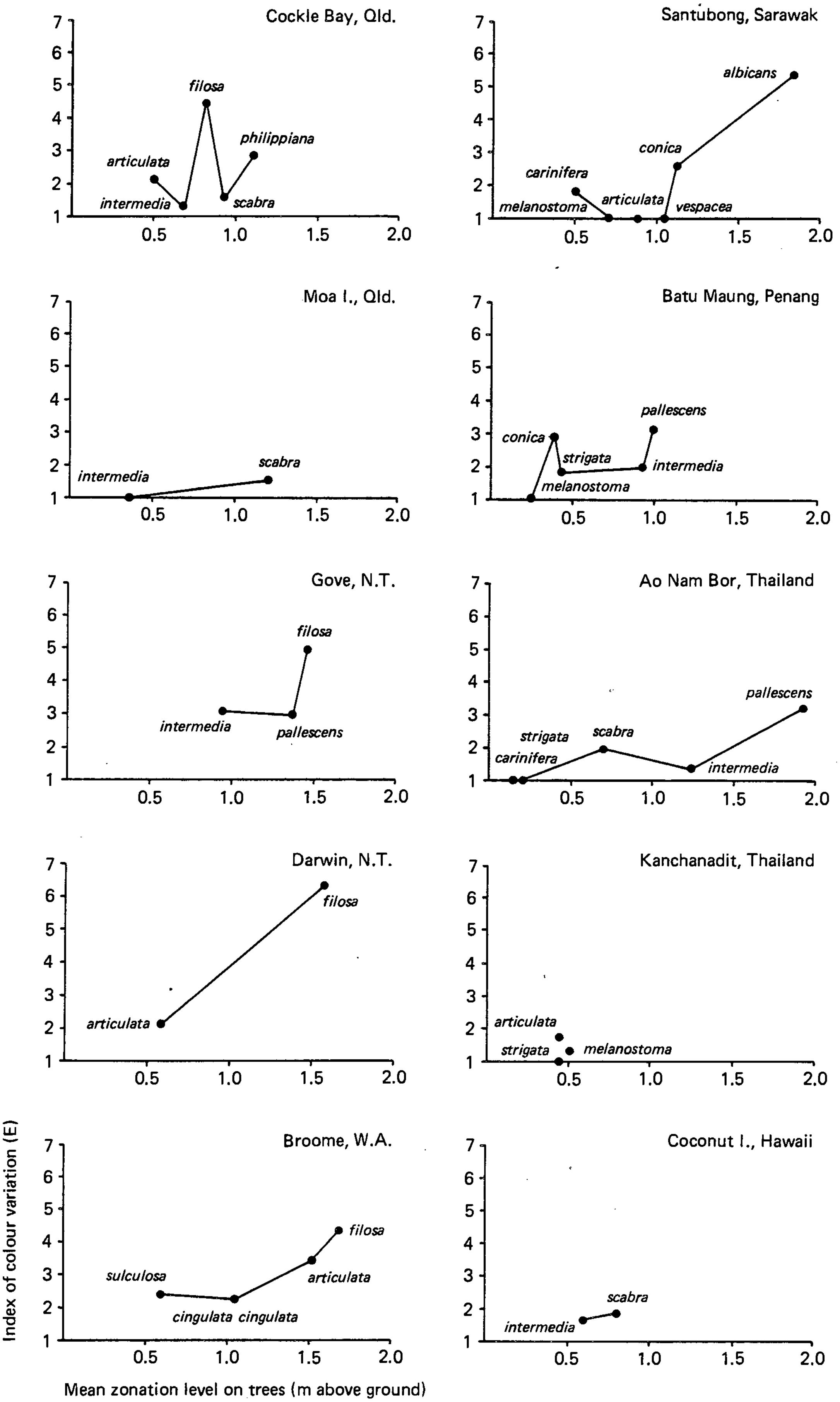


Table 15.1 Correlation coefficients between index of shell colour variation (E) and three measures of zonation level on mangrove transects with two or more *Littoraria* species.

Locality	Number of species	Correlation coefficients of E with measures of zonation level[A]		
		>GR	>CD	HZ
Cockle Bay, Qld.	5	0.243	0.579	0.774
Moa I., Qld.	2	1.000	1.000	-1.000
Gove, N.T.	3	0.592	0.699	-0.449
Darwin, N.T.	2	1.000	1.000	1.000
Broome, W.A.	4	0.874	0.192	-0.495
Santubong, Sarawak	6	0.850 *	0.886 *	0.328
Batu Maung, Penang	5	0.553	0.815	0.593
Ao Nam-Bor, Thailand	5	0.850	0.545	-0.098
Kanchanadit, Thailand	3	-0.141	-0.141	-0.141
Coconut I., Hawaii	2	1.000	1.000	-

[A] >GR, weighted mean height above ground; >CD, weighted mean height above chart datum; HZ, weighted mean distance from seaward edge of forest; * indicates probability between 0.01 and 0.05, ** less than 0.01.

Fig. 15.3 Relationship between index of shell colour variation (E) and vertical zonation above the ground of *Littoraria* species, at localities in Australia, South-east Asia and Hawaii. See Chapter 11 for descriptions of transects through mangrove forests at these localities.


Cockle Bay, Qld.
articulata
intermedia
filosa
scabra
philippiana
Santubong, Sarawak
carinifera
melanostoma
articulata
vespacea
conica
albicans
Moa I., Qld.
intermedia
scabra
Batu Maung, Penang
conica
strigata
melanostoma
intermedia
pallescens
Gove, N.T.
intermedia
pallescens
filosa
Ao Nam Bor, Thailand
strigata
carinifera
scabra
intermedia
pallescens
Darwin, N.T.
articulata
filosa
Kanchanadit, Thailand
articulata
strigata
melanostoma
Broome, W.A.
sulculosa
cingulata cingulata
articulata
filosa
Coconut I., Hawaii
intermedia
scabra
Index of colour variation (E)
Mean zonation level on trees (m above ground)
1
2
3
4
5
6
7
0.5
1.0
1.5
2.0

15.4.2 Geographical distribution of colour forms

Within the polymorphic species of *Littoraria* there appears to be little geographical variation in the presence of colour forms. This is demonstrated by the two most conspicuously polymorphic species, *L. filosa* and *L. pallescens* (Figs 15.4, 15.5), in which even the uncommon pink morphs are found throughout most of the respective geographical ranges. At the present state of knowledge it is difficult to assess possible geographical variation in the proportions of the colour forms. Many of the samples represented in Figures 15.4 and 15.5 are from museum collections, in which precise habitat data is often lacking, and in which collector bias, particularly towards unusual or bright colour forms, is a possibility.

L. filosa is only common on *Avicennia* trees (Section 11.4.3) and it is therefore likely that most of the museum samples were collected from this habitat, as were the majority of those collected personally. If the samples are indeed representative of this species, it appears that the proportion of brown shells may be higher in northern parts of the range, while paler shells predominate in southern samples. In the case of *L. pallescens* there was much greater variability in the proportions of colour forms in the available samples. This variability probably reflects the tree species from which the samples were taken, since there is an association between microhabitat and colour in this species (Section 15.4.3). Some regional forms of both *L. filosa* and *L. pallescens* can be recognized by virtue of distinctive shell colour patterns and sculpture (Sections 9.2.3.7, 9.2.3.3).

Amongst the variable (non-polymorphic) species, there are distinctive regional colour forms in *L. intermedia* and *L. articulata* (Sections 9.2.3.5, 9.2.4.6). *L. cingulata* is an interesting case, in which the southern subspecies *L. c. pristissini* is polymorphic, while the nominate subspecies is not (Sections 9.2.3.8, 9.2.3.9).

Fig. 15.4 Geographical variation in proportions of shell colour classes in samples of *Littoraria filosa* from Australia and the Arafura Sea. Unshaded, yellow; light stipple, yellow-brown; dark stipple, brown; black, pink; see Section 15.2 for definitions of colour classes. Details of samples:

A *Avicennia*; Broome, W.A.; DGR; n = 94.

B Walsh Point, Admiralty Gulf, W.A.; WAM 685-81; n = 25.

C Bolang, S.W. Timor; RNHL; n = 30.

D *Avicennia*; Ludmilla Creek, Darwin, N.T.; DGR; n = 115.

E *Aegialitis*; Gove Peninsula, N.T.; DGR; n = 26.

F Merauke, Irian Jaya; AMS C119935; n = 70.

G *Aegialitis*; St. Paul's Mission, Moa I., Qld.; DGR; n = 25.

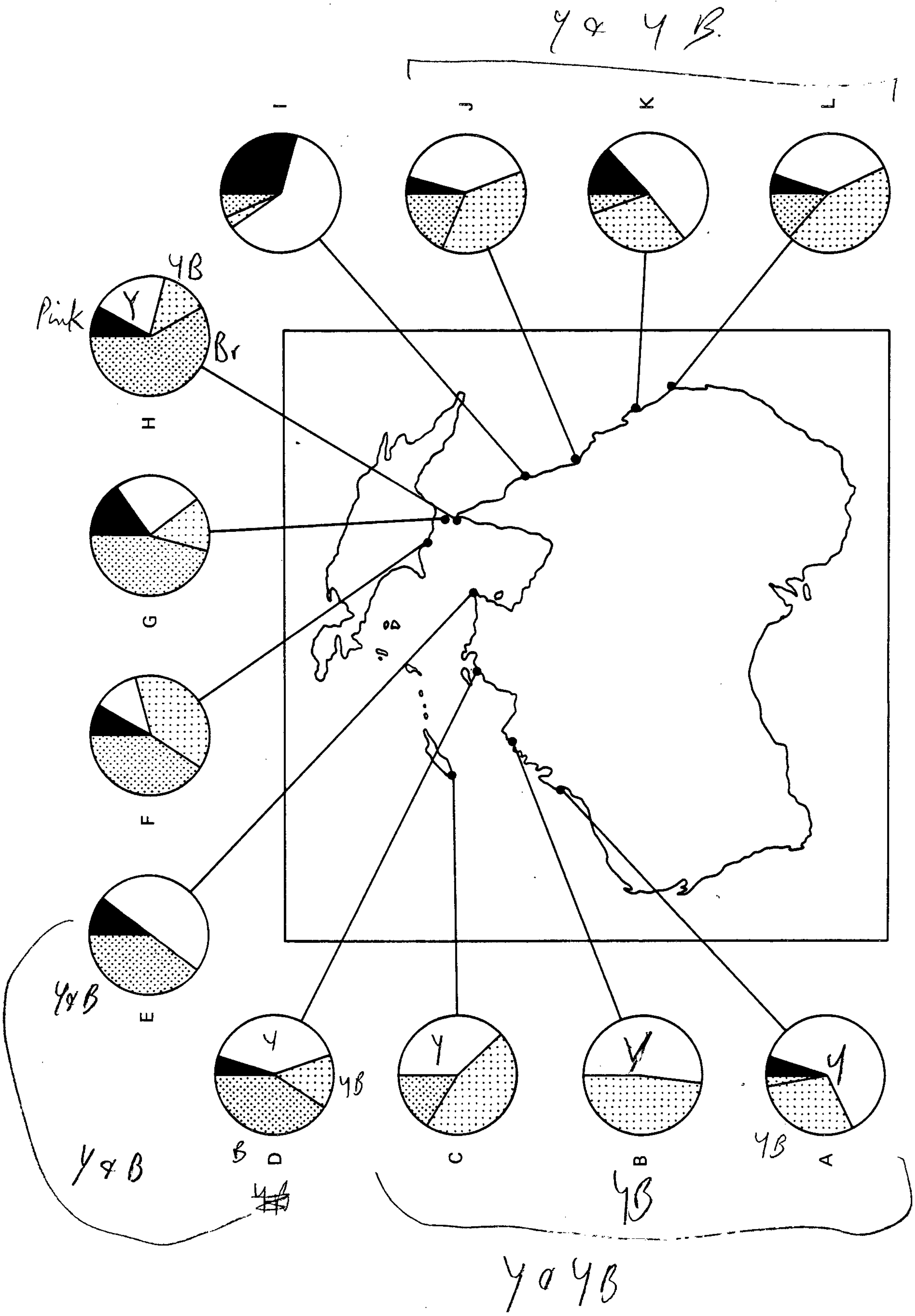
H *Avicennia*; Thursday I., Qld.; DGR; n = 38.

I Cooktown, Qld.; AMS C72095; n = 39.

J *Avicennia*; Cockle Bay, Magnetic I., Qld.; DGR; n = 129.

K Yeppoon, Qld.; AMS C87097; n = 94.

L Elliot River, Pialba, Qld.; QM MO10116; n = 21.



