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The taxonomy and biology of fishes of the genus *Parapercis* (Teleostei: Mugiloididae) in Great Barrier Reef waters

Thesis submitted by

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RESUBMISSION

This thesis was lodged for resubmission on September 6, 1984 after certain modifications suggested by the examiners had been carried out

G.J. Stroud

ABSTRACT

This study was initiated as an investigation into the taxonomy and biology of fishes of the mugiloidid genus *Parapercis* from the Great Barrier Reef Province.

Nine species of *Parapercis* were found to inhabit Great Barrier Reef waters: *Parapercis cylindrica*, *P. hexophtalma*, *P. cephalopunctata*, *P. clathrata*, *P. xanthozona*, *P. nebulosa*, *P. diplospilus*, *P. snyderi*, plus one undescribed species. Detailed descriptions and a key to these species are presented.

The habitats in which *Parapercis* are most commonly encountered and the pattern of species occupancy within each of these habitats are described along with seasonal patterns of abundance.

The interrelationships between the morphology of the alimentary tract, the food taken, and feeding behaviour were investigated. A division was made into three groups, namely (1) small crustacean, algal, and polychaete feeders; (2) polychaete, large crustacean, and small crustacean feeders; and (3) large crustacean and fish feeders. All species are diurnal and utilize specialized feeding strategies in which vision plays a key role.

The social behaviour and organization of *Parapercis cylindrica* was investigated in detail. The basic social unit in this species is a harem consisting of a single male, two or three adult females, and a variable number of subadult females. Within each harem, individuals are arranged into a very stable, size-dependent, linear dominance hierarchy with the male always highest in status. Each female of the harem holds a relatively permanent territory which is defended against equivalent-sized or smaller females. The male maintains a permanent territory which encompasses all the territories of his females, and which he defends against other males. He also visits and aggressively interacts with each female of his harem at frequent, essentially regular intervals throughout the day. Motor patterns associated with male-male and male-female agonistic encounters are described. When the male dies, the dominant (largest) female of the harem changes sex and assumes control of the harem, provided she is large and aggressive enough to resist invasions of the harem by neighbouring males.

Parapercis cylindrica has a polygynous mating system and a male mates almost exclusively with the females of his harem. Motor patterns associated with courtship and spawning are described. Reproductive activity takes place every day and is restricted to the evening crepuscular period. It is suggested that the combination of strong site attachment, lack of mobility and clumped distributions of females, in creating a potential for mate monopolization by large males, has led to the development of the haremic social/mating system in this species.

Spawning activity in *P. cylindrica* is essentially restricted to between August and March each year although some harems spawn the year round. Settlement of juveniles of *P. cylindrica* and most other *Parapercis* species peaks in November each year. Evidence for the year round presence of juveniles was obtained for all species but *P. hexophtalma*.

Parapercis cylindrica, *P. hexophtalma*, *P. clathrata*, *P. xanthozona*, *P. nebulosa and P.* sp. 1 are monandric protogynous hermaphrodites. Each with the exception of *P. nebulosa*, is sexually dichromatic. Sex reversal in *P. cylindrica* is under social control and is completed approximately 20 days after the time of its initiation. The adaptiveness of protogynous sex reversal and its relationship to the social system in *P. cylindrica* is discussed.

DECLARATION

I declare that this thesis is my own work and has not been submitted in any form for another degree or diploma of any university or other institute of tertiary education. Information derived from the published or unpublished work of others has been acknowledged in the text and a list of references is given.

G. J. Stroud

June 1982

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PART I

TAXONOMY

INTRODUCTION

Mugiloidid fishes of the genus *Parapercis*, the so-called "weeverfishes" or "sand-weevers", are elongate, percoid fishes of small to moderate size which are essentially restricted to the tropical and temperate regions of the Indian and Pacific oceans. They are characteristically demersal and occur in both shallow inshore and deep offshore waters. Although most species are of little commercial value, a few are known to provide important sources of food in some countries (Fourmanoir, 1957; Munro, 1967; Kuronuma and Abe, 1972; Rau and Rau, 1980).

In addition to *Parapercis* Bleeker (1863), Cantwell (1964) recognized two other genera within the family Mugiloididae, *Mugiloides* Lacépède (1803) and *Prolatilus* Gill (1865), but neglected to include *Kochichthys* Kamohara (1961). On the basis of osteological evidence, McDowall (1973) has also assigned the genus *Cheimarrichthys* Haast (1874) to the Mugiloididae.

Parapercis is by far the dominant genus in terms of species number and is the only mugiloidid genus found in Australian waters. Both *Mugiloides* and *Prolatilus* are confined to the eastern coast of South America and may be distinguished from *Parapercis* by their greater vertebral and fin ray counts. The sole representative of the genus *Kochichthys* is *K. flavofasciata* (Kamohara, 1936) from Japan, which differs from *Parapercis* in having fewer dorsal spines and the lower jaw much shorter than the upper. There is but a single species of *Cheimarrichthys*, the diadromous *C. fosteri* Haast (1874), which is endemic to New Zealand (McDowall, 1973) and the only species of non-marine mugiloidid. The non-protractile nature and inferior position of the mouth serve to distinguish this genus from *Parapercis*.

The present investigation arose from a study of the general biology and ecology of members of the genus *Parapercis* at Lizard Island, Great Barrier

Reef Province (see Part II), when taxonomic confusion, and certain descriptive inadequacies in the literature pertaining to this group, became evident.

Emphasis in this investigation has been placed on external morphological characters, which allow good separation of the species of *Parapercis* occurring within the Great Barrier Reef region. The following characters and their various combinations proved to be the most important diagnostically: (1) the number of oblique rows of scales crossing the lateral line, counting from the upper angle of the gill opening to the base of the caudal fin; (2) the number of scales in a zig-zag row around the least vertical depth of the caudal peduncle; (3) the spinous dorsal count, shape, and site of connection to the soft dorsal; (4) the pectoral fin count; (5) the presence/absence of palatine teeth; (6) the number of enlarged canines in the outer tooth row of the lower jaw (dentically intact specimens); and (7) the colour pattern.

Although most morphometric measurements show a great deal of interspecific overlap, some, such as length of longest dorsal spine, length of longest pelvic ray, and interorbital width, are still useful for species separation and/or defining species groups.

There is a tendency for some of the enlarged lower jaw canines to be lost, not only during the life of the fish but also on collection and/or handling thereafter. It is therefore unfortunate that Schultz's (1968) key, the most recent to the species of *Parapercis* of the Indo-Pacific region, relies almost entirely on this character to split the genus into main species groups. Such reliance has undoubtedly contributed to much of the existing confusion. Caution in the use of Schultz's key is recommended if (1) the dentition appears damaged in any way; (2) an odd number of canines is counted; or (3) distinct excavations which appear to have held enlarged canines, are present in the outer region of the lower jaw.

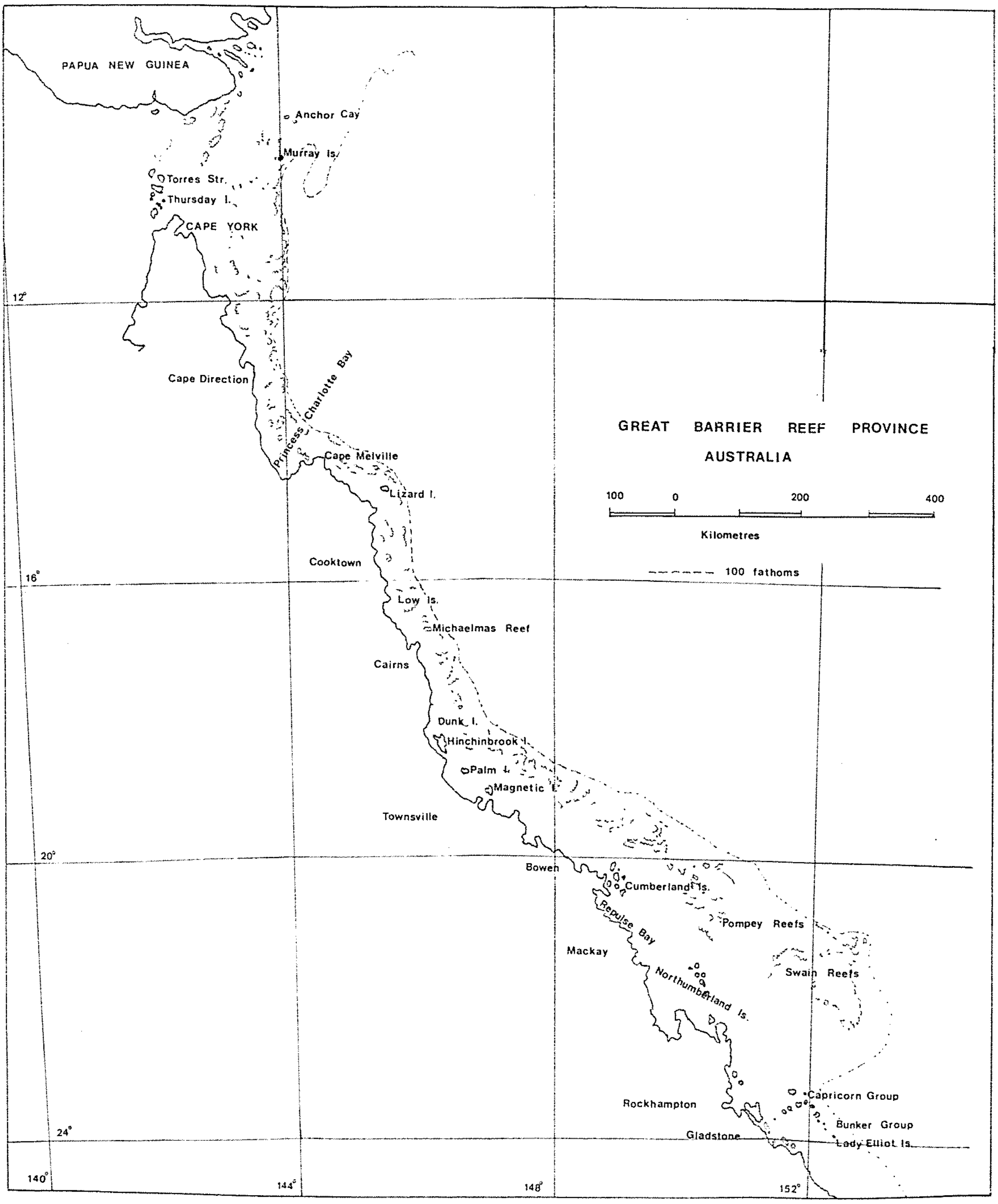
The colour pattern is invaluable in identifying members of the genus *Parapercis* in the field (i.e. underwater or freshly caught) and is also of great value when specimens are recently and/or well preserved. Some care must be exercised, however, when separating species by colour pattern alone since (1) poorly preserved specimens tend to fade quickly and in time lose most, if not all, of their colour pattern; (2) the colour pattern for some species varies with geographical locality; and (3) sexual dichromatism appears widespread amongst the members of this genus, particularly the tropical species. More than half the number of species of *Parapercis* examined in this study were found to be sexually dichromatic (see Part II). It seems probable that on closer inspection, additional cases of sexual dichromatism will be discovered amongst both tropical and temperate water members of this genus. Cantwell (1964), in revising the genus *Parapercis*, unfortunately overlooked sexual dichromatism within the group. Consequently, particular attention has been paid to description of colour patterns in the present study.

The term "Great Barrier Reef Province" as used throughout this study is defined (cf. Bennett, 1971) as the area lying between Anchor Cay (lat. 9°22'S) in the north, Lady Elliot Island (lat. 24°07'S) in the south, and bounded east and west by the edge of the Continental Shelf (which is considered as lying along the 100 fathom line) and the coast of the mainland, respectively (Fig. 1). The present review recognizes a total of nine species of *Parapercis* from this region. Additions to the known mugiloidid fauna of the Great Barrier Reef Province remain a distinct possibility, as exploratory sampling is lacking along much of the coastline and outer reefs, especially in depths greater than 70 metres.

The author recognizes a total of 19 species of *Parapercis* from Australian waters (11 of these from Queensland) and between 45 and 48 species on a world wide basis. To confirm the latter a world wide revision

Figure 1

Map of the Great Barrier Reef Province, Australia


GREAT BARRIER REEF PROVINCE
AUSTRALIA
100
0
200
400
Kilometres
100 fathoms
PAPUA NEW GUINEA
Anchor Cay
Murray Is.
Torres Str.
Thursday I.
CAPE YORK
12°
Cape Direction
Princess Charlotte Bay
Cape Melville
Lizard I.
Cooktown
16°
Low Is.
Michaelmas Reef
Cairns
Dunk I.
Hinchinbrook I.
Palm I.
Magnetic I.
Townsville
20°
Bowen
Cumberland Is.
Repulse Bay
Pompey Reefs
Mackay
Northumberland Is.
Swain Reefs
Rockhampton
Capricorn Group
Bunker Group
Gladstone
Lady Elliot Is.
24°
140°
144°
148°
152°

of *Parapercis* is needed and it is hoped that the present investigation, although regional, may provide a basis for more extensive treatment.

HISTORICAL RESUMÉ

Bloch (1792) was the first author to describe a member of the genus *Parapercis*, as a *Sciaena* species from an unknown type locality. Cuvier and Valenciennes (1829) made a comprehensive study of the genus *Parapercis* (ascribed by them to the genus *Percis*) and recorded 13 nominal species. Günther (1860), in a less detailed work, also listed 13 nominal species for the genus *Parapercis* (also ascribed to *Percis*). Bleeker (1863a) erected the genus *Parapercis* using *Sciaena cylindrica* Bloch as the type in a list of fishes from Ternate and, up to 1878, provided many short descriptions and records of *Parapercis* species from the East Indies and New Guinea. Taxonomic descriptions and records, usually only a few species at a time, constituted the remainder of the work on this genus prior to 1900.

Martin and Montalban (1935) and de Beaufort and Chapman (1951) gave excellent treatments of the Philippine and Indo-Australian Archipelago *Parapercis* species respectively. Jordan et al. (1913), Okada (1938), Kamohara (1960), and more recently Masuda et al. (1975), provided reviews of the group for Japan. Reviews on a regional basis were also given by Smith (1965) for Southern Africa, Munro (1955, 1967) for Ceylon and New Guinea, Fowler (1956, 1959) for China and Fiji, and Schultz et al. (1960) for the Marshall and Marianas Islands.

With regard to the Australian mugiloidids, McCulloch's (1914) paper on the "Endeavour" collection, which included a checklist and key to Australian species of *Parapercis*, is of major importance. Checklists of Australian mugiloidids were also given by McCulloch (1929) and Whitley (1964b). Some of the more important papers encompassing the genus

Parapercis on a regional basis include Ogilby (1911), McCulloch and Whitley (1925), and Marshall (1964) for Queensland; Waite (1899) and McCulloch (1927) for New South Wales; Waite (1923, 1928) and Scott et al. (1974) for South Australia; and Serventy (1937), Whitley (1948), and Allen (1976) for Western Australia.

The mugiloidids of the Great Barrier Reef Province have been largely neglected, with most of the literature consisting of locality records only. In their checklist of Queensland fishes, McCulloch and Whitley (1925) recorded four species of *Parapercis* from Great Barrier Reef waters: *P. cylindrica* (Bloch), *P. nebulosa* (Quoy and Gaimard), *P. hexophtalma* (Ehrenberg) and *P. xanthozona* (Bleeker). Whitley (1926, 1927a, 1932) listed only the one species, *P. cylindrica*, amongst fishes collected from North-West Islet, Michaelmas Cay, and Low Isles. More recent records from within the Great Barrier Reef Province are those of Woodland and Slack-Smith (1963) for Heron Island (*P. cylindrica, P. hexophtalma*), Whitley (1964) for the Swain Reefs (*P. cylindrica*), Goldman (1973) for One Tree Island (*P. cylindrica, P. hexophtalma*), Goeden (1974) for Heron Island and Wistari Reef (*P. cylindrica, P. hexophtalma*), and Paxton et al. (MS.) for the Lizard Island region (*P. cylindrica, P. hexophtalma, P. xanthozona, P. clathrata*, plus an unidentified species described later in this study as *Parapercis* sp. 1).

Cantwell (1964) revised the genus *Parapercis*, recognising a total of 26 species, all from the Indo-Pacific region. Schultz (1968) extensively expanded and modified Cantwell's key in a supplementary paper. Not included amongst the 32 species recognised by Schultz were *P. elongata* Fourmanoir (1965)[1] and *P. guezei* Fourmanoir (1966) from Vietnam and

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[1] Fourmanoir first described *P. elongata* in 1965 under the name *Parapercis* sp., although it was referred to as *P. elongata* in the text of the description and in the index. He later redescribed the species in full (Fourmanoir, 1967).

Réunion respectively, and the Atlantic species *P. atlantica* (Vaillant, 1887). Since Schultz's publication, six additional species have been described: *P. dockinsi* McCosker (1971) from the eastern Pacific, *P. gushikeni* Yoshino (1975) from southern Japan, *P. biordinis* Allen (1976) from Western Australia, *P. cephalus* Kotthaus (1977) from southern India, *P. flavescens* Fourmanoir and Rivaton (1979) from New Caledonia, and *P. diplospilus* Gomon (1980) from the Philippine Islands.

METHODS AND MATERIALS

Identification of each species is based upon comparison of field material from the Great Barrier Province, with that from Australian and selected overseas museums, and with published descriptions. It was not possible to examine the type specimens of each species, most of which are housed in European museums. Reference to type material may be necessary for complete verification of identifications and nomenclature used in this study.

Field material was collected using a variety of methods, with size of the fish generally dictating the particular method adopted. Coral reef *Parapercis* of large size (i.e. greater than about 15 cm total length) were captured by SCUBA diving and using a miniature Hawaiian sling(cf. Randall, 1963). Large individuals of species inhabiting coastal and deeper offshore waters away from reefs were sampled with an 11 metre otter trawl (32 mm mesh) operated from the RV *James Kirby* (James Cook University of North Queensland, Townsville) and RV *Lady Basten* (Australian Institute of Marine Science, Townsville).

Smaller *Parapercis* specimens were collected by SCUBA diving using ichthyocides, anaesthetics and nets. In most cases, a sudden movement towards an individual was all that was necessary to induce it to seek cover under rubble or in a coral cavity. A small net (80 cm diameter, 6 mm mesh) with a weighted perimeter was then placed over the rubble or entrance to the coral cavity, and the area sprayed with a small amount of "Chemfish collector" (a rotenone extract) or quinaldine, from a plastic bottle. This usually succeeded in bringing the fish out from cover and into the net. Juveniles were collected in a similar way, except that a plastic bag was utilized rather than a net.

Additional material was examined from the collections of various Australian and overseas museums. Material collected from outside the Great Barrier Reef Province was also examined for some species to allow comparison with the Great Barrier Reef forms and to provide additional information on distribution. This latter material is listed in the species accounts under the heading "Comparative Material".

Abbreviations used in the subsequent text for museums and collections are as follows: AMS - Australian Museum, Sydney; FMNH - Field Museum of Natural History, Chicago; GJS - Author collection; MCZ - Museum of Comparative Zoology, Harvard University; MNHN - Muséum National d'Histoire Naturelle, Paris; QM - Queensland Museum, Brisbane; USNM - National Museum of Natural History, Smithsonian Institution, Washington, D.C.; WAM - Western Australian Museum, Perth.

For all material listed, the museum/collection abbreviation, registration number, locality of capture, and in parentheses, the standard length(s) of the specimen(s) examined, are given.

Synonymies list all references that could be found, and are grouped under original names, new combinations, misapplied names and misspellings.

Morphometric measurements were taken in accordance with those defined by Hubbs and Lagler (1947) using needlepoint dial calipers or an ocular micrometer, on the left side of the fish. Accuracy of measurement was to the nearest 0.1 mm. All proportions are expressed in standard length unless otherwise specified, with the mean given first followed by a range in parentheses. Total length, standard length, and head length are abbreviated as TL, SL, and HL respectively.

Scale and fin ray counts employed follow those of Cantwell(1964), with the following abbreviations (partly after Munro, 1967) given in the descriptions:

A. - Number of spines and rays in the anal fin.

C. - Number of branched rays in the caudal fin.

Ch. - Number of scale rows crossing an imaginary line from the eye to the preopercular angle.

C.Ped. - Number of scales in a zig-zag row around the least vertical depth of the caudal peduncle.

D. - Number of spines and rays in the dorsal fin.

G.R. - Number of gill rakers on the anterior right arch, counted as those above and below the bend in the arch.

L.lat. - Number of oblique scale rows crossing the lateral line from the upper angle of the gill opening to the structural caudal base.

P. - Number of rays in the pectoral fin.

Pred. - Number of scale rows before the dorsal, counted to one side of the midline.

Tr. - Number of scales between the back and abdomen, counted in two parts; the first obliquely down and back from the first soft dorsal ray to the lateral line; the second obliquely up and back from the anterior margin of the anus to the lateral line; the lateral line scale is not counted.

V. - Number of spines and rays in the ventral or pelvic fins.

Summaries of counts and measurements are based on Great Barrier Reef specimens unless stated otherwise.

Colouration in life was recorded with the aid of underwater photographs and *in situ* descriptions written on an underwater slate. For those species exhibiting sexual dichromatism the following terminology (partly after Warner and Robertson, 1978) is used:

Initial phase (IP) - The colour pattern characteristic of adult females.

Terminal phase (TP) - The colour pattern characteristic of adult males.

Species distributions (i.e. both Great Barrier Reef Province and world) are given first in broad geographical terms, then in terms of localities with the respective authorities for these. Localities without authorities are based upon material examined in the present study.

SYSTEMATIC ACCOUNTS

Genus *Parapercis* Bleeker

Parapercis Bleeker, 1863a, p.236 (type-species *Sciaena cylindrica* Bloch = *Percis cylindrica* Cuvier and Valenciennes, by monotypy)

Neopercis Steindachner and Döderlein, 1885, p.212 (type-species *Parapercis ramsayi* Steindachner, by original designation)

Osurus Jordan and Evermann, 1903, p.206 (type-species *Percis schauinslandi* Steindachner, by original designation)

Chilias Ogilby, 1911, p.40 (type-species *Percis stricticeps* De Vis, by original designation)

Parapercichthys Whitley and Phillipps, 1939, p.235 (type-species *Enchelyopus colias* Bloch and Schneider, by original designation)

DIAGNOSIS: Body elongate, robust and cylindrical. Head somewhat depressed. Snout depressed. Eye more or less entering upper profile of head. Snout naked; opercular bones and upper part of head behind eyes scaly. Scales on body ctenoid; those of head, jugular region and abdomen often cycloid. Opercle with a single spine; pre- and subopercle with or without spines.

Mouth moderate, slightly oblique; jaws equal or lower jaw protruding. Lips thick. Upper jaw protractile. Both jaws with a row of hooked conical teeth, inside of which occurs a band of villiform teeth. Three to six canine teeth in outer row on either side of symphysis of lower jaw. Vomerine teeth present; palatine teeth present or absent. Spinous dorsal rounded or progressively higher posteriorly. Dorsal with four, five, or rarely six spines, and 19-24 rays; soft portion much higher than spinous portion. Anal similar to, but shorter than soft dorsal, with one weak spine and 16-19 branched rays. Pelvics with a short spine and five branched rays, fourth much longer than others; their insertion below or slightly in advance of pectorals. Caudal fin often slightly rounded in young; truncate to deeply crescentric with age, consisting of 13-15 branched rays. Lateral line complete, curved upward anteriorly. Abdominal vertebrae 10, caudal vertebrae 18-22.

DISTRIBUTION: Confined to the tropical and temperate regions of the Indian and Pacific oceans, with the exception of one species from the north-east Atlantic.

DISCUSSION: Prior to Bleeker (1853b) introducing the genus *Parapercis*, the generic name *Percis* had been widely used for this group of fishes. Bloch and Schneider (1801) erected the genus *Percis* by designating *Percis maculata* as its type-species. However, this species does not fit within the limits of the genus *Parapercis* Bleeker, hence *Percis* Bloch and Schneider and *Parapercis* Bleeker cannot be considered synonymous (Cantwell, 1964). The genus *Percis* of Bleeker (1844), Dumeril (1856) and Günther (1880a), although synonymous with *Parapercis* Bleeker, is preoccupied by *Percis* Scopoli (1777) which was introduced for *Cottus japonicus* Pallas of the family Agonidae.

The genus *Neopercis* was established by Steindachner and Döderlein (1885) based on *Parapercis ramsayi* Steinachner. The only character they gave to distinguish *Neopercis* from *Parapercis* Bleeker was the presence of palatine teeth. McCulloch (1914) later showed palatine teeth were present in *Parapercis cylindrica*, the type-species of *Parapercis* Bleeker. Hence *Neopercis* must be regarded as a junior synonym of *Parapercis*.

Jordan and Evermann (1903) erected the genus *Osurus* using *Percis schauinslandi* Steindachner as its type species. The only character used to distinguish *Osurus* from *Parapercis* was the deeply forked caudal fin of their type. I agree with Cantwell (1964) in considering this character to be insufficient for generic separation.

Ogilby (1911) introduced the genus *Chilias*, the type species being *Percis stricticeps* De Vis. The only character given in the diagnosis of *Chilias* that differs from *Parapercis*, is the absence of lower jaw villiform teeth. McCulloch (1913) later showed that lower jaw villiform teeth were in fact present in *Chilias stricticeps* (De Vis) and, therefore, concluded that *Chilias* and *Parapercis* were synonymous.

Whitley and Phillipps (1939) erected the family Parapercichthyidae and genus *Parapercichthys* using *Enchelyopus colias* Bloch and Schneider as the type species. Greenwood et al. (1966) have since incorporated the Parapercichthyidae into the Mugiloididae. In distinguishing *Parapercichthys* from *Parapercis*, Whitley and Phillipps (loc. cit.) wrote: "The genotype of *Parapercis* is *cylindrica*, a relatively large scaled species with 50 scales in the lateral line, while *colias* has 66. Vomerine and palatine teeth present in *cylindrica* are absent from *colias*." Cantwell (1964) noted that the number of scales in the lateral line within the genus *Parapercis* ranged from about 40 to 90. He also examined 17 specimens of the type species of *Parapercichthys* and found that all possessed a small number of vomerine teeth. Within the genus *Parapercis*, palatine teeth may be present or absent. Taking the above into account, I find no valid reason for separating *Parapercichthys* and *Parapercis* and consequently synonymize them.

KEY TO THE SPECIES OF *Parapercis* FROM THE GREAT BARRIER REEF PROVINCE

1a. Palatine teeth present.

2a. Oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 48-54; circum-peduncle scales 23-26; pectoral rays 15-16.

3a. Nine dark vertical bars on side below lateral line extending to midventral line; lower lip and branchiostegal membrane with pigment spots; 10 enlarged canines in outer tooth row of lower jaw .... *cylindrica* (Bloch)

3b. Dark vertical bands on side below lateral line not reaching midventral line; lower lip and branchiostegal membrane unpigmented; eight enlarged canines in outer tooth row of lower jaw .... sp. 1

2b. Oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 39-43; circum-peduncle scales 18-20; pectoral rays 13-14 .... *snyderi* Jordan and Starks

1b. Palatine teeth absent.

4a. Last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine.

5a. Three to eight small black ocelli on side of body ventrally; jaws equal or only just subequal; eight enlarged canines in outer tooth row of lower jaw ...... *hexophtalma* (Ehrenberg)

5b. Colouration not as above; lower jaw much longer than upper; six enlarged canines in outer tooth row of lower jaw.

6a. Dorsal spines IV; subopercle entire; dark blotch below ventral base of pectoral fin.

7a. Caudal fin with large centro-basal blackish blotch; side of body with nine distinct vertical bars, more or less evenly pigmented throughout their length; anterior margin of opercle and subopercle with a dark vertical bar extending downwards on to interopercle; a pair of oblong brownish black spots above opercle near rear of post-temporal fork ..... *cephalopunctata* (Seale)

7b. Caudal fin with several scattered small dark spots and/or one (ventro-basal) or two (one dorso-basal, the other ventro-basal) dark horizontal bars; a small intense dark spot or horizontal bar just below midside in each of nine scarcely discernible lateral vertical bars; opercle and subopercle without a dark vertical bar; a single brownish black rounded spot above opercle near rear of post-temporal fork, this spot encircled with a narrow, dark bordered whitish ring in larger individuals (i.e. greater than about 140 mm total length) .... *clathrata* Ogilby

6b. Dorsal spines V; subopercle terminating in a single, large, blunt, flat spine and/or about five small sharp spines; no dark blotch below ventral base of pectoral fin .... *xanthozona* (Bleeker)

4b. Last dorsal spine connected by membrane to first soft dorsal ray near base of ray.

8a. Oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 79-86; circum-peduncle scales 36-40; most individuals with three dark lines joining eyes across interorbital ...... *nebulosa* (Quoy and Gaimard)

8b. Oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 55-56 ; circum-peduncle scales 20-22; no dark lines joining eyes across interorbital ....*diplospilus* Gomon

Parapercis cylindrica (Bloch)

(Plate 1, Fig. 2)

Sciaena cylindrica Bloch, 1792, p.42; —— 1797, p.37, pl.299, fig. 1 (type locality unknown); Lacépède, 1802, p.309.

Bodianus sebae Bloch and Schneider, 1801, p.335 (type locality, East Indies).

Percis cylindrica Cuvier and Valenciennes, 1829, pp.267-268; Bleeker, 1851, pp.235-236; Günther, 1860, p.239; Fowler, 1927, p.295-296.

Parapercis cylindrica Bleeker, 1863a, p.236; Waite, 1900, p.209; Ogilby,

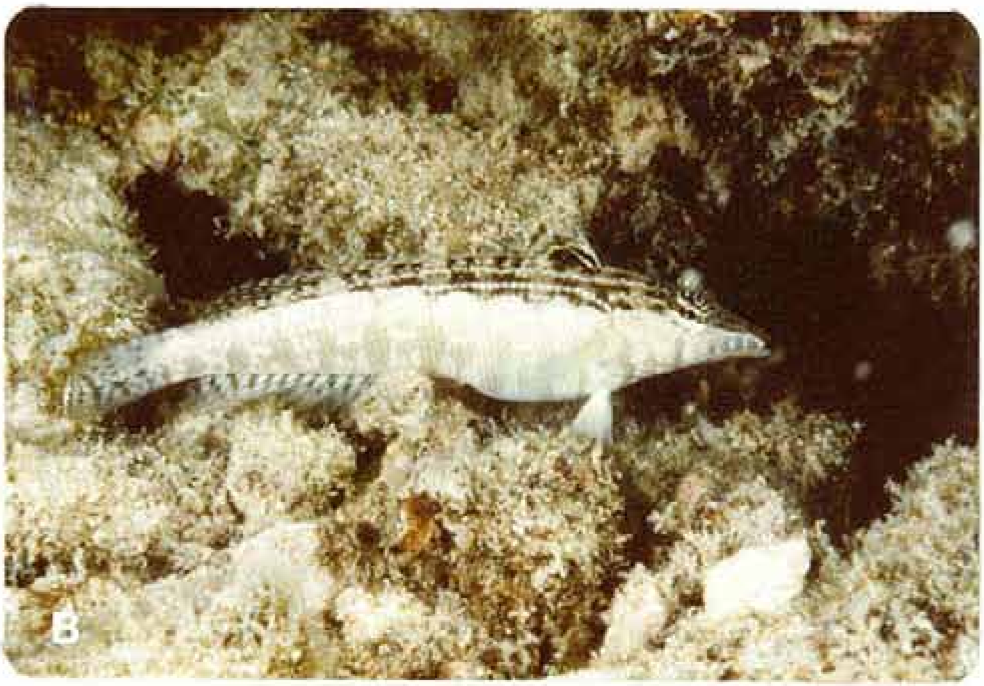
Plate 1

Parapercis cylindrica

A. Terminal phase individual, approx. 90 mm SL, Lizard Island in 8 m depth

B. Initial phase individual, approx. 55 mm SL, Palfrey Island in 6 m depth


A


B

1911, p.49; Weber, 1913, p.519; McCulloch, 1914, p.154; Cockerell, 1915, p.45; McCulloch and Whitley, 1925, p.173; Giltay, 1933, p.81; Martin and Montalban, 1935, pp.216-217, pl. 1, fig. 1; Herre, 1936, p.395; de Beaufort and Chapman, 1951, pp.19-21; Matsubara, 1955, pp.691-692; Fowler, 1956, pp.981-982; —— 1959, p.497, fig. 209; Kamohara, 1960, pp.2-3, pl. 1, fig. 1; Schultz et al., 1960, pp.272-273, pl. 112B; Woodland and Slack-Smith, 1963, p.46; Cantwell, 1964, pp.262, 264, figs. 1E, 2E, 8A; Marshall, 1964, p.329; Whitley, 1964a, p.151; —— 1964b, p.52; Munro, 1967, p.445; Schultz, 1968, p.2; Grant, 1975, p.439; Masuda et al., 1975, p.258, pl. 81F; Allen et al., 1976, p.424.

Parapercis cylindricus Whitley, 1927b, p.7.

Chilias synaphodesmus Fowler, 1946, pp.212-213, 170, fig. 38 (type locality, Ryukyu Is.).

Cilias synaphodesmus Matsubara, 1955, p.693.

MATERIAL EXAMINED:

Great Barrier Reef Province - 28 specimens, 20.1 to 97.1 mm SL. GJS: P.625, North Direction I. (29.1); P.613, Eyrie Reef (20.1); P.782, South I. (38.4, 51.7); P.764, Palfrey Is. (50.9); P.778, Lizard I. lagoon (56.8); P.772, SW end Lizard I. (62.0); P.450, Macgillivray's Reef (60.6, 78.2); P.565, Yonge Reef (76.7, 90.0); P.818, Tijou Reef (87.3); P.812, Haggerstone I. (54.0); —— MCZ: 36755, Gladstone, Qld (76.2); 38508, Eclipse I., Palm Group (91.0); 36947, Cairns, Qld (48.5, 51.0, 53.2); —— QM: I. 11351, Lady Musgrave I., Bunker Group (76.3); I. 9330, Heron I., Capricorn Group (86.6); I. 11689, One Tree I., Capricorn Group (75.7); I. 13303, Bushy I., 50 mls ENE of Mackay (86.3); I. 12950, Lindeman I., Cumberland Group (96.6); I. 11349, Curacoa I., Palm Group (97.1); I. 3819, Dunk I. (83.1); I. 3821, Murray I., Torres

Strait (86.3); I. 6363, Yorke I., Torres Strait (80.2); I. 1092, Darnley I., Torres Strait (73.7).

Comparative Material - 3 specimens, 58.2 to 96.3 mm SL. AMS: I. 17785-001, Sydney Harbour, NSW (58.2); —— MCZ: 50621, Dumaguete, Philippines (96.3, 66.8).

DIAGNOSIS: Palatine teeth present; 10 enlarged canines in outer tooth row of lower jaw; middle dorsal spines longest; last dorsal spine connected by membrane to base of first soft dorsal ray; oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 50-54; circum-peduncle scales 24-26; nine dark vertical bars on side below lateral line extending to midventral line; lower lip with a brown spot at tip.

DESCRIPTION: D. V, 20-21. A. I, 16-18 . . P. 15-16. V. I, 5. C. 8 + 7. G.R. (2-4) + (5-9). L.lat. 50-54. Tr. (3-4) + (14-17). C.Ped. 24-26. Pred. 4-7. Ch. 5-7.

Body elongate, moderately compressed, greatest depth 4.5 (4.0-5.1); least depth of caudal peduncle 3.2 (3.0-3.7) in HL; snout tip to dorsal fin origin 3.3 (3.0-3.6); tip of lower jaw to anal fin origin 2.1 (2.0-2.2); dorsal profile more arched than ventral profile; head small, pointed, 3.4 (3.0-3.6); snout 2.9 (2.6-3.2) in HL, acutely rounded at tip; eye small, moderately high, almost equidistant between tip of snout and edge of opercle, its diameter 3.4 (2.9-3.9) in HL; interorbital width 13.7 (11.2-17.6), postorbital length 2.5 (2.3-2.8), in HL; mouth small, oblique; jaws equal; lips narrow; premaxillaries not very protractile; maxillary almost entirely concealed by preorbital, extending to, or a little behind, vertical through anterior edge of orbit; snout tip to rear edge of maxillary 2.8 (2.5-3.2) in HL. Opercle with spine at upper angle; interopercle and subopercle terminating in a spine, that of the former sometimes blunt.

Teeth in two series on both jaws. Outer series of upper jaw a single row of enlarged teeth, coarser in front, terminating in one short curved canine on each side; inner series a band of dense villiform teeth with width of band decreasing posteriorly. Lower jaw with an outer series of five enlarged canines on each side at front increasing in size latero-posteriorly; inner-series a band of villiform teeth mesially, continuing postero-laterally to a single row of small conical teeth. Palatine teeth present. Vomer with villiform teeth.

Dorsal originating above rearmost tip of fleshy operculum; length of dorsal base 1.6 (1.5-1.7); last dorsal spine connected by membrane to base of first soft dorsal ray forming a deep notch between spinous and soft portions; third dorsal spine longest, 2.7 (2.4-3.3) in HL; soft dorsal rays longer than spines; anal inserted below fifth soft dorsal ray, its basal length 2.3 (2.2-2.4); pectoral small, rounded, length of longest ray 5.1 (4.5-5.6), reaching to or slightly posterior to vertical through anal origin; pelvic fin slender, fourth soft ray longest, 3.5 (3.0-4.3), reaching as far as sixth anal ray; caudal slightly rounded with upper lobe pointed and slightly produced in large individuals.

Snout, interorbital space, interopercle, and occiput naked; remainder of body with ctenoid scales; scales present proximally on caudal and pectorals; dorsal, anal, and pelvics naked.

Colouration in life - Background greyish white to yellowish, with nine purplish brown vertical bands on lower sides, the middle ones spindle-shaped, each band extending to midventral line. Bluish brown reticulated pattern above lateral line. V-shaped purplish brown band across jugular region. Vertical purplish brown bar extending from lower margin of eye over cheek; a yellowish band bordered on each side by brown, more developed in TP than in IP individuals, extending from tip of upper lip to front of eye. Lower lip with a brown spot at tip and another on side, the latter darker and more oblong in TP than in IP individuals; side of upper lip with either a long dark brown bar (TP), or about six alternating brown and white vertical bands (IP), the white bands generally narrower than the brown ones. Upper third of eye with irregular brown blotches (TP) or six to nine narrow dark lines radiating from pupil (IP). Branchiostegal membrane with several intense black bars (TP), or a number of scattered light brown pigment spots (IP) (Fig. 2). Interopercle with one to three intense black blotches and/or a black bar running along the posterior half of its lower margin (TP), or a few light brown pigment spots (IP). Large black blotch on basal half of spinous dorsal between spines II and V, above this a narrow yellow band bordered dorsally by a thin black submarginal band; a black spot at base of all but alternate third soft dorsal rays, thereby forming pairs of black spots along soft dorsal base; soft dorsal with oblong dusky areas anteriorly, gradually becoming defined as small spots posteriorly; distal margin of soft dorsal white. Anal fin with many small dusky spots sometimes fused to form vertical bands, its base chalky white. Pectorals yellowish brown. Pelvics bluish grey overall with a few scattered dark spots, often a purplish brown blotch at each fin base. Caudal fin with many dark blackish brown spots, a white margin, and a submarginal dusky border.

Juveniles and small subadults (i.e. less than about 40 mm TL) with an ocellus, a little greater than pupil diameter, at base of upper third of caudal; otherwise, colouration as above for IP.

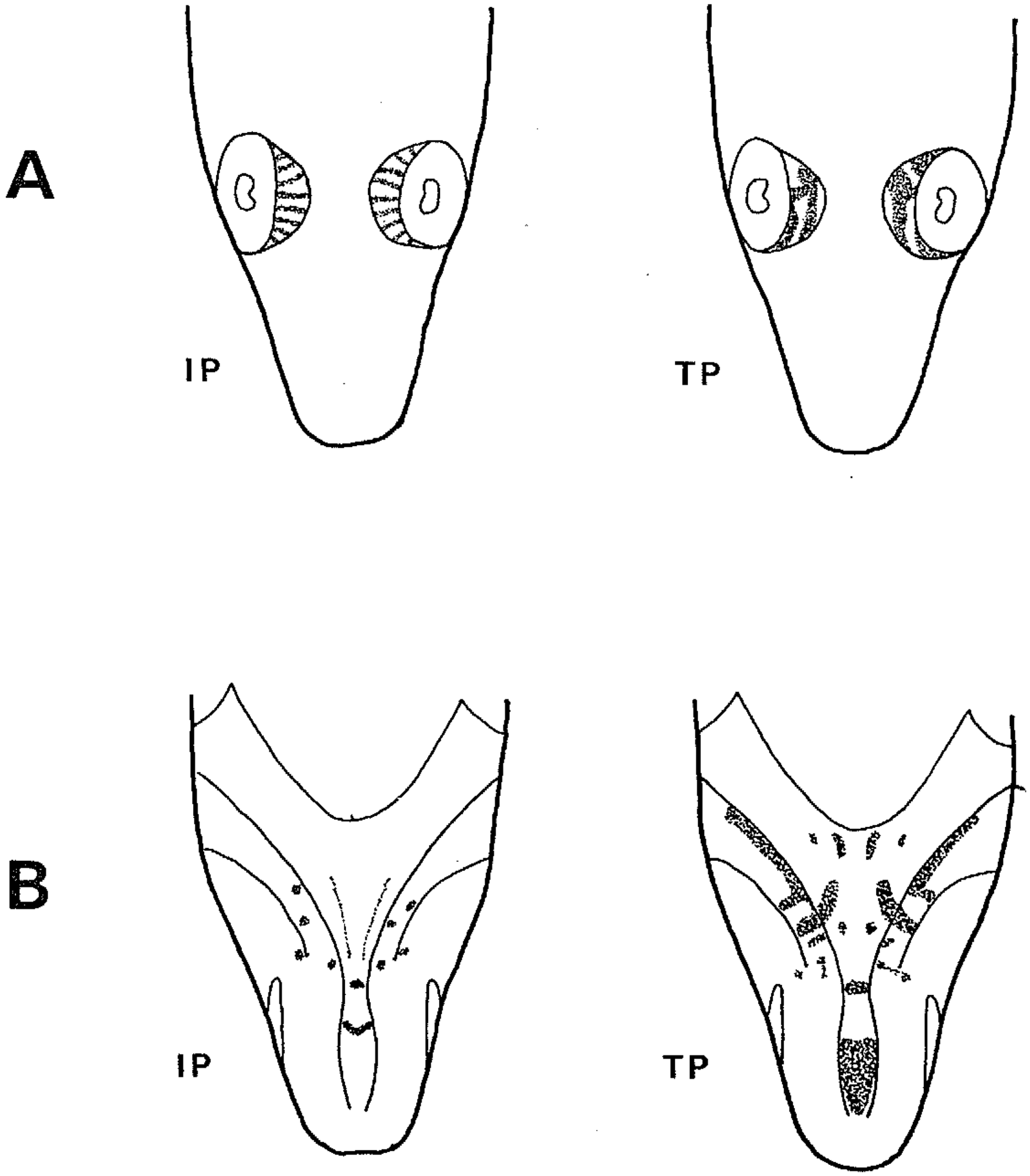
Colouration in alcohol - Vertical bands on sides of body dark brown; reticulated pattern above lateral line dark brown; narrow band above spinous dorsal blotch white or transparent; pectorals whitish; pelvics

Figure 2

Diagram showing differences in eye and branchiostegal pigmentation for the sexual colour phases of *Parapercis cylindrica*

A. Eye pigmentation (dorsal view)

B. Branchiostegal pigmentation (ventral view)


A
IP
TP
B
IP
TP

creamy white overall with a few scattered small dark spots. Remainder of colouration as in life.

DISTRIBUTION:

Great Barrier Reef Province - Widespread throughout the entire Great Barrier Reef Province.

Bunker Group - Lady Musgrave I.; Capricorn Group - Heron I. (Woodland and Slack-Smith, 1963), North-West I. (Whitley, 1926), One Tree I. (Goldman, 1973), Wistari Reef (Goeden, 1974); Gladstone; Swain Reefs (Whitley, 1964a); Bushy I.; Hayman I. (Cantwell, 1964); Lindeman I.; Curacoa I.; Eclipse I. (Cantwell, 1964); Dunk I. (Ogilby, 1911); Cairns (Cantwell, 1964); Green I. (Cantwell, 1964); Michaelmas Cay (Whitley, 1927a); Low Isles (Whitley, 1932); North Direction I. (Paxton et al., MS); Linnet Reef (Paxton et al., MS); South I.; Palfrey I.; Lizard I. (Paxton et al., MS); Macgillivray's Reef; Yonge Reef (Paxton et al., MS); Tijou Reef; Haggerstone I.; Sir Charles Hardy I. (Günther, 1860); Torres Strait - Murray Is. (Ogilby, 1911), Darnley I. (Cockerell, 1915), Yorke I.

World - Widespread throughout the Indo-Australian Archipelago and western Pacific as far north as the Ryukyu Islands and south to Sydney, Australia; the Friendly Islands and western Malaya appear to form the eastern and western limits of distribution, respectively.

East Indies (Cuvier and Valenciennes, 1829; Bleeker, 1851, 1857, 1858a, 1860; Günther, 1860; Bleeker, 1861, 1863a,b,c, 1864, 1865a,b,c,d, 1873a; Weber, 1895, 1913; de Beaufort, 1913; Whitley, 1926; Giltay, 1933; de Beaufort and Chapman, 1951). West New Guinea (Bleeker, 1878; Weber, 1913; Munro, 1967). South Vietnam (Whitley, 1926). Philippines (Günther, 1860; Seale and Bean, 1907; Fowler, 1927; Herre, 1933, 1934; Martin and Montalban, 1935). China (Günther, 1860; Bleeker, 1873b; de Beaufort and

Chapman, 1951; Fowler, 1956). Southern Japan (Fowler, 1946; Aoyagi, 1954; Kamohara, 1960; Masuda et al., 1975). Lord Howe I. (Waite, 1900; Allen et al., 1976). Admiralty Is. (Waite, 1900). Northern Marshall Is. (Schultz et al., 1960). New Caledonia (Whitley, 1961; Plessis and Fourmanoir, 1966). New Hebrides (Herre, 1931). Fiji Is. (Schmeltz, 1869; Whitley, 1927b; Herre, 1936; Fowler, 1959). Friendly Is. (Whitley, 1926).

Additional Australian records include: Queensland - "Queensland" (Whitley, 1926; McCulloch, 1929; de Beaufort and Chapman, 1951; Marshall, 1964); Moreton Bay (Ogilby, 1911). New South Wales - Sydney Harbour.

A record of *P. cylindrica* from Madagascar by Vivien (1973) appears doubtful and probably refers to *P. hexophtalma* (Ehrenberg).

DISCUSSION: *P. cylindrica* appears allied to *P. haackei* (Steindachner), a temperate water species from South Australia and Western Australia, and to the tropical species *Parapercis* sp. 1 (described later in this review). *P. cylindrica* differs from *P. haackei* most notably in having (1) fewer soft dorsal rays (20-21 versus 22), (2) fewer soft anal rays (17 versus 18), (3) the interorbital naked (versus interorbital scaled), and (4) a dark spot at the tip of the lower lip (versus no dark spot at tip of lower lip) [data for *P. haackei* from Cantwell (1964) and Schultz (1968)]. *P. cylindrica* can be distinguished from *Parapercis* sp. 1 on the basis of dentition, circum-peduncle scale count and colour pattern (see pp.29-30).

REMARKS: This is one of the commonest species of *Parapercis* found within the Great Barrier Reef Province. *P. cylindrica* inhabits reef flats and shallow slopes and is often found in great abundance over rubble areas supporting a heavy growth of algal turf. It is rarely encountered below 15 m depth.

Maximum recorded total length for this species is 126 mm (Cantwell, 1964). The largest individual examined during the present study measured 118.0 mm TL (97.1 mm SL) and was collected from Curacoa Island, Palm Group, northern Queensland.

Parapercis sp. 1

(Plate 2, Fig. 3)

MATERIAL EXAMINED:

Great Barrier Reef Province - 21 specimens, 25.3 to 68.5 mm SL. AMS: I. 18767-034. Linnet Reef (25.3, 46.5, 51.5); I. 19108-051, lagoon, Lizard I. (30.7, 32.0, 37.9, 60.7); I. 19465-003, Watsons Bay, Lizard I. (60.1); I. 19470-007, Granite Bluff, Lizard I. (55.1); — GJS: P.790, lagoon, One Tree I., Capricorn Group (68.5); P.626, North Direction I. (45.0); P.575, Eyrie Reef (43.4, 57.1); P.780, South I. (51.6); P.758, Palfrey I. (45.8); P.773, lagoon, Lizard I. (56.0, 62.6, 64.9, 67.2); P.813, Haggerstone I. (33.6); P.804, Halfway I. (38.4).

Comparative Material - 2 specimens, 27.0 to 51.2 mm SL. AMS: I. 17262-036, Manubada I., Port Moresby, Papua New Guinea (51.2); I. 17503-002, Blanche Bay, Rabaul, New Britain (27.0).

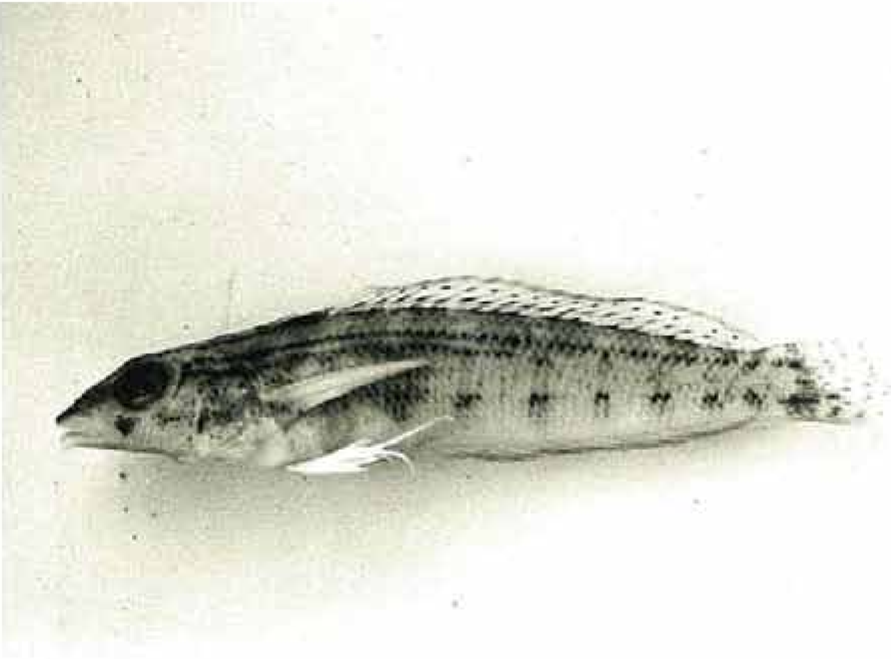
DIAGNOSIS: Palatine teeth present; eight enlarged canines in outer tooth row of lower jaw; middle dorsal spines longest; last dorsal spine connected by membrane to base of first soft dorsal ray; oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 48-52; circum-peduncle scales 23-26; three narrow dark longitudinal

Plate 2

Parapercis sp. 1

A. Terminal phase individual, 60.1 mm SL, collected from Long Reef, Lizard Island

B. Initial phase individual, approx. 45 mm SL, Palfrey Island in 12 m depth




B

lines on head and side of body, the first running from occiput to base of 1st, 2nd, or 3rd soft dorsal ray, the second and third lines running from the posterior margin of orbit back along side of body.

DESCRIPTION: D. V-VI (rarely VI), 20-21. A. I, 16-18. P. 15. V. I, 5. C. (7-8) + (6-7). G.R. (3-5) + (8-10). L.lat. 48-52. Tr. (3-4) + (12-15). C.Ped. 23-26. Pred. 4-6. Ch. 4-6.

Body elongate, moderately compressed, greatest depth 4.9 (4.3-5.5); least depth of caudal peduncle 3.2 (2.8-3.5) in HL; snout tip to dorsal fin origin 3.3 (3.2-3.5); tip of lower jaw to anal fin origin 2.1 (1.9-2.3); dorsal profile slightly more convex than ventral profile; head 3.4 (3.2-3.6); snout 3.2 (2.8-3.7) in HL; eye small, moderately high, almost equidistant between tip of snout and edge of opercle, its diameter 3.2 (2.9-3.7) in HL; interorbital width 11.5 (9.8-14.6); postorbital length 2.4 (2.2-2.7) in HL; mouth small oblique; jaws equal, though upper heavier; lips moderately narrow; premaxillaries not very protractile; maxillary just reaching a vertical through anterior edge of orbit; snout tip to rear edge of maxillary 2.8 (2.5-3.4) in HL. Opercle with spine at upper angle; subopercle terminating in a spine; interopercle entire.

Teeth in two series on both jaws. Outer series of upper jaw consisting of two or three large canines on each side at front, followed by four or five smaller canines, another large canine and about 20 closely spaced small uniserial pointed teeth; inner series a band of dense villiform teeth, with width of band decreasing posteriorly. Outer series of lower jaw with four enlarged canine teeth on each side at front increasing in size latero-posteriorly, followed by a gap and then four or five small canines, one large canine, and about 18 small uniserial pointed teeth; inner series of lower jaw a band of villiform teeth which is usually divided at the midline. Palatine and vomerine teeth present.

Dorsal originating above upper part of pectoral base; length of dorsal base 1.6 (1.5-1.8); last dorsal spine connected by membrane to base of first soft dorsal ray forming a deep notch between spinous and soft portions; third dorsal spine longest, 2.9 (2.5-3.5) in HL; soft dorsal higher than spinous dorsal; anal inserted below fifth or sixth soft dorsal ray, its basal length 2.2 (2.0-2.4); height of anal less than soft dorsal; pectoral small, rounded, length of longest ray 4.9 (4.5-5.2), reaching to a vertical through about third anal ray; pelvic fin slender, fourth soft ray longest, 3.4 (3.0-3.9), reaching to between fifth and seventh anal rays; caudal fin truncate, shorter than head.

Snout, interorbital space, and occiput naked; remainder of body with ctenoid scales; scales present proximally on caudal and pectorals; dorsal, anal, and pelvics naked.

Colouration in life - Background light cream; four dark brown U-shaped markings on sides, the two posterior markings completely above, the two anterior markings extending to just below, the lateral line; eight or nine dark vertical bars on side below lateral line not reaching midventral line; a faint brown line originating at pectoral insert, extending to caudal base, with concentrations of pigment present at its intersection with lateral vertical bars. Two dark narrow lines approximately a scale's width apart passing back from posterior margin of orbit to origin of lateral line, the upper running just above lateral line for about half its length and then diverging to continue to caudal base, the other running just below lateral line for about half its length; a narrow dark line originating at occiput and running posteriorly to base of first to third soft dorsal ray. Dark narrow line extending from anterior margin of orbit to snout tip; ventral margin of orbit with bluish-purple hue. Prominent dark brownish black bar about equal in length to pupil diameter (TP), or a light brown spot, 1.3-2.0 in pupil diameter surrounded by a halo of yellow pigment (IP), at posterior base of pectoral. Light brown band extending from posterior lower margin of orbit to posterior edge of maxillary. Spinous dorsal in TP individuals with a large dark brownish black blotch between third and fifth spines bordered anteriorly and ventrally by numerous dark brown pigment spots which extend from about midway between second and third spines to just beyond fifth spine; in IP individuals, a small dark brownish black blotch between third and fourth spines bordered anteriorly, posteriorly, and ventrally by yellowish tan pigment spots which extend from second to just beyond fifth spine; spinous dorsal of both sexes with a narrow submarginal band of dark brown pigment spots running from first to fifth spine (Fig. 3). Soft dorsal with two rows of brownish black spots, the basal row sometimes coalesced forming a longitudinal band, and the outer margin of fin dusky (TP), or with two or three (usually three) longitudinal rows of brownish black spots and the remainder of fin hyaline (IP). Anal pale tan with a submarginal transparent longitudinal band. Paired fins hyaline. Caudal with scattered brownish black spots of small size, decreasing in intensity and diameter distally.

Colouration in alcohol - The yellow pigment associated with the spinous dorsal and pectoral base of the female, the bluish purple hue around the ventral margin of the orbit, and the anal fin pigmentation all disappear upon preservation; remainder of colouration as in life.

DISTRIBUTION:

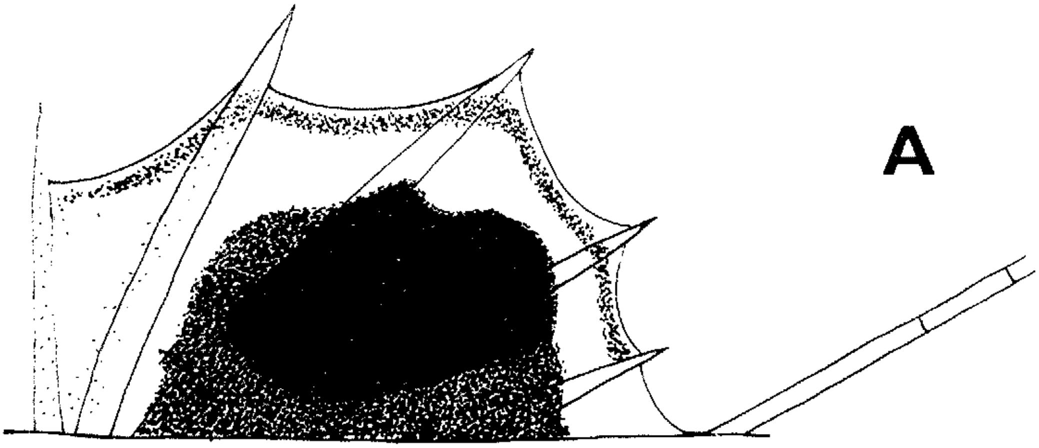
Great Barrier Reef Province - Collected from the northern and extreme southern regions of the Great Barrier Reef Province. Further

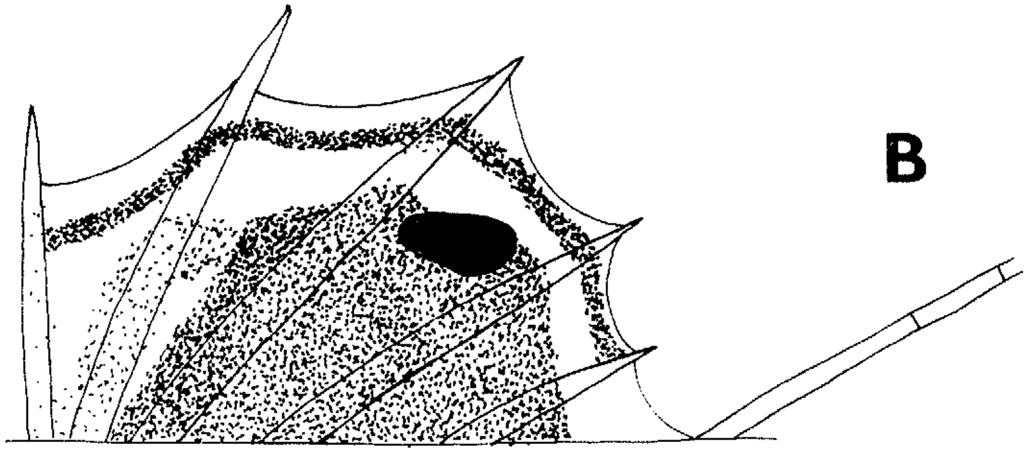
Figure 3

Arrangement and pigmentation of spinous dorsal in *Parapercis* sp. 1

A. Terminal phase

B. Initial phase


A


B

sampling will probably show this species to occur over the entire length of the Great Barrier Reef Province.

Capricorn Group - One Tree I.; Linnet Reef (Paxton et al., MS); North Direction I.; Eyrie Reef; South I.; Palfrey I.; Lizard I. (Paxton et al., MS); Haggerstone I.; Halfway I.

World - Presently known only from the Great Barrier Reef Province, Papua New Guinea, and New Britain.

Papua New Guinea - Manubada I. New Britain - Rabaul.

DISCUSSION: *Parapercis* sp. 1 appears allied to *P. snyderi* Jordan and Starks and *P. cylindrica* (Bloch). It differs meristically from *P. snyderi* in having a greater number of scales in the lateral line (48-52 versus 39-43), from the lateral line to the anus (12-15 versus 11-12), and around the caudal peduncle (23-26 versus 18-20). There is also a significant colour difference between that of *Parapercis* sp. 1 and *P. snyderi* (c.f. Plate 2 and Figure 4).

Parapercis sp. 1 may be separated from *P. cylindrica* on the basis of a lower number of enlarged canines in the outer tooth row of the lower jaw (8 versus 10) and slightly greater circum-peduncle scale count (23-26 versus 20-24). There is also an apparent difference in maximum size between these two species. *Parapercis* sp. 1 grows to about 90 mm TL compared with at least 120 mm TL for *P. cylindrica*. The final basis for separation is that of pigmentation. Some major differences include: (1) the overall colouration, which is much lighter in *Parapercis* sp. 1 than in *P. cylindrica*; (2) the lower lip and branchiostegal pigmentation, which is absent in *Parapercis* sp. 1 but present in *P. cylindrica*; and (3) the lateral vertical bars, which do not extend to the midventral line in *Parapercis* sp. 1, but do in *P. cylindrica*.

Underwater, some difficulty may be experienced distinguishing early juvenile stadia of *Parapercis* sp. 1 and *P. cylindrica*. However, juveniles and small subadults of the latter species (i.e. less than about 40mm TL) possess a small ocellus at the base of the upper caudal rays, this being absent in juvenile *Parapercis* sp. 1.

REMARKS: *Parapercis* sp. 1 inhabits fringing reefs of continental islands, inner reefs, coastal reefs and lagoons, at depths ranging from 3 to 30m. The commonest habitat is the interface between the sand of the off-reef floor and the sand rubble region of lower reef slopes.

