CHAPTER ONE

GENERAL INTRODUCTION

1.1 Background literature

Matuta lunaris (Forskål) (Crustacea: Decapoda) is a common inhabitant of tropical sandy shores. It has a widespread distribution which extends from the Red Sea, South Africa, to Asia and Australia. Despite its common occurrence, there have been few published studies on this species, apart from taxonomic descriptions (Barnard, 1950, Tyndale-Biscoe & George, 1962, Sakai, 1965 and Romimohtarto, 1972) and area records (Chhapgar, 1957, Sankarankutty, 1962, Guinot, 1966 and Vannini, 1976). Biological work on *M. lunaris* has been restricted to the functional morphology of the stridulatory organs (Guinot-Dumortier & Dumortier, 1960, 1961) and anterolateral denticulations (Garstang, 1897 a, b), chromosome appearance (Niyama, 1942, Redfield *et al*, 1980), larval morphology and development (Hasmi, 1969, Rajabai, 1959 and Terada, 1983) and notes on its breeding biology (Pillay & Nair, 1976) and feeding behaviour (Seiler, 1976). Many aspects of the general biology of *M. lunaris*, however, have not been studied. In Australia, for example, only two studies of *M. lunaris* have been undertaken: a) chromosomal analysis by Redfield *et al*. (1980) and b) systematic descriptions by Tyndale-Biscoe & George (1962).

Matuta lunaris is not a commercial species in Australia. However, it has been reported to be of importance in the diet of people living in Third World countries such as India where *M. lunaris* is eaten by the poor population (Chhapgar, 1959 in: Guinot, 1966). *M. lunaris* is also fished in West Pakistan and in

the Gulf of Siam. In Madras and in the Philippines, *M. lunaris* is considered to be an important edible brachyuran species along with *Portunus* spp. and *Scylla serrata* (Guinot, 1966 and Schreiber & Cases, 1984).

1.2 Aim of the study

The aim of the present study was to investigate the following aspects of the biology of *M. lunaris*: 1) relative growth, 2) feeding biology, 3) reproductive biology, 4) absolute growth and 5) population biology. *M. lunaris* is ideally suited for this kind of study because it is abundant, easy to obtain, identify and hardy in aquaria. It can be collected throughout the year and has a restricted distribution in the intertidal and subtidal areas.

1.3 Systematics

Matuta lunaris is a member of the family Calappidae, a group of burrowing crabs which is distinguished by the location of their inhalent branchial openings. In the Calappidae, these are located in front of the basal segment of the cheliped. Unlike most brachyurans, however, the inhalent current does not enter directly at these points but flows in at the eye sockets and is carried along a canal in the surface of the pterygostomian region (Hale, 1927). The Calappidae is subdivided into two subfamilies, the Calappinae (the 'box crabs') and the Matutinae (the 'sand crabs'). This subdivision is based primarily on the location of the palp of the third maxilliped. In the Matutinae, it is hidden beneath the merus which is elongate and pointed at the tip but in the Calappinae, where the merus is not elongate, it is exposed (Hale, 1927 and

Sakai, 1965). In the field, species in the Calappinae are distiguished by a winglike expansion on each side of the carapace which covers the walking legs, whereas species in the Matutinae are characterized by flattened swimming legs and a prominent lateral spine or tubercule on each side of the carapace.

The Matutinae contains the single genus, *Matuta*, which is represented both in the Indo-Pacific and Atlantic oceans (Romimohtarto, 1972). At present, it contains 7 species, 5 of which have been recorded in Australia. These are: *M. lunaris*, *M. banksii*, *M. inermis*, *M. granulosa* and *M. planipes*. Only two species were recorded in the study area and local nearshore regions: *M. lunaris* and *M. granulosa*. *M. granulosa* was rare and only occurred offshore.

The systematic position of *M. lunaris* is as follows:

PHYLUM	Arthropoda
SUBPHYLUM	Crustacea
CLASS	Malacostraca
ORDER	Decapoda
SUBORDER	Reptantia
SECTION	Brachyura
SUBSECTION	Oxystomata
FAMILY	Calappidae
SUBFAMILY	Matutinae
GENUS	*Matuta*
SPECIES	*M. lunaris*

M. lunaris was first described by Forskål in 1775 as *Cancer lunaris* (Tyndale-Biscoe & George, 1962). Species that have since been synonomised with *M. lunaris* included *M. victor* (Alcock, 1896 in: Romimohtarto, 1962) and *M. victrix* (Lanchester, 1900). Additional descriptions of *M. lunaris* have been made by Miers (1877), Tyndale-Biscoe & George (1962), Sakai (1965) and Romimohtarto (1972).

In this study, *M. lunaris* was identified by the possession of an accessory stridulating organ with 24 - 26 striae on the outer face of the dactylus in males greater than 46.5 mm full carapace width (Chapter 1 and Romimohtarto, 1972), two well developed lateral spines on the carapace and at least two distinct spines on the outer face of the propodus (Tyndale-Biscoe & George, 1962). In addition, *M. lunaris* was differentiated from other closely related species by the following features: the absence of a postero-lateral tubercule on the carapace (present in *M. banksii*) and the absence of a distinct red patch at the base of the lateral spines (present in *M. granulosa*, Plate 1.1c). The carapace of *M. lunaris* is relatively flat and covered with red spots. In the present study, however, considerable variation in the general appearance of the carapace was found. Most individuals had fine red spots scattered over the carapace, some of which occasionally formed loops and lines (Plate 1.1a). A few individuals had more numerous darker red spots scattered over the carapace (Plate 1.1b). No morphological nor sex-related differences, however, corresponded with these colour variations. In Australia, therefore, the colour pattern of the carapace appears to be variable. Because of these colour variations, the species descriptions of Miers (1877) which were based primarily

Plate 1.1

Dorsal views of *Matuta lunaris* and *M. granulosa*, showing their characteristic shape, colour and carapace patterns.

a. *Matuta lunaris* Forskål

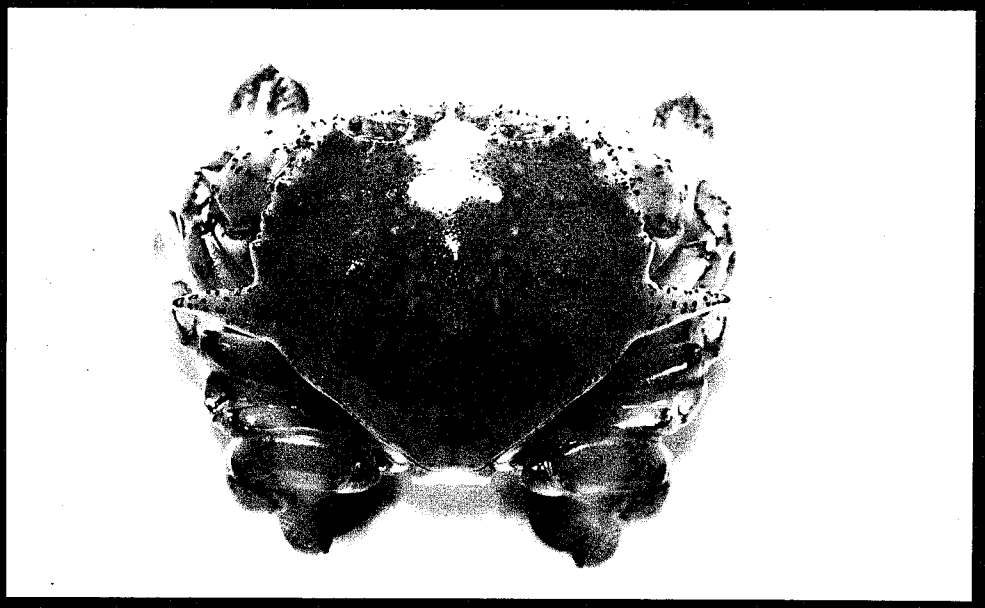
Typical carapace appearance.

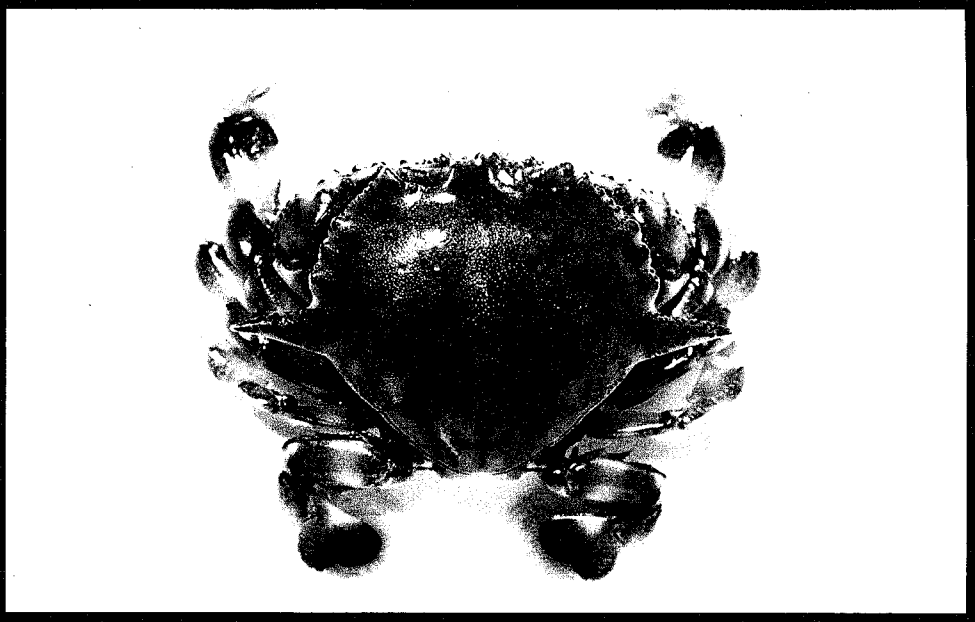
b. *M. lunaris*

Occasional colour variant.

c. *Matuta granulosa* (Miers)

Scale: 1 mm divisions





on the carapace were of little use in this study.

1.4 Geographic Distribution

1.4.1 World

The type locality of *Matuta lunaris* is the Red Sea (Forskål, 1775 in: Tyndale-Biscoe & George, 1962). It has since been recorded from the tropical beaches of several Indo-Pacific localities. In the Indian ocean, *M. lunaris* has been recorded on the east coast of Africa (Barnard, 1950), Natal (Guinot, 1966), Somalia (Vannini, 1976), Pakistan (Hashmi, 1969) and India (Chappgar, 1957 and Pillai & Nair, 1976). There are also records of collections from Madagascar (Guinot, 1966), the Andaman and Nicobar Islands (Sankarankutty, 1962), the Gulf of Siam (Guinot, 1966), Singapore and Indonesia (Romimohtarto, 1972). Miers (1877) recorded *M. lunaris* from Sri Lanka, however the species identification by Miers is questionable (see Chapter 3).

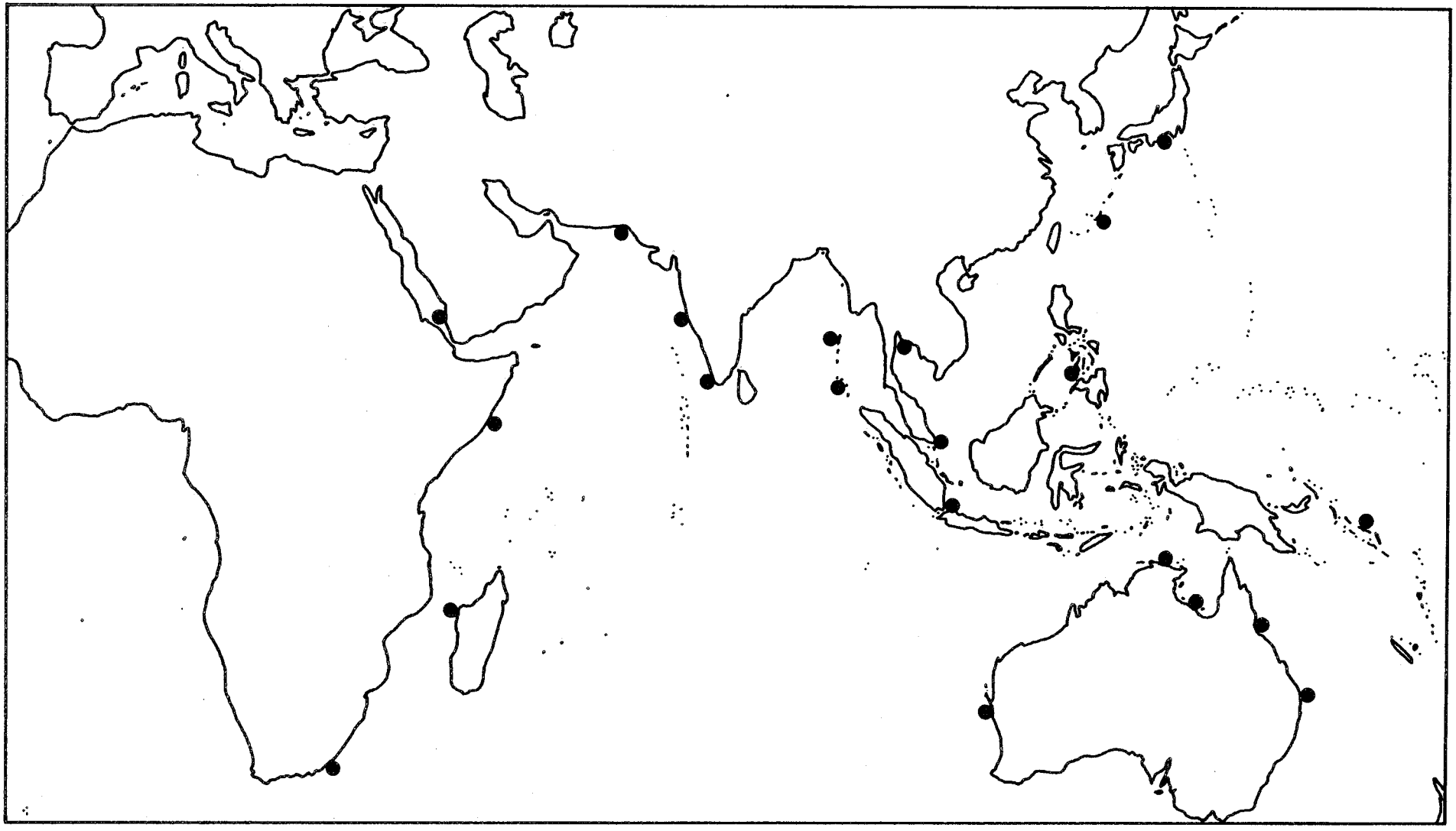
In the Pacific Ocean, *M. lunaris* has been recorded as far north as Japan (Sakai, 1965) and as far east as Fiji (pers. obs., Australian Museum collections). It has also been recorded in the Philippines (Schreiber & Cases, 1984), the Solomon Islands (Australian Museum collections) and Australia (Tyndale-Biscoe & George, 1962).

The world distribution of *M. lunaris* is summarized in Figure 1.1.

Figure 1.1

The geographic distribution of *Matuta lunaris* in the Indo-Pacific region.

● = area records



1.4.2 Australia

In Australia, *M. lunaris* has been recorded in four states: Western Australia, Northern Territory, Queensland and New South Wales. There are no records of *M. lunaris* in Victoria, Tasmania and South Australia, although other *Matuta* species have been recorded in these states. A summary of the distribution of *Matuta* species in Australia is given in Table 1.1, whilst the distribution pattern of *M. lunaris* in Australia is shown in Figure 1.2.

M. lunaris has been recorded in New South Wales from Port Jackson and Newcastle. In Queensland, it has been recorded from Moreton Bay, Cape Capricorn, Great Keppel Island, Bowen, Townsville, the Palm Islands, Cooktown and Albatross Bay. In the Northern Territory, it has been recorded from North Island, Cape Arnhem and Darwin, whilst in Western Australia, it has been recorded from Fremantle, Shark Bay, Carnavon and Yampi Sound. These area records are based on the material in the reference collection of the Australian Museum (pers. obs.).

1.4.3 Local

In this study, *Matuta lunaris* was recorded from several beaches in the Townsville region, including Magnetic Is. and Hinchinbrook Is. On the mainland, *M. lunaris* was found at Saunders beach, Shelley beach, Pallarenda beach, the mouth of Three Mile Creek and South Townsville beaches. In Magnetic island, *M. lunaris* was only found in three out of the seven bays surveyed, namely: Horseshoe, Radical and Florence bays. None were found at Arthur, Geoffrey, Picnic and Cockle bays. Of the other nearby islands surveyed,

Figure 1.2

The distribution pattern of *Matuta lunaris* in Australia, based on the reference collections of the Australian Museum.

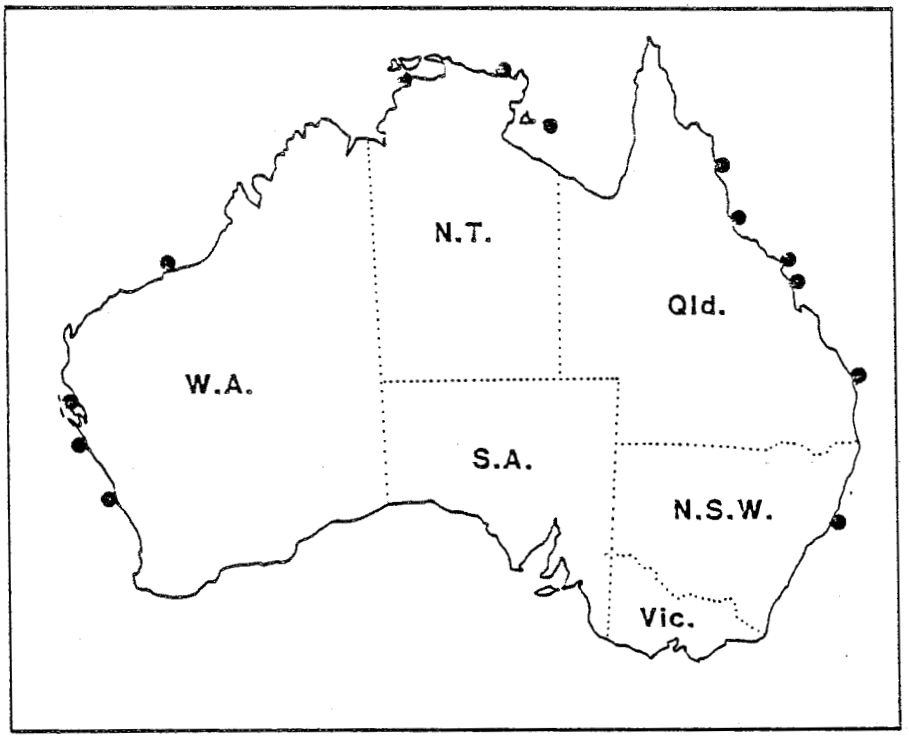


Table 1.1 The distribution of *Maxuta* species in Australia, based on the reference collections of the Australian Museum.

Species Name	W.A.	N.T.	Qld.	N.S.W.	Vic./Tas.	S.A.
M. lunaris	+	+	+	+	-	-
M. granulosa	+	+	+	-	-	-
M. inermis	+	+	+	-	-	-
M. planipes	+	+	+	-	-	-
M. banksii	+	-	+	+	-	-

M. lunaris was found only at Shepherds Bay on Hinchinbrook Island. None were found at Pioneer bay, Orpheus Island. Recent work on the benthic community of the Cleveland Bay has reported the irregular occurrence of a related species, *M. granulosa*, in the inshore stations (6-20 m deep) but no *M. lunaris* (P. Arnold, pers. comm.). The local distributions of *M. lunaris* and *M. granulosa* in the Townsville region are shown in Figure 1.3.