Y & Y B.
I
J
K
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YB
Y
Pink
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Y&B
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Y
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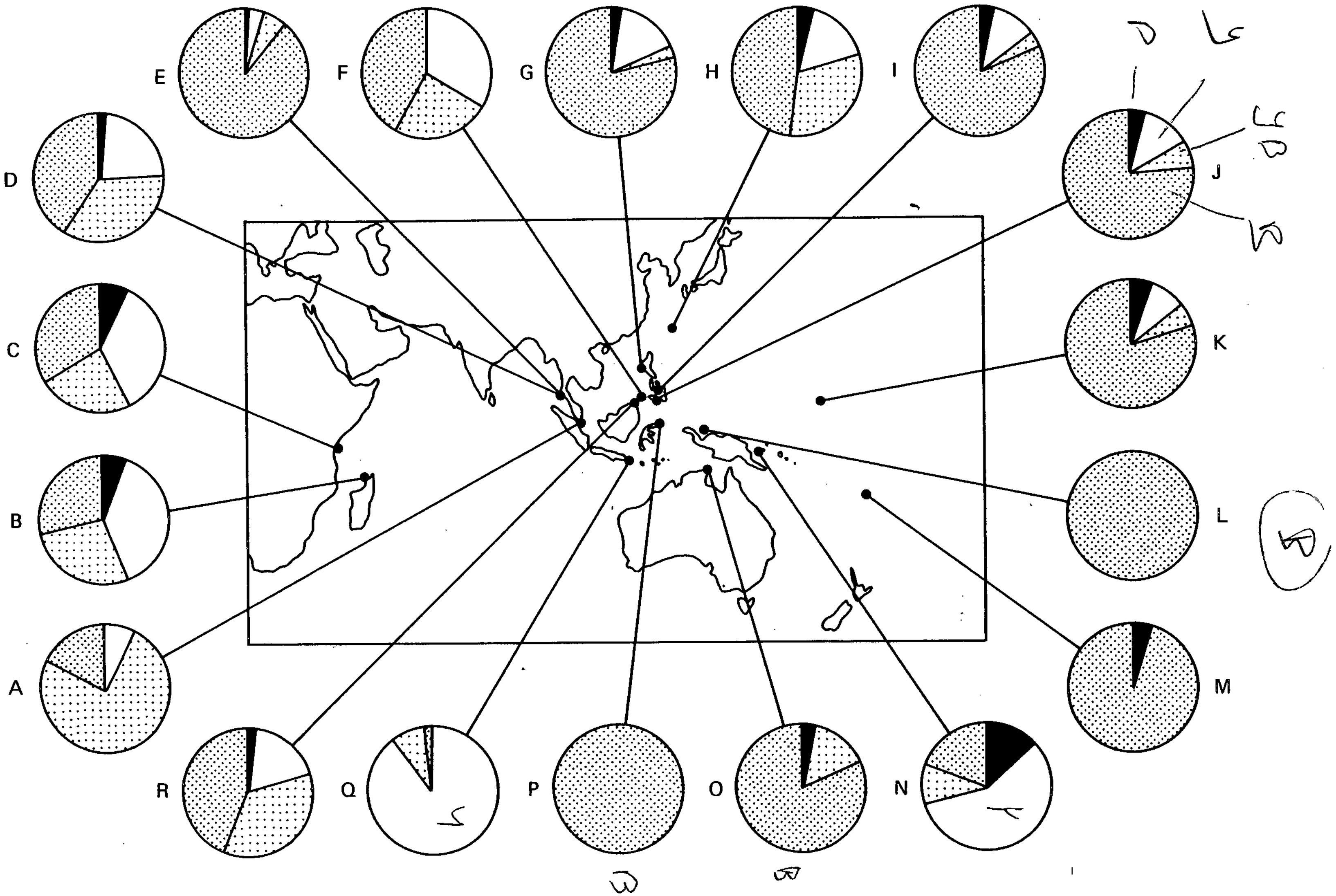
YB
A
Y & YB

Fig. 15.5 Geographical variation in proportions of shell colour classes in samples of *Littoraria pallescens* from the Indo-Pacific. Unshaded, yellow; light stipple, yellow-brown; dark stipple, brown; black, pink; see Section 15.2 for definitions of colour classes. Details of samples:

A *Avicennia*; Ubin I., Singapore; DGR; n = 37.
B Nossi Bé, Madagascar; ANSP 258985; n = 141.
C Chukwani, Zanzibar; ANSP 214826; n = 138.
D *Sonneratia*; Ao Nam Bor, Phuket I., Thailand; DGR; n = 96.
E *Rhizophora*, in shade; Ao Nam Bor, Phuket I., Thailand; DGR; n = 97.
F Siasi I., Sulu Arch., Philippines; ANSP 318551; n = 32.
G Calapan, Mindoro I., Philippines; MCZ; n = 38.
H *Sonneratia*; Ishigaki City, Okinawa, Japan; BMNH; n = 35.
I Leleboon I., Samar I., Philippines; USNM 601227; n = 106.
J Tapiantana I., Philippines; USNM 233255; n = 190.
K *Rhizophora* and *Sonneratia*; Kusaie I., Caroline Is.; USNM 609503; n = 112.
L Samberbaba, Japen I., Irian Jaya; ANSP 106824; n = 93.
M N.W. Viti Levu, Fiji; MCZ 265753; n = 23.
N Kumbun I., New Britain; ANSP 254266; n = 72.
O *Rhizophora*; Gove Peninsula, N.T.; DGR; n = 64.
P Likupang, Sulawesi; USNM 336984; n = 30.
Q Bali; MCZ 229272; n = 149.
R Po Bui I., Sandakan, Sabah; USNM 233252; n = 171.


A
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C
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YB
B
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Y
B
B

15.4.3 Variation between microhabitats in the proportions of colour forms

The most obvious aspect of environmental patchiness in the habitat of *Littoraria* species is the availability of different tree species. Comparisons of the colour proportions of several species from *Avicennia* and *Rhizophora* trees at the same locality are summarized in Table 15.2. The number of samples is not large, since some species are mainly restricted to a particular tree (Section 11.4.3), while at some localities only one or other of these two principal tree species occurred commonly in the zone occupied by snails. Nevertheless, the observations can be generalized from personal experience at many localities. Samples of both *L. scabra* and *L. philippiana* from stands of *Avicennia* trees invariably showed a lesser degree of shell patterning than samples from *Rhizophora*. The proportion of yellow to pink ground colours in *L. philippiana* did not appear to be affected by microhabitat. On the basis of small collections made at Singapore, *L. lutea* seemed to vary in the same way as *L. philippiana*. The effect was less striking in *L. intermedia* and *L. articulata*, but samples from *Avicennia* trees were sometimes noticeably paler. Some species showed no differences between *Rhizophora* and *Avicennia* trees; for example, *L. melanostoma* was uniformly pale on both at Kanchanadit, Thailand.

L. filosa stands out amongst the other polymorphic species as one relatively little affected by tree species. At some localities (e.g. Ludmilla Creek, Darwin; Table 15.2) there was no discernible difference in colour proportions on *Avicennia* and *Rhizophora* trees. In samples from Cockle Bay, however, brown shells were more prevalent on *Rhizophora*. It should be noted that there was still a high frequency of yellow non-patterned shells on *Rhizophora* trees, whereas in other polymorphic species (*L. philippiana, L. lutea, L. pallescens*) this was not so.

At Ao Nam-Bor on Phuket Island, Thailand, significant differences

Table 15.2 Comparisons of shell colour proportions of *Littoraria* species on *Avicennia* and *Rhizophora* trees.

Species	Locality	Tree sp.[B]	n	Proportions in colour classes[A]										χ^2	d.f.	P
				Y0	Y1	Y2	Y3	B4	B5	P0	P1	P2	P3			
L. scabra	Cockle Bay, Qld.	A	29			.38	.48	.10	.03					52.9	2	<.001 **
		R	52					.17	.83							
L. scabra	Orpheus I., Qld.	A	15		.07	.20	.60	.13						37.6	1	<.001 **
		R	31					.03	.97							
L. philippiana	Cockle Bay, Qld.	A	47			.17	.11	.40	.23		.04	.02	.02	37.2	2	<.001 **
		R	160			.01	.01	.23	.69		.03	.02	.02			
L. intermedia	Cockle Bay, Qld.	A	19					.16	.84							
		R	99					.02	.98							
L. filosa	Cockle Bay, Qld.	A	132	.35		.20	.20	.20	.03	.01		.01		14.0	3	.003 **
		R	52	.27	.04	.04	.15	.42	.04		.04					
L. filosa	Darwin, N.T.	A	115	.13	.27	.07	.08	.28	.12	.01	.03	.01		4.9	5	.423
		R	112	.10	.22	.11	.13	.33	.12							
L. articulata	Cockle Bay, Qld.	A	97			.04	.19	.62	.15					16.4	2	<.001 **
		R	86				.03	.67	.29							
L. articulata	Darwin, N.T.	A	108				.10	.74	.16					3.6	2	.165
		R	69				.03	.77	.20							
L. lutea	Ubin I., Singapore	A	28		.36	.64								–	–	–
		R	14		.14	.14	.07	.50	.14							

[A] see Section 15.2 for definitions of colour classes.

[B] A, *Avicennia*; R, *Rhizophora*.

in the proportions of colour forms of *L. pallescens* were found between samples from three microhabitats (Table 15.3). The sample from *Sonneratia* leaves in sunlight showed a high proportion of yellow and lightly patterned shells, while the two samples from *Rhizophora* differed only in the proportions of Y3, B4 and B5 shells, the darker shells predominating in the shaded forest habitat.

Another aspect of microenvironmental variation concerns the distinction between bark and leaf substrates on a single tree species. At Kurnell, N.S.W., *L. luteola* was collected from the foliage of *Avicennia* bushes in open positions on the edge of a belt of trees, and from the trunks of *Avicennia* trees in the dense forest behind, where there was no foliage at levels occupied by the snails. Comparison of the samples was complicated by a marked difference between the colour proportions of the sexes, but when males and females were compared separately, those from trunks in the forest were shown to be significantly darker than those from foliage (Table 15.4).

A few species of the genus *Littoraria*, while typical of mangrove habitats, may also be found on rocky shores (Section 11.4.4). *L. intermedia* is most notable amongst these, and in various parts of its extensive range samples from rocky shores show paler and more variable shells than those from mangrove habitats (e.g. Hawaiian Is. and Queensland, pers. obs.; Okinawa and Diego Garcia, specimens in BMNH).

To test the implication of a direct influence of microhabitat upon shell colour, transfer experiments were carried out at Cockle Bay. These were of limited success, for various reasons. Firstly, the strongest environmental effects are to be expected in *L. scabra* and *L. philippiana*, in which colour proportions showed greatest differences between tree species (Table 15.2). Juveniles of both these species were relatively rare, and both were found most frequently upon *Rhizophora* trees, on which colour forms were dark. Consequently, only small numbers of juvenile pale shells were

Table 15.3 Comparison of shell colour proportions of *Littoraria pallescens* in different habitats at Ao Nam-Bor, Phuket Island, Thailand.

Habitat	Sample	n	Proportions in colour classes									
			YO	Y1	Y2	Y3	B4	B5	PO	P1	P2	P3
Sonneratia foliage, in sun	A	96	.16	.06	.08	.27	.33	.07	.02			
Rhizophora foliage, in sun	B	104	.03	.02	.05	.12	.33	.44	.01	.01		
Rhizophora foliage, in deep shade	C	97	.02	.01	.04	.03	.15	.73		.01		

Comparisons: A,B: χ^2 = 43.7, d.f. = 5, P = <.001 **
A,C: χ^2 = 91.8, d.f. = 5, P = <.001 **
B,C: χ^2 = 18.7, d.f. = 4, P = .001 **

Table 15.4 Comparison of shell colour proportions of *Littoraria luteola* in different microhabitats at Bonna Point, Kurnell Peninsula, Botany Bay, N.S.W.

Habitat	Sex	n	Proportions in colour classes										χ^2 A	d.f.	P
			YO	Y1	Y2	Y	B4	B5	PO	P1	P2	P3			
Avicennia foliage, in sun	♀	42	.02	.10	.40	.19	.10	.07	.07	.05			34.6	4	<.001 **
	♂	59			.03	.22	.58	.10	.02	.02	.03				
Avicennia trunks, in shade	♀	22		.09	.09	.23	.18	.41					2.7	2	.258
	♂	57			.02	.11	.28	.49		.02	.05	.04			

A χ^2 for comparison of males and females in same habitat.
For comparisons of same sex in different habitats:
Females: χ^2 = 13.6, d.f. = 2, P = .001 **
Males : χ^2 = 24.0, d.f. = 3, P = <.001 **

available for transfer from *Avicennia* trees. Secondly, *L. filosa* did not survive in netting sleeves on bark substrates, while the other species showed abnormally low growth in these sleeves. Finally, transfer of individually marked snails without confinement was hampered by the high loss rate of juvenile snails and the difficulty of marking the smallest individuals.

Of *L. scabra*, two pale (Y2) individuals, about 8 mm in height, showed significant darkening of the newly grown shell (B4) after four months in a sleeve on a *Rhizophora* root, although the height increments during this time were only 3 to 6% of those expected (see growth curve, Fig. 13.19). Another pale shell confined on an *Avicennia* trunk showed similarly slow growth, but no darkening in colour. Of the uncaged snails transferred, both of the two pale shells from *Avicennia* trees became slightly darker (Y2 to Y3, size 15 mm) after a month on a *Rhizophora* tree, during which time growth rate was normal. However, the reciprocal transfers of brown shells to *Avicennia* trees revealed no lightening in colour after one or two months.