The largest individual examined during the present study measured 85.8 mm TL (68.5 mm SL) and was collected from One Tree Island, Capricorn Group, southern Queensland.

Parapercis snyderi

(Fig. 4)

Parapercis snyderi Jordan and Starks, 1905, pp.210-211, fig.10(type locality, Korea); Jordan et al., 1913, p.365, fig.323; Kamohara, 1938, p.1451; Okada, 1938, pp.252-253; Fowler, 1956, pp.980-981; Tomiyama and Abe, 1958, p.121, fig.357; Kamohara, 1960, pp.3-4; Cantwell, 1964, p.264, figs.1D,2D,8B; Schultz, 1968, p.3; Masuda et al., 1975, p.258, pl.81I

Neopercis snyderi Jordan and Metz, 1913, p.41, fig.35.

Cilias snyderi Matsubara, 1955, p.693.

Parapercis cylindrica Burgess and Axelrod, 1975, p.1422, pl.52; Fourmanoir and Laboute, 1976, p.134(non Bloch, 1792).

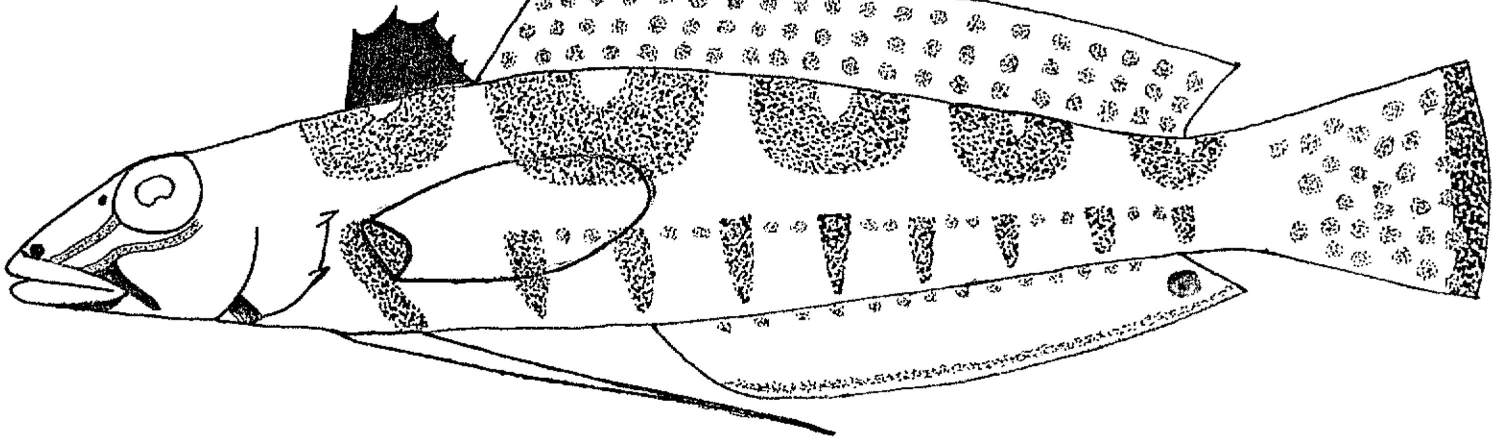
MATERIAL EXAMINED:

Great Barrier Reef Province - 8 specimens, 28.2 to 55.1 mm SL.
GJS: P.1086, Decapolis Reef (45.6); P.1088, 4 km NW of Nymph I. (28.2, 30.9, 46.0); P.1087, 20 km NW of Nymph I. (53.0, 53.8, 55.1); P.1060 6 km E of Turtle Head I., Cape York (42.6).

DIAGNOSIS: Palatine teeth present; eight enlarged canines in outer tooth row of lower jaw; middle dorsal spines longest; last dorsal spine connected by membrane to base of first soft dorsal ray; oblique scale

Figure 4

Diagram of *Parapercis snyderi* showing major features of colour pattern



rows crossing lateral line from upper angle of gill opening to caudal base 39-43; circum-peduncle scales 18-20; an ocellus on membrane between last two branched anal rays.

DESCRIPTION: D. V, 21. A. I, 17. P. 13-14. V. I, 5. C. (7-8) + 7. G.R. (2-4) + (8-9). L.lat. 39-43. Tr. (3-4) + (11-12). C.Ped. 18-20. Pred. 3-5. Ch. 4-5.

Body moderately elongate, a little compressed, greatest depth 4.9 (4.5-5.2); least depth of caudal peduncle 3.0 (2.5-3.3) in HL; snout tip to dorsal fin origin 3.4 (3.0-3.5); tip of lower jaw to anal fin origin 2.1 (2.0-2.2); predorsal profile rising gently to anterior edge of eye, then arching to dorsal fin origin; head small, pointed, as deep as wide, 3.3 (3.2-3.5); snout 3.4 (3.1-3.6) in HL; eye small, reaching dorsal profile, closer to tip of snout than edge of opercle, its diameter 3.2 (2.9-3.5) in HL; interorbital width 13.6 (11.4-16.1), postorbital length 2.3 (2.1-2.4), in HL; mouth moderately small, oblique; jaws equal, or the lower very slightly projecting beyond the upper; lips moderately narrow; maxillary extending a little behind vertical through anterior edge of orbit but not quite as far as pupil; snout tip to rear edge of maxillary 2.6 (2.3-2.9) in HL. Opercle with spine at upper angle; subopercle terminating in a somewhat smaller spine, which may or may not be divided irregularly at its tip into two or three points; interopercle and preopercle entire.

Teeth in two series on both jaws. Outer series of upper jaw consisting of three large canines on each side of front, followed by five smaller canines, and about 20 closely spaced small uniserial pointed teeth; inner series a band of dense villiform teeth, with width of band decreasing posteriorly. Outer series of lower jaw with four enlarged canines on each side at front increasing in size latero-posteriorly, followed by a gap and then four or five small canines, and about 15 small uniserial pointed teeth; inner series of lower jaw a band of villiform teeth which is sometimes separated at the midline. Palatine teeth present. Vomer with two rows of villiform teeth.

Dorsal originating above rearmost tip of fleshy operculum; length of dorsal base 1.6 (1.5-1.7); last dorsal spine connected by membrane to base of first soft dorsal ray forming a deep notch between spinous and soft portions; third dorsal spine longest, 3.1 (2.9-3.2) in HL; soft dorsal higher than spinous dorsal; anal inserted below fourth or fifth soft dorsal ray, its basal length 2.3 (2.1-2.4); pectoral small, rounded, length of longest ray 5.0 (4.6-5.2), reaching to vertical through about third anal ray; pelvic fin slender, fourth soft ray longest, 3.1 (2.7-3.4), reaching as far as sixth or seventh anal ray; caudal fin truncate, longest caudal ray 4.5 (4.1-4.9).

Snout, interorbital space, interopercle, and occiput naked; remainder of body with ctenoid scales; scales present proximally on caudal and pectorals; dorsal, anal, and pelvics naked.

Colouration in life - Background pinkish red, abdomen lighter than back; five V-shaped dark brownish black blotches on back, one under spinous dorsal, the other four under soft dorsal. Pale lateral band extending from pectoral to caudal base, below which are nine vertical light brown bars which do not reach the midventral line; upper ends of vertical bars connected by a horizontal series of small orange spots which decrease in intensity posteriorly. Narrow bright blue bar running from anterior lower margin of orbit to front of upper lip; a similar blue bar running from just behind orbit, along lower margin of orbit, to middle of upper lip. Upper region of snout with four small dark brownish black spots, each forming the corner of a square or rectangle. Upper lip light brown with two small dark spots on each side and one large oblong spot at tip; lower lip with one small dark spot on each side plus another at tip. Oblique brownish black blotch behind rear edge of maxillary. Dark brownish black line on each side beneath lower jaw following run of lower lip but not extending to midventral line. White blotch on lower edge of subopercle. One to three white blotches on interopercle alternating with dark brown blotches. Membrane between dorsal spines, black; soft dorsal greyish with three or four small ocelli (orange spots ringed with dark grey) between each ray, and a yellowish marginal band. Anal greyish with a pink submarginal band and an ocellus (black spot approximately half pupil size ringed with silver) on membrane between last two branched anal rays. Large ocellus (bright orange blotch with a dark brown margin) on both anterior and posterior of pectoral base. Paired fins pinkish yellow. Caudal fin yellowish tan with numerous scattered orange spots, often with a dusky margin in larger individuals.

Colouration in alcohol - Background creamy white; horizontal series of orange spots, blue snout bars, and orange caudal spots all lost on preservation; orange ocelli of soft dorsal, yellowish margin of soft dorsal, and pink submarginal band of anal become transparent; ocellus on pectoral base disappears (only dark margin present); paired fins hyaline. Remainder of colouration as in life.

DISTRIBUTION:

Great Barrier Reef Province - Collected from the northern end of the Great Barrier Reef Province only.

Decapolis Reef; off Lizard I. (sight record, 9/5/77); Yonge Reef (sight record, 8/8/76); off Nymph I.; off Turtle Head I., Cape York.

World - Recorded from the central Indo-Pacific and south-west Pacific. Material collected during the present study represents the first record of this species from Australian waters.

Japan- Nagasaki (Jordan and Starks, 1905; Jordan et al., 1913); Tosa (Kamohara, 1958); Honzu (Kamohara, 1938; Okada, 1938); "Southern Japan" (Masuda et al., 1975). Korea (Jordan and Starks, 1905; Jordan and Metz, 1913). Taiwan (Kamohara,1938; Okada, 1938). China (Fowler, 1956). New Hebrides (Fourmanoir and Laboute, 1976). New Caledonia (Burgess and Axelrod, 1975).

DISCUSSION: The differences in meristics and pigmentation between *Parapercis snyderi* and the allied *Parapercis* sp. 1 have been discussed previously(see p.29).

Individuals of *P. snyderi* from Japan and Taiwan are generally more melanistic than those from the Great Barrier Reef and other southern localities (e.g. New Caledonia). Whilst this may be simply a manifestation of the differing substrates on which they were collected, detailed comparative studies might conceivably reveal the population of *P. snyderi* to be divisible into northern and southern species (J.E. Randall, pers. comm.).

REMARKS: *Parapercis snyderi* inhabits the off-reef floor adjacent to coastal reefs, fringing reefs of continental islands, inner reefs and outer reefs, at depths ranging from 10 to 37m. It appears to be associated with weed beds and/or mud substrata.

Maximum recorded total length for this species is 100mm(Kamohara, 1960). The largest individual examined during the present study measured 66.1 mm TL (55.1 mm SL) and was collected off Nymph Island, northern Queensland.

Parapercis hexophtalma (Ehrenberg)

(Plates 3-4)

Percis cylindrica Rüppell, 1828, pp.19-20, pl.5. fig.2 (type locality, Djetta and Massaua, Red Sea) (non Bloch, 1792).

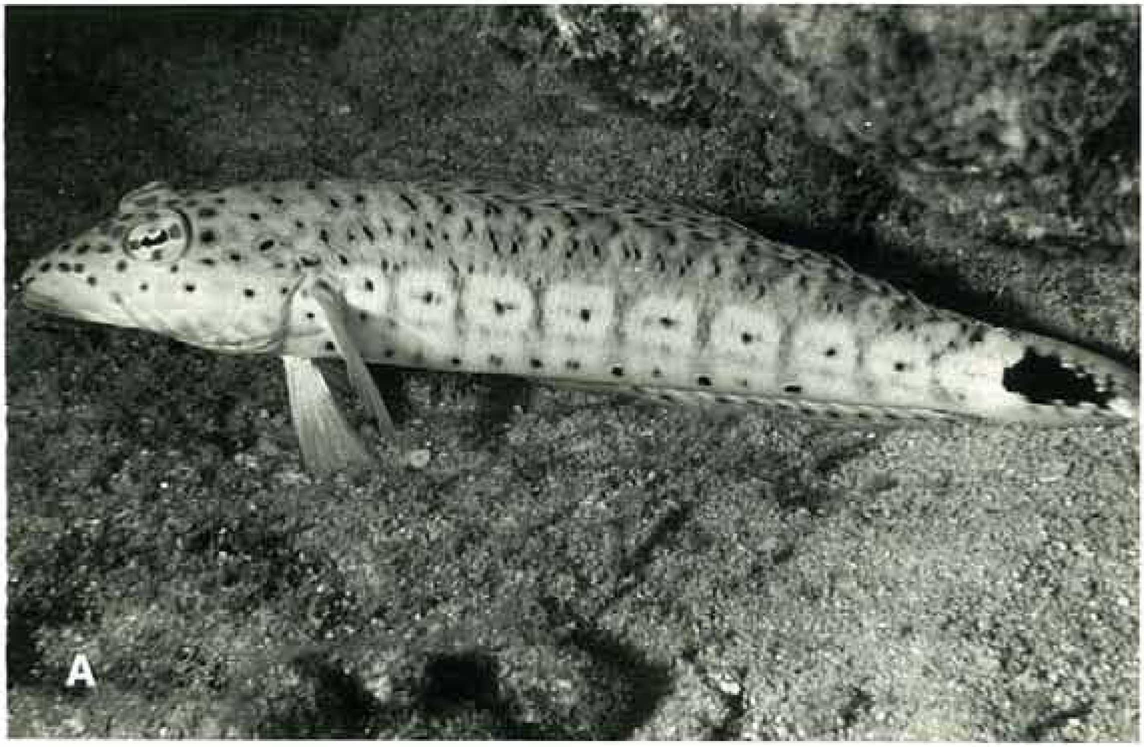
Percis hexophtalma Ehrenberg, in Cuvier and Valenciennes, 1829,pp.271-272

Plate 3

Parapercis hexophtalma

A. Terminal phase individual, approx. 175 mm SL, Palfrey Island in 9 m depth

B. Initial phase individual, approx. 110 mm SL, Palfrey Island in 9 m depth


A


B

Plate 4

Parapercis hexophtalma

Initial phase individual, 82 mm SL, photographed immediately after collection at Haggerstone Island

(type locality, Massaua, Red Sea).

Percis polyophtalma Ehrenberg, in Cuvier and Valenciennes, 1829, pp. 272-273 (type locality, Massaua, Red Sea).

Percis caudimaculata Rüppell, 1835, p.98 (substitute for *Percis cylindrica* Rüppell, 1828); Bleeker, 1849, pp.54-55; —— 1853c, pp.163-164; —— 1858b, p.459; —— 1860, p.43.

Percis hexophthalma Bleeker, 1845, p.527; Günther, 1860, p.239; Playfair and Günther, 1866, pp.68-69; Day, 1876, pp.262-264; pl. 57, fig. 4; Günther, 1880b, p.35.

Pinguipes didikuar Thiolliere, 1856, pp.499-500 (type locality, Woodlark I., Melanesia).

Percis polyophthalma Playfair and Günther, 1866, p.68; Klunzinger, 1870, pp.816-817; —— 1884, pp.122-123.

Parapercis hexophthalmus Bleeker, 1868a, p.272; —— 1875, p.78; —— 1878, p.53; Whitley, 1927b, p.7; McCulloch, 1929, p.332; Whitley, 1961, p.65; Marshall, 1964, pp.328-329.

Percis caudimaculatum Haly, 1875, p.269 (type locality, North China).

Parapercis hexophthalma Jordan and Snyder, 1902, pp.463, 466; Ogilby, 1911, p.40; Snyder, 1912, p.516; Barnard, 1927, p.442; Martin and Montalban, 1935, pp.219-220, pl. 2, fig. 1; Marshall, 1950, pp. 192-193, fig. 2; de Beaufort and Chapman, 1951, pp.24-25; Fourmanoir, 1957, pp.17-18, fig. 11A, B; Fowler, 1959, pp.495-496; Woodland and Slack-Smith, 1963, p.46; Cantwell, 1964, pp.268, 270, figs. 1J, 3J, 9B; Smith, 1965, p.117, pls. 13, 104; Munro, 1967, p.446, pl. 62, fig. 852; Schultz, 1968, p.5.

Parapercis polyophthalmus McCulloch, 1914, p.154.

Parapercis polyophthalma McCulloch and Whitley, 1925, p.173; Cantwell, 1964, pp.270-271, figs. 1J, 3J, 9C; Schultz, 1968, pp.5, 15-16; Masuda et al., 1975, p.258, pl. 81G; Allen et al., 1976, p.425;

Fourmanoir and Laboute, 1976, p.134.

Parapercis hexophtalma Giltay, 1933, p.82; Fourmanoir, 1954, p.214; Fowler, 1956, pp.984-985.

Chilias hexophtalma Fowler, 1946, p.211; —— 1957, pp.69-70, fig. 2.

Cilias hexophthalma Matsubara, 1955, p.692.

Parapercis hexophalma Kamohara, 1960, pp.4-5.

Parapercis cylindrica Smith and Smith, 1963, p.13, pl. 8C; Burgess and Axelrod, 1973, pp.776-777, pl. 277-278; —— 1974, p.932, pl. 166; —— 1976, p.1810, pl. 254-255 (non Bloch, 1792).

Paraperus hexophthalma Bennett, 1971, plate on p.166.

MATERIAL EXAMINED:

Great Barrier Reef Province - 50 specimens, 29.2 to 193.9 mm SL. AMS: I. 11964, Murray I., Torres Strait (164.7); - GJS: P.998, Fitzroy I. (150.7); P.827, No Name Reef #2 (17°52'S, 146°43'E) (110.0); P.618, North Direction I. (29.2, 30.0, 83.2, 97.2, 127.9, 161.6); P.705, P.706, Eyrie Reef (61.0, 62.4, 78.4, 93.4, 140.8; 149.3, 160.0, 172.3, 187.2, 193.9); P.37, P.101, Bird I., Lizard Group (66.8, 78.4; 147.4); P.180, Palfrey I., Lizard Group (79.2, 98.8, 171.1); P.68, Lizard I., Lizard Group (128.8, 138.7, 186.3, 191.0); P.399, P.89, P.52, Macgillivray's Reef (123.3, 162.2; 170.3, 174.5; 174.6, 182.7); P.1, P.34, Yonge Reef (86.2, 139.5, 188.1; 117.5, 121.5); P.18, Carter Reef (182.4); P.507, Day Reef (101.4, 111.8); P.814, Haggerstone I. (79.4); - MCZ: 36756, Cairns (154.8); - QM: I. 11747, One Tree I., Capricorn Group (175.0); I. 12539, Palm I. (165.1); I. 16081, NE of Eves Reef off Cape Melville (13°56'S, 144°36'E) (59.0); I. 14/1732, Raine I. (171.7); I. 14990, Tobin Cay, Torres Strait (158.1).

Comparative Material - 69 specimens, 48.0 to 193.2 mm SL. FMNH: 4030, Red Sea (158.6); 74056, Imma I., Maldives (96.7, 97.3, 99.5, 105.2, 110.7, 135.1, 139.7, 140.6, 144.8); 55531, Okinawa, Ryukyu Is. (159.8); 37097, 37096, 37095, Fiji (143.4; 148.2; 166.2); - MCZ: 3657, Red Sea (134.6); 1018, 1070, 4493, 12891, 26960, Zanzibar (183.5; 177.5, 187.8; 128.7, 139.0, 147.6, 156.9; 130.1, 151.7; 187.6); 12888, Society Is. (154.9); - MNHN: 1966-488, 1966-489, Ras Zeiti, Gulf of Suez (168.0; 175.8); 1977-965, A.3111, Red Sea (127.1; 161.3); 2376, Madagascar (181.0); 2289, Zanzibar (193.2); 1977-716, 60-68, Golfe de Tadjoura (108.5; 129.0, 148.3, 153.6); - QM: I.5211, Flat Rock, S. Queensland (186.5); - USNM: VGS 69-2 (uncat.), El Himeira, Gulf of Aqaba (48.0, 97.4, 126.9, 128.1); 49310, Red Sea (151.8); VGS 69-10 (uncat.), Sciuma I., Red Sea (57.9, 76.6, 85.7, 85.8, 87.6, 120.6, 137.8, 158.4, 166.3); 200743 Admirantes Is. (105.0, 110.3); HA 67-59 (uncat.), Aldabra (108.3); 200698, East Ambariobe - Nossi Be, Madagascar (99.3, 99.6, 157.7); 55926, 122332, Luzon, Philippines (132.1; 160.5); 122333, Cebu Market, Philippines (162.0); 122546, 122484, Biri Channel, Philippines (100.3; 157.7); 75862, Ryukyu Is.? (158.7); 75501, Naha, Okinawa (95.5, 141.0, 144.5, 163.4); 82926, 82927, Fiji (168.3; 180.2).

DIAGNOSIS: Palatine teeth absent, eight enlarged canines in outer tooth row of lower jaw; middle dorsal spines longest; last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 63-70; three to eight small ocelli on side of body ventrally; a large oblong black blotch on middle of caudal fin.

DESCRIPTION: D. V-VI (rarely VI), 20-22. A. I, 16-18. P. 17-19. V. I, 5. C. 8 + 7. G.R. (4-8) + (8-11). L.lat. 63-70. Tr. (6-9) + (15-18). C.Ped. 28-34. Pred. 10-13.

Body elongate, subcylindrical, greatest depth 5.6 (4.7-6.6); least depth of caudal peduncle 3.1 (2.8-3.6) in HL; snout tip to dorsal fin origin 3.3 (3.1-3.5); tip of lower jaw to anal fin origin 2.2 (2.0-2.4); dorsal profile of head region more arched than ventral profile; head 3.4 (3.2-3.6); snout 2.7 (2.3-3.0) in HL; eye large, moderately high, nearer tip of snout that edge of opercle, its diameter 4.1 (3.4-4.8) in HL; interorbital width 12.4 (8.0-22.8), postorbital length 2.2 (2.1-2.5) in HL; mouth large, oblique; jaws equal or only just subequal; lips broad, fleshy; premaxillaries protractile; maxillary concealed by preorbital, reaching a little behind vertical through anterior edge of orbit; snout tip to rear edge of maxillary 2.6 (2.3-3.1) in HL. Opercle with spine at upper angle; preopercle, interopercle, and subopercle entire.

Teeth in two series on both jaws. Outer series of upper jaw consisting of three large canines on each side at front, followed by three or four smaller canines, another two or three large canines, and about 20 closely spaced small uniserial pointed teeth; inner series a band of dense villiform teeth, with width of band decreasing posteriorly. Outer series of lower jaw with four enlarged canines on each side at front increasing in size latero-posteriorly, followed by a gap and then about seven small canines, four larger canines (increasing in size posteriorly), and about 15 small uniserial pointed teeth; inner series of lower jaw a band of villiform teeth which may or may not be separated at the midline. Palatine teeth absent. Vomer with a patch of curved teeth, consisting of two or more rows, those of the anterior row larger than the others.

Dorsal originating above or just behind pectoral base; length of dorsal base 1.6 (1.5-1.7); last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; fourth dorsal spine longest, 4.0 (3.6-4.8) in HL; soft dorsal higher than spinous dorsal; anal inserted below fifth soft dorsal ray, its basal length 2.3

(2.1-2.5); height of anal a little less than soft dorsal; pectoral rounded, length of longest ray 5.5 (5.0-5.9), reaching to a vertical through about third anal ray; pelvic fin with rays broadened and much thickened near tips, fourth soft ray longest, 4.4 (3.7-5.2), reaching to between second and fourth anal rays; caudal fin rounded in young; caudal fin in adults and larger subadults (i.e. individuals greater than about 80 mm TL) rounded except for one or two of the upper rays which project in a sharp point.

Snout, interorbital space, and occiput naked; remainder of body with ctenoid scales except for cheeks, jugular region, abdomen, and behind occiput which have cycloid scales; cheeks covered with 10-16 rows of small cycloid scales, more or less embedded in the skin; scales present proximally on caudal and pectorals; dorsal, anal, and pelvics naked.

Colouration in life - Background greyish, with back brownish grey and abdomen greyish white; upper two thirds of body with many small spots, with centres generally lighter than margins. Two horizontal rows of dark brown spots or oblong dashes at midside, one running from the upper part, the other from the lower part of pectoral base to base of caudal fin; seven or eight dark brown vertical bands crossing these horizontal rows forming eight or nine somewhat rectangular spaces, each containing one or several horizontally arranged dark brown spots or dashes. IP individuals with a row of five to eight conspicuous ocelli (brownish black spots ringed with lemon yellow) below midside, running from below pectoral fin base to above rear of anal fin base; the anterior three ocelli generally smaller and less distinct than the others; ocelli connected to rectangular spaces by continuations of lateral vertical bands. TP individuals with a similar row of markings, but several of the anterior ones reduced to undefined dusky spots, leaving only two to four ocelli per side. Both IP and TP individuals with head greenish grey, bluish white beneath; snout, interorbital space, and occiput with scattered orange blotches, some with brown centres; a C-shaped orange blotch often joining orbits at their anterior edges. IP individuals with two horizontal rows of brownish black spots extending across cheek, opercle, and subopercle. TP individuals with one horizontal row of brownish black spots extending across upper cheek and opercle, and four to seven brown oblique bars (maximum bar width 13.4-28.9, mean 19.3, in HL), sometimes fork-shaped, running across lower cheek; each cheek bar terminating dorsally in an indistinct spot; a few cheek bars extending on to interopercle and subopercle. Spinous dorsal of both sexes with a large bluish black spot on membrane between spines II and IV; this spot bordered anteriorly, posteriorly, and dorsally by a lemon yellow band with a narrow brownish black margin; remainder of spinous dorsal white. Soft dorsal yellowish, narrowly edged in white, with a narrow submarginal dusky band; a small brown spot directly behind each ray on lower margin of this dusky band, forming a row of small spots near fin margin; remainder of membrane between soft dorsal rays with two to four large brownish black spots or dashes which form longitudinal rows along fin. Anal fin yellowish, edged in white, with an indistinct dusky submargin, a single median longitudinal row of large brownish black spots, and a narrow dusky basal band. Pectoral fin whitish with about three dark brown spots on anterior base, one on scaled portion of fin rays; posterior base with one or more dark brown streaks or spots. Pelvics whitish. Caudal fin with a large median oblong black blotch surrounded by many small black spots; a whitish area directly behind oblong black blotch; usually a narrow white posterior margin and an indistinct dusky submargin to fin. Caudal in juveniles and small subadults (i.e. individuals less than about 80 mm TL) with black blotch extending ventrally and posteriorly to tip of lower branched rays, the remainder of fin white.

Colouration in alcohol - Background creamy brown with back darker brown and belly creamy white; the yellowish pigmentation of the dorsal and anal fins, and the bluish tint associated with the spinous dorsal, are both lost on preservation; the orange spots present on the snout, interorbital space, and occiput, plus the yellow rings of the body ocelli, fade to creamy white. Remainder of colouration as in life.

DISTRIBUTION:

Great Barrier Reef Province - Widespread throughout the entire Great Barrier Reef Province.

Bunker Group - Lady Musgrave I. (Fowler, 1957); Capricorn Group - One Tree I. (Goldman, 1973), Heron I. (Woodland and Slack-Smith, 1963), Wistari Reef (Goeden, 1974); Palm I.; Fitzroy I.; Cairns; No Name Reef #2 (17°52'S, 146°43'E); North Direction I.; Decapolis Reef (Paxton et al., MS); Eyrie Reef; Bird I.; Palfrey I.; Lizard I. (Paxton et al., MS); Macgillivray's Reef; Yonge Reef; Carter Reef; Day Reef; NE of Eves Reef off Cape Melville (13°56'S, 144°36'E); Haggerstone I.; Raine I.; Torres Strait - Murray Is. (McCulloch, 1913), Tobin Cay; "Great Barrier Reef" (Bennett, 1971; Burgess and Axelrod, 1976).

World - Widespread throughout the Indo-Pacific from the Red Sea and East African coast as far south as Durban, to the central and western Pacific as far north as southern Japan and south to southern Queensland, Australia; the Society Islands appear to form the eastern limit of distribution.

Red Sea (Rüppell, 1828; Cuvier and Valenciennes, 1829; Günther, 1860; Klunzinger, 1870, 1844; Tortonese, 1968). Golfe de Tadjoura. East Africa (Playfair and Günther, 1866; Klunzinger, 1870; Day, 1876; Barnard, 1927;

Smith, 1965; Talbot, 1965). Seychelles (Cuvier and Valenciennes, 1831; Smith and Smith, 1963; Schultz, 1968). Admirantes Is. (Schultz, 1968). Aldabra (Smith, 1955). Comores Is. (Fourmanoir, 1954). Madagascar (Bleeker, 1875; Fourmanoir, 1957; Schultz, 1968). Réunion (Bleeker, 1875). Maldive Is. (Burgess and Axelrod, 1973). India (McCulloch, 1929; de Beaufort and Chapman, 1951). Andaman Is. (Day, 1876). Cocos-Keeling Is. (Bleeker, 1858b; Marshall, 1950). East Indies (Bleeker, 1849, 1853c, 1860, 1868a; Weber, 1913; de Beaufort and Chapman, 1951; Sumadhiharga, 1977). West New Guinea (Bleeker, 1878; de Beaufort and Chapman, 1951). North Vietnam (Tonkin) (de Beaufort and Chapman, 1951; Matsubara, 1955). Taiwan (de Beaufort and Chapman, 1951; Fowler, 1956; Burgess and Axelrod, 1974). China (Haly, 1875; Fowler, 1956). Southern Japan (Jordan and Snyder, 1902; Snyder, 1912; Fowler, 1946, 1956; Aoyagi, 1954; Masuda et al., 1975). Philippines (Evermann and Seale, 1907; Martin and Montalban, 1935). Papua New Guinea (Munro, 1967). Solomon Is. (Herre, 1931a; Giltay, 1933; Seale, 1935; Rofen, 1958). Woodlark I. (Thiolliere, 1856). Louisiade Archipelago (Günther, 1860; Klunzinger, 1870). Lord Howe I. (Allen et al., 1976). New Caledonia (Whitley, 1961; Fourmanoir and Laboute, 1976). New Hebrides (Herre, 1931b; Fowler, 1944; Fourmanoir and Laboute, 1976). Santa Cruz Is. (Cantwell, 1964). Fiji Is. (Schmeltz, 1879; Günther, 1880b; Whitley, 1927b; Fowler, 1928, 1929). Samoan Is. (Jordan and Seale, 1905). Society Is. (Fowler, 1928, 1938).

Additional Australian records include: Queensland - "Queensland" (McCulloch, 1929; de Beaufort and Chapman, 1951; Marshall, 1964); Flat Rock, near Brisbane, southern Queensland.

DISCUSSION: Günther (1860) synonymised *P. hexophtalma* (Ehrenberg) and *P. polyophtalma* (Ehrenberg) but later (Playfair and Günther, 1866) separated them for the same reasons advanced by Cuvier and Valenciennes

(1829) after their examination of Ehrenberg's type material: that *P. hexophtalma* possesses three lateral ocelli and several oblique bars across the cheek and opercle whereas *P. polyophtalma* has six or seven lateral ocelli and the sides of the head dotted. To the present day argument still exists as to whether or not *P. hexophtalma* and *P. polyophtalma* are colour forms of the same species. Some authors consider each to be valid (Cantwell, 1964; Schultz, 1968; Masuda et al., 1975; Fourmanoir and Laboute, 1976), whilst others synonymise the two (Barnard, 1927; Marshall, 1950; de Beaufort and Chapman, 1951; Fourmanoir, 1957; Smith, 1965). Marshall (1950) suggested that *P. hexophtalma* and *P. polyophtalma* were male and female forms respectively, of the same species, and that protogynous sex reversal might be implicated in the life history of this species. Marshall's (loc. cit.) suggestions have been confirmed by work carried out during the present study and will be discussed in more detail later (see Part II).

The number and form of the cheek bars of TP *P. hexophtalma* vary with geographical locality. Individuals from the Red Sea, Indian Ocean, Fiji and Society Islands, possess a greater number of cheek bars than their conspecifics from the Great Barrier Reef Province, Melanesia, New Caledonia, and New Hebrides. In addition, the bars exhibited by individuals from the former group of localities are narrower and originate higher up the cheek, often radiating from just below the eye. TP *P. hexophtalma* from the Philippines and Southern Japan generally possess only two cheek bars, the most distinctive of the two arching across the lower cheek from just behind the rear edge of the maxillary to the rounded angle of the preopercle.

The specific name *hexophtalma* has been frequently misspelt, almost since the time the species was described. The present author follows Ehrenberg's (in Cuvier and Valenciennes, 1829) original spelling of the specific name as there is no evidence of an inadvertant error in the original publication, and the form of the name is correct (see Article s 26-30 and 32, International Code of Zoological Nomenclature, revised edition, 1964).

REMARKS: An extremely common mugiloidid in Great Barrier Reef waters, *P. hexophtalma* inhabits reef flats, lagoons, and reef slopes of continental islands, coastal, inner and outer reefs, at depths ranging from 2 to 20 m. This species is often found in great abundance within shallow patch reef areas, particularly around staghorn coral (*Acropora spp.*) thickets which are separated from one another by long expanses of sand.

Maximum recorded total length for *P. hexophtalma* is 305 mm (Marshall, 1964). The largest individual examined during the present study measured 234.3 mm TL (193.9 mm SL) and was collected from Eyrie Reef, northern Queensland.

Parapercis cephalopunctata (Seale)

(Plate 5, Fig. 5)

Percis tetracanthus Bleeker, 1853b, pp.458-459 (type locality, Batavia): —— 1857, p.371; Günther, 1860, p.241; Kner and Steindachner, 1866, pp.362-363, fig. 18; Günther, 1876, p.158, pl. 93, fig. B (non Lacépède, 1801, 1802).

Parapercis tetracanthus Bleeker, 1865b, p.149; —— 1865d, p.288; Jordan and Seale, 1905, p.414; Whitley, 1927b, p.7; Fowler, 1928, p.424; —— 1934a, p.445; —— 1938, pp.177, 185, 300; Schultz, 1943; p.369 (non Lacépède, 1801, 1802).

Plate 5

Parapercis cephalopunctata, approx. 135 mm SL, Green Island in 2 m depth

Percis cephalopunctatus Seale, 1901, p.124 (type locality, Guam).

Parapercis tetracantha Snyder, 1912, p.516 (non Lacépède, 1801, 1802).

Percis quadrispinosus Weber, 1913, p.519 (substitute name for *Percis tetracanthus* Bleeker).

Parapercis quadrispinosus Giltay, 1933, p.82.

Parapercis quadrispinosa Herre, 1934, p.95; de Beaufort and Chapman, 1951, pp.15-18; Munro, 1955, p.198, pl. 589; Fowler, 1956, pp.986-987.

Parapercis montillai Martin and Montalban, 1935, pp.224-225, pl. 3, fig. 2 (type locality, Philippines).

Parapercis cephalopunctatus Randall, 1955, p.208; Schultz et al., 1960, pp.270-271, pl. 112C-E; Burgess and Axelrod, 1973, pp.778-779, pls. 279-280; —— 1974, p.932, pl. 165.

Parapercis clathrata Fowler, 1959, pp.496-497 (non Martin and Montalban, 1935).

Parapercis cephalopunctata Cantwell, 1964, pp.267-268, figs. 1C, 2C, 8E; Schultz, 1968, p.4; Masuda et al., 1975, p.259, pl. 81M.

MATERIAL EXAMINED:

Great Barrier Reef Province - 3 specimens, 96.3 to 139.5 mm SL. AMS: I. 20209-003, One Tree I., Capricorn Group (96.3); - GJS: P.1052, NW end of Wheeler Reef, off Townsville (136.2, 139.5).

Comparative Material - 2 specimens, 115.0 and 125.0 mm SL. MCZ: 12889, Society Is. (115.0, 125.0).

DIAGNOSIS: Palatine teeth absent; six enlarged canines in outer tooth row of lower jaw; dorsal IV, 21; last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; side of body with nine distinct vertical bars, more or less evenly pigmented throughout their length; anterior margin of opercle and subopercle with a dark verticle bar extending downwards on to interopercle.

DESCRIPTION: D. IV, 21. A. I, 17. P. 17. V. I, 5. C. 8 + 7. G.R. (5-6) + (9-10). L.lat. 57-59. Tr. (6-7) + (14-15). C.Ped. 26-27. Pred. 8-11.

Body elongate, subcylindrical, greatest depth 5.9 (5.7-6.2); least depth of caudal peduncle 3.2 (2.6-3.6) in HL; snout tip to dorsal fin origin 3.0 (3.0-3.1); tip of lower jaw to anal fin origin 2.1 (2.1-2.2); dorsal profile more arched than ventral profile; head 3.3 (3.3-3.4), somewhat depressed; snout 3.0 (2.8-3.4) in HL; eye moderately large, nearer tip of snout than angle of opercular opening, its diameter 4.8 (4.5-5.2) in HL; interorbital width 21.3 (17.4-26.0), postorbital length 2.1 (2.0-2.1), in HL; mouth large, oblique; lower jaw projecting beyond upper; lips moderately broad; premaxillaries protractile; maxillary partly concealed by preorbital, extending to, or a little behind, vertical through anterior edge of orbit; snout tip to rear edge of maxillary 2.9 (2.7-3.2) in HL. Opercle with spine at upper angle; subopercle terminating in a flat pointed spine, or in a sharp edge which may or may not be divided at the tip irregularly into two or three points; interopercle and preopercle entire.

Teeth in two series on both jaws. Outer series of upper consisting of two large canines on each side at front, followed by three smaller canines, another two large canines and about 20 closely spaced small uniserial pointed teeth; inner series a band of dense villiform teeth, with width of band decreasing posteriorly. Outer series of lower jaw with three enlarged canine teeth on each side at front increasing in size postero-laterally, followed by a gap and then nine or ten canines (increasing in size posteriorly), and about 10 small uniserial pointed teeth; inner series of lower jaw a band of villiform teeth decreasing in width postero-laterally, and usually divided at the midline. Palatine teeth absent. Vomer with a patch of villiform teeth.

Dorsal originating just behind vertical through upper part of pectoral base; length of dorsal base 1.6 (1.6-1.7); last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; third dorsal spine longest, 4.9 (4.4-5.2) in HL; soft dorsal higher than spinous dorsal; anal inserted below fifth soft dorsal ray, its basal length 2.4 (2.3-2.5); height of anal about equal to that of soft dorsal; pectoral rounded, length of longest ray 6.0 (5.8-6.1), not quite reaching or just reaching vertical through anal origin; pelvic fin pointed with rays broadened near tips, fourth soft ray longest, 5.0 (4.5-5.5), reaching to between anus and anal fin origin; caudal rounded.

Snout, interorbital space, and occiput naked; remainder of body with ctenoid scales except for cheeks, jugular region, abdomen, and behind occiput which have cycloid scales; cheeks covered with about 12 rows of small cycloid scales, more or less embedded in the skin; scales present proximally on pectorals and on basal half of caudal; dorsal, anal, and pelvics naked.

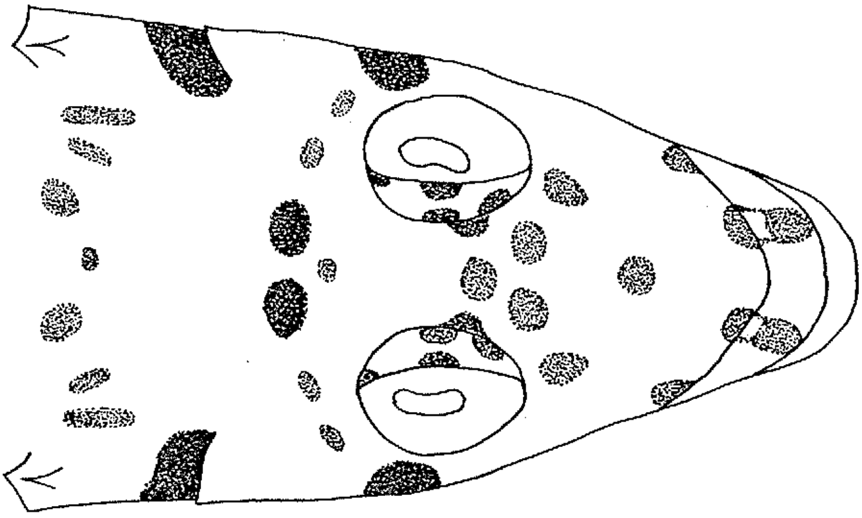
Colouration in life - Background whitish; sides with about nine vertical reddish brown bars, each broadest below lateral line, fading ventrally so that they do not always reach the midventral line; a large brownish black blotch at lower base of pectoral fin extending behind fin to upper base forming an additional lateral bar, the middle of this bar with a white vertical streak; lateral vertical bars branching dorsally into two, each branch joining with its neighbour to form a reddish brown W-shaped pattern along the upper sides and back. Narrow reddish brown line extending from lower base of pectoral fin to lower base of caudal fin; just above this line and alternating with the vertical reddish brown bands, nine reddish brown spots almost as large as eye, with whitish margins. Dorsal surface of head with several reddish brown spots, pupil size or a little smaller (Fig. 5A); a prominent pair of spots on occiput followed by another pair near mid-dorsal line of head about midway between occiput and dorsal fin origin; a pair of oblong brownish black spots above operculum near rear of post-temporal fork; snout with about nine brownish black spots, four just anterior to eyes the most prominent. Upper lip with a large brownish blotch postero-laterally, extending down over lower lip, gradually fading to yellowish orange, and continuing as a transverse band beneath lower jaw to meet its counterpart at midventral line; remainder of upper lip light brown or with two to four small brown spots. Lower lip with five small brown spots, two laterally on each side, and one at tip. Three large brownish blotches on cheek; the first blotch behind rear edge of maxillary; the second about half the size of the first, below infero-posterior border of eye; the third, about the same size as the first and sometimes connected to the second, near rounded angle of preopercle; first and third cheek blotches continuing as yellowish orange transverse bands on throat and interopercle respectively, with only the former band reaching the mid ventral line. Dark vertical bar running down anterior margin of opercle and subopercle, and on to interopercle. Basal membrane between dorsal spines I-III dusky; remainder of spinous dorsal yellowish white. Soft dorsal pale yellow with an indistinct reddish brown submarginal band and two longitudinal rows of reddish brown spots, one of these rows median, the other basal; basal row of spots much darker than median row, the former consisting of pairs of spots formed where W-shaped bars of back meet their counterparts along mid-dorsal line. Anal fin pale yellowish, with or without a narrow reddish marginal band. Pectoral and pelvic fins bright yellow, the anterior half of the latter sometimes whitish. Caudal fin with a large centro-basal blackish blotch, a postero-median white

Figure 5

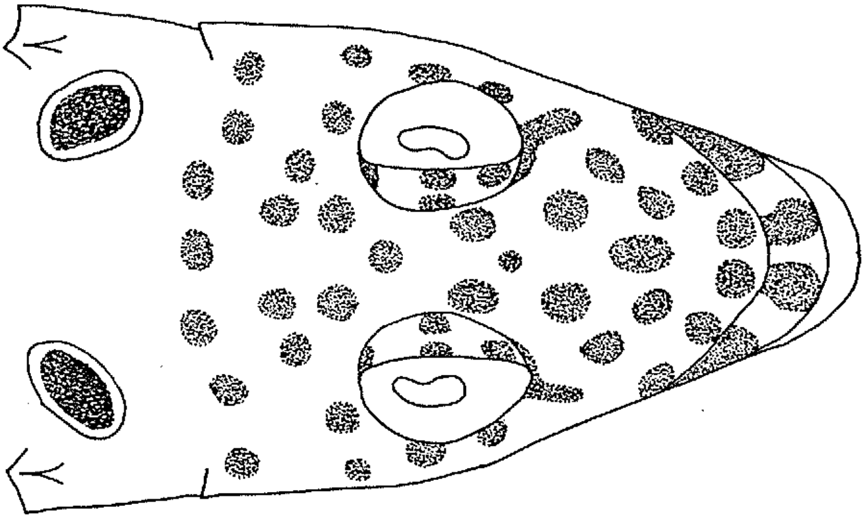
Diagram showing pattern of spots of dorsal surface of head of *Parapercis cephalopunctata* and *P. clathrata*

A. *P. cephalopunctata*

B. *P. clathrata*



A



B

blotch, and a dusky marginal band; remainder of fin with small scattered blackish spots.

Colouration in alcohol - Background whitish; back, lateral vertical bands, and all other reddish brown markings in life, lose their reddish tint; the yellowish orange transverse bars of lower jaw, throat, and interopercle become a pale brown; the yellowish pigmentation associated with the dorsal, anal, and pectorals fades to white on preservation; pelvics pale yellow. Remainder of colouration as in life.

DISTRIBUTION:

Great Barrier Reef Province - Presently known only from the central and extreme southern regions of the Great Barrier Reef Province.

Capricorn Group - One Tree I.; Wheeler Reef, off Townsville; Green I.; off Cairns (photographic record, 2/5/76, G. Stroud).

World - Widespread throughout the Indo-West Pacific from Mauritius and the Maldive Islands to the central and western Pacific, as far north as the Ryukyu Islands, and south to One Tree Island at the southern extremity of the Great Barrier Reef Province; the Tuamotu Archipelago appears to form the eastern limit of distribution.

Mauritius (Cantwell, 1964). Maldive Is. (Burgess and Axelrod, 1973). Sri Lanka (Ceylon) (Munro, 1955; Cantwell, 1964). East Indies (Bleeker, 1853b, 1857, 1865b,d; Günther, 1860; de Beaufort and Chapman, 1951). Philippines (Herre, 1934; Martin and Montalban, 1935). Taiwan (Fowler, 1956; Burgess and Axelrod, 1974). Ryukyu Is. (Snyder, 1912; Fowler, 1956; Masuda et al., 1975). Palau Is. (Günther, 1876). Guam (Seale, 1901; Jones and Chase, 1975). Caroline Is. (Cantwell, 1964). Marshall Is. (Schultz et al., 1960; Cantwell, 1964). Gilbert Is. (Günther, 1876; Randall, 1955). New Hebrides (Fowler, 1934a). Fiji Is. (Günther, 1860, 1876; Schmeltz, 1866, 1879; Garman, 1903; Whitley, 1927b; Fowler, 1928, 1959). Samoan Is. (Kner and Steindachner, 1866; Jordan and Seale, 1905; Schultz, 1943). Phoenix Is. (Schultz, 1943; Cantwell, 1964). Fanning I. (Chave and Eckert, 1974). Caroline Is. (Cantwell, 1964). Society Is. (Günther, 1876; Fowler, 1928, 1938; Cantwell, 1964). Tuamotu Archipelago (Cantwell, 1964).

DISCUSSION: *P. cephalopunctata* (Seale) has been frequently confused with *P. clathrata* Ogilby and *P. tetracantha* (Lacépède). Both *P. cephalopunctata* and *P. clathrata* differ from *P. tetracantha* in meristics and colouration, the most important meristic difference being the presence of four dorsal spines in *P. cephalopunctata* and *P. clathrata*, versus five in *P. tetracantha*.[1] *P. cephalopunctata* is closely related to *P. clathrata* and differs chiefly in regard to colour pattern. Some major differences include: (1) *cephalopunctata* with nine dark lateral vertical bars, more or less evenly pigmented throughout their length and extending on to abdomen, the posterior bars generally reaching midventral line; *clathrata* with a small intense dark spot or horizontal bar just below midside in each of nine scarcely discernible lateral vertical bars, these bars seldom extending to abdomen, the posterior ones rarely reaching midventral line; (2) *cephalopunctata* with two dark spots on occiput; *clathrata* with six or seven dark spots on occiput; (3) *cephalopunctata* with about nine dark spots on snout; *clathrata* with about 13 dark spots on snout (Fig. 5); (4) *cephalopunctata* with five small dark spots on lower lip; *clathrata* with uniformly pigmented, non-spotted lower lip; (5) *cephalopunctata* with transverse bands on throat and beneath lower jaw; no such bands in *clathrata*; (6) *cephalopunctata* with three large roundish dark blotches on cheek; cheek of *clathrata* with two or three, somewhat indistinct,

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[1] Cuvier and Valenciennes (1829:268) examined the type specimen of *P. tetracantha* (Lacépède) and concluded that Lacépède had failed to enumerate the spines correctly; hence the misleading name of this species.

blotches generally broken up into many oblique bars and irregular spots in larger individuals (i.e. greater than about 140 mm TL); (7) *cephalopunctata* with a dark vertical bar running down anterior margin of opercle and subopercle, and on to interopercle; no such bar in *clathrata*; (8) larger individuals of *clathrata* (i.e. greater than about 140 mm TL) with a large ocellus above opercle near rear of post-temporal fork; larger individuals of *cephalopunctata* without ocellus above opercle; (9) caudal fin of *cephalopunctata* with a large centro-basal blackish blotch; caudal fin of *clathrata* with several small dark spots and/or one (ventro-basal) or two (one dorso-basal, the other ventro-basal) dark horizontal bars. In addition, *cephalopunctata* appears to have a slightly greater HL/eye diameter ratio than *clathrata* (4.5-5.2 versus 3.6-4.5).

Lacépède (1800, 1801)[1] described *Labrus tetracanthus* and later (1802) *Bodianus tetracanthus* from collections in the Muséum National d'Histoire Naturelle, Paris. According to Cuvier and Valenciennes (1829:268) both species are of the genus *Percis* (*Percis* C&V = *Parapercis* Bl). They examined the type of *Labrus tetracanthus*, found five, not four dorsal spines and therefore decided to change the name of this species to *Percis cancellata*. However, Lacépède's failure to enumerate the spines correctly does not confer on any subsequent author authority to change the name. Consequently, *Parapercis tetracantha* (Lacepede) [= *Labrus tetracanthus* Lacépède (1801)] is accepted as a valid name for this species (Cantwell, 1964; Schultz, 1968). *Bodianus tetracanthus* Lacépède (1802), the second *tetracanthus* species described by Lacépède, will be a synonym of *Parapercis clathrata* Ogilby by neotypy (see pp.65-66).

Apparently unaware of Lacépède's *Labrus tetracanthus* and *Bodianus tetracanthus*, Bleeker (1853b) described yet another species under this

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[1] Lacépède (1800: pl. 13, fig. 3) first illustrated, then later (1801:428 and 473) described, *Labrus tetracanthus*.

trivial name, *Percis tetracanthus*, from Batavia. *Parapercis tetracantha* (Lacépède) [= *Labrus tetracanthus* Lacépède] is clearly separable from *Percis tetracanthus* Bleeker on the basis of meristics and colouration. Although both *Parapercis clathrata* Ogilby [= *Bodianus tetracanthus* Lacépède] and *P. cephalopunctata* (Seale) fit Bleeker's description of *Percis tetracanthus* well, I consider *Parapercis cephalopunctata* (Seale) rather than *P. clathrata* Ogilby to be conspecific with *Percis tetracanthus* Bleeker since Bleeker (1853b:458) makes specific mention of the presence in his specimens of (1) nine dark reddish lateral transverse bands (these bands are more characteristic of *cephalopunctata*; those of *clathrata* being scarcely discernible) and (2) three dark reddish blotches on the side of the head (these blotches are obvious in *cephalopunctata*; those of *clathrata* being less distinct and, in individuals greater than about 140 mm TL, generally broken up into many oblique bars and irregular spots). In addition, he makes no mention of ocelli in his specimens, the largest of which measured 170 mm TL (*cephalopunctata* lacks ocelli at all sizes; *clathrata* greater than about 140 mm TL possess a large ocellus above each opercle). Although *Percis tetracanthus* Bleeker (1853b) is a senior synonym of *Parapercis cephalopunctata* (Seale, 1901), the latter name is used since Bleeker's (1853b) *tetracanthus* is preoccupied by Lacépède's (1801) *tetracanthus*.

Seale's (1901) original spelling of *cephalopunctatus* is amended to *cephalopunctata* under Article 30 rendered by the International Code of Zoological Nomenclature (1964).

REMARKS: *P. cephalopunctata* appears to be relatively rare within the Great Barrier Reef Province but it is likely that further sampling will show this species to be more abundant than presently believed. The author sighted several individuals of this species over the reef flat of

Wheeler Reef, off Townsville, at one to two metres depth. All were encountered over areas consisting of compacted calcareous rubble, scattered live coral colonies and occasional sand patches.

Maximum recorded total length for this species is 178 mm (Munro, 1955). The largest individual examined during the present study measured 166.3 mm TL (139.5 mm SL) and was collected from Wheeler Reef, northern Queensland.

Parapercis clathrata Ogilby

(Plate 6, Fig. 5)

Bodianus tetracanthus Lacépède, 1802, pp.285 and 302 (type locality, unknown) (non Lacépède, 1801; non Bleeker, 1853b)

Parapercis clathrata Ogilby, 1911, p.41 [substitute name for *Percis tetracanthus* (Lacépède, 1802) = *Bodianus tetracanthus* Lacépède, 1802]; Martin and Montalban, 1935, pp.222-224, pl. 3, fig. 1; Schultz et al., 1960, pp.268-270, pl. 112A; Cantwell, 1964, p.268, figs. 1C, 2C, 9A; Schultz, 1968, p.3-4; Burgess and Axelrod, 1974, p.932, pl. 164; —— 1975, p.1422, pl. 51.

Parapercis cephalopunctata Allen, 1976, pp.29-30 (non Seale, 1901).

MATERIAL EXAMINED:

Great Barrier Reef Province - 19 specimens, 36.9 to 145.4 mm SL. AMS: I. 20547-016, One Tree I. (36.9, 91.0); —— GJS: P.122, South I. (99.5, 114.4); P.342, Lizard I. (92.9, 113.9, 119.1, 134.6); P.274, Macgillivray's Reef (56.4, 69.3, 75.9, 95.0, 119.2, 145.4); P.6, Yonge Reef (74.8, 113.7, 114.4); P.830, No-Name Reef (14°56'S, 144°36'E), off Cape Melville (72.2, 90.6).

Plate 6

Parapercis clathrata

A. Terminal phase individual approx. 130 mm SL, North Point, Lizard Island in 9 m depth

B. Initial phase individual approx. 115 mm SL, North Point, Lizard Island in 9 m depth


A


B

Comparative Material - 11 specimens, 41.7 to 159.9 mm SL. GJS: P.1043, Osprey Reef, Coral Sea (116.3); —— MCZ: 46961, Trincomalee Bay, Ceylon (41.7, 42.3); —— QM: I.10231, Warrora Station, N.W. Australia (156.9); —— WAM: P.26665-003, Dirk Hartog I., N.W. Australia (159.9); P.25369-006, P.25367-006, North-West Cape, N.W. Australia (44.2; 121.5); P.24582, Kendrew Is., Dampier Archipelago, N.W. Australia (54.7); P.26125-005, P.26081-015, P.26092, Christmas I., Indian Ocean (107.8; 122.9; 133.9).

DIAGNOSIS: Palatine teeth absent; six enlarged canines in outer tooth row of lower jaw; dorsal IV, 21; last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; a small intense dark spot or horizontal bar, approximately pupil size, below midside in each of nine scarcely discernible lateral vertical bars; larger specimens (i.e. greater than about 140 mm TL) with a large ocellus above opercle near rear of post-temporal fork.

DESCRIPTION: D. IV, 21. A. I, 17. P. 17-18. V. I, 5. C. 8 + 7. G.R. (5-7) + (8-12). L.lat. 57-60. Tr. (6-7) + (13-14). C.Ped. 26-28. Pred. 10-12.

Body elongate, subcylindrical, greatest depth 6.3 (5.5-7.4); least depth of caudal peduncle 3.8 (3.5-4.1) in HL; snout tip to dorsal fin origin 3.0 (2.9-3.0); tip of lower jaw to anal fin origin 2.1 (2.0-2.2); dorsal profile more arched than ventral profile; head 3.2 (3.1-3.3), somewhat depressed, snout 2.9 (2.7-3.2) in HL; eye moderately large, nearer tip of snout than angle of opercular opening, its diameter 4.1 (3.6-4.5) in HL; interorbital width 19.0 (12.1-25.4), postorbital length 2.1 (1.9-2.3) in HL; mouth large, oblique; lower jaw projecting beyond upper; lips moderately broad; premaxillaries protractile; maxillary partly concealed by preorbital, extending to, or a little beyond, vertical through anterior edge of orbit; snout tip to rear edge of maxillary 2.9 (2.7-3.3) in HL. Opercle with a strong spine at upper angle; subopercle terminating in a flat pointed spine or in a sharp edge; interopercle and preopercle entire.

Teeth in two series on both jaws. Outer series of upper consisting of two large canines on each side at front, followed by two or three smaller canines, another two large canines and one small canine, and finally by about 20 closely spaced small uniserial pointed teeth; inner series a band of dense villiform teeth with width of band decreasing posteriorly. Outer series of lower jaw with three enlarged canine teeth on each side at front increasing in size postero-laterally, followed by a gap and then eight to ten canines (increasing in size posteriorly), and about 10 small uniserial pointed teeth; inner series of lower jaw a band of villiform teeth decreasing in width postero-laterally and usually divided at the midline. Palatine teeth absent. Vomer with a patch of villiform teeth.

Dorsal originating just behind upper part of pectoral base; length of dorsal base 1.7 (1.6-1.9); last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; third dorsal spine longest, 4.6 (4.2-5.1) in HL; soft dorsal higher than spinous dorsal; anal inserted below fifth soft dorsal ray, its basal length 2.4 (2.4-2.6); anal fin height about equal to that of soft dorsal; pectoral rounded, length of longest ray 5.8 (5.1-6.1), not quite reaching or just reaching vertical through anal fin origin; pelvic fin pointed, with rays broadened near tips, fourth soft ray longest 4.6 (3.9-5.4), reaching to between anus and anal fin origin or further; caudal fin rounded.

Snout, interorbital space, and occiput naked; remainder of body with ctenoid scales except for cheeks, jugular region, abdomen, and behind occiput which have cycloid scales; cheeks covered with about 12 rows of small cycloid scales, more or less embedded in the skin; scales present proximally on pectorals and on basal half of caudal; dorsal, anal, and pelvics naked.

Colouration in life - Background grey; body greyish brown above, whitish below, the pale portion set off by a narrow line of brown dots extending from rearmost tip of fleshy operculum to upper caudal base; a brownish W-shaped pattern along upper sides and back. A series of nine prominent blackish spots and/or horizontal bars along sides below lateral line, one spot/bar in each of nine scarcely discernible pale reddish vertical bands; a prominent blackish spot or horizontal bar below base of pectoral fin, in line with, and forming an additional member of this series; all series members connected by a narrow reddish line extending from below pectoral base to lower caudal base; nine indistinct light brown spots about pupil size, midway between this line and dark/light border of upper side, alternating with lateral vertical bars. Dorsal surface of head with numerous roundish dark brown spots (Fig. 5B). Prominent brownish black spot above opercle near rear of post-temporal fork which may (TP i.e. individuals greater than about 140 mm TL), or may not (IP i.e. individuals less than about 140 mm TL) be encircled with a narrow, dark bordered white ring. Upper lip greyish with four to six dark brown blotches, the most prominent being a pair of rounded spots at anterior tip and a large oblong blotch laterally; posterior tip of maxillary silvery white; lower lip bright orange with an indistinct narrow brown band extending along upper margin; two closely spaced dark brown spots, less than pupil size, just below infero-median margin of eye. Large blotch on cheek behind rear edge of maxillary, bright orange-red and generally broken up into two or more oblique bars in TP, pale reddish brown and somewhat indistinct in IP; an irregular silvery white blotch immediately posterior to this first cheek blotch. IP individuals with a large, somewhat indistinct blotch near rounded angle of preopercle, composed of numerous minute, widely spaced, reddish brown dots; in TP individuals this blotch more distinct and generally broken up into about four oblique orange-red bars which extend downwards on to interopercle and subopercle. Both IP and TP individuals with small scattered reddish brown spots on opercle. Spinous dorsal membrane hyaline or slightly dusky. Soft dorsal yellowish white with an indistinct reddish brown submarginal band and two longitudinal rows of reddish brown spots, one of these rows median, the other basal; basal row of spots much darker than median row, the former consisting of pairs of spots formed where W-shaped bars of back meet along mid-dorsal line. Anal fin pale yellow on basal half merging into pale pink near outer margin; a longitudinal row of small reddish brown spots, closer to fin margin than base, present or absent; some individuals with about four widely spaced reddish brown spots forming a longitudinal row at base of fin. Pectoral fin pale yellowish. Basal half of pelvic fin silvery white; remainder of fin pale yellowish. Caudal fin with several scattered small dark spots and/or one (ventro-basal) or two (one dorso-basal, the other ventro-basal) dark horizontal bars; middle rays of posterior half of fin with a silvery white blotch.

Colouration in alcohol - Background cream; body light brown above, creamy white below; the lateral vertical bands and midside pigmentation usually fade so that only the series of blackish spots/horizontal bars remain; the narrow reddish line connecting the series of blackish spots/ bars disappears or becomes a pale tan colour; the orange-red colour of the lower lip and cheeks fades to brown; dorsal and anal fins colourless except for the longitudinal rows of dark spots which lose their reddish tint; paired fins colourless. Remainder of colouration as in life.

DISTRIBUTION:

Great Barrier Reef Province - Widespread throughout the entire Great Barrier Reef Province.

Capricorn Group - One Tree I.; Wheeler Reef, off Townsville (sight record, 9/12/78); Keeper Reef, off Townsville (sight record, 7/4/76); Green I. (photographic record, 2/5/76, G. Stroud); South I.; Lizard I. (Paxton et al., MS); Macgillivray's Reef; Yonge Reef (Paxton et al., MS); No-Name Reef (14°56'S, 144°36'E), off Cape Melville; Halfway I. (sight record, 18/2/79, G. Stroud).

World - Known from Sri Lanka (Ceylon), Christmas Island, and North-Western Australia in the Indian Ocean, as well as the East Indies, Philippines, Taiwan, Great Barrier Reef Province, Coral Sea, Melanesia, and Micronesia.