Figure 1.3

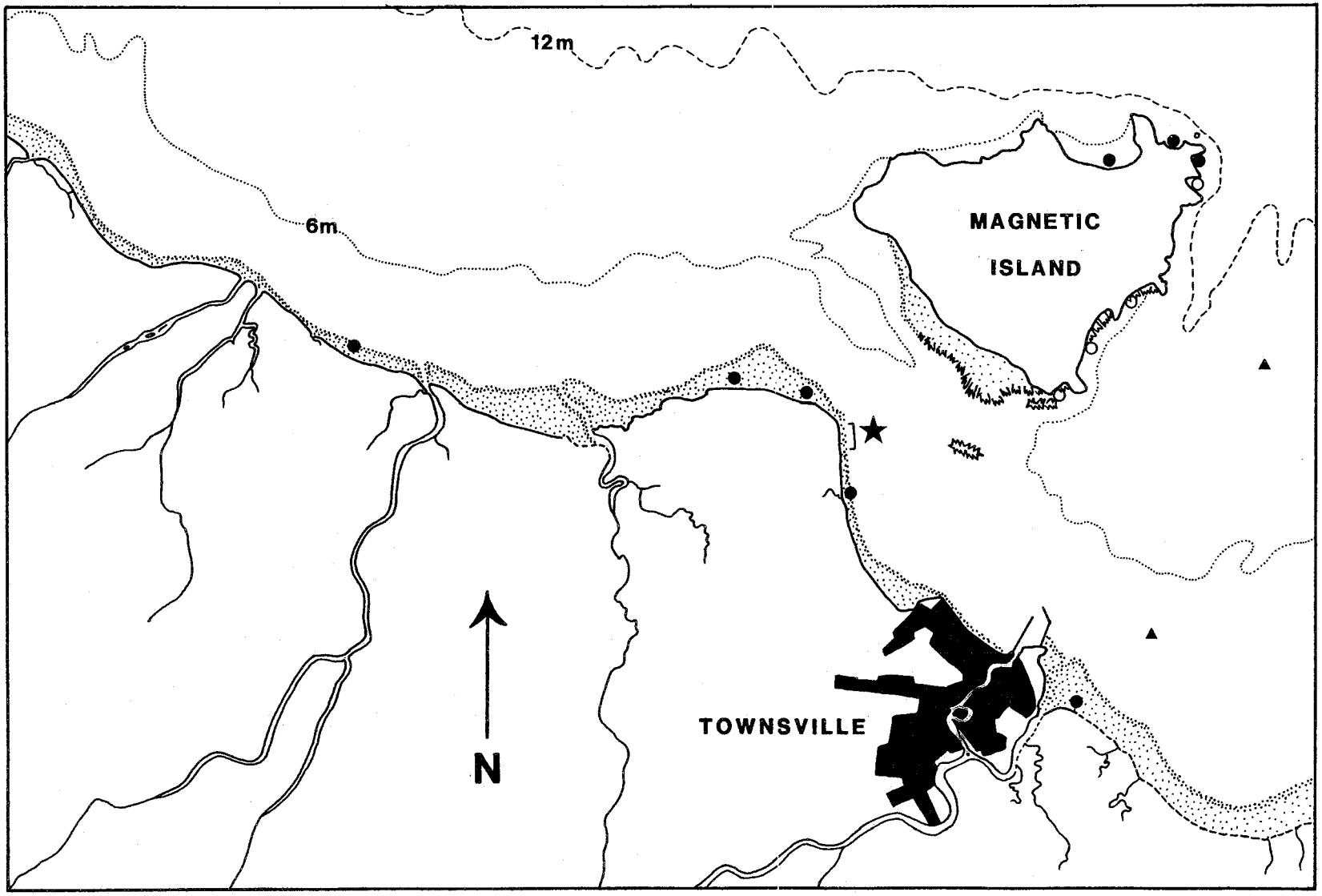
A map of the Townsville region including Magnetic Island, showing the study area and the local distribution of *M. lunaris*. and *M. granulosa*.

● *M. lunaris* present

○ *M. lunaris* absent

★ Study area

▲ *M. granulosa* present


12m
6m
MAGNETIC
ISLAND
TOWNSVILLE
N

CHAPTER TWO

SAMPLING METHODS AND THE STUDY AREA

2.1 Sampling methods

The specimens used in this study were collected between the months of January and February, 1984 and April, 1984 to May, 1985. Sampling was undertaken during the mid-falling tide, approximately three hours after the previous high tide. To avoid any variability in reproductive states as a result of lunar cycles, all samples were collected within two days of the full moon of each month. A summary of sampling days and tidal heights is given in Figure 2.1.

Sampling was carried out using two types of nets. A large 10 m x 1 m nylon beach seine net with a 25-mm mesh (12.5 mm square) was used to catch crabs greater than 20 mm in size. The weighted net was dragged along the substratum by means of two wooden poles attached at each ends (Plate 2.1a). When in use, the effective catching area, *i.e.* gape, of the large net was approximately 7 meters, resulting in a sample area of approximately 250 m^2. Smaller and newly settled crabs were caught using a 1.7 m long x 1 m x 0.4 m gape fine conical net with a 3.5 mm mesh (2 mm square), made from an old mosquito netting (Plate 2.1b). The gape of the net was maintained by 3 floats attached to the opening of the net. A 1.55 m long, 36 mm x 6 mm thick chain with 1 kg. lead weights at each end was attached to the bottom edge of the opening of the net to ensure that this remained close to the substratum. The net was dragged by means of two 4 m ropes attached to the lead weights. Specimens were collected in a 150 ml plastic bottle which was attached at the funnel end of the net. The size

Figure 2.1

A summary of sampling days and tidal heights during the study period between April, 1984 and May, 1985.

Sampling dates:	1984 –	1985 –
	April 8	January 7
	May 16	February 6
	June 16	March 7
	July 16	April 6
	August 13	May 7
	September 12	
	October 10	
	November 7	
	December 7	

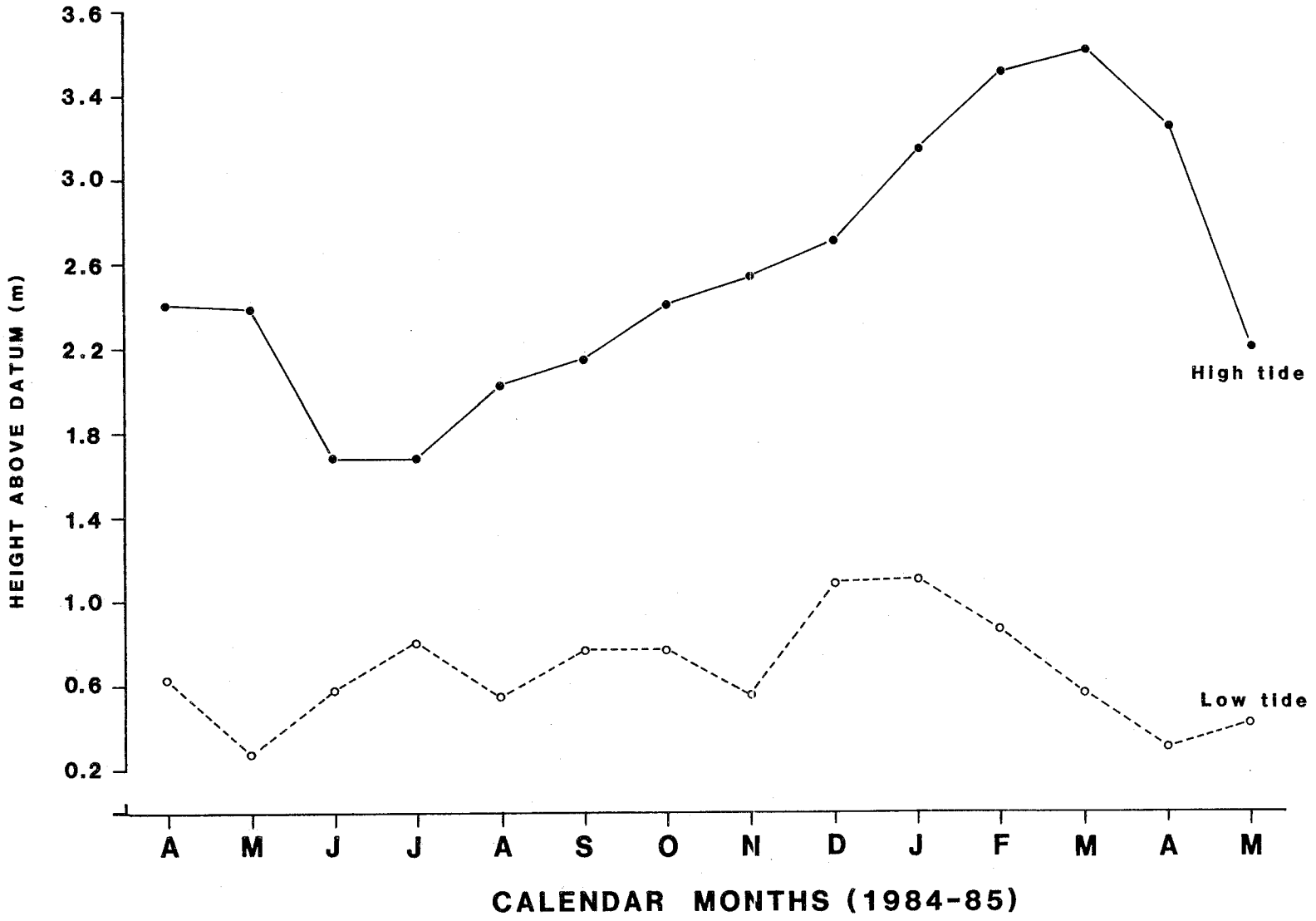

3.6
3.4
3.0
2.6
2.2
1.8
1.4
1.0
0.6
0.2
HEIGHT ABOVE DATUM (m)
High tide
Low tide
A
M
J
J
A
S
O
N
D
J
F
M
A
M
CALENDAR MONTHS (1984-85)

Plate 2.1

The two types of nets used in this study.

a. A large 10 m x 1 m, 25-mm mesh beach seine net.

b. A small 1.7 m long x 1 m x 0.4 m gape, fine meshed net.

ranges of crabs caught in the two types of nets, based on the samples obtained for the population study (Chapter 7), are given in Figure 2.2.

The nets were dragged along the substratum parallel to the shore in the surf zone, in 0.2–0.7 m of water. Each drag was of 3 minute duration and covered a distance of approximately 36 m. Crabs used for the morphometric and reproductive studies were maintained in fresh seawater and taken to the laboratory for analyses. Crabs used in the analyses of the feeding biology were placed on ice immediately after capture whilst crabs collected for population studies were sexed, measured and returned to the surf zone shortly after capture.

The methods of analysis of these samples are described in the succeeding chapters.

2.2 Study Area

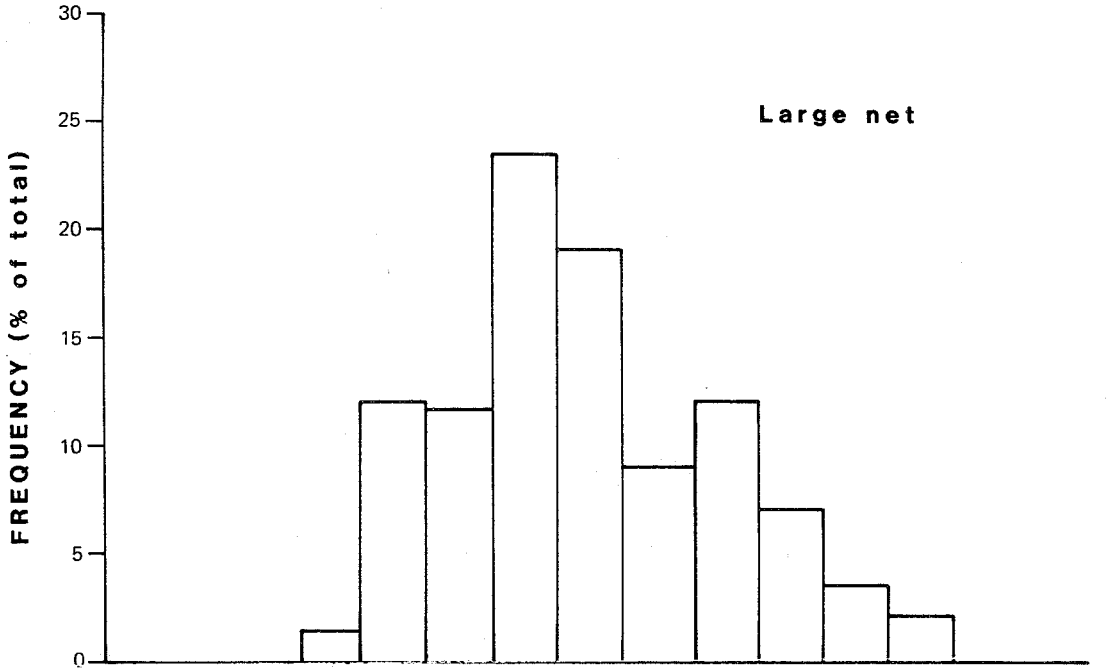
The specimens used in this study were collected from Pallarenda beach, Townsville, Queensland (19°11.8'S, 146°46.6'E). This location was selected as the main study area because of the abundance of *M. lunaris* in the surf zone and its accessibility. Within the study area, two sampling sites were established, namely 'A' and 'B' (Plate 2.2). Site 'A' was a 'non-destructive' population study area where the individuals caught were returned to the surf zone shortly after capture. Site 'B' was the 'destructive' reproduction study area where the individuals caught were taken to the laboratory for analysis. A 150 m gap was established between sites 'A' and 'B' in order to minimize the interactive effects of

Figure 2.2

The size ranges of crabs caught in the two types of nets used in this study.

Large net, n = 1206

Small net, n = 129


Large net
FREQUENCY (% of total)
30
25
20
15
10
5
0

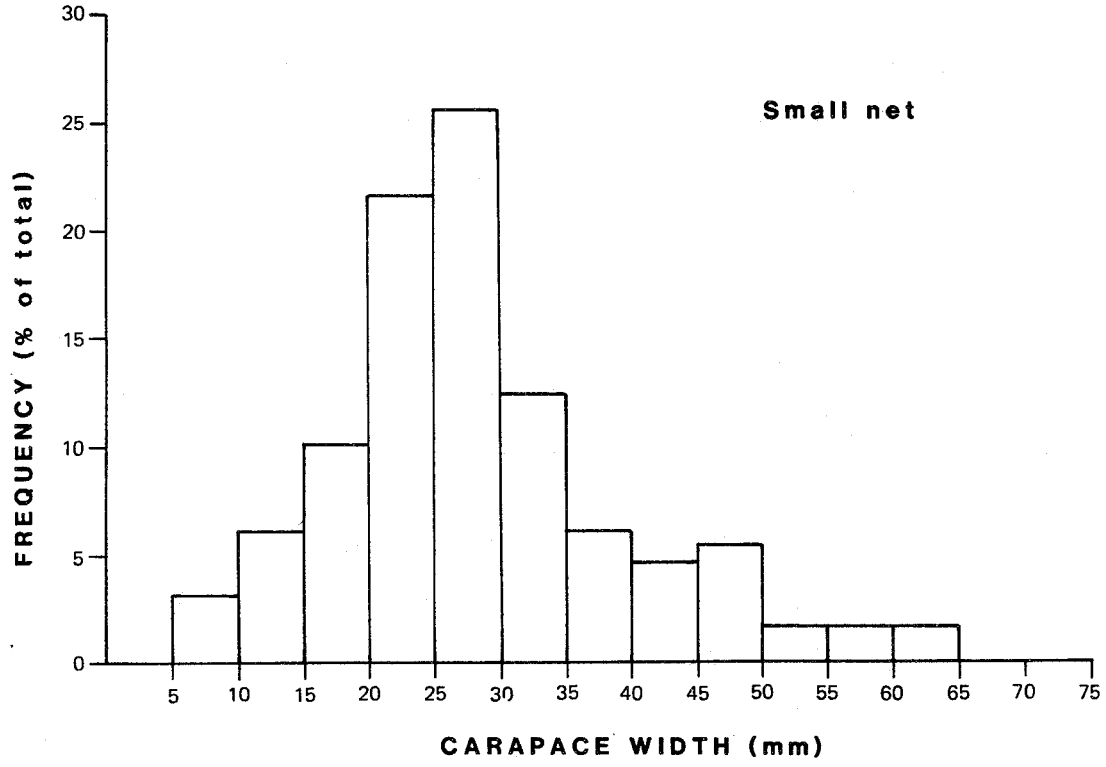

Small net
FREQUENCY (% of total)
30
25
20
15
10
5
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
CARAPACE WIDTH (mm)

Plate 2.2

An aerial photograph of the study area in Pallarenda beach showing the location of study sites A and B.

A - study site A for population studies

B - study site B for growth, feeding and reproductive studies.

x - the point where the photographs in Plate 2.3 were taken.


X

sampling in both sites.

The following topographical description of the study area, uses the terminology of Hopley (1970 and pers. comm.), Bird (1971) and Davis (1972). Pallarenda beach is a medium energy beach where there is a distinctive upper and lower beach portion. The upper beach portion is steep and is composed of coarse carbonate sediments of terrigenous origin and a small amount of biogenic material which is primarily of molluscan origin. In comparison, the lower beach portion has a gently sloping profile and is composed entirely of fine terrigenous sand and silt. During low tide, the exposed lower beach portion of Pallarenda is expansive and consists of a system of sand ridges and runnels. In the study area, the lower beach portion is composed of two sand ridges separated by a shallow runnel (Plates 2.3a, b). The first ridge is low and is bordered on the landward size by a narrow gutter at the base of the upper beach face and on the seaward side, by the shallow runnel. In most parts of the first ridge, there is a thin film of water covering the surface as a result of the damming effect by the second ridge which is distinctly raised. Sampling in this study was carried out in the surf zone during a midfalling tide which is in the region of the lower beach at this time.

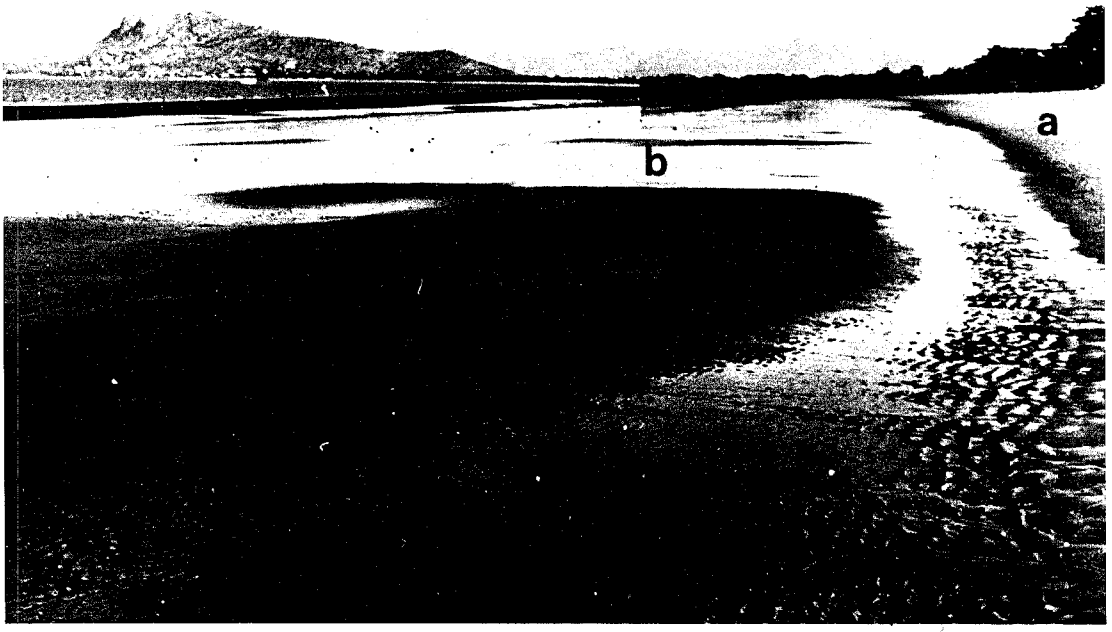
The faunal composition of the study area, based on visual surveys and analyses of the by-catch during sampling, is summarized in Table 2.1. Among the teleosts, the tetraodontids (pufferfishes) and ambassids (glass perches) were found regularly throughout the sampling period, whilst seasonal occurrence was noted in most species particularly the juvenile cynoglossids (tongue soles).

Plate 2.3

Photographs of the two study sites A and B, taken from point x (Plate 2.2), showing the upper beach area (a) and the flat lower beach region (b).

a. The population study site A.

b. The growth, reproduction and feeding study site B.


a
b


a

Table 2.1 A summary of the faunal composition of the study area based ocular surveys and sampling by-catch.

A. INVERTEBRATES

Echinoderms
*Arachnoides placenta**

Molluscs

Bivalves
Tellina australis
Mesodesma altenai
Mactra dissimilis
Dosinia kapiewi

Gastropods
*Nassarius dorsatus**
Polinices sp.
Isanda coronata

Crustaceans

Anomurans
Clibanarius sp.
Diogenes sp.

Brachyurans
Portunus pelagicus
P. sanguinelentus

Others
Penaeus merguiensis
P. esculentus
Ascetes sp.*

Other invertebrates
Balanoglossus sp.