In the case of *L. philippiana*, six out of seven pale shells (P0, Y1, Y3, sizes 8 to 20 mm) from *Avicennia* trees showed significant darkening of the newly grown shell when confined on *Rhizophora* trunks. Again growth was abnormally slow (25 to 30% of that expected). Eleven similar individuals confined on *Avicennia* trunks or foliage showed equally slow growth, but no darkening of the shell. Of 50 marked snails (8 to 15 mm) transferred between tree species, half were recovered after two months. Of these only 17 were combinations which might have been expected to produce colour change, while others were controls. No colour changes were observed in any of these individuals of *L. philippiana*.

Of *L. filosa*, all individuals confined on bark, of either tree species, died. Of 200 transfers performed, none showed colour change. No colour changes were ever observed in those small juveniles caged on leaves of *Avicennia* during investigations of growth rate (under which conditions survival and growth were high, Section 13.3.3).

In the species investigated at Cockle Bay, shell colour and pattern were constant throughout the course of growth in most specimens collected in the field. In *L. philippiana* some pale shells showed a tendency towards gradual darkening of the final whorl, as was typical in *L. lutea* (Section 9.2.3.2). This tendency was also apparent in some yellow shells of *L. filosa* (scored Y1) from Darwin and the Torres Strait. If shell pattern is influenced by substrate, it is to be expected that some shells should be found in the field showing evidence of abrupt pattern change during the course of growth. Such shells were occasionally found in *L. scabra* and *L. philippiana* at Cockle Bay. In *L. filosa* from Cockle Bay the only evidence of pattern change was the finding of five yellow shells with flecks of pigment on the ribs close to the outer lip, all from *Rhizophora* trees.

Several previous authors have mentioned a possible connection between dark pigmentation and a slow growth rate (Section 15.5.1). Although insufficient data were available for the calculation of growth rates of the predominantly dark shells of *L. philippiana* on *Rhizophora* trees (since few juveniles were present), inspection of growth increments of the 96 individually marked shells showed that they did not grow more slowly than paler shells on *Avicennia* trees (Section 13.3.3). In *L. filosa* the growth rate data for individually numbered snails on *Avicennia* was reanalysed by analysis of covariance, which showed no significant differences amongst the slopes of the regressions of growth increment on initial shell size for each of the three colour classes (Y, YB, BP) during any of the 13 monthly intervals.

15.4.4 The distribution of colour forms of *L. filosa* on *Avicennia* trees at Cockle Bay, and evidence of natural selection

In the survey carried out in February 1981, no differences could be detected in the colour proportions of *L. filosa* on *Avicennia* trees in sunny and shaded positions (Table 15.5). The distribution of colour forms was found to be homogeneous between leafy and relatively bare trees in the range of shell sizes below 10 mm. In larger snails a significantly different distribution was found, with yellow shells occurring in a higher proportion on leafy trees, and brown shells on relatively bare trees (Table 15.5). Comparing the two size classes, on relatively bare trees the increased proportion of brown shells amongst large individuals was not significant, but on leafy trees a significant difference was found between small and large snails, with a greater proportion of yellow shells in the latter.

When a similar survey was repeated in July 1981, the snails were more abundant (Fig. 13.10). Here the shells were divided into four size classes, and although none of the differences in colour proportions on bare and leafy trees was significant when comparisons were made within size classes, in three out of four cases brown shells were relatively more abundant on the bare trees, and yellow shells were always relatively more abundant on the leafy trees (Table 15.6). When all size classes were combined, the difference between the colour proportions was significant.

In the third set of observations, snails representing a single cohort were scored for colour when juvenile and again when adult. In this case the colour proportions of the juveniles (3-6 mm) were homogeneous on leafy and bare trees, while as adults ($\geq$15 mm) the increased proportions of brown shells on bare trees and of yellow shells on leafy trees were highly significant (Table 15.7).

Table 15.5 Shell colour proportions of *Littoraria filosa*, on *Avicennia* trees classified by relative area of leaves and bark and by exposure to sunlight, at Cockle Bay on 8 February 1981.

Size class (mm)	Sun or shade	Bare trees[A]				Leafy trees[B]			
		n	Y	YB	BP	n	Y	YB	BP
≤10	sun	25	.32	.52	.16	107	.24	.42	.34
≤10	shade	10	.20	.30	.50	66	.21	.42	.36
>10	sun	49	.29	.41	.31	61	.37	.41	.21
>10	shade	23	.04	.61	.35	68	.40	.38	.22

A leaf : trunk index = 0–3 (see Section 15.3 for details); see Section 15.2 for definitions of colour classes.

B leaf : trunk index = 4–8.

Comparisons of numbers in colour classes, by χ^2 contingency tests:

Size class	Sun or shade	Tree type	χ^2	d.f.	P
≤10	comparison	bare	sample size too small		
≤10	comparison	leafy	0.2	2	.887
>10	comparison	bare	0.0	1	.920
>10	comparison	leafy	0.1	2	.937
≤10	sun	comparison	3.0	2	.221
≤10	shade	comparison	sample size too small		
>10	sun	comparison	1.6	2	.452
>10	shade	comparison	10.2	2	.006 **
≤10	all	comparison	1.2	2	.563
>10	all	comparison	7.1	2	.028 *
comparison	all	bare	0.9	2	.634
comparison	all	leafy	8.1	2	.018 *

Table 15.6 Shell colour proportions of *Littoraria filosa* on *Avicennia* trees classified by relative area of leaves and bark, at Cockle Bay on 11 July 1981. Abbreviations as in Table 15.5.

Size class (mm)	Sun or shade	Bare trees				Leafy trees			
		n	Y	YB	BP	n	Y	YB	BP
≤7	sun	130	.26	.42	.32	450	.36	.40	.24
7-12	sun	158	.32	.47	.21	458	.33	.50	.17
12-17	sun	34	.24	.62	.15	119	.40	.42	.18
>17	sun	29	.24	.41	.34	69	.38	.42	.20

Comparisons of numbers in colour classes on the two tree types, by χ^2 contingency tests:

Size class (mm)	χ^2	d.f.	P
≤7	4.8	2	.093
7-12	1.5	2	.463
12-17	4.4	2	.111
>17	2.8	2	.247
>7	3.1	2	.217
≤12	4.2	2	.120
>12	5.0	2	.084
all	6.9	2	.031 *

Table 15.7 Changing shell colour proportions of *Littoraria filosa* on *Avicennia* trees classified by relative area of leaves and bark, over four month interval, at Cockle Bay.

Size class	Date	Bare trees[A]				Leafy trees[B]				χ^2	d.f.	P
		n	Y	YB	BP	n	Y	YB	BP			
3-6	17/5/1982	183	.30	.50	.20	474	.30	.53	.16	1.5	2	.463
≥15	11/9/1982	67	.13	.36	.51	252	.40	.36	.24	23.2	2	<.001 **

[A] leaf : trunk index = 0 (see Section 15.3).
[B] Leaf : trunk index = 8.
Comparison between dates by χ^2 contingency tests:
on bare trees: $\chi^2 = 23.6$, d.f. = 2, $P < .001$ **
on leafy trees: $\chi^2 = 20.1$, d.f. = 2, $P < .001$ **

Table 15.8 Comparisons of shell colour proportions between the sexes of *Littoraria filosa* at two localities.

Locality	Sex	n	Proportions in colour classes							χ^2	d.f.	P
			Y0	Y1	Y2	Y3	B4	B5	P			
Cockle Bay,[A] Qld.	♂	603	.34	.01	.18	.23	.18	.03	.03	15.6	6	.016 *
	♀	654	.34	.02	.21	.24	.12	.02	.05			
Ludmilla Creek,[B] Darwin, N.T.	♂	103	.12	.28	.08	.07	.30	.13	.03	4.1	5	.537
	♀	123	.10	.24	.11	.14	.29	.10	.02			

[A] sample = all snails marked during mark and recapture experiment on *Avicennia* trees.
[B] sample = snails from *Avicennia* and *Rhizophora* trees combined (see Table 15.2).

15.4.5 Observations on the behaviour, loss rate and sex of the colour forms of *L. filosa*

When a comparison was made between the proportions of the colour forms in the two sexes of *L. filosa* (taking as the sample all individually numbered shells of the mark and recapture experiment), a significant difference was found, due largely to the slightly greater proportion of brown (B4) shells amongst the males in the large sample (Table 15.8). In a smaller sample from Darwin no significant difference was apparent. It may be noted that in the samples of *L. luteola* from Kurnell, N.S.W., male shells were likewise darker than females (Table 15.4).

Regarding the behaviour of colour forms and their detailed distribution upon the trees, the forms appeared to be distributed rather uniformly on the two trees used for the mark and recapture experiment. Vertical levels were analysed on 13 dates and on only two of these was colour a significant factor in the analysis of covariance. On these two occasions the mean level of brown shells (adjusted for shell size) was slightly higher than those of yellow and yellow-brown shells, but since the differences were only between 0.1 and 0.4 m, a correlation between level and colour is regarded as of negligible importance. The distribution of colour forms on leaf and bark substrates is summarized in Table 15.9. Since *Avicennia* twigs are green, they are included in the same substrate category as leaves. A slight tendency for yellow shells to be more frequent on the green substrate is evident from the figures, but the difference was not significant. When comparisons were made between the colour proportions found in direct sunlight and in shade, a significantly higher proportion of yellow shells was found to occur in sunlight (Table 15.10).

From the results detailed in Section 15.4.4, it might be anticipated that on the leafy trees on which the mark and recapture experiment was performed, yellow snails would have shown a higher

Table 15.9 Comparison of shell colour proportions of *Littoraria filosa* on leaves and bark of *Avicennia* trees at Cockle Bay.

Substrate	n	Colour proportions			χ^2	P
		Y	YB	BP		
leaves and twigs	685	.43	.42	.14	3.8	.152
bark	427	.39	.43	.18		

Table 15.10 Comparison of shell colour proportions of *Littoraria filosa* in sun and shade on *Avicennia* trees at Cockle Bay.

Sun or shade	n	Colour proportions			χ^2	P
		Y	YB	BP		
sun	206	.49	.37	.15	7.1	.029 *
shade	642	.38	.46	.16		

survivorship than brown shells. In fact the difference between yellow and brown shells, while in the direction expected, was too small to be significant (mean survivorship of yellow snails = 72.1% per month (95% confidence range 65.8 – 77.8%), for brown snails 68.1% (63.3 – 72.8%), t = 1.13, d.f. = 20, P = 0.273). The instantaneous loss rates per month were almost identical for yellow and brown shells (for yellow μ = 0.374 (± 95% confidence limits 0.067), for brown μ = 0.373 (± 0.042); t for comparison of slopes of survivorship curves = 0.014, d.f. = 13, P = 0.989).

15.4.6 Temperature effects and seasonal differences in proportions of colour forms of *L. filosa*

The temperatures attained by empty shells of six colour classes of *L. filosa* in direct sunlight are given in Table 15.11. In order of increasing temperature, the non-faded colour classes were: yellow < pink < yellow-brown = brown (differences between all but the last two significant at $P < 0.05$, when compared by t tests). The difference between the mean temperatures of yellow and brown shells was 2.6°C. Faded yellow shells appeared almost white, but were not significantly cooler than normal yellow shells, although faded brown shells, appearing lilac grey, reached a significantly lower temperature than normal brown shells. Only a few temperature records of living snails in the field were made (Table 15.12). Although snails were not sufficiently common to permit standardization of substrate, situation and method of attachment, body temperatures were significantly lower in the yellow than brown shells in this small sample (difference between means 1.1°C); shell temperatures were also lower, but not significantly so.

The proportions of colour forms of *L. filosa* did not remain homogeneous throughout the year, as ascertained from the mark and recapture experiment (Fig. 15.6; comparing proportions in the three

Table 15.11 Surface temperatures of empty shells of *Littoraria filosa* in full sunlight.

Shell colour	Mean temp. (°C) (n = 10)	95% confidence limits
Yellow (YO)	37.9	±0.3
Faded yellow (YO)	37.6	±0.2
Yellow-brown (Y2, Y3)	40.3	±0.5
Pink (PO)	38.5	±0.4
Brown (B4, B5)	40.5	±0.2
Faded brown (B4, B5)	39.9	±0.4

Weather conditions: air temperature 36.8°C; cloudless sky; slight breeze.
Date: 10 January 1981.