Sri Lanka. Christmas I. (McKay, 1974; Allen and Steene, 1979). East Indies (Sumadhiharga, 1977). Philippines (Martin and Montalban, 1935). Taiwan (Burgess and Axelrod, 1974). Osprey Reef, Coral Sea. Papua New Guinea (Burgess and Axelrod, 1975). New Britain (photographic record, R. Steene, ident. G. Stroud). Marianas Is. (Kami et al., 1968; Jones and Chase, 1975). Caroline Is. (Cantwell, 1964). Marshall Is. (Hiatt and Strasburg, 1960; Schultz et al., 1960; Cantwell, 1964).

Additional Australian records include: N.W. Australia - Warrora Station; Dirt Hartog I.; North-West Cape (Allen, 1976); Dampier Archipelago (Allen, 1976).

DISCUSSION: Counts, proportions, and gross external morphology indicate *P. clathrata* Ogilby is closely related to *P. cephalopunctata* (Seale). As shown previously, these two species are separable primarily on the basis of colour pattern (see pp.55-56).

Ogilby (1911) introduced the name *Parapercis clathrata* in a list of *Parapercis* species which he considered likely to inhabit Queensland waters, with the following words: "*Parapercis clathrata*; nom. subst. for *Percis tetracanthus* Lacépède, ibid., iv, 1803, pp.285 and 302: inadmissable on account of the preceding species." The preceding species is given as "*Parapercis tetracantha* (Lacépède), Poiss., iii, 1802, pp.473 and 488 = *Percis cancellata* Cuvier and Valenciennes, ibid., p.268." Although Ogilby did not provide a description or lodge any specimens, it is apparent from the page numbers cited that he substituted *Parapercis clathrata* for *Bodianus tetracanthus* Lacépède (1802) and not for *Labrus tetracanthus* (1801) [= *Parapercis tetracantha* (Lacépède)] (see p.56). Martin and Montalban (1935) gave a figure and detailed description of a species collected from the Philippines which they called *Parapercis clathrata* Ogilby. Subsequent authors (e.g. Cantwell, 1964; Schultz, 1968) have followed Martin and Montalban and, as a result, *P. clathrata* has become the accepted name for this species. However, some doubt exists as to whether the species described by Martin and Montalban is the same species as *Bodianus tetracanthus* Lacépède (1802) i.e. the species upon which *Parapercis clathrata* Ogilby is based. Lacépède (1802:285 and 302) described *Bodianus tetracanthus* after a single specimen collected from an unknown locality and says no more than: "Four spinous rays and 21 branched rays to the dorsal fin; 17 rays to the anal fin; posterior of opercle with two spines; head somewhat depressed and broader than the body; upper lip thick and protractile; the teeth slender, hooked and unequal." (translated from the French). The only important species diagnostic character he gives is the dorsal count of IV, 21; a dorsal count which is exhibited by only two known members of the genus *Parapercis*, *P. cephalopunctata* (Seale) and the species called *P. clathrata* Ogilby by Martin and Montalban (1935). Whilst

Martin and Montalban's species could quite possibly be the same species as *Bodianus tetracanthus* Lacépède, the obvious short-comings of Lacépède's (1802) description coupled with the loss of the type specimen of *Bodianus tetracanthus* over 150 years ago [Cuvier and Valenciennes (1829:268) could not locate the type] makes it impossible to determine whether *Bodianus tetracanthus* Lacépède is synonymous with *Parapercis cephalopunctata* (Seale), or with the species called *Parapercis clathrata* by Martin and Montalban (1935). Despite this, the name *Parapercis clathrata* Ogilby is widely used for the species which Martin and Montalban (1935) described under that name. In the interests of stability of the nomenclature it is therefore recommended that a specimen be selected from Martin and Montalban's material and designated neotype of *Bodianus tetracanthus* Lacépède (1802) [= *Parapercis clathrata* Ogilby (1911)] and lodged in the Muséum National d'Histoire Naturelle, Paris.

REMARKS: *P. clathrata* inhabits fringing reefs of continental islands, inner reefs, and outer reefs, at depths ranging from 3 to 65 m. This species was never observed or collected over reef flat areas within the Great Barrier Reef Province, in marked contrast to the closely allied *P. cephalopunctata*. The author observed both *P. clathrata* and *P. cephalopunctata* at Wheeler Reef, off Townsville, the former species (both sexual colour phases observed) over the upper reef slopes, the latter species over the reef flat.

Maximum recorded length for this species is 139.6mm SL (Burgess and Axelrod, 1974). The largest individual examined from the Great Barrier Reef Province during the present study measured 145.4 mm SL (172.6 mm TL) and was collected at Macgillivray's Reef, near Lizard Island. An individual from Dirk Hartog Island, N.W. Australia, which was examined (WAM: P.26665-003), measured 159.9 mm SL (190.6 mm TL), thus representing a new maximum length record for this species.

Parapercis xanthozona (Bleeker)

(Plate 7)

Percis xanthozona Bleeker, 1849, p.55 (type locality, Malay-Moluccan Archipelago); Günther, 1860, p.240; Bleeker, 1861, p.56; Playfair and Günther, 1866, p.69, pl. 8, fig. 3; Weber, 1895, p.267; Steindachner, 1900, p.427.

Percis pleurostigma Sauvage, 1891, pp.317-318 (type locality, Mauritius).

Parapercis atromaculata Fowler, 1904, pp.548-549, pl. 24, lower fig. (type locality, Pandang, Sumatra).

Parapercis xanthozoma Jordan and Seale, 1905, p.414.

Parapercis xanthozona Seale, 1906; p.86; McCulloch, 1914, p.154; McCulloch and Whitley, 1925, p.173; Fowler, 1928, p.425; McCulloch, 1929, p.332; Herre, 1931a, p.9; Giltay, 1933, p.82; de Beaufort and Chapman, 1951, pp.22-23; Kamohara, 1960, pp.6-7; Cantwell, 1964, p.273, figs. 1H, 2H, 9E; Munro, 1967, p.445; pl. 62, fig. 851; Schultz, 1968, p.4.

Parapercis hexophthalmus Jordan and Seale, 1907, p.46 (non Ehrenberg, 1829).

Parapercis dorsonebulosa Martin and Montalban, 1935, pp.220-222, pl. 2, fig. 2 (type locality, Catbalogan, Balabac I., Philippines).

Neopercis xanthozona Kamohara, 1938, p.1452; Matsubara, 1955, p.691; Kamohara, 1958, p.67.

Parapercis hexophtalma Fourmanoir and Laboute, 1976, p.134 (non Ehrenberg, 1829).

MATERIAL EXAMINED:

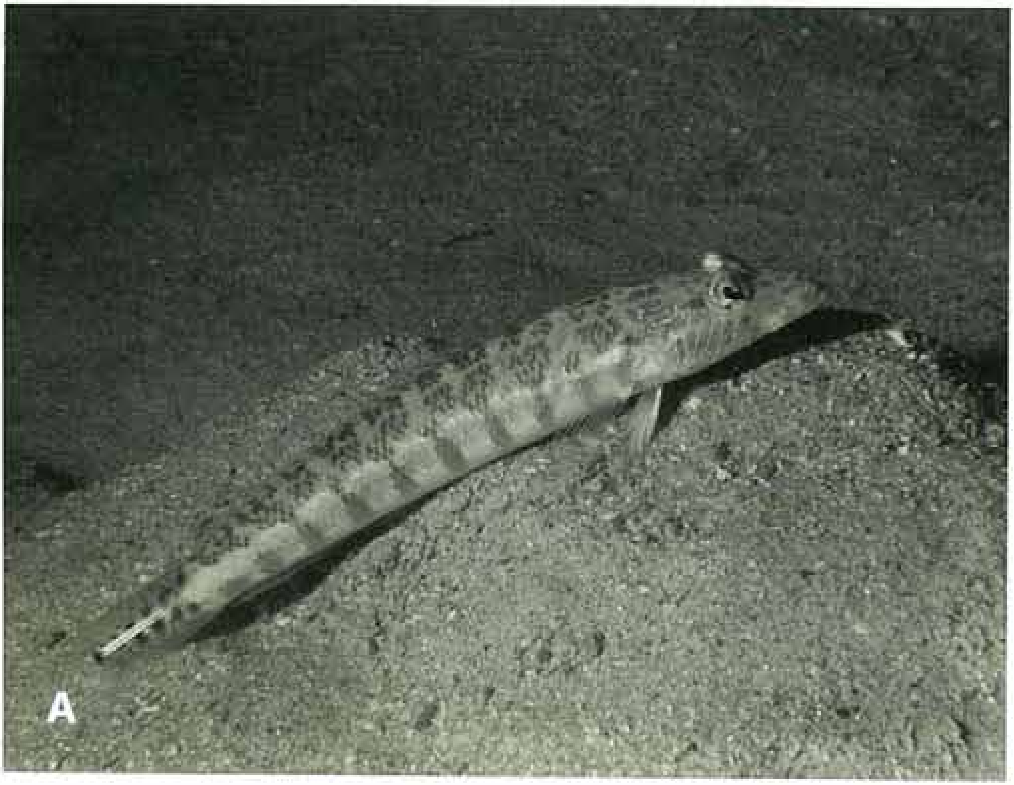
<u>Great Barrier Reef Province</u> - 18 specimens, 19.9 to 138.1 SL. AMS:

Plate 7

Parapercis xanthozona

A. Terminal phase individual approx. 140 mm SL, South Island in 10 m depth

B. Initial phase individual approx. 110 mm SL, Palfrey Island in 11 m depth


A


B

I.18739-039, lagoon, Lizard I. (131.4); —— GJS: P.828, No-Name Reef #2 (17°52'S, 146°43'E) (75.5); P.542, North Direction I. (111.0, 121.7); P.248, Eyrie Reef (94.4, 111.4); P.561, South I. (63.8); P.170, Palfrey I. (26.3); P.121, Bird I. (41.0); P.116, lagoon, Lizard I. (103.2); P.131, Aborigine Bluff, Lizard I. (33.7); P.55, Macgillivray's Reef (110.4, 138.1); P.820, Clack Reef (19.9, 77.8); P.815, Haggerstone I. (68.9, 74.4); P.803, Halfway I. (95.5).

Comparative Material - 2 specimens, 47.8 and 51.8 mm SL. MNHN: 1980-648, New Caledonia (47.8, 51.8).

DIAGNOSIS: Palatine teeth absent; six enlarged canines in outer tooth row of lower jaw; dorsal V, 21; last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 58-64; circum-peduncle scales 27-30; lower side of body with nine dark vertical bands which fade ventrally, not reaching midventral line; a pale longitudinal band extending from pectoral axil to midbase of caudal fin; larger individuals (i.e. greater than about 140 mm TL) with 7-12 narrow, oblique, light bars running across cheek, opercle, and subopercle.

DESCRIPTION: D. V, 21. A. I, 16-18. P. 16-18. V. I, 5. C. 8 + 7. G.R. (5-7) + (9-12). L.lat. 58-64. Tr. (5-7) + (13-15). C.Ped. 27-30. Pred. 9-11.

Body elongate, subcylindrical, rather depressed anteriorly and compressed posteriorly, greatest depth 6.0 (5.3-6.7); least depth of caudal peduncle 3.6 (3.5-3.9) in HL; snout tip to dorsal origin 3.1 (2.8-3.2); tip of lower jaw to anal origin 2.1 (1.9-2.3); dorsal and ventral profiles arched to about same extent; head 3.3 (3.0-3.4), somewhat depressed; snout 2.9 (2.7-3.7) in HL; eye moderately large, projecting little if at all above head profile, closer to tip of snout than rear edge of fleshy operculum; eye diameter 3.9 (3.4-4.7) in HL; interorbital width 24.5 (18.4-44.0), postorbital length 2.2 (2.1-2.3), in HL; mouth large, oblique; lower jaw projecting beyond upper; lips broad; premaxillaries protractile; maxillary almost entirely concealed under preorbital, extending to a vertical through anterior edge of orbit; snout tip to rear edge of maxillary 2.8 (2.6-3.0) in HL. Opercle with spine at upper angle; subopercle terminating in a single large blunt flat spine and/or about five small sharp spines; preopercle and interopercle entire.

Teeth in two series on both jaws. Outer series of upper jaw consisting of two large canines on each side at front, followed by four smaller canines, another two large canines, and about 18 closely spaced small uniserial pointed teeth; inner series a band of dense villiform teeth, with width of band decreasing posteriorly. Outer series of lower jaw with three enlarged canine teeth on each side at front increasing in size latero-posteriorly, followed by a gap and then four small canines, two larger canines, and about 12 small uniserial pointed teeth; inner series of lower jaw a band of villiform teeth which is usually divided at the midline. Palatine teeth absent. Vomer with a patch of about 20 villiform teeth, anterior row with the largest teeth.

Dorsal originating just behind vertical through upper pectoral base; length of dorsal base 1.7 (1.6-1.8); last dorsal spine connected by membrane to first soft dorsal ray at about level of tip of last spine; third or fourth dorsal spine longest, 4.2 (3.8-5.1) in HL; soft dorsal higher than spinous dorsal; anal inserted below fifth soft dorsal ray, its basal length 2.3 (2.2-2.4); height of anal slightly less than soft dorsal; pectoral rounded, length of longest ray 5.8 (4.0-7.6), reaching to, or a little behind, vertical through anal fin origin; pelvic fin pointed, fourth soft ray longest 4.6 (3.9-6.1), reaching to about third anal ray; caudal fin rounded with a projecting, pointed upper lobe.

Snout, interorbital space, and occiput naked; remainder of body with ctenoid scales except for cheeks, jugular region, abdomen, and behind occiput which have cycloid scales; cheeks covered with about 12 rows of small cycloid scales, more or less embedded in the skin; scales present proximally on pectorals and basal half of caudal; dorsal, anal, and pelvics naked.

Colouration in life - Background light tan. Abdomen whitish. Back and upper sides with nine or ten dark brown saddles, usually one below spinous dorsal, eight below soft dorsal (these paired and joined ventrally forming four U-shaped markings), and one on upper region of caudal peduncle; dark saddles ending at a whitish longitudinal band which extends from pectoral axil to mid-base of caudal fin; nine or ten vertical dark brown bars beneath this whitish band fading ventrally so that they do not reach the midventral line; an indistinct brownish line connecting these bars at their border with whitish lateral band; some individuals with narrow extensions to vertical bars which penetrate, and occasionally traverse, white lateral band. Dorsal surface of head light brown; eight to ten small dark brown spots behind eyes; about ten larger dark brown spots, each darkest around its periphery, on snout, the most prominent being a pair just anterior to interorbital. Upper lip with six dark brown spots (about same size as snout spots), each spot generally darkest around its periphery; lower lip with three dark blotches, one at anterior tip, and one oblong blotch laterally on each side. Throat, branchiostegal membrane, interopercle unpigmented. Two brown blotches on cheek, the first below infero-anterior margin of eye, the second, made up of numerous minute brown dots, larger but less distinct than the first, below infero-posterior margin of eye, extending nearly to upper angle of preopercle. Opercle and subopercle overall light brown with a few scattered brown spots; cheek, opercle, and subopercle may (TP i.e. individuals greater than about 140 mm TL) or may not (IP i.e. individuals less than about 140 mm TL) be traversed by 7-12 narrow, oblique, dark bordered, whitish bars. Base of spinous dorsal with a dark brown blotch between first and fourth spines. Soft dorsal pale yellow with three longitudinal rows (one each basal, median, and submarginal) of small dark brown spots; often an indistinct narrow brown band near edge of fin above submarginal row of spots. Anal fin pale yellow with a narrow reddish brown submarginal band, and with or without a median longitudinal row of dark brown spots. Pectoral fin hyaline, an orange blotch at its base. Basal half of pelvic fin white, outer half hyaline. Caudal fin with a bright white blotch on posterior two thirds of middle rays; this blotch bordered dorsally and ventrally by brownish black spots which generally form longitudinal rows extending to hind margin of fin.

Colouration in alcohol - Background brownish tan; back overall dusky brown with groups of dark brown margined scales where U-shaped markings were present (the latter markings often indistinct in preserved specimens); abdomen creamy white; oblique cheek bars of TP, and whitish lateral band common to both IP and TP, fade to creamy white; dark line connecting vertical bars on lower sides disappears or becomes scarcely discernible; yellowish tint of soft dorsal, yellowish and reddish tint of anal, whitish pigmentation of pelvics, orange patch on pectoral base, and the majority of snout spots, are lost on preservation. Remainder of colouration as in life.

DISTRIBUTION:

Great Barrier Reef Province - Known only from the central and northern regions of the Great Barrier Reef Province.

Keeper Reef (sight record, 7/4/76); No-Name Reef #2 (17°52'S, 146°43'E); North Direction I.; Eyrie Reef; South I.; Palfrey I.; Bird I.; Lizard I. (Paxton et al., MS); Macgillivray's Reef; Clack Reef; Haggerstone I.; Halfway I.; Torres Strait - Thursday I. (Weber, 1895).

World - Widespread throughout the Indo-West Pacific from Zanzibar off the East African coast, to the western Pacific as far north as southern Japan and south to about Townsville, Queensland; the Samoan Islands appear to form the eastern limit of distribution.

Zanzibar (Playfair and Günther, 1866; Sauvage, 1891). Madagascar (de Beaufort and Chapman, 1951). Mauritius (Sauvage, 1891). East Indies (Bleeker, 1849; Günther, 1860; Bleeker, 1861; Playfair and Günther, 1866; Sauvage, 1891; Steindachner, 1900; Fowler, 1904; Jordan and Seale, 1905; Giltay, 1933; de Beaufort and Chapman, 1951). Gulf of Siam (Cantwell, 1964). Philippines (Jordan and Seale, 1907; Martin and Montalban, 1935). Indo-China (de Beaufort and Chapman, 1951). Southern Japan (Kamohara, 1958, 1960). Papua New Guinea (Munro, 1967). Solomon Is. (Seale, 1906; Fowler, 1928, Herre, 1931a). New Caledonia (Fourmanoir and Laboute, 1976). New Hebrides (Fourmanoir and Laboute, 1976). Fiji Is. (Cantwell, 1964). Samoan Is. (Jordan and Seale, 1905).

Additional Australian records include: "Queensland" (McCulloch, 1929; Giltay, 1933; de Beaufort and Chapman, 1951).

DISCUSSION: The closest relative of *Parapercis xanthozona* (Bleeker) is *Parapercis stricticeps* (De Vis). These species differ in dentition, morphometrics, and colour pattern, though especially the latter. Major differences are as follows: (1) *xanthozona* with throat, interopercle, and branchiostegal membrane unpigmented; *stricticeps* with either scattered brownish black pigment spots, or four brownish black transverse bars, on throat, interopercle, and branchiostegal membrane; (2) large individuals (i.e. greater than about 140 mm TL) of *xanthozona* with 7-12 narrow, oblique, dark bordered whitish bars running across cheek, opercle, and subopercle; large individuals of *stricticeps* with two brownish black bars on cheek, the first somewhat triangular, just behind rear edge of maxillary, the second bar beginning at infero-median margin of eye, running slightly obliquely across cheek to lower angle of preopercle, and then on to interopercle; (3) snout of *xanthozona* with about ten dark brown spots and no bars; *stricticeps* with a dark brown bar extending from anterior margin of eye through nostrils almost to edge of snout, plus about five spots on middle of snout; (4) *xanthozona* with a median, *stricticeps* with a basal, single longitudinal row of dark brown spots on anal fin, when these are present.

Cantwell (1964) places *Parapercis stricticeps* (De Vis) in the synonymy of *Parapercis xanthozona* (Bleeker). However, after examining the holotype of the former, plus several other specimens under this name in the collections of the Australian and Queensland Museum it is clear that *P. xanthozona* and *P. stricticeps* are separate species [*P. stricticeps* material examined. —— AMS: I. 19696-008, South Solitary I., New South Wales (87.5, 120.5); I. 19159-004, Sydney Harbour, New South Wales (43.0); —— QM: I. 1708, holotype of *Percis stricticeps* De Vis, Southport, southern Queensland (145.2); I. 5991, Mooloolabah, southern Queensland (138.6, 176.4)].

REMARKS: A rather common mugiloidid of central and northern Great Barrier Reef waters, *P. xanthozona* inhabits lagoons and/or reef slopes of inner reefs, coastal reefs, and continental island fringing reefs, at depths ranging from 3 to 35 m. This species is most commonly encountered at the interface between the sand of the off-reef floor and the sand-rubble region of lower reef slopes.

Maximum recorded total length of *P. xanthozona* is 195 mm (Kamohara, 1938; Cantwell, 1964). The largest individual examined during the present study measured 164.9 mm TL (138.1 mm SL) and was collected from Macgillivray's Reef, near Lizard Island, northern Queensland.

Parapercis nebulosa (Quoy and Gaimard)

(Fig. 6)

Percis nebulosa Quoy and Gaimard, 1824, pp.349-350 (type locality, Shark Bay, N.W. Australia); Cuvier and Valenciennes, 1829, pp. 260-264; Günther, 1860, pp.237-238; Castelnau, 1879, p.351; Macleay, 1881, pp.563-564.

Percis emeryana Richardson, 1842, pp.130-131 (type locality, Depuch I., N.W. Australia); —— 1843, p.4, pl. 1, fig. 1; Bleeker, 1853a, p.26; —— 1855, p.6.

Dentex fasciatus Solander, in Richardson, 1846, p.211 (type locality, Australia).

Parapercis nebulosa Bleeker, 1875, p.78; Ogilby, 1911, p.40; McCulloch and Whitley, 1925, p.173; Whitley, 1964b, p.52.

Percis coxii Ramsay, 1884, p.179 (type locality, Port Jackson, New South Wales).

Percis concinna De Vis, 1885, p.546 (type locality, Moreton Bay, S. Queensland).

Percis coxi Waite, 1899, p.111.

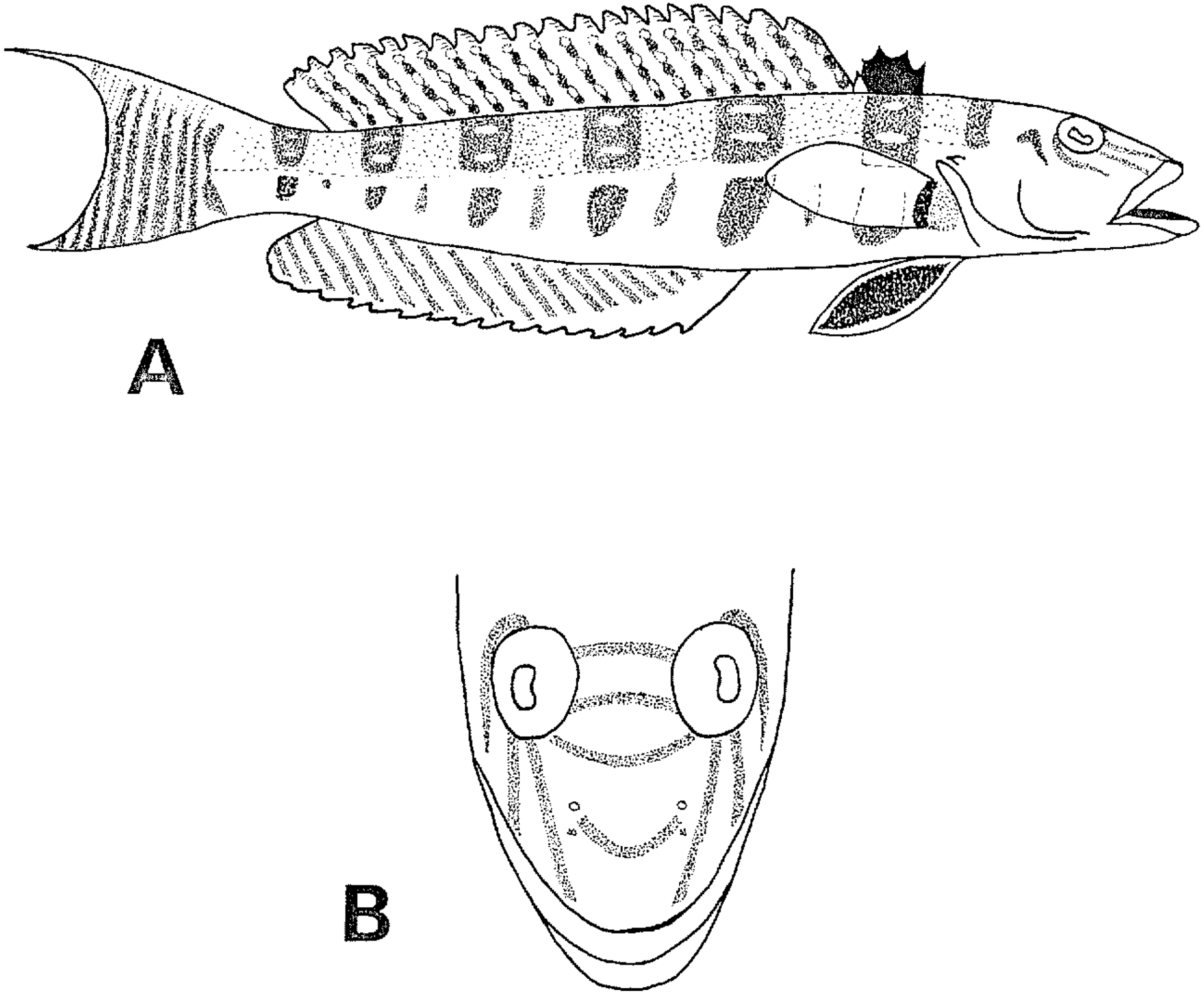
Parapercis nebulosus Waite, 1899, p.111; —— 1904, p.49; —— 1905, p.75; McCulloch, 1914, p.156; —— 1927, p.75; —— 1929, p.331; Whitley, 1940, p.425; —— 1948, p.27; Ogilby, 1954, pp.84-85, fig. 99;

Figure 6

Diagram of *Parapercis nebulosa* showing major features of colour pattern

A. Lateral view

B. Pattern of lines on snout and interorbital (dorsal view)


A
B

Marshall, 1964, p.329, col. pl. 49; Burgess and Axelrod, 1974, p.933, pl. 167; Grant, 1975, p.439.

Parapercis emeryana Cantwell, 1964, pp.258-259, figs. 1Q, 3Q, 7C; Schultz, 1968, p.3; Allen, 1976, pp.29-30.

MATERIAL EXAMINED:

Great Barrier Reef Province - 21 specimens, 83.5 to 184.7 mm SL. GJS: P.127, off Cape Bowling Green (19°03'S, 147°07'E) (117.2, 184.7); P.125, off Cape Cleveland (19°01'S, 146°53'E) (119.9, 178.1); P.751, off John Brewer Reef (102.8, 136.0, 145.9); P.826, 10 mls. N.W. of Nymph I. (14°33'S, 145°06'E) (83.5, 95.1, 101.8); P.819, Princess Charlotte Bay (119.9); P.806, 1-9 mls. E. of Capt. Billy's Creek (11°37'S, 142°56'E) (129.9, 133.5, 138.2, 148.6, 149.2, 165.7, 175.5); P.801, 3 mls. E. of Turtle Head I., Cape York (106.9); —— QM: I. 13444, Palm I. (164.4); I. 16357, off Warrior Reefs, Torres Strait (9°40'S, 142°56'E) (172.7).

Comparative Material - 10 specimens, 66.5 to 197.0 mm SL. AMS: I. 18199-001, Balmoral Beach, Sydney Harbour, N.S.W. (66.5); I. 17279-002, Seal Rocks, N.S.W. (151.6); I. 16486-001, mouth of Clarence River, N.S.W. (150.1, 152.2, 175.2, 197.0); I. 11025, mouth of Wide Bay, S. Queensland (144.8); IB. 3022, Exmouth Gulf, N.W. Australia (113.0); —— QM: I. 742, Great Sandy Strait, S. Queensland (180.6); I. 10310, Exmouth Gulf, N.W. Australia (93.9).

DIAGNOSIS: Palatine teeth absent; six enlarged canines in outer tooth row of lower jaw; last dorsal spine connected by membrane to base of first soft dorsal ray; total gill rakers 17-21; circum-peduncle scales 36-40; spinous dorsal black between spines I and V; a narrow dark band on posterior two-thirds of lower lip; most individuals with three dark (blue in life) lines joining the eyes across interorbital.

DESCRIPTION: D. V, 22. A. I, 18. P. 16-17. V. I, 5. C. 8 + 7. G.R. (6 + 8) + (11-13). L.lat. 79-86. Tr. (11-13) + (19-21). C.Ped. 36-40. Pred. 12-15.

Body elongate, moderately compressed, greatest depth 5.7 (4.9-6.6); least depth of caudal peduncle 3.2 (3.0-3.5) in HL; snout tip to dorsal origin 3.6 (3.1-3.8); tip of lower jaw to anal origin 2.3 (2.1-2.4); dorsal profile only slightly more arched than ventral profile; head 3.6 (3.3-3.8), moderately large, rounded, somewhat depressed; snout with a parabolic contour, 2.9 (2.6-3.3) in HL; eye large, directed obliquely upwards, moderately high, closer to tip of snout than edge of opercle, its diameter 3.8 (2.8-4.6) in HL; interorbital width 9.5 (6.1-13.2), postorbital length 2.1 (2.0-2.3) in HL; mouth large, oblique; lower jaw projecting beyond upper; lips moderately broad; premaxillaries weakly protractile; maxillary concealed by preorbital, extending a little behind vertical through anterior edge of orbit; snout tip to rear edge of maxillary 2.4 (2.1-2.9) in HL. Opercle with spine at upper angle; subopercle terminating in a spine which may or may not be divided irregularly into two or three points; interopercle and preopercle entire.

Teeth in two series on both jaws. Outer series of upper jaw consisting of two large canines on each side at front, followed by one or two smaller canines, another four large canines, and about 15 closely spaced small uniserial pointed teeth; inner series a band of dense villiform teeth, with width of band decreasing posteriorly. Outer series of lower jaw with three enlarged canine teeth on each side at front increasing in size latero-posteriorly, followed by a gap and then about five small canines, four larger canines increasing in size posteriorly, and about 12 small uniserial pointed teeth; inner series of lower jaw a band of villiform teeth which is divided at the midline. Palatine teeth absent. Vomer with a row of six to eight villiform teeth.

Dorsal originating above or slightly behind upper part of pectoral base; length of dorsal base 1.5 (1.5-1.6); last dorsal spine connected by membrane to base of soft dorsal ray forming a deep notch between spinous and soft portions; third dorsal spine longest, 3.8 (3.6-4.5) in HL; soft dorsal higher than spinous dorsal; anal inserted below fifth soft dorsal ray, its basal length 2.1 (2.0-2.2); height of anal slightly less than soft dorsal; pectoral small, rounded, length of longest ray 6.1 (5.6-6.8), reaching to or beyond vertical through anal opening; pelvic fin pointed with rays broadened near tips, fourth soft ray longest 5.6 (5.0-6.2), generally reaching to between anus and anal fin origin. Caudal fin in young individuals slightly emarginate with the outer angles pointed; older individuals with outer rays produced into filaments, the upper lobe usually more developed than the lower lobe.

Snout, interorbital space, and occiput naked; remainder of body with ctenoid scales except for jugular region, abdomen, and anterior third of cheek which have cycloid scales; posterior two-thirds of cheek with about 12 rows of small, finely ctenoid scales, more or less embedded in the skin; scales present proximally on pectorals and basal half of caudal; dorsal, anal, and pelvics naked.

Colouration in life - Background reddish pink on back and upper sides, primrose yellow on lower sides, fading to white on abdomen. Six slightly oblique, dark red bands on back extending from dorsal midline to lower sides, one under spinous dorsal, four under soft dorsal, and one on caudal peduncle; an indistinct pale pink mid-lateral band extending from behind upper pectoral base to mid-base of caudal dividing these lateral bands into two segments; each upper segment square to rectangular in outline with light interruptions in its centre; lower segment smaller than upper, more rounded in outline, and without lighter centre. Head pink with a broad red band running downwards from behind eye to rounded angle of preopercle, and a narrow dark red band extending from just above upper angle of opercle to nape, the latter band reaching the dorsal midline; occiput with or without a dark red bar; eye scarlet with a black pupil, the scarlet colour entering pupil above causing it to appear dented. Most individuals with a network of narrow blue lines across the snout, interorbital, and cheeks (Fig. 6B), their number and arrangement as follows: (1) three between eyes across interorbital; (2) two extending from anterior margin of each orbit to upper lip; (3) a curved one across snout between the two pairs of nostrils; and (4) one running across upper part of cheek following curve of orbit, not quite reaching upper lip. Upper lip reddish brown anteriorly, remainder pinkish; a narrow brownish black band on posterior two thirds of lower lip. Spinous dorsal black between spines I and V; membrane whitish between last dorsal spine and first soft dorsal ray; soft dorsal pinkish with six to eight alternating white and pale pink spots on membrane behind each ray. Anal white with a broad dark red submarginal band, and oblique pink stripes and spots on remainder of fin. Pectoral hyaline pink with a pearly silvery spot at base followed by a dark spot on scaled portion of fin. Pelvic fin with rays whitish, membrane blackish, and a pinkish tinge distally. Caudal pinkish, dark red on ventral edge grading into orange-yellow on dorsal edge, with four to eight wavy transverse reddish brown bars on posterior two-thirds of fin; caudal fin in young individuals with two dark red spots, one ventro-basal, the other dorso-basal, and fewer transverse bars.

Colouration in alcohol - Background light brown above, creamy white below; oblique bands on back and sides of body, plus all other dark red markings, fade to dark brown; pale pinkish mid-lateral band cream in colour and much more distinct; blue lines of snout, interorbital, and cheeks, if present in life, fade to dark brown, or disappear completely; soft dorsal almost hyaline with six to eight alternating white and brown spots on membrane behind each ray; dark red sub-marginal band, and pinkish oblique bars and spots of anal become dark brown and light tan respectively; paired fins lose their pinkish tinge; caudal fin fades to a creamy colour, brownish black on its ventral edge grading into creamy white on its dorsal edge; wavy transverse reddish brown bars of caudal fin fade to light brown forming alternate white and dark bars; the two reddish brown spots on the caudal base of young individuals become brownish black on preservation. Remainder of colouration as in life.

DISTRIBUTION:

Great Barrier Reef Province - Widespread throughout the entire Great Barrier Reef Province.

Off Bustard Head Lighthouse (McCulloch, 1914); off Cape Bowling Green; off Cape Cleveland; Palm I.; off John Brewer Reef; 10 mls N.W. of Nymph I.; Princess Charlotte Bay; 1-9 mls. E. of Capt. Billy's Creek; 3 mls. E. of Turtle Head I., Cape York; off Warrior Reefs, Torres Strait.

World - Known from Madagascar, Réunion, Mauritius, and Western Australia in the Indian Ocean, and from Taiwan and the eastern coast of Australia as far south as Port Jackson (New South Wales) in the western Pacific.

Madagascar (Bleeker, 1875). Réunion (Cuvier and Valenciennes, 1829; Bleeker, 1875). Mauritius (Günther, 1860). Taiwan (Burgess and Axelrod, 1974).

Additional Australian records include: Western Australia - "Western Australia" (McCulloch, 1929; Whitley, 1948; Marshall, 1964; Allen, 1976); Mandurah (Waite, 1905); Shark Bay (Quoy and Gaimard, 1824; Cuvier and Valenciennes, 1829; Günther, 1860); Exmouth Gulf (Cantwell, 1964); Dampier Archipelago (Cantwell, 1964); Depuch I. (Richardson, 1842; Günther, 1860). New South Wales - "New South Wales" (Waite, 1904;

McCulloch, 1929); Port Jackson (Castlenau, 1879; Ramsay, 1884; Waite, 1899; Ogilby, 1911; McCulloch, 1927); Seal Rocks; mouth of Clarence River. Queensland - "Queensland" (Ogilby, 1911; McCulloch, 1929; Ogilby, 1954; Marshall, 1964; Grant, 1975); Moreton Bay (De Vis, 1885); 22 mls. N.W. of Double I. Point (McCulloch, 1914); Great Sandy Strait; Fraser I. (McCulloch, 1914); Bustard Head Lighthouse (McCulloch, 1914).

DISCUSSION: The species from the Persian Gulf, Gulf of Oman, Seychelles, Aldabra, and east coast of Arabia, referred to as *Parapercis nebulosa* by Barnard (1927) and others (e.g. Fowler, 1934b; Smith and Smith, 1963; Cantwell, 1964; Smith, 1965; Schultz, 1968), is not the true *nebulosa* originally described by Quoy and Gaimard (1824) from specimens collected at Shark Bay, N.W. Australia. These two species, whilst obviously closely related, show important differences in gill raker count, number of scales from lateral line to first soft dorsal ray, dentition, caudal fin shape, and colour pattern (Table 1).

Specimens from Great Barrier Reef waters agree well with Quoy and Gaimard's (loc. cit.) original description of *Percis nebulosa* and also with Cuvier and Valenciennes (1829) description of this species (the latter authors examined Quoy and Gaimard's specimens from Shark Bay plus other specimens from Réunion). In their description, Quoy and Gaimard (1824) mention a black spinous dorsal, a silvery spot at the pectoral base, and a forked caudal fin filamentous at its two margins. Cuvier and Valenciennes (1829) also make mention of (1) two rows of five or six large brown blotches on the side of the body, those in the row above the lateral line square in outline, those in the row below the lateral line smaller and more rounded; (2) each blotch of the upper row reaching the dorsal fin base and possessing light interruptions in its centre; (3) white and brown spots on the soft dorsal; and (4) white bars across the

Table 1. Characters which separate *Parapercis nebulosa* Barnard, 1927 from *P. nebulosa* (Quoy and Gaimard, 1829)

	Parapercis nebulosa Barnard, 1927*	*Parapercis nebulosa* (Quoy and Gaimard, 1824)
Scales from lateral line to 1st soft dorsal ray	8-10	11-13
Total gill rakers	11-17 (usually 13-14)	17-21 (usually 18-20)
Longest dorsal spine	IV	III
Number of vomerine teeth	4	6-8
Caudal fin shape	Rounded in young; rounded to truncate in larger individuals	Slightly emarginate with outer angles pointed in young; larger individuals with outer rays produced into filaments
Pigmentation of back	8 large black V-shaped markings	6 large square/rectangular shaped markings
Pigmentation of pale midlateral band	Dark edged on its dorsal and ventral margins	Without dark edging
Pigmentation of lower sides	8-9 vertical black bars which may or may not reach midventral line	6 roundish blotches which never reach midventral line
Pigmentation of lower lip	No narrow dark band	A narrow dark band on posterior two-thirds of lower lip
Pigmentation of pectoral fin base	Large black blotch	Large pearly-silver blotch
Pigmentation of spinous dorsal fin	Pale overall, indistinctly spotted with fine dark brown specks	Jet black between spines I and V
Pigmentation of soft dorsal fin	As above	6-8 alternating white and light brown spots on membrane behind each ray
Pigmentation of caudal fin	Many small dark spots; no alternating white and dark wavy transverse bars	No small dark spots; several alternating white and dark wavy transverse bars

* Data for this species from the literature (Barnard, 1927; Smith and Smith, 1963; Cantwell, 1964) and a 164.2 mm SL specimen (MNHN:02-153) from the Persian Gulf.

caudal fin. Neither Quoy and Gaimard (loc. cit.) or Cuvier and Valenciennes (loc. cit.) made mention of dark bars joining the eyes across the inter-orbital, however, this is not surprising since it was found that these bars may or may not be present in the living animal, and if present, often fade and disappear on preservation, even after only a short period of time.

REMARKS: *Parapercis nebulosa* (Quoy and Gaimard) inhabits the off-reef floor adjacent to coastal reefs, fringing reefs of continental islands and inner reefs of the Great Barrier Reef Province. Although occasionally encountered in water as shallow as 5 m (N.E. Milward, pers. comm.), *P. nebulosa* is essentially a deepwater species apparently most abundant between 15 and 58 m depth.

Maximum recorded total length for this species is 343 mm (Grant, 1975). The largest individual examined during the present study from the Great Barrier Reef Province measured 231.5 mm TL (184.7 mm SL) and was trawled off Cape Bowling Green, near Townsville, at a depth of 21 m.

Parapercis diplospilus

(Fig. 7)

Parapercis diplospilus Gomon, 1980 , pp. 989-996, figs. 1,2 (type locality Visayan Sea, Philippine Islands).

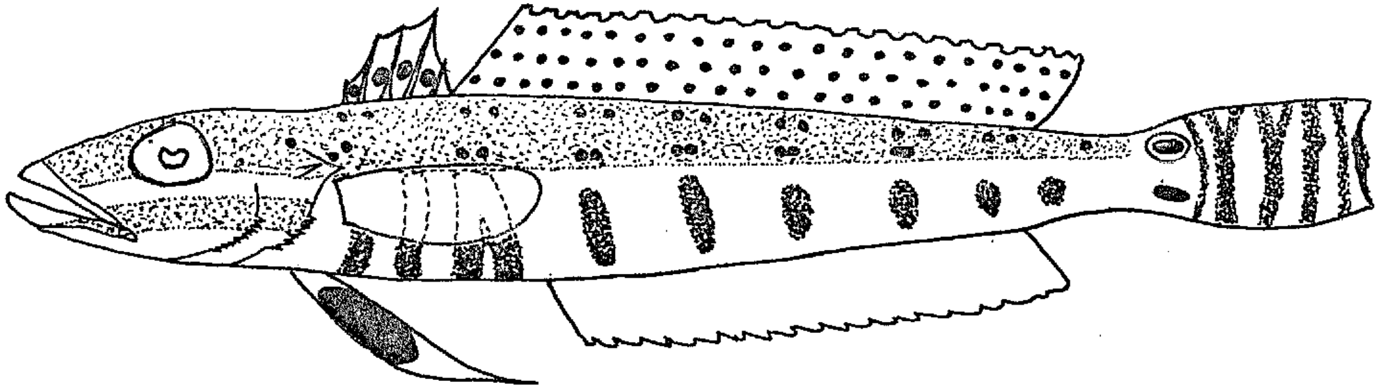
MATERIAL EXAMINED:

Great Barrier Reef Province - 2 specimens, 61.7 and 69.5 mm SL. GJS: P.1042, deepwater off Townsville (19°08'S, 146°55'E) (61.7); —— QM: I. 11015, North Palm I. (69.5).

Comparative Material - 1 specimen, 69.0 mm SL. QM: I. 13049, west of Moreton I. (69.0); 3 specimens, 64.0-76.9, AMS: I.21362-001, Visayan Sea, Philippine Islands, paratypes of *Parapercis diplospilus* Gomon.

Figure 7

Diagram of *Parapercis diplospilus* showing major features of colour pattern



DIAGNOSIS: Palatine teeth absent; 8-12 (usually 8) enlarged canines in outer tooth row of lower jaw; middle dorsal spines longest; last dorsal spine connected by membrane to base of first soft dorsal ray; oblique scale rows crossing lateral line from upper angle of gill opening to caudal base 55-56; circum-peduncle scales 21-22; two prominent dark spots on caudal base, the upper one ocellated, the lower of equal size or slightly more oblong, and not ocellated.

DESCRIPTION: D. V, 21-22. A. I, 18. P. 15-16. V. I, 5. C. 8 + 7. G.R. (2-5) + (7-9). L.lat. 50-55. Tr. 3 + (10-11). C.Ped. 21-22. Pred. 7-11. Ch. 5-6.

Body elongate, greatest depth 6.3 (6.2-6.3); least depth of caudal peduncle 3.6 (3.4-3.8) in HL; snout tip to dorsal origin 3.5 (3.4-3.5); tip of lower jaw to anal origin 2.2; dorsal and ventral profiles about evenly arched; head 3.7 (3.6-3.8); snout length 3.6 (3.5-3.8) in HL; eye moderately large, just reaching head profile, slightly closer to tip of snout than edge of opercle, its diameter 3.1 (3.0-3.2) in HL; interorbital width 19.3 (19.1-19.5), postorbital length 2.1 (2.0-2.1), in HL; mouth moderately large, oblique; lower jaw projecting beyond upper; lips narrow, premaxillaries protractile; maxillary almost entirely concealed by preorbital extending to vertical through anterior edge of orbit; snout tip to rear edge of maxillary 3.4 (3.3-3.4) in HL. Opercle with a strong spine at upper angle; subopercle with 11-16 small spines along posterior margin; interopercle terminating in a spine or sharp point; preopercle with one to five small spines on margin of angular portion.

Teeth in two series on both jaws. Outer series of upper jaw a single row of large, curved, conical teeth decreasing in size posteriorly; inner series a band of dense villiform teeth with width of band decreasing posteriorly. Outer series of lower jaw with 4-6 (usually 4) enlarged canines on each side at front; inner series a band of villiform teeth mesially, continuing postero-laterally to a single row of small conical teeth. Palatine teeth absent. Vomer with a patch of small villiform teeth in two or three rows.

Dorsal originating above rearmost tip of fleshy operculum; length of dorsal base 1.6 (1.5-1.6); last dorsal spine connected by membrane to base of first soft dorsal ray forming a deep notch between spinous and soft portions; fourth dorsal spine longest, 3.1 (3.0-3.1) in HL; soft dorsal higher than spinous dorsal; anal fin inserted below fifth soft dorsal ray, its basal length 2.2 (2.1-2.2); pectoral fin acutely rounded, length of longest ray 5.5 (5.3-5.7), reaching to or slightly posterior to vertical through anal fin origin; pelvic fin slender, pointed, fourth soft ray longest, 5.4 (5.1-5.7), reaching to or slightly posterior to anal fin origin; caudal fin truncate, outermost rays slightly produced.

Snout and interorbital space naked; remainder of body with ctenoid scales; scales present proximally on caudal and pectorals; dorsal, anal, and pelvics naked.

Colouration in alcohol - Background creamy tan; free edges of body scales and scale pockets above lateral line dark pigmented giving upper half of body an overall dark brown appearance. A longitudinal row of about 14 small brown spots grouped into seven pairs on back near base of dorsal fin (one pair under spinous dorsal, six under soft dorsal); a similar longitudinal row of about six paired spots (some pairs may be coalesced forming a single large spot) along mid-side of body. Ventral half of body paler with about 10 dark brown vertical or oblique bars, the posterior four often reduced to small blotches; first bar extending from just behind pectoral base to just behind pelvic base; second bar usually extending to midventral line; third bar not reaching midventral line; fourth and fifth bars reaching midventral line and forming a dark

U-shaped ring round anal opening. Scaled portion of dorsal head surface with same tesselated appearance as upper body. Snout and remainder of unscaled portion of head overall light brown, the former with about four short dark brown bars. Narrow dark brown bar running from posterior edge of opercle across cheek and on to lateral portion of lips; this bar sometimes indistinct and broken up into two small blotches on cheek, and one on opercle. Upper lip with two light brown spots anteriorly; lower lip and chin with many, branchiostegal membrane and isthmus with few, scattered dark brown melanophores. Spinous dorsal with four large, somewhat diffuse dark brown spots (one spot on membrane between each spine) forming a band between spines I and V. Soft dorsal with three or four (usually three) longitudinal rows of dark brown spots on membranes; remainder of fin hyaline. Anal fin with dark brown melanophores on anterior halves of membranes directly behind rays; posterior halves without melanophores. Distal margin of pectoral fin with scattered dark brown melanophores; base and scaled portion of fin with an oblique dark brown bar. Anterior two-thirds of pelvic fin with a large brownish black blotch. Two prominent dark spots about pupil size at base of caudal fin, dorsal one surrounded by a narrow whitish ring, thus forming an ocellus; ventral one non-ocellate and slightly more elongate than upper spot; remainder of fin with about three brownish black vertical bars and middle fin rays edged distally in the same colour.

DISTRIBUTION:

<u>Great Barrier Reef Province</u> - Known from the central region of the Great Barrier Reef Province.

Off Townsville (19°08'S, 146°55'E); North Palm I.

<u>World</u> - Known only from the Philippine Islands, Great Barrier Reef and Moreton Bay, southern Queensland. Material collected during the

present study represents the first record of this species from Australian waters.

Visayan Sea, Philippine Islands(Gomon, 1980); additional Australian record: Moreton Bay , southern Queensland.

DISCUSSION: *Parapercis diplospilus* is allied to *Parapercis ommatura* Jordan and Snyder(1902) but may be distinguished by its possessing the following characters: circum-peduncle scales 21-22 against 23-26; scales from lateral line to anus 10-11 against 12-13; caudal fin truncate with outer rays slightly produced rather than broadly rounded; one stripe or two blotches on cheek against two stripes; caudal with a prominent ventro-basal dark spot against none, in *P. ommatura* [data for *P. ommatura* from Jordan and Snyder(1902), Kamohara(1960) and Cantwell(1964)] . Greatest body depth and least fleshy interorbital width are smaller in *P. diplospilus* than in *P. ommatura* at small sizes, however the latter species is more slender with a narrower interorbital space at larger sizes(Gomon, 1980).

Gomon(1980) described *P. diplospilus* from 21 specimens collected from the Philippine Islands. Specimens from Great Barrier Reef waters agree well with Gomon's description except that they have fewer lateral line scales(55-56 against 58-60) and a longer 4th dorsal spine(7.7-9.4% SL against 6.4-7.8%SL) and snout(7.3-8.1%SL against 6.5-7.1%SL) than the Philippine specimens.

REMARKS: *Parapercis diplospilus* although apparently rare within the Great Barrier Reef Province, is quite common in Moreton Bay off Brisbane. The individuals examined in the present study were all collected in coastal waters at depths ranging from 28 to 40m. Maximum recorded length for this species is 78.0 mm SL (Gomon, 1980). The largest individual examined measured 69.5 mm SL and was trawled off North Palm Island, near Townsville.

MERISTICS

A summary of fin ray, scale, and gill raker counts is given for all nine species in Tables 2-5 (based on Great Barrier Reef material only). Without exception, the first anal element was a weak spine and the pelvic count I, 5.

The number of enlarged canine teeth in the front tooth row of the lower jaw varied between 6 and 12 (dentically intact specimens), generally being either 6, 8, 10 or 12. *Parapercis diplospilus* was the only species to show intaspecific variation in this count (i.e. 8-12).

MORPHOMETRICS

The numbers and size ranges of individuals examined, together with the ranges of all morphometric ratios, are presented in Figures 8-15 (Great Barrier Reef material only). It can be seen that there is considerable interspecific overlap for all morphometric characters and that no single species can be completely separated from the others using any one character.

Cantwell (1964) dismissed the use of morphometrics in his revision of the genus *Parapercis* stating that (p.241): "These show more variation , both within and among species, than the meristic data, and therefore are not used at all." Although reference to the above figures shows that there is indeed considerable intraspecific variability and interspecific overlap, it is felt that morphometric characters can still prove extremely useful for species separation and/or defining species groups, particularly in a regional situation. For example, Figures 8-15 may be used as a multi-choice key by beginning at Figure 8 and working through to Figure 15 using a process of elimination.

Table 2. Frequency distributions of fin element counts for species of *Parapercis* from Great Barrier Reef waters.

Species	Dorsal						Anal				Pectoral							Caudal (branched)					
	IV	V	VI	20	21	22	I	16	17	18	13	14	15	16	17	18	19	7	8	+	6	7	8
cylindrica		28		3	21		28	1	26	1			23	5					28			28	
hexophtalma		49	1	1	48	1	50	2	46	2					4	40	6		50			50	
cephalopunctata	3				3		3		3						3				3			3	
clathrata	17				17		17		17						14	3			17			17	
xanthozona		18			18		18	2	15	1				3	12	3			18			18	
nebulosa		21				21	21			21				3	18				21			21	
sp. 1		20	1	2	19		21	1	19	1			21					18	3		2	19	
snyderi		8				8	8		8		2	6						7	1			8	
diplospilus		2			1	1	2			2			1	1					2			2	

Table 3. Frequency distributions of lateral line and circum-peduncle scale counts for species of *Parapercis* from Great Barrier Reef waters

Species	Oblique scale rows/lateral line											Circum-peduncle scales								
	35 -39	40 -44	45 -49	50 -54	55 -59	60 -64	65 -69	70 -74	75 -79	80 -84	85 -89	15 -17	18 -20	21 -23	24 -26	27 -29	30 -32	33 -35	36 -38	39 -41
cylindrica				27											21					
hexophtalma						6	34	7								1	44			
cephalopunctata					3										2	1				
clathrata					5	8									10	5				
xanthozona					7	9										7	10			
nebulosa									2	17	1								14	5
sp. 1			6	15										7	11					
snyderi	1	5											6							
diplospilus					1									2						

Table 4. Frequency distribution of scale counts above and below lateral line for species of *Parapercis* from Great Barrier Reef waters

Species	Scales from lateral line to first soft dorsal ray											Scales from lateral line to anus											
	3	4	5	6	7	8	9	10	11	12	13	10	11	12	13	14	15	16	17	18	19	20	21
cylindrica	5	23														3	10	11	3				
hexophtalma				2	27	14	2										14	19	2	3			
cephalopunctata				1	2											2	1						
clathrata				8	7										8	5							
xanthozona			2	9	6										5	8	3						
nebulosa									5	11	5										12	5	2
sp. 1	13	8												2	7	8	1						
snyderi	7	1											4	2									
diplospilus	2											1	1										

Table 5. Frequency distributions of predorsal scale and gill raker counts for species of *Parapercis* from Great Barrier Reef waters

Species	Predorsal scales													Gill rakers																
	3	4	5	6	7	8	9	10	11	12	13	14	15	2	3	4	5	6	7	8	+	5	6	7	8	9	10	11	12	13
cylindrica		4	7	11	1									3	19	5						1	6	19		1				
hexophtalma								2	14	23	2					2	6	36	6	1					1	20	25	4		
cephalopunctata						1		1	1								2	1								1	2			
clathrata								8	4	4							1	8	6	1					1		6	6	3	
xanthozona							2	7	5								1	13	4							1	1	6	10	
nebulosa										7	5	5	3					7	13	1								3	11	7
sp. 1		8	9	1											4	13	2								3	11	5			
snyderi	1	3	2											2	3	3									7	1				
diplospilus					1				1					1		1								1	1					

Figure 8

Size range and number of specimens examined; ratio of length of longest spine in HL

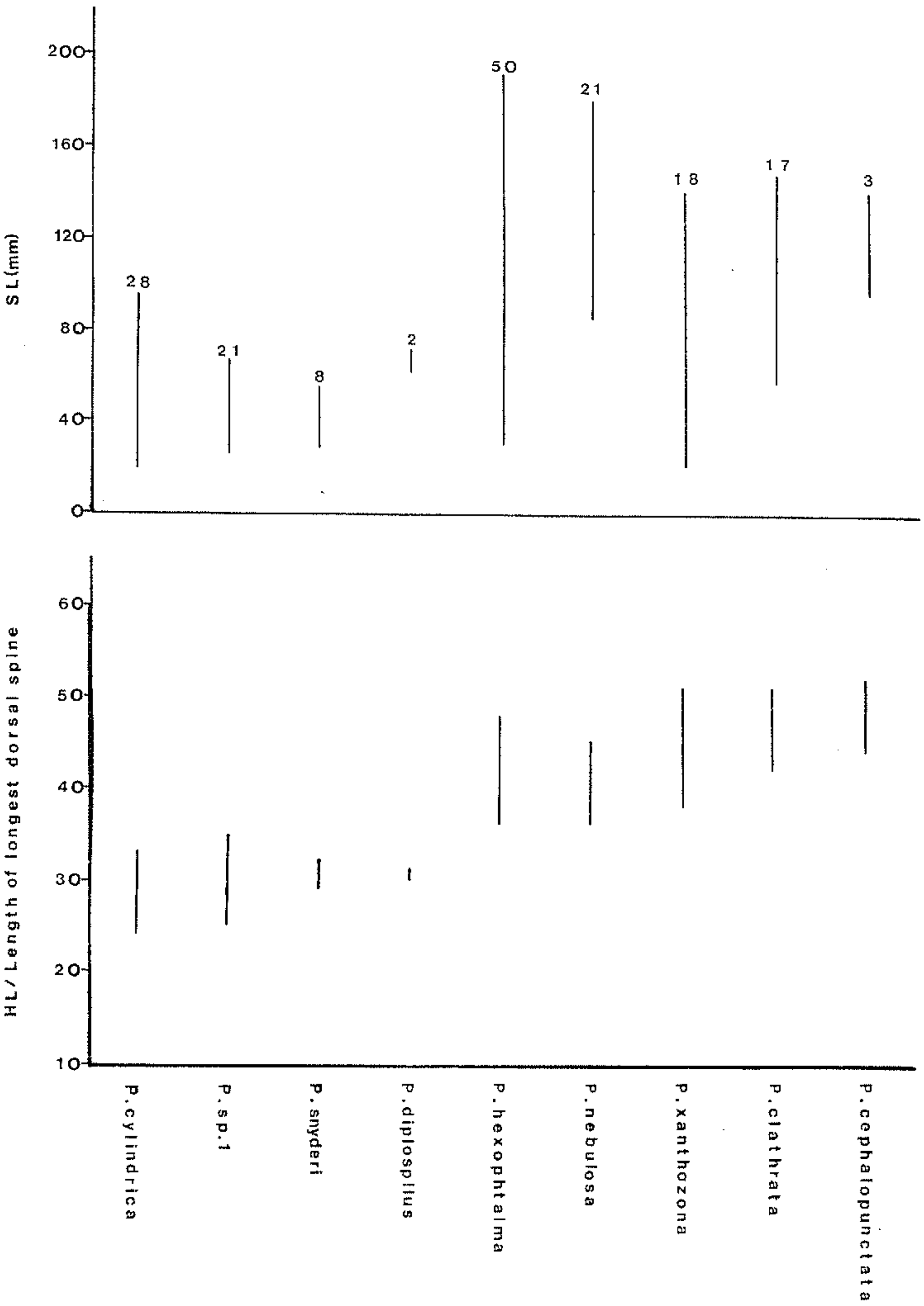

SL(mm)
0
40
80
120
160
200
28
21
8
2
50
21
18
17
3
HL/Length of longest dorsal spine
10
20
30
40
50
60
P.cylindrica
P.sp.1
P.snyderi
P.diplospilus
P.hexophtalma
P.nebulosa
P.xanthozona
P.clathrata
P.cephalopunctata

Figure 9

Ratios of interorbital width in HL, body depth in SL

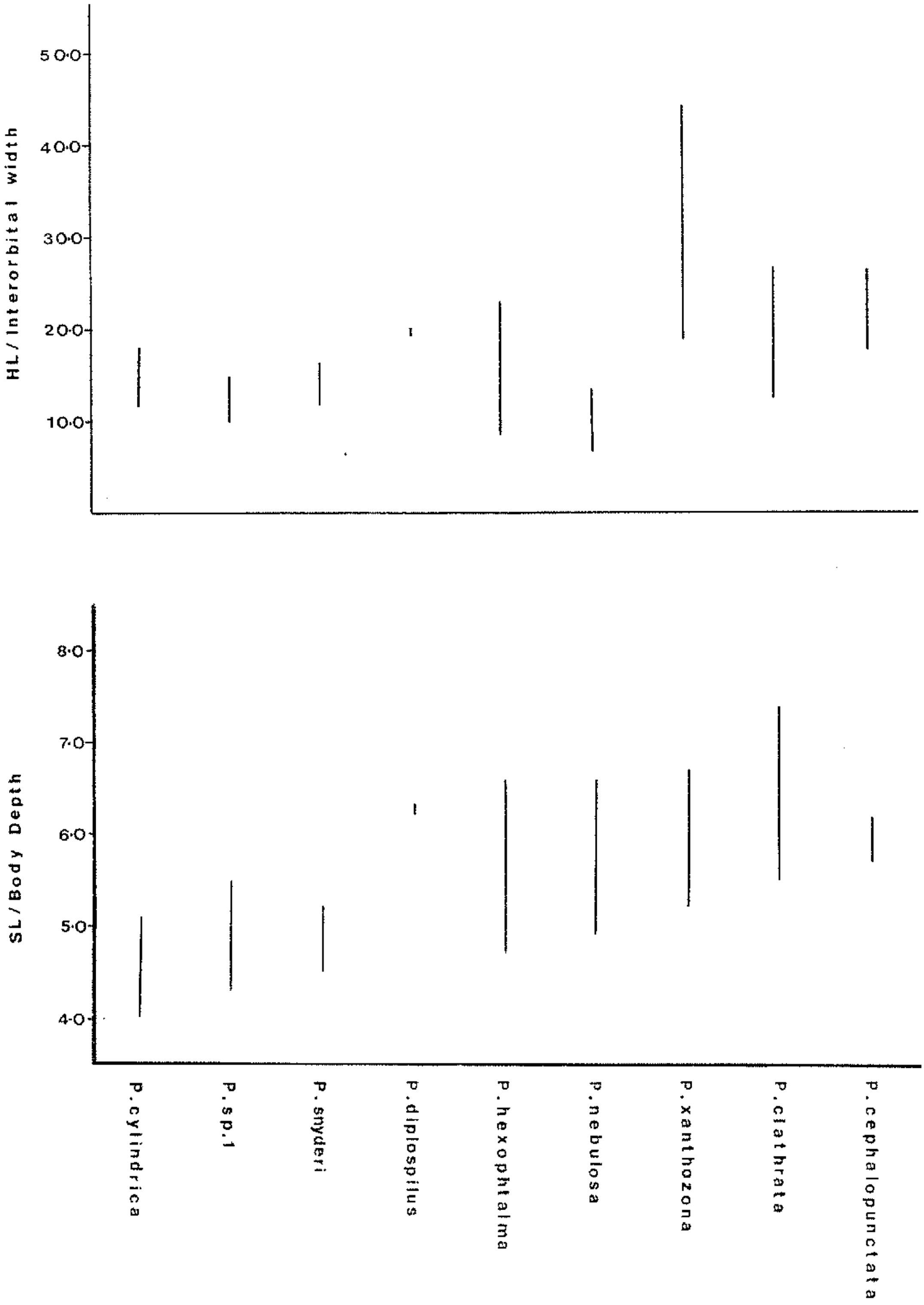

HL / Interorbital width
50·0
40·0
30·0
20·0
10·0
SL / Body Depth
8·0
7·0
6·0
5·0
4·0
P. cylindrica
P. sp. 1
P. snyderi
P. diplospilus
P. hexophtalma
P. nebulosa
P. xanthozona
P. clathrata
P. cephalopunctata