B. VERTEBRATES

Teleosts
Leiognathus splendens
*Cynoglossus bilineatus**
Chorinemus tol
Lutjanus fluviflamma
Tylosurus strongylorus
Arrhamphus sclerolepsis
Sillago sihama
*Sillago ciliata**
Trachinotus blochi
Priopidichthyes gymnocephalus
*Ambassis buruensis**
Terapon puta
*Chelonodon patoca** ++
Arothron reticularis
Drepane punctata
Upeneus vittatus
Leptobrama mulleri
Sardinella jusieu
Paraplagusia guttata
*Stolephorus devisi**
Gerres splendens
Scutengraulis hamiltoni
Platycephalus indicus
Mugil dussumieri
Pomadacys maculata
Caranx sexfasciatus
Gaza minuta
Leiognathus nuchalis

* – common and occurred in relatively large numbers

++ – known predators of M. lunaris (based on intestinal analyses)

Among the invertebrates, several species of gastropods, namely *Conuber* sp. and *Polinices* sp., and the sand dollar, *Arachnoides placenta*, occurred regularly in the study area. In addition, *Balanoglossus* sp. worm casts were often observed on the seaward edge of the lower beach during low tide. Among the crustaceans, the sand shrimp, *Ascetes* sp. and several species of hermit crabs were frequently found in the study area, whilst juvenile prawns such as *Penaeus merguiensis* and *P. esculentus* occurred irregularly. Of the larger crustaceans, however, only *M. lunaris* occurred in abundance throughout the study period. Juvenile *Portunus pelagicus* and *P. sanguinolentus* were also found but only in some months of the year and in low numbers.

CHAPTER THREE

Relative Growth

3.1 Introduction

The value of morphometric studies in understanding the biology of Crustacea, particularly brachyuran crabs, is well established. The rigid exoskeleton and the resultant discontinuous growth of crustaceans enable quantitative studies of growth patterns and stadia. In brachyurans, morphometric data have been used extensively in: a) taxonomy, for example in the genera *Macrophthalmus* (Barnes, 1967, 1968) and *Portunus* (Stephenson, 1967); b) the evaluation of sex and sexual maturity in the Ocypodidae (Haley, 1969, 1973, Paulraj *et al.*, 1982), Portunidae (Ryan, 1967c, Lewis, 1977 and Du Preez & McLachlan, 1984a), Grapsidae (Hiatt, 1948), Raninidae (Fielding & Haley, 1976), Xanthidae (Finney & Abele, 1981), Majidae (Hartnoll, 1963, 1965) and Corystidae (Hartnoll, 1972); c) the analysis of ontogenetic changes in form (Weymouth & Mackay, 1936, Sandon, 1937, Gray & Newcombe, 1938, Mackay, 1942, 1943a, b, Needham, 1950, Teissier, 1960, Hartnoll, 1963, 1965a, 1972); d) relating form and function as an ecological tool (Aldrich, 1976, Brown *et al.*, 1979, Elner, 1978 and Blundon & Kennedy, 1982) and e) determining the size and age of crabs in commercial fisheries (Allen, 1962, Poole, 1967, Williams & Lee, 1980 and Hancock & Edwards, 1966 in: Hartnoll, 1982).

In the Matutidae, including *Matuta lunaris*, morphometric data have only been used in taxonomy (Hale, 1927, Sakai, 1965 and Romimohtarto, 1972). Studies of relative growth and ontogenetic variations in form and function are lacking. In this chapter,

morphometric analysis of *M. lunaris* will be used to define relative growth patterns in male and female crabs and to determine the effect of size, sex and sexual maturity upon the growth patterns of different body parts. In addition, this chapter will form the morphological basis for the feeding and reproductive studies in Chapters 4 and 5.

3.2 Materials and Methods

3.2.1 The samples

The crabs used in this study were collected from Site 'B', Pallarenda beach, Townsville, between the months of January and July, 1984 using the methods described in Chapter 2. All crabs were brought alive to the laboratory for morphometric analysis. All measurements were made on freshly killed specimens.

3.2.2 The measurements

Measurements were taken to the nearest 0.1 mm using either a metric vernier caliper or an ocular micrometer. The following measurements were made:

1) full carapace width (FCW): Figure 3.1, the distance across the carapace from the tip of the lateral spines.
2) short carapace width (SCW): Figure 3.1, the distance across the carapace from the anterior base of the lateral spines.
3) carapace length (CL): Figure 3.1, the distance across the carapace along the median line from the anterior to the extreme posterior margin of the carapace.
4) body depth (BD): the distance between the mid-dorsal aspect of the carapace to the mid-ventral aspect of the sternal plate.

5) distance between eyes (ED): Figure 3.1, the distance between the bases of the ocular peduncles measured from the inner margin of the orbit.

6) propodus length (PL): Figure 3.2, the maximum distance from the tip of the propodus to the articulation with the carpus.

7) chela width (CHW): Figure 3.2, the distance between the frontal (from the base of the second spine) and the rear aspects of the propodus.

8) chela depth (CD): Figure 3.2, the maximum distance between the dorsal and ventral margins of the propodus.

9) chela gape (CG): the maximum distance between the inner margins of the dactylus and the propodus, when the chela is open.

10) dactylus length (DL): Figure 3.2, the distance from the tip of the dactylus to the articulation with the propodus.

11) chela spine height (CSH): Figure 3.2, the distance from the base of the first chela spine to the tip, measured using an ocular micrometer.

12) abdominal width (AW): Figure 3.3, the distance between the margins of the fourth abdominal segment in females and the fifth in males.

13) thoracic width (TW): Figure 3.3, the distance across the thoracic sternum between the notches at the bases of the second periopods.

14) total lateral spine length (TLSL): the difference between full carapace width (FCW) and short carapace width (SCW), *i.e.* the length of both lateral spines.

15) pleopod length (PLL): Figure 3.4, the length of the first pleopod (gonopod).

Figure 3.1

The dorsal aspect of *M. lunaris* showing the measurements of the following morphological characters:

FCW	full carapace width
SCW	short carapace width
CL	carapace length
ED	distance between the eyes

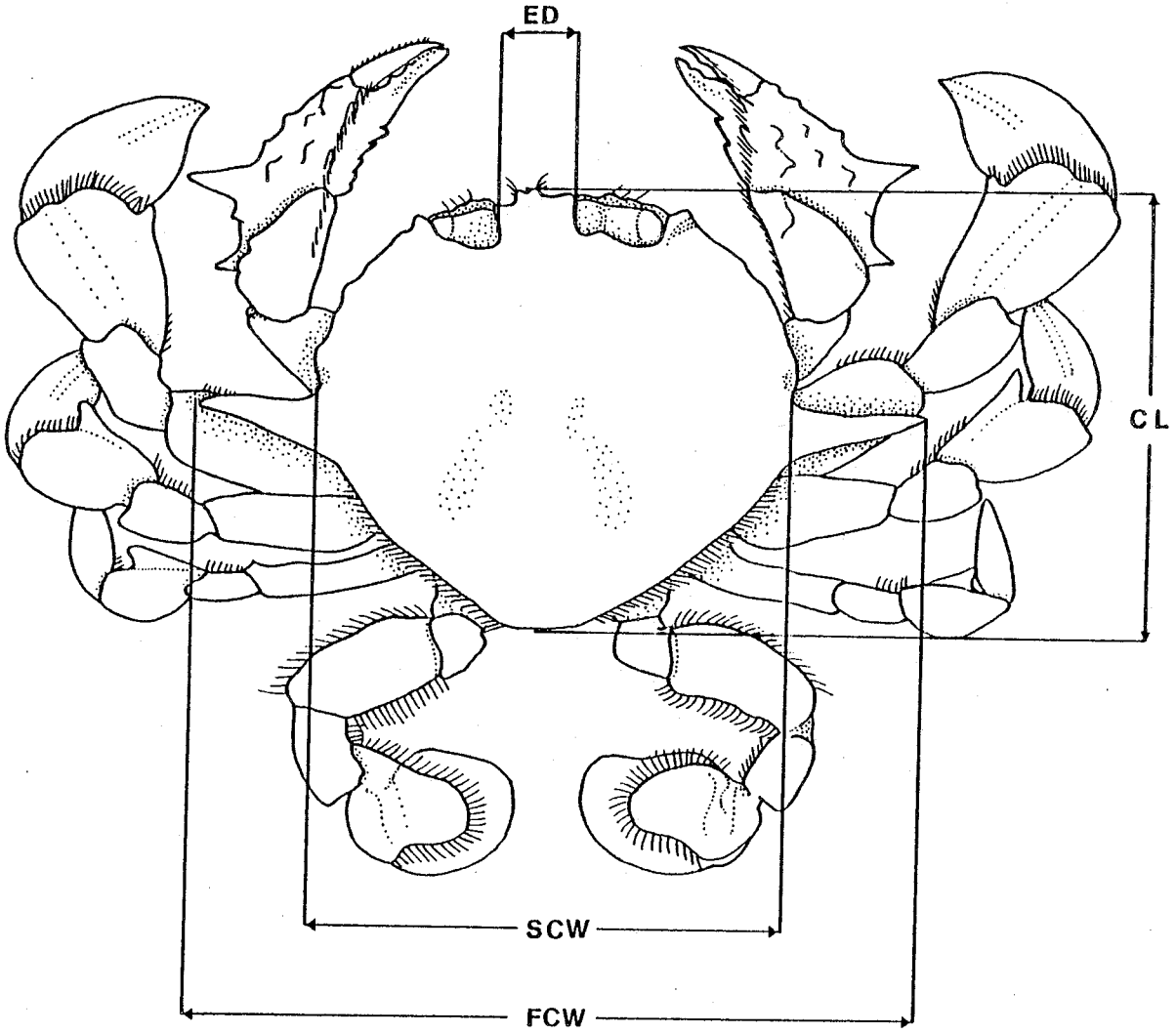

ED
CL
SCW
FCW

Figure 3.2

Details of the left chela of *M. lunaris* showing the measurements of the following morphological characters:

PL propodus length

CHW chela width

CD chela depth

DL dactylus length

CSH chela spine height

3.2A Adult male

upper: frontal aspect

lower: ventral aspect

so secondary stridulating organ

3.2B Adult female

upper: frontal aspect

lower: ventral aspect

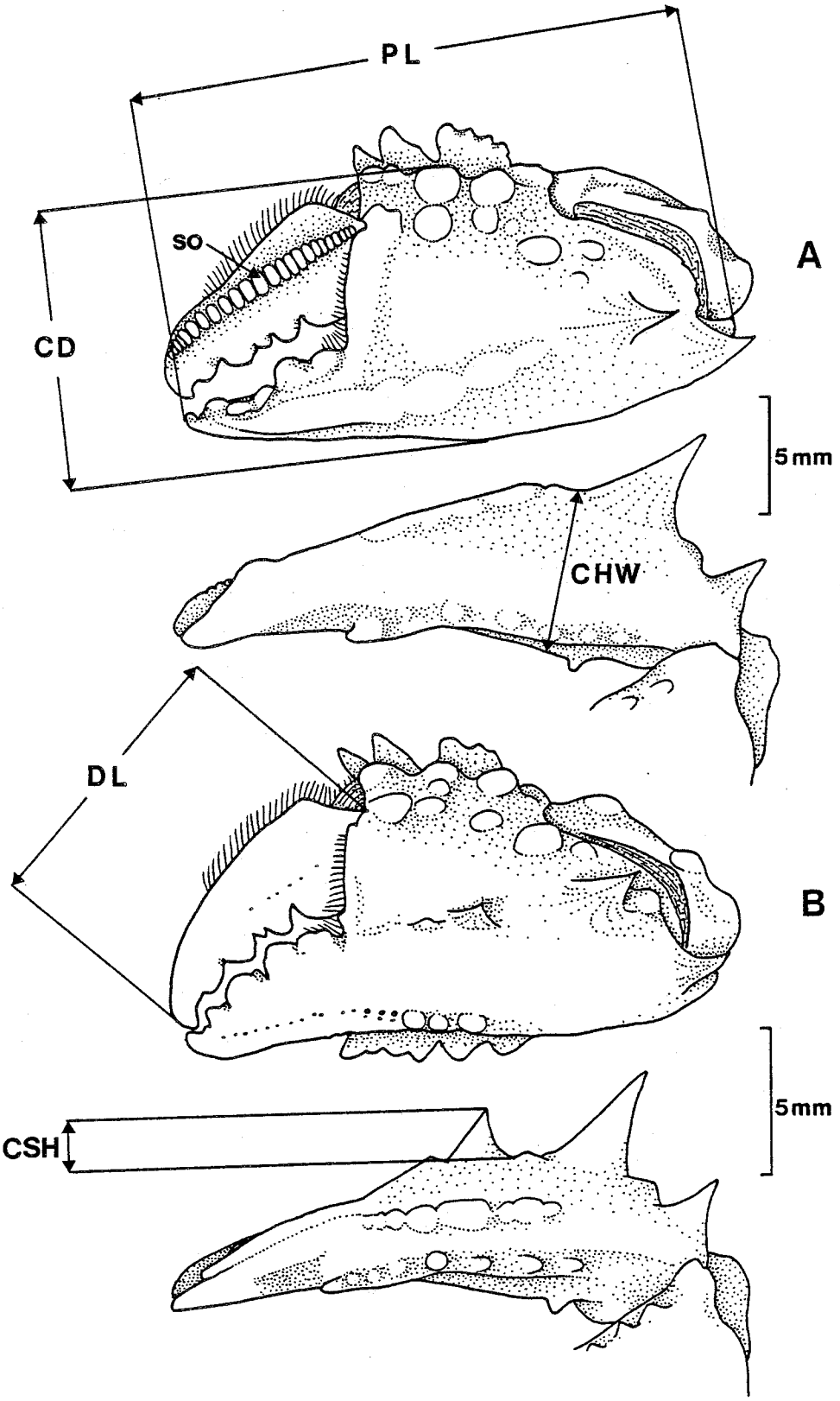

PL
SO
A
CD
5mm
CHW
DL
B
5mm
CSH

Figure 3.3

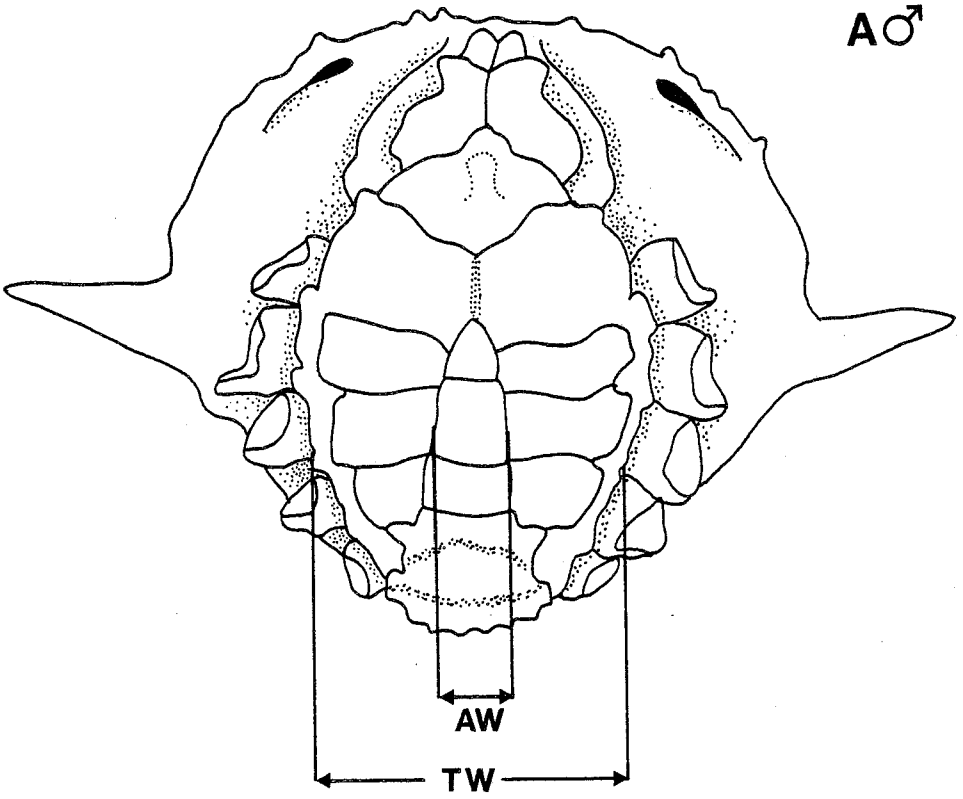
The ventral aspect of *M. lunaris* showing the measurements of the following morphological characters:

AW abdominal width

TW thoracic width

3.3A Adult male

3.3B Adult female


A♂
AW
TW

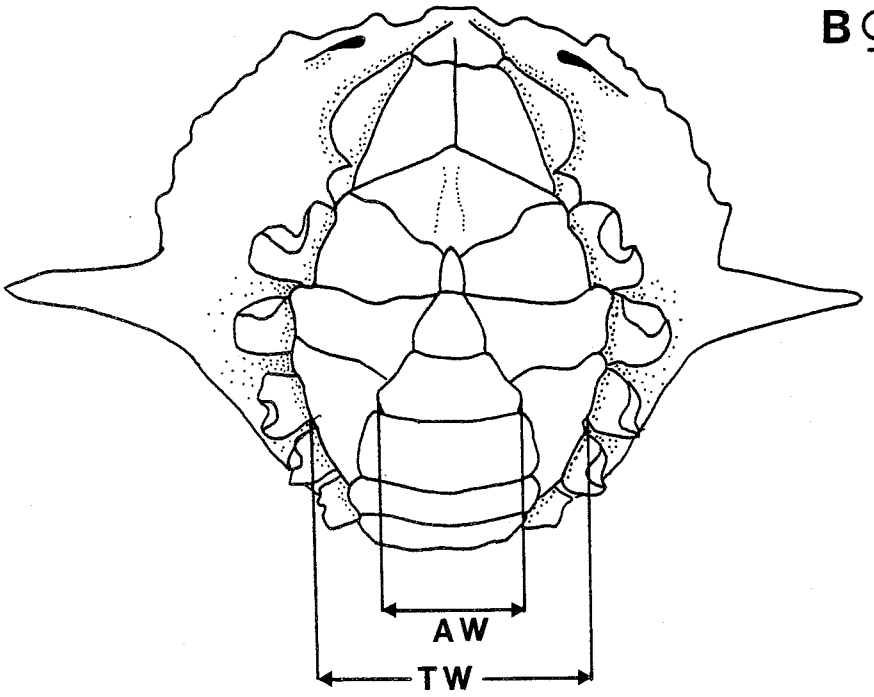

B♀
AW
TW

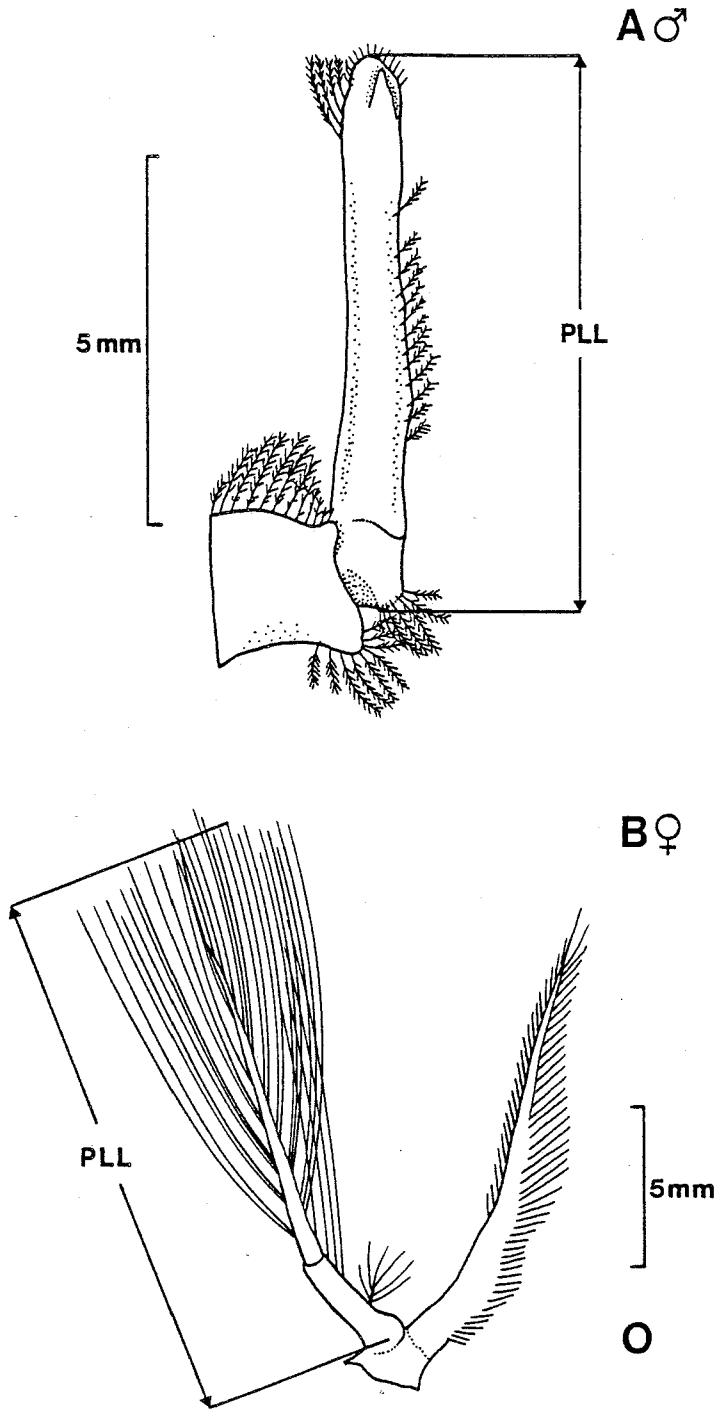
Figure 3.4

Details of the first pleopods of *M. lunaris*.