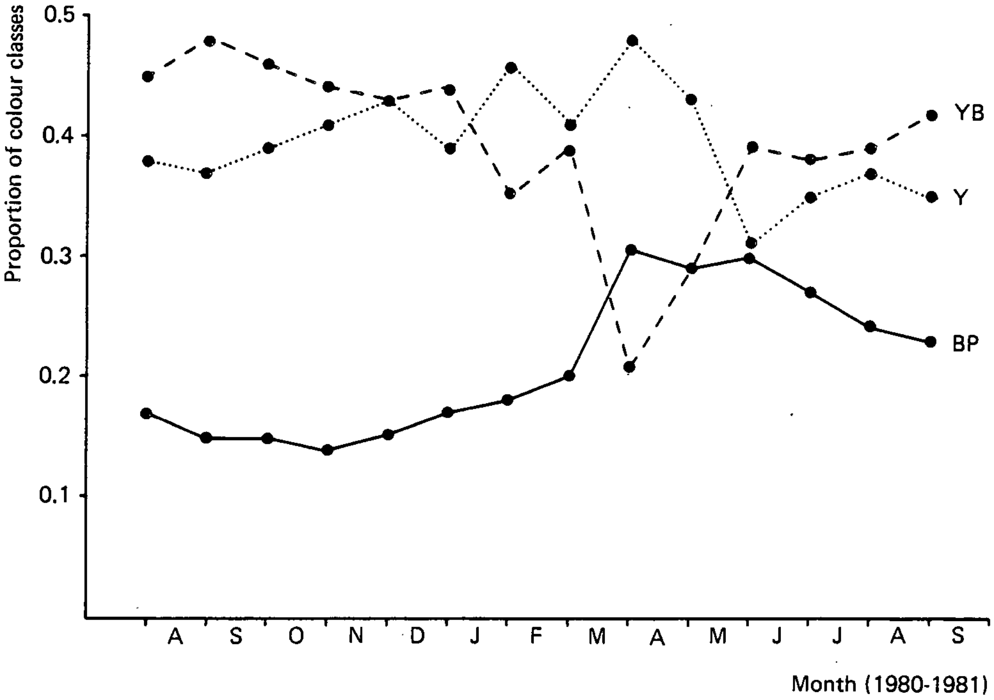
Table 15.12 Shell surface and body temperatures of *Littoraria filosa* on *Avicennia* trees at Cockle Bay.

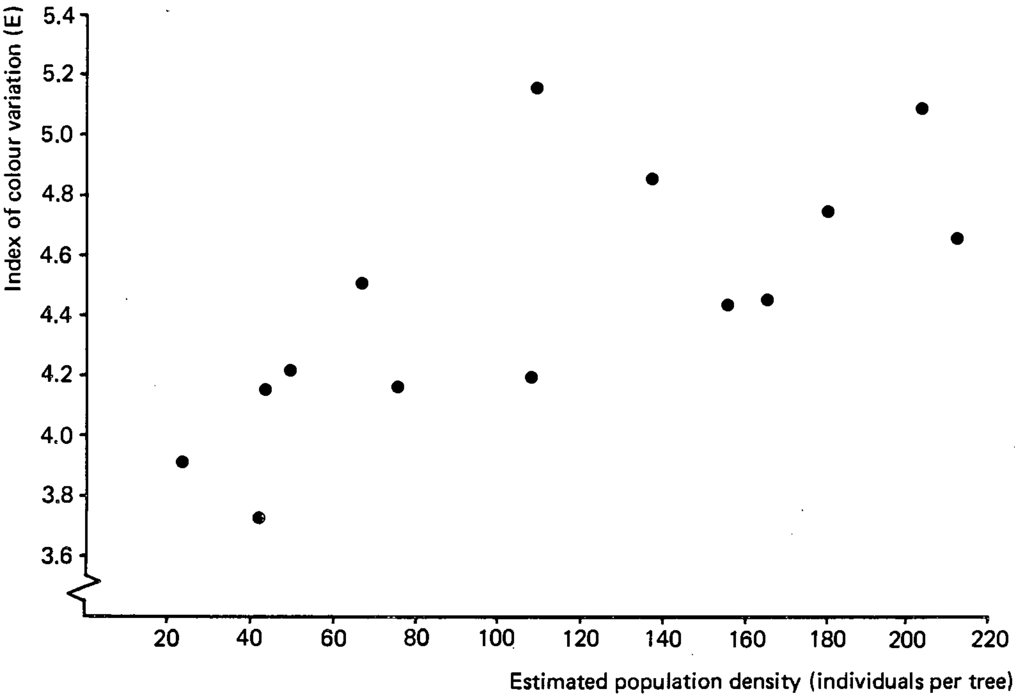
Shell colour	n	Mean shell surface temp. (°C)	95% confidence limits	Mean body temp. (°C)	95% confidence limits
Yellow (YO)	8	33.4	±0.6	32.5	±0.7
Brown (B4, B5)	13	34.0	±0.6	33.6	±0.7

Weather conditions: air temperature 31.9°C; cloud cover 0.1; light breeze.
Date: 8 January 1981.
t-tests: shell surface temperature: $t = 1.35$, $P = 0.193$; body temperature: $t = 2.16$, $P = 0.04$ *

Fig. 15.6 Annual variation in proportions of shell colour classes of *Littoraria filosa* on *Avicennia* trees at Cockle Bay. Y, yellow; YB, yellow-brown; BP, brown and pink; see Section 15.2 for definitions of colour classes.

Fig. 15.7 Correlation between index of colour variation (E) and estimated population density of *Littoraria filosa* on *Avicennia* trees at Cockle Bay. Data from monthly samples of mark and recapture experiment, from August 1980 to September 1981.


Proportion of colour classes
0.5
0.4
0.3
0.2
0.1
YB
Y
BP
A
S
O
N
D
J
F
M
A
M
J
J
A
S
Month (1980-1981)


Index of colour variation (E)
5.4
5.2
5.0
4.8
4.6
4.4
4.2
4.0
3.8
3.6
20
40
60
80
100
120
140
160
180
200
220
Estimated population density (individuals per tree)

colour classes Y, YB and BP, $\chi^2 = 87.5$, d.f. = 26, $P < 0.001$). During the months January to March the proportion of yellow-brown shells dropped sharply, while that of yellow and of brown (including pink) shells rose. By September 1981 the proportions found 13 months earlier were almost restored. The January to March interval corresponded with the periods of peak spawning (Fig. 13.2), lowest population density (Fig. 13.10) and highest temperature and rainfall (Fig. 13.17) for the year.

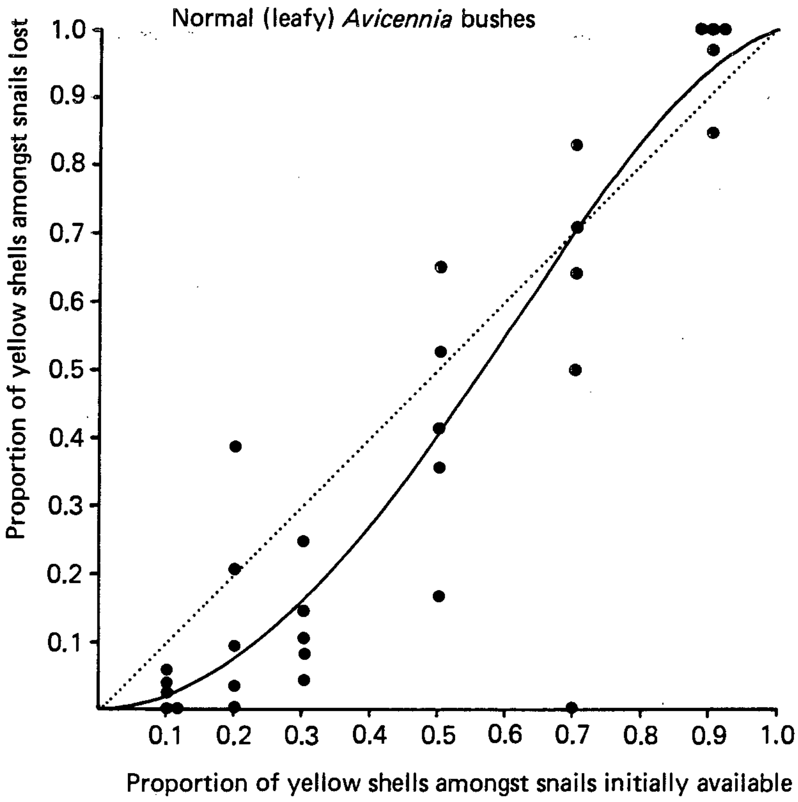
Conceivably, the shells found dead, but attached to the trees, could have been killed by climatic effects. The colour proportions amongst the 34 dead shells found were as follows: 0.44 Y, 0.38 YB, 0.18 BP. These proportions did not differ significantly from the average throughout the year amongst living snails ($\chi^2 = 0.528$, d.f. = 2, $P = 0.768$).

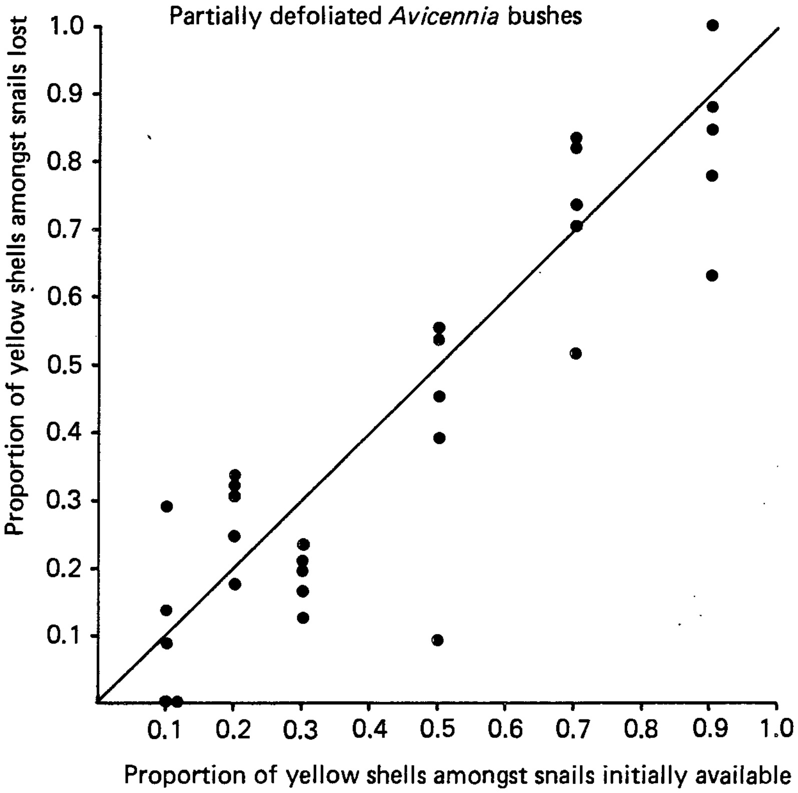
15.4.7 Frequency-dependent selection in *L. filosa*

On leafy *Avicennia* bushes the slope (b) of the regression of the logarithm of the relative number of yellow shells lost (e) on the logarithm of the relative number available (A) was 1.455 (±0.332, 95% confidence limits). Since this value was significantly greater than unity ($t = 3.802$, d.f. = 4, $P = 0.019$), there was evidence of a significant frequency-dependent component in the disappearance of yellow and brown shells. The plot of the proportion of yellow shells lost against the proportion available is therefore an S-shaped curve (Fig. 15.8). The tendency towards a higher loss of yellow shells irrespective of their frequency was estimated by the value of the coefficient $V = 0.768$ (95% confidence range 0.545–1.079). Since this was not significantly less than unity ($t = 2.176$, d.f. = 4, $P = 0.095$) this tendency was not significant.

On relatively bare bushes, however, there was no evidence of a

Fig. 15.8 Evidence for apostatic selection acting on *Littoraria filosa* on *Avicennia* bushes at Cockle Bay. Each point represents shell colour proportions in initial population, and proportion amongst snails lost after two weeks. Curve for leafy bushes fitted from calculated values of b and V, and relationship between $e_1/(e_1 + e_2)$ and $A_1/(A_1 + A_2)$ given in Section 15.3. Curve for defoliated bushes did not differ significantly from the line of equality.


Normal (leafy) *Avicennia* bushes
Proportion of yellow shells amongst snails lost
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Proportion of yellow shells amongst snails initially available


Partially defoliated *Avicennia* bushes
Proportion of yellow shells amongst snails lost
1.0
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0.1 0.2 0.3 0.4 0.5 0.6 0.7 0.8 0.9 1.0
Proportion of yellow shells amongst snails initially available

frequency-dependent effect ($b = 0.937 \pm 0.286$, $t = 0.616$, d.f. = 4, $P = 0.571$). Again the estimate of V was not significantly different from unity ($V = 0.816$ (0.513-1.306), $t = 1.254$, d.f. = 4, $P = 0.278$). Comparing the parameter estimates on leafy and bare trees, only the value of b differed significantly ($t = 3.282$, d.f. = 8, $P = 0.011$).

The proportions of all snails lost during the two week intervals, irrespective of colour, showed no significant differences according to the proportions of colours initially released (leafy trees: $F = 0.612$, d.f. = 7,32, $P = 0.742$; bare trees: $F = 0.460$, d.f. = 7,32, $P = 0.856$). However, significant differences were found between the rates of loss from individual trees (leafy trees: $F = 2.383$, d.f. = 7,32, $P = 0.044$; bare trees: $F = 2.646$, d.f. = 7,32, $P = 0.028$), suggesting that the precaution in the experimental design of rotating treatments between trees was necessary. Greater proportions of snails were lost from bare than leafy trees (mean loss on leafy trees = 25.1% per two week interval (95% confidence range 20.5-30.2%), on bare trees = 38.6% (31.0-46.3%), comparing arcsine transformed proportions: $t = 3.002$, d.f. = 76, $P = 0.004$).

The average immigration rates on the four leafy and four bare trees, by which the results were corrected, were closely similar, declining steadily over the course of the experiment from 8 to 2 snails per tree (in keeping with the declining natural population density during this season). Of the immigrant snails 33% (28-39%) were yellow.