Figure 10

Ratios of eye diameter in HL, length of longest pelvic ray in SL

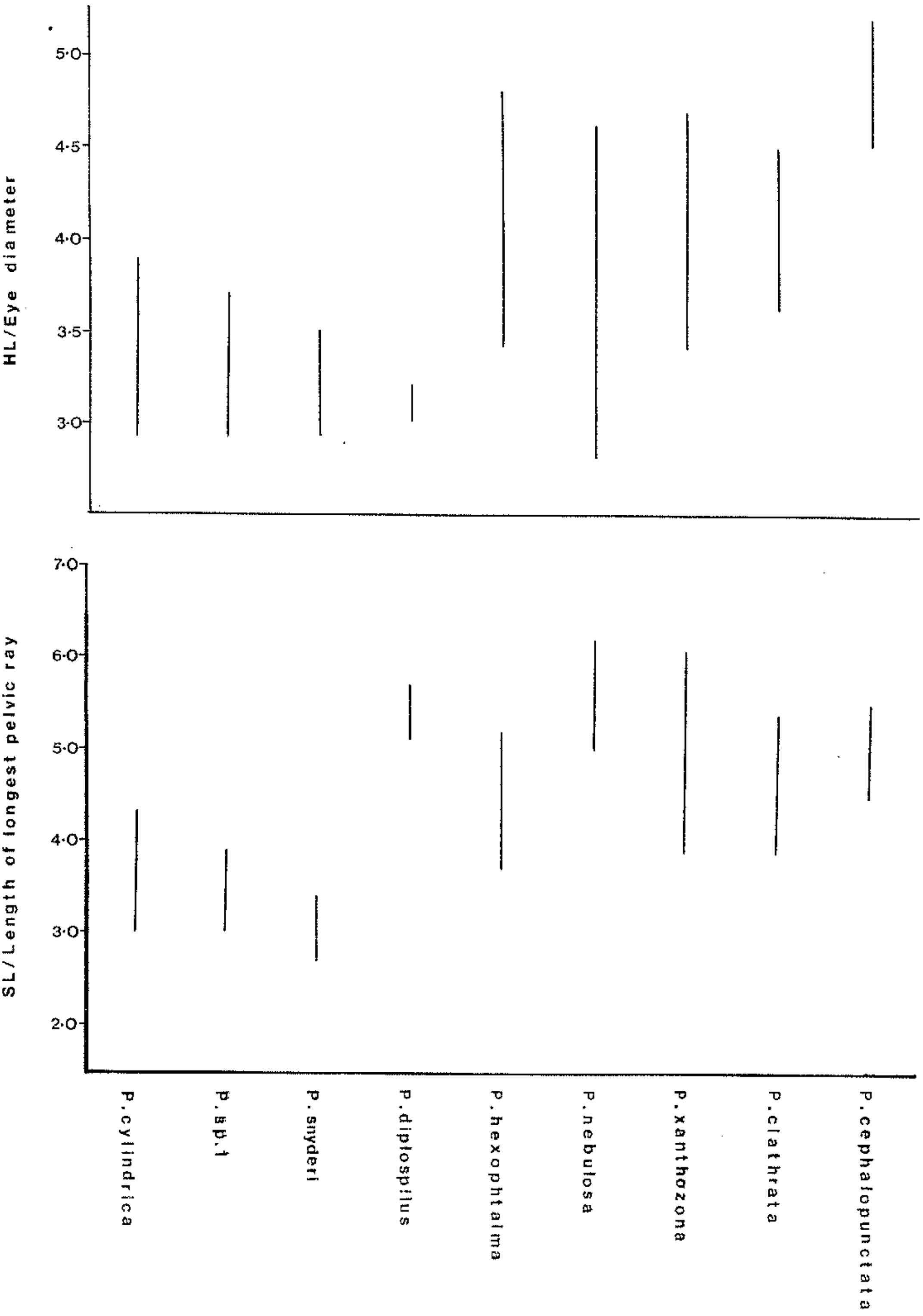

HL/Eye diameter
5·0
4·5
4·0
3·5
3·0
SL/Length of longest pelvic ray
7·0
6·0
5·0
4·0
3·0
2·0
P.cylindrica
P.sp.1
P.snyderi
P.diplospilus
P.hexophtalma
P.nebulosa
P.xanthozona
P.clathrata
P.cephalopunctata

Figure 11

Ratios of length of longest pectoral ray, head length, in SL

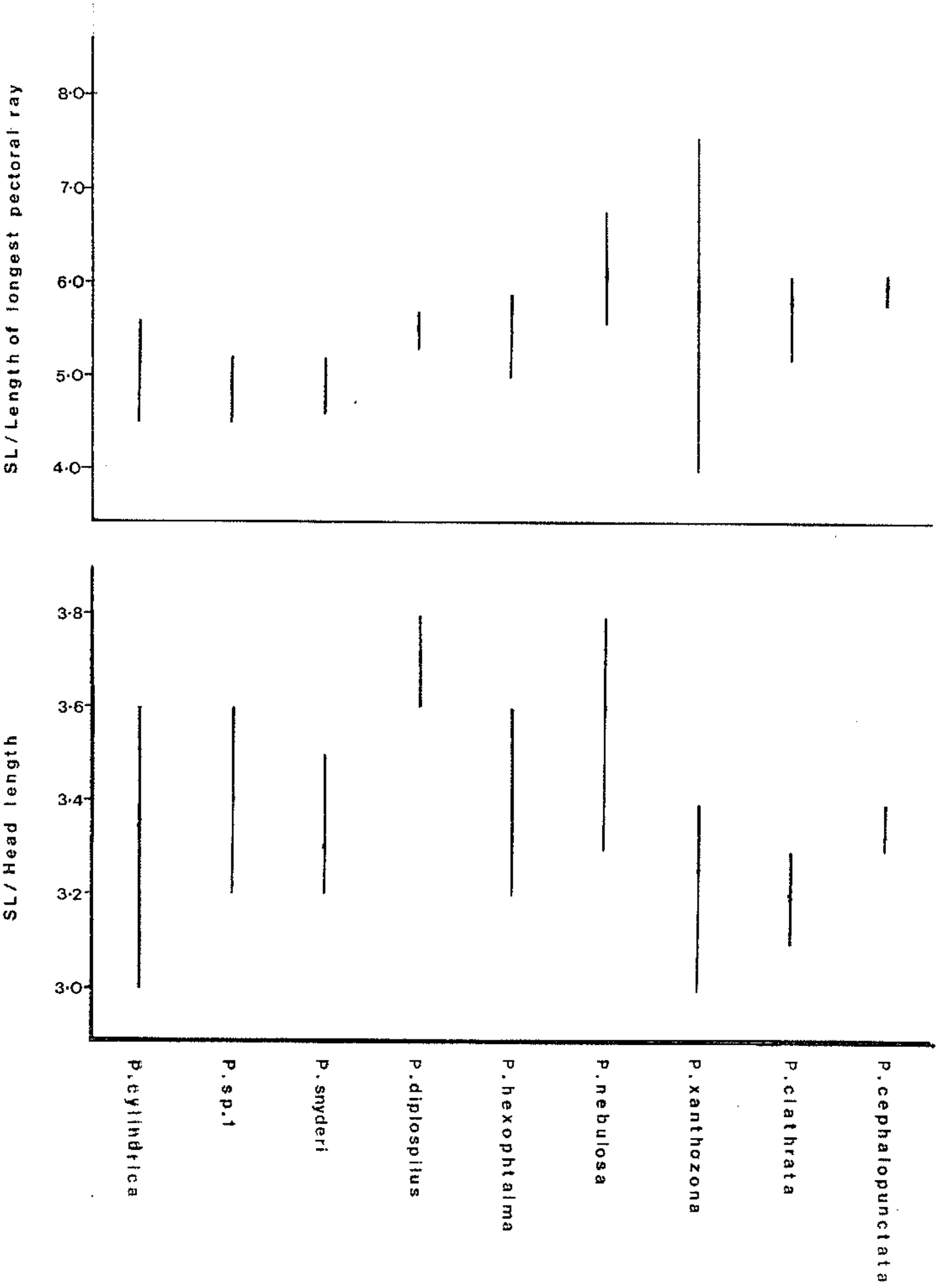

SL / Length of longest pectoral ray
8·0
7·0
6·0
5·0
4·0
SL / Head length
3·8
3·6
3·4
3·2
3·0
P. cylindrica
P. s.p. 1
P. snyderi
P. diplospilus
P. hexophtalma
P. nebulosa
P. xanthozona
P. clathrata
P. cephalopunctata

Figure 12

Ratios of postorbital length, least depth of caudal peduncle, in HL

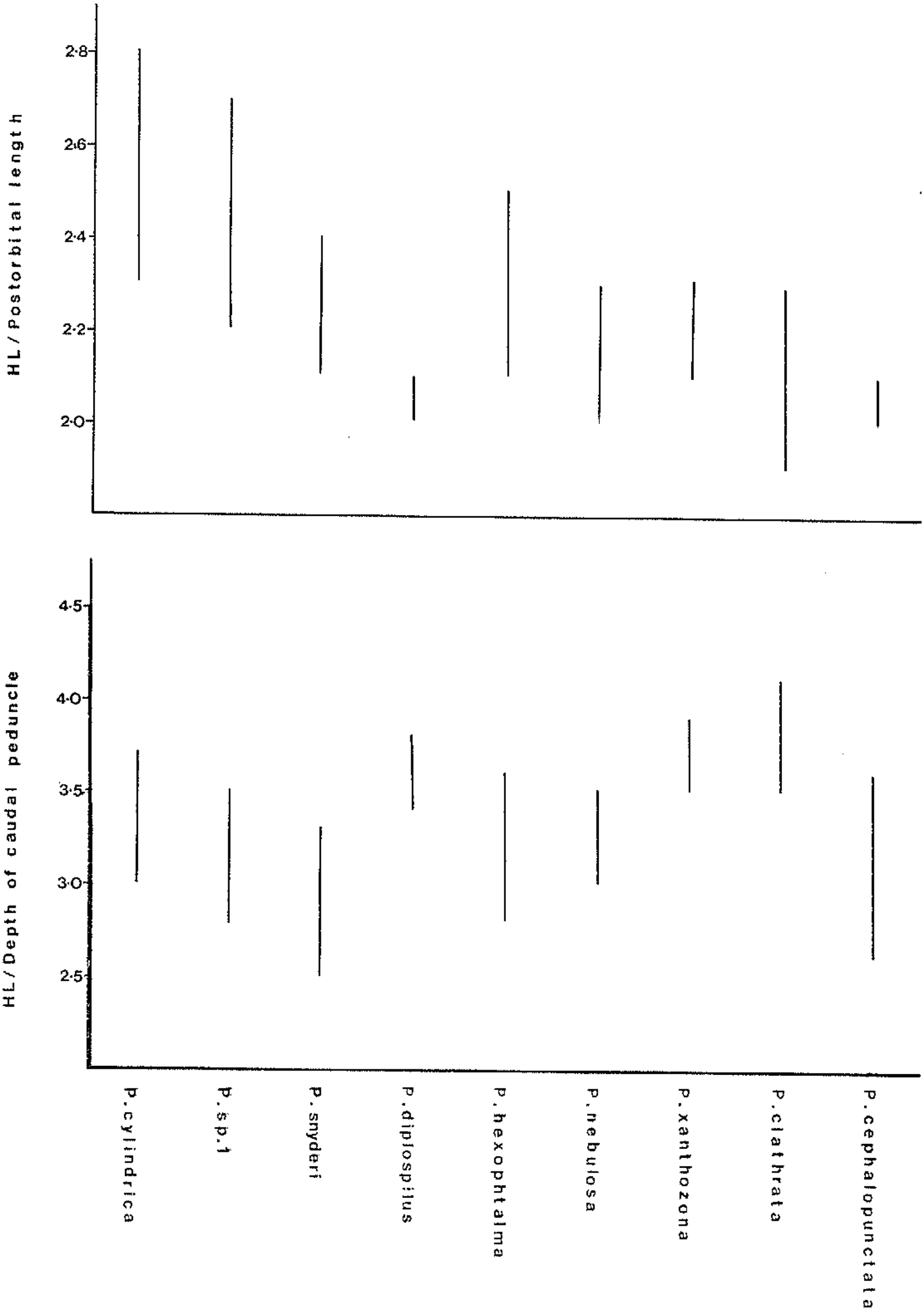

HL / Postorbital length
2·8
2·6
2·4
2·2
2·0
HL / Depth of caudal peduncle
4·5
4·0
3·5
3·0
2·5
P. cylindrica
P. s.p.1
P. snyderi
P. diplospilus
P. hexophtalma
P. nebulosa
P. xanthozona
P. clathrata
P. cephalopunctata

Figure 13

Ratios of length of longest caudal ray in SL, snout length in HL

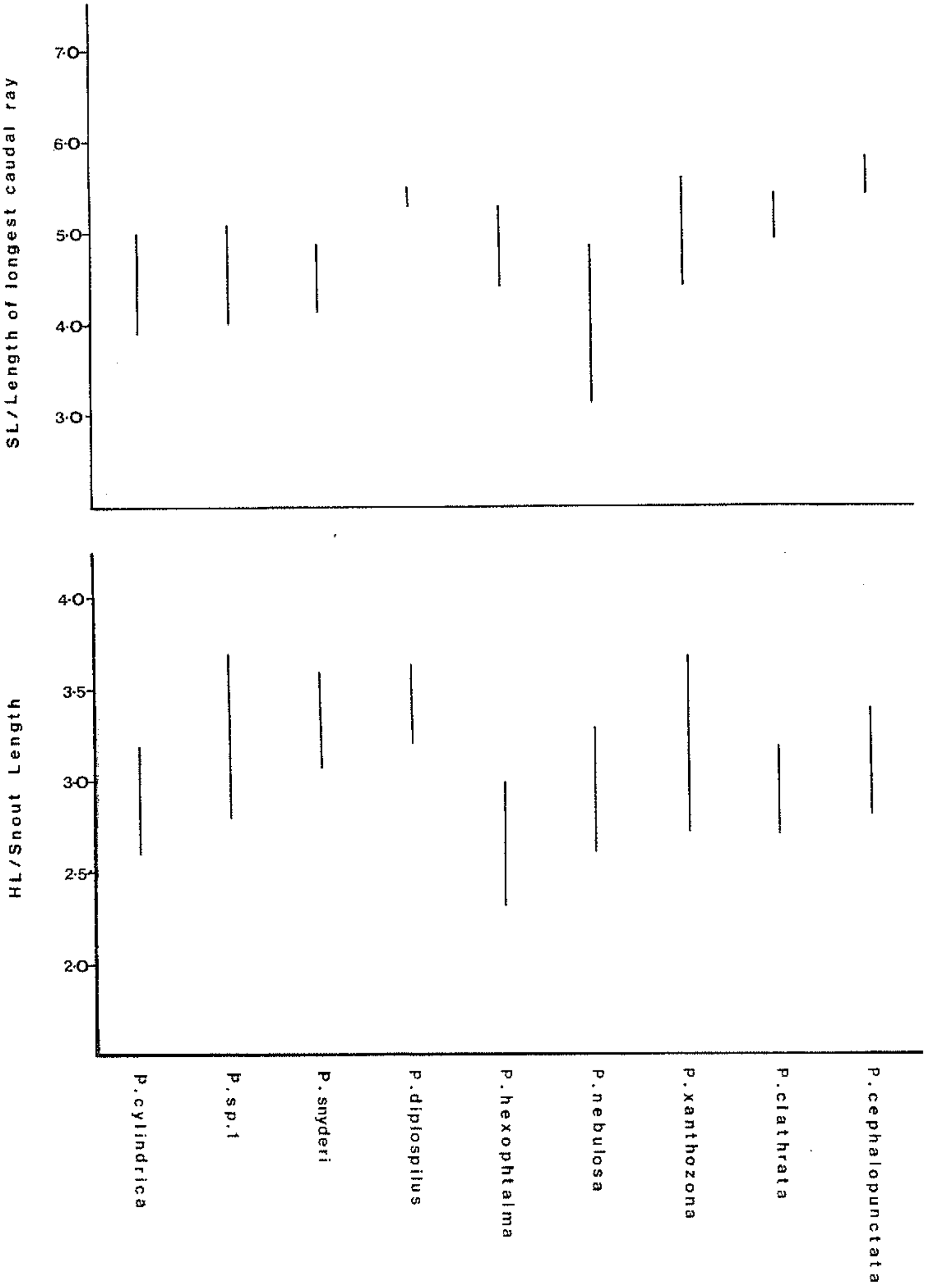

SL/Length of longest caudal ray
7·0
6·0
5·0
4·0
3·0
HL/Snout Length
4·0
3·5
3·0
2·5
2·0
P.cylindrica
P.sp.1
P.snyderi
P.diplospilus
P.hexophtalma
P.nebulosa
P.xanthozona
P.clathrata
P.cephalopunctata

Figure 14

Ratios of distance from snout tip to rear edge of maxillary in HL, length of dorsal base in SL

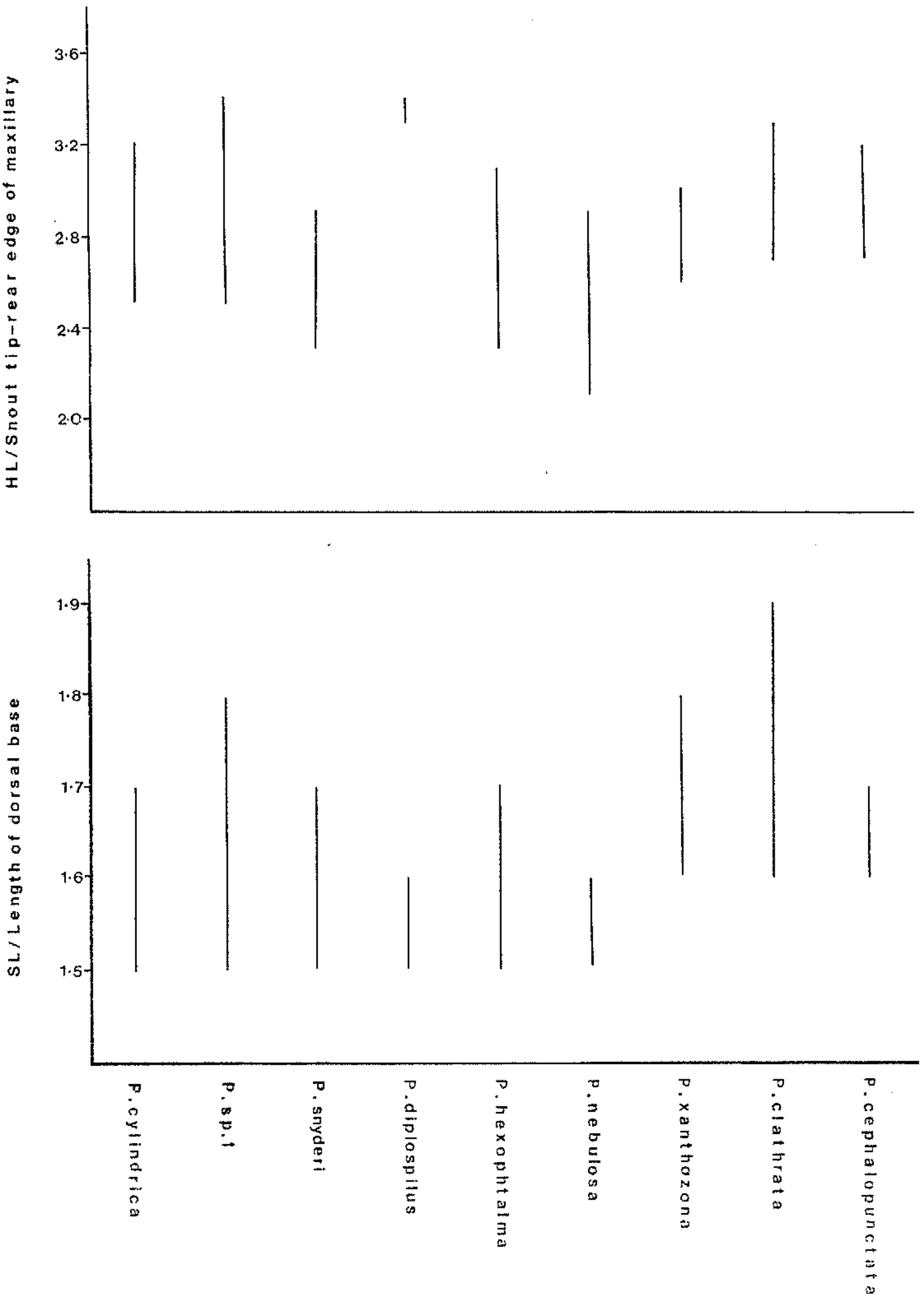
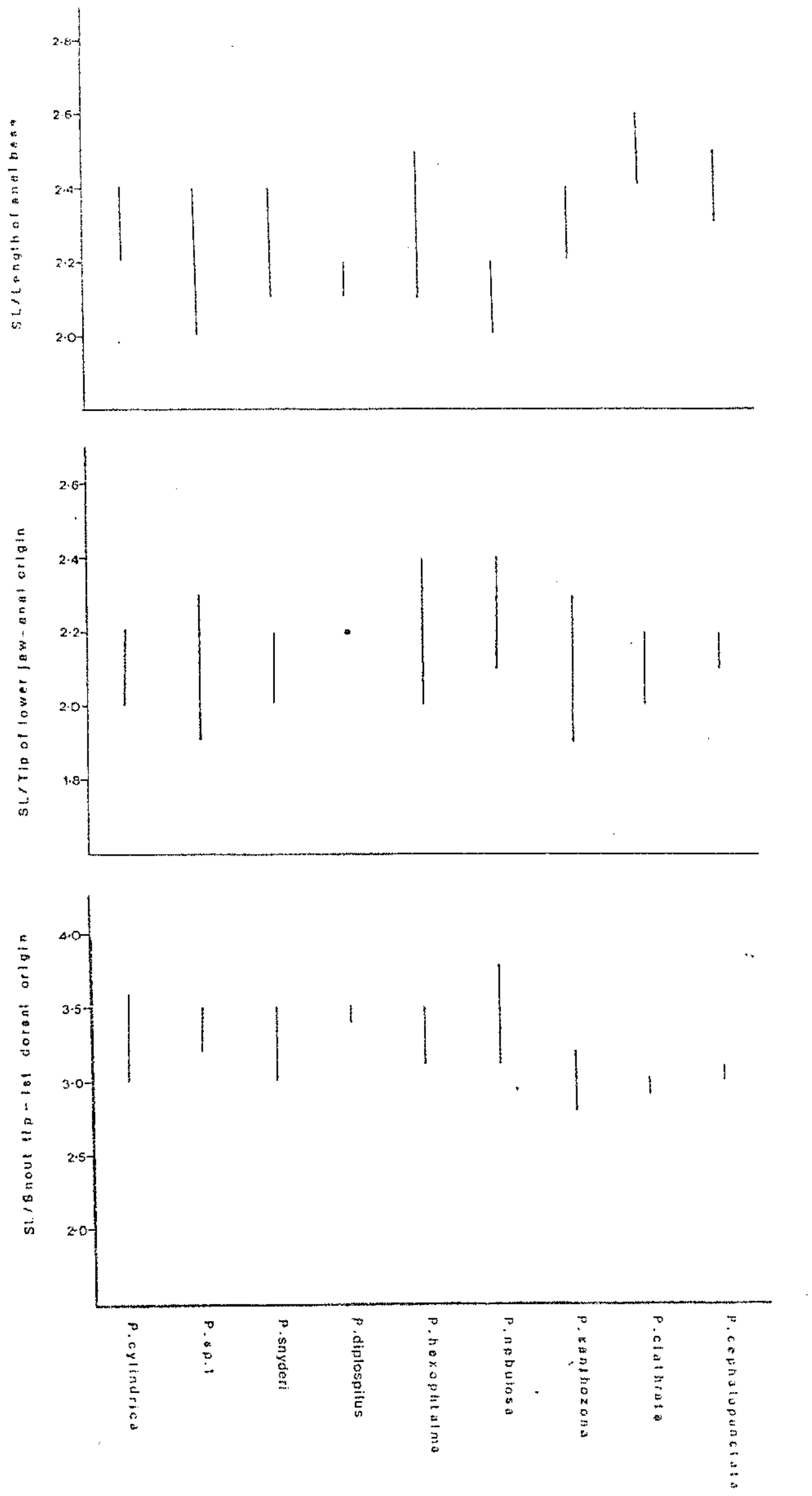

HL/Snout tip–rear edge of maxillary
3·6
3·2
2·8
2·4
2·0
SL/Length of dorsal base
1·9
1·8
1·7
1·6
1·5
P.cylindrica
P.sp.1
P.snyderi
P.diplospilus
P.hexophtalma
P.nebulosa
P.xanthozona
P.clathrata
P.cephalopunctata

Figure 15

Ratios of length of anal base, distance from lower jaw tip to anal origin, distance from snout tip to 1st dorsal origin, in SL


SL/Length of anal base
2·8
2·6
2·4
2·2
2·0
SL/Tip of lower jaw - anal origin
2·6
2·4
2·2
2·0
1·8
SL/Snout tip - 1st dorsal origin
4·0
3·5
3·0
2·5
2·0
P.cylindrica
P.sp.1
P.snyderi
P.diplospilus
P.hexophtalma
P.nebulosa
P.xanthozona
P.clathrata
P.cephalopunctata

Based on ranges of measurements from the material examined, the most useful morphometric ratios (i.e. those showing least interspecific overlap) proved to be (1) length of longest dorsal spine in HL; (2) interorbital width in HL; (3) body depth in SL; (4) eye diameter in HL; and (5) length of longest pectoral ray in SL. At least two species-groups become apparent after examination of these and the other ratios shown in Figures 8-15. One group consists of *Parapercis cylindrica*, *Parapercis* sp. 1, and *P. snyderi*; the other *P. diplospilus*, *P. nebulosa*, *P. hexophtalma*, *P. xanthozona*, *P. cephalopunctata*, and *P. clathrata*. This supports Cantwell's (1966) system of *Parapercis* relationships fairly well. His system, which was based on meristic data, distinguished six species-groups within the genus. *P. cylindrica* and *P. snyderi* were placed in Group II, *P. nebulosa* in Group III, and *P. hexophtalma*, *P. xanthozona*, *P. cephalopunctata*, and *P. clathrata* in Group IV. It therefore appears that morphometrics may be of at least some help in defining species-groups within the genus *Parapercis*.

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PART II

BIOLOGY

Chapter 1 INTRODUCTION

Adaptive radiation within the percoid fishes has given rise to numerous semi-sedentary bottom living forms (Gosline, 1971). Fishes which have successfully adopted this mode of life show a number of similarities in their morphology, anatomy and locomotion (Alexander, 1967; Gibson, 1969; Wirtz, 1978). Members of the genus *Parapercis*, for example, lack swimbladders but possess large, independently moving eyes set forward and high on the head, compressed and somewhat elongate bodies, and scales of small size. They also swim by synchronous adduction of the pectoral fins, generally in short "hopping" movements, and utilize the pelvic fins as supports when resting. These six features are common to many benthic fishes and may be interpreted as convergent adaptions to an existence in contact with the substratum (Jones and Marshall, 1953; Wickler, 1960; Abel, 1961; Alexander, 1967; Gibson, 1969; Lewis, 1976; Willoughby, 1976; Wirtz, 1978).

Surprisingly little work has been undertaken on the biology of members of the genus *Parapercis* despite the widespread distribution and abundance of this group throughout the Indo-Pacific region. Data are either unavailable or very limited for most species, with much of the available information being obtained from either observations made incidental to taxonomic studies, or from broad investigations not solely concerned with *Parapercis*. In contrast much attention has been given to the biology of two other groups of benthic fishes, the gobies (Gobiidae) and the blennies (Blenniidae), though much of this work involves species that do not occur on coral reefs (e.g. Thomson and Bennett, 1953; Wickler, 1957; Porumb, 1961; Abel, 1962; Reese, 1964; Gibson, 1969; Stephens et al., 1970).

The temperate water mugiloidid, *Parapercis colias*, which is endemic to the New Zealand region, is the most comprehensively studied weeverfish from a biological viewpoint. Graham (1939, 1953) and Doak (1972) discussed the diet, spawning season and general distribution of this commercially important food and baitfish (Munro, 1967; Robertson, 1973). In addition, egg and larval development in *P. colias* has been described by Robertson (1973).

Less data are available on coral reef species of *Parapercis*. Hiatt and Strasburg (1960) described the food, feeding habits and local distribution of *P. cephalopunctata* and *P. clathrata* in a broad investigation of the ecological relationships of coral reef fishes of the Marshall Islands. Although a total of only 28 stomachs were examined, their study was the most detailed to date on the feeding ecology of coral reef *Parapercis*. Other literature containing information on *Parapercis* food and/or feeding habits, such as that by Smith (1965), Low (1971), Goldman (1973), Goeden (1974) and Burgess and Axelrod (1975), gives general feeding categories (e.g. carnivorous, omnivorous) rather than detailed accounts of diet.

Marshall (1950), in a checklist of fishes from the Cocos-Keeling Islands, suggested that *Parapercis hexophtalma* was sexually dichromatic and might exhibit protogynous hermaphroditism similar to that found in fishes of the family Labridae. Marshall's suggestions were based on the size distribution of the colour phases and sexes of only 16 individuals whose gonads had been examined macroscopically. Although cited by Atz (1964) and Allen et al. (1976) as evidence for sexual dichromatism and/or protogynous hermaphroditism within the family Mugiloididae, his work had not been confirmed histologically until the present time.

Egg and larval development in *Parapercis sexfasciata* and nine unidentified species of mugiloidids from southern Japan have been described in a series of papers by Mito (1956; 1960; 1962). Additional early life history data were provided by Russell et al. (1977), who described the recruitment pattern of *P. cylindrica* to artificial reefs in One Tree Island lagoon at the southern end of the Great Barrier Reef.

In marked contrast to the gobies and blennies whose reproductive behaviour has been more thoroughly studied than any other group of marine teleosts, except for the pomacentrids (Reese, 1964), no information is available on the reproductive behaviour, mating systems, or social systems of weeverfishes.

The possibility of behavioural adaptations to a benthic existence, the suggestion of protogynous hermaphroditism, and the paucity of ecological and behavioural data suggested that weeverfishes should be further studied, particularly from the aspects of their feeding ecology, social structure, and reproductive biology. It was felt that studying a single species of *Parapercis* in detail would contribute more to an understanding of the biology of this group of fishes than adopting a comparative approach and obtaining less complete information for several species. Therefore, a broad but detailed study was undertaken of *Parapercis cylindrica*, a species chosen for its abundance within the study areas, low mobility and variable colour pattern which enabled individual fishes to be recognized in the field. The major objectives of the study were as follows: (1) to determine whether sexual dichromatism occurs in *P. cylindrica* and, if so, to examine the nature and extent of this dichromatism; (2) to describe the social units in which *P. cylindrica* live and the behavioural mechanisms underlying the relationships within and between social units; (3) to examine the ecological background of *P. cylindrica* with a view to its possible role in determining the structure of the social and mating system of this species; (4) to determine whether protogynous hermaphroditism is a life history characteristic of *P. cylindrica* and, if so, investigate its relationship to the social organization observed in this species.

Data are presented on spatial distribution, food and feeding habits, social organization, and reproductive biology of *Parapercis cylindrica*. Information was collected for other species of *Parapercis*, when possible, to gain additional insight into the selective pressures which have acted upon these fishes. However, these supplementary data were not always sufficiently numerous to allow quantitative comparison. Consequently, discussion of these other species is limited primarily to those chapters on distribution and abundance (Chapter 3), food and feeding habits (Chapter 4), and reproductive biology (Chapter 6).

Chapter 2 STUDY AREAS

Field work was conducted within the Lizard Island region at the northern end of the Great Barrier Reef Province (Fig. 16) between August 1976 and April 1979. The Lizard Island Research Station, situated at the south-western end of Lizard Island, provided an ideal base for the study. Twelve study periods totalling 15.8 months were spent at Lizard Island, during which an estimated 3000 hours of underwater observations were made on *Parapercis*.

General observations and collections were made at several localities within the Lizard Island region, particularly Eyrie Reef and North Direction Island (Fig. 16). Little collecting was carried out around Lizard Island and its associated islands (i.e. Palfrey I., South I., Bird I.), since this general area was reserved for long term monitoring of "natural" populations and other detailed observational studies.

Situated 20 nautical miles off the mainland coast, Lizard Island (145°28'E, 14°40'S) is a 360 m high, granite, continental island, covering an area of approximately seven square kilometres. It is well vegetated and possesses diverse terrestrial habitats, such as open grassland (*Themeda* covers more than 50 per cent of the island), pandanus and mangrove swamps, eucalyptus scrub, and small patches of rainforest (Saunders, 1978). The island is surrounded by an extensive fringing reef and connected to neighbouring Palfrey, South, and Bird Islands by a well developed reef enclosing a 10 m deep lagoon (Fig. 17). The lagoon is penetrated by only one major channel, approximately 15 m deep, situated at its north-eastern end. Water flow into the lagoon is via this channel, and by wave and tidal transport primarily over the windward reef face between South Island and

Figure 16

Map of the Lizard Island region, northern Great Barrier Reef Province.

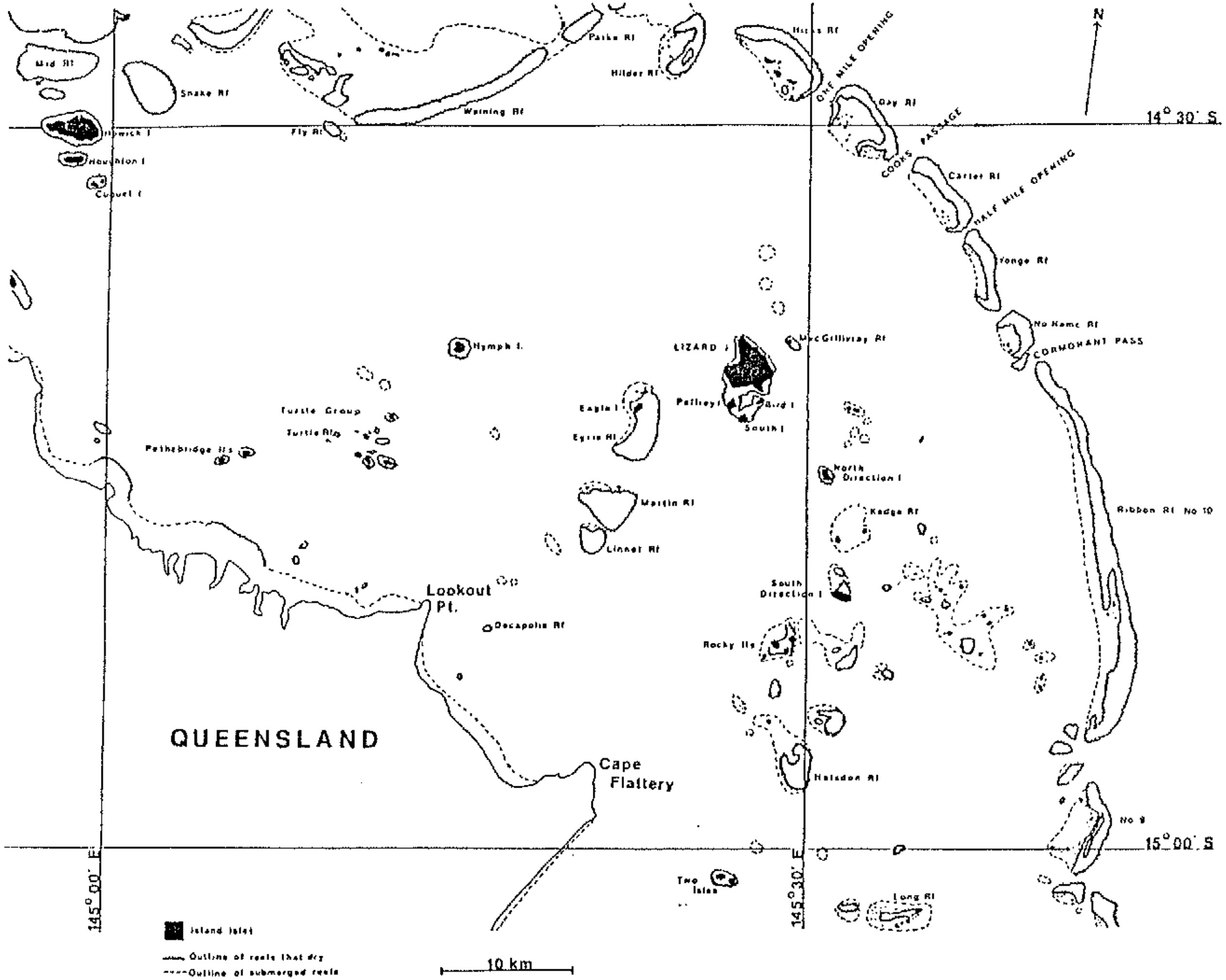
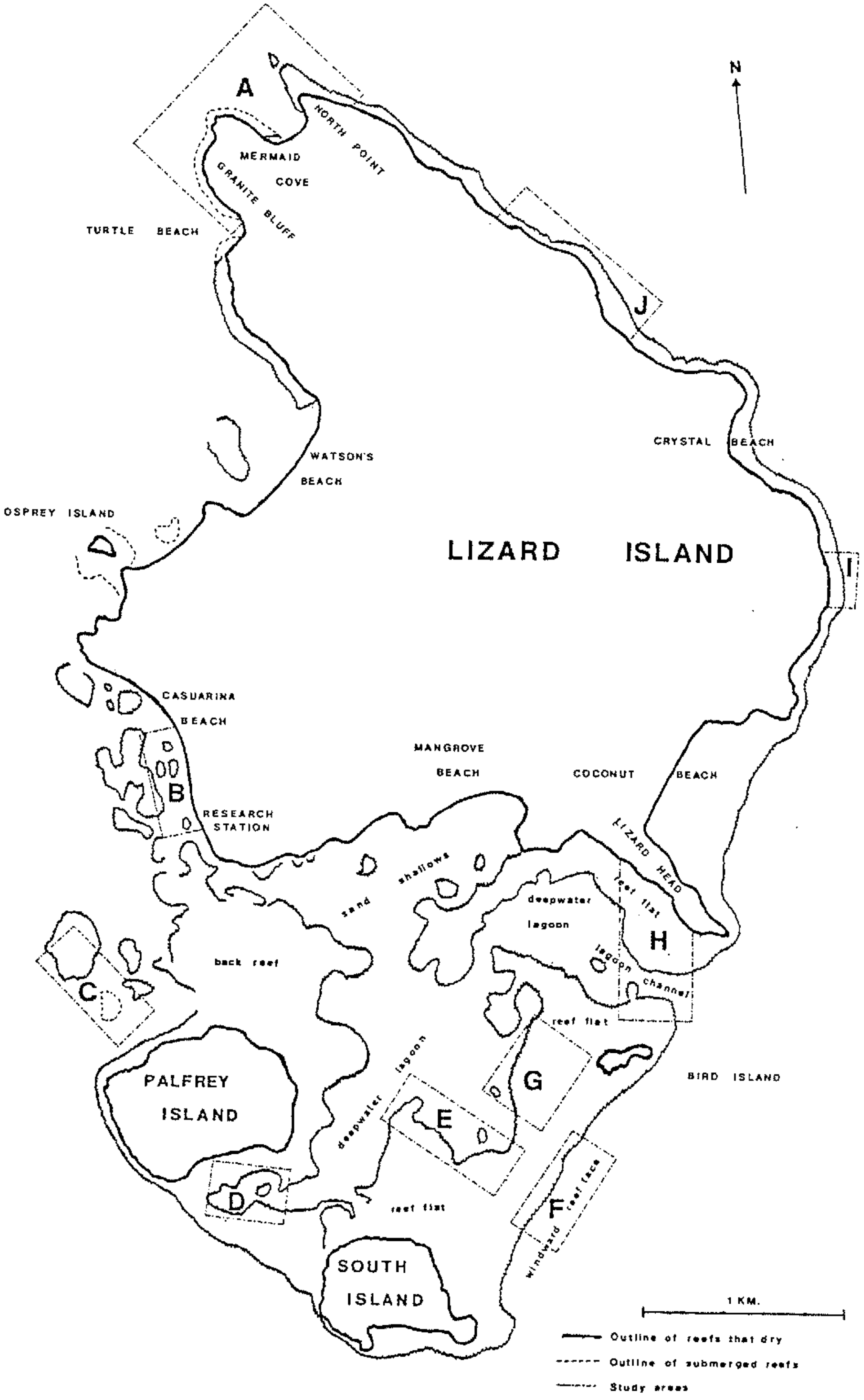
Mid Rf
Snake Rf
Howick I
Houghton I
Coquet I
Fly Rf
Waining Rf
Parke Rf
Hilder Rf
Hicks Rf
ONE MILE OPENING
Day Rf
COOKS PASSAGE
Carter Rf
HALF MILE OPENING
Yonge Rf
No Name Rf
CORMORANT PASS
N
14° 30' S
Nymph I.
LIZARD I
MacGillivray Rf
Turtle Group
Turtle Rfs
Pethebridge Ils
Eagle I
Eyrie Rf
Palfrey I
Bird I
South I
North Direction I
Martin Rf
Linnet Rf
Kedge Rf
Ribbon Rf No 10
Lookout Pt.
Decapolis Rf
South Direction I
Rocky Ils
QUEENSLAND
Cape Flattery
Halsdon Rf
No 9
15° 00' S
145° 00' E
145° 30' E
Two Isles
Long Rf
Island Islet
Outline of reefs that dry
Outline of submerged reefs
10 km

Figure 17

Map of Lizard Island and its associated reefs and islands showing the location of study areas where observational work on *Parapercis* was undertaken.

A. Mermaid Cove study area
B. Casuarina Beach study area
C. Palfrey Island study area
D. South-western lagoon study area
E. Leeward Bird-South Island study area
F. Windward Bird-South Island study area
G. Bird Island study area
H. Lagoon entrance study area
I. North-east face study area


N
A
NORTH POINT
MERMAID
COVE
GRANITE BLUFF
TURTLE BEACH
J
WATSON'S
BEACH
CRYSTAL BEACH
OSPREY ISLAND
LIZARD ISLAND
I
CASUARINA
BEACH
MANGROVE
BEACH
COCONUT
BEACH
B
RESEARCH
STATION
LIZARD HEAD
sand shallows
deepwater
lagoon
reef flat
H
back reef
lagoon channel
C
reef flat
G
BIRD ISLAND
PALFREY
ISLAND
deepwater lagoon
E
F
windward reef face
D
reef flat
SOUTH
ISLAND
1 KM.
Outline of reefs that dry
Outline of submerged reefs
Study areas

Bird Island. Once within the lagoon, surface circulation is mostly a function of wind (Barnes et al., 1976; Hamner, 1976).

The fringing reefs of Lizard Island have been under physiographical study by workers at James Cook University and the Australian Institute of Science (AIMS) for some time now. Since the results of this work will be published in the near future, only a simplified description of the Lizard Island reefs will be given here. The following description utilizes the terminology of Goldman and Talbot (1976):

The eastern side of Lizard Island possesses a fringing reef which extends from the tip of Lizard Head to North Point (Fig. 17). This reef, although generally quite narrow, becomes very wide near Coconut Beach and forms an extensive reef flat which is usually exposed at low water. The outer margin of this eastern fringing reef lacks a well developed algal rim and falls away in a vertical or slightly undercut cliff to a depth of 4 to 10 m, depending on the locality. The region below this cliff, which never emerges at low water, is characterized by rich coral growth and scattered sand-rubble patches. As one travels deeper, the slope becomes gentler in aspect and possesses fewer, but larger, coral outcrops and more extensive sand-rubble patches. The transition to the off-reef floor begins at a depth of about 20 m and is characterized by scattered tallus and a few clumps of living coral. The off-reef floor is reached at about 35 m and is an open, undulating plain consisting of a mixture of sand, shell and *Halimeda* fragments.

On the western side of the island, a fringing reef runs from the western end of Mermaid Cove, around Granite Bluff, to the northern end of Turtle Beach (Fig. 17). The inner, and uppermost section of this reef, forms a shelf which comes to within 5 m of the surface. This shelf is covered in tabulate and delicate ramose corals and extends out from shore approximately 20 m before sloping down at an angle of about 45 degrees to a depth of 9 to

17 m. At this depth, the bottom evens out and is dotted with large, isolated coral outcrops that contain many ledges and crevices and support heavy growths of soft corals. The areas between these coral outcrops are filled with a sand-rubble or sand-shell mixture. The off-reef floor is reached at about 30 m and is of a similar nature to that described for the off-reef floor on the eastern side of the island, except for the addition of a surface layer of detrital mud. Fringing reef also extends from the southern end of Turtle Beach to Watson's Beach. The shelf here slopes away more gently than the Mermaid Cove/Granite Bluff reef and terminates on a flat sandy bottom in 10 m of water. The remainder of the western side of Lizard Island consists of localized areas of fringing reef and sand beaches, with shallow submerged coral formations offshore.

On the southern, lagoonal side of the island is a large, shallow (1-2 m) sand flat covering the area from Research Station Point to Mangrove Beach. A relatively wide reef flat, often exposed at low water, extends from Mangrove Beach to the tip of Lizard Head (Fig. 17). For most of its length, the outer margin of this reef drops off vertically to a depth of about 3 m. At the base of this small wall, the substratum generally consists of sand and/or rubble with small, isolated coral colonies. The bottom then slopes away gently to the sandy lagoon floor.

A shallow (2-3 m) back reef area extends from Research Station Point to Palfrey Island (Fig. 17). The lagoonal rim of this reef is covered with rich, luxurious coral growth. Leeward (i.e. north-west) of this margin is a zone of small coral heads on a sandy, algal filmed bottom. The most leeward zone of this shallow back reef is essentially a sand flat with few coral heads and extensive algal filming. This sand flat eventually gives way to several large patch reefs (longest axis 90-200 m) and deeper leeward reef development. Of particular note is a large, isolated patch reef situated approximately 300 m off the north-western tip of Palfrey Island. This reef possesses a roughly elliptical summit measuring about 120 m along its longest axis and rises to within 2 m of the surface at mean low tide. Both the summit and sides are covered with rich coral growth dominated by large (3-6 m diameter) *Porites* colonies and dense thickets of branched *Acropora*. The sides fall away sharply to a depth of approximately 5 m before sloping down at an angle of about 40 degrees and eventually terminating on a flat, sandy bottom in 9 m of water.

Fringing reef extends around the western side of Palfrey Island and continues to the south-eastern tip of South Island (Fig. 17). This reef possesses essentially the same structural features as the fringing reef on the eastern side of Lizard Island.

A well developed reef connects South Island with Bird Island (Fig. 17). This reef receives the full impact of the south-east tradewinds, which blow consistently at 15 to 25 knots from May through to October, and exhibits zonation typical of many exposed coral reefs. The outer margin possesses a distinct algal rim and, below low tide level, is dissected by numerous surge channels, which empty out on to the windward reef slope. The upper region of this slope drops off at an angle of 70 to 90 degrees and is covered with rich coral growth, particularly branching and tabulate forms. Below this region the slope becomes more gentle in aspect and is covered with large coral outcrops separated from one another by extensive sand and/or rubble patches. The transition to the off-reef floor begins at a depth of about 25 m and is characterized by scattered tallus and a few colonies of both soft and hard corals. The off-reef floor is reached at about 35 m and is of the same nature as that described for the off-reef floor on the eastern side of Lizard Island.

Leeward of the windward reef face between South Island and Bird Island is a wide, shallow (1-2 m) reef flat (Fig. 17). The outer half of this reef flat is predominantly a hard substrate zone of impacted carbonate rock where overall coral cover is very low. Small patch reefs and thickets of staghorn coral (*Acropora* spp.) separated by expanses of sand are much more common on the inner or lagoonal half of this reef flat.

The lagoon is approximately 10 m deep, its floor consisting of coarse, mounded sand. No living coral, coral rubble, or reef rock is present on the lagoon floor except in the vicinity of the lagoon channel.

The outer margins of the fringing reefs associated with Bird Island and Lizard Head form the sides of the lagoon channel (Fig. 17). Each side consists of a short, near vertical wall of coral terminating at a depth of approximately 5 m. A gently sloping sand-rubble shelf, with isolated colonies of *Pocillopora, Acropora*, and massive corals, extends out a distance of about 10 m from this wall before changing to a substratum of corase sand. This sand-rubble/sand interface occurs at a depth of approximately 7 m. From here, the bottom slopes away at an angle of about 40 degrees towards the channel floor. The latter, while overall flat and sandy, has considerable relief due to scattered limestone outcroppings, rubble patches, and both hard and soft coral colonies. Gorgonian-type soft corals are particularly abundant in this region.

All of the above reef areas of Lizard and its associated islands were explored as a preliminary to the *Parapercis* study. Consequent upon this, ten study areas were established for detailed observational work (see Fig. 17): (A) Mermaid Cove; (B) Casuarina Beach; (C) Palfrey Island; (D) South-western lagoon; (E) Leeward Bird-South Island; (F) Windward Bird-South Island; (G) Bird Island; (H) Lagoon entrance; (I) Coconut/Crystal Beach; and (J) North-eastern face. All ten areas supported large numbers of *Parapercis* and, with the exception of study areas F and I, were workable year-round regardless of prevailing weather conditions (cyclones excepted). As such they proved ideal locations for regular, long term observations on *Parapercis*.

Chapter 3 DISTRIBUTION AND ABUNDANCE

3.1 Introduction

Information on species abundance, local distribution and general habitat requirements of fishes of the genus *Parapercis* is meagre. Much of the available data has arisen from either broad ecological (e.g. Hiatt and Strasburg, 1960; Goldman, 1973; Chave and Eckert, 1974; Jones and Chase, 1975) or taxonomic (e.g. Marshall, 1950; Fourmanoir, 1957; Schultz et al., 1960; Woodland and Slack-Smith, 1963; Fourmanoir and Laboute, 1976) studies of fish communities.

Little attention has been given to description of the ecological conditions in which *Parapercis* are found within Great Barrier Reef waters. Woodland and Slack-Smith (1963) recorded *P. hexophtalma* from the lagoon and north-western outer reef flat of Heron Island, and also noted *P. cylindrica* to be common on sandy bottoms about coral. Low (1971) and Sale and Dybdahl (1975) observed *P. cylindrica* on the southern outer reef flat of Heron Island. Goldman (1973) noted the presence of *P. cylindrica* and *P. hexophtalma* within reef flat zones at One Tree Island, the former being the more abundant of the two species. Russell et al. (1974) and Talbot et al. (1978) recorded *P. cylindrica* and *P. hexophtalma* amongst fishes recruited to a series of artificial reefs in One Tree Island lagoon and, in an additional paper (Russell et al., 1977), described long term fluctuations in abundance of newly metamorphosed *P. cylindrica* on these reefs.

The major objectives of this section of the study were to describe, for the Lizard Island reefs, (1) the habitats in which *Parapercis* are most commonly encountered and (2) the pattern of species occupancy within each of these habitats.

3.2 Methods and Materials

3.2.1 Species studied Data were collected for the following species: *Parapercis cylindrica, P. hexophtalma, P. xanthozona, P. clathrata*, and an undescribed species, *P.* sp. 1 (see Part I).

3.2.2 Field observations Observations were made by SCUBA and snorkelling and recorded underwater on roughened PVC sheets using a normal carbon pencil.

Observations were concentrated in those habitats deemed to support, by subjective estimates, an abundance of *Parapercis* species and/or individuals. The relative proportions of different substrate components in these habitats were estimated by running several 30 m line transects in areas judged typical of each habitat. Along each line transect, changes in the substrate types were recorded with an accuracy of ± 10.0 cm and the amount of line crossing a particular substrate component expressed as a percentage of the total length of the transect. The results for all transects in a habitat were pooled to give a mean percentage figure for each substrate type.

Individuals of each species were divided into three size classes: juvenile, subadult, and adult. The juvenile size class was comprised of newly settled post-larvae and immature individuals of very small size. Hence, the presence of juveniles was taken to indicate recruitment. Subadults were immature individuals of intermediate size between juveniles and adults. Adults were individuals of a size such that they were considered to have reached sexual maturity. Size limits for these three classes (Table 6) were established by examination of collected specimens. Visual estimates of length were checked by collection and measurement of previously estimated individuals and were found to be accurate within ± 6%.

The distribution of adults and subadults was investigated by counting

Table 6. Designated size limits of juvenile, subadult and adult *Parapercis*

Species	SIZE CLASS		
	Juvenile	Subadult	Adult
P. cylindrica	*TL ⩽ 25	25 < TL ⩽ 55	TL > 55
P. hexophtalma	TL ⩽ 40	40 < TL ⩽ 100	TL > 100
P. xanthozona	TL ⩽ 40	40 < TL ⩽ 100	TL > 100
P. clathrata	TL ⩽ 40	40 < TL ⩽ 100	TL > 100
P. sp. 1	TL ⩽ 20	20 < TL ⩽ 45	TL > 45

*TL = total length in mm

individuals over 50 x 5 m temporary strip transects which had been laid in locations judged typical of each habitat. A total of 49 transects were run, seven in each habitat. Of these, 31 were run outside Lizard Island lagoon and 18 inside (Fig. 18).

Data on (1) distribution of juveniles and (2) general population stability (resilience) were obtained by conducting long term observations over permanent study sites located within major *Parapercis* habitats. Twenty such study sites, each measuring 9 x 12 m were established around Lizard Island (Fig. 18). Of these, five were located within reef flat habitats (i.e. one algal reef flat site; two coral-rich reef flat sites; two shallow patch reef sites) and five within each of the open reef slope, shallow reef slope/floor transition and deep reef slope/floor transition habitats. Each study site was delimited and further subdivided into three 3 x 12 m lanes by polythene ropes staked to the substratum. Fish present in the twenty study sites were visually censused 11 times between November 1976 and November 1978 (mean sampling interval 2.1 months). The actual census technique was as follows: counts were made whilst swimming an "S" shaped path over the study site i.e. the observer first worked down one of the two outer lanes then up the middle lane, before finally working down the remaining (outer) lane. Two such swims were made over each study site per sampling period. On the first swim, only adults and subadults were counted; this slow swim was carried out approximately 1 m above the substratum. The second swim (perhaps better described as a "finger-walk" over the substratum rather than an actual swim) was undertaken with the observer's head about 30 cm above the substratum; only juveniles were counted on this swim.

Figure 18

Map of Lizard Island and associated islands showing the location of transect sites and permanent study sites

Transect sites: short lines labelled T_{1-49}

Permanent study sites: dots labelled G_{1-20}

Algal reef flat sites: T_{1-7}, G_2

Coral-rich reef flat sites: T_{8-14}; G_{4-5}

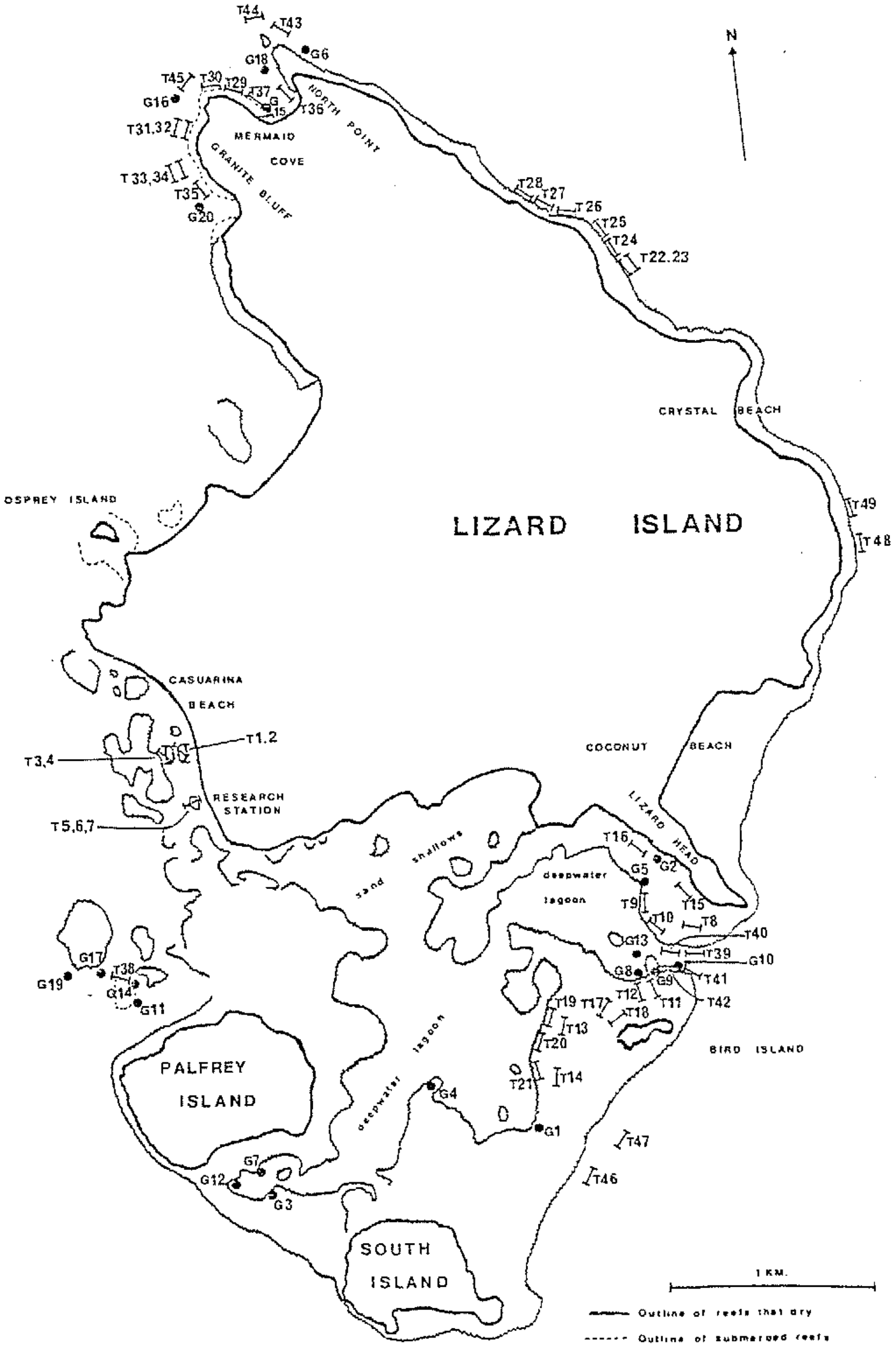
Shallow patch reef sites: T_{15-21}; G_1, G_3

Open reef slope sites: T_{22-28}; G_{6-10}

Closed reef slope sites: T_{29-35}

Shallow reef slope/floor transition sites: T_{36-42}; G_{11-15}

Deep reef slope/floor transition sites: T_{43-49}; G_{16-20}


N
LIZARD ISLAND
NORTH POINT
MERMAID COVE
GRANITE BLUFF
CRYSTAL BEACH
OSPREY ISLAND
CASUARINA BEACH
RESEARCH STATION
COCONUT BEACH
LIZARD HEAD
sand shallows
deepwater lagoon
deepwater lagoon
BIRD ISLAND
PALFREY ISLAND
SOUTH ISLAND
T44
T43
G6
G18
T45
T30
T29
T37
G15
T36
G16
T31,32
T33,34
T35
G20
T28
T27
T26
T25
T24
T22.23
T49
T48
T1.2
T3,4
T5,6,7
T16
G5
G2
T9
T15
T10
T8
G13
T40
T39
G10
G8
G9
T41
T12
T11
T42
T19
T17
T18
T13
T20
T21
T14
G17
T38
G19
G14
G11
G4
G1
T47
T46
G7
G12
G3
1 KM.
Outline of reefs that dry
Outline of submerged reefs

3.3 Results

3.3.1 Description of habitats On the basis of subjective estimates of abundance, seven distinct *Parapercis* habitats were recognized for the Lizard Island reefs:

I. ALGAL REEF FLAT HABITAT (Plate 8A). This habitat is frequently exposed at low spring tides and is characterized by extensive areas of algal-covered, impacted carbonate rock separated by small (longest axis ⩽ 1 m) sand or sand-rubble patches. The algal mat on the carbonate rock surface is particularly thick (3-6 cm), with the calcareous red alga, *Amphiroa fragilissima*, predominating. Additional algal species colonizing the carbonate rock surface include *Bornetella oligospora* and *Halimeda cylindracea* (both Chlorophyta), *Laurencia papillosa* and *Tolypiocladia glomerulata* (both Rhodophyta), and *Dictyota* sp. (Phaeophyta). The sea-grass *Thalassia hemprichii* (Anthophyta) is occasionally found in the sand and/or sand-rubble patches between the areas of rock. Live coral cover is extremely low and usually consists of a few colonies of the hard corals *Goniastrea palauensis*, *G. aspera*, *Favia amicorum*, *F. pallida*, and *Pocillopora damicornis*, together with the soft corals *Sarcophyton trocheliophorum*, *Xenia elongata*, and *Lobophytum* sp. The small foram *Marginopora vertebralis* and an unidentified species of cup sponge occupy the remainder of the carbonate rock surface.

II. CORAL-RICH REEF FLAT HABITAT (Plate 8B). This deeper (0.5-2.5 m) reef flat habitat is generally semi-exposed at low spring tides and is characterised by extensive hard coral growth with frequently interspersed sand and/or rubble patches. The hard coral cover is dominated by *Acropora formosa* thickets and *A. hyacinthus* plates. Less common are *A. cuneata*, *A. humilis*, *A. intermedia*, *Pocillopora damicornis*, and the massive corals *Montastrea magnistellata* and *Goniastrea pectinata*. Soft coral cover is very low and usually consists of a few scattered clumps of *Sarcophyton trochelio-*

Plate 8

Lizard Island habitat types

A. Algal reef flat

B. Coral-rich reef flat


A


B

phorum and *Lobophytum* sp.. Colonies of the stinging hydroid *Aglaophenia cupressina* are often found growing around the dead bases of the *Acropora* thickets. Algal growth is poor; only a light algal film and the occasional clump of *Halimeda cylindracea* or *Chlorodesmis fastigiata* are present on dead coral surfaces.