PLL pleopod length

3.4A Adult male

3.4B Adult female


A♂
5mm
PLL
B♀
PLL
5mm
O

16) chela volume (CV): the multiplication product of chela depth, width and propodus length.

Relative growth is defined as the change during ontogeny in the proportions of a particular dimension relative to a reference measurement (Hartnoll, 1982). In this study, the full carapace width (FCW) was chosen as the measure of body size and the reference measurement, for comparisons with other brachyuran literature. Lewis (1977) found the short carapace width (SCW) more suitable as reference measurement in *Bathynectes superbus* (Brachyura: Portunidae) since the anterolateral spines were frequently broken. In *M. lunaris*, however, this was only rarely observed and damaged crabs were not included in the morphometric analyses. All 15 characters were analyzed in relation to carapace width.

To assess shape changes within a particular body part, several other variables were also designated as reference measurements. Dactylus length, chela width, chela depth, chela gape, chela spine height and chela volume were analyzed against propodus length. The width of the abdomen was compared with thorax width and pleopod length with abdomen width.

3.2.3 The statistical analysis

Three approaches were used in the analysis of results in this study: 1) direct plots; 2) linear regressions of transformed data and 3) plots of relative proportions. Direct plots were used to show the nature of the relationship between the reference measurement and the other characters. Linear regressions of logarithmically transformed data were used to quantify allometric

and isometric patterns. Relative proportions of each morphological character were used to assess growth trends, determine inflection points in relationships and to demonstrate any differences between characters which exhibit isometry but are significantly different between sexes.

Huxley (1924 in: Hartnoll, 1978) demonstrated that relative growth can be satisfactorily described by the simple allometry equation, $y = Bx^{\alpha}$, where y is the dependent variable, x is the reference dimension or independent variable, B is the y-intercept and α is the regression coefficient, also known as allometric growth constant or relative growth rate (Hartnoll, 1982). Although Zar (1968) has questioned the reliability of log transformations, the logarithmic transformation of this equation has been found to describe clearly most patterns of relative growth (*e.g.* Gould, 1966, Sprent, 1972, Hartnoll, 1974, 1978a, 1982, Lewis, 1977, Finney & Abele, 1981 and Paulraj *et al.*, 1982). The theoretical considerations of this technique have been discussed in detail by Finney and Abele (1981).

In this study, all measurements were transformed to log base 10 and Least-Squares regressions were performed. The regression coefficient of each variable was tested against the isometric standard of 1 using a t-test to determine its allometric status (following Finney & Abele, 1981; t-test procedure in Zar, 1974). If the regression coefficient is significantly less than 1, negative allometry exists. If the regression coefficient is significantly greater than 1, there is positive allometry. Isometry exists when the regression coefficient does not differ significantly from 1. In

the case of chelae volume, an isometric standard of 3 was used. In addition, male and female regression coefficients were compared using a paired t-test following Finney & Abele (1981).

In order to evaluate the growth phase patterns within a single sex, the data was divided into juvenile (immature) and adult (mature) groups. The cut-off point was selected after preliminary analysis of morphological and histological data (following Newcombe *et al.*, 1949, Knudsen, 1960, Haley, 1969, 1973, Fielding & Haley, 1976 and Finney & Abele, 1981) since the onset of maturity (*i.e.* puberty moult) in brachyurans does not occur at a specific size, rather over a particular size range (Hartnoll, 1982). Regression coefficients were calculated from logarithmically transformed data and tested for significance to determine the allometric status of each variable in juvenile and adult phases.

Barnes (1966, 1968) used relative proportions to define species in the ocypode genus, *Macrophthalmus*, noting the importance of determining the degree or rate of variation in these proportions with an increase in size. In this study, relative proportions of the given variables versus the reference dimension were calculated and plotted against carapace width.

Regression lines and statistics were calculated using Statpack Version 4 (STP) on the James Cook University computer. In addition, bivariate scatterplots of each regression and relative proportions were generated and examined.

3.3 Results

3.3.1 Relative growth patterns

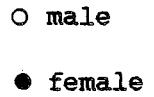
Initial analyses of the 15 morphological characters using direct linear plots against carapace width showed two basic forms: 1) plots with no indication of any abrupt change with increasing size, *i.e.* a straight line or a smoothly curved line (Figs. 3.5, 3.6 and Appendix I), and 2) plots with a marked inflection indicating changes in proportions with increasing size (Figs. 3.7, 3.8, 3.9 and Appendix I). Of the 15 characters examined, only three showed marked inflections with increasing size: abdomen width, chelae spine height and pleopod length (Figs. 3.7, 3.8, 3.9).

Further analyses using linear regressions on log transformed data quantified the relative growth status of the 15 characters. The results relating to this aspect are summarized in Table 3.1. In males, two characters exhibited isometry: body depth and chelae gape whilst all the other characters exhibited allometry. In females, four characters displayed isometric growth: body depth, thoracic width, chelae gape and total lateral spine length whilst the other characters displayed allometry.

The relative proportions of these characters versus the reference dimension, when plotted, clearly demonstrated the variability of the growth patterns during ontogeny. As the size of the crab increased, there was a decrease in the relative proportions of the carapace length, the eye distance and the short carapace width in both sexes and in the thoracic width and the chela spine height in males (Fig. 3.10 and Appendix I). In comparison, there

Figure 3.5

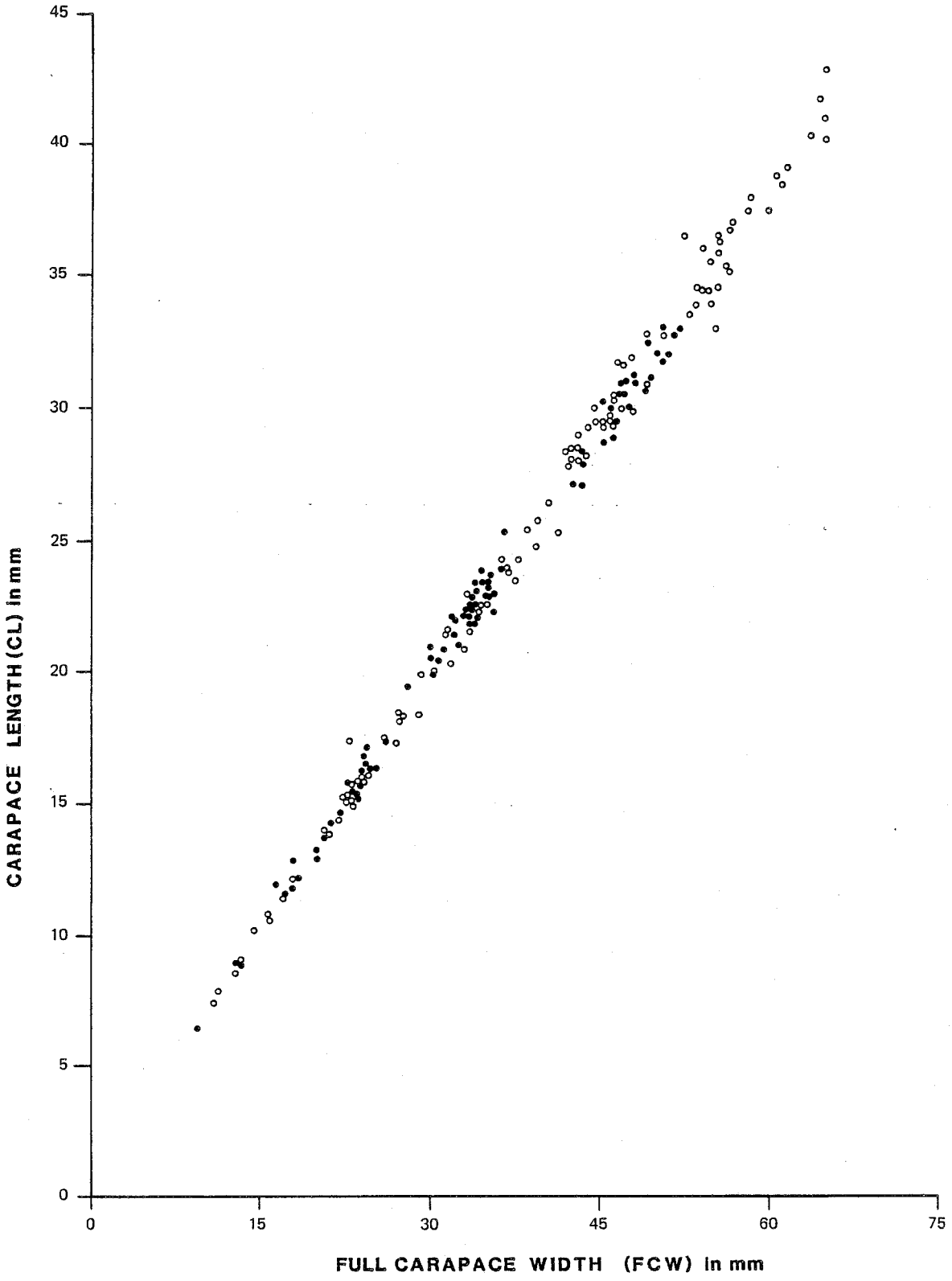
A direct linear plot showing the relationship between the carapace length and the reference dimension, carapace width.



This is an example of a plot which shows no indication of any abrupt change in the growth pattern with increasing size. Other morphological characters which exhibit a similar relationship (*i.e.* when plotted against carapace width) are:

short carapace width	chela depth
eye distance	chela gape
body depth	dactylus length
lateral spine length	thoracic width
propodus length	chela volume
chela width	

Computer-generated scatterplots of these characters against carapace width are given in Appendix I.


45
40
35
30
25
20
15
10
5
0
CARAPACE LENGTH (CL) in mm
0
15
30
45
60
75
FULL CARAPACE WIDTH (FCW) in mm

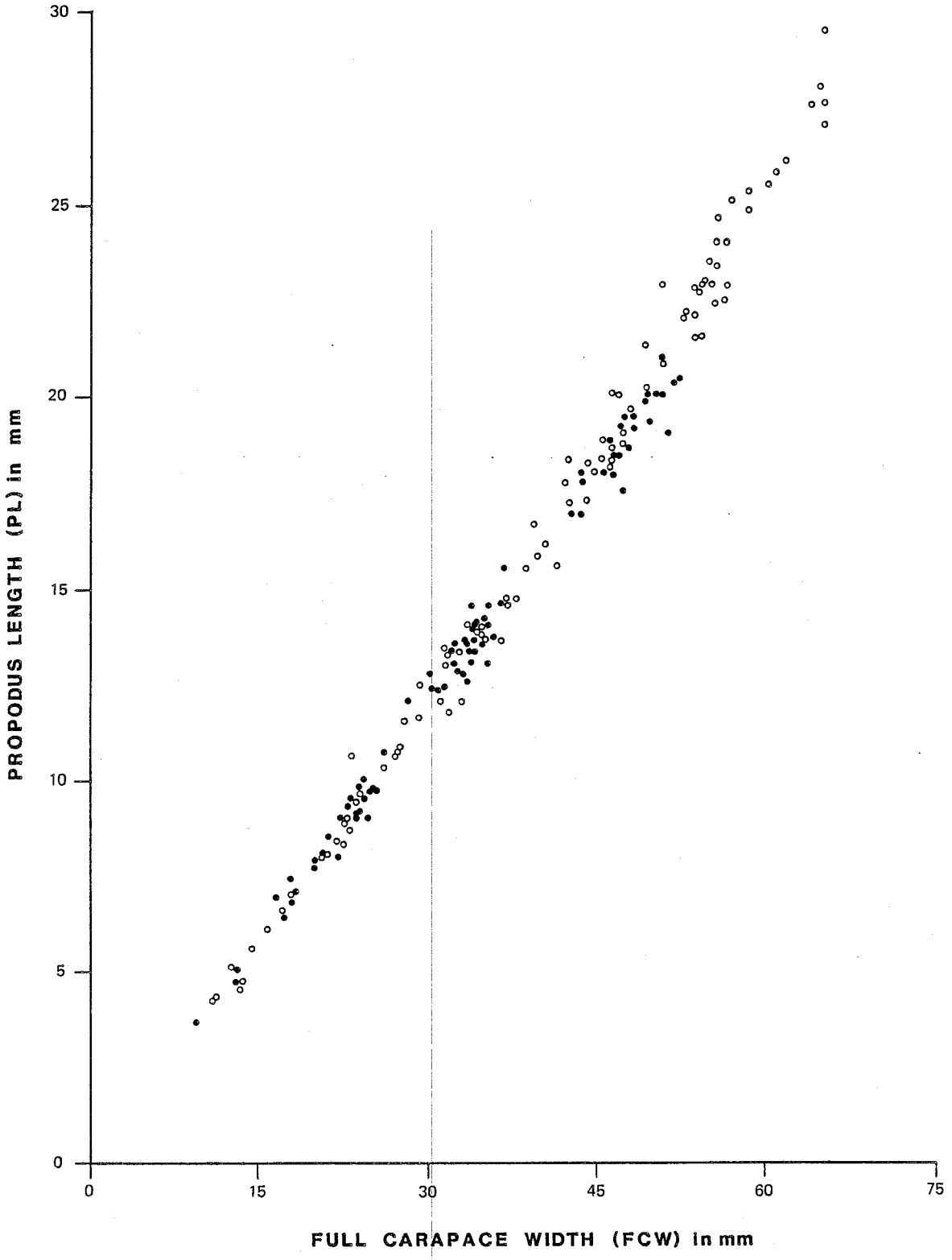

30
25
20
15
10
5
0
PROPODUS LENGTH (PL) in mm
0
15
30
45
60
75
FULL CARAPACE WIDTH (FCW) in mm

Figure 3.7

A direct linear plot showing the relationship between the abdominal width and the reference dimension, carapace width.

○ male

● female

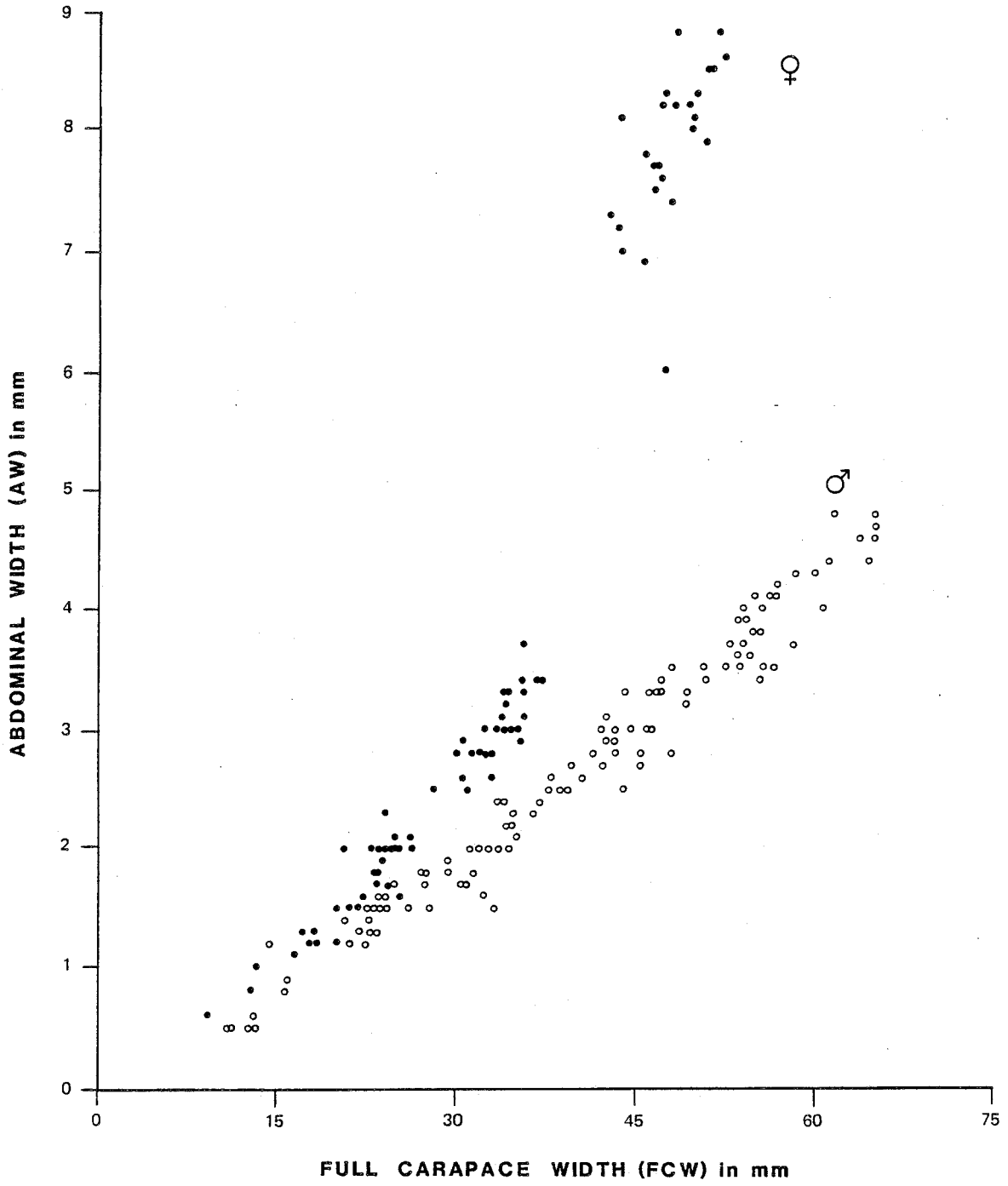

ABDOMINAL WIDTH (AW) in mm
FULL CARAPACE WIDTH (FCW) in mm
♀
♂
0
1
2
3
4
5
6
7
8
9
0
15
30
45
60
75

Figure 3.8

A direct linear plot showing the relationship between the pleopod length and the reference dimension, carapace width.