A significant positive correlation ($r = 0.700$, $P = 0.005$) was found between the index of colour variation (E) and the population density over 14 months on the two trees used for the mark and recapture experiment (Fig. 15.7).

15.5 Discussion

15.5.1 The basis of shell colour variation: genetic or environmental?

Evidence for the action of natural selection on populations has usually been derived in the first instance from correlations between phenotypic and environmental variation. However, an evolutionary interpretation is only justified if the phenotypic variation is of genetic origin. The genetic basis of colour polymorphism is well understood in *Cepaea* and some other pulmonates (reviews by Jones *et al.*, 1977; Clarke *et al.*, 1978), but because of the relative difficulty of breeding prosobranchs, knowledge of their genetics is meagre. In the Littorinidae no details of the inheritance of colour patterns have been published, but it is reported that breeding experiments have confirmed the genetic basis of colour polymorphism in *Littorina mariae* (Reimchen, 1979) and *Littorina saxatilis* (T. Warwick, quoted in Raffaelli, 1982). In the former there are four principal colour morphs, but in the latter a large number of discrete colour and banding patterns have been described (Pettitt, 1973a). The polymorphism of *Littoraria* species is rather different, since only two discrete shell ground colours can be recognized, while there is continuous variation in the degree of superimposed patterning. The basis of the variation in *Littoraria* may therefore not be the same as that in *Littorina*.

Despite the lack of evidence from breeding experiments, it is impossible to believe that there is not a strong genetic component in the determination of shell colour in the polymorphic species of *Littoraria*. Discrete categories of pink and yellow ground colours, and of patterned and non-patterned shells can be recognized. In *L. filosa*, the most strikingly variable species, all colour forms can be found together on single trees, with little evidence of segregation in separate microhabitats. Very few natural shells, and none artificially transferred between habitats, show signs of colour change during life. Further support for the genetic determination of shell colour is derived from the similarity of the colour range amongst polymorphic species of the subgenus *Littorinopsis*, which suggests the possibility of an homologous genetic basis. The relative rarity of pink, patterned shells in *L. filosa* and *L. pallescens* is reminiscent of the linkage disequilibrium effects in *Cepaea* (Clarke *et al.*, 1978). In *Nucella lapillus*, a species with direct development and therefore limited dispersal, the local distribution of unique colour forms has been cited as evidence of the genetic basis of the polymorphism (Berry & Crothers, 1974). In the widely dispersed *Littoraria* species geographical variation can be recognized on a grand scale (Chapter 9), but this is equivocal evidence for genetic determination.

Amongst both polymorphic and variable species of *Littoraria*, there are some which show predictable associations between the degree of patterning of the shell and the substrate upon which they are found. In particular, shells from *Avicennia* trees (and perhaps from *Sonneratia* also) show less dense patterning, appearing paler and in polymorphic species more colourful, than shells from *Rhizophora* trees (Section 15.4.3). Of course such associations could be explained by selection, but this would have to be strong indeed to produce the differences which can be found between adjacent trees. If the shells were being selected on the basis of their colour by a predator, it is understandable that dark shells might be more readily overlooked on the darker bark of *Rhizophora* trees, but be relatively conspicuous on the paler, greenish brown, bark of *Avicennia* trees. However, the visual properties of, for example, *Rhizophora* and *Sonneratia* foliage appear similar, yet marked differences in the colour proportions of *L. pallescens* were found between these habitats at Phuket Island, Thailand (Table 15.3). Complex hypotheses involving linkage or pleiotropic effects could be proposed in which the selective advantage of a colour form could be unrelated to the phenotypic expression of shell colour (Sacchi, 1969; Raffaelli, 1979b; Berry, 1983), but the simpler hypothesis of a direct influence of the environment upon colour, perhaps through a dietary effect, adequately accounts for the facts presently known.

The suggestion of a direct effect of the environment upon shell pigmentation is not new. An early example was the work of Moore (1936) on the influence of a diet of mussels or barnacles on the shell colour of *Nucella lapillus*, although subsequent experiments have thrown some doubt on the results (Berry & Crothers, 1974; Spight, 1976; Berry, 1983). The relationship between diet and shell colour has been more convincingly demonstrated in the herbivorous archaeogastropods *Turbo* (Ino, 1949), *Haliotis* (Leighton, 1961) and *Austrocochlea* (Creese & Underwood, 1976; Underwood & Creese, 1976). Other possible environmental influences include water chemistry (D. Neumann, quoted in Heller, 1979), sunlight (D. Dagan, quoted in Heller, 1979) and temperature (Struhsaker, 1970).

The evidence on this subject in *Littoraria* species is poor. The differences in colour proportions on different tree species at the same locality do not preclude a selective explanation, and furthermore confound the possible effects of substrate and of sunlight, since *Rhizophora* trees develop more dense, shady canopies than *Avicennia* trees. In *L. pallescens* at Phuket Island, samples from *Rhizophora* trees in the sun and shade were more similar to each other than either was to a sample from *Sonneratia* trees in a sunny position, but differences between the samples from *Rhizophora* were still significant (Table 15.3). Whether this was because of sunlight, selection or migration from nearby *Sonneratia* trees could not be determined. Precise habitat details are available for only a few of the samples of *L. pallescens* represented in Figure 15.5, but there is an apparent division into those with more than 75% and those with less than 50% of brown shells, which could reflect the tree species from which they were collected. In the case of *L. luteola* at Kurnell, N.S.W., the difference between samples from trunks and leaves of *Avicennia* (Table 15.4) may again be accounted for by the effects of substrate, sunlight or selection. The darker colouration of males in this species is noteworthy. Sexual dimorphism in shell size is marked (Table 9.12), and if a vertical size gradient exists, as in the species at Cockle Bay (Section 12.3.4), it may be that the smaller males spend more time at lower, shadier levels, on bark rather than leaf substrates. In *L. filosa* substrate appeared to have little influence on pigmentation, and the slightly greater proportion of brown shells amongst males could be a sex-linked effect.

Although some colour changes were produced by transferral of snails between tree species at Cockle Bay, the experiments were unsatisfactory (Section 15.4.3). They should be repeated at a locality where large numbers of pale and dark forms are available for experimentation. An obvious candidate for such trials is *L. pallescens*, abundant on *Rhizophora*, *Sonneratia* and *Avicennia* trees (Figs. 11.9, 11.10, 11.12), and suspected of showing a marked susceptibility to substrate effects.

During the attempted transfer experiments it was observed that caged snails grew at a much slower rate than that of unconfined marked individuals. Since only the shells confined on *Rhizophora* trunks showed darkening of the shell increment, this effect cannot be ascribed entirely to the slowing of growth. Several authors have noted a connection between slow growth and darker patterning (Comfort, 1951; Struhsaker, 1970), but no detailed accounts have been traced. Some gastropods show colour allometry (Gould, 1971), which could be related to growth rate. The lack of pattern change in the larger, individually marked and unconfined shells, and the rarity of natural changes in the field, suggest that snails may be susceptible to an environmental influence only when very small.

In summary, it seems probable that the ground colour of the polymorphic *Littoraria* species is determined genetically. In *L. filosa*, shell pattern may be controlled in the same way, although variation amongst patterned shells is continuous. In several other species (including *L. scabra*, *L. philippiana*, *L. intermedia*, *L. pallescens*, *L. luteola* and *L. lutea*) it is suggested that the expression of shell patterning is at least partially influenced by the environment, possibly through a dietary effect. The evidence for an environmental component is poor, but such an effect would explain the associations between shell colouration and tree species which can be found in these species. A genetic basis of shell colouration with a degree of phenotypic plasticity has also been proposed for *Acmaea digitalis* (Giesel, 1970) and *Theodoxus jordani* (Heller, 1979).

15.5.2 The agents of natural selection

The evidence for the action of natural selection upon colour forms of *Littoraria* species is derived from the observations made at Cockle Bay on the distribution of *L. filosa* on *Avicennia* trees with relatively few and with many leaves (Section 15.4.4). Amongst the smallest snails, the proportions of the three main colour classes were not significantly different on bare and leafy trees, but the larger sizes showed relatively greater proportions of yellow shells on leafy trees and of brown shells on bare trees. This effect was most striking when snails representing a juvenile cohort were re-scored after a period of four months. When snails were most abundant, in July, the contrast between samples from bare and leafy trees was less clear. The interpretation of these results in terms of visual selection is dependent upon the observations that shell colouration does not change with age in this species, nor appear to be significantly affected by the environment (Section 15.4.3).

If this is true, the difference in colour proportions in samples of *L. filosa* from *Rhizophora* and *Avicennia* trees at Cockle Bay (Table 15.2) could also be explained by selection. Even if there is a small environmental component in the determination of shell patterning in *L. filosa*, and allowing that a change in pattern of a shell by one degree (e.g. Y3 to B4) could be overlooked in the continuum of variation, it is obvious, from the examination of many thousands of specimens, that larger changes do not occur. If the data of Tables 15.5 and 15.7 are re-analysed using only two colour classes, YO against all others combined, the results remain significant ($P < 0.05$), although the difference between the proportions on *Avicennia* and *Rhizophora* trees (Table 15.2) is then not significant. These two colour classes are so distinct that any change from one to the other on the whorls of a shell could not have been overlooked. The different colour proportions of small and large snails on *Avicennia* trees therefore cannot be accounted for by a direct environmental influence together with inaccurate colour scoring.

Since natural selection appeared to favour yellow shells on trees with abundant foliage, and brown shells when the background was predominantly brown bark, the most obvious hypothesis is that shells are selected on the basis of their colour by visual predators. Visual selection by birds has been amply demonstrated in *Cepaea* (reviews by Jones *et al.*, 1977; Clarke *et al.*, 1978), and in some situations is believed to maintain the cryptic resemblance of shells to their background. For example, brown, pink and unbanded shells predominate in woodlands, and yellow and banded shells in meadows. In a review of the predators of *Littorina* species in the north Atlantic, Pettitt (1975) concluded that birds and crabs were the most significant, and since both have colour vision, could together be responsible for visual selection leading to the cryptic resemblance of shells to their backgrounds (Pettitt, 1973b). Heller (1975b) found red shells of *Littorina saxatilis* (as *Littorina rudis*) and *Littorina nigrolineata* to be more abundant on red sandstone rocks, and yellow shells on sheltered shores with a cover of brown algae, and likewise suggested that visual selection was responsible, although without any direct evidence. Recent workers have revised Heller's concept of *Littorina saxatilis* (review by Raffaelli, 1982), casting some doubt on the validity of his observations on this 'species'.

From the exclusion cage experiment (Section 14.3.2) it appears that crabs are the major predators of *L. filosa*. Since some crabs are known to possess colour vision (Hyatt, 1975) they could in theory impose visual selection on their prey. However, the *Metopograpsus* species are probably most active at night (Section 14.3.1) and may therefore not hunt visually. *Thalamita crenata* may be a more important crab predator of *L. filosa* (Section 14.4.2), but little is known of its foraging behaviour.

The results of the exclusion cage experiment (Section 14.3.2) suggest that birds were not significant predators of *L. filosa* in the 7 to 12 mm size range. It remains possible that birds prey upon smaller snails (Pettitt, 1975; Liddy, in press; Section 14.4.1). Even if birds are indeed quantitatively insignificant predators of *L. filosa*, they could in theory be the most important selective agents if they alone amongst the predators select prey on the basis of colour (Pettitt, 1975).

Some fish are also known to possess colour vision (Pettitt, 1975). *Blennius pholis* has been shown to impose selection for crypsis on *Littorina mariae* (Reimchen, 1979), and blennies have also been implicated in a study of a freshwater neritid (Heller, 1979). Octopus may prey selectively on *Nerita* species (Safriel, 1969). Since *Littoraria* species remain above the water level (Section 12.3.1), such entirely aquatic predators are unlikely to be significant.

For a conclusive demonstration of selection of colour forms by predators in the field, it would be necessary to monitor colour proportions on trees from which various potential predators were excluded by cages of different designs. Such an undertaking was precluded in the present study by the relatively low natural density of snails, and the consequently large number of cages that would have been required to detect significant differences.

Shell pigmentation affects not only the visual properties of snails, but also their absorption of solar energy, and hence their thermal properties. In *Cepaea*, climate has been invoked as a selective agent responsible for high frequencies of brown shells in frost hollows on sand dunes (Cain, 1968), of yellow shells at high and low altitudes in long valleys (Arnold, 1968) and for the predominance of yellow shells in the warmer and more southerly regions of Europe (Jones *et al.*, 1977). It is believed that yellow shells are more resistant to overheating in sunlight, while pink and brown shells absorb heat more rapidly and so maintain activity for longer periods in cold climates. Both laboratory and field experiments designed to demonstrate these effects have, however, been severely criticised (Clarke *et al.*, 1978), so that the evidence for climatic selection is poor. The most convincing evidence for selective heat death has been provided by Richardson (1974), who found that in a sand dune habitat *Cepaea nemoralis* frequently experienced temperatures near its lethal limit, and that among snails presumed to have been killed by overheating, yellow shells were represented at a lower frequency than in the population as a whole.