III. SHALLOW PATCH REEF HABITAT (Plate 9A). This shallow water (0.5-2.5 m) habitat becomes semi-exposed at low spring tides and is usually found in reef flat areas adjacent to the lagoon periphery. It is characterized by small (longest axis 3-6 m), isolated patch reefs separated from one another by 2-4 m expanses of sand. Dense thickets of *Acropora grandis* usually dominate these patch reefs, with several other species of hard corals being common components e.g. *Acropora pulchra*, *Seratiopora hystrix*, *Goniopora lobata*. The green algal species *Halimeda micronesica* and *Bryopsis indica* are generally found growing at the base of the *Acropora* thickets. Scattered clumps of the soft corals *Sarcophyton trocheliophorum* and the branching, fan-like *Isis* sp. are occasionally present in the central region of individual patch reefs.

IV. OPEN REEF SLOPE HABITAT (Plate 9B). This structurally complex habitat occurs on gently sloping reef faces in depths of 10 m or less and is characterized by relatively small colonies of both hard (branching, massive, tabulate) and soft corals. Sand and/or rubble filled spaces of 1-3 m are present between these colonies, thus giving an overall appearance of openness. Coverage by hard corals is more than twice that of soft corals, the dominant species of the former being *Acropora grandis*, *A. formosa*, and *Pocillopora damicornis*. Dominant soft corals include *Isis* sp. and *Sinularia* sp. The calcareous rhodophyte *Amphiroa fragilissima* and the phaeophyte *Lobophora variegata* are reasonably common on dead coral surfaces within this habitat.

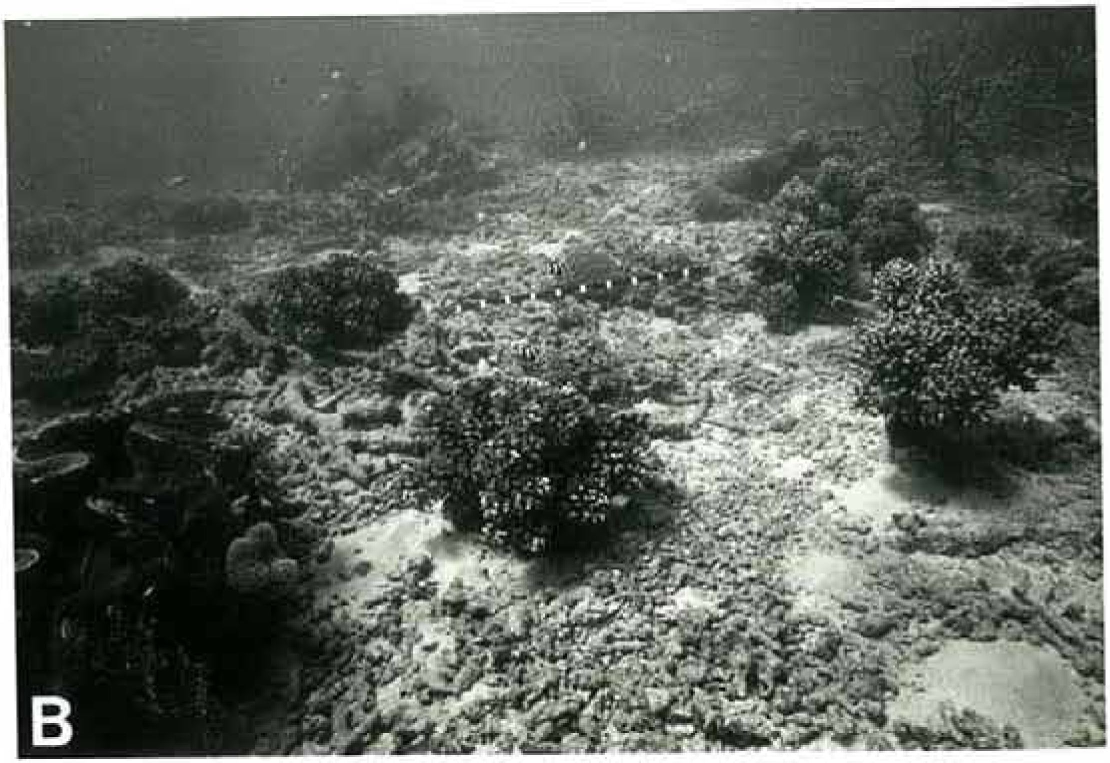
Plate 9

Lizard Island habitat types

A. Shallow patch reef

B. Open reef slope


A


B

V. CLOSED REEF SLOPE HABITAT (Plate 10A). This habitat is similar to the open reef slope habitat. However, the spaces between coral colonies are smaller (0.5-1 m) and filled with impacted carbonate rock rather than sand/rubble. Dominant hard corals include *Stylophora pistillata*, *Pocillopora damicornis*, *Acropora sarmentosa*, and *A. florida*. Small colonies of faviid and poritid corals are also often in abundance. The branching soft coral *Isis* sp. and, to a lesser extent, the soft corals *Sinularia* sp., *Cladiella* sp., *Sarcophyton trocheliophorum*, and *Litophyton* sp. are common within this habitat. The impacted carbonate rock surface between the coral colonies supports a thin algal film, scattered clumps of the brown algae *Lobophora variegata* and *Dictyota* sp., and occasional patches of crustose coralline algae.

VI. SHALLOW REEF SLOPE/FLOOR TRANSITION HABITAT (Plate 10B). This shallow water (< 10m) habitat is common around the lagoon periphery and represents the transition zone between the lower reef slope and the sandy, "off-reef" (generally lagoon) floor. The major structural components of this habitat are sand and general calcareous rubble (Table 7). A few small, scattered colonies of the hard corals *Pocillopora damicornis*, *Acropora formosa*, and *Porites australiensis* are also present, along with occasional colonies of the soft coral *Sinularia* sp. The only other conspicuous sessile organism of note is the green algal species *Chlorodesmis fastigiata*, which is often found in scattered clumps over dead coral surfaces.

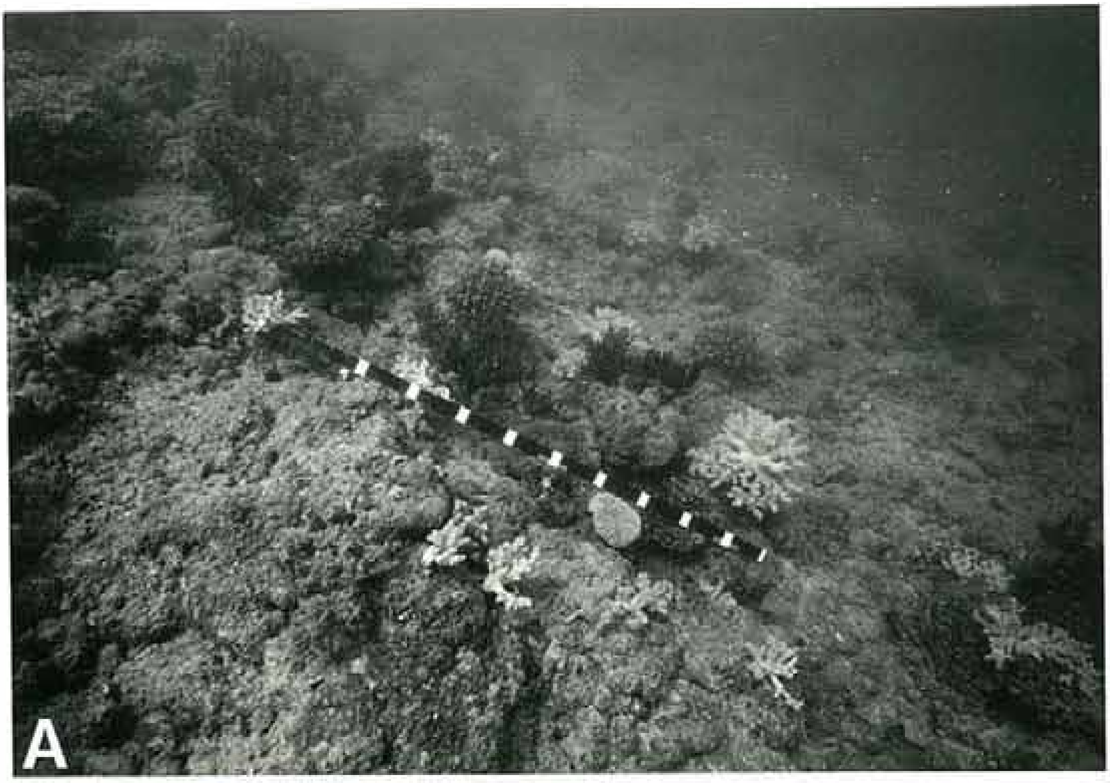
VII. DEEP REEF SLOPE/FLOOR TRANSITION HABITAT (Plate 11). This deep water (20-35 m) habitat is the transition zone between the lower reef slope and the off-reef floor proper. As with the shallow reef slope/floor transition habitat, the major structural components are sand and general calcareous rubble (Table 7). Hard coral cover is very low and is usually dominated by small colonies of *Turbinaria stellulata*, *Montipora verrucosa*, *Favia favus*, and *Platygyra* sp. Soft corals are uncommon and essentially restricted to the upper

Plate 10

Lizard Island habitat types

A. Closed reef slope

B. Shallow reef slope/floor transition


A

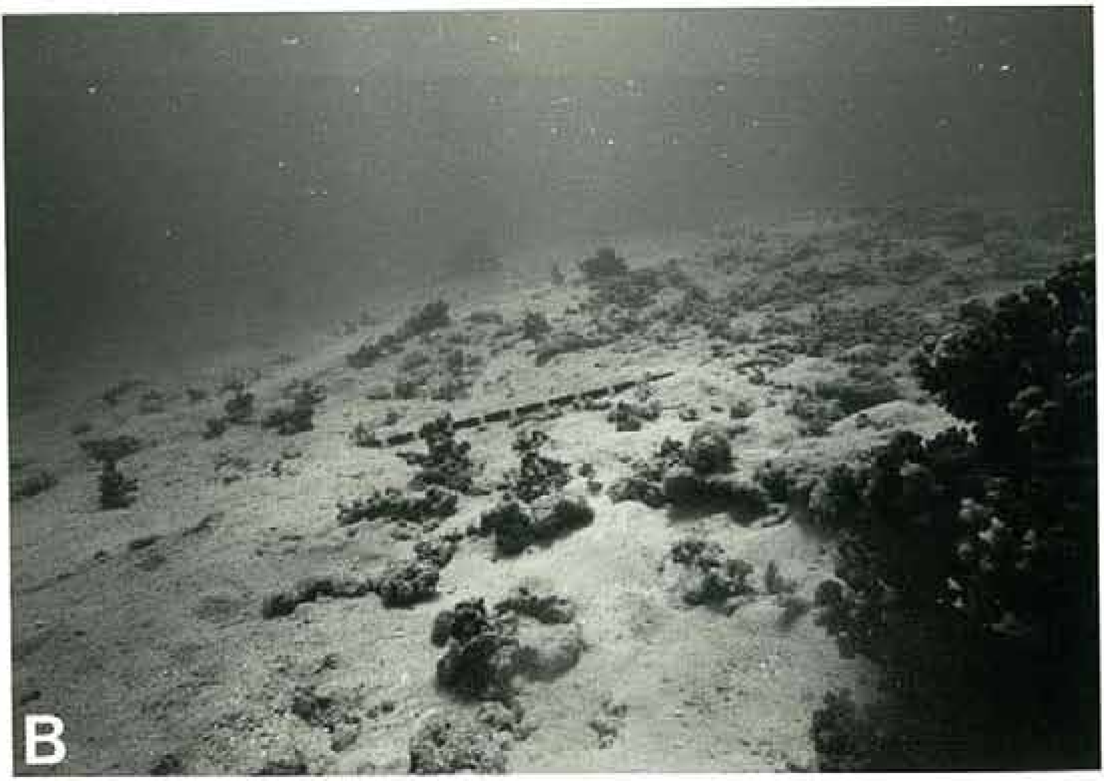

B

Table 7. Relative proportions of different substrate components in seven *Parapercis* habitats [a]

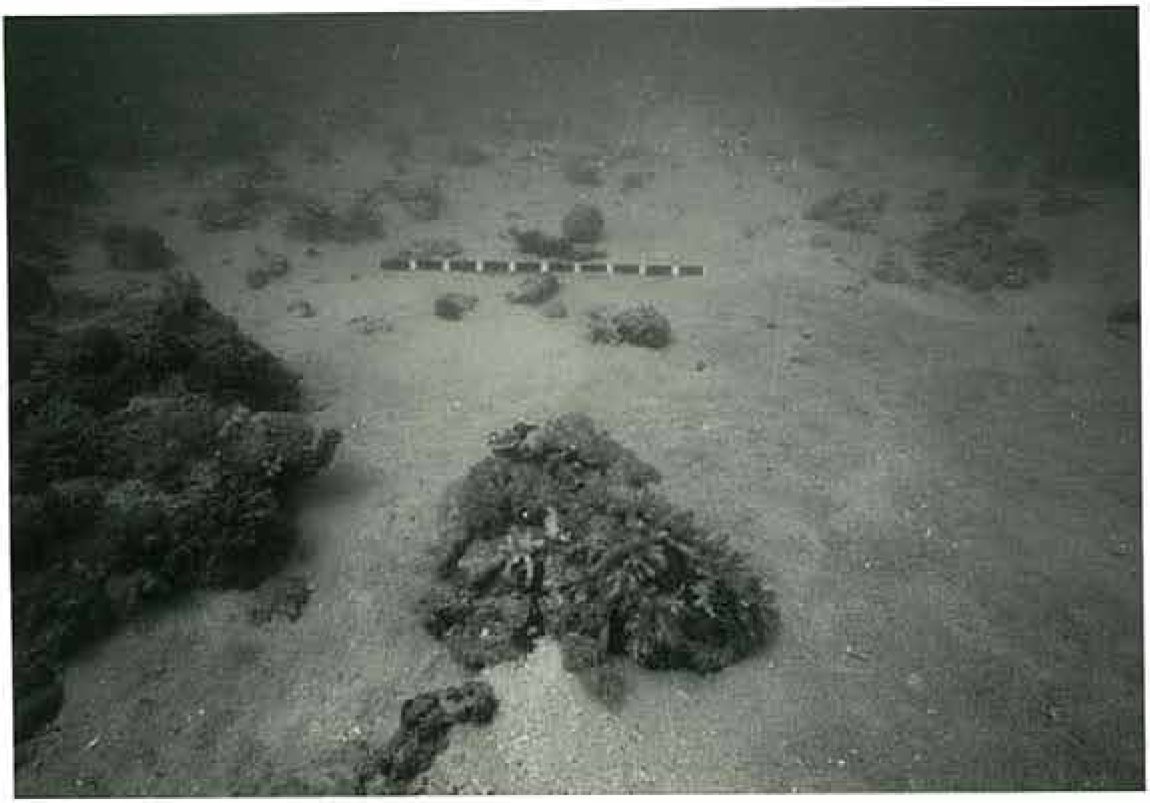
Habitat	S	GCR/S	GCR	IC	BR/S	BR	DM	DP	HC	SC	MA	MC	n
Algal reef flat	17.3	10.1	5.1	1.3	0.2	-	0.3	-	2.9	4.8	57.8	0.2	5
Coral-rich reef flat	4.9	4.3	4.0	2.0	8.2	10.0	0.9	3.2	58.8	1.0	2.6	0.1	4
Shallow patch reef	35.4	3.2	1.8	0.3	4.0	3.3	1.5	-	41.6	7.7	1.2	-	6
Open reef slope	17.5	25.1	18.1	3.7	0.6	0.7	0.6	1.0	20.4	8.8	2.5	1.0	5
Closed reef slope	1.2	5.2	1.8	39.8	2.9	1.5	0.4	3.2	30.2	11.4	2.1	0.3	5
Shallow reef slope/ floor transition	61.6	10.7	13.0	2.1	1.7	1.4	1.3	-	5.1	1.0	2.0	0.1	6
Deep reef slope/ floor transition	75.0	4.3	8.6	5.7	0.1	0.1	0.2	-	1.5	2.4	1.2	0.9	4

[a] Values given: mean percentages calculated from pooled 30 m line transects

KEY:
GCR/S = general calcareous rubble in sand
GCR = general calcareous rubble
IC = impacted carbonate rock
BR/S = rubble derived from branching corals in sand
BR = rubble derived from branching corals
DM = dead massive corals
DP = dead plate corals
HC = living hard corals
SC = soft corals
MA = macroscopic algae
MC = miscellaneous (e.g. sponges)
n = number of 30 m line transects run

Plate 11

Lizard Island habitat type: deep reef slope/floor transition



region of the habitat where they occur on small (< 60 cm), scattered, impacted carbonate rock boulders; dominant genera include *Sinularia*, *Cladiella*, and *Dendronephthya*. Several conspicuous algal species occupy dead coral surfaces, particularly *Dictyopteris delicatula*, *Lobophora variegata*, and *Gelidiopsis* sp.

Estimates of the relative proportions of different substrate components in each of the above seven habitats are presented in Table 7.

3.3.2 Distribution of subadults and adults Table 8 gives the numbers of subadult and adult *Parapercis* observed along transects within the various habitats. A comparison of the subadult and adult distributions indicates that, for each species, individuals of both size classes are restricted to the same habitats.

To facilitate statistical analysis, data for subadults and adults were pooled. *Parapercis clathrata* was excluded from analysis since only six individuals were counted along the combined 49 transects (Table 8). Table 9 shows *P. cylindrica, P. hexophtalma, P. xanthozona* and *P.* sp. 1 to be unevenly distributed within and between the seven habitats. The highly significant G-value (G-test of independence, $P < 0.001$; Sokal and Rohlf, 1969) suggests that the abundance of each species is dependent upon habitat type.

Parapercis cylindrica and *P. hexophtalma* were most abundant within the algal reef flat and shallow patch reef habitats respectively (Table 9). The former species, which had exclusive occupancy of the algal reef flat habitat, was recorded from all habitats except the deep reef slope/floor transition habitat. The latter species was rarely encountered within the shallow reef slope/floor and deep reef slope/floor transition habitats and was not recorded from the algal reef flat and closed reef slope habitats.

Table 8. Numbers of subadult and adult *Parapercis* observed along transects within various habitats at Lizard Island[a]

Species	REEF FLAT HABITATS						REEF SLOPE HABITATS				REEF SLOPE/FLOOR TRANSITION HABITATS					
	Algal reef flat		Coral-rich reef flat		Shallow patch reef		Open reef slope		Closed reef slope		Shallow slope/ floor transition		Deep slope/ floor transition		Total no.	
	SA	A	SA	A	SA	A	SA	A	SA	A	SA	A	SA	A	SA	A
P. cylindrica	19	269	6	17	1	21	3	73	7	60	5	57	–	–	41	497
P. hexophtalma	–	–	8	19	1	52	5	34	–	–	1	2	1	3	16	110
P. xanthozona	–	–	–	–	–	–	–	–	1	13	4	28	7	48	12	89
P. clathrata	–	–	–	–	–	–	2	4	–	–	–	–	–	–	2	4
P. sp. 1	–	–	–	–	–	–	3	3	–	–	24	59	11	125	38	187
Total no.	19	269	14	36	2	73	13	114	8	73	34	146	19	176	109	887

[a] Numbers under habitat headings refer to the actual number of subadults and adults of a species observed on seven combined 50 x 5m transects.

KEY: A = adult
SA = subadult

Table 9. Contingency table comparing the four most abundant *Parapercis* species with habitat type[a]

Species	REEF FLAT HABITATS			REEF SLOPE HABITATS		REEF SLOPE/FLOOR TRANSITION HABITATS		
	Algal reef flat	Coral-rich reef flat	Shallow patch reef	Open reef slope	Closed reef slope	Shallow slope/ floor transition	Deep slope/ floor transition	Total no.
P. cylindrica	288 (100.0)	23 (46.0)	22 (29.3)	76 (62.8)	67 (82.7)	62 (34.4)	– (–)	538
P. hexophtalma	– (–)	27 (54.0)	53 (70.7)	39 (32.2)	– (–)	3 (1.7)	4 (2.1)	126
P. xanthozona	– (–)	– (–)	– (–)	– (–)	14 (17.3)	32 (17.8)	55 (28.2)	101
P. sp. 1	– (–)	– (–)	– (–)	6 (5.0)	– (–)	83 (46.1)	136 (69.7)	225
Total no.	288	50	75	121	81	180	195	990

[a] Numbers without parentheses under habitat headings refer to the adult number (adults and subadults pooled) of a species observed on seven combined 50 x 5m transects; numbers in parentheses = % species composition within a habitat; G-test of independence, $G = 1210.0$, $P < 0.001$ (Sokal and Rohlf, 1969).

P. xanthozona was most abundant within the deep reef slope/floor transition habitat (Table 9). This species was recorded from only two other habitats, these being the closed reef slope and shallow reef slope/floor transition habitats.

Parapercis sp. 1 was common within both the shallow reef slope/floor and deep reef slope/floor transition habitats, though primarily the latter (Table 9). Few individuals of this species were observed within the open reef slope habitat and none were recorded from the closed reef slope habitat. *P.* sp. 1, like *P. xanthozona* was absent from the reef flat habitats, i.e. algal reef flat, coral-rich reef flat, shallow patch reef.

In summary, three (*P. hexophtalma, P. xanthozona, P.* sp. 1) of the four species predominated in particular habitats in which generally one other species was also common. Only one species (*P. cylindrica*) had exclusive occupancy of a habitat type.

3.3.3 Distribution of juveniles A summary of juvenile abundance within major habitats is presented in Table 10. The highly significant G-value (G-test of independence, $P < 0.001$; Sokal and Rohlf, 1969) suggests that juveniles of the four species examined were not randomly distributed.

The distribution of juveniles resembled that of the adults (cf. Tables 9 and 10) with the following exceptions: (1) the presence of juvenile *P. cylindrica* within the deep reef slope/floor transition habitat (adult *P. cylindrica* were absent from this habitat); (2) the presence of juvenile *P.* sp. 1 within the reef flat habitats (adult *P.* sp. 1 were absent from these habitats); and (3) the large number of juvenile *P.* sp. 1 observed within the open reef slope habitat (adult *P.* sp. 1 were rarely encountered within this habitat).

Table 10. Numbers of juvenile *Parapercis* recorded from study sites within major habitats for the period November 1976 to November 1978[a]

Species	Reef flat sites[b]		Open reef slope sites		Shallow slope/floor transition sites		Deep slope/floor transition sites		Total no.
P. cylindrica	244	(80.8)	152	(62.3)	61	(46.9)	21	(7.8)	478
P. hexophtalma	25	(8.3)	25	(10.2)	2	(1.5)	2	(0.7)	54
P. xanthozona	-	(-)	2	(0.8)	3	(2.3)	32	(11.9)	37
P. sp. 1	33	(10.9)	65	(26.6)	64	(49.2)	213	(79.5)	375
Total no.	302		244		130		268		944

[a] Numbers without parentheses under habitat headings refer to the total number of juveniles observed over five 9 x 12m study sites sampled 11 times between Nov. 1976 and Nov. 1978; numbers in parentheses = % species composition within a habitat; G-test of independence, $G = 485.2$, $P < 0.001$ (Sokal and Rohlf, 1969).

[b] Includes one algal reef flat site, two coral-rich reef flat sites, and two shallow patch reef sites.

3.3.4 Population changes through time Figures 19-21 show the fluctuations in juvenile, subadult and adult abundance of *Parapercis* species within various habitats for the period November 1976 to November 1978. Only those habitats in which a species comprised >2% of the total number of adults (i.e. of all *Parapercis* species) counted in three successive censuses were included.

Despite the high sample variances, general seasonal patterns of change in juvenile and subadult abundances are nonetheless evident. Recruit (i.e. juvenile) abundance of *P. cylindrica* was lowest from April to June (inclusive) and generally highest in the month of November (Fig. 19). This summer peak in the number of juveniles, whilst evident in all three habitat types, was particularly marked in the reef flat habitats and was generally followed about two months later by a peak in subadult abundance (Fig. 19). The peak in subadult abudance at this time presumably reflected individuals comprising the prior peak in juveniles growing into the subadult size class.

Consistent seasonal patterns of change in the numbers of juveniles and subadults, not unlike those observed in *P. cylindrica*, were also recorded for *P.* sp. 1 in the deep slope/floor transition habitat. Recruit abundance was lowest from July to September(inclusive) and highest in November of each year (Fig. 20). In addition, a peak in the number of subadults of this species occurred approximately two months after the peak in juvenile abundance (Fig. 20). No consistent seasonal patterns of change in juvenile and subadult numbers of *P.* sp. 1 were observed in the open reef slope and shallow slope/floor transition habitats (Fig. 20).

Juvenile *P. hexophtalma* reached peak abundance , in both reef flat and open reef slope habitats, in November of each year (Fig. 21A,B). The period of least recruitment however, varied between the two habitat types. Recruits were absent from the reef flat habitats from February 1977-April 1977 and from May 1978-June 1978, whilst in the open reef slope habitat

Figure 19

Temporal changes in the mean numbers of juvenile, subadult and adult individuals of *P. cylindrica* per study site in three habitat types. Vertical lines indicate 95% confidence limits. The data are based on regular censuses of five 9×12 m sites within each habitat type.

Key:

Juveniles	■
Subadults	▨
Adults	□

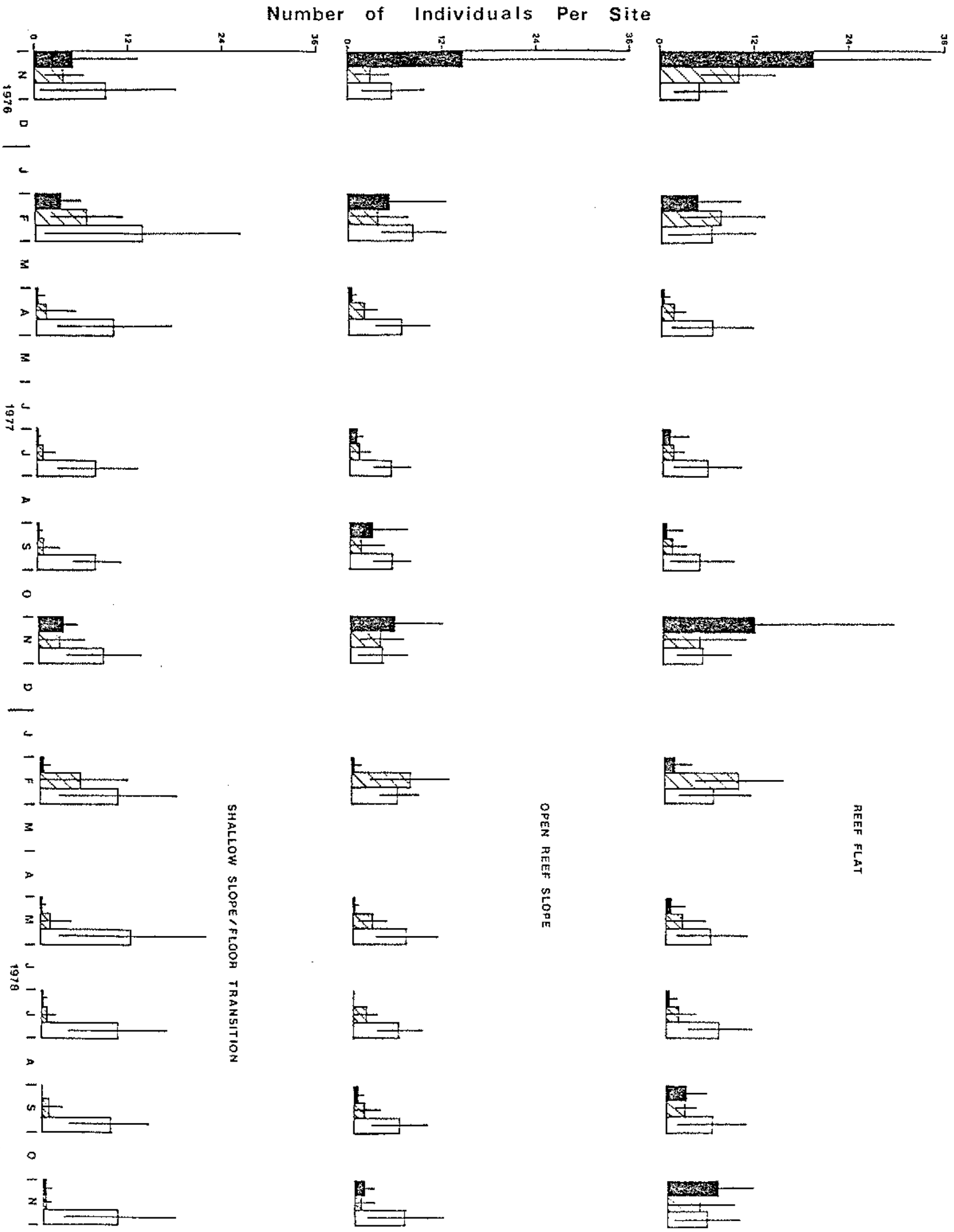

Number of Individuals Per Site
0
12
24
36
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1976
1977
1978
SHALLOW SLOPE/FLOOR TRANSITION
OPEN REEF SLOPE
REEF FLAT

Figure 20

Temporal changes in the mean numbers of juvenile, subadult and adult individuals of *Parapercis* sp. 1 per study site in three habitat types. Vertical lines indicate 95% confidence limits. The data are based on regular censuses of five 9×12 m sites within each habitat type.

Key:

Juveniles ■
Subadults ▨
Adults □

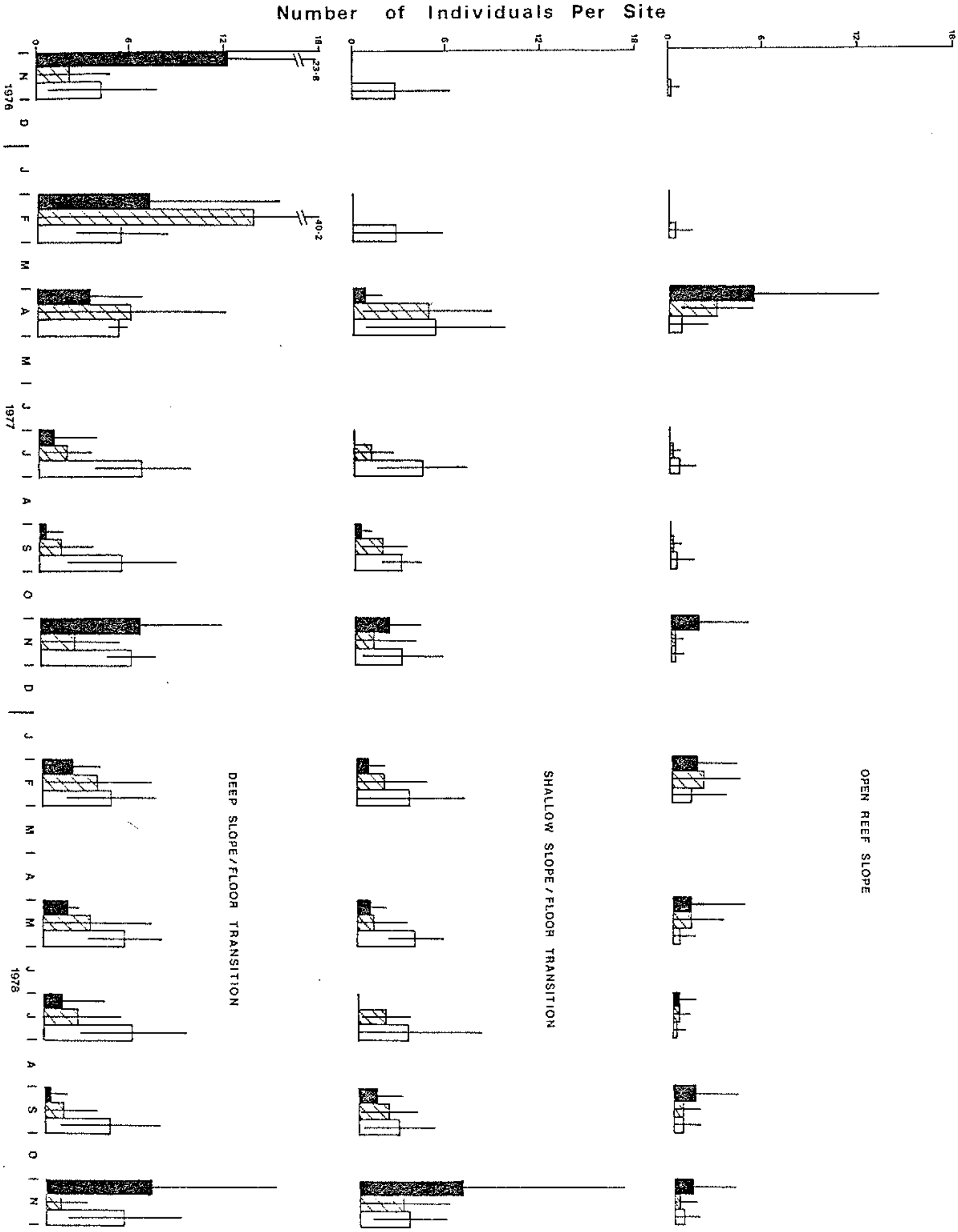

Number of Individuals Per Site
0
6
12
18
23·8
40·2
N
D
J
F
M
A
M
J
J
A
S
O
N
D
J
F
M
A
M
J
J
A
S
O
N
1976
1977
1978
DEEP SLOPE / FLOOR TRANSITION
SHALLOW SLOPE / FLOOR TRANSITION
OPEN REEF SLOPE

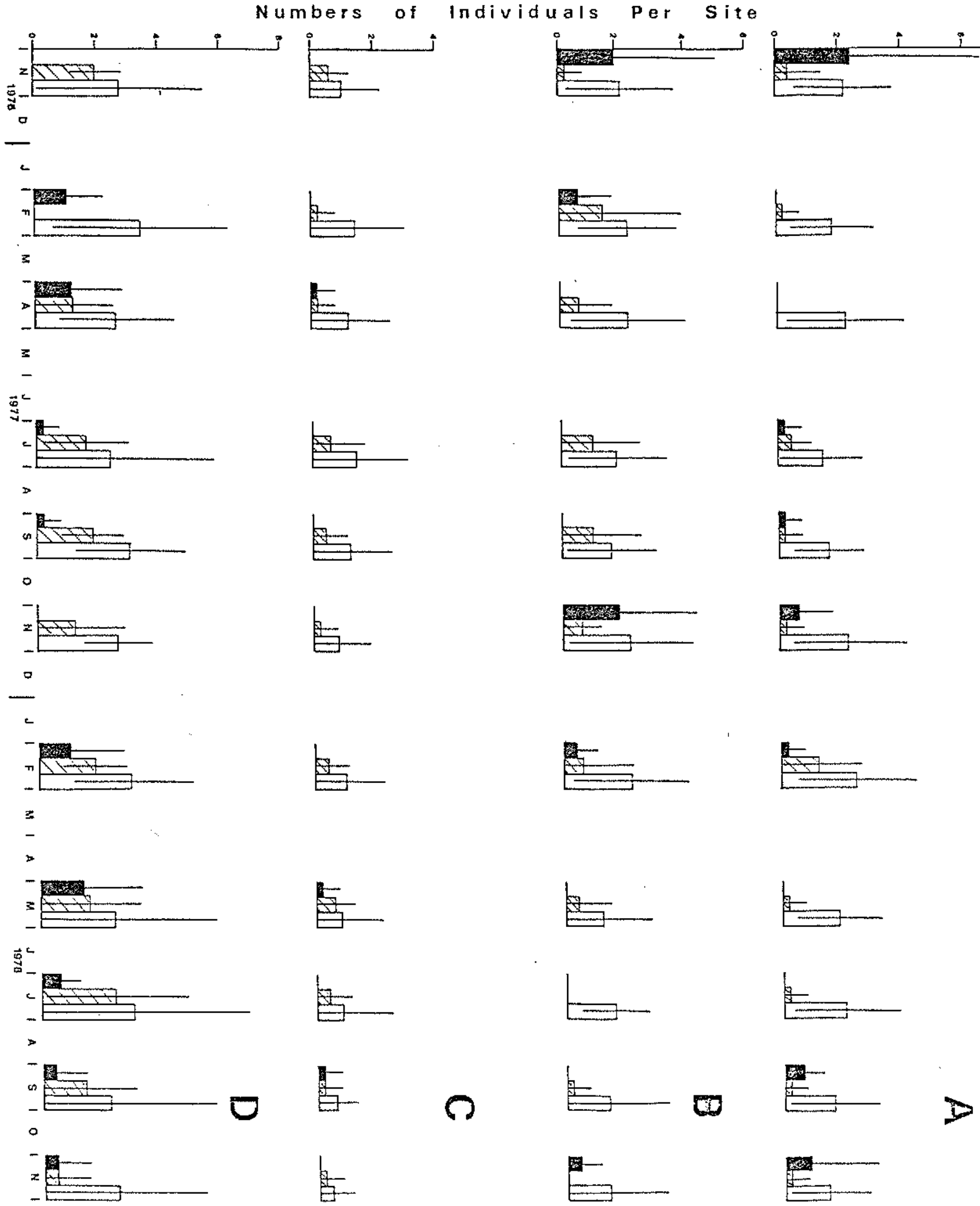
Figure 21

Temporal changes in the mean number of juvenile, subadult and adult individuals of *P. hexophtalma* and *P. xanthozona* per study site in different habitat types. Vertical lines indicate 95% confidence limits. The data are based on regular censuses of five 9×12 m sites within each habitat type.

A. *P. hexophtalma, REEF FLAT*
B. *P. hexophtalma, OPEN REEF SLOPE*
C. *P. xanthozona, SHALLOW SLOPE/FLOOR TRANSITION*
D. *P. xanthozona, DEEP SLOPE/FLOOR TRANSITION*

Key:

Juveniles ■
Subadults ▨
Adults □


Numbers of Individuals Per Site
0
2
4
6
8
0
2
4
0
2
4
6
0
2
4
6
8
1976
N
D
J
F
M
A
M
J
1977
J
A
S
O
N
D
J
F
M
A
M
J
1978
J
A
S
O
N
D
C
B
A

they were absent from April 1977-September 1977 and from May 1978-September 1978 (Fig. 21A,B). It appears that,unlike the other species of *Parapercis* studied, recruitment may not be year round for this species.

Within the deep slope/floor habitat, *P. xanthozona* showed peak recruitment during November (Fig. 21D). The numbers of recruits recorded within the shallow slope/floor transition habitat (Fig. 21C) are unfortunately too small to allow one to make any meaningful comparisons with the deeper habitat type in terms of the timing of recruitment.

Figures 19-21 show that whilst the number of juveniles and/or subadults of each species generally underwent large fluctuations over the two year census period, the number of adults in most cases remained remarkably constant. Linear regressions of the mean number of adults on time in months were calculated for each species in each habitat type to investigate this apparent constancy of numbers. Whilst the number of adult *P. xanthozona* decreased significantly in the shallow slope/floor transition habitat ($F_{1,9} = 12.24$, $p < 0.01$) over the two year period, no significant change in either direction was recorded for this species in the deep slope/floor transition habitat ($F_{1,9} = 2.61$, $p > 0.05$). Adult abundances of *P. cylindrica*, *P.* sp. 1 and *P. hexophtalma* did not change significantly over the two year period in all habitats tested (F tests, all $p > 0.05$).

Year-to-year variability in recruitment of *P. cylindrica* was examined by testing for differences between the November 1976, 1977 and 1978 recruitment peaks in each habitat type using a Kruskal-Wallace Test (Siegal, 1956). These three recruitment peaks were significantly different in the shallow slope/floor transition habitat ($H_{corr.} = 7.05$, $n_i = 5$, $p < 0.05$) however did not differ in either the reef flat ($H_{corr.} = 3.69$, $n_i = 5$, $p > 0.05$) or open reef slope habitats ($H_{corr.} = 2.83$, $n_i = 5$, $p > 0.05$).

3.4 Discussion

The data demonstrate that *Parapercis* species, like most coral reef fishes, are habitat specialists on a broad scale (Goldman and Talbot, 1976; Sale, 1977, 1980). While there is multi-specific use of six of the seven habitats, it is apparent from the species abundance figures (Table 9) that there is (1) specialization of *P. xanthozona* and *P.* sp. 1 on the reef slope/floor transition habitats and (2) specialization of *P. hexophtalma* and *P. cylindrica* on the reef flat habitats. Numerous authors have documented similar cases of large scale habitat specialization amongst coral reef fishes (Hiatt and Strasburg, 1960; Gosline, 1965; Talbot, 1965; Jones, 1968; Talbot and Goldman, 1972; Key, 1973; Vivien, 1973; Chave and Eckert, 1974; Fishelson et al., 1974; Hobson, 1974; Jones and Chase, 1975; Clarke, 1977; Fricke, 1977; Waldner and Robertson, 1980).

Members of the genus *Parapercis* pass through a planktonic larval phase before metamorphosis and subsequent settlement as juveniles (Mito, 1956; Breder and Rosen, 1966). The distributions of newly settled juveniles closely resemble those of their adults (cf. Tables 9 and 10), hence there appears to be little or no change in habitat requirements with growth (cf. Sale, 1969; Emery, 1973; Clarke, 1977; Itzkowitz, 1977). In addition, the relative constancy of adult numbers in the various habitats observed over the two year census period suggests that habitat occupancy patterns were not changing appreciably through time. Juveniles of *Parapercis* sp. 1 did occupy, to a limited extent, the reef flat habitats and those of *P. cylindrica*, the deep reef slope/floor transition habitat from which their adults were respectively absent. All evidence from observations and records suggests emigration of recruits from these habitats was minimal and that individuals settling out therein did not survive to maturity. Consequently it appears that these habitats may be suboptimal for juvenile *Parapercis* sp. 1 and *P. cylindrica*.

The pattern of habitat segregation observed in the *Parapercis* species examined in this study could be the result of (1) interspecific differences in ecological requirements and habitat preferences of the larvae; (2) interactions (competitive, mutualistic, predatory) between newly settled recruits and prior residents of their own or other species; or (3) some combination of these effects. An observational approach, such as the one employed in the present study, is unfortunately insufficient to separate these effects (Sale, 1980).

The data on population changes through time suggest that settlement of juvenile *Parapercis* at Lizard Island is markedly seasonal. Although evidence for the year round presence of juveniles was obtained for all but one species (*P. hexophtalma*), most *Parapercis* settlement occurred between September and February of each year with a peak in November (Figs. 19; 20; 21A,B). An exception was *P. xanthozona* which settled predominantly between February and July reaching a peak in April-May (Fig. 21D). Such peaks in recruitment presumably reflect spawning activity by a large proportion of the population at an earlier time. The low number of recruits recorded at other times of the year suggests that only a very small proportion of the population of each species continue spawning throughout the whole year. These results generally agree with the work of Russell et al. (1977) who examined the recruitment patterns of fishes to artificial reefs in One Tree Island lagoon at the southern end of the Great Barrier Reef. They found that although there was some recruitment throughout the whole year, most settlement occurred from September to May with a marked peak for the majority of species in January-February. *P. cylindrica* was observed to settle on the artificial reefs during the months of November, February and May in one year of their three year study but was absent for the other two years.

Many other reef fish groups besides *Parapercis* show seasonal patterns in spawning and recruitment at Lizard Island, northern Great Barrier Reef. These patterns are similar if not identical to those described by Russell et al. (1977) for One Tree Island fishes (Anderson and Talbot, pers. comm.). Indeed many similar seasonal patterns in spawning and recruitment of coral reef fishes have been noted by researchers working in other geographical areas, albeit at different times of the year and/or showing more than one spawning/recruitment peak (Erdman, 1956 ; Fourmanoir, 1963; Vatanachi, 1972; Munro et al., 1973; Watson and Leis, 1974; Powles, 1975; Luckhurst and Luckhurst, 1977; Johannes, 1978). The available evidence suggests that such patterns may have arisen as responses to local seasonal changes in food availability for larvae or newly settled juveniles (Russell et al., 1977), or to variable patterns of water circulation which favour local retention of larvae (Watson and Leis, 1974; Johannes, 1978). Whilst water temperature plays an important role in the timing of spawning of fishes in temperate regions (Quasim, 1955), there appears to be little correlation between spawning seasons and water temperature regimes in different tropical regions (Johannes, 1978; Sale, 1980).

In addition to seasonally varying recruitment, the results showed year-to-year variabilty in recruitment of *P. cylindrica* to occur in at least one habitat (shallow slope/floor transition). Differences in recruitment or larval abundance from year-to-year have been observed in many other species of coral reef fishes (Gosline and Brock, 1960; Powles, 1975 ;Kami and Ikehara, 1976; Luckhurst and Luckhurst, 1977; Russell et al., 1977). Such differences could be due to a number of factors including breeding irregularities (Russell et al., 1977), chance factors in dispersal (Russell et al., loc. cit.), and/or changing environmental conditions from one year to the next which affect larval or recruit survival (Allen, 1975). Clearly, information is required on transport of larvae by water masses, duration of larval life, weather patterns etc., to satisfactorily explain the year-to-year variability observed in the recruitment of various species of reef fishes.

In contrast to the large fluctuations observed in juvenile and subadult abundance, the numbers of adults of each *Parapercis* species remained relatively constant over the two year study period (Figs. 19-21). Such persistence in numbers differs from much of the available data on other reef fish species and assemlages for which adult numbers have been monitored over the long term (though admittedly these types of studies are not paticularly numerous in the literature). Sale (1978b, 1979) monitored three species of territorial pomacentrids within the same habitat patches for 3½ years and found there were marked changes in the number of adults of each species over this time period. Similarly, Itzkowitz (1977) found adult numbers of two species of *Eupomacentrus (= Stegastes)* to vary considerably over a 12 month period. Sale (1980), in discussing the results of his own work (Sale, 1978b, 1979) as well as interpreting that of others (e.g. Smith and Tyler, 1973b; Ogden and Ehrlich, 1977), concluded that coral reef fish assemblages are not particularly persistent in structure. The relative constancy of adult numbers observed in *Parapercis* over time may be due to, for at least some species, (1) the nature of the social system (small, stable, haremic groups) and (2) differential mortality between the size classes. Indeed Robertson (1974), working on the cleaner wrasse *Labroides dimidiatus*, a species remarkably similar in social structure to *Parapercis*, observed no large scale fluctuations in the numbers of adults in his three study areas over a 2½ year period.

Chapter 4 FOOD AND FEEDING HABITS

4.1 Introduction

Several authors have placed weeverfishes in broad feeding categories e.g. carnivorous (Smith, 1965; Munro, 1967; Goeden, 1974; Burgess and Axelrod, 1975), omnivorous (Low, 1971). However, few workers have given detailed accounts of diet.

Graham (1939; 1953), in a qualitative study of the food of the fishes of Otago Harbour (New Zealand), examined 400-500 stomachs of the temperate water species, *Parapercis colias*. He found a total of 16 fish species, 11 crustacean species (including three crabs and one stomatopod), nine mollusc species, five polychaete species, two algal species, and miscellaneous actinozoans. Graham concluded that *P. colias* is both carnivorous and phytophagous, feeding on a mixture of nekton, benthos, and macrophyton (although he suggested that algae may be taken incidentally with other items in the diet).

Hiatt and Strasburg (1960) gave a detailed account of the diet of *Parapercis cephalopunctata* based upon the examination of 26 specimens. Stomach contents comprised crustaceans (xanthiid, maiid, and portunid crabs; palaemonid and other shrimps; stomatopods; *Galathea* sp.) and fishes (*Apogon novemfasciatus* and unidentifiable fish fragments). Hiatt and Strasburg also examined the gut contents of two specimens of *P. clathrata* finding shrimp fragments in one and a portunid crab in the other. They concluded that both *P. cephalopunctata* and *P. clathrata* are voracious, demersal carnivores, which feed on crustaceans and small fishes.

The remainder of the published information concerning the diets of

Parapercis species is limited to brief qualitative statements on general food preferences for which no data are presented. Quoy and Gaimard (1824) noted *P. nebulosa* to feed on small crustaceans, in their description of this species from Shark Bay, Western Australia. Low (1971) recorded *P. cylindrica* as omnivorous in a table listing the diets of fishes having agonistic and non-agonistic encounters with the damselfish *Pomacentrus flavicauda*. In an ecological study of the fishes of One Tree Island, Great Barrier Reef, Goldman (1973) described *Parapercis cylindrica* and *P. hexophtalma* as benthic invertebrate feeders. Russell (1975) considered the numbers of fishes on his artificial reefs to be affected by predation by *P. colias* and commented as follows (p.305): "*P. colias* is a voracious carnivore and followed the observer about during surveys, snapping at any small crustaceans and fishes which were disturbed". Harmelin-Vivien (1979) suggested *P. hexophtalma* fed on small crustaceans of the bottom sediments at Tuléar Reef, Madagascar, and Coleman (1980), in a popular account of the temperate water fishes of Australia, listed *P. haackei, P. ramsayi* and *P. stricticeps* (given as *P. xanthozona*) as crustacean feeders.

The only published account of *Parapercis* feeding behaviour is that given by Hiatt and Strasburg (1960) for *P. cephalopunctata* and *P. clathrata*. They describe both species as camouflaged, lying on exposed sandy substrates, on rocky surfaces, or beneath coral heads in wait for their prey, which, when sufficiently close, they capture with a rapid dash of one to three feet along the bottom or into midwater.

The main objects of this investigation were (1) to describe and compare the diets and feeding behaviour of *Parapercis* species on the Great Barrier Reef and (2) to examine the diet of a single species, *P. cylindrica*, in relation to time of year, sex, and growth.

4.2 Methods and materials

4.2.1 Species studied Data on general diet composition and feeding behaviour were collected for *Parapercis cylindrica, P. hexophtalma, P. clathrata, P. xanthozona, P. nebulosa*, and an undescribed species *P.* sp. 1 (see Part I). Analyses of diet with respect to time of year, sex, and growth were carried out for *P. cylindrica* only.

4.2.2 Field procedures Specimens were collected by spear, ichthyocides, anaesthetics, nets, or otter-trawl as outlined in Part I (see pp.7-8). Upon capture each individual was placed in a numbered polythene bag and locality, date, time, and depth recorded on an underwater slate. Gut cavities were syringe injected with concentrated formaldehyde within one hour of capture.

Data on feeding behaviour were collected through direct observations whilst SCUBA diving and supplemented by movie footage taken with a Canon Auto-Zoom Super 8 movie camera in an underwater housing.

4.2.3 Laboratory procedures Fish were weighed and measured, after which alimentary tracts were removed and placed individually into numbered vials containing buffered 10% formolsaline. After a few days the formolsaline was replaced with 40% isopropyl alcohol solution. Data on species, locality, date, time, and depth of capture, total length, standard length, weight, colour phase, and sex were recorded on numbered registration cards for cross-reference with gut analyses.

Preliminary investigation revealed that food in the intestinal portion of the alimentary tract of all species was, in general, in a state of advanced digestion. Consequently only stomach contents were used in the food analyses.

Hynes (1950), Pillay (1952), Windell (1971), and, more recently, Berg (1979) have critically reviewed the methods most commonly used for analysing the stomach contents of fishes. After much consideration of the various advantages and disadvantages of each particular method, it was decided to adopt a modified "points" method similar to that recommended by Hynes (1950). Firstly, each stomach was opened and allotted either zero, 5, 10, 15, or 20 points for fullness according to the following criteria:

A. Stomach collapsed, no food present ..... 0 pts.

B. Food occupying approximately ¼ total volume of stomach; wall feels thick and hard when pressed between forceps 5 pts.

C. Stomach with food occupying approximately ½ total stomach volume, generally along most of its length; inner surface is longitudinally pleated and the wall feels thick and hard between forceps ..... 10 pts.

D. Stomach nearly filled with food, but some space remains and a small region of the wall feels thick and hard; shallow longitudinal pleats internally ..... 15 pts.

E. Stomach full; internal pleats shallow or absent; entire wall feels soft and can be idented with forceps in the intact stomach ..... 20 pts.

Next, the stomach contents were emptied into a petri dish containing 40% isopropyl alcohol and sorted into major taxonomic groups with the aid of a stereo-microscope. Identification of food items was carried to species level when condition of the material (i.e. state of digestion and completeness), and present systematic knowledge of the particular group concerned, permitted. The number of points allotted to each stomach was divided amongst the various food items (categories) according to their contribution, in terms of estimated volume, to stomach fullness.

Intermediate values to 0.5 were allowed. The food points for each food item/category were then summed and divided by the total number of points allocated to all stomachs analysed in the sample. This statistic expressed in percentage form gives the relative volumes of food items making up the diet, i.e. % diet composition.

To investigate whether there was any correlation between diet and digestive tract morphology, lengths were measured of the (1) buccal and pharyngeal cavity (i.e. from lips to oesophagus), (2) oesophagus and stomach (i.e. up to pyloric valve), (3) intestine (i.e. midgut), and (4) rectum (i.e. intestino-rectal valve to anus) for each of five individuals of each species. Lengths are expressed as percentages of the whole uncoiled tract, i.e. from lips to anus.

4.3 Results

4.3.1 General composition of diets

4.3.1.1 *Parapercis cylindrica* A total of 378 specimens (20-91 mm SL) were collected, 15 of which had empty guts. The results of the food analysis of the remaining 363 individuals are given diagrammatically in Figure 22A. In terms of percentage of diet composition, crustaceans are clearly the most important food (40.0%), followed by algae (21.8%), polychaetes (12.0%), echinoderms (5.6%), and molluscs (5.0%).

Table 11 presents the food analysis in more detail. Dominant crustaceans included gammaridean amphipods (8.7%), natantian decapods (6.7%) and brachyurans (6.3%), with lesser contributions being made by isopods (3.2%), anomurans (3.0%), anisopods (2.8%), and harpacticoid copepods (1.9%). The most important food group amongst the echinoderms were the ophiuroids, which contributed 5.0% toward the diet. Of the

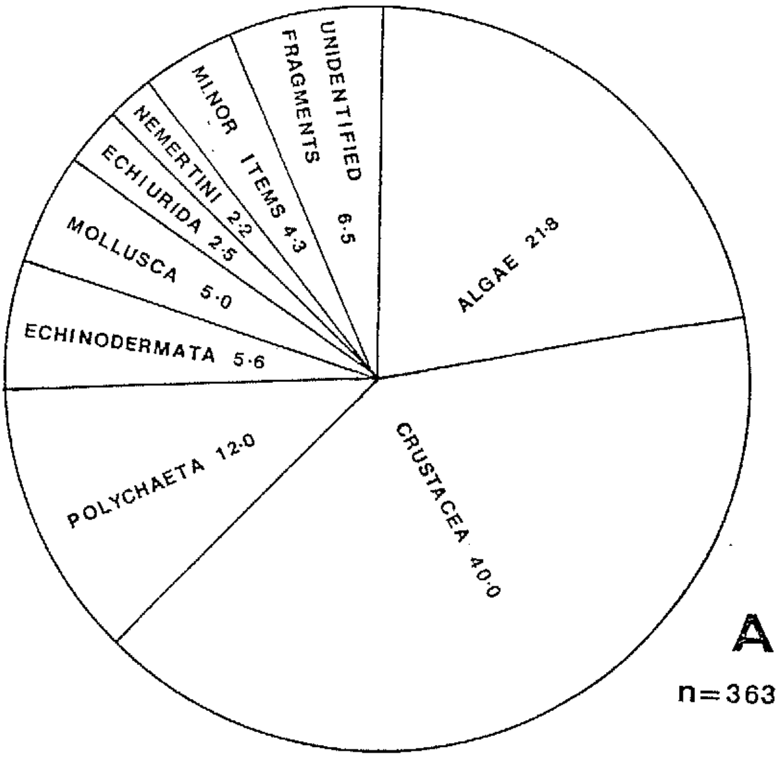
Figure 22

General diet composition of *Parapercis cylindrica* and *P. hexophtalma* from the northern Great Barrier Reef

A. *P. cylindrica*

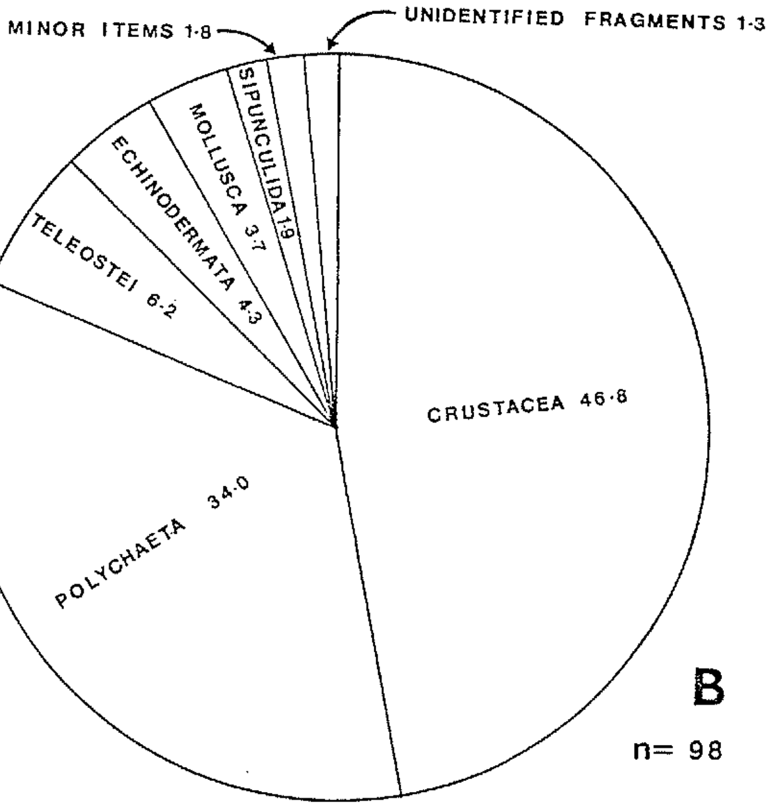
B. *P. hexophtalma*

Values represent % diet composition


UNIDENTIFIED FRAGMENTS 6·5
MINOR ITEMS 4·3
NEMERTINI 2·2
ECHIURIDA 2·5
MOLLUSCA 5·0
ECHINODERMATA 5·6
POLYCHAETA 12·0
CRUSTACEA 40·0
ALGAE 21·8

A

n=363


MINOR ITEMS 1·8
UNIDENTIFIED FRAGMENTS 1·3
SIPUNCULIDA 1·9
MOLLUSCA 3·7
ECHINODERMATA 4·3
TELEOSTEI 6·2
POLYCHAETA 34·0
CRUSTACEA 46·8

B

n= 98

Table 11. Detailed food analysis of 363 specimens of *Parapercis cylindrica* collected from the northern Great Barrier Reef

Food category	% Diet composition (n = 363)		
CRUSTACEA	40.0		
Gammaridean amphipods		8.7	
Natantian decapods		6.7	
Brachyurans		6.3	
Isopods		3.2	
Anomurans		3.0	
Anisopods		2.8	
Harpacticoid copepods		1.9	
Other Crustacea		4.4	
Ostracods			1.3
Stomatopods			0.9
Mysids			0.8
Cumaceans			0.7
Cyclopoid copepods			0.3
Reptantian decapods			0.3
Caprellid amphipods			0.1
Crustacean fragments		3.0	
ALGAE	21.8		
Filamentous green algae		14.1	
Other algae		7.7	
POLYCHAETA	12.0		
Sedentary polychaetes		6.2	
Errant polychaetes		5.8	
ECHINODERMATA	5.6		
Ophiuroids		5.0	
Echinoids		0.6	
Crinoids		Tr	

Table 11 (continued)

Food category	% Diet composition (n = 363)	
MOLLUSCA	5.0	
Prosobranch gastropods		3.5
Bivalves		0.7
Opisthobranchs		0.5
Amphineurans		0.3
ECHIURIDA	2.5	
NEMERTINI	2.2	
MINOR ITEMS	4.3	
Sand		2.5
Teleosteans		0.8
Foraminiferans		0.3
Sipunculids		0.3
Fish eggs		0.1
Turbellarians		0.1
Anthozoans		0.1
Hydroids		Tr
Bryozoans		Tr
Sponges		Tr
UNIDENTIFIED FRAGMENTS	6.5	

n = number of guts used in analysis
Tr = trace (< 0.1%)

molluscs, prosobranch gastropods were by far the dominant group (3.5%); bivalves (0.7%), opisthobranchs (0.5%), and amphineurans (0.3%) were of relatively little importance in the diet.

4.3.1.2 *Parapercis hexophtalma* A total of 108 specimens (25-195 mm SL) were examined, 10 of which had empty guts. Figure 22B gives the general diet composition of the remaining 98 individuals. The most important food groups were crustaceans (46.9%) and polychaetes (34.0%), followed by fishes (6.2%), echinoderms (4.3%), and molluscs (3.7%).

Brachyurans (16.5%), natantian decapods (10.5%), gammaridean amphipods (6.7%), and anomurans (4.4%) were the dominant groups amongst the crustaceans (Table 12). Sedentary polychaetes constituted 31.1% of the diet, whilst errant polychaetes made up the remaining 2.9% of the "Polychaeta" category. Ophiuroids (2.9%) and echinoids (1.4%) were the only echinoderms recorded. Mollusc groups comprised bivalves (1.8%), prosobranch gastropods (1.6%), and occasional amphineurans (0.3%).

4.3.1.3 *Parapercis clathrata* Seventeen individuals (55-135 mm SL) of this species were collected for food analysis and of these, two had empty stomachs. The general diet composition of the remaining 15 individuals is presented in Figure 23A. It is immediately apparent that the major foods of *P. clathrata* are crustaceans (68.5%) and fishes (29.8%).