○ male

● female

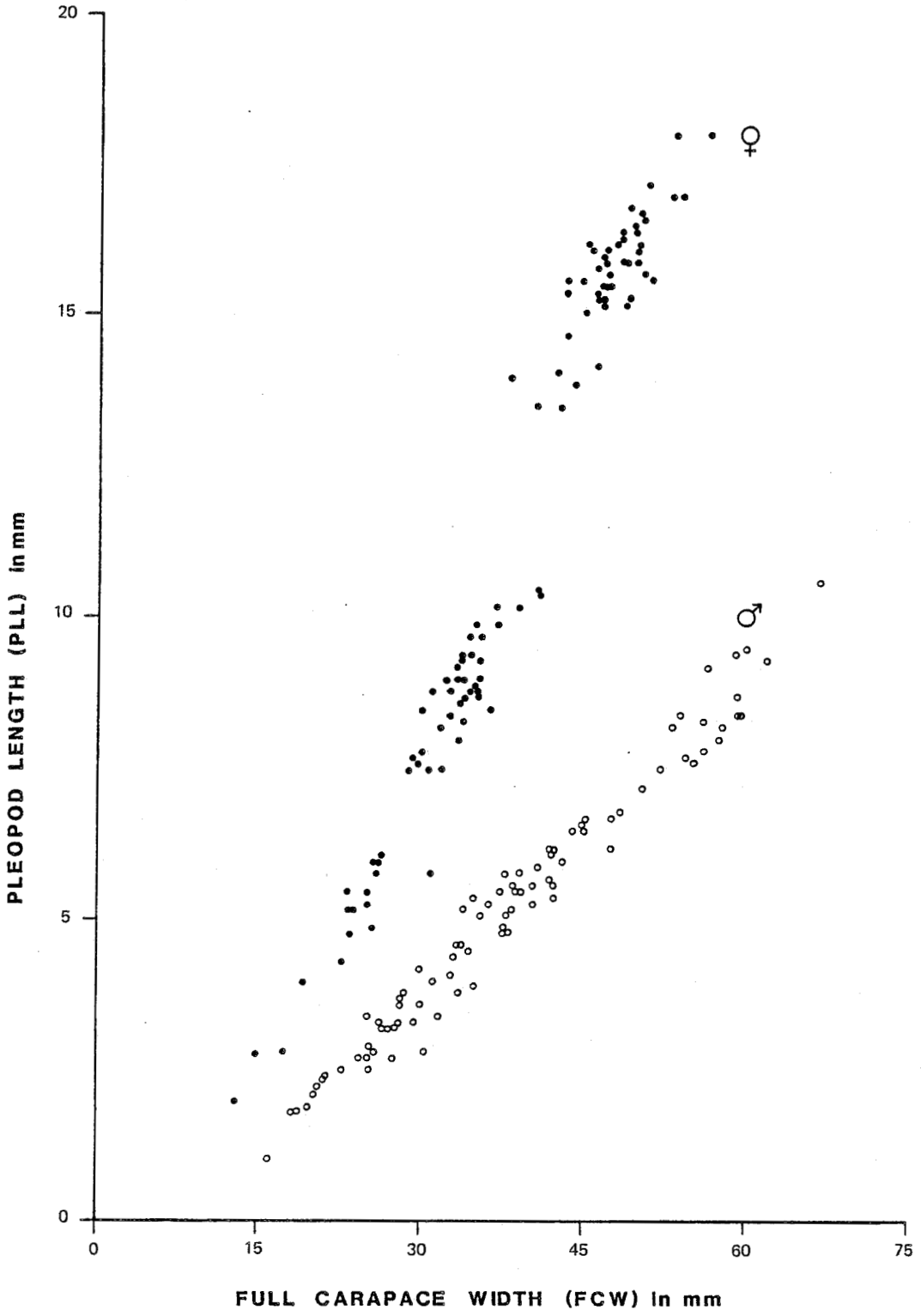

20
15
10
5
0
0
15
30
45
60
75
♀
♂
PLEOPOD LENGTH (PLL) in mm
FULL CARAPACE WIDTH (FCW) in mm

Figure 3.9

A direct linear plot showing the relationship between the chela spine height and the reference dimension, carapace width.

○ male

● female

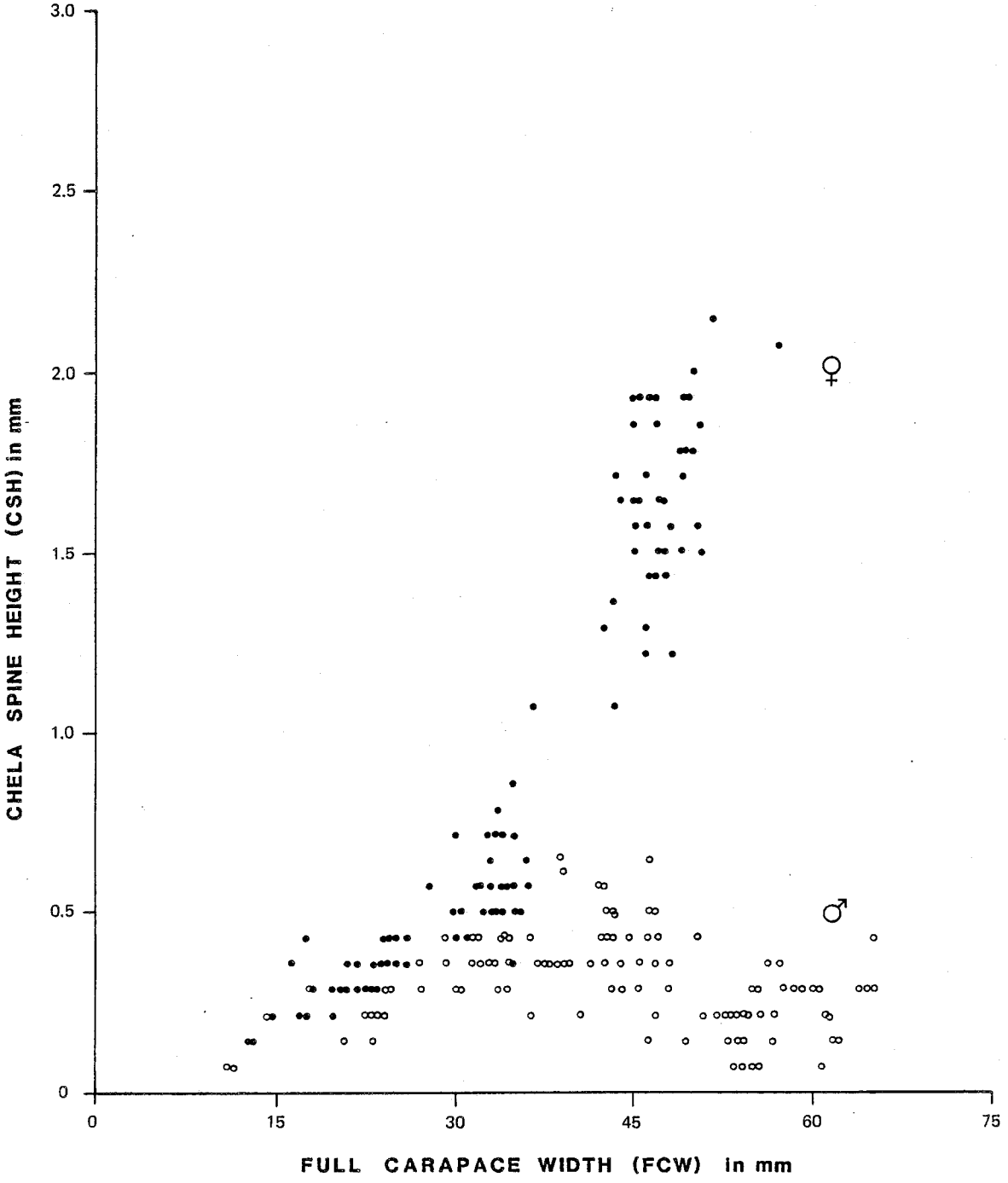

3.0
2.5
2.0
1.5
1.0
0.5
0
CHELA SPINE HEIGHT (CSH) in mm
0
15
30
45
60
75
FULL CARAPACE WIDTH (FCW) in mm
♀
♂

Table 3.1 A summary of allometric statistics for *M. lunaris*.

Morphological Characters (y)	Sex	Equation	S.E.	Correlation Coefficient (r)	F	t-value	p†	Allometric Status‡
A. Relative to carapace width (x)								
Short carapace width	M	$\log y = 0.960 \log x - 0.099$	0.012	0.993	6215.0	3.2726	***	–
	F	$\log y = 0.920 \log x - 0.041$	0.016	0.982	3436.0	5.0819	***	–
Carapace length	M	$\log y = 0.954 \log x - 0.118$	0.005	0.998	30600.0	8.5268	***	–
	F	$\log y = 0.942 \log x - 0.102$	0.020	0.979	2119.0	2.8178	**	–
Body depth	M	$\log y = 1.003 \log x - 0.491$	0.024	0.965	1729.0	0.1295	ns	I
	F	$\log y = 1.051 \log x - 0.545$	0.030	0.964	1209.0	1.6852	ns	I
Eye distance	M	$\log y = 0.853 \log x - 0.554$	0.013	0.986	4336.0	11.3608	***	–
	F	$\log y = 0.866 \log x - 0.572$	0.044	0.902	395.0	3.0849	**	–
Propodus length	M	$\log y = 1.063 \log x - 0.492$	0.011	0.994	10190.0	5.9797	***	+
	F	$\log y = 1.021 \log x - 0.431$	0.010	0.995	9594.0	2.0467	*	+
Chela width	M	$\log y = 1.178 \log x - 1.273$	0.026	0.978	2063.0	6.8755	***	+
	F	$\log y = 1.095 \log x - 1.129$	0.017	0.988	4404.0	5.7701	***	+
Chela depth	M	$\log y = 1.064 \log x - 0.811$	0.011	0.995	9410.0	5.8482	***	+
	F	$\log y = 1.031 \log x - 0.756$	0.009	0.995	13060.0	3.4581	***	+
Chela gape	M	$\log y = 1.012 \log x - 0.712$	0.039	0.939	682.8	0.3033	ns	I
	F	$\log y = 1.017 \log x - 0.718$	0.033	0.947	922.7	0.5113	ns	I
Dactylus length	M	$\log y = 1.133 \log x - 0.895$	0.012	0.994	9538.0	11.4318	***	+
	F	$\log y = 1.090 \log x - 0.832$	0.015	0.992	5266.0	5.9966	***	+
Chela spine height	M	$\log y = 0.114 \log x - 0.776$	0.0965	0.100	1.4	9.1860	***	–
	F	$\log y = 2.008 \log x - 3.224$	0.065	0.943	955.0	15.5136	***	+
Abdominal width	M	$\log y = 1.171 \log x - 1.457$	0.002	0.979	2944.0	7.9514	***	+
	F	$\log y = 1.765 \log x - 2.140$	0.051	0.964	1204.0	15.0413	***	+
Thoracic width	M	$\log y = 0.966 \log x - 0.411$	0.010	0.993	9169.0	3.3377	**	–
	F	$\log y = 1.002 \log x - 0.458$	0.012	0.994	7895.0	0.1587	ns	I
Lateral spines	M	$\log y = 1.047 \log x - 0.568$	0.019	0.978	2802.0	2.3760	*	+
	F	$\log y = 1.076 \log x - 0.631$	0.042	0.937	649.0	1.8066	ns	I
Pleopod length	M	$\log y = 1.330 \log x - 1.396$	0.030	0.979	1854.0	10.6857	***	+
	F	$\log y = 1.596 \log x - 1.483$	0.028	0.985	3163.0	21.0024	***	+
Chela volume	M	$\log y = 3.299 \log x - 2.568$	0.040	0.993	6842.0	7.4891	***	+
	F	$\log y = 3.148 \log x - 2.319$	0.028	0.996	13000.0	5.3662	***	+
B. Relative to propodus length (x)								
Chela width	M	$\log y = 1.116 \log x - 0.733$	0.022	0.983	2584.0	5.2711	***	+
	F	$\log y = 1.069 \log x - 0.661$	0.015	0.989	4825.0	4.5021	***	+
Chela depth	M	$\log y = 1.006 \log x - 0.320$	0.008	0.997	17540.0	0.0724	ns	I
	F	$\log y = 1.007 \log x - 0.315$	0.007	0.997	17600.0	0.0897	ns	I
Chela gape	M	$\log y = 0.949 \log x - 0.238$	0.038	0.934	631.0	1.342	ns	I
	F	$\log y = 0.995 \log x - 0.286$	0.032	0.951	994.6	0.134	ns	I
Dactylus length	M	$\log y = 1.059 \log x + 0.364$	0.011	0.994	9746.0	5.5111	***	+
	F	$\log y = 1.064 \log x + 0.368$	0.013	0.993	6641.0	4.9105	***	+
Chela spine height	M	$\log y = 0.089 \log x - 0.701$	0.091	00.084	1.0	10.0437	***	–
	F	$\log y = 1.929 \log x - 2.337$	0.073	0.926	707.4	12.8065	***	+
Chela volume	M	$\log y = 3.121 \log x - 1.053$	0.025	0.997	15120.0	4.7735	***	+
	F	$\log y = 3.076 \log x - 0.975$	0.020	0.998	23570.0	3.7972	***	+
C. Relative to Abdominal width (x)								
Pleopod length	M	$\log y = 1.202 \log x + 0.201$	0.039	0.958	911.2	5.0671	***	+
	F	$\log y = 0.758 \log x + 0.456$	0.027	0.944	815.8	9.1334	***	+
D. Relative to thoracic width (x)								
Abdominal width	M	$\log y = 1.200 \log x - 0.944$	0.024	0.976	2503.0	8.3282	***	+
	F	$\log y = 1.740 \log x - 1.311$	0.055	0.958	1012.0	13.5320	***	+

† – ns = not significant, $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$

‡ – based on testing the slope against a standard of 1 (or 3 for volume), $\alpha = 0.05$
+ = positive allometry, I = isometry, – = negative allometry

was an increase in the relative proportions of the propodus length, the dactylus length, the chela width, the abdomen width and the pleopod length in both sexes, the chela depth in males and the chela spine height in females (Fig. 3.11 and Appendix I). Abrupt changes in relative proportions were apparent in the chela spine height of both sexes and in the abdominal width of females.

3.3.2 Sex-related differences in relative growth patterns

A comparison between male and female regression coefficients using a paired t-test revealed 9 characters which were significantly different between the sexes: propodus length, dactylus length, chela depth, chela width, chela volume, abdominal width, pleopod length, thoracic width and chelae spine height. These are summarized in Table 3.2. From the plots of relative measurements versus the reference dimension, several morphological characters also varied between sexes in terms of absolute values (*e.g.* lateral spine length). These variations, however, were not found to be significant in the t-test.

3.3.3 Relative growth patterns before and after sexual maturity

Preliminary analyses of morphological and histological data showed differences in the size at sexual maturity in male and female *M. lunaris*. Males become sexually mature at sizes greater than 43.0 mm FCW, whereas females became sexually mature at sizes greater than 39.0 mm FCW. The results pertaining to the relative growth patterns of males greater or lesser than 43.0 mm FCW and females greater or lesser than 39.0 mm FCW are summarized in Table 3.3.

Figure 3.10

The relationship between the relative eye distance (ED/FCW) and the reference dimension, carapace width.

This is an example of a plot showing a decrease in the relative proportions with increasing size. Other morphological characters which show a similar trend are:

short carapace width
carapace length
thoracic width in males
chela spine height in males

Computer-generated scatterplots of the relative proportions of these characters against carapace width are given in Appendix I.

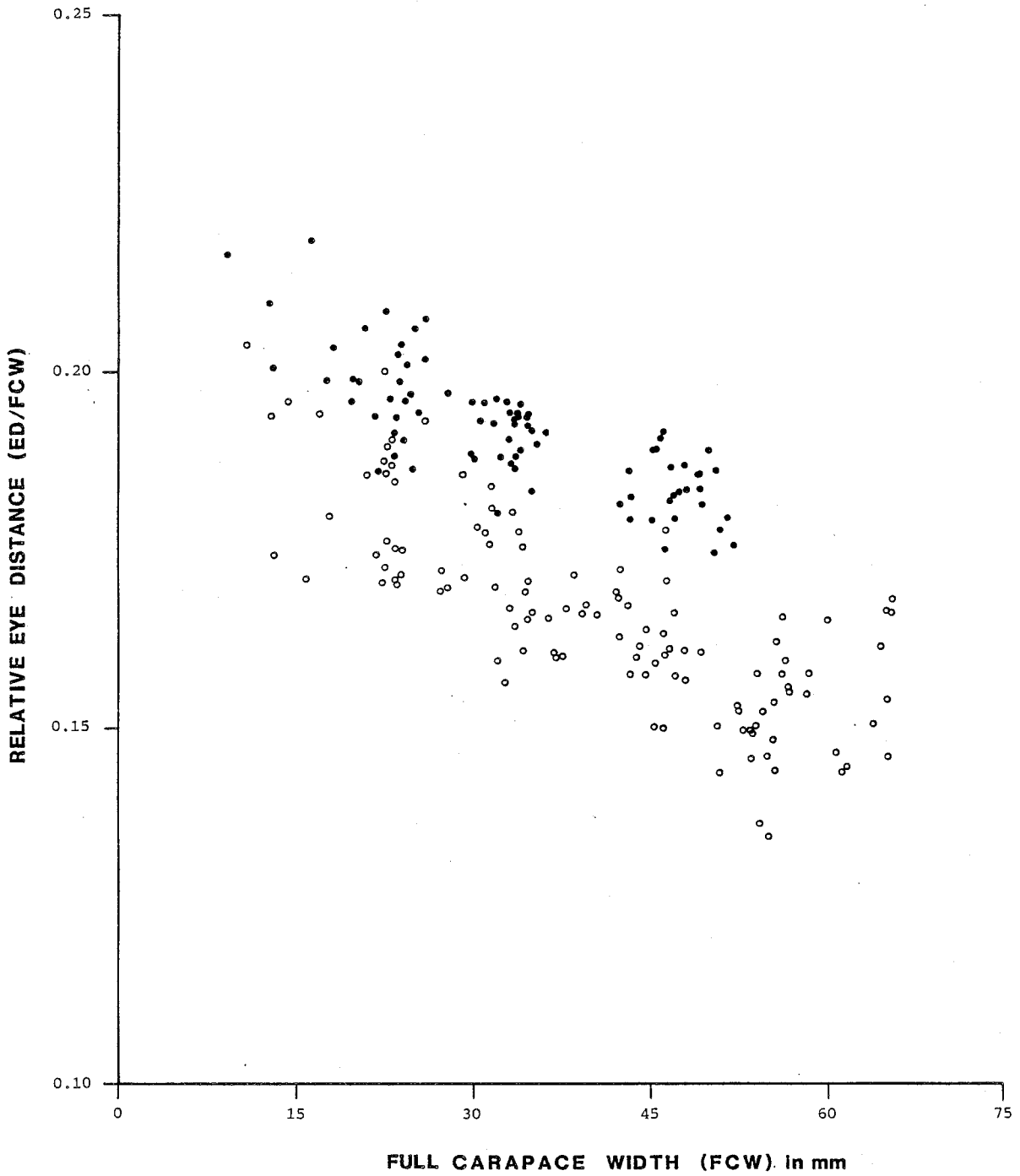

0.25
0.20
0.15
0.10
RELATIVE EYE DISTANCE (ED/FCW)
0
15
30
45
60
75
FULL CARAPACE WIDTH (FCW) in mm

Figure 3.11

The relationship between the relative dactylus length (DL/FCW) and the reference dimension, carapace width.

This is an example of a plot showing an increase in the relative proportions with increasing size. Other morphological characters which show a similar trend are:

propodus length
chela width
abdomen width
pleopod length
chela depth in males
chela spine height in females

Computer-generated scatterplots of the relative proportions of these characters against carapace width are given in Appendix I.

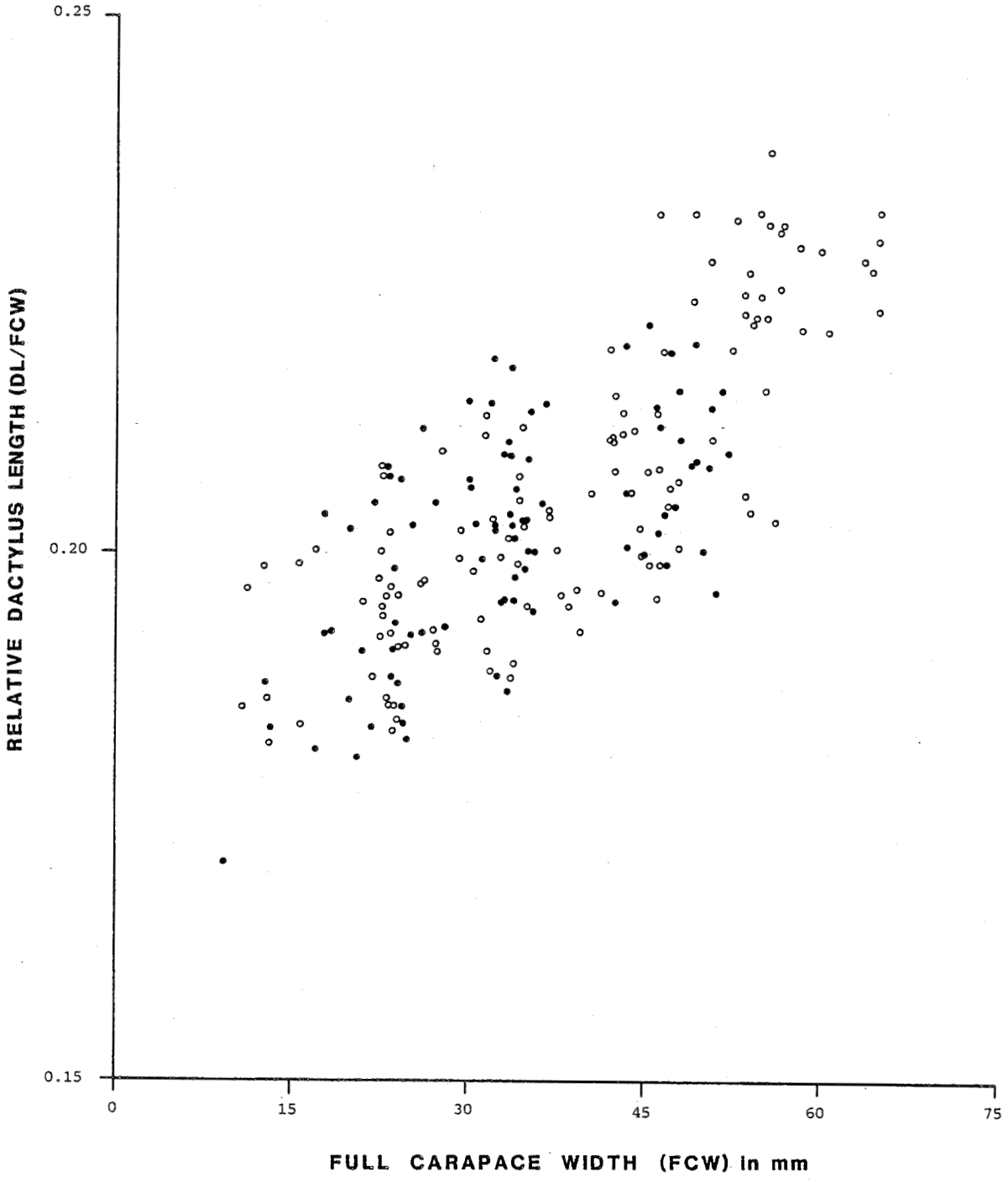

0.25
0.20
0.15
RELATIVE DACTYLUS LENGTH (DL/FCW)
0
15
30
45
60
75
FULL CARAPACE WIDTH (FCW) in mm

Table 3.2 Comparison of male and female allometric coefficients using a paired *t*-test.