There is no clear evidence for similar climatic effects in *Littoraria* species. Investigations at Cockle Bay failed to find differences in colour proportions of *L. filosa* on *Avicennia* trees in sunny and shaded situations (Section 15.4.4). At Phuket Island, Thailand, a sample of *L. pallescens* from *Rhizophora* trees in open situations was significantly paler than one from a shaded forest, but the sites were 200 m apart and the principal differences lay in the relative proportions of the two shades of brown shells (Section 15.4.3). The dead shells found attached to trees at Cockle Bay could perhaps have died from overheating or dehydration, but the small sample provided no evidence of differential susceptibility of colour forms (Section 15.4.6). Likewise, the annual changes in colour proportions of *L. filosa* were not consistent with an hypothesis of climatic selection, since proportions of both yellow and brown shells increased during the summer months (Fig. 15.6). There was no obvious change in the appearance of the background which could explain the changed frequencies during the summer in terms of visual selection.

Direct measurement of the temperatures attained by empty and living shells of *L. filosa* showed differences of up to 2.6°C in surface temperature and 1.1°C in tissue temperature between yellow and brown shells. These figures are similar to the 1 to 2°C differences recorded between colour morphs of *Cepaea* (Richardson, 1974; Heath, 1975) and to the 1 to 3°C differences between two *Nodilittorina* species with dark and pale shells (Markel, 1971). Such a small difference may well be significant for the survival of *Cepaea* in open habitats where temperatures close to the lethal limit of 43°C are frequently experienced (Richardson, 1974). The lethal limits of *Littoraria* species are not known, but in two tropical *Nodilittorina* species have been measured as 47 to 53°C, some 10°C above the maximum recorded tissue temperatures (Markel, 1971). It is possible that in contrast to *Cepaea*, tropical littorinids may seldom suffer heat death, and that climatic selection may be insignificant. The exclusion cage experiment designed to investigate sources of mortality of *L. filosa* provided no evidence for mortality caused by insolation (Section 14.4.1). Even if temperature differences between colour forms are not sufficient to cause selective mortality, they may affect behaviour, perhaps accounting for the higher proportions of yellow *L. filosa* found exposed to direct sunlight. A similar effect has been suggested to account for behavioural differences between the morphs of *Cepaea* (Jones, 1982). Alternatively, the unpigmented yellow snails could be less sensitive to strong light, as proposed by Sacchi (1966) for *Littorina obtusata*.

If heat death were an important selective force in littorinids, it would be predicted that tropical species and those from the highest supralittoral levels should be palest in colour. *Littoraria coccinea* and *L. undulata* from high levels on rocky shores are amongst the palest in the genus, while *L. pintado* from a similar habitat is variable in pigmentation, but sometimes quite dark (see figures in Rosewater, 1970). Most mangrove-associated species probably experience less intense insolation, for even leaf-dwelling species are usually shaded by foliage. It may be noted that in *L. albicans*, a species from foliage at high levels, all large adult shells fade to white. Other pale species such as *L. melanostoma* and *L. sulculosa* are not associated with particularly high level or open habitats. In general the mangrove-associated species from higher levels are more variable and vivid in colouration, whereas climatic selection would be expected to favour uniformly pale shells. In other littorinid genera, Vermeij (1971b, 1973a) has noted the occurrence of paler species at higher intertidal levels on rocky shores. The tendency is by no means general (Markel, 1971; Bandel & Kadolsky, 1982), perhaps because crypsis may be a more important consideration than the thermal properties of the shell.

Latitudinal clines in *Nodilittorina africana* and *Melarhaphe neritoides* have been interpreted as a response to temperature (Hughes, 1979a). The geographical distribution of colour forms in *Littoraria* species does not support the possibility of climatic selection; populations of *L. filosa* from lower latitudes appear somewhat darker, the reverse of the anticipated trend. Neither direct nor indirect lines of evidence indicate an important role for climatic selection in the *Littoraria* species of mangrove habitats.

In several polymorphic intertidal gastropods investigators have failed to find correlations between morph frequencies and background or habitat, which could be explained by climatic or visual selection, and have concluded that selection acts on pleiotropic characters of the alleles for colour, unrelated to the appearance of the shell. In *Nucella lapillus* this suggestion has been made by Berry (1983), who noted the existence of different physiological tolerances among the several banding morphs, and also proposed that some morphs may be favoured at high population densities. Aspects of density-dependent selection will be considered in Section 15.5.3. Pleiotropic effects have also been invoked in *Littorina obtusata* and *Littorina mariae* (Sacchi, 1969) and in *Littorina saxatilis* (Raffaelli, 1979b), to explain associations of morph frequencies with conditions of exposure to wave action. The distribution of the colour morphs of *Littorina obtusata* in estuarine and polluted areas (Smith, 1976) may imply physiological differences between them. However, most recent authors have argued that visual selection is important in *Littorina* species (Heller, 1975b; Smith, 1976; Reimchen, 1979; Raffaelli, 1982).

15.5.3 The maintenance of the polymorphism

If acting alone, both visual and climatic selection should impose directional or stabilizing effects, producing optimally adapted monomorphic populations. In fact, the occurrence of a similar and probably homologous polymorphism in ten species of *Littoraria* (Section 15.2) suggests that it has been maintained during evolution from a common ancestral stock. To account for the persistence and stability of natural genetic polymorphisms, four principal hypotheses have been advanced (Jones *et al.*, 1977; Clarke *et al.*, 1978). These involve random processes with selective neutrality, a balance between disruptive selection and gene flow in a heterogeneous environment, frequency- and density-dependent selection, and heterozygote advantage.

Early work on the polymorphism of *Cepaea* gave rise to the suggestion that colour variation was adaptively neutral, allele frequencies being determined by their rate of origin by mutation and rate of loss by the random process of genetic drift. While small and isolated colonies of *Cepaea* may be subject to random drift, and the founder effect may account for some cases of anomalous allele frequencies, there is now abundant evidence for the influence of selection on the polymorphism (Jones *et al.*, 1977). The polymorphism of littorinids has been relatively little studied in comparison, but in the same way earlier workers failed to find consistent patterns of phenotypic frequencies (Fischer-Piette *et al.*, 1964;

Fischer-Piette & Gaillard, 1968), perhaps because of inadequate taxonomic knowledge. More recent work has suggested that shell colour may well be adaptive, even if the selective mechanisms are poorly understood (Heller, 1975b; Smith, 1976; Reimchen, 1979; Raffaelli, 1982).

Several lines of evidence militate against the importance of random processes in polymorphic *Littoraria* species. There is a consistent association between polymorphism and a habitat amongst foliage, while the species typical of visually uniform bark substrates are less variable (Section 15.4.1), as also observed by Cook (1983) amongst three species at one locality. It has, however, been argued that *Littoraria* species at high levels on trees have escaped the constraints of visual selection for crypsis by ground-dwelling predators, allowing variation to be freely expressed (Rosewater, 1970). Further evidence against the idea of adaptively neutral variation is provided by the observation that in all the polymorphic species of which large samples are available (*L. filosa*, Fig. 15.4; *L. pallescens*, Fig. 15.5; *L. philippiana*; *L. lutea*; *L. luteola*; *L. cingulata pristissini*; *L. albicans*; see Chapter 9) the pink shelled forms are present at similarly low frequencies, almost always less than 10%, suggesting maintenance by selection. Furthermore, at least in *L. filosa*, there is some, albeit indirect, evidence for visual and frequency-dependent selection. On theoretical grounds it seems unlikely that random genetic drift can be important, for the species are probably widely dispersed in the planktonic larval stage (Section 7.2), leading to a large effective population size and ensuring gene flow between geographically distant populations. For the same reason, founder effects are probably not significant, and there is no evidence of unusual colour proportions in peripheral populations, which could be attributed to such effects. In contrast, amongst the prosobranchs with nonplanktotrophic development, including some species of *Littorina* (Section 13.4.1), dispersal must be restricted, and founder and area effects should be considered (Sacchi, 1974; Berry & Crothers, 1974).

The three hypotheses which invoke the action of natural selection to explain the maintenance of balanced polymorphisms are to a considerable degree interconnected. The processes involved are not mutually exclusive, and might operate together upon polymorphic species or populations.

It has been suggested that in a heterogeneous environment selection might act in different directions on parts of a population, so that over the population as a whole selection would be disruptive, and a polymorphism could be maintained by a balance between selection in different habitats and migration between them. In the literature, discussions of the consequences of selection and migration in a diverse environment have often been confused by a failure to recognize the significance of the scale of the patches in a heterogeneous environment, relative to the size and dispersibility of the animal concerned (a concept referred to as environmental grain).

The theoretical model was initially developed by Levene (1953), Levins & MacArthur (1966), Levins (1968), Maynard Smith (1970) and Gillespie (1974). Assuming random mating in the population, and random distribution of the offspring over the environmental patches, this 'fitness set' model predicts that without heterozygote advantage, polymorphism cannot be stable in a fine-grained environment, but only in a coarse-grained one. If the heterozygote is favoured, polymorphism may be stable under both conditions, but is more so when the grain is coarse. The model has been applied to polymorphic gastropods in which morphs are cryptic on different backgrounds and mis-matched individuals are selected by visual predators, for example *Crepidula convexa* on dark and light stones or shells (Hoagland, 1977), *Littorina obtusata* and *Littorina mariae* on the holdfast and frond of brown algae (Smith, 1976; Reimchen 1979). In these examples the juveniles may well be distributed at random, but there is a continuum of increasing patch size relative to the dispersal capability of the animal. Thus in *Cepaea* adjacent subpopulations may experience visual (Cain & Sheppard, 1954) or climatic (Jones, 1973) selection in different directions, while gene flow between them maintains relatively high frequencies of inappropriate morphs. On the largest scale of environmental grain, the species as a whole may be polymorphic, while individual populations differ in gene frequency or even tend towards monomorphism under the action of directional selection, as in *Littorina* species with nonplanktotrophic development on long coastlines (Heller, 1975b; Naylor & Begon, 1982) and *Theodoxus* in bodies of fresh water (Heller, 1979).

In the case of environmental variation within the range of single populations (as addressed by the fitness set model), the maintenance of a stable polymorphism is more likely if there is selection by the morphs of the habitat in which they are most fit (Maynard Smith, 1970; Maynard Smith & Hoekstra, 1980). Such habitat choice may well be common, for it will be favoured by selection (Johnson, 1981). In helicid pulmonates there is evidence that banded morphs seek shaded habitats (Johnson, 1981; Jones, 1982), and even if this is a direct consequence of the thermal properties of the shells, it may still promote polymorphism. Amongst intertidal prosobranchs differential behaviour of colour morphs was proposed by Giesel (1970) to account for the distribution of the limpet *Acmaea digitalis* on rocks and barnacle colonies, although the possibility of a direct dietary effect on colour was not adequately considered (Underwood, 1979). Sacchi (1966a) has shown that the yellow, unpigmented morph of *Littorina obtusata* is less disturbed by strong light, and is therefore more often to be found on the surface of algal fronds than are the darker cryptic morphs.

The possibility of balanced polymorphism in a fine-grained environment has been considered in detail by Endler (1978). Polymorphism may be stable if the morphs are equally cryptic. One way in which this may occur is if the environmental grain is extremely fine, on a scale smaller than the size of the animal, such that each colour pattern appears as a different random sample of the background. One possible example is the exceptionally diverse polymorphism of the neritid *Clithon oualaniensis* (Grüneberg, 1976), in which shell patterns resemble the coloured sand grains on which they are often found (pers. obs.). Endler believes that equivalent crypsis of some morphs, and therefore a degree of selective neutrality, may be more common than has been supposed, perhaps explaining some of the anomalous 'area effects' in *Cepaea*. If, on the other hand, morphs are not equally cryptic, polymorphism is still possible if there is a precise mimicry of environmental elements of the same size range as the animal. A variety of frequency-dependent selection may then maintain the morphs in the same proportions as the background elements which they imitate. Amongst molluscs, possible examples include juvenile *Donax* in shell sand (Schneider, 1982), *Nerita* species on pebbles (Safriel, 1969) and *Littorina obtusata* amongst the receptacles and bladders of fucoid seaweeds (Smith, 1976). At still larger grain size (but still fine-grained relative to the mobility of the animal), with unequal crypsis among morphs, the morph which is cryptic in the most common environmental patch will replace those which are on average less cryptic. This will be so unless there is habitat selection or if there is apostatic selection, to balance the disadvantage of a less cryptic morph by a selective advantage at low frequencies. In both these cases density- or frequency-dependent effects will allow 'tracking' of temporal and spatial changes in background patterns, since the frequencies of the morphs at equilibrium will be related to the proportional areas of the different backgrounds available (Endler, 1978).