By far the most important crustacean group in the diet was the Brachyura which accounted for 50.3% of the total diet (Table 13). Food groups making up the remaining 18.2% of the Crustacea category were, in order of importance, natantian decapods (9.7%), crustacean fragments (3.4%), gammaridean amphipods (3.1%), and anomurans (2.0%). *Cryptocentrus koumansi*, a gobiid fish, accounted for 10.9% of the diet; the digested fragments of fishes contributed a further 18.9%. Miscellaneous groups such

Table 12. Detailed food analysis of 98 specimens of *Parapercis hexophtalma* collected from the northern Great Barrier Reef.

Food category	% Diet composition (n = 98)		
CRUSTACEA	46.9		
Brachyurans		16.5	
Xanthidae			2.1
Majiidae			1.0
Calappidae (*Calappa* sp.)			0.7
Parthenopidae			0.5
Portunidae			0.3
Leucosiidae (*Leucosia* sp.)			0.2
Other brachyurans			11.7
Natantian decapods		10.5	
Synapheidae			1.0
Hippolytidae			0.5
Other natantian decapods			9.0
Gammaridean amphipods		6.7	
Anomurans		4.4	
Galatheidae			2.6
Paguridae			1.8
Macrurans (Thalassinidea)		2.5	
Callianassidae			2.2
Upogebiidae			0.3
Isopods		2.5	
Aegidae			0.8
Eurycidae			0.6
Sphaeomidae			0.6
Idoteidae			0.5
Gnathidae			Tr
Other Crustacea		3.8	
Ostracods			0.7
Stomatopods			0.7
Cumaceans			0.6
Anisopods (Paratanaidae)			0.5
Crustacean fragments			0.5

Table 12 (continued)

Food category	% Diet composition (n = 98)		
Copepods			0.4
Caprellid amphipods			0.3
Crab megalops			Tr
POLYCHAETA	34.0		
Sedentary polychaetes		31.1	
Errant polychaetes		2.9	
TELEOSTEI	6.2		
ECHINODERMATA	4.3		
Ophiuroids		2.9	
Echinoids		1.4	
MOLLUSCA	3.7		
Bivalves		1.8	
Prosobranch gastropods		1.6	
Amphineurans		0.3	
SIPUNCULIDA	1.9		
MINOR ITEMS	1.8		
Nemerteans		0.5	
Echiurids		0.5	
Branchiostomids (Amphioxiformes)		0.5	
Foraminiferans		0.2	
Teleostean eggs		Tr	
Sponges		Tr	
UNIDENTIFIED FRAGMENTS	1.3		

n = number of guts used in analysis
Tr = trace (< 0.1%)

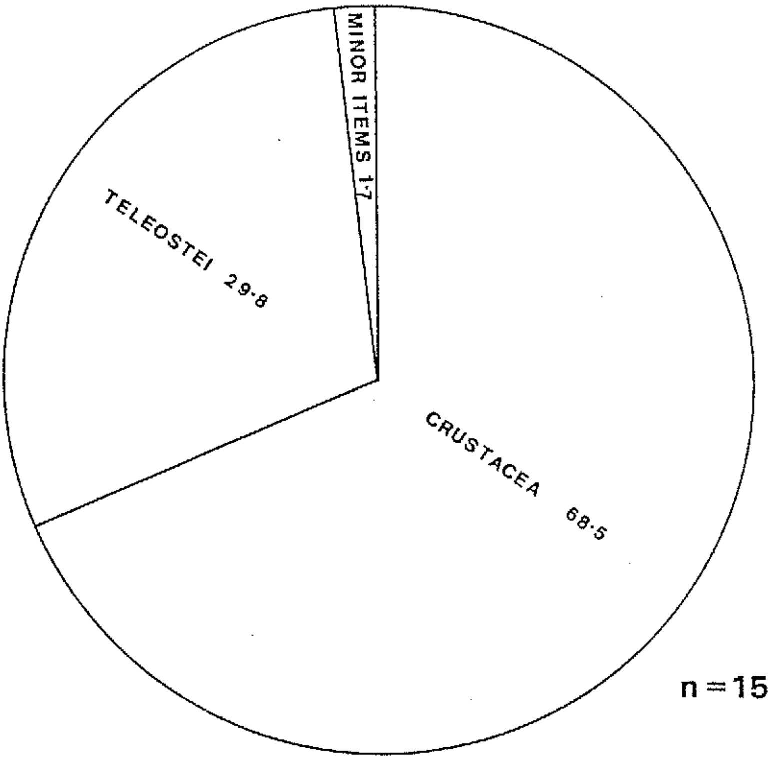
Figure 23

General diet composition of *Parapercis clathrata* and *P. xanthozona* from the northern Great Barrier Reef

A. *P. clathrata*

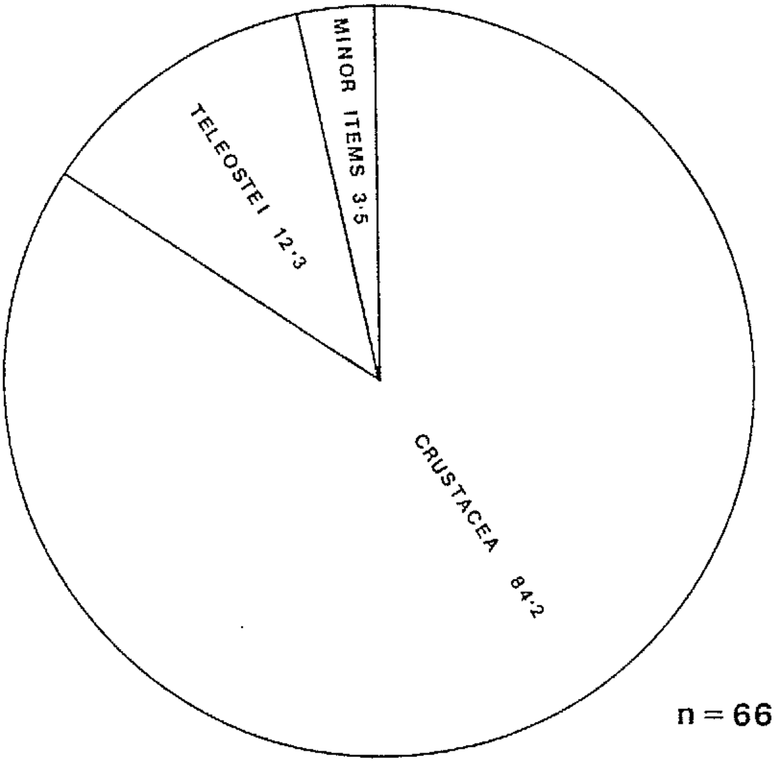
B. *P. xanthozona*

Values represent % diet composition


MINOR ITEMS 1·7
TELEOSTEI 29·8
CRUSTACEA 68·5

A

n = 15


MINOR ITEMS 3·5
TELEOSTEI 12·3
CRUSTACEA 84·2

B

n = 66

Table 13. Detailed food analysis of 15 specimens of *Parapercis clathrata* collected from the northern Great Barrier Reef

Food category	% Diet composition (n = 15)		
CRUSTACEA	68.5		
Brachyurans		50.3	
Natantian decapods		9.7	
Crustacean fragments		3.4	
Gammaridean amphipods		3.1	
Anomurans		2.0	
Paguridae			1.4
Galatheidae			0.6
TELEOSTEI	29.8		
Gobiidae (*Cryptocentrus koumansi*)		10.9	
Other teleosteans		18.9	
MINOR ITEMS	1.7		
Prosobranch gastropods		1.1	
Hydroids		0.3	
Sand grains		0.3	

n = number of guts used in the analysis

as prosobranch gastropods and hydroids, were of little importance to the diet, together making up only 1.7%.

4.3.1.4 *Parapercis xanthozona* Seventy-three individuals (27-138 mm SL) were examined, seven of which had empty guts. Figure 23B shows the general diet composition of the remaining 66 individuals. Crustaceans were by far the major food source constituting 84.2% of all food consumed. Much less important were fishes which accounted for 12.3% of the diet.

Dominant groups amongst the crustaceans included natantian decapods (26.5%) and brachyurans (26.0%), followed by anomurans (15.9%) and stomatopods (9.4%) (Table 14). Of lesser importance were gammaridean amphipods and mysids which contributed 3.0% and 1.3% respectively to the diet. Minor groups, together, made up 3.5% of the total diet and included ophiuroids (1.4%), prosobranch gastropods (1.0%), sedentary polychaetes (0.6%), bivalves (0.1%), and echinoids (0.1%).

4.3.1.5 *Parapercis nebulosa* A total of 19 individuals (84-187 mm SL) were collected, 17 by otter-trawl and the other two by spear; five individuals had empty guts thus leaving 14 individuals for the analysis. The results, in terms of general diet composition are shown in Figure 24A. It can be seen that crustaceans were the most important food type, comprising two-thirds of the total food eaten. Polychaetes were the next most important food type contributing 19.8% to the diet, followed by fishes and branchiostomids (Amphioxiformes) which together made up 10.8% of the diet.

Table 15 shows the food analysis in more detail. Brachyurans and natantian decapods were the dominant groups amongst the crustaceans, comprising 27.2% and 21.7% respectively of the total food eaten. The next most important crustacean groups were anomurans (4.6%) and stomatopods

Table 14. Detailed food analysis of 66 specimens of *Parapercis xanthozona* collected from the northern Great Barrier Reef

Food category	% Diet composition (n = 66)		
CRUSTACEA	84.2		
Natantian decapods		26.5	
Synalpheidae			4.2
Other natantian decapods			22.3
Brachyurans		26.0	
Xanthidae			5.0
Portunidae (*Thalamita* sp.)			4.1
Majiidae			1.9
Calappidae			1.5
Leucosiidae			0.6
Other brachyurans			12.9
Anomurans		15.9	
Galatheidae			9.4
Paguridae			6.3
Porcellanidae			0.2
Stomatopods		9.4	
Gammaridean amphipods		3.0	
Other Crustacea		3.4	
Mysids			1.3
Crustacean fragments			1.2
Ostracods			0.6
Crab megalops			0.1
Isopoda			0.1
Harpacticoid copepods			Tr
Anisopoda			Tr
TELEOSTEI	12.3		
MINOR ITEMS	3.5		
Ophiuroids		1.4	
Prosobranch gastropods		1.0	
Sedentary polychaetes		0.6	

Table 14 (continued)

Food category	% Diet composition (n = 66)
Unidentified fragments	0.2
Bivalves	0.1
Echinoids	0.1
Foraminiferans	Tr

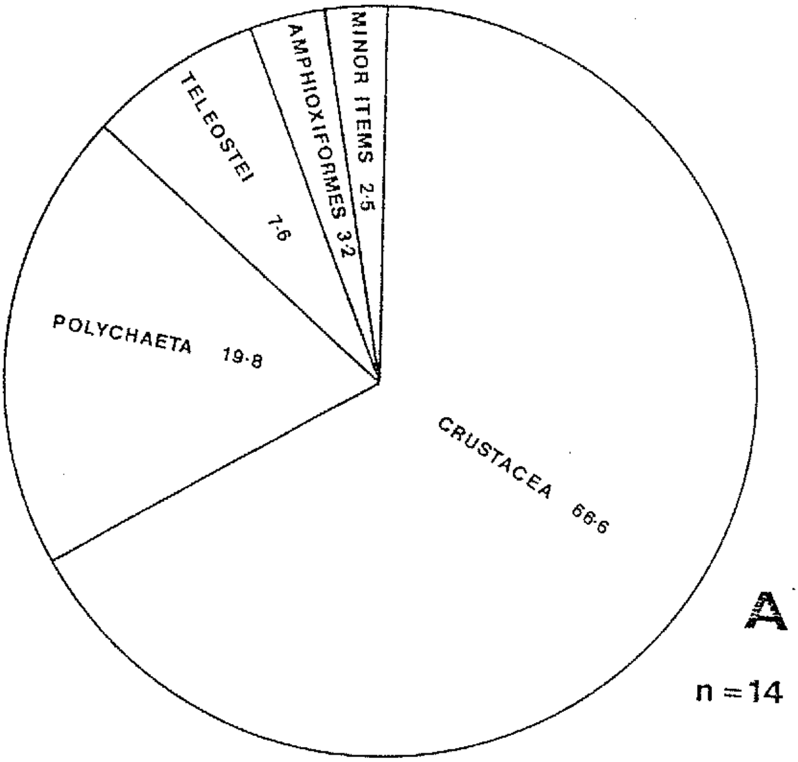
n = number of guts used in analysis
Tr = trace (< 0.1%)

Figure 24

General diet composition of *Parapercis nebulosa* and *P.* sp.1 from the northern Great Barrier Reef

A. *P. nebulosa*

B. *P.* sp.1


MINOR ITEMS 2·5
AMPHIOXIFORMES 3·2
TELEOSTEI 7·6
POLYCHAETA 19·8
CRUSTACEA 66·6
A
n = 14

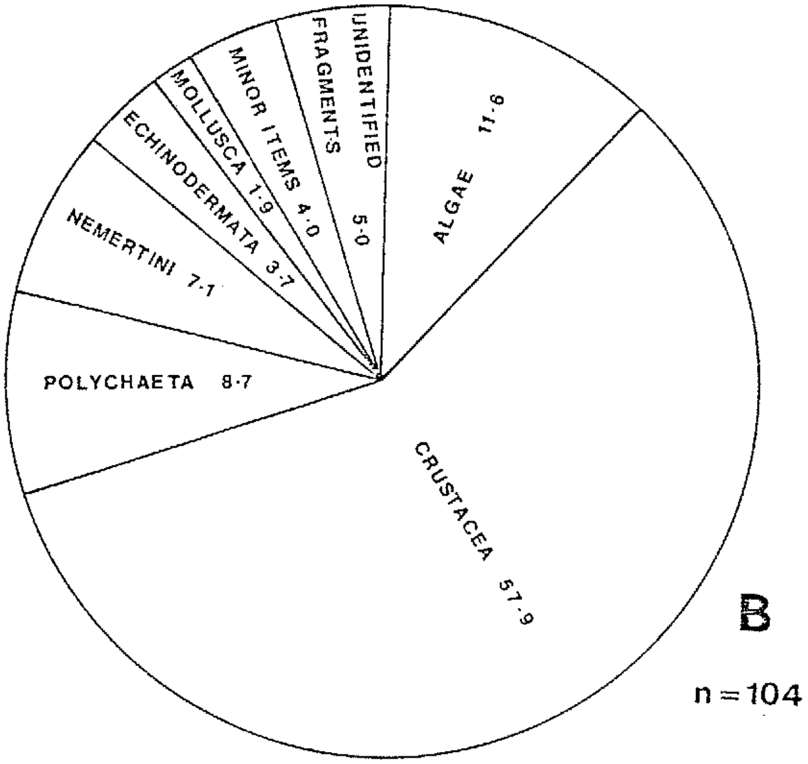

UNIDENTIFIED FRAGMENTS 5·0
ALGAE 11·6
MINOR ITEMS 4·0
MOLLUSCA 1·9
ECHINODERMATA 3·7
NEMERTINI 7·1
POLYCHAETA 8·7
CRUSTACEA 57·9
B
n = 104

Table 15. Detailed food analysis of 14 specimens of *Parapercis nebulosa* collected from the northern Great Barrier Reef

Food category	% Diet composition (n = 14)		
CRUSTACEA	66.6		
Brachyurans		27.2	
Portunidae			10.8
Other brachyurans			16.4
Natantian decapods		21.7	
Synalpheidae			2.8
Other natantian decapods			18.9
Anomurans		4.6	
Galatheidae			3.8
Porcellanidae			0.8
Ostracods		4.3	
Mysids		2.7	
Isopods		2.4	
Stomatopods		2.2	
Other Crustacea		1.5	
Gammaridean amphipods			1.0
Cumaceans			0.5
POLYCHAETA	19.8		
Errant polychaetes		10.3	
Sedentary polychaetes		9.5	
TELEOSTEI	7.6		
Mugiloididae (*Parapercis diplospilus*)		6.5	
Other teleosteans		1.1	
AMPHIOXIFORMES (Branchiostomidae)	3.2		
MINOR ITEMS	2.5		
Ophiuroids		1.4	
Unidentified fragments		0.8	
Foraminiferans		0.3	

n = number of guts used in analysis

(2.2%). The Polychaeta comprised both errant and sedentary groups, which contributed 10.3% and 9.5% respectively, to the diet. Amongst the fishes eaten, *Parapercis diplospilus* formed 6.5% of the diet with another 1.0% being made up of unidentifiable fish fragments. Of the minor groups, ophiuroids were the most notable contributing 1.4% to the total diet.

4.3.1.6 *Parapercis* sp. 1 A total of 111 specimens (28-64 mm SL) were collected, seven of which had empty guts. The general diet composition of the remaining 104 individuals is presented in Figure 24B Crustaceans were the most important food type taken contributing 57.9% to the total diet. Algae were the next most important item (11.6%), followed by polychaetes (8.7%), nemerteans (7.1%), echinoderms (3.7%), and molluscs (1.9%).

Natantian decapods were the most important group amongst the crustaceans, comprising 11.7% of the total food eaten (Table 16). Harpacticoid copepods were of slightly lesser importance (7.2%) and were followed closely by ostracods (6.9%), gammaridean amphipods (6.7%), and crustacean fragments (6.0%). The next most important crustacean groups were mysids (4.7%), brachyurans (4.1%), and cumaceans (4.0%), isopods (2.5%), and anomurans (1.6%). The other crustacean groups present were of relatively minor importance in the diet. Both errant and sedentary polychaetes were taken, forming 4.3% and 4.4% of the diet respectively. The Echinodermata were almost wholly made up of ophiuroids (3.7%); echinoids were found in only trace amounts. Molluscs comprised mainly prosobranch gastropods (1.3%), although some bivalves (0.6%) were taken.

4.3.2 Diet comparisons Table 17 compares the % diet compositions (major food categories only) of the six *Parapercis* species examined. Small crustaceans, algae and polychaetes dominate the diets of *P. cylindrica* and *P.* sp. 1 in contrast to the strictly carnivorous diets of the other four species. *P. hexophtalma* and *P. nebulosa* feed predominantly on polychaetes and both small and large crustaceans whereas *P. clathrata* and *P. xanthozona* take fishes and large crustaceans almost exclusively.

Table 16. Detailed food analysis of 104 specimens of *Parapercis* sp. 1 collected from the northern Great Barrier Reef

Food category	% Diet composition (n = 104)		
CRUSTACEA	57.9		
Natantian decapods		11.7	
Harpacticoid copepods		7.2	
Ostracods		6.9	
Gammaridean amphipods		6.7	
Crustacean fragments		6.0	
Mysids		4.7	
Brachyurans		4.1	
Cumaceans		4.0	
Isopods		2.5	
Serolidae			1.9
Idoteidae			0.6
Anomurans		1.6	
Galatheidae			1.3
Paguridae			0.3
Other Crustacea		2.5	
Cyclopoid copepods			1.0
Crab megalops			0.8
Anisopods			0.4
Caprellid amphipods			0.3
ALGAE	11.6		
Filamentous green algae		5.7	
Other algae		5.9	
POLYCHAETA	8.7		
Sedentary polychaetes		4.4	
Errant polychaetes		4.3	
NEMERTINI	7.1		
ECHINODERMATA	3.7		
Ophiuroids		3.7	
Echinoids		Tr	

Table 16 (continued)

Food category	% Diet composition (n = 104)	
MOLLUSCA	1.9	
Prosobranch gastropods		1.3
Bivalves		0.6
MINOR ITEMS	4.0	
Sand grains		1.2
Pedicellarids (Entoprocta)		1.1
Teleosteans		0.9
Foraminiferans		0.4
Sipunculids		0.2
Teleostean eggs		0.1
Hydroids		Tr
UNIDENTIFIED FRAGMENTS	5.0	

n = number of guts used in analysis
Tr = trace (< 0.1%)

Table 17. Comparison of the diets of six *Parapercis* species from the northern Great Barrier Reef (major food categories only; content figures represent % diet composition)

Food category	*P. cylindrica* (n=363)		*P.* sp. 1 (n=104)		*P. hexophtalma* (n=98)		*P. nebulosa* (n=14)		*P. clathrata* (n=15)		*P. xanthozona* (n=66)	
ALGAE	21.8		11.6		–		–		–		–	
CRUSTACEA	40.0		57.9		46.9		66.6		68.5		84.2	
Brachyurans		6.3		4.1		16.5		27.2		50.3		26.0
Natantian decapods		6.7		11.7		10.5		21.7		9.7		26.5
Anomurans		3.0		1.6		4.4		4.6		2.0		15.9
Stomatopods		0.9		–		0.7		2.2		–		9.4
Macrurans		–		–		2.5		–		–		–
Gammaridean amphipods		8.7		6.7		6.7		1.0		3.1		3.0
Mysids		0.8		4.7		–		2.7		–		1.3
Ostracods		1.3		6.9		0.7		4.3		–		0.6
Harpacticoid copepods		1.9		7.2		0.4		–		–		Tr
Cyclopoid copepods		0.3		1.0		–		–		–		–
Isopods		3.2		2.5		2.5		2.4		–		0.1
Anisopods		2.8		0.4		0.5		–		–		Tr
Cumaceans		0.7		4.0		0.6		0.5		–		–
POLYCHAETA	12.0		8.7		34.0		19.8		–		0.6	
Sedentary		6.2		4.4		31.1		9.5		–		0.6
Errant		5.8		4.3		2.9		10.3		–		–
TELEOSTEI	0.8		0.9		6.2		7.6		29.8		12.3	
ECHINODERMATA	5.6		3.7		4.3		1.4		–		1.5	
MOLLUSCA	5.0		1.9		3.7		–		1.1		1.1	

n = number of guts used in analysis

Tr = trace (<0.1%).

There appears to be some differences in diet composition from species to species within each of the above three general feeding groups. Comparing *P. cylindrica* and *P.* sp. 1, the former ate a higher percentage of algae (21.8% vs. 11.6%), but a lower percentage of crustaceans (40.0% vs. 57.9%), than the latter (Table 17). The percentage of diet composition for various crustacean groups also varied between *P. cylindrica* and *P.* sp. 1, namely the contributions to the diets by natantian decapods (6.7% vs. 11.7%), anomurans (3.0% vs. 1.6%), anisopods (2.8% vs. 0.4%), and harpacticoid copepods (1.9% vs. 7.2%).

The diets of *P. hexophtalma* and *P. nebulosa* differed from each other in the quantities of crustaceans (46.9% vs. 66.6%), errant polychaetes (2.9% vs. 10.3%), and sedentary polychaetes (31.1% vs. 9.5%) eaten, in addition to less important food items such as echinoderms (4.3% vs. 1.4%) and molluscs (3.7% vs. 0%) (Table 17). The contributions made by various crustacean groups to the diets of *P. hexophtalma* and *P. nebulosa* also varied, particularly those of brachyurans (16.5% vs. 27.2%), natantian decapods (10.5% vs. 21.7%), gammaridean amphipods (6.5% vs. 1.0%), and ostracods (0.7% vs. 4.3%).

Results of the food analyses showed differences between the diets of *P. clathrata* and *P. xanthozona* in terms of the proportion of crustaceans (68.5% vs. 84.2%) and fishes (29.8% vs. 12.3%) eaten by these two species (Table 17). In addition, differences were evident in the percentages of certain crustacean groups making up the diets of *P. clathrata* and *P. xanthozona,* notably brachyurans (50.3% vs. 26.0%), natantian decapods (9.7% vs. 26.5%), anomurans (2.0% vs. 15.9%), and stomatopods (0% vs. 9.4%).

4.3.3 Variations in diet with sex of fish The general diet compositions of 223 female and 140 male *Parapercis cylindrica* are compared in Figure 25. It can be seen that the diets of females and males were quite similar though the proportions of crustaceans (42.8% versus 36.1%), echiurids (0.9% versus 4.9%), algae (20.6% versus 23.6%), and echinoderms (4.8% versus 6.9%) differed somewhat.

Sexual differences with respect to the various crustacean groups

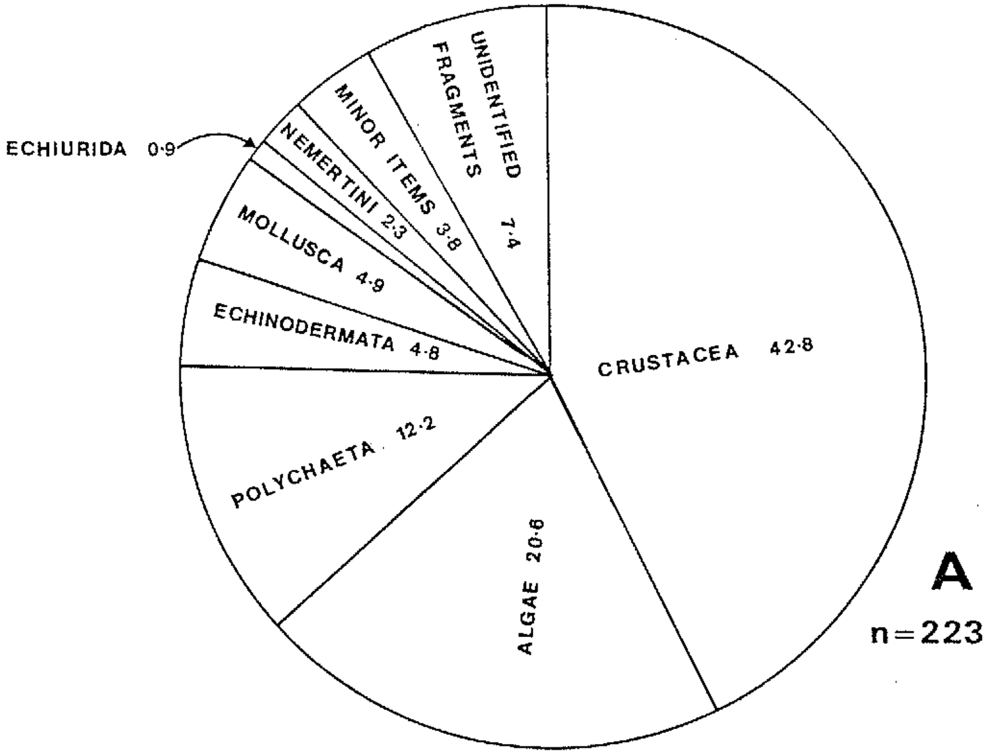
Figure 25

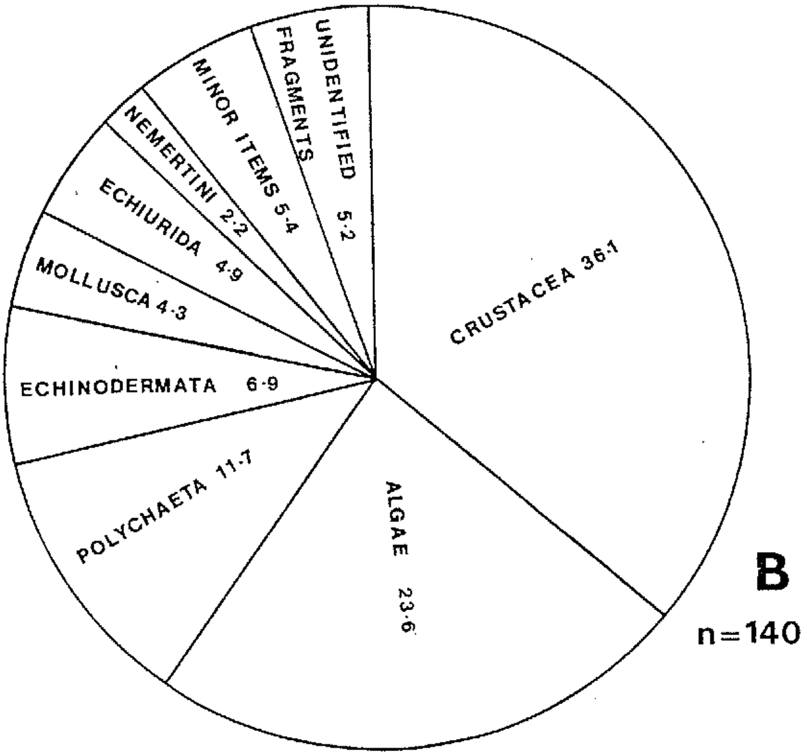
Comparison of the diets of female and male *Parapercis cylindrica*

A. Female

B. Male

Values represent % diet composition


ECHIURIDA 0·9
UNIDENTIFIED FRAGMENTS 7·4
MINOR ITEMS 3·8
NEMERTINI 2·3
MOLLUSCA 4·9
ECHINODERMATA 4·8
CRUSTACEA 42·8
POLYCHAETA 12·2
ALGAE 20·6
A
n=223


UNIDENTIFIED FRAGMENTS 5·2
MINOR ITEMS 5·4
NEMERTINI 2·2
ECHIURIDA 4·9
MOLLUSCA 4·3
ECHINODERMATA 6·9
CRUSTACEA 36·1
POLYCHAETA 11·7
ALGAE 23·6
B
n=140

in the diet were present to a degree (Table 18). Males had a greater proportion of brachyurans in their diet compared with females (8.4% versus 4.9%), but lesser proportions of gammaridean amphipods (6.3% versus 10.3%), isopods (1.7% versus 4.2%), anisopods (1.6% versus 3.6%), and harpacticoid copepods (0.7% versus 2.7%).

4.3.4 Variations in diet with growth The general diet compositions of *Parapercis cylindrica* in four different size-classes are compared in Figure 26. The most apparent feeding patterns with growth were (1) a decrease in the proportion of crustaceans and (2) an increase in the proportion of echiurids. Other patterns include the absence of echinoderms and molluscs, and a lower algal proportion, in the diet of the smallest size-class.

Table 19 shows the diet composition of *Parapercis cylindrica* in different size-classes for crustacean food types. It can be seen that there were decreases in the proportions of gammaridean amphipods, isopods, anisopods, and harpacticoid copepods with growth. Concomitant with these decreases were increases in the proportions of natantian decapods and brachyurans.

4.3.5 Seasonal differences in diet The general diet compositions of *Parapercis cylindrica* for each season of the year are presented in Figure 27.

In autumn, crustaceans were the dominant food type (38.0%), followed by algae (29.3%), polychaetes (7.9%), echinoderms (5.2%), molluscs (4.6%), nemerteans (3.3%), and echiurids (2.3%). The diet composition in winter was very similar to that of autumn with the exception of slight decreases in the importance of echinoderms and molluscs.

In spring, the importance of crustaceans, polychaetes, echinoderms, molluscs, and echiurids increased, whilst that of algae and nemerteans decreased. Crustaceans were the dominant food type (45.6%), followed by polychaetes (13.0%), algae (11.4%), molluscs (5.2%), echinoderms (4.8%), echiurids (3.6%), and nemerteans (1.0%).

Table 18. Variations in diet composition with sex in *Parapercis cylindrica* : crustaceans only

Food category	% Diet composition	
	Female (n = 223)	Male (n = 140)
Gammaridean amphipods	10.3	6.3
Natantian decapods	6.7	6.7
Brachyurans	4.9	8.4
Isopods	4.2	3.9
Anisopods	3.6	1.6
Harpacticoid copepods	2.7	0.7
Ostracods	1.5	1.0
Stomatopods	0.7	1.3
Mysids	1.1	0.4
Cumaceans	1.0	0.2
Cyclopoid copepods	0.3	0.2
Reptantian decapods	-	0.9
Caprellid amphipods	0.2	Tr
Crustacean fragments	3.2	2.7

n = number of guts used in analysis
Tr = trace (< 0.1%)

Figure 26

General diet composition of *Parapercis cylindrica* in different size classes

A. 20-37 mm SL

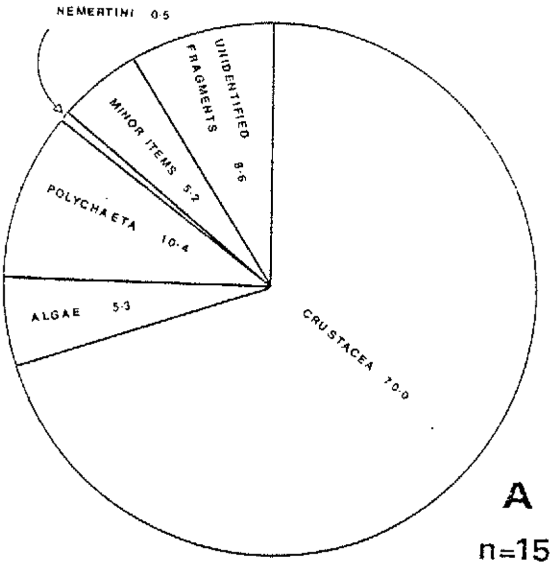
B. 38-55 mm SL

C. 56-73 mm SL

D. 74-91 mm SL

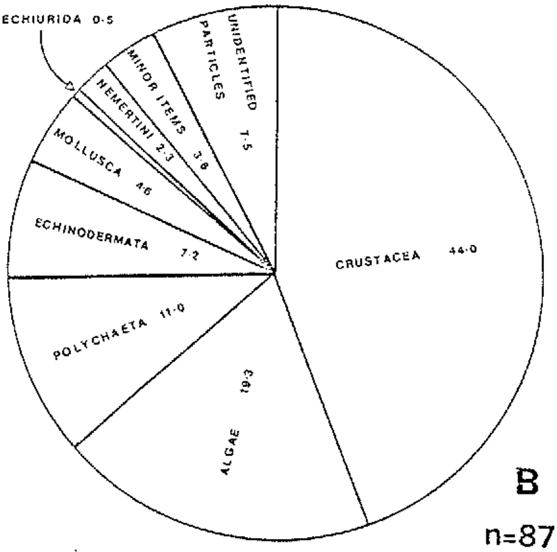
SL = standard length

Values represent % diet composition



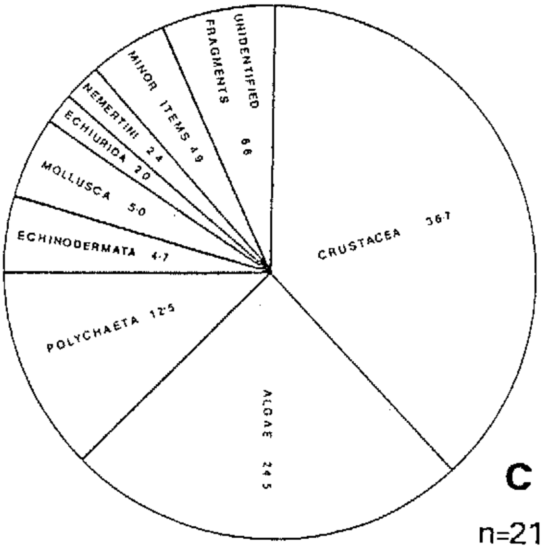
A

n=15



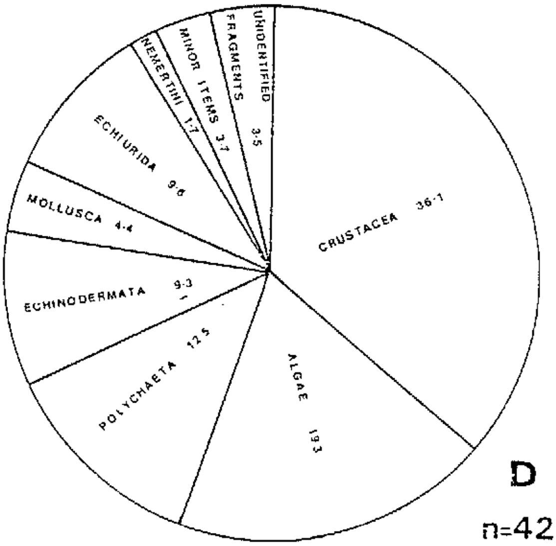
B

n=87



C

n=219



D

n=42

Table 19. Diet composition of *Parapercis cylindrica* in different size-classes : crustaceans only

Food category	% Diet composition			
	20-37* (n=15)	38-55 (n=87)	56-73 (n=219)	74-91 (n=42)
Gammaridean amphipods	16.2	11.5	7.5	5.8
Natantian decapods	4.3	8.4	5.0	12.3
Brachyurans	4.8	3.6	5.6	12.2
Isopods	16.7	4.2	2.2	0.6
Anomurans	-	3.5	3.5	1.1
Anisopods	6.4	2.7	3.0	0.7
Harpacticoid copepods	5.2	2.5	1.7	0.5
Ostracods	2.1	1.4	1.4	0.6
Stomatopods	-	-	1.6	-
Mysids	3.8	1.0	0.7	-
Cumaceans	6.7	0.3	0.5	0.1
Cyclopoid copepods	-	0.2	0.4	-
Reptantian decapods	-	1.4	-	-
Caprellid amphipods	-	0.2	Tr	0.1
Crustacean fragments	3.8	2.3	4.2	2.1

n = number of guts used in analysis
Tr = trace (< 0.1%)

* size-class in mm standard length

Figure 27

General diet composition of *Parapercis cylindrica* collected during different seasons of the year

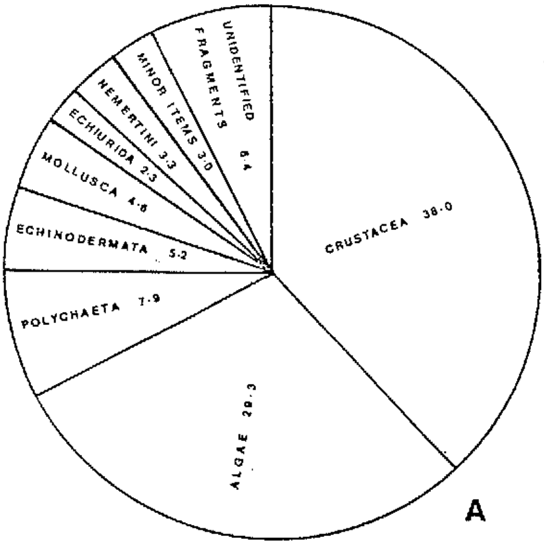
A. Autumn (March-May 1977)

B. Winter (June-August 1977)

C. Spring (September-November 1977)

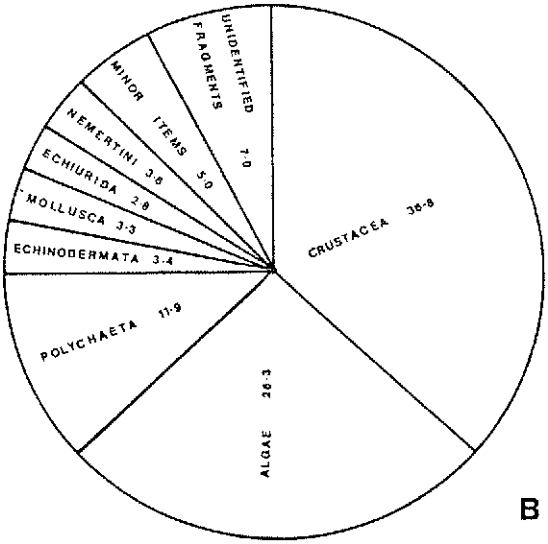
D. Summer (December 1977-February 1978)

Values represent % diet composition



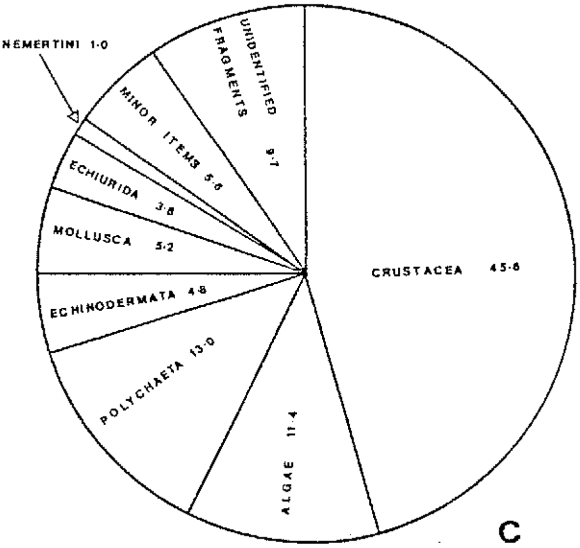
A

n= 81



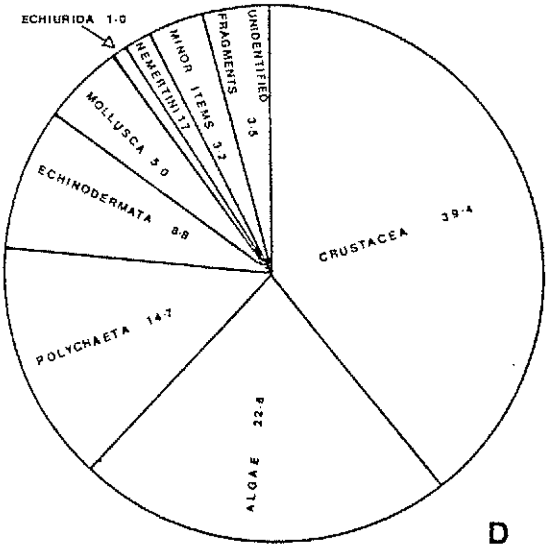
B

n=86



C

n=101



D

n=95

In summer, the importance of algae, polychaetes, and echinoderms increased, whilst that of crustaceans and echiurids decreased. The resulting diet composition consisted of crustaceans being the dominant food type (39.4%), followed by algae (22.6%), polychaetes (14.7%), echinoderms (8.8%), molluscs (5.0%), nemerteans (1.7%), and echiurids (1.0%).

4.3.6 Morphology of the digestive tract Figure 28 shows the relative lengths of different regions of the alimentary canal in *Parapercis cylindrica, P.* sp. 1, *P. hexophtalma, P. nebulosa, P. clathrata,* and *P. xanthozona.* It can be seen that these species fall into three groups on the basis of gut morphology. The buccal and pharyngeal cavities together with the oesophagus and the stomach form about 40% of the alimentary tract in *P. cylindrica* and *P.* sp. 1, about 55% in *P. hexophtalma* and *P. nebulosa,* and about 65% in *P. clathrata* and *P. xanthozona.* Conversely, the length of the intestine together with that of the rectum constitute about 60% of the alimentary canal in *P. cylindrica* and P. sp. 1, about 45% in *P. hexophtalma* and *P. nebulosa,* and about 35% in *P. clathrata* and *P. xanthozona.*

4.3.7 Feeding behaviour

4.3.7.1 *Parapercis cylindrica* During the day, this relatively small weeverfish was observed to feed actively over a sand/rubble substratum. Locomotion and the resting position of *P. cylindrica* is common to all members of the genus *Parapercis.* When resting on the substrate, the anterior of the body is propped up on the pelvic fins. Slow to moderate forward locomotion is achieved solely by repeated synchronous adduction of the pectoral fins. Use of the caudal fin for propulsion is restricted to times when short bursts of rapid swimming are required, i.e. when capturing prey and avoiding predation.

The feeding strategy of *P. cylindrica* is a distinctly visual one and consists of picking at relatively small, cryptic organisms generally residing (1) on, or just beneath, the surface of the sand or (2) amongst algal-covered coral rubble. In the latter case, both prey and the algal cover it is utilizing are ingested. The basic feeding sequence begins

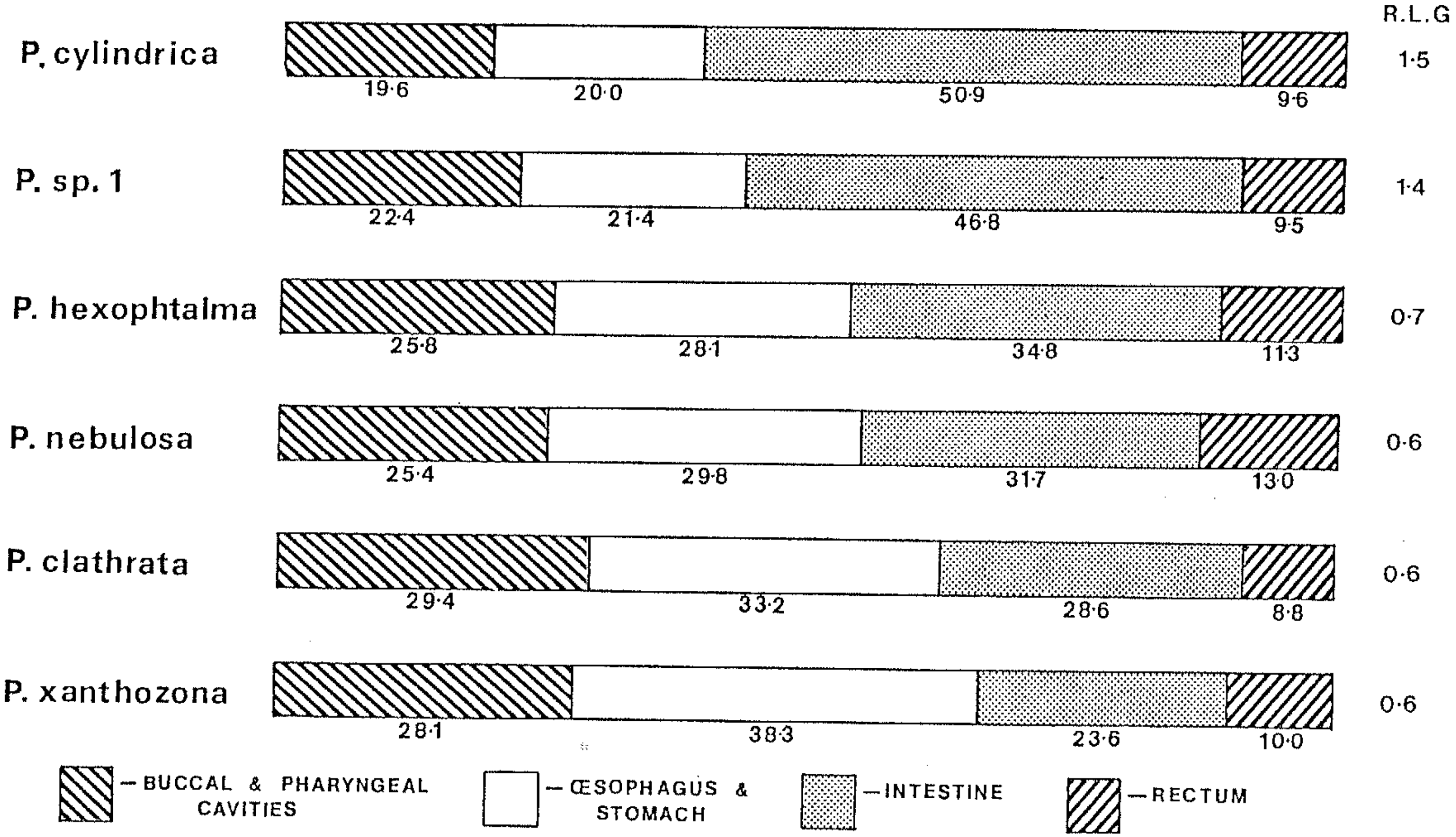
Figure 28

Relative lengths of different regions of the alimentary canal in six *Parapercis* species

Lengths expressed as percentages of the whole uncoiled tract, i.e. from lips to anus; values given represent mean percentages based on examination of five specimens of each species

R.L.G. = Gut length relative to fish length (Al=Hussaini, 1947)
= Length from oesophagus to anus/Standard length

Values given represent mean R.L.G. for five specimens of each species


R.L.G
P. cylindrica
19·6
20·0
50·9
9·6
1·5
P. sp. 1
22·4
21·4
46·8
9·5
1·4
P. hexophtalma
25·8
28·1
34·8
11·3
0·7
P. nebulosa
25·4
29·8
31·7
13·0
0·6
P. clathrata
29·4
33·2
28·6
8·8
0·6
P. xanthozona
28·1
38·3
23·6
10·0
0·6
— BUCCAL & PHARYNGEAL CAVITIES
— ŒSOPHAGUS & STOMACH
— INTESTINE
— RECTUM

with *P. cylindrica* scanning the surface of the substratum, whilst adopting the resting position as described above. When prey is detected, presumably through irregular contours or movement, visual fixation occurs for a few seconds after which the fish makes a rapid dash towards the prey in an effort to capture it. This rapid dash of approximately 5-10 cm is achieved by a single, posterior sweep of both pectoral fins in conjunction with a simultaneous strong sweep of the caudal fin. The prey is then grasped and held by the canines present in the jaws; if the food is attached to the substrate, it is torn loose by lateral movements of the head and body. After ingestion, scanning is resumed.

P. cylindrica also capitalizes on prey driven from cover by the foraging activities of habitat disturbing fishes, such as the mullids *Parupeneus trifasciatus* and *P. cyclostomus*, the wrasses *Coris gaimard* and *Hemipteronotus taeniourus*, and the dasyatid rays *Taeniura lymma* and *Dasyatis kuhli*.

After dark, *Parapercis cylindrica* adopts a slightly different colouration (characterized by darkening of the head and paling of the body), secretes itself under coral rubble or in reef crevices, and remains inactive until daylight (Plate 12). Feeding is thus restricted to the day.

4.3.7.2 *Parapercis* sp. 1 This species was observed to feed actively during daylight hours, generally over expanses of sand adjacent to rubble slopes. The feeding strategy of *Parapercis* sp. 1 is almost identical to that of *P. cylindrica*. Relatively small, cryptic organisms hiding on, or just under the surface of the sand or amongst the algal film covering the substratum, plus the algae itself, are taken with the same search, detection, and capture behaviour.

Besides capitalizing on prey driven from cover by the foraging activities of various fishes, *Parapercis* sp. 1 also takes advantage of the shifting nature of its habitat. Sand movement amongst the hummocks and depressions comprising the sandy habitat of *Parapercis* sp. 1 was of common occurrence and this was observed to be a powerful visual attractant to *P.* sp. 1, which took full advantage of prey uncovered in this way. This species commonly formed loose associations with holothurians,

Plate 12

Night-time photograph of *Parapercis cylindrica* resting in shelter site and exhibiting nocturnal colouration

since sand movement was often precipitated by the latter's feeding activities. *Parapercis* sp. 1 was often observed at the aboral end of *Actinopyga miliaris*, snapping at small prey uncovered due to the disturbance of the substratum by emission of the faeçal pellets of the holothurian (Plate 13). Occasionally, *Parapercis* sp. 1 was observed to even feed on the faecal pellets themselves.

After dark, *Parapercis* sp. 1 retreats to the sand/rubble slope interface where it secretes itself under rubble and remains inactive until daylight.

4.3.7.3 *Parapercis hexophtalma* This species utilizes a feeding strategy not found in other *Parapercis* species, that of disturbing the habitat to uncover prey. Digging behaviour was observed frequently and involved two to three second bouts of rapid beating of the caudal and pectoral fins with the pelvics folded against the body and the fish lying flat on the surface of the sand (Fig. 29). The sweeping action of the caudal and pectorals results in substantial sand being removed from the area and the subsequent formation of a depression. After completing a bout of caudal and pectoral beating, the fish would turn around, lower its body to the substratum (i.e. with consequent folding of the pelvics against the body), and then inspect the surface of the sand in the depression for uncovered prey (Plate 14). If prey was detected, the fish would make a rapid dash, by way of a single posterior sweep of the pectoral fins and a strong sweep of the caudal fin, to make the capture. If no prey was observed, another bout of caudal and pectoral beating would generally take place followed by inspection of the depression once again. *P. hexophtalma* often excavate for prey in this way under small coral heads at the coral/sand interface and consequently form additional sites in which they can shelter from predators (Plate 15). Besides capturing prey exposed by their digging activities, *P. hexophtalma* also pick at any prey they detect on the substratum, in much the same way as *P. cylindrica*, whilst en route to digging sites.

On one particular occasion whilst the author was spearing fishes for gut analyses, an individual of *P. cylindrica* removed itself from

Plate 13

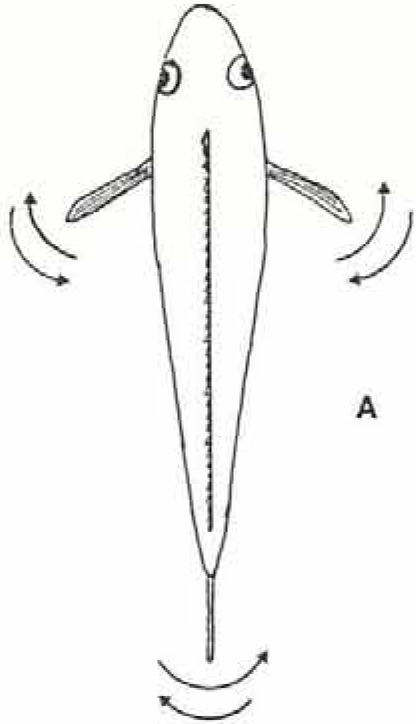
Parapercis sp. 1 feeding on prey which has been uncovered due to disturbance of the substratum by the holothurian *Actinopyga miliaris*

Figure 29

Digging behaviour in *Parapercis hexophtalma*

A. Dorsal view

B. Lateral view



A

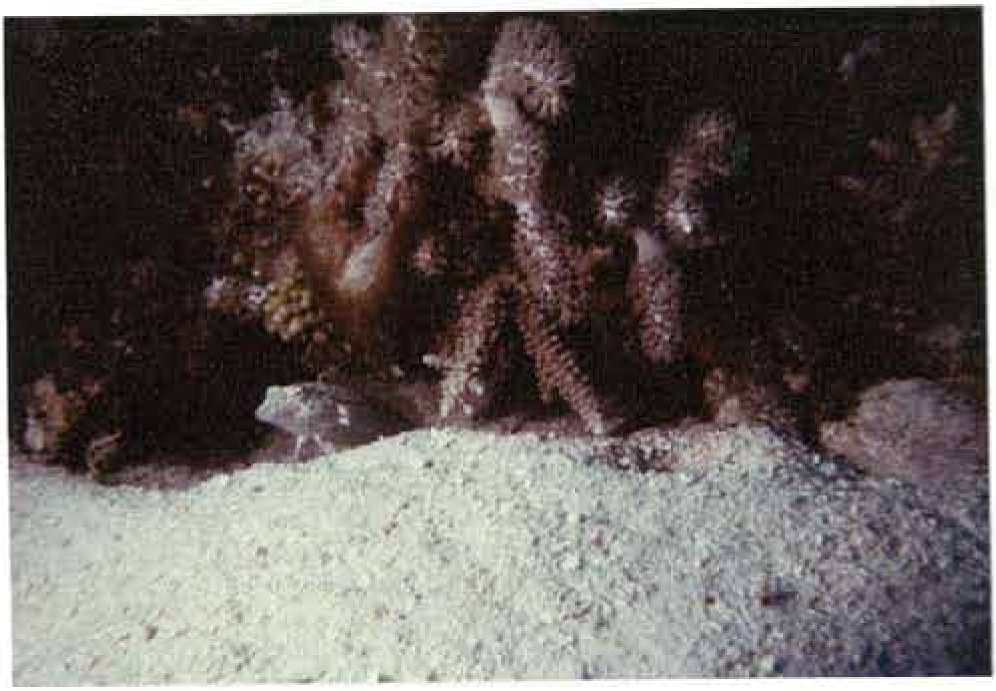
B

Plate 14

Parapercis hexophtalma inspecting the sand depression it has just excavated, for potential prey

Plate 15

Parapercis hexophtalma resting after excavating for prey underneath a small coral head at a coral/sand interface



the spear and dashed towards cover. At that moment, a large terminal phase *P. hexophtalma* darted upon the wounded fish, captured and then swallowed it. Although hardly a natural situation, such behaviour does suggest that *P. hexophtalma* takes advantage of the vulnerability of prey when the latter is under stress.

P. hexophtalma is a strictly diurnal species;at night an individual will "sleep" under a small coral head, often in a depression it has dug during the day.

4.3.7.4 *Parapercis clathrata* Individuals of this species ambush crustaceans and small fishes by lying motionless on or under pieces of coral rubble (Plate 16). When the potential prey comes within striking distance, approximately one metre, the fish makes a rapid dash forward to seize it. The camouflage colouration of *P. clathrata* ensures that this species is relatively inconspicuous when resting on the substrate and it is able to take its prey by surprise. The author observed *P. clathrata* preying in this way upon gobiid fishes, particularly the yellow-headed goby, *Valenciennia strigatus*.

Individuals of *Parapercis clathrata* "sleep" under pieces of coral rubble at night and remain inactive until daylight.

4.3.7.5 *Parapercis xanthozona* The main feeding strategy of this species is one of stalking its prey. Observations were made of *P. xanthozona* attacking the goby *Cryptocentrus koumansi*. The sequence of events was as follows: (1) visual fixation of the prey, (2) short, slow movements in the direction of the prey, by way of bouts of pectoral sculling, until within attacking range, and (3) rapid dash of about one metre to grasp prey.

P. xanthozona was also observed to pick at relatively large cryptic prey hiding just beneath the surface of the sand. Upon detection of the prey, presumably through movement or irregular contours, visual fixation occurred for a few seconds after which the fish made a rapid lunge to seize the prey in its jaws.

Plate 16

Parapercis clathrata lying under coral rubble in readiness to ambush prey

This species, like the other *Parapercis* species mentioned above, is nocturnally inactive, "sleeping" within reef crevices.

4.3.7.6 *Parapercis nebulosa* Observations on the feeding behaviour of this deepwater species are restricted to those made during a 30 minute midday dive to 51 metres on the off-reef floor adjacent to Wheeler Reef, near Townsville. During this dive, *P. nebulosa* was observed to move over the substratum in the short "hops" characteristic of *Parapercis* species, occasionally visually fixating, then picking at both large and small, cryptic and non-cryptic prey hiding amongst the foraminiferans, silt, weed, and dead molluscs comprising the benthic habitat. No digging behaviour was observed.

Nocturnal observations were not carried out on this species, hence one cannot rule out feeding activity at this time as well as during the day.

4.4 Discussion

On the basis of the food analyses presented above, it is possible to divide the six *Parapercis* species examined into three general feeding groups as follows:

I. Small crustacean, algal, and polychaete feeders: *P. cylindrica*, *P.* sp. 1.

II. Polychaete, large crustacean, and small crustacean feeders: *P. hexophtalma*, *P. nebulosa*.

III. Large crustacean and fish feeders: *P. clathrata*, *P. xanthozona*.

The relative lengths of the different sections of the alimentary tract for each species (see Fig. 28) agree with this grouping. The buccal and pharyngeal cavities, together with the oesophagus and stomach form only about 40% of the total length of the whole tract in Group I species, about 55% in Group II species, and about 65% in Group III species. Group

III species, i.e. the large crustacean and fish feeders, thus have considerable storage capacity for the relatively bulky prey which they seize quickly and swallow intact. This storage capacity is not required by Group I species due to the small size of the food items they take. Also the presence of algae in their diet necessitates a longer time for digestion and absorption and hence a much greater relative intestinal length than in Group III species (see Fig. 28). Group II species take up a somewhat intermediate position between these two extremes.

The inter-relationship between the morphology of the alimentary tract and the particular feeding category (i.e. Group I, II, or III) a species belongs to, as outlined above, suggests that *Parapercis* species show some degree of food specialization. However, it is unclear whether the differences observed between the diets of species within each broad feeding group reflect (1) differences in the availability of certain food items due to differing habitat types or (2) active preference or avoidance of particular food items. Knowledge of the quantities of different food organisms available to each species is required to separate these two effects and this was unfortunately beyond the scope of the present study. In any case, of the six species of *Parapercis* examined, no two are identical in diet composition, consequently potential competition through dietary overlap is minimized.

Dietary changes with growth have been documented for many fishes (Steven, 1930; Hynes, 1950; McDowall, 1965; Godfriaux, 1969; Pollard, 1973; Keast, 1978; Targett, 1978). In *P. cylindrica*, the main dietary trend with growth was an increase in the proportion of larger food types consumed, i.e. brachyurans, echinoderms, and echiurids, with a corresponding decrease in the consumption of smaller food types, such as gammaridean amphipods, isopods, anisopods, and harpacticoid copepods. Such changes presumably reflect (1) the strength and ability of larger fish to feed on larger organisms (Hynes, 1950; McDowall, 1965) and (2) the changes in diet required to maintain an optimal energy response, i.e. with increase in fish size the energy expenditure in capturing and assimilating small prey is too high for the amount of energy returned, hence larger organisms are taken to satisfy energy requirements (Steven, 1930; Allen, 1935). The results also show the algal component in the diets of juveniles (20-37 mm.SL size-class) to be of much lesser importance than in the diets of individuals belonging to larger size-classes. That omnivorous fishes utilize plant food for metabolic energy and animal food for growth is well known (Migata and Hashimoto, 1949; Menzel, 1959; Fischer, 1970, 1972a, 1972b, 1973). The lesser importance of algae in the diet of juveniles may reflect the absence of amino acids and other essential nutrients in this type of food at a time of the life history when maximum energy for development and growth is required. With maturity, and a slowing down of the growth rate, the fish would be able to obtain a greater proportion of its growth requirements from algae, hence one might expect the consumption of algae to increase.

The differences observed between the diets of the sexes in *Parapercis cylindrica*, namely the greater proportion of larger food types (e.g. brachyurans, echinoderms) in the diet of males compared with females can probably be explained by the larger size of the male fish (see Fig. 66,p.326). In addition, some differences may be attributable to the larger feeding areas and greater mobility of males compared with females (see Chapter 5).

Seasonal fluctuations in the diet of *P. cylindrica* tended to be somewhat irregular and probably reflect seasonal changes in the availability of the various food organisms, rather than specific seasonal changes in food preferences by the fish.

Of the six *Parapercis* species studied, at least five are inactive during night-time. All feed actively during the day and utilize specialized feeding strategies in which vision plays a key role. That *Parapercis* species have diurnalhabits agrees with the suggestion of Hobson (1974) that whilst nocturnal and crepuscular habits predominate among the more generalized (primitive) coral reef fishes, e.g. Carangidae, Holocentridae, Apogonidae, Serranidae, diurnal habits predominate among the more advanced, specialized forms, including most of the higher Perciformes (which includes the genus *Parapercis*) and Tetraodontiformes.