Morphological Character	Allometric Coefficients Relative to FCW		p†
	Male	Female	
Short carapace width	0.9604	0.9296	ns
Carapace length	0.9535	0.9423	ns
Body depth	1.0031	1.0509	ns
Eye distance	0.8528	0.8657	ns
Propodus length	1.0629	1.0213	**
Chela width	1.1784	1.0952	**
Chela depth	1.0642	1.0312	*
Chela gape	1.0118	1.0171	ns
Dactylus length	1.1326	1.0900	*
Chela spine height	0.1139	2.0076	***
Abdominal width	1.1715	1.7650	***
Thoracic width	0.9663	1.0017	*
Lateral spine length	1.0472	1.0762	ns
Pleopod length	1.3302	1.5962	***
Chela volume	3.2987	3.1482	***

† : ns = not significantly different, $p > 0.05$
* = significant difference, $p < 0.05$
** = strong significant difference, $p < 0.01$
*** = very strong significant difference, $p < 0.001$

Table 3.3 The allometric status of pre-puberty and post-puberty phases of *M. lunaris*.

Morphological Character	Sex	PRE-PUBERTY Allometric Coefficient	p†	Allometric Status‡	POST-PUBERTY Allometric Coefficient	p†	Allometric Status‡
A) Relative to carapace width							
Short carapace width	M	0.8782	***	-	0.9156	*	-
	F	0.9758	ns	I	0.6733	*	-
Carapace length	M	0.9559	***	-	0.9124	*	-
	F	0.9432	ns	I	0.8335	**	-
Body depth	M	1.0453	ns	I	0.9134	ns	I
	F	1.1350	**	+	0.9297	ns	I
Eye distance	M	0.8801	***	-	0.8383	*	-
	F	0.8594	ns	I	0.6759	**	-
Propodus length	M	1.0584	***	+	1.2054	**	+
	F	1.0445	*	+	0.8195	*	-
Chela width	M	1.0975	ns	I	1.2750	ns	I
	F	1.0668	*	+	1.2314	**	+
Chela depth	M	1.0235	ns	I	1.1395	*	+
	F	1.0541	***	+	1.0411	ns	I
Chela gape	M	1.0865	ns	I	1.0092	ns	I
	F	1.0788	ns	I	0.9876	ns	I
Dactylus length	M	1.0935	***	+	1.2409	***	+
	F	1.1043	***	+	0.9887	ns	I
Chela spine height	M	0.9532	ns	I	-1.5692	***	-
	F	1.3294	***	+	1.2985	ns	I
Abdominal width	M	1.2058	***	+	1.2277	**	+
	F	1.3305	***	+	1.9281	*	+
Thoracic width	M	0.9677	ns	I	0.9563	ns	I
	F	1.0131	ns	I	0.9758	ns	I
Lateral spines	M	1.0146	ns	I	1.1805	*	+
	F	1.0577	ns	I	1.1175	ns	I
Pleopod length	M	1.4443	***	+	1.0412	ns	I
	F	1.5704	***	+	1.2976	*	+
Chela volume	M	3.1445	**	+	3.5445	*	+
	F	3.1728	***	+	3.2726	ns	I
B) Relative to propodus length							
Chela width	M	1.0668	ns	I	1.1706	*	+
	F	1.0129	ns	I	1.1936	**	+
Chela depth	M	0.9959	ns	I	1.0000	ns	I
	F	1.0004	ns	I	0.9949	ns	I
Chelae gape	M	1.0474	ns	I	0.9080	ns	I
	F	1.0317	ns	I	0.8990	ns	I
Dactylus length	M	1.0271	ns	I	0.9464	ns	I
	F	1.0516	*	+	1.2017	ns	I
Chela spine height	M	0.9063	ns	I	-1.0947	***	-
	F	1.1976	*	+	1.1876	ns	I
Chela volume	M	3.0627	ns	I	3.1707	ns	I
	F	3.0134	ns	I	3.1886	ns	I
C) Relative to abdomen width							
Pleopod length	M	1.4007	***	+	0.9527	ns	I
	F	0.9588	ns	I	0.3692	***	-
D) Relative to thoracic width							
Abdominal width	M	1.2166	***	+	1.2291	**	+
	F	1.2979	***	+	1.5232	ns	I

† : ns = not significant, $p > 0.05$, * = $p < 0.05$, ** = $p < 0.01$, *** = $p < 0.001$.

‡ : based on testing the slope against a standard of 1 (or 3 for volume), $\alpha = 0.05$
+ = positive allometry, I = isometry, - = negative allometry

There are nine possible combinations of growth patterns before and after sexual maturity which may reflect the following growth conditions:

1) absence of any change in the type of relative growth pattern before and after sexual maturity,
2) a change in the relative growth pattern of the character after maturity, with a decrease in the relative growth rate, and
3) a change in the relative growth pattern after sexual maturity, with an increase in the relative growth rate.

A summary of morphological characters demonstrating these combinations of growth patterns is given in Table 3.4.

3.3.4 Sexual dimorphism

Although the individuals of both sexes of *M. lunaris* appeared very similar in the field, several morphological differences were apparent upon detailed examination. The female abdomen is wider than that of the male, with the width becoming more pronounced with increasing size. Likewise, the first chelae spine on the propodus becomes more prominent with increasing size in females whereas it becomes reduced in males. A ribbing on the dorsal aspect of the dactylus is present in large males but absent in smaller males and all females.

A comparison of the allometric statistics of male and female *M. lunaris* have shown the following differences (from Tables 3.1, 3.2, 3.3 and 3.4):

1) The propodus is relatively longer and larger in males than in females. Both sexes show positive allometry in all chelae

Table 3.4 Relative growth patterns of both sexes before and after sexual maturity, showing the different growth combinations.

	Relative Growth Pattern		Significance	Morphological Characters	
	PRE-PUBERTY	POST-PUBERTY		MALE	FEMALE
1)	I	I	Type of relative growth pattern remains constant. No change at the onset of maturity.	Body depth Thoracic width Chela gape Chela gape* Dactylus length* Chela depth* Chela volume*	Lateral spine length Thoracic width Chela gape Chela gape*
2)	-	-	Type of relative growth pattern remains constant. No change at the onset of maturity.	Carapace length Eye distance Short carapace length	
3)	+	+	Type of relative growth pattern remains constant. No change at the onset of maturity.	Propodus length Dactylus length Abdominal width Chela volume Abdominal width***	Chela width Pleopod length Abdominal width
4)	I	-	Type of relative growth pattern changes at the onset of maturity. Relative growth rate decreases.	Chela spine length	Carapace length Eye distance Short carapace width Pleopod length**
5)	+	I	Type of relative growth pattern changes at the onset of maturity. Relative growth rate decreases.	Pleopod length Chela width Pleopod length**	Chela depth Dactylus length Chela volume Body depth Chela spine height Chela spine height* Dactylus length* Abdominal width***
6)	+	-	Type of relative growth pattern changes at the onset of maturity. Relative growth rate decreases.		Propodus length
7)	I	+	Type of relative growth pattern changes at the onset of maturity. Relative growth rate increases.	Lateral spine length Chela depth Chela width*	Chela width* Chela volume*
8)	-	+	Type of relative growth pattern changes at the onset of maturity. Relative growth rate increases.	none	none
9)	-	I	Type of relative growth pattern changes at the at the onset of maturity. Relative growth rate increases.	none	none

I = isometry, + = positive allometry, - = negative allometry

* : relative to propodus length, ** : relative to abdominal width, *** : relative to thoracic width.

dimensions before maturity except chela depth in males. At the onset of maturity, however, both sexes show differences in the growth patterns of all chelae dimensions (Table 3.3). Only the propodus length in males continues to exhibit positive allometry with the level of the allometric coefficient increasing from 1.06 to 1.21.

2) The dactylus length in both sexes exhibit positive allometry before maturity. Upon maturity, the length of the dactylus in females becomes isometric whereas in males, it continues to be positively allometric. Relative to propodus length, the dactylus length in males increases isometrically throughout ontogeny whereas in females, it exhibits positive allometry before maturity and changes into isometry at maturity.

3) In terms of absolute measurements, the female abdomen is wider than that of the male. Although the abdomen width in both sexes show positive allometry before and after maturity, the allometric coefficients differ significantly between sexes ($t = 9.1416$, d.f. = 198, $p << 0.001$). In addition, the levels of allometry increased from 1.33 to 1.93 at maturity in females and from 1.21 to 1.23 at maturity in males. In relation to the thoracic width, the abdomen width of males exhibit positive allometry after maturity whereas females exhibit isometry.

4) Although the thoracic width of both sexes show isometry throughout ontogeny, in terms of absolute measurements, males tend to have narrower thoracic plates than females.

5) Apart from the abdomen, the most striking sexually dimorphic character in *M. lunaris* is the height of the first chela

spine. In males, the chela spine height is isometric with carapace width and propodus length before maturity. At the onset of maturity, however, the chela spine becomes markedly reduced, exhibiting a very strong negative allometry. In females, however, the chela spine is positively allometric with carapace width and propodus length before maturity and becomes isometric after maturity.

6) The male and female pleopods of *M. lunaris* differ in form (Fig. 3.4) although in terms of relative growth, both sexes exhibit positive allometry in pleopod length before maturity. At the onset of maturity, the pleopod length in females continues to exhibit positive allometry whereas in males it exhibits isometry. In contrast with the changes in the allometric coefficients of the abdomen width, the level of allometry decreases in both sexes, from 1.57 to 1.30 at maturity in females and from 1.44 to 1.04 in males. In relation to abdomen width, the pleopod length in males exhibits isometry after maturity whereas females exhibits negative allometry.

3.4 Discussion

3.4.1 Functional interpretations

Growth in the Crustacea is a discontinuous process because of the rigid exoskeleton. Like most crustaceans, crabs often undergo substantial changes in form during successive moults. These changes result from the differences in the growth rates of various parts of the body relative to other parts. This may occur gradually over a series of moults or become apparent at a single moult, such as that between the final immature and first mature instars. These changes

which occur during development are referred to as relative or allometric growth (Hartnoll, 1982).

In this study, relative growth in *M. lunaris* showed three basic patterns: isometry, positive allometry and negative allometry. These patterns varied between parts of the body and between the same parts, not only in the two sexes but also in the different phases of growth within each sex. The extent of these variations between sexes and between growth phases may be indicative of the functional role of each morphological character. In this context, therefore, the 15 morphological characters may be classified into three groups:

1) Those characters which exhibit isometry throughout ontogeny suggesting functional roles which are independent of size, sex or sexual maturity.
2) Those characters which exhibit allometry sometime during ontogeny but with no marked inflection at sexual maturity, suggesting size-related functional roles other than that of reproduction.
3) Those characters which exhibit allometry during ontogeny and show marked variations at the onset of maturity, suggesting possible roles in the reproductive biology of the species.

In order to understand the functional implications of the growth patterns of morphological characters, however, it is necessary to consider these characters as part of functional units rather than as isolated character states (Hartnoll, 1974). In this study therefore, three functional units were recognized: 1) the carapace, 2) the chela and 3) the abdomen and its associated structures. The growth patterns of the 15 characters studied in *M. lunaris* will therefore be discussed in relation to these

functional units.

3.4.1.1 The carapace

In this study, five carapace dimensions have been considered: carapace length, distance between eyes, lateral spine length, short carapace width and body depth. With the exception of the lateral spine length in females and body depth in both sexes, the relationships between the reference measurement and the other carapace dimensions are allometric in both sexes indicating that the ratios of the dimensions are not constant throughout development. There are, however, no discernible discontinuities in the growth patterns of these dimensions, and no significant differences between the sexes have been found. This suggests that these patterns are not related to sex or sexual maturity.

The functional implications of these pattens are unclear, with the possible exception of the relative growth of the eye distance which appears to be related to vision. In *M. lunaris*, the distance between the eyes is negatively allometric in both sexes, *i.e.* the relative distance between the eyes become smaller as the crab grows larger. It is likely that there is a limit to the advantages gained by increasing the distance between the eyes in a turbid environment such as that inhabited by *M. lunaris*. The advantages of better resolution with increased distance between the eyes may be achieved at small sizes. In larger crabs, however, these advantages maybe outweighed by the disadvantage of consequent structural changes in the nerve complex. Negative allometry appears to be advantageous whenever isometry or positive allometry diminishes the efficiency of an organ or is energetically expensive (Hartnoll, 1974). As the

growth pattern of the distance between the eyes in *M. lunaris* is probably related to photoreception and visual acuity, it is therefore unlikely to be affected by sex or sexual maturity. These interpretations are tentative and require further investigation. A similar non-puberty related decrease in the relative distance between the eyes has also been recorded in *B. superbus* (Lewis, 1977) and in *Carcinus maenas* (Williams & Needham, 1941).

It is interesting to note that the lateral spine length in males exhibits positive allometry at sexual maturity. This may be related to the role played by the male in reproductive behaviour. Observations of the specimens in this study suggest that mating is of the "soft-female" type (Chapter 5) where copulation occurs between a hard-shelled male and a soft-shelled newly moulted female. Hartnoll (1969) has stated that the advantages of this type of mating is that the hard male is able to protect the female during the vulnerable post-ecdysis period. This, however, transfers vulnerability to the male crab. Longer lateral spines, if used for protection, may then be more important to males than to females at this time, and may account for the positively allometric growth of the lateral spines in male *M. lunaris*.

3.4.1.2 The chelae

In brachyurans, the chelae have a variety of functions. These are used as tools in feeding and in behavioural patterns such as courtship, territoriality and maintenance of status in a hierarchy (Warner, 1977). The extent of these functions, however, is largely determined by the size and shape of the chelae. In behavioural interactions, large chelae would be more advantageous as these tend

to maximize the apparent size of the individual thus enabling the individual to appear formidable (Warner, 1977). This has been observed in ocypodids and many semi-terrestrial grapsids (Schöne, 1968). In addition, heavily built chelae are also advantageous in feeding as they enable crabs such as *Cancer pagurus* (Ebling *et al.*, 1964), *Calappa hepatica* (Vermeij, 1982) and several xanthid species (Warner, 1977 and Zipser & Vermeij, 1978) to crack open mollusc shells.

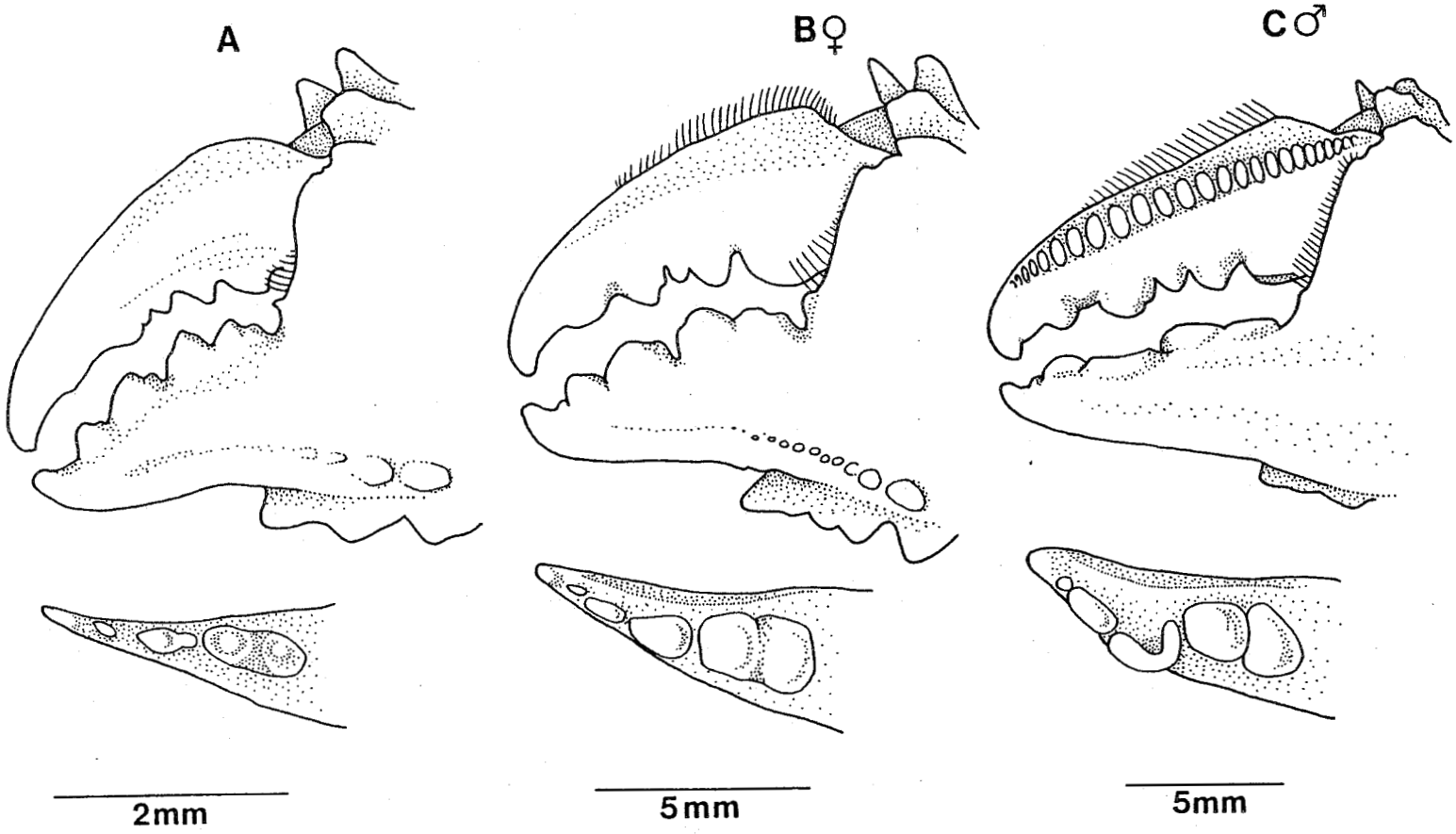
Allometric growth of the chela is common in brachyurans (*e.g.* Hartnoll, 1974, Lewis, 1977, Finney & Abele, 1981 and Paulraj *et al.*, 1982), the degree of which usually varies between sexes and between species. In *M. lunaris*, all except one of the chela dimensions exhibited allometric growth during ontogeny. Chela gape remained isometric with carapace width whereas propodus length, chela depth, chela width and dactylus length showed positive allometry during ontogeny but with no marked inflection at the onset of maturity. The height of the first chela spine in females exhibited strong positive allometry with a marked inflection at maturity. There was a significant difference in all the chela dimensions between the sexes although this was most notable only in the chela spine height.

The degree of variation in the growth patterns of these chelae dimensions may be related to the functions of the chelae in the feeding and reproduction of *M. lunaris*. The lack of distinct discontinuities in the growth patterns of propodus length, chelae depth, chelae width and dactylus length at the onset of maturity, however, suggests that these dimensions are not associated with

reproduction. These allometric differences are more likely, therefore, to be related to feeding.

There is a general increase in all the relative measurements of the chela during ontogeny and this is most clearly demonstrated in the chela volume of both male and female *M. lunaris*. The increase in the chela volume is primarily the result of an increase in the width of the chela relative to propodus length rather than an increase in depth. This results in a more robust chela. Such a chela is capable of a strong crushing action (Warner, 1977). A possible correlation between the absolute force of the chela and the size of the apodeme muscle in decapods has been reported (Brown *et al.*, 1979 and Warner *et al.*, 1982). It is therefore probable that in *M. lunaris*, an increase in the relative width and volume of the chela may result in an increase in the relative size of the apodeme muscle within the chela which may in turn markedly increase its strength. Studies in the cheliped biomechanics of *M. lunaris* are needed to assess this proposal.