Theoretical considerations predict that the diversity of polymorphisms maintained by selection in fine-grained environments should increase with the pattern complexity of the background (Levins, 1968; Endler, 1978). Amongst terrestrial pulmonates, those from dense woodland are less likely to be polymorphic than those from more open, vegetated habitats (Clarke *et al.*, 1978). Several authors have noted that the most highly polymorphic pulmonates are tree-climbing forms, such as species of *Liguus*, *Partula*, *Limicolaria* and *Cepaea* (Clarke, 1962a; Owen, 1965b; Clarke *et al.*, 1978). This observation has been taken as evidence for apostatic selection, since snails may become more conspicuous to predators when they climb above the ground (Clarke, 1962a; Jones *et al.*, 1977). However, Endler (1978) has argued that climbing species experience a greater diversity of backgrounds, on which a wider variety of morphs may be equally cryptic. The association between habitat and morph diversity has also been noted in the intertidal environment (Heller, 1975b; Smith, 1975, 1976; Schneider, 1982). The genus *Littoraria* provides a clear example of this correlation, since in assemblages in various parts of the Indo-Pacific province the most strikingly polymorphic species are found on the visually diverse background of mangrove foliage, while the more uniform species occur on bark and rocks (Section 15.4.1). It must be emphasized that the two explanations of these observations are not necessarily mutually exclusive. They may in fact be complementary, since apostatic selection maintains morphs in frequencies proportional to their relative crypsis (Clarke & O'Donald, 1964; Endler, 1978).

In considering whether any of these ideas on the maintenance of polymorphism in a heterogeneous environment might apply to *Littoraria* species, discussions will be confined to *L. filosa*. In the present study this species has been investigated in greatest detail, and there is evidence both of a strong genetic component of the colour variation and of visual selection on backgrounds of different colour. The nature of the environmental grain experienced by this species must be considered. On the largest, geographical, scale, colour proportions do vary (Fig. 15.4) and since the species is probably widely dispersed (Section 7.2), recruitment from several distant populations could conceivably maintain or enhance local variability. The possible importance of this coarse-grained effect cannot be judged. It has been found that, at least at Cockle Bay, there are differences in the proportions of colour forms on *Avicennia* and *Rhizophora* trees, with brown shells being a little more common on the latter. Tree species cannot, however, be a significant aspect of coarse environmental grain, since *L. filosa* is uncommon on *Rhizophora*, and rare patches do not promote polymorphism

(Levins, 1968; Gillespie, 1974). The same argument dismisses the importance of *Avicennia* trees with relatively few and with many leaves, since the great majority of trees at the seaward edge of the forest, where *L. filosa* is most common, possess abundant foliage.

Within individual *Avicennia* trees, the habitat of *L. filosa* may be divided into the relatively uniform substrate of bark and the visually diverse foliage. The bark is greenish brown, sometimes variegated by paler patches where scales of bark have been shed. The foliage consists of a mosaic of lanceolate leaves 10 by 2 cm, with bright green and shining upper surfaces and silver green, tomentose lower surfaces, occasional vivid yellow senescent leaves, pale green twigs and glimpses of brown branches, the whole dappled with sunlight and shadow (Fig. 15.1). Flowers appear in December (pers. obs. at Cockle Bay), and are small (5 mm) and inconspicuous, golden or orange in colour and borne in open terminal clusters, while fruits are green and about 3 cm in diameter. The environment is clearly fine-grained, for the snails are highly mobile, moving freely between foliage and branches (Chapter 12). The seasonal change in the visual quality of the background appears negligible.

As discussed above, in a fine-grained environment polymorphism may be stable if the morphs are equally cryptic (Endler, 1978). Whilst it is difficult to determine how a predator might perceive its prey, it is clearly not the case that all colour forms are random samples of an extremely fine background pattern. Furthermore, if morphs are equally cryptic, their frequencies should not respond to differences in the proportions of background elements, yet the comparison of relatively bare and leafy *Avicennia* trees suggests that this is so. A precise mimicry of background elements appears unlikely, for as in *Cepaea* (Clarke, 1962a) none of the colour forms appears truly cryptic. Yellow forms are proportionately more common than expected if they were a close mimic of senescent leaves, while pink shells are conspicuous against all elements of the background. Cook (1983) has suggested that on *Rhizophora* trees yellow shells of *L. pallescens* resemble leaf buds, brown shells twigs, and pink shells the occasional orange-brown blemishes on the leaves, but in fact yellow and pink shells are highly conspicuous. It should also be noted that *L. pallescens* is probably subject to a direct environmental influence upon colour (Section 15.4.3). It could perhaps be argued that if the visual predator perceives a mosaic of patches of colour of leaves, branches and sun flecks, as might be so if acuity were poor or hunting were from a distance, then the colour forms of *L. filosa* might effectively imitate background elements. However, there is still the difficulty of the highly conspicuous pink form.

Not only spatial heterogeneity, but also temporal variability of an environment may promote diversity of a polymorphism. For example, some populations of *Cepaea* experience cyclic visual selection, brown shells being favoured on leafless backgrounds in winter, yellow shells amongst new foliage in spring, and brown shells beneath tall herbage in summer (Carter, 1968). A similar process might operate on *Littorina obtusata*, of which yellow shells are only cryptic while receptacles are present on the food plant *Fucus* (Smith, 1976). Climatic effects might also introduce a cyclic component to selection. The colour proportions of *L. filosa* did indeed appear to change in a regular manner over the year of observation at Cockle Bay (Section 15.4.6), although the changes were not in the direction that might have been predicted as an outcome of climatic selection, nor did the appearance of the background change noticeably during the year. A cyclic effect which may be significant is that during the wet summer months a higher proportion of the snails occurred on the leaves than at other times (Section 12.3.5). Pleiotropy or heterogeneous recruitment from the plankton (Johnson & Black, 1982) could also be invoked to account for the changing colour proportions during the year. Temporal variation should be examined over a number of years before conclusions can be drawn.

The two final conditions permitting polymorphism in a fine-grained environment are habitat choice and apostatic selection. No evidence for substrate selection was found in *L. filosa*, there being no significant departure from a random distribution of colour forms on green and brown substrates (Section 15.4.5), but apostatic selection remains a strong possibility.

The term 'apostatic selection' was first coined by Clarke (1962a), although similar concepts had been discussed by earlier authors (review by Allen, 1974). The name describes the tendency of a predator to specialize on the most common type of a polymorphic prey, while overlooking rarer types. Since the selective advantage of a particular morph is inversely related to its frequency in the population, this is a special case of the more general concept of frequency-dependent selection (review by Ayala & Campbell, 1974), and the behaviour of the predator will tend to maintain a balanced polymorphism in the prey. By concentrating on one or a small number of prey types, predators may be able to hunt more effectively for cryptic prey. In vertebrates such behaviour is described as the formation of a search image, 'a perceptual change in the ability of a predator to detect familiar cryptic prey' (Lawrence & Allen, 1983). There is considerable evidence that birds hunt in this way, derived from laboratory experiments (Cook & Miller, 1977) and studies of wild birds provided with artificial polymorphic baits (Croze, 1970; Allen, 1972, 1974) or with baited polymorphic snail shells (Harvey *et al.*, 1975). However, the importance of this behaviour in the wild remains a matter of speculation (Lawrence & Allen, 1983). Search images are rapidly learned, after only two or three experiences with prey, and are very specific, so that birds can discriminate between shells differing in colour shade and in sculpture (Croze, 1970). Hunting by search image is a special case of a widespread tendency of many predators, from protozoans to vertebrates, to exert frequency-dependent selection on their prey by specializing on the most abundant of several alternative prey morphs or species, a phenomenon known as 'switching' (review by Murdoch & Oaten, 1975).

Both the experimental and theoretical approach suggest that apostatic selection is only likely to operate if certain conditions are met. The selective effect of a predator will depend upon its rate of encounter with the prey. If the prey is rare, it may be encountered too rarely for a search image to be formed for even the most frequent morph, so that apostates will gain no advantage (Clarke, 1962a). In laboratory and field experiments, apostatic selection has been shown to become more effective as the prey density is increased (Croze, 1970; Cook & Miller, 1977), and in natural populations of *Limicolaria* (Owen, 1965a, b) and *Donax* (Smith, 1971) the diversity of the polymorphism is highest where density is greatest. Smith (1976) found no correlation between morph diversity and population density on a geographical scale in *Littorina obtusata*. Some authors have reported that at very high densities selection of both artificial baits and natural prey becomes directional (Allen, 1972; Smith, 1975), perhaps because search images are formed even for the less frequent morphs, which may be more conspicuous (Clarke, 1962a). However, some results have shown apostatic selection of baits to continue at very high densities (Harvey *et al.*, 1974). Greenwood (1969) has argued that since predators are responsible for a smaller proportion of deaths at high prey densities, apostatic selection will then be less effective even if there is no change in hunting behaviour.

It was originally suggested that the likelihood of apostatic selection should increase as prey became more conspicuous, as for example in snails climbing trees (Clarke, 1962a), in bivalves on a monotonous sand background (Smith, 1975) and in species living at high densities in monospecific communities (A.H. Clarke, 1978). Nevertheless, it is now clear that apostasis and crypsis are intimately related, that most morphs are to some extent cryptic, and that visually complex backgrounds permit a greater diversity of morphs to be maintained (Croze, 1970; Endler, 1978; Schneider, 1982).

Concerning the predator, if a visual polymorphism is to be maintained by search image formation, learning ability and visual acuity are required, although colour vision may not be necessary.

Murdoch & Oaten (1975) have generalized that the phenomenon of switching is shown by those predators in which the averaged preference for alternative prey is weak, but the preference shown by individuals is strong and variable. The maximum diversity of polymorphism is expected to occur at intermediate predation intensities, for at high intensities prey will be selected for more precise resemblance to the background (Endler, 1978).

In respect of most of these conditions, *L. filosa* and other polymorphic *Littoraria* species are likely subjects for apostatic selection. They are usually common and found on foliage, which presents a complex background pattern. The major predators are crabs (Chapter 14), which probably have colour vision (Hyatt, 1975; Warner, 1977) and may show some learning ability (Schöne, 1961; Warner, 1977). It has been speculated that birds may also be significant predators of small snails (Section 15.5.2).

It is easy to understand how apostatic selection might maintain one or a few rare morphs amongst a common type, but in many natural polymorphisms several colour forms are common. It has been shown by Clarke & O'Donald (1964; see also Endler, 1978) that in a polymorphic prey maintained at equilibrium by apostatic selection, the morphs are represented in proportion to their degree of crypsis. Although the relative crypsis of morphs as perceived by a predator may be different from that estimated by the human observer, in the case of predators with colour vision and good visual acuity the difference may not be great. It is therefore significant that in *L. filosa* the most common colour forms are usually yellow-brown and yellow, which appear most cryptic amongst leaves, while the proportion of brown shells increases on bark substrates, and the highly conspicuous pink shells are always represented at the lowest frequency. A similar explanation in terms of apostatic selection may apply to *Littorina obtusata*, in which the three common morphs (reticulate brown, green and yellow) are all cryptic on certain backgrounds, while the striking banded and orange forms are rare (Smith, 1976). Clarke (1962a) suggested that under the influence of apostatic selection, polymorphisms should increase in diversity, but there is apparently some limitation, for when presented with a continuously graded series of baits, birds exert disruptive selection (Allen, quoted in Clarke *et al.*, 1978). In natural polymorphic prey the morphs often appear distinct, and in *Cepaea* the shell patterns seem to emphasize the distinctions (Clarke *et al.*, 1978). Whether selection can maintain continuous variation, as within the variously pigmented yellow-brown and brown shells of *L. filosa*, is not clear. It might be that the pigmented shells are equally cryptic and therefore not discriminated by predators. It may be noted that only a rather small proportion of shells fall into the categories Y1 and Y2, intermediate between unpigmented and darkly pigmented shells.

Another consequence of apostatic selection is that polymorphic prey suffer less predation than monomorphic prey (Croze, 1970) and can live at higher densities (Smith, 1975). This effect was not evident in *L. filosa*, in which loss rates were too variable to detect differences between subpopulations with different colour frequencies (Section 15.4.7).

Although the mechanism is plausible and theoretically sound, the evidence for the maintenance of natural polymorphisms by apostatic selection is mostly indirect. Experiments with artificial baits have shown that the hunting behaviour of some birds is consistent with the search image model, but gathering data under natural conditions is beset with problems (Murdoch & Oaten, 1975). Amongst molluscs there is little evidence for apostatic selection, even in *Cepaea*. Clarke (1962b, 1969) has argued that the negative correlation between morph frequencies of two *Cepaea* species in mixed colonies implies a selective advantage of uncommon forms, since predators do not discriminate between the species, but Carter (1967) has produced conflicting evidence. In an artificial population of *Cepaea* species, it has been shown that thrushes preferentially selected the most frequent and conspicuous form, until it reached a low and stable frequency (Bantock *et al.*, 1975). Crabs prey upon the bivalve *Donax*, apparently exerting apostatic selection at moderate prey densities and directional selection at high densities (Smith, 1975; but see Schneider, 1982, for a critical review of the evidence). However, all these observations are merely consistent with the hypothesis, and do not prove that apostatic selection can maintain natural polymorphisms. Apostatic selection has also been invoked to account for polymorphisms in other marine molluscs, including *Nerita* species (Safriel, 1969), *Littorina saxatilis* (Heller, 1975b, as *Littorina rudis*) and others (A.H. Clarke, 1978), although without evidence. General observations on the occurrence of non-mimetic polymorphisms are also consistent with the hypothesis, for they are most prevalent in common species (Clarke *et al.*, 1978; A.H. Clarke, 1978), on backgrounds of diverse pattern (Endler, 1978), in prey subject to visual predation (Clarke, 1969) and in the tropics where interactions between predators and prey are believed to be well developed (A.H. Clarke, 1978).