Parapercis cylindrica and *P.* sp. 1 have virtually identical feeding strategies, that of visually scanning the algae and the surface of the sand, then picking at small cryptic organisms hiding thereon. Similar scan-and-pick feeding strategies have been shown to occur in some coral reef labrids (Hobson, 1974) and stream-dwelling salmonids (Kalleberg, 1958; Keenleyside, 1962).

Although many diurnal fishes that feed on benthic invertebrates frequently take algae along with prey items, in many cases its ingestion is probably incidental and not used as a food source (Hobson, 1968). Both *P. cylindrica* and *P.* sp. 1 ingest algae along with their small cryptic prey; however, the high proportion of algae in the stomach contents and the long intestines of these two species suggest that they are true omnivores. This is in agreement with the findings of Low (1971), who listed *P. cylindrica* as being omnivorous in nature.

Parapercis cylindrica and *P.* sp. 1 also capitalize on prey driven from cover by the foraging activities of other fishes. This additional feeding strategy is used by many fishes. Keenleyside (1979) noted that small freshwater cyprinids can often be seen following catostomids that are sucking up and sorting out bottom materials, periodically darting in to feed on the exposed prey. Many coral reef labrids follow close to the feeding jaws of larger herbivores that disturb the substratum, to snap up tiny crustaceans driven from cover (Hobson, 1968, 1974). Several species of the labrid genus *Halichoeres* follow mullids or ostraciontids and snatch prey as the sand is disturbed by these fishes (Longley, 1927; Hobson, 1968, 1974). The present author has also observed scolopsids on the Great Barrier Reef feeding on prey organisms disturbed by digging mullids.

In contrast to the feeding strategies of *P. cylindrica* and *P.* sp. 1, *P. hexophtalma* disturbs the habitat by rapid movement of its caudal and pectoral fins, and then picks at the uncovered prey. Several other reef fishes utilize this strategy of uncovering organisms buried in the soft substrate through active disturbance of the habitat. The trunk fish *Lactophrys triqueter* directs jets of water from its mouth to disturb the sandy substrate and uncover small organisms upon which it feeds (Longley, 1927). By rapidly undulating its dorsal and anal fins whilst lying on its side or by directing a jet of water from its mouth, the eastern Pacific balistid *Sufflamen verres* generates considerable sand movement thereby uncovering its buried prey (Hobson, 1965, 1968). In a slightly different strategy, the labrids *Coris gaimard* and *Hemipteronotus taeniourus* overturn pieces of coral rubble in sand/rubble areas with their snout or jaws and feed on the exposed organisms (Hobson, 1974; pers. obs.).

The feeding strategy employed by *P. clathrata,* that of hunting by ambush; is utilized by several other groups of coral reef fishes. In all these fishes, surprising the prey is of the utmost importance and is accomplished by (1) camouflage colouration, (2) hiding under cover, (3) remaining motionless, or some combination of these (Curio, 1976). Besides *P. clathrata,* other ambushers on coral reefs include some serranids, synodontids, scorpaenids, bothids, and platycephalids (Hiatt and Strasburg, 1960; Hobson, 1968, 1974). The latter four groups, like *P. clathrata,* depend heavily on camouflage to remain unseen by their potential prey.

P. xanthozona has a similar but slightly more active feeding technique than *P. clathrata* in that it stalks its prey for a time before making a rapid lunge to seize it. Most fishes which stalk their prey, generally do so away from the bottom in mid- to upper-waters, and are characterized by long attenuated bodies, e.g. aulostomids, fistulariids (Hobson, 1974). *P. xanthozona* differs in that it is not particularly attenuated in body shape and feeds close to the substratum. Another exception to this generalization would be the flounder *Paralichthys dentatus* which captures small epibenthic shrimps by a stalking strategy (Olla *et al.*, 1972; Keenleyside, 1979).

Parapercis nebulosa, on the basis of the limited observations made, preys on both large and small, cryptic and non-cryptic organisms residing amid benthic cover, utilizing a similar scan-and-pick foraging strategy to that of *P. cylindrica* and *P.* sp. 1. Additional observations are required on *P. nebulosa* to examine its feeding behaviour more closely.

That there is considerable diversity in the food and feeding habits of members of the genus *Parapercis* is apparent from the above account. *Parapercis clathrata* and *P. xanthozona,* both of which feed on large crustaceans and fishes, have retained the generalized predaceous feeding mechanism (*sensu* Hobson, 1974) but have adopted specialized feeding strategies such as ambushing or stalking their prey. *Parapercis hexophtalma,* also a strictly carnivorous species, on the other hand utilizes specialized digging techniques to uncover its benthic invertebrate prey. In considerable contrast to these species, *Parapercis cylindrica* and *P.* sp. 1 possess specialized feeding strategies and mechanisms which enable them to feed on both small, cryptic, benthic prey and algae. Hence, weeverfishes join several other groups of coral reef fishes, e.g. chaetodontids, pomacentrids, blenniids, in having both omnivorous and strictly carnivorous members.

Chapter 5 SOCIAL BEHAVIOUR AND ORGANIZATION

5.1 Introduction

The development of SCUBA diving and related techniques has given considerable impetus to the study of the social organization and behaviour of coral reef fishes (Ehrlich, 1975; Sale, 1978c; Reese, 1978; Keenleyside, 1979; De Boer, 1980). Most of these studies have centred around the conspicuous or "visible" (*sensu* Sale, 1978c) members of the reef fish community, notably the damselfishes (Pomacentridae), butterflyfishes (Chaetodontidae), surgeonfishes (Acanthuridae), wrasses (Labridae), and parrotfishes (Scaridae). In contrast, little attention has been paid to the abundant, bottom-dwelling, cryptic fishes, which inhabit coral reefs (Ehrlich, 1975; Sale, 1978c).

The only available information on the social units of coral reef *Parapercis* species is that given by Hiatt and Strasburg (1960), who noted that *P. cephalopunctata* and *P. clathrata* lived solitarily on the reefs they examined. Unfortunately, supportive data for their observations were not given. No information is available on the social units of temperate *Parapercis* species.

Space-related behaviour, one of the most important determinants of social behaviour in animals (Reese, 1978), has similarly been neglected for *Parapercis* species. Talbot et al. (1978) listed *P. cylindrica* and *P. hexophtalma* as residents on their artificial reefs in One Tree Island lagoon, at the southern end of the Great Barrier Reef Province, and suggested that they probably spent their entire lives on the same small area of reef (generally $< 1m^2$). Sale and Dybdahl (1975) recorded *P. cylindrica* as a common resident on small (25-30 cm diam.), live coral colonies in an experimental habitat at Heron Island, southern Great Barrier Reef Province. They wrote: "Many of the commonest species in the collections are known to be sedentary enough to have restricted their activities to the immediate vicinity of the unit [coral colony] from which they were collected" (p.1346). Although listed as one of the most abundant species in the collections, *P. cylindrica* was not specifically mentioned in the text and hence it is not definite from their paper whether the above statement is applicable to this species.

Data on the space-related behaviour of temperate species of *Parapercis* are almost as limited as that for the tropical species. Graham (1953) reported that in southern New Zealand, *Parapercis colias* emigrate from coastal to offshore waters in May of each year. In his popular account of the rocky reef fishes of New Zealand, Doak (1972) states that such movement of *P. colias* is not apparent in northern New Zealand waters. He observed individuals at several locations showing distinct territoriality and staying in the same areas all year round. Some support for Doak's observations is provided by the work of Russell (1975) who listed *P. colias* as resident on an artificial reef approximately 25 m^2 in area, situated off the north-eastern coast of New Zealand.

The objective of this section of the study was to describe the social behaviour and resulting social organization of *Parapercis cylindrica* with particular emphasis placed on (1) the behavioural mechanisms, space-related or otherwise, underlying the relationships within and between social units, (2) the mating system, and (3) the pattern of courtship and spawning.

5.2 Methods and Materials

5.2.1 Study sites Long term observations on (1) the spatial relationships within and between social groups and (2) the general social organization of *P. cylindrica* were conducted over four 9 x 12 m study sites which had been established around Lizard Island. Two sites were located at the lagoon entrance (G_8, G_{10}), one was situated approximately 300 m off the north-western tip of Palfrey Island (G_{14}), and the other was located on the western side of Mermaid Cove (G_{15}) (Fig. 30). Each study site was delimited and further subdivided into three 3 x 12 m lanes by means of polythene ropes staked to the substratum. Weeverfishes accommodated very rapidly to the presence of these ropes, ignoring them within a few days of establishment.

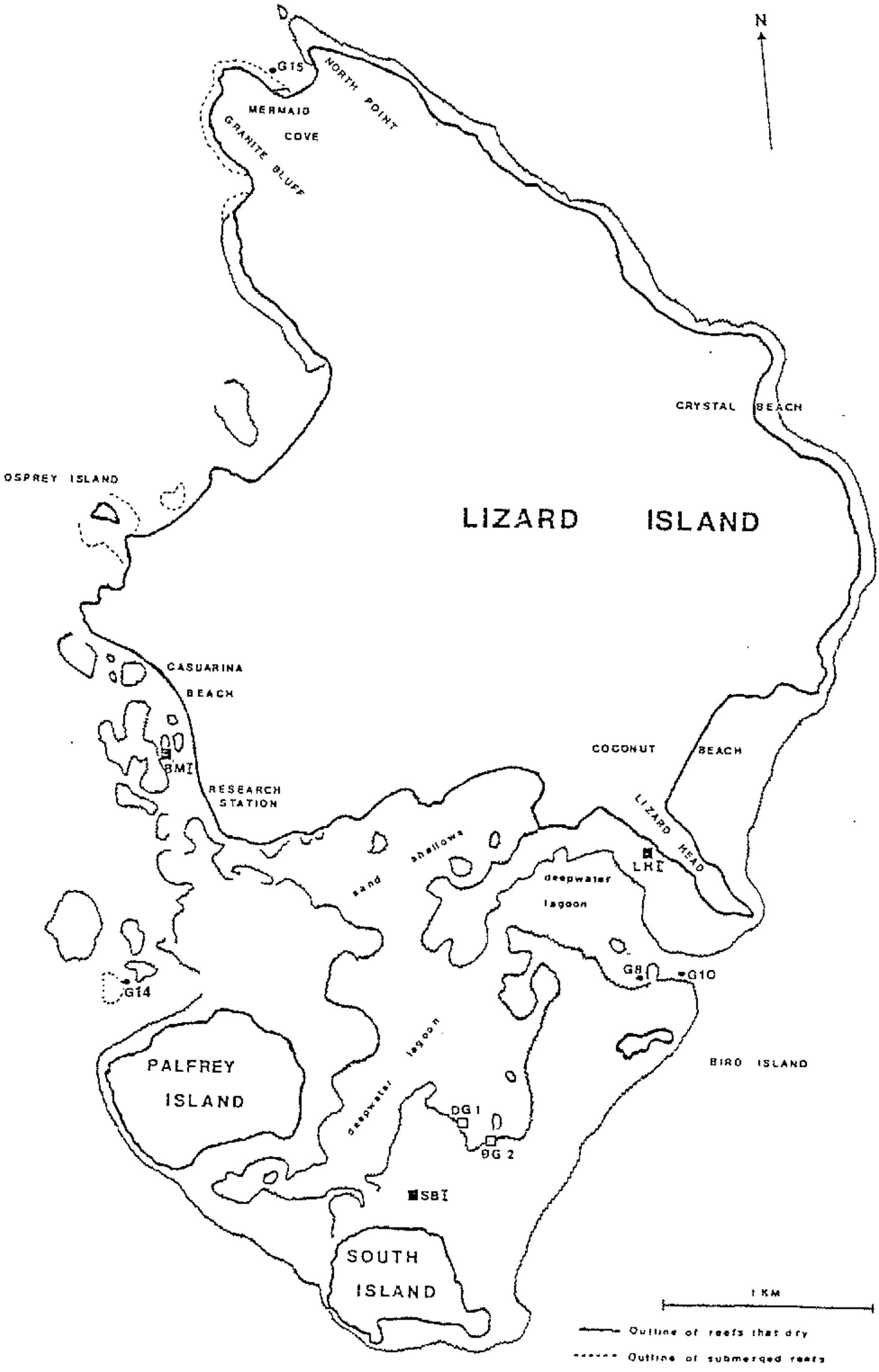
Intensive, short term observations on groups of *P. cylindrica* were undertaken within two study sites (DG-1, DG-2), each measuring about 100 m² in area, located on the leeward reef margin approximately mid-way between Bird Island and South Island (Fig. 30). Neither study site was delimited or subdivided by ropes staked to the substratum. Experiments on individual recognition of group members and intruders were also carried out within these two study sites.

Experiments involving the removal of males and investigations of the consequent effect of this on spatial relationships within social groups, were conducted within three, shallow, reef flat study sites; the first (LHI) situated on the northern side of Lizard Head, the second (SBI) approximately 200 m north of South Island, and the third (BMI) about 150 m off Casuarina Beach near the Research Station (Fig. 30). Each of these study sites measured approximately 40 m² in area and supported a single social group of *P. cylindrica*. The study sites were not delimited or subdivided by ropes staked to the substratum.

Figure 30

Map of Lizard Island and associated reefs and islands showing the location of study sites where observations and experiments on the social organization of *Parapercis cylindrica* were undertaken

- ● G_8, G_{10}, G_{14}, G_{15}: long term observational sites (refer text p. 203)
- ☐ DG-1, DG-2: short term observational and experimental sites (refer text p. 203)
- ■ LHI, SBI, BMI: male removal experimental sites (refer text, p. 203)


N
G15
NORTH POINT
MERMAID
COVE
GRANITE BLUFF
CRYSTAL BEACH
OSPREY ISLAND
LIZARD ISLAND
CASUARINA
BEACH
BMI
RESEARCH
STATION
COCONUT BEACH
LIZARD HEAD
LHI
sand shallows
deepwater
lagoon
G8
G10
G14
PALFREY
ISLAND
BIRD ISLAND
deepwater lagoon
DG1
DG 2
SBI
SOUTH
ISLAND
1 KM
Outline of reefs that dry
Outline of submerged reefs

Substrate maps for each of the above nine study sites (see Appendix 2) were prepared by careful tape measurements and plotted on to roughened P.V.C. sheets.

5.2.2 Observations All observations were made in the field whilst using SCUBA and snorkelling equipment. Movements and territorial boundaries of *P. cylindrica* were mapped over study sites G_8, G_{10}, G_{14}, and G_{18} at approximately bimonthly intervals (mean interval 2.3 months) between September 1976 and September 1978. The experiments and intensive observations made on social groups within study sites DG-1 and DG-2 were conducted during August and early September 1976. Observations on social groups in which males had been experimentally removed, i.e. those within study sites LHI, BMI and SBI, were made between late May and early July 1978.

5.2.3 Age/sex classification Individuals of *Parapercis cylindrica* were graded into four age(size)/sex categories, the characteristics of which are as follows:

1. Juvenile females: Newly settled post-larvae or individuals of small size (total length $\leq$ 25 mm). Sexually immature. Initial phase colouration.
2. Subadult females: Individuals of intermediate size between juveniles and adults (25 mm $<$ total length $\leq$ 55 mm). Sexually immature. Initial phase colouration.
3. Adult females: Individuals of moderate to large size (total length $>$ 55 mm). Sexually mature. Initial phase colouration.
4. Males: Individuals of large size (total length generally $>$ 75 mm). Sexually mature. Terminal phase colouration. All males are derived from adult females through sex reversal (see Chapter 6) hence there

are no juvenile or subadult categories for this gender. Criteria for these four categories were established by gonad examination and length measurements of collected specimens.

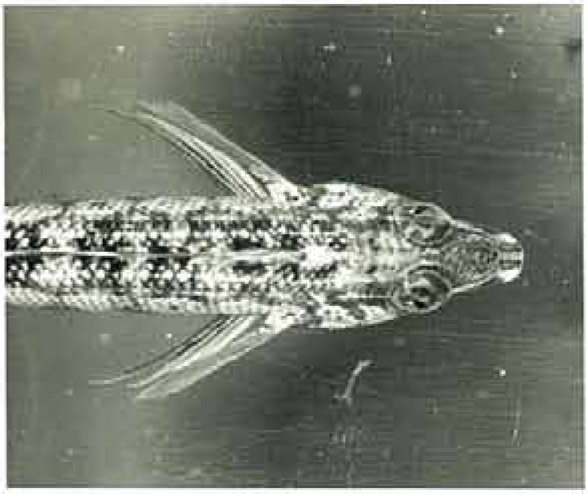
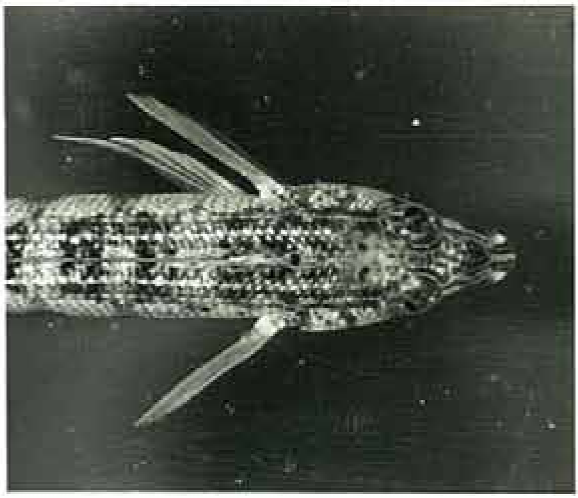
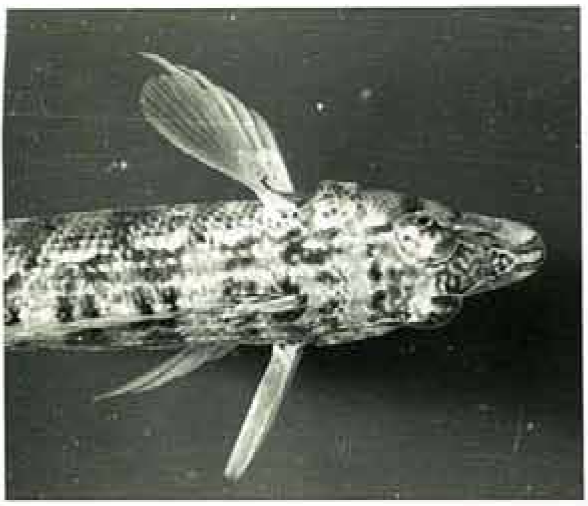
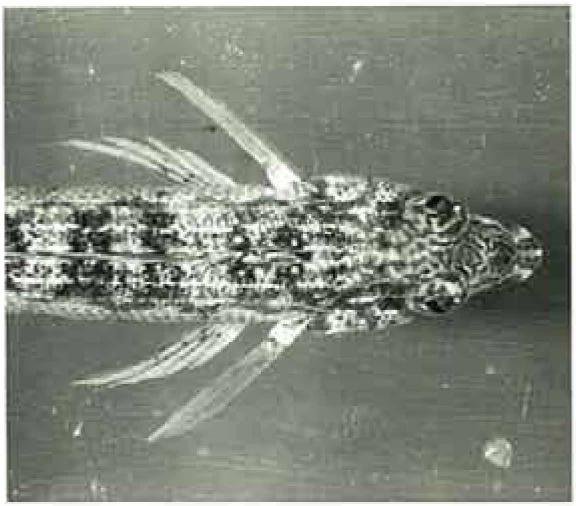
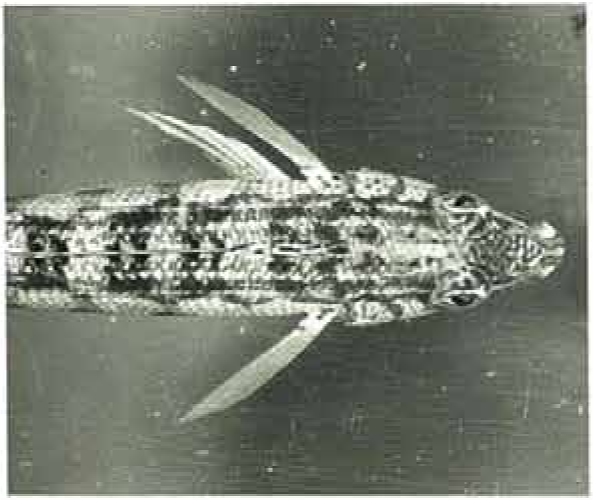
The sexual dichromatism which occurs in *P. cylindrica* made determination of sex underwater a simple task. Males have a characteristic colouration [i.e. terminal phase (TP) colouration] the main features of which are (1) a dark brown bar along the side of the upper lip and (2) irregular brown blotches on the upper third of the eye. In contrast, the colouration of females [i.e. initial phase (IP) colouration] is characterized by the presence of (1) about six alternating brown and white vertical bands along the side of the upper lip and (2) six to nine narrow dark lines radiating from the pupil over the upper third of the eye (see Part I, p.19, Fig. 2).

Field estimates of total length to the nearest mm were made by placing a clear, plastic ruler (length 150 mm) near the individual to be measured. *Parapercis cylindrica* is an extremely inquisitive fish by nature and would soon approach, inspect, and often rest on the ruler thus allowing relatively accurate (within ± 6%) measurements to be taken.

5.2.4 Recognition of individuals in the field Preliminary investigations showed that individuals could be recognized by variations in the pattern of lines, bars, and blotches on the interorbital, snout, and front of the upper lip (Plate 17). A figure showing the pattern of head markings for each individual of a study site was drawn up on a sheet of "Draftex" (transparent waterproof paper), along with data on size and sex. This sheet was carried in the field for each mapping/observation period in order to check identifications. Slight changes in the colour pattern sometimes occurred with growth, hence the figures were regularly

Plate 17

Individual variation in the pattern of lines, bars, and blotches on the interorbital, snout, and front of the upper lip of *P. cylindrica*

checked and adjusted where need be. This technique of using variations in the colour pattern to recognize individuals was used for all fishes except those below about 15 mm total length. Individuals of such small size lacked sufficient variation of colour pattern to enable discrimination. Consequently, information on these small individuals is based on repeatedly seeing an individual of the "same" size (allowing for growth) at the same location and assuming it was one and the same individual. This assumption is not unreasonable considering the extremely limited home range of these sized individuals.

5.2.5 Recording social behaviour Data were recorded underwater on roughened P.V.C. sheets and Draftex sheets using a normal carbon pencil. Aspects of the behaviour were timed on a waterproof watch and stop-watch, and photographed using (1) a Nikonos II underwater camera with strobe and (2) a Canon F1 camera in an underwater housing with strobe. Complex social encounters were filmed with a Canon Auto 200 m movie camera in an underwater housing.

Because of the inquisitive nature of *P. cylindrica*, a diver's presence is initially a disturbing influence on their behaviour. After a short time (generally about five minutes for regularly visited study sites), however, they become habituated to the observer's presence, so that satisfactory observations of their behaviour can be made from as little as three metres away. No attempt was made to record behaviour before this habituation process was complete and individuals were exhibiting no reaction to the presence of the observer. Consequently, it is believed that the results obtained accurately reflect the normal behaviour patterns of *P. cylindrica*.

5.2.6 Mapping the movements and territories of individuals Movements of fishes were plotted, using a normal carbon pencil, on to Draftex sheets which overlaid a prepared substrate map of the study site (see 5.2.1). In the laboratory, movements drawn on the Draftex sheets were ink-traced on to normal paper.

For the purposes of this study, a territory is defined as a defended area (Noble, 1939). The territorial boundaries of an individual of *P. cylindrica* were determined by noting (1) the location of its agonistic interactions with conspecifics and (2) the limits of its movements, since preliminary model-bottle experiments (cf. Myrberg and Thresher, 1974) and observations had shown territory and home range to coincide for this species.

The path swum by an individual during a 30 minute period was drawn on the map along with the location of any social encounters. Three such mapping sessions totalling 90 minutes were made for each individual of a study site and a composite territory map drawn up from the three component maps. Composite territory maps of individuals residing within long-term study sites during each bimonthly mapping period (see 5.2.2) are presented in Appendix 2.

The frequency with which an individual visited various regions of its territory was investigated by plotting the position of the fish at 30 second intervals. Five observations periods, each ranging from 60 to 90 minutes, were conducted per individual.

5.3 Results

5.3.1 Size and composition of the social unit Individuals of *P. cylindrica* occur in groups which, because of their stable nature and agonistic, sexual, and spatial inter-individual relationships, can be regarded as social units.

At Lizard Island, *P. cylindrica* was mostly encountered in social units of 3 or 4 individuals (Fig. 31). Each social unit comprised a single male and a variable number of adult, subadult, and juvenile females (Table 22). Minimum social unit size was 2 individuals, these being without exception a male:adult female pair (Fig. 32). The largest social unit observed contained 20 individuals which included a male, 10 adult females, and 9 subadult females.

The male:adult female and male:total female sex-ratios were 1:2.32 and 1:4.32 respectively (see Table 22), thus showing a considerable bias towards females.

5.3.2 Agonistic interactions within and between social units

5.3.2.1 *Motor patterns associated with agonistic encounters* Agonistic behaviour in *P. cylindrica* was found to be characterized by 17 motor patterns, each of which is described below.

(i) Fin-Spread: The spinous dorsal, soft dorsal, anal, and caudal fins are maximally spread (Plate 18).

(ii) Partial-Fin-Spread: This motor pattern is the same as the Fin-Spread except for the position of the spinous dorsal which is kept folded.

(iii) Gular-Expansion: The branchiostegal membranes are expanded and the opercula flared out (Plate 18). Normally a series of Gular-Expansions take place with each one lasting approximately two seconds.

(iv) Fin-Spread-Approach: A slow swim towards, but not right up to, another individual during which time the unpaired fins of the performer are kept maximally spread. The caudal fin is not utilized for propulsion.

Figure 31

Frequency distribution of social unit sizes of *Parapercis cylindrica* at Lizard Island

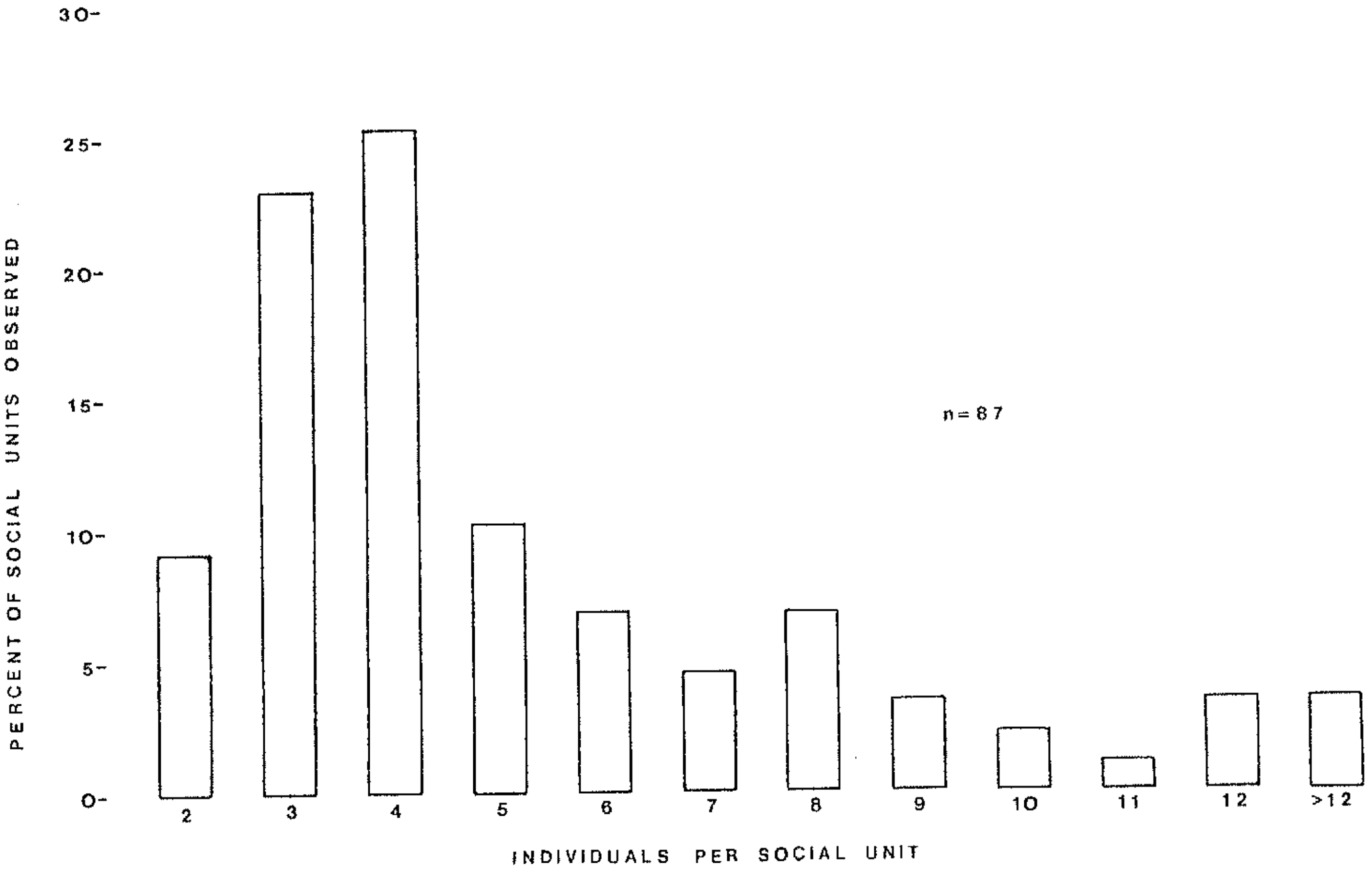

30
25
20
15
10
5
0
PERCENT OF SOCIAL UNITS OBSERVED
n = 87
2
3
4
5
6
7
8
9
10
11
12
>12
INDIVIDUALS PER SOCIAL UNIT

Table 20. Composition of *Parapercis cylindrica* social units observed at Lizard Island[a]

Age/sex dategory	Individuals[b]	Mean ± SD
Males	87	1.00 ± 0.00
Adult females	202	2.32 ± 1.41
Subadult females	136	1.56 ± 2.11
Juvenile females	38	0.44 ± 1.03
Total no. individuals in social unit		5.32 ± 3.25

[a] Number of social units observed = 87

[b] Denotes total number of individuals of a category observed for all social units

Figure 32

Percentage occurrence of different age/sex categories in *Parapercis cylindrica* social units of various sizes

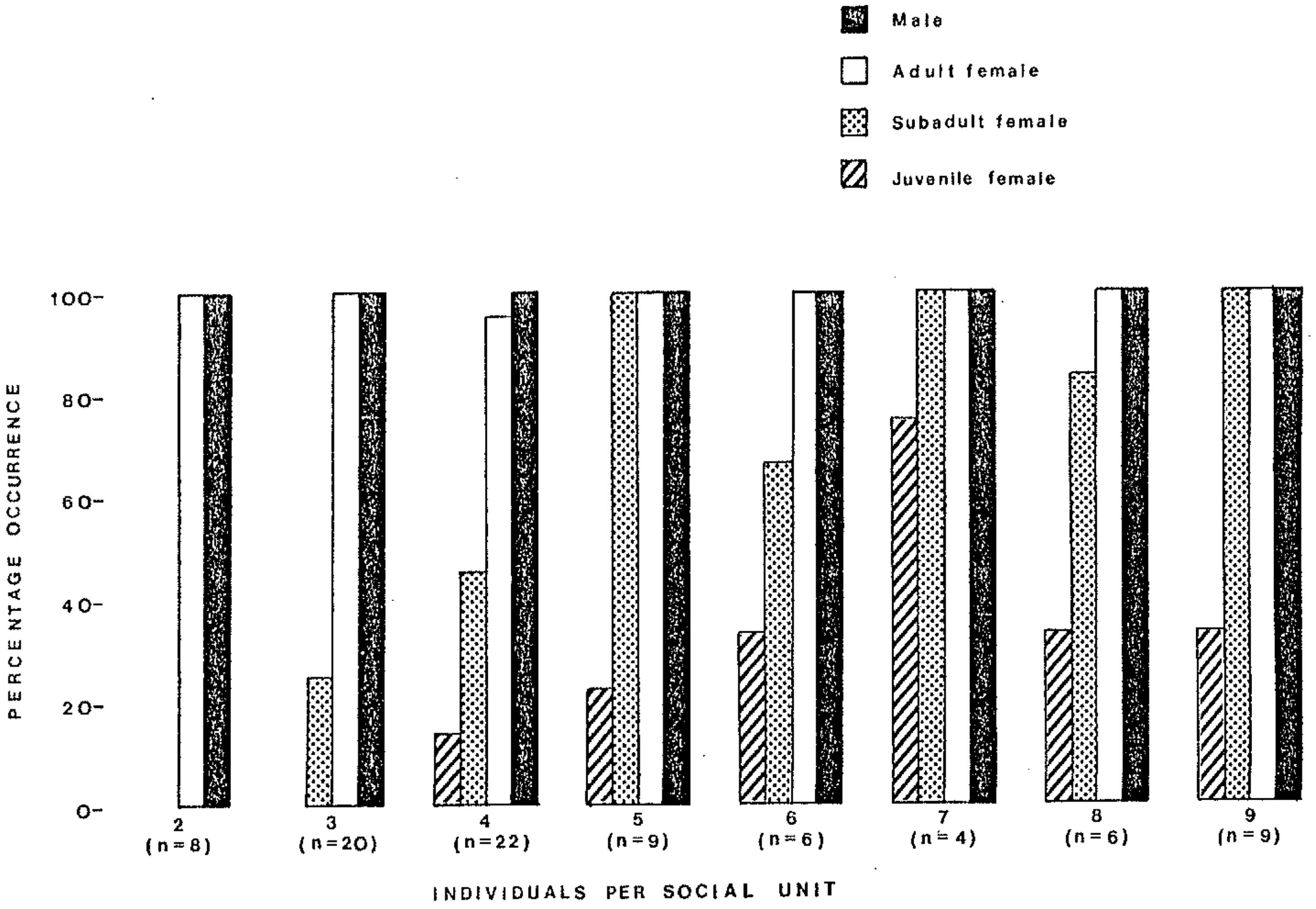

Male
Adult female
Subadult female
Juvenile female
PERCENTAGE OCCURRENCE
100
80
60
40
20
0
2 (n=8)
3 (n=20)
4 (n=22)
5 (n=9)
6 (n=6)
7 (n=4)
8 (n=6)
9 (n=9)
INDIVIDUALS PER SOCIAL UNIT

Plate 18

Underwater photograph of an agonistic encounter between male individuals of *Parapercis cylindrica*

This encounter was induced (for photographic purposes) by placing a foreign male in a large, mesh-topped, clear glass bottle and then introducing this into the territory of another male. The two fishes are in a T-formation with the territory holder (left) performing Fin-Spread and Gular-Expansion. The foreign male is executing a Fin-Spread.

(v) Spinous dorsal-Approach: A slow swim towards, and right up to another individual during which the spinous dorsal fin of the performer is kept maximally spread; the soft dorsal, anal, and caudal fins are only partly spread (Plate 19). The caudal fin is not used for propulsion during the performance of this motor pattern.

(vi) Reverse Body-Sigmoid: A Reverse Body-Sigmoid is distinguished by (a) the fin and body postures of the performer and (b) the relative orientations of the performer and receiver during its execution.

(a) Fin and body postures: With the caudal fin folded and the dorsal and anal fins partly spread, the body is flexed into a "Ƨ" shape i.e. reverse sigmoid. The first, and main, point of flexion is the abdominal region; the second, below about midway along the soft dorsal fin (Plate 20).

(b) Orientation: Beginning from a position parallel to, slightly left of, and facing in the same direction as, the receiver, the performer slowly swims 180 degrees around the front of the receiver thus ending the swim facing in the opposite direction to that of the receiver (Plate 20, Fig. 33A). The performer, whose abdominal flexion is orientated towards the receiver, is no greater than four centimetres away from the receiver during the swim. This 180 degree swim is achieved by movement of the pectoral fins only.

The Reverse Body-Sigmoid is approximately three seconds in duration.

(vii) Head-Bob: The anterior half of the body is slowly lowered and raised in the dorsal-ventral plane by a levering action of the ventral fins. The downward and upward movements together take approximately two seconds.

Plate 19

A male individual of *Parapercis cylindrica* performing a Spinous dorsal-Approach

Plate 20

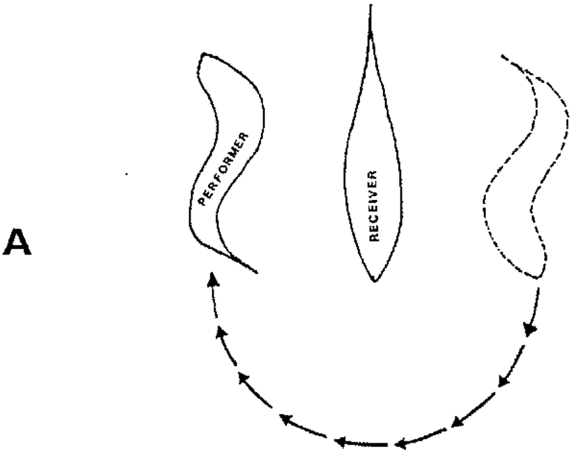
A female individual of *P. cylindrica* (foreground) performing a Reverse Body-Sigmoid to a male conspecific

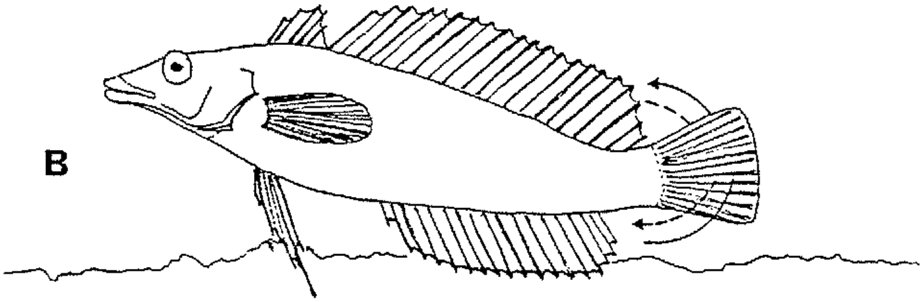
Figure 33

Motor patterns associated with agonistic encounters

A. Reverse Body-Sigmoid

B. Tail-Beat


A
PERFORMER
RECEIVER


B

(viii) Tail-Beat: A relatively slow, laterally directed motion of the posterior section of the body is termed a Tail-Beat. Tail-Beats generally occur in series and are always accompanied by Fin-Spread. Although the performer remains on the substrate while Tail-Beating, the hind portion of its body is slightly curved upward and the tail thus raised off the substrate (Fig. 33B).

(ix) Butt: A forceful striking of the receiver by the snout of the performer. Most butts are aimed at the flank of the receiver.

(x) Bite: The performer actually snaps at, or closes its jaws on, some portion of the receiver's body. If the receiver is Fleeing (see below), the target of the bite is the caudal fin; if the receiver is stationary, the target is either the mouth, operculum or flank.

(xi) Jaw-Lock: If Biting is directed towards the mouth of the opponent both individuals may lock jaws as shown in Figure 34A. This motor pattern is uncommon and observed only between pairs of females of equal or near-equal size.

(xii) Half-Circle: Beginning from a tail-head or T-formation with the receiver, the performer swims around quickly in a small half circle which results in bringing the performer either face to face or back into a T-formation with the receiver (Fig. 34B).

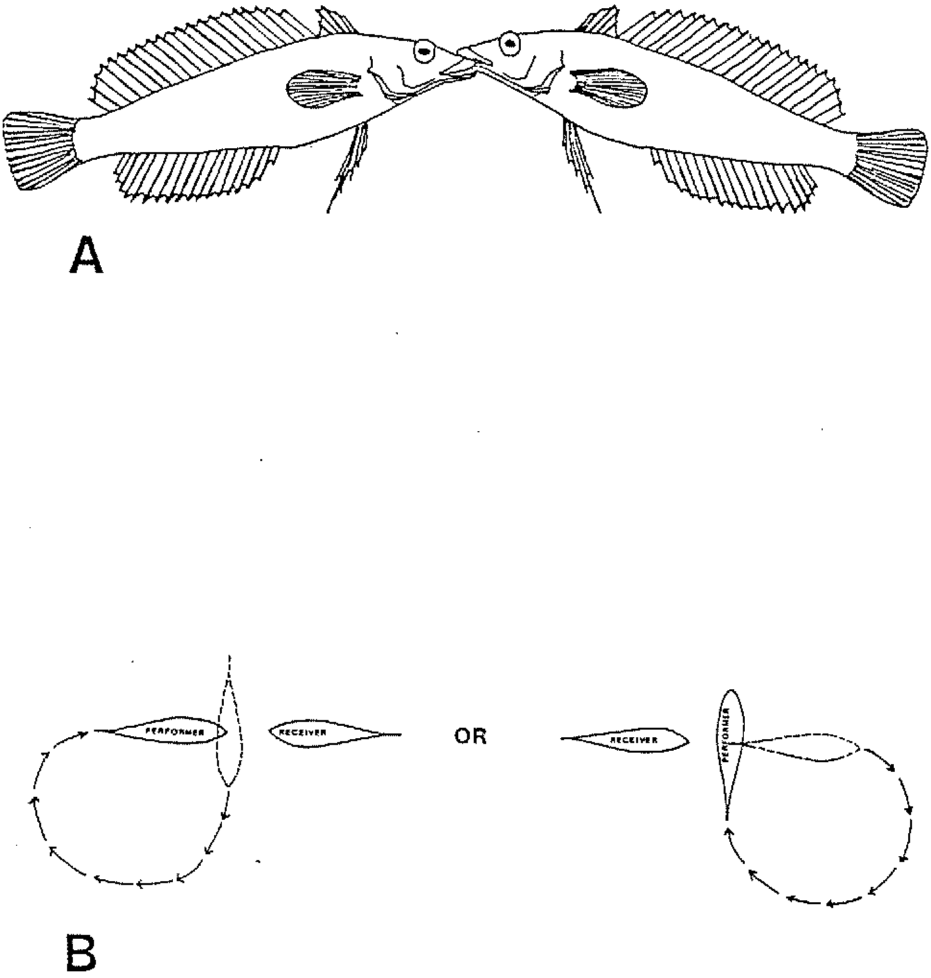
(xiii) Carrousel: The two adversaries swim rapidly head to tail in a small circle, each trying to Bite the tail of the other. As the fishes circle, both perform Fin-Spreads and rise above the substrate. The pectorals provide the primary propulsive force while the caudal and ventral fins are used as rudders and provide stabilization.

Figure 34

Motor patterns associated with agonistic encounters

A. Jaw-Lock

B. Half-Circle


A
PERFORMER
RECEIVER
OR
RECEIVER
PERFORMER
B

(xiv) Frontal-Thrust: A rapid swimming toward, and right up to, an approaching or stationary adversary. During this movement, the performer's unpaired fins are maximally spread and its mouth opened slightly. Primary propulsion is provided by the caudal fin. The Frontal-Thrust usually results in physical contact with the adversary.

(xv) Chase: Pursuit of a Fleeing individual by the performer; the latter's unpaired fins are maximally spread, its mouth is open slightly, and its caudal fin provides the main propulsion.

(xvi) Retreat: The performer moves away from its opponent for a distance of no greater than 10 centimetres. This is carried out by either (1) normal swimming or (2) facing the other fish and backing away using the pectorals in reverse motion.

(xvii) Flee: Rapid swimming by an individual that is being Chased. During Fleeing the unpaired fins of the performer are kept folded and the mouth is closed. Propulsion is provided primarily by movement of the caudal fin.

A comparison of agonistic motor patterns performed by the sexes in *P. cylindrica* is presented in Table 21. It can be seen that 12 of the above 17 motor patterns were common to both sexes. Spinous dorsal-Approach and Head-Bob were performed by males but were absent from the behavioural repertoire of females. Females performed Partial-Fin-Spread, Reverse Body-Sigmoid, and Jaw-Lock; these motor patterns were not executed by males.

5.3.2.2 *The nature of agonistic encounters* Interactants in agonistic encounters were, with few exceptions, conspecific *Parapercis cylindrica*; interspecific aggression is virtually absent [see (c) below]. The nature

Table 21. Comparison of agonistic motor patterns performed by the sexes in *Parapercis cylindrica*

Motor Pattern	Recorded from	
	Male	Female
Fin-Spread	+	+
Partial-Fin-Spread	—	+
Gular-Expansion	+	+
Fin-Spread-Approach	+	+
Spinous dorsal-Approach	+	—
Reverse Body-Sigmoid	—	+
Head-Bob	+	—
Tail-Beat	+	+
Butt	+	+
Bite	+	+
Jaw-Lock	—	+
Half-Circle	+	+
Carrousel	+	+
Frontal-Thrust	+	+
Chase	+	+
Retreat	+	+
Flee	+	+

of agonistic encounters varied according to whether the interactants were members of (a) the same social unit, i.e. agonism within the social unit; or (b) different social units, i.e. agonism between social units.

(a) Agonism within the social unit

(i) Male-Female encounters: When a male observes a female of the same social unit he immediately makes a Spinous dorsal-Approach and then adopts a resting position beside her. The female then reacts in one of two ways - either she performs a Reverse Body-Sigmoid around the male, or she simply remains still. If the female takes the former course of action, the male is appeased and either swims away or begins to feed with no further aggression being shown towards the female. If, however, the female remains still, the male performs a Frontal-Thrust followed by a Butt and, very farely, a Bite. The female responds to this by Fleeing and is then Chased by the male until she disappears from his sight.

(ii) Female-Female encounters: If one (*A*) of the female interactants (*A*, *B*) is conspicuously larger in size than the other (*B*), then the encounter will be brief and very simple in form. Immediately *A* observes *B*, it performs a Frontal-Thrust; if *B* does not Flee in time, it is then Butted and Bitten by *A*. *B* then Flees and is Chased by *A* until the former disappears from the latter's sight.

If *B* is almost as large as *A*, then instead of *B* Fleeing when *A* performs a Frontal-Thrust, *B* Retreats and executes a Half-Circle; this results in bringing *B* to a position where it forms the top bar of a T-formation with *A*. Whilst in this T-formation, *B* performs a Partial-Fin-Spread. *A* responds with another Frontal-Thrust after which *B* either Flees (and is subsequently Chased by *A*) or repeats the Retreat → Half-Circle → Partial-Fin-Spread sequence. This latter sequence may be repeated several times, each time in response to a Frontal-Thrust from *A*, however, the encounter always terminates with *B* taking flight.

Two females of equivalent size (i.e. within 3 mm total length of each other) belonging to the same social unit, although uncommon, nevertheless, did occur. Encounters between such females were observed to be quite complex, the most frequent sequence of which is described as follows: Upon seeing *B*, *A* attacks with a Frontal-Thrust. *B* then Retreats and executes a Half-Circle thus bringing it to form the top bar of a T-formation with *A*. Whilst in this position, *B* performs a Fin-Spread in association with several Gular-Expansions and one or more Tail-Beats. If the attack is still pressed by way of another Frontal-Thrust from *A*, *B* once again Retreats and performs the Half-Circle → Fin-Spread/Gular-Expansion/Tail-Beat sequence. If *A* does not press the attack, *B* retaliates by performing a Half-Circle followed by a Frontal-Thrust. *A* responds by Retreating and then performing a Half-Circle → Fin-Spread/Gular-Expansion/Tail-Beat as described above. If *B* attacks with another Frontal-Thrust at this stage, *A* again Retreats and performs the Half-Circle → Fin-Spread/Gular-Expansion/Tail-Beat sequence. However, if *B* does not attack, *A* executes a Half-Circle and takes the offensive once again with a Frontal-Thrust. At any stage the encounter may end by the flight of either of the interactants, though Fleeing usually occurs in response to a Frontal-Thrust by the other opponent. The Fleeing individual is Chased by its opponent, i.e. the winner of the encounter, until the former disappears from the sight of the latter.

If, in the above encounter, *A* attacks *B* with a Frontal-Thrust whilst *B* is executing a Half-Circle, then both individuals will go into a Carrousel; a motor pattern which is terminated only by the flight of one of the interactants.

Females of equivalent size were occasionally observed to attack each other simultaneously with Frontal-Thrusts. When this occurred, a Jaw-Lock resulted. This extremely intense aggressive act was terminated in the same way as the Carrousel, i.e. only by the flight of one of the interactants.

(b) Agonism between social units

(i) Male-Male encounters: The majority of male-male encounters occur at the mutual border separating the territories of neighbouring males. Border encounters are characterized by the following sequence of aggressive exchanges:

One territorial resident (*B*) approaches the mutual border of his, and his neighbour's (*A*) territory. *B* stops close to the border and begins to feed. Upon observing *B*, *A* immediately makes a Fin-Spread-Approach and takes up a resting position approximately 50 centimetres from *B* and begins to feed. If *B* swims away from the border at this stage, *A* will also swim away. However, if *B* moves closer to, or actually on to, the border then *A* responds by orientating its head and body towards *B* and repeatedly performing Head-Bob. In response to this, *B* may either (1) swim away, or (2) orientate itself towards *A* so that both fish are facing each other and then Head-Bob repeatedly. If the latter occurs, *A* responds by performing a Half-Circle which brings it to a position where it forms the top bar of a T-formation with *B*. Upon reaching this position *A* executes a Fin-Spread and a series of Gular-Expansions. The response of *B* at this stage dictates whether the encounter will proceed to a lower or higher level of intensity. If *B* stops Head-Bobbing and begins to feed, then *A* will also stop and begin to feed; and after 10 seconds or so, *B*, and then *A*, will swim away from each other, returning to more central areas within their territories. However, if *B* stops Head-Bobbing and then, instead of feeding, performs a Fin-Spread, the encounter will pass to a higher level of intensity:

A and *B* take up a position parallel to each other (either head to head or head to tail) and perform a series of Tail-Beats accompanied by Fin-Spreads and Gular-Expansions. This behaviour is often terminated by the flight of one of the interactants; the Fleeing individual is Chased by its opponent. Alternatively, this behaviour may be followed by *A* performing a Half-Circle, Frontal-Thrust and a Butt. In response to this, *B* makes a Retreat, performs a Half-Circle (bringing him into a T-formation with*A*), and then executes several Tail-Beats accompanied by Fin-Spreads and Gular-Expansions. *B* then performs a Half-Circle, Frontal-Thrust and a Butt. *A* responds to this attack in the same way as described above for when *B* is attacked with a Frontal Thrust from *A*, i.e. Retreat → Half-Circle → Tail-Beating (plus Fin-Spreads and Gular-Expansions) → Half-Circle → Frontal-Thrust → Butt. At any stage the encounter may be terminated by the flight of either of the interactants, though Fleeing usually occurs in response to a Frontal-Thrust by the other opponent. If one individual attacks his opponent with a Frontal-Thrust whilst the latter individual is performing a Half-Circle then the usual result is a Carrousel. This act is terminated only by the flight of one of the interactants.

When a male comes upon another male which has actually intruded into its territory, it immediately attacks the intruder by way of a Frontal-Thrust. Without exception, the intruder Flees and is Chased by the territory holder. Upon both individuals reaching the territory border, a border dispute, as described above, generally takes place.

(ii) Male-Female encounters: Occasionally a male encounters a female from another social unit which has intruded into his territory. If such an encounter takes place during the daily sexual period (see 5.3.4.1) then the male may attempt to court the foreign female. However, if the encounter occurs outside this period, the usual reaction of the male is to overtly attack the intruding female and drive her out of his territory. Upon observing the intruder, the male performs a Frontal-Thrust which results in the female Fleeing; the male Chases her until she crosses the border of his territory, and in many cases, well beyond the border.

(iii) Female-Female encounters: Females from other social units caught intruding into the territory of a resident female are overtly attacked and driven off even though the resident might be much smaller in size than the intruder.

(c) Interspecific aggressive encounters

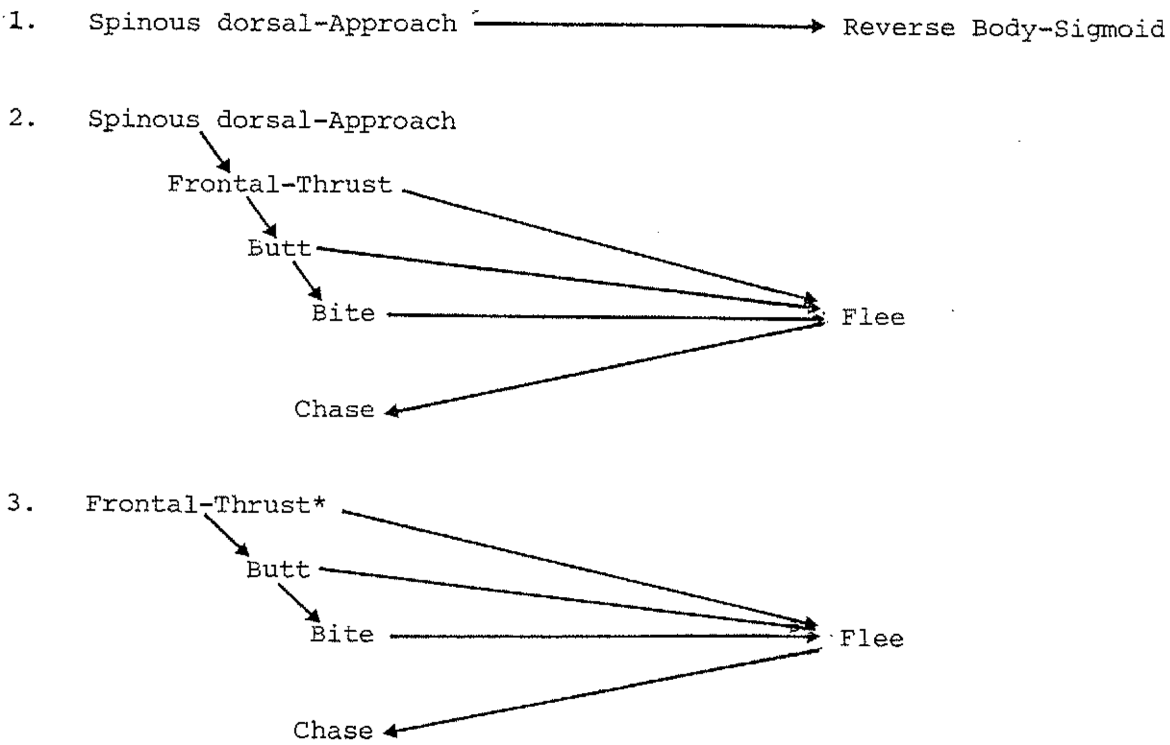
In contrast to those species of coral reef fishes which exhibit interspecific territoriality (see Low, 1971; Myrberg and Thresher, 1974); individuals of *Parapercis cylindrica*, in most cases, do not attack and repel other species which they encounter within their territories. Indeed, the space occupied by a single male *P. cylindrica* will often contain several gobiids, blenniids, and pomacentrids, they themselves with territories.

Large individuals of *P. cylindrica* were seen to chase scolopsid juveniles (*Scolopsis bilineatus, S. margaritifer*) in addition to pomacentrid juveniles (*Dischistodus perspicillatus, Pomacentrus flavicauda*); they also occasionally chased labrids (*Coris variegata, Thalassoma lunare*) and gobiids (*Amblygobius phalaena, Cryptocentrus* sp.). Such chases were uncommon, were of short duration, and generally did not proceed as far as the territorial border of the *P. cylindrica* individual involved. Far more common, were attacks on *P. cylindrica* by other species, particularly the pomacentrids *Dischistodus perspicillatus, Pomacentrus amboinensis,* and *P. flavicauda*. The congener, *Parapercis hexophtalma,* was also observed to attack and chase away *Parapercis cylindrica* on a few occasions.

5.3.2.3. *Dominance relationships within the social unit* Agonistic encounters between members of the same social unit were characterized by three frequent and easily identifiable sequences of aggressive behaviour which produced, on the part of the receiver, a particular submissive reaction:

Aggressive action(s)/reaction of fish A

Submissive reaction of fish B



Intensive observations were made on social units of *P. cylindrica* during which the frequency with which each individual directed any of the above three *aggressive displays* towards another social unit member, was recorded. The dominance relationships within each social unit were then determined by examining the distribution of aggressive displays amongst the members of the social unit.

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* Spinous dorsal-Approach does not precede this motor pattern.

The dominance relationships within a social unit of five *P. cylindrica* (1 ♂, 2 adult ♀♀, 1 subadult ♀, 1 juvenile ♀) present over study site DG-1 and observed for a total of 65 hours (780 minutes observation per individual in 60-90 minute periods) are presented in Figure 35. The male, DC, the largest individual within the social unit, was dominant over all other individuals. The largest female of the social unit, adult female DB, was dominant over all females (i.e. DE, DA, DD) but was subordinate to male DC; adult female DE was subordinate to male DC and adult female DB, but was dominant over subadult female DA and juvenile female DD; subadult female DA was subordinate to male DC and both adult females (DB, DE) but was dominant over juvenile female DD; and juvenile female DD was subordinate to all members of the social unit. Figure 35 shows the total number of aggressive displays directed by an individual to be perfectly correlated with rank and that aggressive displays occurred in only one direction, i.e. they were directed from higher ranking to lower ranking individuals only. It is also apparent that size (total length) of an individual was perfectly correlated with rank within the social unit. The dominance relationships within this social unit are thus characteristic of a linear, size-dependent, dominance hierarchy.

The dominance relationships within a slightly larger social unit than that above, are presented in Figure 36. This social unit, situated within study site DG-2, was comprised of six individuals (1 ♂, 3 adult ♀♀, 1 subadult ♀, 1 juvenile ♀) and was observed for a total of 72 hours (720 minutes observation per individual in 60-90 minute periods) over an eight day period. As in the previous social unit, the male, in this case DI, was the largest and most dominant individual in the social unit. Adult female DF, whilst subordinate to male DI, was larger than, and dominant over, all other females within the social unit. Adult females DG and DH

Figure 35

Rank order by aggressive dominance in a social unit of five *Parapercis cylindrica*

KEY:

(i)

95% = % Aggressive displays directed at individual to which arrow points by individual from whose line arrow extends

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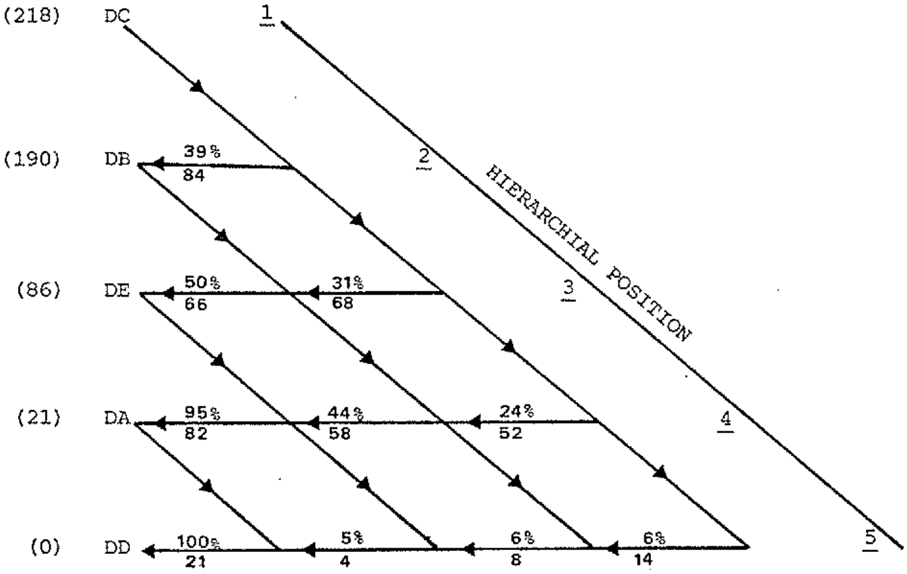
82 = No. Aggressive displays directed at individual to which arrow points by individual from whose line arrow extends

(ii) TL = total length of individual

(iii) Numbers in parentheses refer to the total number of aggressive displays performed by each individual

(iv) An aggressive display is defined as a Spinous dorsal-Approach and/or a Frontal-Thrust followed by a Chase (see text

Study period: 14-20 August 1976
Study site: DG-1
Total observation time = 65 hrs
Observation time/individual = 780 mins
Total aggressive displays recorded = 457



Social unit composition:
DC = 101 mm TL, ♂
DB = 78 mm TL, ♀
DE = 63 mm TL, ♀
DA = 41 mm TL, ♀
DD = 25 mm TL, ♀

Figure 36

Rank order by agressive dominance in a social unit of six *Parapercis cylindrica*

<u>KEY</u>:

(i)

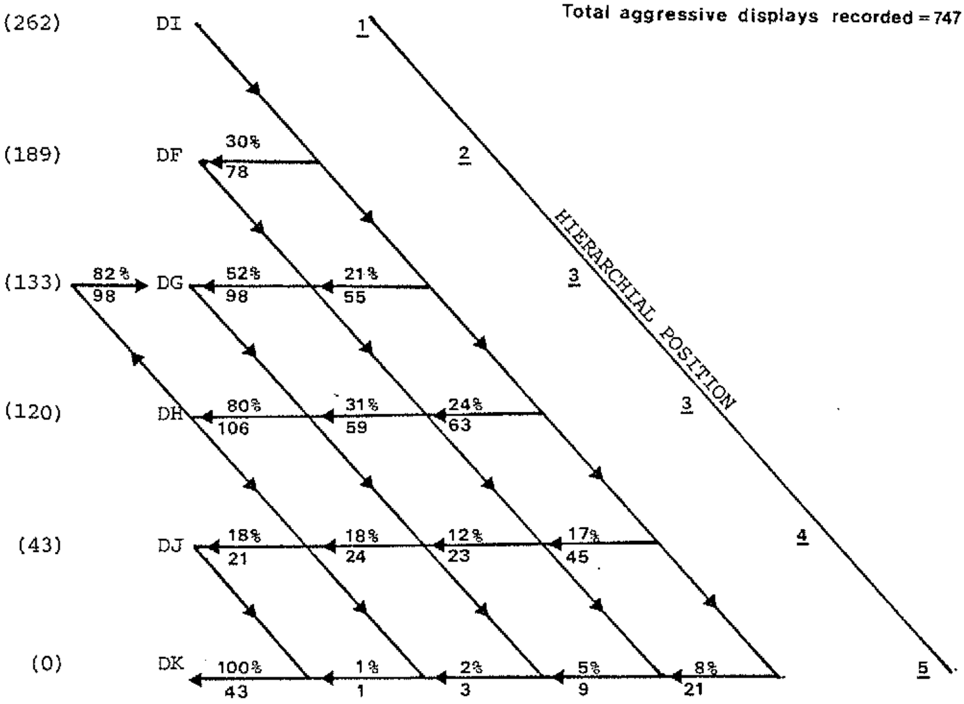
80% =	% Aggressive displays directed at individual to which arrow points by individual from whose line arrow extends
106 =	No. Aggressive displays directed at individual to which arrow points by individual from whose line arrow extends

(ii) TL = total length of individual

(iii) Numbers in parentheses refer to the total number of aggressive displays performed by each individual

(iv) An aggressive display is defined as a Spinous dorsal-Approach and/or a Frontal-Thrust followed by a Chase (see text

Study period: 21-28 August 1976
Study site: DG-2
Total observation time = 72 hrs
Observation time/individual = 720 mins
Total aggressive displays recorded = 747



Social unit composition:

DI = 105 mm TL, ♂
DF = 89 mm TL, ♀
DH = 71 mm TL, ♀
DG = 70 mm TL, ♀
DJ = 45 mm TL, ♀
DK = 25 mm TL, ♀

were equivalent in size (total length) and directed aggressive displays at one another with approximately the same frequency. Consequently, DG and DH were considered to hold the same rank within the social unit; both were subordinate to male DI and adult female DF but were dominant over subadult female DJ and juvenile female DK. Subadult female DJ was subordinate to male DI, adult females DF, DG and DH, but was dominant over juvenile DK; juvenile DK was however, subordinate to all individuals within the social unit. There was a highly significant correlation between the total number of aggressive displays directed by individuals and rank within the social unit (Spearman Rank Correlation Coefficient $r_s = 0.99$, $P < 0.01$). Similarly, high significance appeared between size (total length) and rank (Spearman Rank Correlation Coefficient $r_s = 0.99$, $P < 0.01$). It is apparent that this social unit, like the previous one discussed, was characterized by an essentially linear, size-dependent, dominance hierarchy.