The dentition of the chela of *M. lunaris* shows variations which correspond with the allometric change in the chela dimensions. Small individuals possess relatively sharp, pointed incisor-like teeth along the dactylus and the propodus (Fig. 3.12). In larger individuals, the teeth on the dactylus are robust and appear worn and blunt. Sharply toothed chela have been associated with a tearing or cutting action (Warner & Jones, 1976) as in the chela of *Pachygrapsus crassipes* (Brown *et al.*, 1979) and *Callinectes sapidus* (Warner, 1977). In contrast, the robust and blunt dentition of the chela suggests a crushing ability (Warner & Jones, 1976) as in the


A
B♀
C♂
2mm
5mm
5mm

'strong' or 'master' chela of *C. maenas* (Elner, 1978), *Daldorfia horrida* (Zipser & Vermeij, 1978), *Menippe mercenaria* (Brown *et al.*, 1979) and *Ovalipes punctatus* (Du Preez, 1984).

Considering the non-puberty related allometric increase of all chela dimensions including chela volume and the size-related change in the chela dentition, there appears to be a change in the mechanical ability of the chela from that of a cutting/tearing device in small individuals to a strong crushing device in larger ones. It is therefore proposed that the chelae of *M. lunaris* are initially adapted for tearing and cutting food material and as the size of *M. lunaris* increases, become increasingly capable of crushing hard or shelled prey items.

Although the growth patterns of most chela dimensions indicate that the primary function of the chela is related to feeding, several morphological features of the chela suggest that a reproductive role is also of importance. For example, there is marked sexual dimorphism of the first chela spine which appears to be related to sexual maturity. In females, the first chela spine exhibits strong positive allometric growth at sizes below 39.0 mm FCW and shifts to isometry at sizes above 39.0 mm FCW, with a marked increase in the relative height. As females become sexually mature at sizes above 39.0 mm FCW (Chapter 5), this strongly suggests that sexual maturity and chela spine height are correlated. The analysis of the moult stages of *M. lunaris* indicate that the female puberty moult occurs around the 38.0 - 40.0 mm size range (Chapter 6). Similar examples of high positive allometry at the prepuberty phase and considerable size increases at the puberty moult are common in

brachyurans (review by Hartnoll, 1982). This serves to bring an organ to a functional size at maturity whilst minimizing the waste of resources which could have resulted had they been at a large size in the immature instars (Hartnoll, 1974). The positive allometry of the female chela spine strongly contrasts with the negative allometry of the male chela spine. This suggests that the spine plays a more important role in females than in males. The function of the chelae spine is unclear, although it may be related to the reproductive behaviour of *M. lunaris*, where males typically grasp the chelae of the immature females during precopulatory attendance. It is probable that the first chela spine in female *M. lunaris* distinguishes a sexually mature female from an immature one. Such a distinguishing feature would prevent the male from grasping unnecessarily with a female which has presumably already mated with another male.

In addition, there are two morphological features of the chela which are found only in adult males: a) a ribbing on the dorsal aspect of the dactylus (Figs. 3.2, 3.12) and b) the lateral migration of the penultimate tooth on the propodus (Fig. 3.12). As with the chela spine in the females, these features appear to be related to sexual maturity as these are only present in adult males. The lateral migration of the penultimate tooth of the propodus is interpreted as a means of accommodating the chela of the female during grasping, without crushing or causing any damage.

The ribbing on the dorsal aspect of the dactylus of male *M. lunaris* has been previously referred to as an accessory stridulating organ (Guinot-Dumortier & Dumortier, 1960, 1961). The

function of the accessory stridulating organ in *M. lunaris* is unknown, although as a male secondary sexual characteristic (Guinot-Dumortier & Dumortier, 1960, 1961 and this study), it is likely to have some role in the reproductive biology of the species. Hilgendorf (1869, in: Guinot-Dumortier & Dumortier, 1960) has observed large male *M. lunaris* to produce a different stridulating sound using the ribbing on the dactylus. In this study, however, it has not been observed to be used for stridulation. Further investigations on the behavioural basis of the accessory stridulating organ are therefore recommended.

Both sexes possess two pairs of primary stridulating organs on the propodus which rub against the tubercules on the pterygostomian region of the body. The function of this stridulating organ in *M. lunaris* is also unknown although Dumortier (1960) has suggested that it is used to produce a protest sound similar to those made by insects in response to any excitation or in the presence of danger. However, there has been no indication of the potential benefits of this behaviour. In this study, *M. lunaris* has been observed to stridulate in aquaria particularly when other individuals are encountered. It is, therefore, suggested that stridulation in *M. lunaris* may be related to social behaviour, for example, spacing between individuals, in the turbid environment of the surf zone where the efficiency of visual signals are reduced.

3.4.1.3 The abdomen

The growth patterns of the abdomen and its associated structures in *M. lunaris* demostrate true sexual dimorphism. In females, the abdomen is broad and exhibits strong positive allometry throughout ontogeny with a pronounced increase in relative width at the onset of maturity. The length of the first pleopod also increases allometrically during development although at the onset of maturity, the level of allometry decreases. In males, the abdomen is narrow and also exhibits positive allometry throughout ontogeny but with only a slight increase in size at at the onset of maturity. The pleopod length is positively allometric before maturity and becomes isometric at puberty. Both sexes exhibit isometry in thoracic width throughout ontogeny.

Allometry and sexual dimorphism of the abdomen is well documented in brachyuran crabs (*e.g.* Ryan, 1967c, Barnes, 1968, Haley, 1973, Hartnoll, 1974, 1982, Finney & Abele, 1980 and Paulraj *et al.*, 1982). In *M. lunaris*, the sexual dimorphism of the abdomen appears to be related to the difference in the function of the male and female pleopods. In males, the abdomen shows only a slight degree of positive allometry, presumably as it serves only to cover and support the pleopods which act as intromittent organs during copulation. The positive allometry of the pleopod before maturity serves to bring the organ to a functional size at puberty. However, upon maturity, the advantages to be gained by a further increase in relative length is minimal as it decreases the ability of the male to mate with a wide size range of females (Hartnoll, 1974). In *M. lunaris*, this may account for the change to isometry in pleopod

length relative to carapace width and abdominal width at the onset of maturity.

The relative growth of the abdomen in female *M. lunaris* adheres to the general brachyuran trend of strong positive allometry relative to carapace width. The possession of a large abdomen at maturity is advantageous as it serves as a cover to facilitate the fixation of eggs to the pleopods and acts as a protective incubatory chamber (Hartnoll, 1974). In addition, a larger abdomen increases the capacity for carrying eggs and thus increases the potential reproductive fitness, as observed in *Trapezia ferruginea* where the number of eggs borne by a female is exponentially related to abdomen size (Finney & Abele, 1980).

As the abdomen can only function together with the thoracic sternum, any further disproportionate increase after maturity would reduce the efficiency of the mechanism and would make walking difficult (Hartnoll, 1982). This may account for the observed isometry of the abdomen width relative to thoracic width at the onset of maturity in female *M. lunaris*. A similar trend has also been observed in *T. ferruginea* (Finney & Abele, 1980).

3.4.2 General considerations

Matuta lunaris is, in many ways, a typical brachyuran in its form and function. It does, however, possess several unique morphological features which appear to be adapted to the surf zone environment, these include: 1) four pairs of well developed swimming legs with paddle-like dactyli segments which are also used for digging into the substratum (Hale, 1927 and Warner, 1977), 2)

frontal openings of the inhalent channel to the gill chamber which enables the crab to respire when buried in the substratum (Hale, 1927), 3) a finely spotted pattern on the carapace which resembles the sandy substratum and 4) stridulatory organs which may be a means of communication in a turbid environment.

The analysis of relative growth patterns and the functional interpretations of the 15 morphological characters selected in this study, have shown variations which appear to be related to size, sex and sexual maturity. Sex-related variations were primarily found in the relative growth patterns of the abdomen and its associated structures and in some chela characters. This results in considerable sexual dimorphism. In crabs, sexual dimorphism reflects the different reproductive roles of the two sexes and facilitates recognition of the opposite sex (Warner, 1977). In aquatic species, mating is primarily mediated by chemical signals, *i.e.* pheromones, although this may also be reinforced by tactile stimuli (Hartnoll, 1969). Sexual recognition is particularly important in crabs like *P. crassipes* and *Dotilla mictryoides* where agonistic behaviour is often used as a basis for courtship and it is necessary for the male to distinguish a receptive female from an aggressive male to avoid unnecessary antagonism (Bovbjerg, 1960 and Schöne, 1968). Likewise, this may be important in *M. lunaris*. As the female puberty moult precedes copulation in *M. lunaris*, it is also important for the male to distinguish an immature pre-ecdysic female from a mature post-ecdysic one in order to minimise unproductive encounters. This recognition may be facilitated by the presence of the relatively long chela spine in mature females. The chela spine probably makes grasping difficult for the male as it is

present in the region where the male typically grasps the chela of the female. The abdomen and its related structures are not directly involved in courtship and in this case, sexual dimorphism is directly related to the differences in the function of the reproductive organs of males and females following the typical brachyuran pattern.

Sexually dimorphic characters and secondary sexual characteristics often result in taxonomic confusion with male and female or immature and mature individuals of the same species being described as separate species or subspecies (Mayr, 1969). In decapod crustaceans, this has been reported in the Porcellanidae (Sankolli, 1967) and in the Portunidae (Stephenson, 1967). In *M. lunaris*, adult male and female crabs and immature individuals have been described as separate species. Miers (1877) described immature ones as *M. lunaris*, adult males as *M.victrix* and adult females as *M.victrix* var. *cerebrepunctata*. This confusion resulted from the use of the number and height of chela spines as basis for species identification.

Size-related, *i.e.* ontogenetic, variations were found in the relative growth patterns of most of the chela dimensions. This results in considerable differences in the functional capabilities of the chelae, as outlined above. In smaller individuals, the chelae appear to be adapted for tearing and cutting whilst in large individuals, the chelae appear to be adapted for crushing (following the observations of Brown *et al.*, 1979 on other species of decapod crustaceans). It is likely that these differences in the functional morphology of the chelae will influence the feeding habits of

M. lunaris and will therefore be reflected in the diet. It has been suggested that comparable changes in chela morphology are responsible for ontogenetic dietary changes in *C. sapidus* (Laughlin, 1982). In order to assess the relationship between chela morphology and feeding in *M. lunaris*, it is therefore necessary to examine the composition of its natural diet. This aspect will be considered in Chapter 4.

CHAPTER FOUR

Feeding Biology

4.1 Introduction

There have been very few published accounts on the feeding biology of *Matuta lunaris*. Previous works were limited to behavioural observations (Seiler, 1976) and records of predation (Ozawa, 1981). Both of these studies, however, were restricted to populations in Japan. Seiler (1976) suggested that *M. lunaris* is a herbivore as it was observed to catch plant materials brought by incoming waves whereas Ozawa (1981) reported *M. lunaris* as one of the major predators of *Suchium monliferum*, a marine gastropod. Apart from these, nothing is known of the natural diet of *M. lunaris*.

The aim of this study is to examine the composition of the natural diet of *M. lunaris* from Pallarenda beach, Townsville, Australia with particular attention to variations in the diet during ontogeny.

4.2 Methods

M. lunaris was collected from Site 'B' (Plate 2.1) at Pallarenda beach on June 17 and July 17, 1984. The crabs were caught using a 10 m x 1 m beach seine net as described in Chapter 2. The crabs were placed in polythene bags packed in ice immediately after capture and were transferred to 10% s.w. formalin within two hours. The carapace was opened to ensure rapid fixation of the stomach and its contents.

A total of 163 crabs were examined. The carapace width and sex of each crab was recorded and the stomach removed. The percentage fullness was estimated for each stomach. The stomach contents of all crabs were examined but only crabs with stomachs more than 25% full were used in the analysis. Williams (1981) recommended a sample size of approximately 30 crabs with at least 50% gut fullness as adequate for a description of natural diet in portunids. In this study, however, stomachs which were at least 25% full still contained most food categories and were therefore included.

In *M. lunaris*, mastication of food by the mouthparts and gastric mill made actual counts and volumetric determinations of food items difficult. Stomach contents were therefore analysed using percentage occurrence and percent points following Williams (1981). The stomach contents were examined in 70% alcohol under an Olympus stereomicroscope. The occurrence of each food type was recorded and, where possible, identified to the generic level. In most cases, however, the stomach contents were too macerated to enable identifications beyond major groupings. In the analyses of results, food items were grouped into major taxonomic categories, *e.g.* Crustacea, Mollusca, etc. and were awarded points on a base 2 logarithmic scale (*i.e.* 1, 2, 4, 8, etc.) based on their estimated volume, following Williams (1981).

The general composition of the natural diet was examined based on the diet of all individuals in the sample. In addition, crabs were grouped into 5 mm full carapace width (FCW) size classes in order to assess ontogenetic changes in the diet. The following variables were calculated for the whole sample and each size class,

following the equations given by Williams (1981):

1) Percent occurrence of each food category:

$$\% \text{ occurrence of food category '}i\text{'} = \frac{b_{ij}}{n_j} \times 100$$

where b is the number of crabs in size class 'j' with stomachs containing food category 'i', and n is the total number of crabs with >25% fullness in size class 'j'.

2) Percent point score of each food category:

$$\% \text{ points of food category '}i\text{'} = \frac{\Sigma a_{ij}}{A_j} \times 100$$

where a is the number of points awarded to food category 'i' in size class 'j', and A_j is the total number of points awarded to all food categories in all crabs in size class 'j'.

3) Percent occurrence of specific food items under the most common food category:

$$\% \text{ occurrence of specific food item '}m\text{'} = \frac{c_{mj}}{b_{ij}} \times 100$$

where c is the number of crabs in size class 'j' with stomachs containing the specific food item 'm', and b is the number of crabs in size class 'j' with stomachs containing food category 'i' which includes the food item 'm'.

4.3 Results

The mean number of food categories found in stomachs of varying degrees of fullness is summarized in Table 4.1. There were no notable difference in the mean number of food categories in stomachs which were greater than 25% full. Of the 163 crabs examined, 131 crabs had a stomach fullness greater than 25% and were therefore used in the analyses. Stomach contents were typically finely fragmented and the identification of most food categories were based on remnants found in the stomach. Brief descriptions of the types of remnants used to identify each food category are given in Table 4.2.

4.3.1 Diet Composition

The diet of *M. lunaris* is composed mainly of crustaceans, molluscs, sand and unidentified organic matter. Fish, algae and seagrass remnants were also found in the stomach contents but these were of minor importance (Table 4.3a) with particularly low percentage point scores. Of the four main food categories, Crustacea had both a high frequency of occurrence and a high percentage point score (Table 4.3a) with anomurans and sergestids being the predominant taxa (Table 4.3b). Mollusca also had high frequency of occurrence and percentage point score (Table 4.3a) with the most common taxa being the bivalves (Table 4.3b). A list of those food items identifiable to the generic or species level is given in Table 4.4. Unidentified organic matter also occurred frequently in the diet and had a relatively high percentage point score although it is thought to be often of molluscan origin, *i.e.* the soft bodies of the bivalves which were scored under the Mollusca

Table 4.1 The distribution of % stomach fullness in the sample population.

% stomach fullness	no. of crabs	mean number of food categories	S.E.
75 - 100	72	3.46	0.1340
50 - 74	47	2.98	0.1505
25 - 49	12	3.17	0.2071
1 - 24	9	1.78	0.1469
0	23	-	-

Total no. of individuals = 163

Table 4.2 A description of food categories based on the types of remnants found in the stomach contents of *M. lunaris*.

Food Category	Type of remnants
CRUSTACEA	
Brachyura	Pieces of carapace and various appendages
Paguridae	Hermit crab cephalothorax, telson, uropods and various appendages
Penaeidae	Pieces of carapace, antennae and eyes
Sergestidae	Whole bodies, head and appendages
Copepoda/Amphipoda	Whole bodies
MOLLUSCA	
Bivalvia	Crushed pieces of shell
Gastropoda	Opercula and pieces of shell
TELEOSTEI	Scales and bones
ALGAE	Small filaments and groups of cells
SEAGRASS	Small pieces of leaf blade
SAND	
ORGANIC DEBRIS	

Table 4.3a A summary of the diet composition of *M. lunaris*.

Food Category	% occurrence	% point score
CRUSTACEA	71.7	34.8
MOLLUSCA	66.4	29.6
TELEOSTEI	3.8	0.9
ALGAE	22.9	1.9
SEAGRASS	11.4	0.7
SAND	76.3	13.8
ORGANIC DEBRIS	54.9	18.1

Table 4.3b Details of the composition of the two most important food categories in the diet of *M. lunaris*.

Food Category	% occurrence
Crustacea	
Paguridae	57.4
Sergestidae	32.9
Penaeidae	10.6
Brachyura	8.5
Copepoda/Amph.	6.3
Mollusca	
Bivalvia	82.76
Gastropoda	17.24

Table 4.4 A summary of the species identifications of several food categories in the diet of *M. lunaris*.

CRUSTACEA

Paguridae

Diogenes sp.

Sergestidae

Ascetes sp.

Penaeidae

Penaeus sp.

Brachyura

Matuta lunaris

MOLLUSCA

Bivalvia

Electroma sp.
Tellina australis
Mactra sp.
Dosinia sp.
Laternula sp.

Gastropoda

Isanda coronata

ALGAE

Rhodophyta

Ceramium

SEAGRASS

Halodule

food category based on their shell remnants. In this study, sand had the highest frequency of occurrence but had a limited percentage point score.

4.3.2 Variation with sex

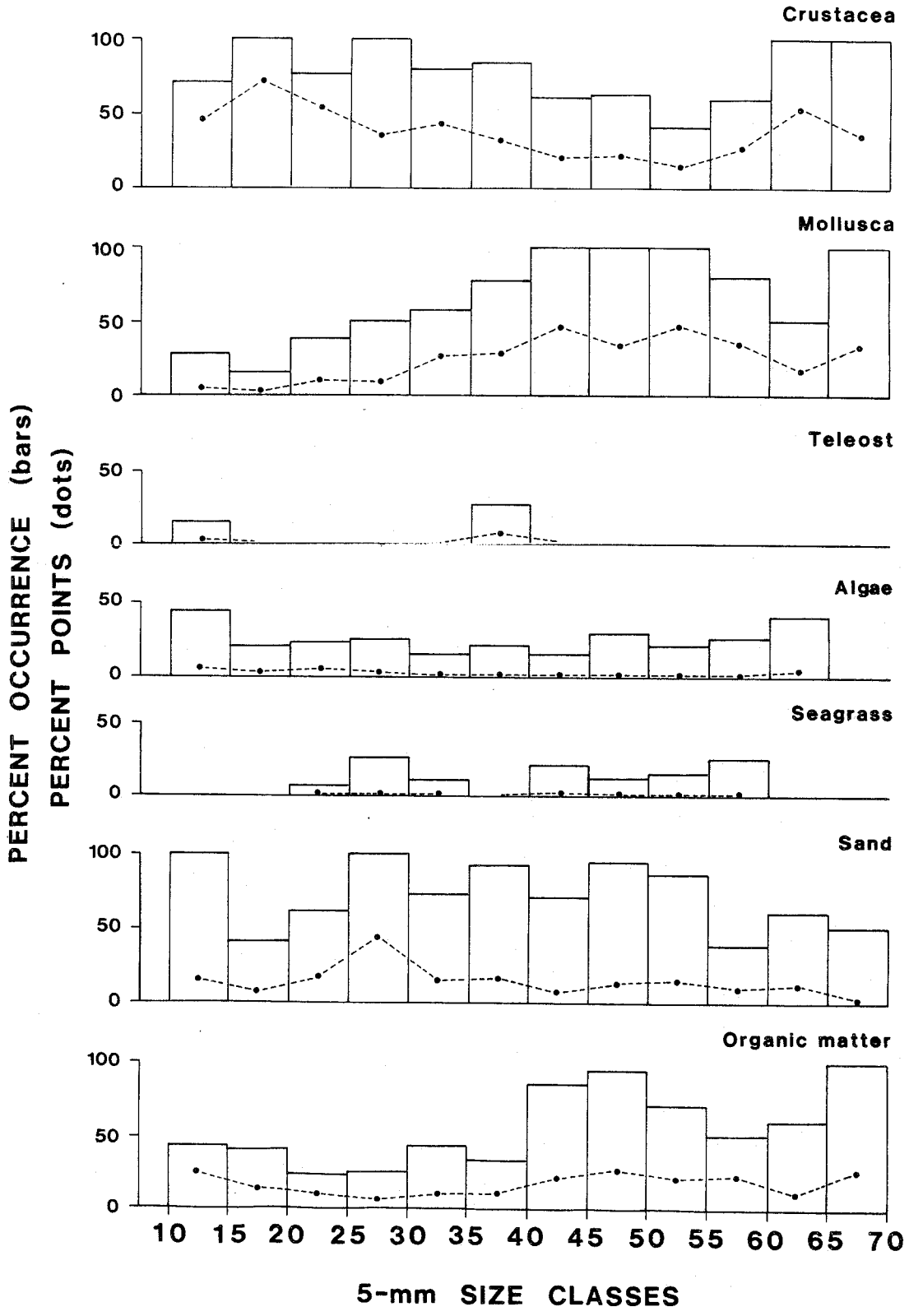
Preliminary analyses of stomach contents showed no apparent differences in the diet composition between male and female *M. lunaris* as all food categories were found in the stomach contents of both sexes in comparable frequencies. Feeding data from both sexes were therefore pooled in the subsequent analyses.