The evidence for the action of apostatic selection on *L. filosa*, while still indirect, is nevertheless more convincing than that available for any other mollusc. Most significantly, it has been shown that there is a frequency-dependent component in the loss of yellow and brown shells from artificially adjusted subpopulations at natural densities on separate *Avicennia* bushes, such that each colour is favoured when present at low frequency (Section 15.4.7). Since predation is believed to be a major source of loss (Section 14.3.2), apostatic selection provides the simplest explanation. The search image behaviour of birds is specific to a small area of search, and is rapidly adjusted by a few encounters with prey (Croze, 1970), so that a bird predator might well change its hunting behaviour from one tree to the next. The frequency-independent 'preference' (or tendency for loss) for brown shells, although not formally significant, might be expected on the basis of superior camouflage of yellow shells amongst foliage, or a pre-existing search image for pigmented shells in general, which are most common in the natural population. The equilibrium frequency predicted by the experiment (at which the proportion lost is equal to the proportion present) was 70% of yellow shells; this was greater than the natural frequency of 35 to 45%, but agreement would not be expected, since in the artificial populations Y1 and Y2 shells were not represented, and Y3 shells under-represented.

Analysis of the results of the same experiment on *Avicennia* bushes largely denuded of leaves revealed no frequency-dependent effect. Conceivably this may have been a consequence of changed hunting behaviour at high prey density (since when the leaves are removed the surface area of a tree is reduced) or on a less visually diverse background. Perhaps more likely is that on leafless trees predators are responsible for a lower proportion of the overall loss (which is higher than on leafy trees), so that loss of colours is more nearly independent of their frequency. A leafless tree caged during the exclusion experiment lost as many snails as an uncaged leafy tree (Section 14.3.2).

Further evidence for the action of apostatic selection on *L. filosa* is less direct. The correlation between the index of colour variation (E) and population density (Fig. 15.7) is in agreement with the idea that apostatic selection becomes more effective with moderate increases in prey density, as discussed above. The finding that brown shells are relatively more common on natural trees with few leaves (Section 15.4.4) is also to be expected, since at the equilibrium maintained by apostatic selection, morphs are represented in proportion to their degree of crypsis (Clarke & O'Donald, 1964; Endler, 1978). Apostatic selection is not the only hypothesis which predicts parallelism of morph frequencies with those of the background pattern, as discussed earlier, but it is the only hypothesis which can account (in terms of visual selection) for the maintenance of the highly conspicuous pink morph at a consistently low frequency in all the polymorphic *Littoraria* species, when the morph is not cryptic on any natural background.

Lastly, the possibilities of the maintenance of polymorphism by heterozygote advantage or by non-random mating must be mentioned.

However, there is as yet no evidence for such effects in *Littoraria*, nor even in the thoroughly investigated genus *Cepaea* (Jones *et al.*, 1977; Clarke *et al.*, 1978).

CHAPTER 16: CONCLUDING DISCUSSION

The taxonomic revision of the *Littoraria scabra* group demonstrates the existence of 20 distinct species throughout the Indo-Pacific province (Chapter 9), largely explaining the extreme variation in shell form of the supposed species '*Littorina scabra*' (Rosewater, 1970). For application to future taxonomic work on the family Littorinidae, the most important results are the demonstration of the value of certain taxonomic characters, including the form of the penis, sperm nurse cells and pallial oviduct (Chapter 5) and the details of shell sculpture and columellar shape (Chapter 4). For the first time, the structure of the pallial oviduct has been described in the principal littorinid genera. Another significant result of the taxonomic work is the phylogenetic analysis of relationships within the Littorinidae (Chapter 8), and the support thereby provided for a new and controversial generic classification of the family (Bandel & Kadolsky, 1982). The *scabra* group is here classified in the genus *Littoraria*, the sister group of the well established genus *Nodilittorina*, and rather distantly related to *Littorina sensu stricto*. Although defined by anatomical details, the genus *Littoraria* is also characterized by the association of all but its most primitive members with mangrove, driftwood and salt marsh habitats, an ecological specialization almost unique in the family.

As a result of the investigation of the ecology of a number of the species of the *scabra* group, it has been possible to account for some of the morphological differences between them in terms of the adaptive significance of the size, shape, sculpture and thickness of the shell (Chapter 14). Several of the newly defined species display conspicuous variability in shell colouration, and again the ecological work provides an interpretation (Chapter 15). Conversely, the taxonomic study puts the ecological work into a new, evolutionary perspective. The phylogenetic analysis of the family

Littorinidae demonstrates consistent patterns not only of anatomy and shell form, but also in the hitherto confusing diversity of developmental types and breeding seasons (Sections 13.4.1, 13.4.2).

Although there exists an extensive literature on many aspects of the ecology of littorinids, the majority of previous work has been carried out on temperate species from rocky shores. The present study is the first detailed account of the ecology of the mangrove-dwelling species of the family in the tropics. As such, comparisons of the findings with available information have been made in the light of both the peculiarities of the mangrove habitat, and the contrasts between tropical and temperate environments.

The habitat provided by a mangrove forest differs from that of a rocky shore chiefly by its structure and microclimate. The trees are a vertical substrate, separated by a soft sediment upon which littorinids cannot crawl or feed. The shore is often gently shelving and of wide horizontal extent, with a well developed zonation of tree species (review by Macnae, 1968). Although the tree species differ in the protection they afford from sun and rain, in general the forest provides a humid, shaded environment and shelter from wave action, thus ameliorating the extreme conditions experienced on exposed rocky shores. As a consequence of these differences, littorinids in mangroves display complex three-dimensional patterns of zonation, with both a vertical component up the trees and a horizontal component through the forest (Chapter 11), whereas on rocky shores zonation patterns predominantly reflect tidal levels. Patterns of zonation in the two habitats also differ in that population densities of tree-dwelling gastropods in mangrove forests are mostly low, and feeding areas of co-occurring species show broad overlap. Intraspecific competitive effects have been reported in the dense aggregations of littorinids on temperate rocky shores, and interspecific competition is suggested by the sequential zonation patterns of some other gastropods in the same habitat, but it seems most unlikely that either effect could contribute to the maintenance of zonation patterns of the mangrove-dwelling littorinids (Section

11.5).

The unusual vertical migratory behaviour of the *Littoraria* species, by which all remain above the water level throughout the tidal cycle (Chapter 12), also appears to be connected with the structure of the forest. The species found at lower levels on the trees follow the rise and fall of the water surface, while those of higher levels may undertake migrations to the water at high tide. Such behaviour, unknown in other littorinids, is made possible by the vertical substrate and by the lack of strong wave action to dislodge snails near the water surface. The behaviour is necessitated by the lack of suitable refuges for snails below the high tide level, such as the crevices occupied by other gastropods on tropical rocky shores (Bertness *et al.*, 1981). The more favourable microclimate amongst mangrove trees, together with the vertical substrate, account for the fact that *Littoraria* species are able to feed at levels higher above the influence of the sea than on any rocky shore.

An obvious difference between temperate and tropical intertidal environments is the higher temperature, and potentially more desiccating conditions, which prevail in the latter. However, it is unclear whether heat or desiccation have directly harmful effects on *Littoraria* species. That this might be so is suggested by the higher mortality of species on *Avicennia* trees than in the shadier *Rhizophora* forest (despite the fact that predation is more severe in the latter) and by the correlation of monthly loss rates with average temperatures (Chapter 13). Furthermore, gradients of increasing shell size at higher vertical levels on the trees were shown by each of the five species examined in detail, even though predation was probably more intense at low levels and smaller shells were more susceptible to predators (Chapter 14), suggesting that only large individuals can tolerate the more rigorous environment at higher levels. Only in the wet tropics are species of *Littoraria* to be found in the landward fringe of the forests, and their absence from this zone in, for example, Australia, may be explained by climatic limitation (Section 11.5.2). Species found at the higher levels on the trees tend to show larger and more heavily sculptured shells, which may be interpreted as adaptations relating to water conservation and dissipation of heat respectively (Chapter 14).

Against the suggestion of mortality induced directly by heat and desiccation, it may be argued that studies of both temperate and tropical littorinids have invariably shown them to tolerate greater extremes of temperature, desiccation and osmotic concentrations than would be experienced in their natural habitat. Natural death of intertidal gastropods from these effects has not yet been conclusively demonstrated in the field, but possible examples mostly involve relatively immobile limpets (review by Underwood, 1979). Since *Littoraria* species are highly mobile and behavioural responses to climatic conditions are well documented (Chapter 12), it may be that mortality is unlikely to be caused directly by climatic factors. Shading of an *Avicennia* tree failed to increase the survival of small *L. filosa*, although the experiment was not carried out at the hottest time of year (Section 14.3.2). As an alternative explanation, it may be that the correlations of loss rate, distribution and shell form with microclimatic conditions are fortuitous, or that the connections are indirect. Further experimental work is clearly necessary. The evidence for a directly harmful effect of monsoonal rainfall is better, although not conclusive. A period of three weeks of almost uninterrupted rain was correlated with greatly increased loss rates, while surviving snails showed reduced growth rates, and appeared to attempt to escape from the influence of the rain by sheltering under leaves and attaching to the substrate by a mucous seal (Chapters 12, 13).

Several aspects of the life history of *Littoraria* species can be related to the tropical climate (Chapter 13). Breeding was continuous, or almost so, in three of the five species at Cockle Bay on Magnetic Island, whereas in temperate latitudes seasonality is more pronounced. The two *Littoraria* species which bred only in the wet summer months were those from the higher levels on the trees. It is suggested that this is a consequence of the highly seasonal rainfall at this locality, and that the species at high levels are partly dependent upon atmospheric moisture for their activity and feeding. At lower levels, species are able to feed near the water level at all seasons. The high temperature probably accounts for the fact that both absolute and relative growth rates of the *Littoraria* species are greater than those recorded for any other littorinids, most of which have been studied in temperate climates. Sexual maturity is achieved more rapidly in these tropical species, although the age structure of the populations and maximum longevity are similar to those of temperate littorinids.

There is an increasing volume of evidence that predation upon intertidal gastropods is more severe in the tropics than in the temperate zones (Chapter 14). This is the first study of predation upon gastropods in the mangrove habitat, and the results suggest that predation is as significant as in other tropical shallow water habitats. At Magnetic Island the major predators upon *Littoraria* species were the tree-climbing crabs of the genus *Metopograpsus* and the swimming crab *Thalamita crenata*. The effects of both were more severe at lower levels on the trees, a case of the general inverse correlation between predation intensity and environmental rigour (Paine, 1976). The influence of predation has been a recurrent theme in the discussions of the results of this work, and can be considered at two levels. In the short-term, predation is a source of mortality, influencing the structure of populations and of the community. In the long-term, predation is an agent of natural selection, producing adaptive patterns of behaviour and of shell morphology and colouration.

The mortality caused by predation was estimated only in artificial populations of 7 to 12 mm snails of *L. filosa* during four months from July to November, when crabs were responsible for the loss of 19% of the snails per month, or 86% of the total mortality. As an indication of the high frequency of attack by crabs, the mean number of repaired breakages per shell (a record of unsuccessful predation attempts) in the three largest *Littoraria* species on *Rhizophora* trees at Cockle Bay were between 2.98 and 3.48. The distribution of repaired breakages over the whorls of the shells, laboratory predation trials, and the abundance of small crabs on the trees, all suggest that in the species found on *Rhizophora* trees the rate of predation was most severe on the smallest snails. This may account for the fact that, despite breeding for most or all of the year, significant recruitment of *L. intermedia* and *L. scabra* occurred only after the peak spawning season (Section 13.3.2). On *Avicennia* trees the *Metopograpsus* species, largely responsible for predation on the smallest snails, are scarce, which may permit the relatively successful recruitment of *L. filosa* on these trees. The population structure of *L. filosa* showed a preponderance of juveniles, in contrast to the populations of *L. intermedia* and *L. scabra*, which were dominated by the larger size classes. The high rates of predation upon *Littoraria* species may explain their generally low population density, despite an apparently favourable habitat. If abundance is indeed limited in this way, predators may be responsible for the probable lack of competition amongst the tree-dwelling gastropods.

The intensity of predation near and below the water level has probably been the selective force responsible for the adoption of a high supralittoral habitat by some species of *Littoraria*, and for the evolution of their unique vertical migratory behaviour. The method of development of the subgenus *Littorinopsis*, in which larvae are brooded in the mantle cavity until the early veliger stage, may also be a response to predation pressure, reducing the time required for spawning at the water surface. Perhaps the clearest reflection of the increasing intensity of predation at lower levels on the trees is the corresponding gradient of increasing thickness of the shells, and therefore of greater resistance to crushing predation.

Natural selection by predators may also have been responsible for the evolution and maintenance of the shell colour polymorphism shown by the species of *Littoraria* which are found at high tidal levels on the foliage of trees. At least in *L. filosa*, the polymorphism is believed to be maintained by apostatic selection (Chapter 15). It is not known whether bird or crab predators are responsible, but the evidence presented for the operation of apostatic selection is the most direct so far available for any mollusc.

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