4.3.3 Ontogenetic variation

Most food categories were found in all size classes except for the teleosts and seagrass (Fig 4.1). Crustacea occurred with high frequency and with consistently high percentage point scores throughout the size range, with the exception of a slight decrease between 40.0 and 60.0 mm FCW. Mollusca were consistently present throughout the size range with a higher frequency of occurrence and percentage point scores in larger size classes. Algae were found in consistently low frequencies and with a very low percentage point score in all size classes. Sand occurred in high frequencies throughout the size range but with relatively low percentage point scores. Unidentified organic matter was found in all size classes. Higher frequencies of occurrence were recorded in the larger size classes but percentage point scores were consistently low. The frequency of occurrence of teleosts in the diet was very low as it was found only in 4 out of 131 stomach contents analysed in this study. Seagrass was only recorded in the stomach contents of

Figure 4.1

The diet composition of *M. lunaris* in 5-mm size classes, expressed as percent occurrence (bars) and percent points (dots) for each food category.


Crustacea
Mollusca
Teleost
Algae
Seagrass
Sand
Organic matter
100
50
0
PERCENT OCCURRENCE (bars)
PERCENT POINTS (dots)
10 15 20 25 30 35 40 45 50 55 60 65 70
5-mm SIZE CLASSES

several intermediate-sized individuals with low frequencies of occurrence and very low percentage point scores.

Analyses of the crustacean food items has shown changes in the frequencies of occurrence of certain taxa with size. Sergestid shrimps occurred at higher frequencies in the stomach contents of the smaller size classes whilst hermit crabs occurred at higher frequencies in the larger size classes (Fig 4.2). A similar trend was found in the occurrence of less common taxa, with harpacticoid copepods and gammarid amphipods being recorded mainly from the stomach contents of the smaller crabs whilst brachyurans and penaeid prawns were found more frequently in larger crabs.

There appears to be a gradual size-related increase in the frequency of occurrence and relative importance based on percentage point scores of Mollusca in the diet. Throughout the size range, the main molluscan taxa recorded were the bivalves although there appeared to be some change in the species composition between size classes (Fig. 4.3). Gastropods were found only in the stomach contents of larger size classes. Some gastropod remnants may have been the result of predation on hermit crabs, although the presence of opercula suggest that gastropods *per se* were ingested.

4.4 Discussion

There is no generally accepted methodology for assessing the diet of brachyuran crabs. The most common methods used in the analyses of stomach contents have included percentage occurrence (Hill, 1976, 1979, Patel *et al.*, 1979, Paul *et al.*, 1979, Paul, 1981 and Williams, 1982), percentage points (Hartnoll, 1963 and Williams,

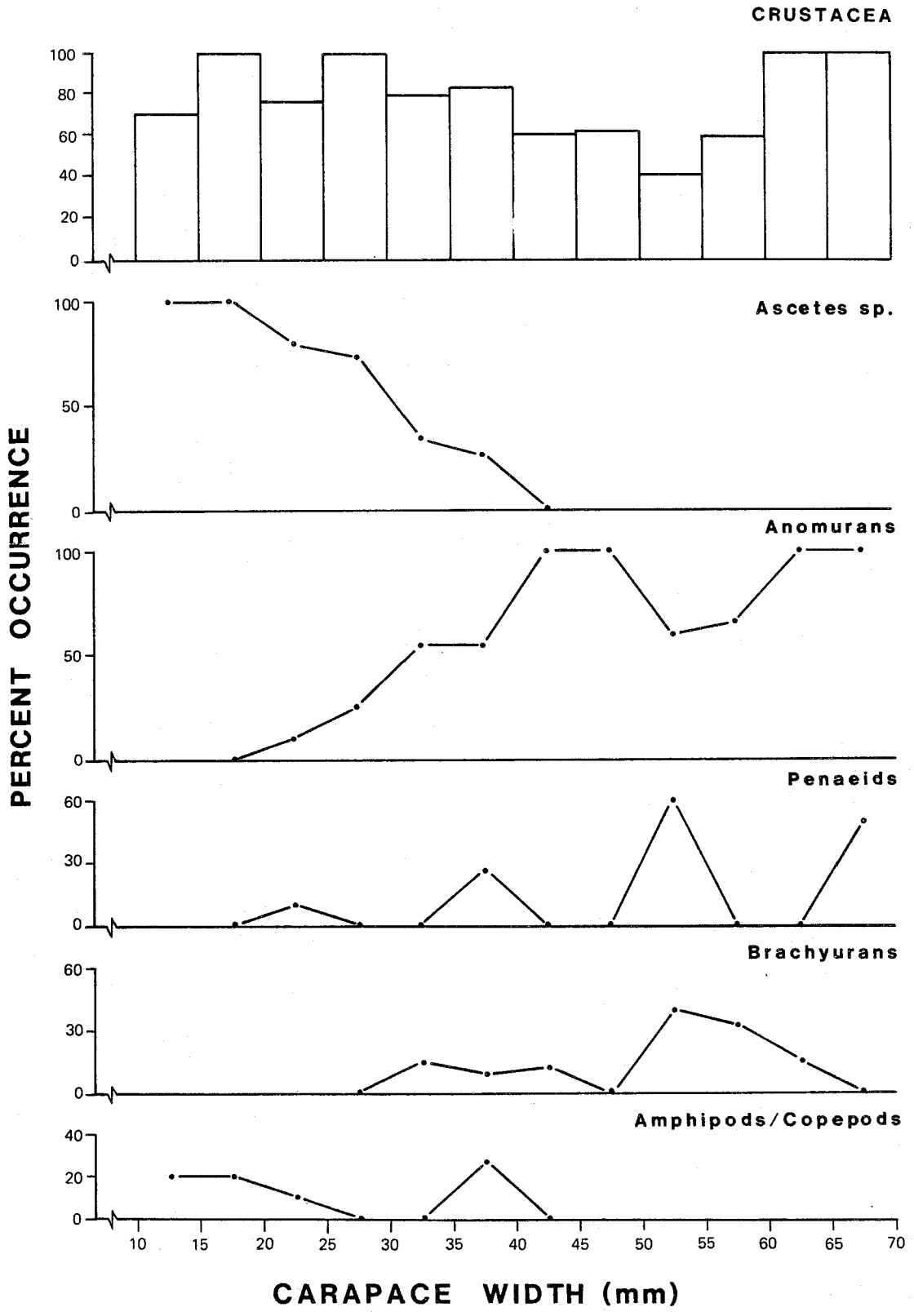
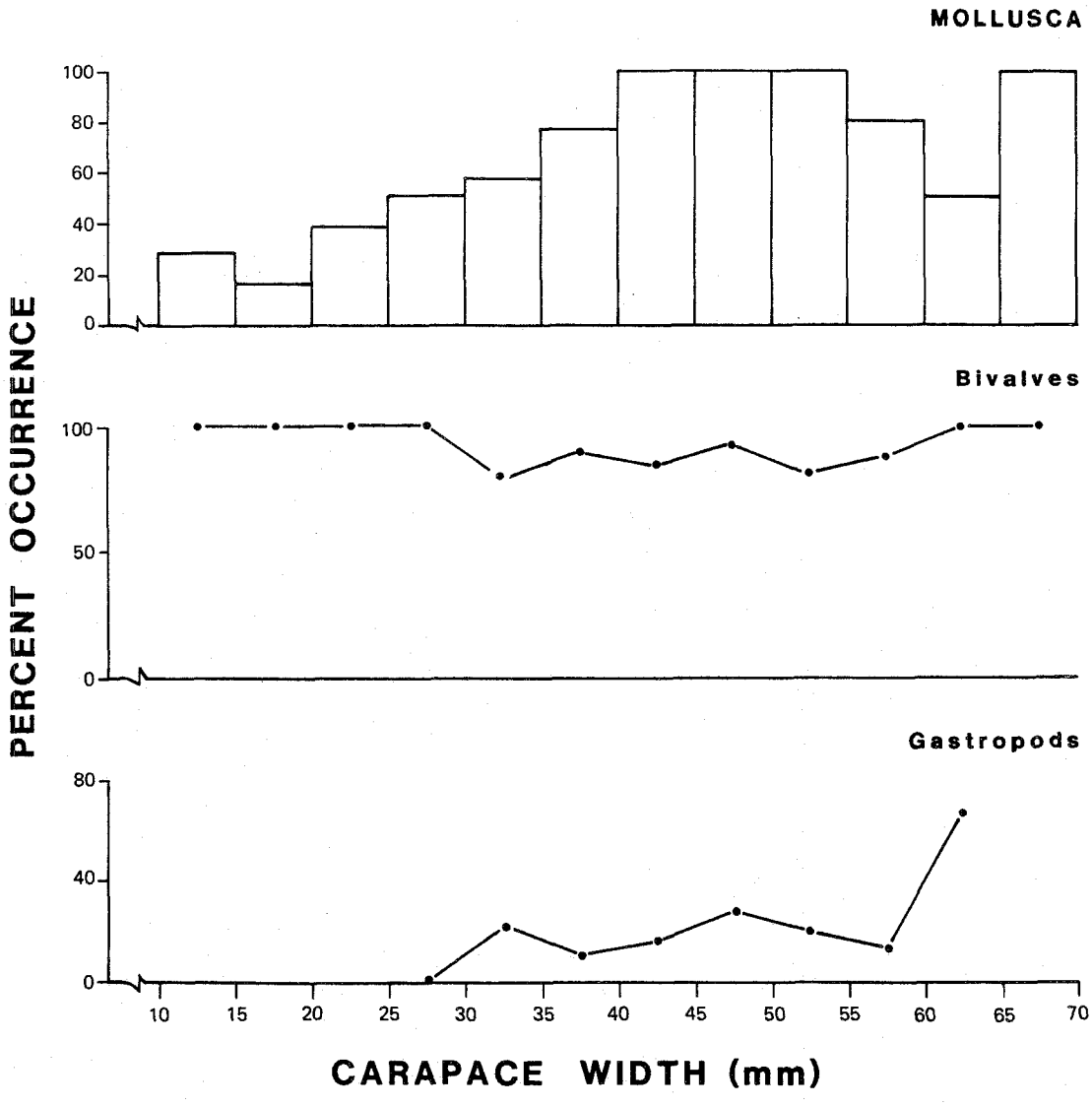

CRUSTACEA
100
80
60
40
20
0
Ascetes sp.
100
50
0
Anomurans
100
50
0
Penaeids
60
30
0
Brachyurans
60
30
0
Amphipods/Copepods
40
20
0
PERCENT OCCURRENCE
10
15
20
25
30
35
40
45
50
55
60
65
70
CARAPACE WIDTH (mm)

Figure 4.3

Details of the molluscan component in the diet of *M. lunaris* during ontogeny, expressed as the percent occurrence of specific food items.


MOLLUSCA
100
80
60
40
20
0
Bivalves
100
50
0
Gastropods
80
40
0
PERCENT OCCURRENCE
10
15
20
25
30
35
40
45
50
55
60
65
70
CARAPACE WIDTH (mm)

1981) and gravimetric analyses (Paul, 1981 and Laughlin, 1982). Fine fragmentation of food items as a result of mastication by the mouth parts and gastric mill and the rejection of some hard parts prior to ingestion, in most cases, make numerical and volumetric determinations difficult (Williams, 1981). In this study, the relatively small stomachs of *M. lunaris* and the finely fragmented nature of the stomach contents precluded any accurate gravimetric, volumetric and numerical analyses. Analyses were therefore based on the occurrrence and point methods.

The points method reflects the relative importance of food items based on their estimated volumes but it tends to underestimate food items possessing soft parts which are often unrecognizable after ingestion, *e.g.* large bivalves without their shells (Williams, 1981). The occurrence method reflects the frequency of inclusion of a food item in the diet but it tends to overestimate the importance of items occurring regularly but only in small quantities, *e.g.* sand. The problems and advantages of the occurrence and point methods and other techniques have been discussed in detail by Hynes (1950) and Hyslop (1980) and briefly by Christensen (1978) based on the analyses of the diet of fishes, and by Williams (1981) based on the analyses of the diet of portunid crabs. However, despite the problems of the occurrence and points methods, when used in combination, both methods do reflect the relative importance of the food items in the diet with the more important ones being ingested more frequently and in greater quantities.

The analyses of the stomach contents of *M. lunaris* indicate that it is almost exclusively carnivorous with crustaceans and molluscs representing the major constituents of its natural diet. Of the 131 crabs used in the analysis, 93 (71.7%) individuals had either sergestid shrimps or hermit crabs in the stomach contents, and in smaller quantities, copepods, penaeid prawns and brachyuran crabs. Cannibalism of small individuals was recorded only in three specimens. Unlike *Callinectes sapidus* (Laughlin, 1982), *Callinectes arcuatus* and *Callinectes toxotes* (Paul, 1981), *M. lunaris* does not consume its own exuviae after a moult, 22 moults having been observed in captivity and exuviae are present in the intertidal region. The stomach contents of 87 (66.4%) individuals also contained mollusc remains which consisted mainly of several bivalve species. Gastropods formed only a small proportion of the diet of *M. lunaris* buttheirinclusion is consistent with the observations of Ozawa (1981) who reports *M. lunaris* as a major predator of *Suchium monilliferum*, a marine gastropod in Japan. The crustacean and molluscan components of the diet were probably the result of predation as these food items were abundant in the sampling area and consistently occurred in the diet.

Remains of large and fast-moving organisms such as fish and penaeid prawns were uncommon in the stomach contents of *M. lunaris*. This suggest that *M. lunaris* is not a predator of highly mobile organisms. Crabs maintained in aquaria together with live fish and prawns did not attempt to catch them although in several instances, weak and injured fishes were immediately caught and eaten. The results of this study indicates that whilst *M. lunaris* is capable of killing weak and injured fish, the teleost and penaeid components in

its diet are probably obtained from scavenging on dead fish and prawns which are occassionally washed up in the surf zone. Similar observations have been found in other brachyurans such as *Scylla serrata* (Hill, 1976), *C. arcuatus* (Paul, 1981), and juvenile *Portunus pelagicus* (Williams, 1982) and *C. sapidus* (Laughlin, 1982).

Plant materials, *i.e.* algae and seagrass were not frequently found in the stomach contents and when found, only occurred in small quantities. Although Seiler (1976) observed *M. lunaris* eating plant materials, it is not known whether *M. lunaris* selectively feeds on plant material or it is merely feeding on the epiphytes associated with the plant, *e.g.* some bivalves. Accidental ingestion of plants has been reported in other carnivorous crabs, including *C. arcuatus* (Paul, 1981) and *P. pelagicus* (Williams, 1982). It is probable that plant materials are not selectively eaten but are accidentally ingested with other food items. It remains to be established whether *M. lunaris* can digest plant material. The low frequency of occurrence of plant materials suggests that plants were only of limited importance in the diet of *M. lunaris*.

Small quantities of sand are frequently found in the stomach contents of *M. lunaris*. It is probable that the presence of sand in the stomach contents is the result of incidental ingestion of sand during feeding with its relative importance being overestimated by the occurrence method. Utilization of the organic matter found on sand grains as observed in many benthic crustaceans including brachyurans (Grahame, 1983), however, is thought to be unlikely in *M. lunaris*. Soft, newly-moulted individuals of *S. serrata* (Hill, 1976) and *P. pelagicus* (Williams, 1982) have been reported to ingest

sand and calcareous particles in the early post-moult condition probably as a source of calcium for hardening of the new exoskeleton. In this study, however, no newly-moulted individuals were included in the analyses as all their stomachs were invariably less than 25% full.

These observations on the natural diet of *M. lunaris* suggest that it is primarily a carnivorous predator of crustaceans and molluscs. The rare occurrence of large, fast-moving organisms suggests that it is also a facultative scavenger. Sand and algae are of limited significance in the diet and are probably only accidentally ingested during feeding.

The diet of *M. lunaris* changes considerably during ontogeny. Although all major food categories were present in the stomach contents of all size classes, there were marked changes in their proportions and in the taxa which comprised these categories. Smaller individuals tended to feed predominantly on sergestid shrimps and copepods, whereas larger individuals fed primarily on hermit crabs, brachyurans and penaeid prawns. Bivalves and gastropods were also consumed in higher frequencies by larger individuals than small individuals with the species composition of bivalves in the diet becoming more varied in the larger size classes. These dietary changes suggest that the feeding strategy of *M. lunaris* changes from that of a predator of small epibenthic invertebrates at small sizes to that of a predator of sessile or slow-moving species at large sizes. *M. lunaris* is also a facultative scavenger throughout ontogeny.

Ontogenetic changes in the diet have also been reported in other brachyurans, including *Carcinus maenas* (Ropes, 1968), *C. sapidus* (Laughlin, 1982), *C. arcuatus* and *C. toxotes* (Paul, 1981), and in other organisms including fish (Helfman, 1978) and amphibians (Christian, 1982). Several factors may lead to changes in the diet during ontogeny. Firstly, life history cycles may place certain size classes in different habitats with different available food items. An example of this is *P. pelagicus*, where small individuals live in the intertidal region but larger individuals live in the subtidal region (Williams, 1982). However, this was not observed in *M. lunaris* as all size classes are present in the surf zone at all times of the year (Chapter 7). Secondly, ontogenetic changes in the functional morphology of the feeding apparatus have been found to affect the feeding habits of several organisms including *C. sapidus* (Laughlin, 1982) and some species of fish (Stoner & Livingston, 1984). In *M. lunaris*, several non-puberty related ontogenetic changes have been found in the relative growth pattens of the chelae. These changes alter the functional abilities of the chelae and are likely to influence the feeding biology of crabs in various size classes. At small sizes, the chelae of *M. lunaris* are adapted for tearing and cutting food, whereas at larger sizes, the chelae are adapted for crushing (Chapter 3). The ontogenetic change in the diet composition strongly correlates with these functional changes, with small and relatively soft crustaceans being fed upon by small individuals, and slow-moving shelled prey being fed upon by large individuals. Similar dietary characteristics which are related to chelae function have been shown in *C. maenas* (Elner, 1978) and *C. sapidus* (Blundon & Kennedy, 1982).

The diet of *M. lunaris* therefore appears to be dependent upon the functional ability of the chela at a given size.

Overall, in terms of its dietary composition, *M. lunaris* is a typical calappid, with the major food items in its diet consisting of various crustaceans and molluscs. In the tropics, calappids, particularly those in the genus *Calappa*, are well known as highly specialized predators of hermit crabs and gastropods (Shoup, 1968, Reese, 1969, McLean & Mariscal, 1973, Miller, 1975, Zipser & Vermeij, 1978 and Vermeij, 1982). *Calappa* spp. possess a highly modified chela, with a large tooth at the base of the dactylus which enables the crab to crush mollusc shells (Shoup, 1968). However, unlike *Calappa* spp., *M. lunaris* has a less specialised chela form which lacks this specialised tooth. This suggests that in terms of feeding, *M. lunaris* is less specialised.

As a predator of slow-moving benthic invertebrates, *M. lunaris* may influence the abundance and distribution of its prey items. The role of brachyurans in the regulation of prey populations has been noted in several other species for instance: *Cancer pagurus*, *Portunus puber*, *C. maenas* (Kitching, *et al.*, 1959 and Muntz, *et al.*, 1965), *C. sapidus* (Virnstein, 1977) and *Panopeus herbstii* (Seed, 1980). The numerical abundance of *M. lunaris* in the surf zone and its carnivorous diet therefore suggest that *M. lunaris* is likely to play an important role in the ecology of tropical sandy shores.