The distributions of aggressive displays given in Figures 35 and 36 show that, in general, (1) an individual directs most aggressive displays towards the individual closest in rank to itself and that (2) there is a consistent decrease in the amount of aggression directed towards those individuals who are further and further removed from a given rank. For example, male DC (rank 1) directed 39% of its aggressive displays (i.e. 39% of the total aggressive displays directed at all fish by DC) at adult female DB (rank 2), 31% at adult female DE (rank 3), 24% at subadult female DA (rank 4), and the remaining 6% at juvenile female DD (rank 5) (Fig.35). Similarly, adult female DF (rank 2) directed 52% and 31% of its aggressive displays at adult females DG and DH (both rank 3) respectively, 12% of its aggressive displays at subadult female DJ (rank 4), and the remaining 5% at juvenile female DK (Fig. 36).

In the initial stages of this study 9 social units of *P. cylindrica* were being regularly mapped, however, by the end of the study, this number had increased to 11 due to social unit division (see p.261). A compendium of the dominance hierarchies within these regularly mapped social units is given in Appendix 1 and can be briefly summarized as follows: without exception, the largest individual of a social unit was a male which totally dominated all of the females in that social unit. If the females of the social unit were distinctly different in size to each other, then a linear rank order according to size resulted, this being maintained by way of spatially-independent dominance relationships, i.e. one individual (in this case the larger of the two interactants) was dominant over the other individual regardless of the locality of interaction. If however, as in the above case of adult females DG and DH (see Fig.36), two (or rarely three) females within the same social unit were of equivalent size (i.e. within 3 mm total length of each other), then the dominance hierarchy became slightly more complicated since equivalent-sized females held the same overall rank and the dominance relationship between them was a spatially-dependent one, i.e. DG was dominant over DH in DG's territory, but DH was dominant over DG in DH's territory.

A total of 13 cases of spatially-dependent dominance relationships were recorded within regularly mapped social units all of which were between equivalent-sized subadult or adult females (Table 22).

The females of a social unit lived within the territorial boundaries of the male of that social unit (see 5.3.4.1), hence all females had the opportunity to interact with the male. Interactions between all combinations of pairs of females however, were not always

Table 22: Spatially-dependent dominance relationships recorded within regularly mapped social units of *P. cylindrica*

Study site	Study period	Social unit	Size class & sex of interactants	Identity & size of interactants[a]	Appendix reference[b]
G_{10}	1	B	subadult females	#9(30TL); #7(30TL)	A1-p366 ; A2-Map 12
"	2	B	" "	#9(45TL); #7(43TL)	A1-p. 366; A2-Map 13
"	7	A	" "	#65(36TL); #93(36TL)	A1-p. 367; A2-Map 18
"	8	A	" "	#85(47TL); #93(47TL)	A1-p. 367; A2-Map 19
G_{15}	5	B	" "	#13(46TL); #14(45TL)	A1-p. 370; A2-Map 37
"	6	B	adult females	#13(56TL); #14(56TL)	A1-p. 370; A2-Map 38
"	7	B_2	" "	#13(66TL); #14(66TL)	A1-p. 371; A2-Map 39
"	8	B_2	" "	#13(74TL); #14(73TL)	A1-p. 371; A2-Map 40
"	9	B_2	" "	#13(78TL); #14(78TL)	A1-p. 371; A2-Map 41
"	10	B_2	" "	#13(84TL); #14(84TL)	A1-p.371; A2-Map 42
"	8	C	" "	#18(62TL); #20(61TL)	A1-p.371; A2-Map 40
"	9	C_2	" "	#18(70TL); #20(70TL)	A1-p.371; A2-Map 41
"	10	C_2	" "	#18(77TL); #20(76TL)	A1-p.371; A2-Map 42

[a] Figure in parentheses refers to total length (TL) of individual in mm.

[b] A1 = Appendix 1, A2 = Appendix 2

possible due to the spatial relationships of the females. Juvenile females and small subadult females for example, in having relatively small areas of movement, often did not have the opportunity to interact with all female individuals of the social unit (Fig. 37A - see subadult females #59, #60 and juvenile females #55 and #57; Fig.37B - see subadult females #22, #26, #33, #51, #58, #55 and juvenile female #61; Fig.37C - see subadult females #56 and #53). When two adult females lived in areas at opposite ends of their male's territory, a similar inopportunity for interaction existed. (Fig.37A - see adult females #4 and #22, #22 and #12; Fig.37B - see adult females #14 and #25; Fig.37C - see adult females #22 and #28, #24 and #28). The dominance hierarchies given here and in Appendix 1 therefore differ accordingly in their completeness.

The stability of any dominance hierarchy is a function of the stabilities of the various dominance relationships within that hierarchy. The dominance relationships between pairs of individuals comprising the hierarchy remained stable until such time as one of the members of the pair died or disappeared from the social unit. This was often a considerable period of time. For example, in social unit A over study site Site G_{15}, #8 was dominant over #9 for a period of 10 months before #9 disappeared from the social unit, during which time #8 had grown from a 70 mm TL* to an 88 mm TL adult female and #9 from a 51 mm TL subadult female to a 78 mm TL adult female (Table 23). Additional examples of the stable nature of dominance relationships between pairs of individuals are listed in detail in Table 23 and include: (1) the domination of #75 by #8 in social unit B over study site G_{10} for a period of 14 months before censusing was terminated, during which time #8 had changed sex and

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*TL = estimated total length.

Figure 37

Examples of dominance hierarchies complicated by the spatial relationships of females within the social unit

A. Social unit over Study site G_8, Study periods 3 (A2-Map 3)
B. Social unit over Study site G_{10}, Study period 3 (A2-Map 14)
C. Social unit over Study site G_{14}, Study period 8 (A2-Map 30)

KEY:

(i) Territory boundaries

- - - - - = Males
🟥 = Dominant females
🟫
🟦 = Other adult females
🟨 = Subadult females
🟩 = Juvenile females

(ii) #1,2,3,...#n = identity number of individual within a particular study site.

(iii) ♂ = male, A = adult female, SA = subadult female, J = juvenile female

(iv) (10,11,12,....nTL) = estimated total length in mm.

(v) #x > #y = #x is dominant over #y regardless of the locality of interaction, i.e. a spatially-independent dominance relationship.

(vi) #x/#y = no pair contact was observed between #x and #y but, due to the small size difference between them, their dominance relationship would probably be a spatially-dependent one.

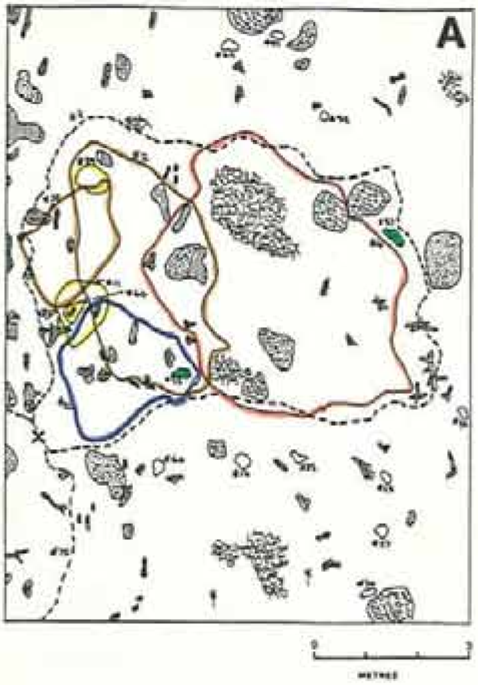
(vii) #x ≯ #y = no pair contact observed between #x and #y, but, due to the large size difference between them, #x would almost certainly be dominant over #y.

(viii) #x ⧖ #y = #x is dominant over #y in #x's territory, but #y is dominant over #x in #y's territory, i.e. a spatially-dependent dominance relationship.

(ix) A2-Map n = refers to Composite Map number in Appendix 2 from which example was taken.

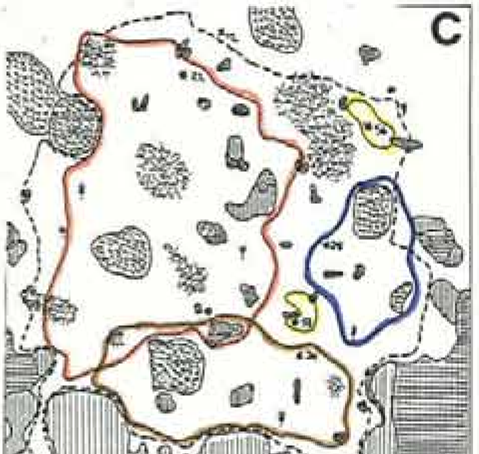
TERRITORY MAP

DOMINANCE HIERARCHY



#3♂ (95TL)>#4A(85TL)>#2A(75TL)>#22A (65TL)/#12A(65TL)>#11SA(55TL)≯#59SA (40TL)≯#60SA(35TL)≯#55J(20TL)/#57J (20TL)

#4♂ (95TL)>#5A(89TL)>#14A(77TL)≯#25A (56TL)≯#22SA(45TL)>#26SA(42TL)≯#33SA (39TL)/#51SA(38TL)≯#58SA(35TL)≯#55SA (32TL)≯#61J(20TL)



#12♂ (108TL)>#22A(85TL)>#24A(75TL)≯ #28A(65TL)≯#56SA(42TL)/#53SA(40TL)

Table 23: Stability of dominance relationships within the social unit

Study site	Social unit	Dominance Relationship[a]	Period of Stability of Dominance Relationship: Study periods	Period of Stability of Dominance Relationship: Time in months	Size and Sex of Interactants[b]: Start of periods	Size and Sex of Interactants[b]: End of period	Appendix Reference[c]
G$_{15}$	A	#8>#9	4-8	10	#8A(70TL); #9SA (51TL)	#8A(88TL): #9A (78TL)	A1-p. 370
G$_{10}$	B	#8>#75	5-11	14	#8A(89TL); #75SA (35TL)	#8♂(96TL); #75A (79TL)	A1-p. 367
G$_{14}$	-	#22>#24	4-10	14	#22A(73TL); #24SA (53TL)	#22♂(88TL); #24A (78TL)	A1-p. 369
G$_{15}$	B	#13⪤#14	5-10	12	#13SA(46TL); #14SA (45TL)	#13A(84TL); #14A (84TL)	A1-p. 370

[a] #1,2,3....#n = identity number of individual (within a particular study site; #x>#y = #x is dominant over #y regardless of the locality of interaction; #x⪤#y = #x is dominant over #y in #x's territory, by #y is dominant over #x in #y's territory, i.e. a spatially-dependent dominance relationship.

[b] ♂ = male, A = adult female, SA = subadult female; (10,11,12....nTL) = estimated total length in mm.

[c] A1 = Appendix 1

and become a male, and #75 had grown from a small subadult into an adult female, the *dominant female* (i.e. the largest and most dominant female) of #8♂'s social unit; (2) the domination of #24 by #22 over study site G_{14} for a period of 14 months before censusing was terminated, during which time #22 had changed sex and become a male, and #24 had grown from a large subadult into an adult female, the dominant female of #22♂'s social unit; (3) the spatially-dependent dominance relationship between #13 and #14, in social unit B over study site G_{15} which was maintained for a period of 12 months before censusing was terminated, during which time #13 and #14 had grown from subadult females into adult *codominant females*.

An individual's position with respect to the top of the dominance hierarchy did not change unless there was death or disappearance of an individual higher in status from the social unit. When one of the females died or disappeared, those females below it in status all advanced one position in rank whilst maintaining their respective dominance-subordinance relationships (Table 24). Similarly, when the male died or disappeared, the dominant female of the social unit assumed his position as male (provided the dominant female was large and aggressive enough to resist any take-over attempts of the social unit by neighbouring males), thus advancing one position in rank to the top of the hierarchy. The females below the "old" dominant female in status in turn advanced one position in rank with the largest and most dominant individual of these becoming the "new" dominant female of the social unit (Table 24). In the 25 cases where a male disappeared from his social unit (including experimental removal), and the social unit was not subsequently taken-over by a neighbouring male, the dominant female was observed to change sex and assume top position in the dominance hierarchy of that social unit.

Table 24: Changes in the dominance hierarchy due to loss of individuals from the social unit

Study site	Social unit	Study period	DOMINANCE HIERARCHY[a]	Remarks	Appendix reference
G_{15}	A	3	#3♂(90TL)>#2A(85TL)>#7A(69TL)>#8A(62TL)≯#9SA(42TL)	Loss of dominant female #2 between censuses; #7, #8 and #9 advance one rank	A1-p.370
G_{15}	A	4	#3♂(94TL)>#7A(75TL)>#8A(70TL)>#9SA(51TL)		A1-p.370
G_{10}	B	8	#15♂(110TL)>#8A(94TL)>#75A(64TL)≯#80A(61TL)>#90SA(42TL)≯#91SA(38TL)>#96SA(29TL)	Loss of male #15 and subadult females #91 and #96; "old" dominant female #8 changes sex advancing one rank; #75, #80 and #90 advance one rank	A1-p.368
G_{10}	B	9	#8♂(95TL)>#75A(70TL)>#80A(67TL)>#90SA(53TL)		A1-p.368

[a] #1,2,3.....#n = identity number of individual within a particular study site; ♂ = male, A = adult female, SA = subadult female; (10,11,12,....nTL) = estimated total length in mm; #x>#y = #x is dominant of #y regardless of the locality of the interaction; #x≯#y = no pair contact was observed between #x and #y, but, due to the large size difference between them, #x would almost certainly be dominant of #y.

5.3.2.4 *Frequency of agonistic encounters between a male and the members of his social unit* Observations were made on male DC (study site DG-1) and male DI (study site DG-2) for 780 and 720 minutes respectively, during which time the number of agonistic encounters each had with other members of their social unit was recorded. Table 25 shows that both male DC and male DI, on average, had an agonistic encounter with each of their adult females, every 9 to 13 minutes. Encounters with subadults were slightly less frequent - male DC interacted with subadult female DA, and male DI with subadult female DJ, every 15 and 16 minutes respectively. Interactions between males and juveniles were the least frequent of all agonistic encounters, presumably as a consequence of the small size and relatively secretive nature of juveniles.

5.3.3 Individual recognition of social unit members and intruders If the male of a social unit encounters a male or female from a different social unit which has intruded into his territory, his immediate reaction is to make an overt attack on the intruder and drive it out of his territory (see pp.226-227). In contrast, the females of his own social unit are permitted to reside within his territory whilst receiving male aggression in a more ritualized form (see p.223). A male *Parapercis cylindrica* therefore has the ability to discriminate between individuals of his own social unit from individuals of different social units. The colour pattern of an individual was considered to be the most likely cue used for this recognition, however it was possible that size, location, and behaviour of the intruder were also important cues.

To investigate the cues upon which individual recognition in *P. cylindrica* is based, two series of "model-bottle" experiments (cf. Myrberg and Thresher, 1974) were conducted, one series each within study sites DG-1 and DG-2. The methodology for each series was identical and was as

Table 25 . Frequency of agonistic encounters between male *P. cylindrica* and members of their social unit[a]

Male identity	Social unit member encountered	Frequency of encounter	Average time between each encounter (mins.)
♂ DC (101 mm TL[b]) Observation time = 780 mins.	♀ DB (78 mm TL)	84	9.3
	♀ DE (63 mm TL)	68	11.5
	♀ DA (41 mm TL)	52	15.0
	♀ DD (25 mm TL)	14	55.7
♂ DI (105 mm TL) Observation time = 720 mins.	♀ DF (89 mm TL)	78	9.2
	♀ DH (71 mm TL)	55	13.1
	♀ DG (70 mm TL)	63	11.4
	♀ DJ (45 mm TL)	45	16.0
	♀ DK (25 mm TL)	21	34.0

[a] ♂-♀ agonistic encounter = Spinous dorsal-Approach only, by ♂; or Spinous dorsal-Approach → Frontal Thrust(→ Butt → Bite) → Chase, by ♂.

[b] TL = estimated total length in mm.

follows: A female individual of the same social unit as that of the male involved in the test series, i.e. a normal "resident" of his territory, was collected by net at least 30 minutes before the start of the test series and placed into a two litre, transparent, mesh-topped, glass jar. Another female individual was collected, this time from a location greater than 200 metres distant from the male involved in the test series (the individual was therefore assumed to have had no prior contact with the test male), and also placed into an identical (but separate) glass jar. To eliminate size as a possible cue for individual recognition, the individual chosen to be this "foreign" female was equal in size to that of the "resident" female above. In each trial of the series, the glass jar containing the "resident" female was placed well into the territory of the male and the number of attacks (i.e. Butts, see p.218) directed at it by the male in a five minute period, recorded. The "resident" female jar was then removed and immediately replaced, in exactly the same location, with the jar containing the "foreign" female. The attack rate by the male was recorded in the same way as above, then the jar was removed. To also eliminate an individual's location as a possible cue for recognition, both "resident" and "foreign" females were placed at the opposite end of the male's territory to which the "resident" female had formerly resided. A total of eight (♂ DC test series, study site DG-1) or nine (♂ DI test series, study site DG-2) paired trials were conducted per series, with the order of presentation of "resident" female and "foreign" female changed on a random basis. There was an interval of 30 minutes between each paired trial, and all paired trials were conducted at times outside the daily reproductive period.

The results of the two series of paired trials are presented in Table 26. It can be seen that male DC attacked the "foreign" female AC at a significantly higher rate than the "resident" female DB (Paired

Table 26. Comparison of attack rates by males on foreign and resident females which had been introduced into male territories[a]

	Individual introduced into male territory	No. of times introduced	Mean attack rate (Butts / 5 min.)
SERIES I ♂ DC (101 mm TL)	Resident ♀ (♀ DB, 78 mm TL)	8	1.25 ± 1.04 SD
	Foreign ♀ (♀ AC, 78 mm TL)	8	14.50 ± 3.07 SD
SERIES II ♂ DI (105 mm TL)	Resident ♀ (♀ DF, 89 mm TL)	9	1.67 ± 1.41 SD
	Foreign ♀ (♀ AD, 88 mm TL)	9	18.68 ± 7.23 SD

[a] Foreign female = female collected > 200 m from the male territory to which it was introduced; Resident female = female formerly (i.e. before the experiment) resident within the male territory to which it was experimentally introduced, i.e. a member of the same social unit as the male.

t-test, $t = 11.52$, $P < 0.001$, $n = 8$). Similarly, the attack rate by male DI against the "foreign" female AD was significantly higher than it was against the "resident" female DF (Paired *t*-test, $t = 7.52$, $P < 0.001$, $n = 9$). In the absence of any obvious difference in behaviour patterns between the "foreign" and "resident" females whilst in their respective glass jars, the results of the experiments suggest that colour pattern, rather than size, location, or behaviour of the intruder, is the cue upon which individual recognition in *P. cylindrica* is based.

5.3.4 Spatial relationships within and between social units

5.3.4.1 *Size and structure of territories* Males defend their territories from both males and females of other social units, though primarily the former. Smaller males are able to successfully defend their territories against larger neighbouring males, hence, in the case of males, prior residence of an area is able to override any size-dominance effect. Territoriality in females, in contrast, is masked somewhat by the size-based dominance hierarchy which occurs within the social unit. The status (size) of a female determines the degree to which she can successfully maintain her territory. If she is the dominant (or codominant) female of the social unit then she will be able to successfully maintain her territory against all other social unit females. However, if she is a low ranking female, she will only be able to successfully defend her territory against females equal or lower in status (i.e. of equivalent or smaller size) than herself - although she may frequently venture unobserved into areas within the territory boundary of a higher ranking female, she will be unable to successfully defend these areas once she is observed and attacked by the more dominant (larger) individual.

Territory sizes for the different age/sex categories of *P. cylindrica*, as determined by planimetry on composite territory maps, are presented in

Table 27. Territory size for different age/sex categories of *Parapercis cylindrica* .

Age/sex category	No. of territories measured	Mean territory size (m^2)
Juvenile females	164	0.10 ± 0.19 SD
Subadult females	89	1.54 ± 2.38 SD
Adult females	135	6.73 ± 4.64 SD
Males	66	32.47 ± 16.52 SD

Table 27. It can be seen that, on average, male territories were almost five times the size of adult female territories, 20 times the size of subadult female territories, and well over 300 times the size of juvenile female territories. Hence, the older and larger an individual is, the greater the size of its territory.

The spatial relationships within male DC's social unit in study site DG-1, as determined by mapping over a two day period during August 1976, are shown in Figure 38 . It is apparent that the females of male DC's social unit lived within the confines of his territory boundary. The dominant female of the social unit, adult female DB, held the largest territory of all the females. Adult female DE held the second largest territory, subadult female DA the next largest, and finally juvenile female DD held the smallest territory of all the females. Whilst there was some overlap between female territories it can be seen that in general, each female resided in its own particular portion of the male DC's territory. Juvenile female DD was an exception to this in that it resided within the area of common overlap between females DB, DE, and DA. In being the lowest ranking individual of the social unit (see Fig. 35), juvenile female DD's residence within this area was dependent upon its

Figure 38

Composite territory map of male DC's social unit within study site DG-1

<u>KEY:</u>

<u>Territory boundaries</u>:

---- = male DC (101 mm TL)

🟥 = adult female DB (dominant female - 78 mm TL)

🟦 = adult female DE (63 mm TL)

🟧 = subadult female DA (41 mm TL)

🟩 = juvenile female DD (25 mm TL)

<u>Substrata</u>:

▤ = Living hard coral - massive or encrusting

▩ = Living hard coral - staghorn *Acropora* spp.

▤ = Dead hard coral

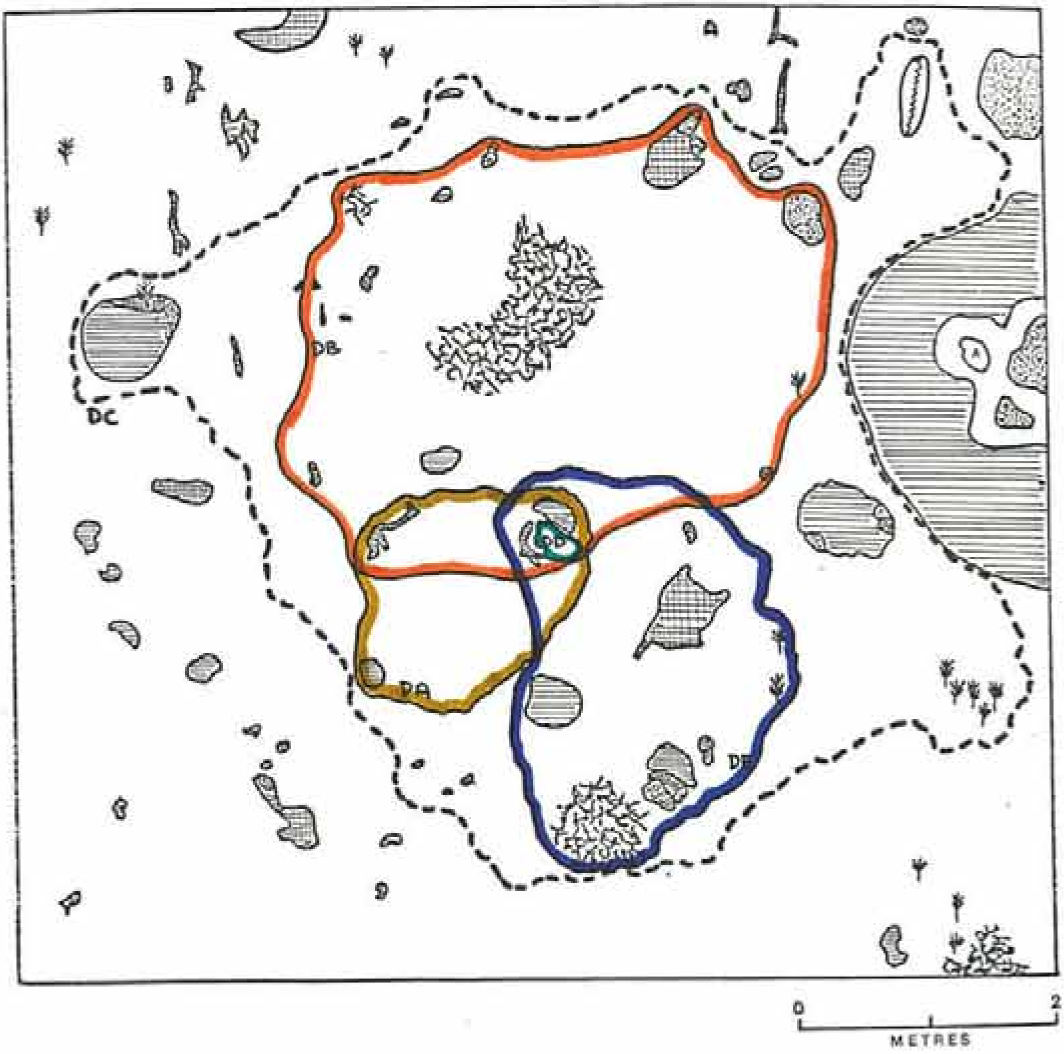
▦ = Soft coral (Alcyonaria)

⚘ = Macroscopic algal clump

Ⓐ = Sea anemone

⬯ = *Tridacna* clam

STUDY SITE DG-1



access to small crevices amongst the coral and coral rubble which provided refuge from attacks by more dominant (larger) individuals.

Fifty-four composite territory maps illustrating the spatial relationships of individuals within regularly mapped social units are presented in Appendix 2. These maps illustrate similar spatial relationships to those described above, namely that (1) the females of a social unit resided within their male's territory (excepting occasional excursions slightly beyond his territory border); (2) in general, each female occupied her own particular portion of the male's territory; and (3) the dominant female of the social unit occupied the largest portion of the male's territory. In those social units where codominant females occurred (i.e. where the two largest females were of equal status), each codominant held approximately the same size territory as the other - their territories were also the largest of all the females within the social unit (Fig.39).

5.3.4.2. *Differential use of space within territories.* Preliminary observations indicated that individuals used some portions of their territories more intensely than other portions. This was examined more closely by plotting an individual's position at 30 second intervals over a considerable time period (five 60-90 minute observation periods per observation series; three observation series per individual). A concentration of points on a particular region of the territory map would thus indicate that activity was concentrated in that portion of the individual's territory. Figures 40-41 show the results of these movement check programs conducted upon male DI (study site DG-2) and male DC (study site DG-1) over a three day period for each. It is apparent that each male concentrated his activities around particular areas within his territory. In the case of DI there were six such

Figure 39

Spatial relationships and dominance hierarchies within social units of *P. cylindrica* containing codominant females

A. Social unit B_2, Study site G_{15}, Study period 10 : Codominant female #13 territory area = 8.29m^2, Codominant female #14 territory area = 6.36m^2 (A2-Map 42).

B. Social unit C_2, Study site G_{15}, Study period 10: Codominant female #18 territory area = 7.54m^2, Codominant female #20 territory area = 8.72m^2 (A2-Map 42).

C. Social unit over Study site SBI, 2/6/78, pre-male removal: Codominant female #1 territory area = 4.31m^2, Codominant female #5 territory area = 3.56m^2, adult female #6 territory area = 1.96m^2, adult female #2 territory area = 1.60m^2, subadult female #4 territory area = 0.82m^2 (A2-Map 47).

KEY:

(i) Territory boundaries:

- - - - = Males

——— = Codominant females

———
——— = Other adult females

——— = Subadult females

——— = Juvenile females

(ii) Dominance hierarchy : As in KEY for Fig.37

(iii) A2-Map n = refers Composite Map number in Appendix 2 from which example was taken.

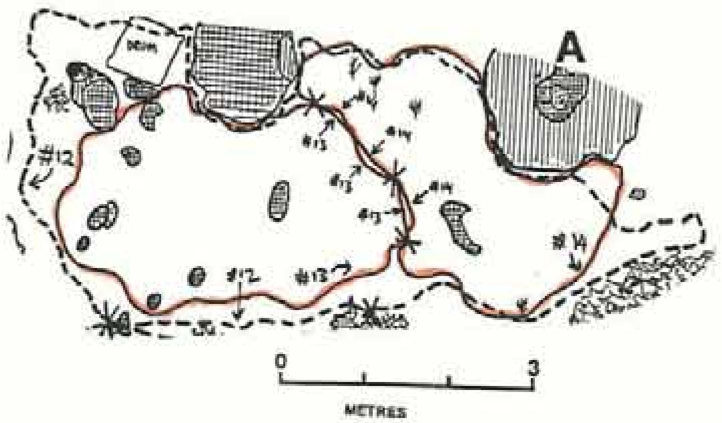
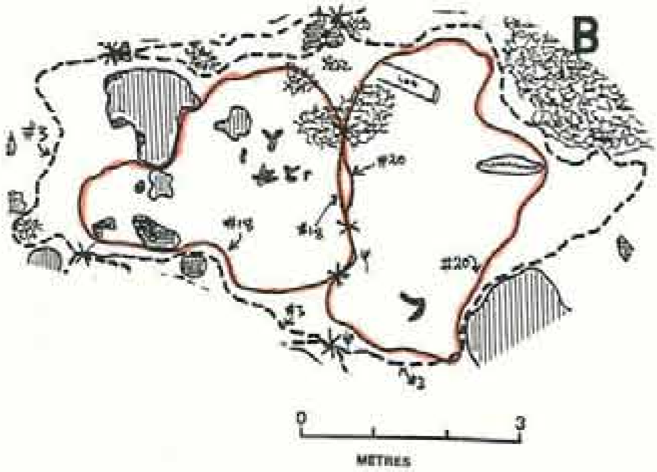
TERRITORY MAP	DOMINANCE HIERARCHY
	#12♂ (95TL)>#13A(84TL)⇔#14A(84 TL)
	#3♂ (102TL)>#18A(77TL)⇔#20A(76 TL)
	#3♂ (80TL)>#1A(82TL)⇔#5A(81TL) >#6A(76TL)≯#2A(57TL)>#4SA(50TL)

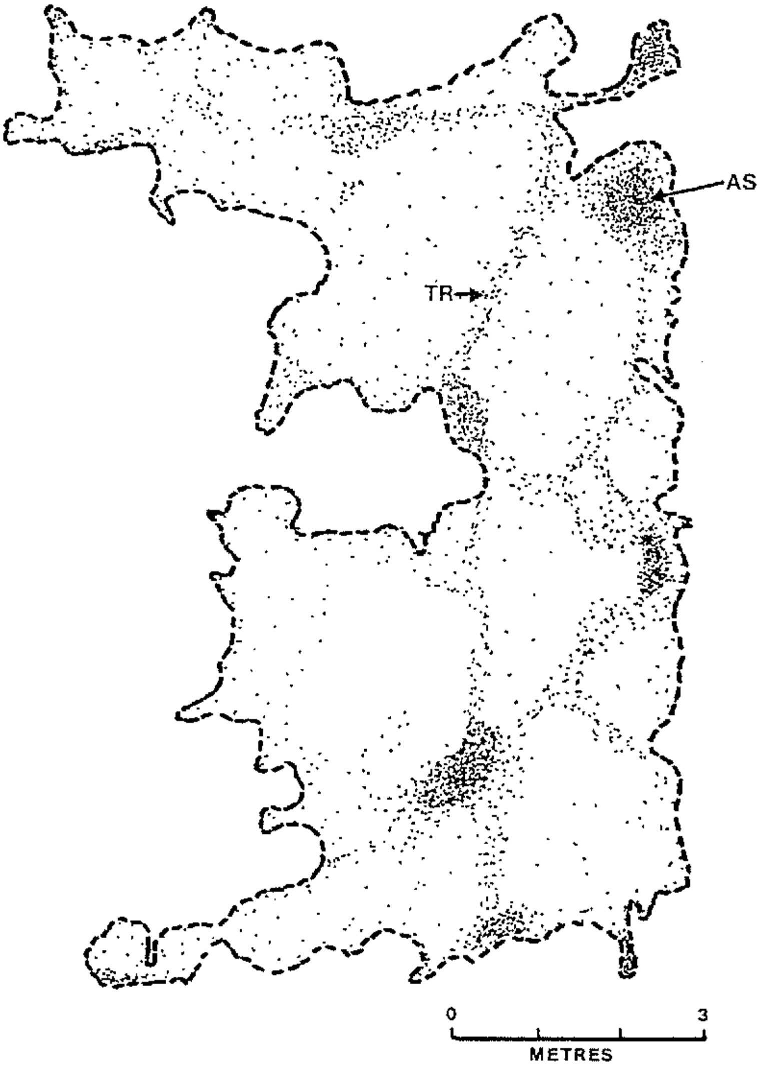
Figure 40

Differential use of space by male DI within his territory

<u>KEY</u>:

(i) AS = Activity site

(ii) TR = Trail



TIME INTERVAL BETWEEN POSITION PLOTS = 30 secs.

TOTAL OBSERVATION TIME = 1200 mins.

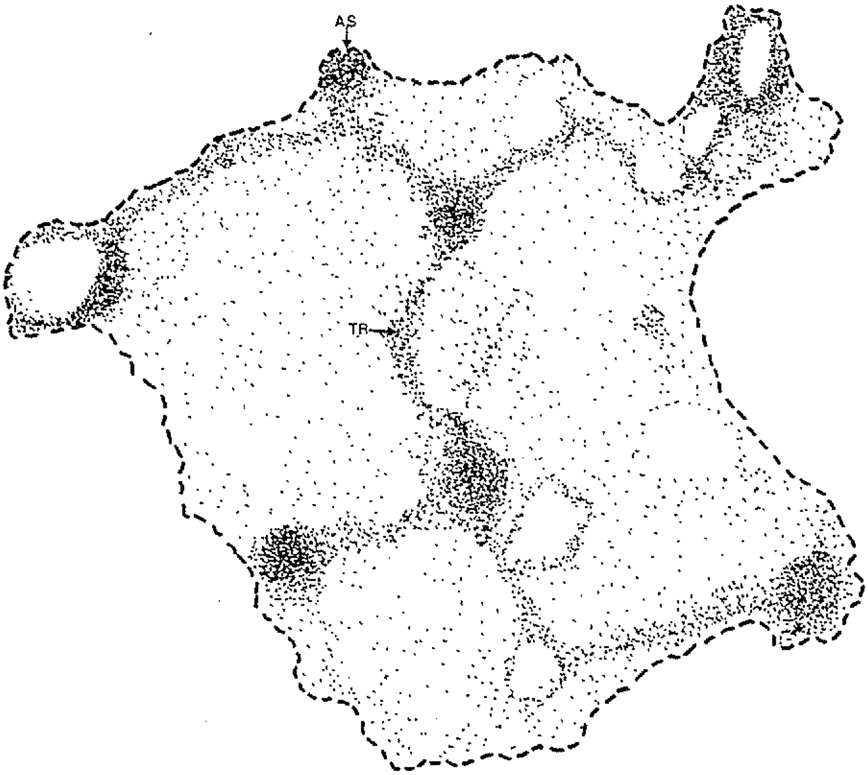
Figure 41

Differential use of space by male DC within his territory

<u>KEY</u>:

(i) AS = Activity site

(ii) TR = Trail



Total observation time=1200 mins
Position plot interval =30 secs

areas, for DC there were seven. These *activity sites,* or areas of concentrated use, were interconnected via *trails* which were regularly used by these individuals to travel from one activity site to another.

Differential use of space within territories appears to be related to social factors as well as simple feeding area preferences. Of the six activity sites of DI shown in Figure 40, four were located within the territories of females belong to male DI's social unit, there being one activity site to each adult or subadult female territory (compare Figs. 40 and 44). Hence male DI concentrated much of its activities in areas where he was likely to encounter the various females of his social unit. The remaining two activity sites were located on, or very near to, DI's territory border and were associated with conspicuous features of the bottom topography. These topographic features (in one case, a soft coral colony; in the other, two pieces of coral rubble) were quite elevated and appeared to provide good vantage points from which DI could survey a considerable amount of his territory and territory border. DI was often observed perching atop these "lookout posts" in between bouts of foraging nearby.

Three of male DC's seven activity sites were located within the territories of females belonging to his social unit, there being one activity site to each adult or subadult female territory (compare Figs.38 and 41). Thus male DC, like male DI discussed above, spent a good deal of his time in areas where he was likely to encounter the females of his social unit. Also, as in the case of male DI, DC's other four activity sites were associated with conspicuous features of the bottom topography (i.e. clam shell, algal colony, brain coral outcrop, piece of coral rubble) and situated very close to his territory border (compare Figs. 38 and 41).

Additional movement check programs conducted on adult and subadult females of the social units of DI and DC showed that those male activity sites located within female territories were more often than not situated close to, or super-imposed upon, the activity sites of females (Figs.42-43). Female activity sites were generally less well defined than male activity sites (an exception being border dispute sites as discussed below) in addition to being fewer in number (Table 28, Figs. 42-43)

Border disputes invariably occurred at those activity sites situated close to, or on, a mutual border separating the territories of neighbouring males or equivalent-sized females. Two such *border dispute sites* are shown in Figure 44 for adult female's DG and DH, two equivalent-sized females belonging to male DI's social unit. The location of a border dispute site generally remained unchanged until the death/disappearance of one or both of the interactants, this often being a considerable period of time, i.e. a year or more (Table 29).

5.3.4.3 *Rates of movement about territories.* The rates of movement of individuals about their territories were estimated by utilizing data methodology of Robertson (1974), the straight line distance between each pair of successive (30 second interval) plotted points was measured and averaged for the sample. A comparison of the rates of movement of males and adult females is presented in Table 30. It is apparent that males move about their territories at a considerably higher rate than adult females.

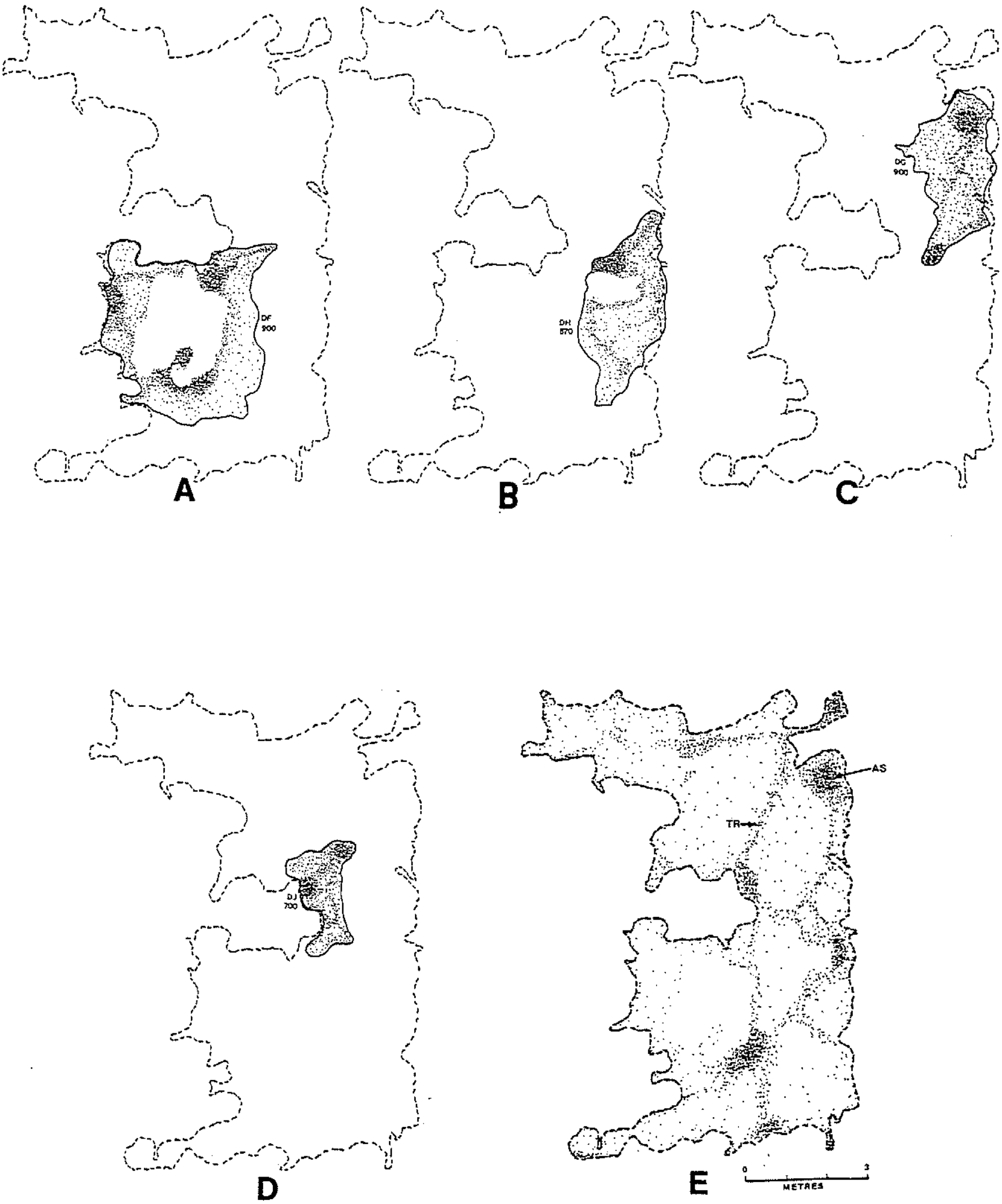
Figure 42

Differential use of space by females of DI's social unit.

A. Adult (dominant) female DF
B. Adult female DH
C. Adult female DG
D. Subadult female DJ
E. Male DI (comparative map)

Key:

(i) Time interval between position plots = 30 secs.
(ii) Number beside female territory = total observation time in minutes on individual.
(iii) ----------- = male territory border
(iv) ———————— = female territory border.



TIME INTERVAL BETWEEN POSITION PLOTS = 30 mins.

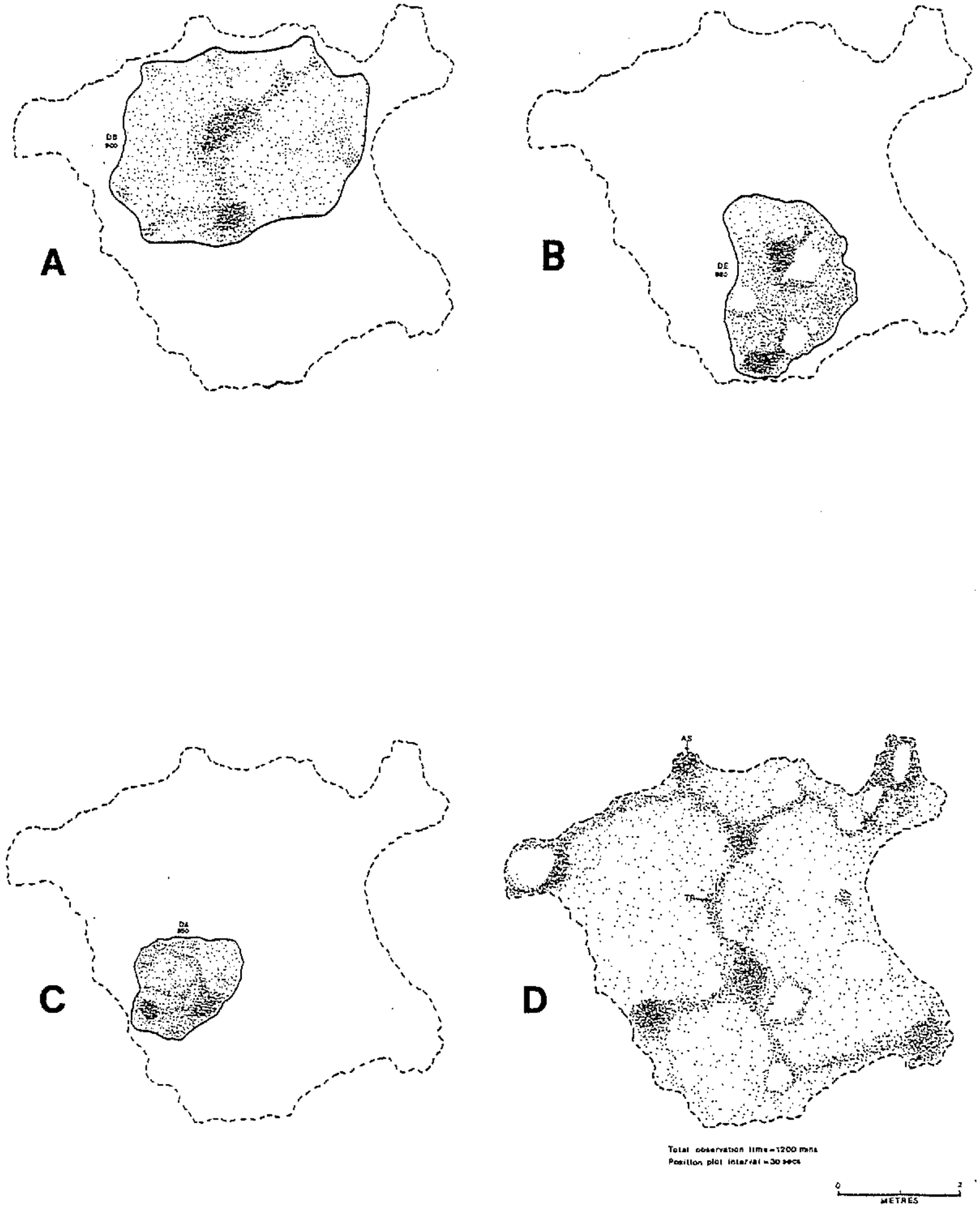
TOTAL OBSERVATION TIME = 1200 mins.

Figure 43

Differential use of space by females of DC's social unit.

A. Adult (dominant) female DB
B. Adult female DE
C. Subadult female DA
D. Male DC (comparative map)

Key: As in Fig. 42



Total observation time = 1200 mins
Position plot interval = 30 secs

Table 28. Number of activity sites of each individual within its territory for two social units of *P. cylindrica*[a]

Social Unit	Identity of individual	Size of individual (mmTL)	Age/Sex Category	No. of activity sites within territory of individual
	DI	105	Male	6
DI's over	DF	89	Adult female	3
study site DG-2	DH	71	Adult female	1
	DG	70	Adult female	2
	DJ	45	Subadult female	2
	DC	101	Male	7
DC's over	DB	78	Adult female	2
study site DG-1	DE	63	Adult female	2
	DA	41	Subadult female	2

[a] Movement check programs were not conducted on juveniles due to their extremely small territory size, consequently these individuals are excluded from the table.

Figure 44

Composite territory map of male DI's social unit within study site DG-2

KEY:

Territory boundaries:

---- = male DI (105 mm TL)

🟥 = adult female DF (dominant female - 89 mm TL)

🟦 = adult female DH (71 mm TL)

🟫 = adult female DG (70 mm TL)

🟧 = subadult female DJ (45 mm TL)

🟩 = juvenile female DK (25 mm TL)

Substrata: Key as in Fig. 38

STUDY SITE DG-2

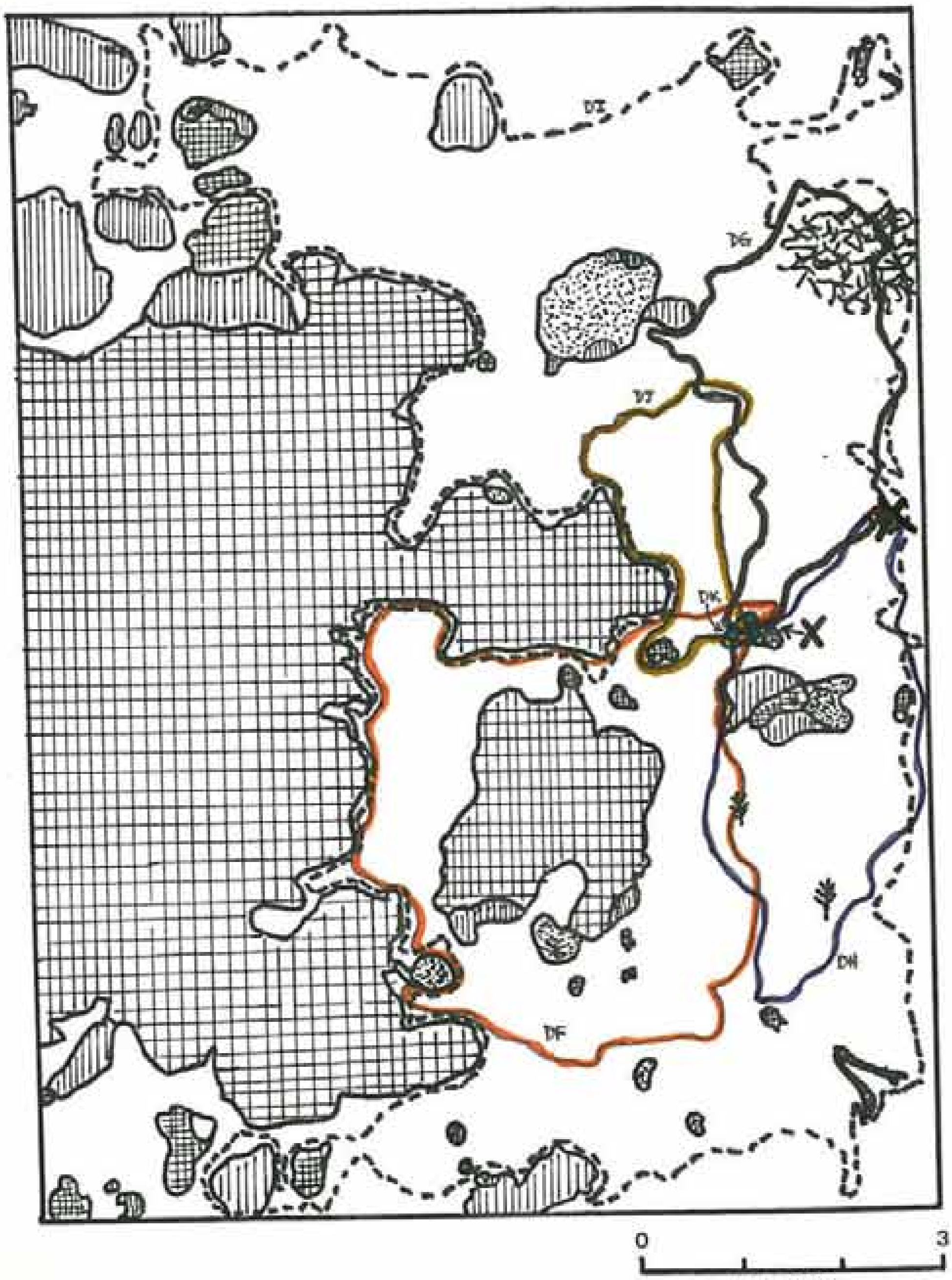


Table 29. Stability of location of border dispute sites for *P. cylindrica*.

Study site	Identities of interactants	No. border dispute sites in common	Time period location of border dispute site remained unchanged		Age/sex category		Appendix[a] reference
			Study periods	Time (months)	Start of period	End of period	
G_{10}	#4 & #5	2	1-7	14	Males	Males	A2-Maps 12-18
G_{10}	#4 & #99	1	1-7	14	Males	Males	A2-Maps 12-18
G_{15}	#5 & #3	1	1-6	12	Males	Males	A2-Maps 33-38
G_{15}	#13 & #14	1	5-10	12	Subadult females	Adult females	A2-Maps 37-42

[a] A2 = Appendix 2

Table 30 Rates of movement of males and adult females about their territories [a]

Age/sex category	No. samples[b] taken	Mean Rate of Movement (cm./sec.)
Male	30	2.7 ± 0.9 SD
Female	75	0.9 ± 0.3 SD

[a] Combined date for two males and five adult females within study sites DG-1 and DG-2

[b] Sample observation time = 30 min.

5.3.4.4. Changes in territorial boundaries and ownership

(i) Males Each male occupied and defended a relatively fixed portion of substratum until his death. Table 31 shows the periods of territorial occupancy of the 14 male *P. cylindrica* which were observed to be resident, at one time or another, over the four long term study sites. It can be seen that the longest period of territorial occupancy by any one male was 22 months and that this individual (#3, study site G_{15}) was still present at the end of the two year census period. Excluding those males still present at the final census, the mean period of territorial occupancy was 13.3 months (SD = 6.5, n= 8) with the shortest period of occupancy by any one male being 2.5 months (#75, study site G_8).

No instance of a male emigrating from its territory, or being driven away and displaced from its territory by another individual, was observed.

Male territories generally underwent slight expansions through time as individuals grew in size (Fig.45). Only one instance of a major contraction of a male's territory was observed during the study. This occurred within study site G_{15} when male #3's social unit was

Table 31. Period of territorial occupancy by male *P. cylindrica* observed over long term study sites

Study site	Male identity	Period of Occupancy of Territory Study periods	 Time (Months)	Appendix Reference[a]
G_8	#3	1-3	5.0	A2-Maps 1-3
"	#75	4-5	2.5	A2-Maps 4-5
"	#12	6-11$^+$	11.4$^+$	A2-Maps 6-11
G_{10}	#4	1-7	14.4	A2-Maps 12-18
"	#99	1-10	21.2	A2-Maps 12-21
"	#58	11$^+$	2 days$^+$	A2-Map 22
"	#15	1-8	16.8	A2-Maps 12-19
"	#8	9-11$^+$	4.3$^+$	A2-Maps 20-22
G_{14}	#12	1-8	17.0	A2-Maps 23-30
"	#22	9-10$^+$	3.2$^+$	A2-Maps 31-32
G_{15}	#3	1-10$^+$	22.0$^+$	A2-Maps 33-42
"	#5	1-6	11.8	A2-Maps 33-38
"	#27	1-8	17.7	A2-Maps 33-40
"	#8	9-10$^+$	2.5$^+$	A2-Maps 41-42

$^+$Denotes individual still present at termination of two year census period.

[a] A2 = Appendix 2.

Figure 45

Changes in the size of four male territories through time.

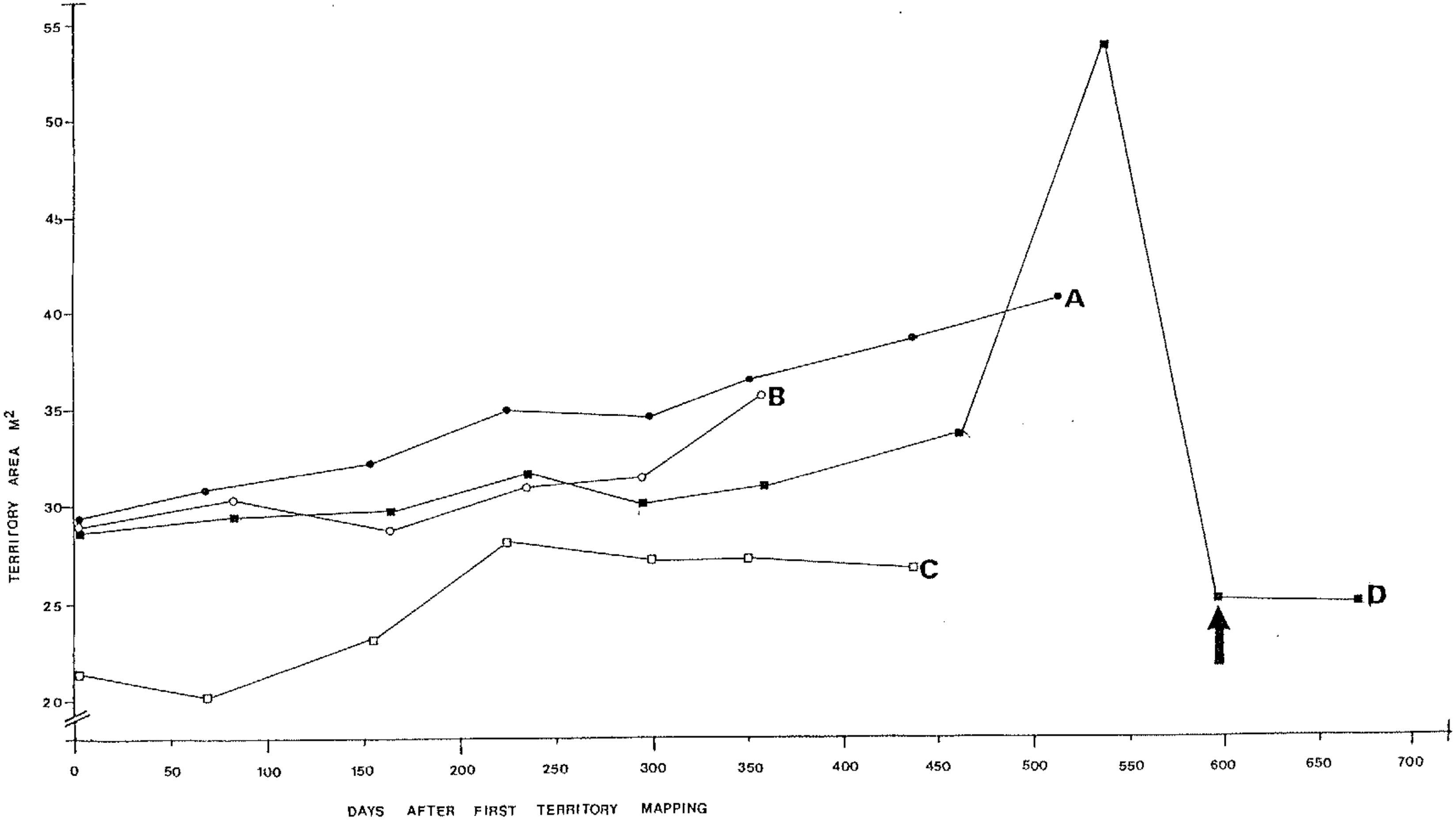
A. #15 (100-110TL), study site G_{10}
Sept.1976-Feb.1978

B. #5 (90-96TL), study site G_{15}
Nov. 1976-Nov.1977

C. #4 (85-102TL), study site G_{10},
Sept.1976-Dec.1977

D. #3 (85-102TL), study site G_{15},
Nov.1976-Sept.1978

Dates refer to the period during which the individual, as a male, was present within a particular study site; figures in parentheses indicate total length of the individual in mm at the beginning and end of this period; males #15, #5 and #4 disappeared and were presumed dead, male #3 was still prsent at the final census; arrow indicates major territory contraction due to social unit division.


TERRITORY AREA M²
55
50
45
40
35
30
25
20
0
50
100
150
200
250
300
350
400
450
500
550
600
650
700
DAYS AFTER FIRST TERRITORY MAPPING
A
B
C
D

split into two smaller social units following sex reversal of the dominant female (#8) of his social unit; in the process, a considerable portion of the territory originally held by male #3 was excised by the "new" male #8 leaving #3's territory considerably reduced in size (Figs. 45D and 46). This was also the only case observed in which a female changed sex whilst in the presence of a male.

Major changes in territory boundaries and ownership occurred with loss of a male from a social unit. A total of 35 male disappearances (21 through natural causes; 14 through experimental removal) were recorded during the study. In 22 of these cases the dominant female underwent sex reversal and assumed control of the social unit following the disappearance of the male. Concomitant with assuming the male role, the individual also extended its territorial boundaries to encompass essentially the same area originally held by the deceased/removed male (Figs. 47-49).

Three of the remaining 13 cases of male disappearance were recorded from social units which contained codominant females rather than a single dominant female. In each case, both codominants changed sex following the disappearance of the male. The remaining members of the social unit and the former territory of the deceased/removed males were divided between the pair of codominants as the two changed sex and extended their territory boundaries; this resulted in two separate social units, each under the control of a "new" male (Fig.50). Potential social unit division also existed in those situations where a dominant female and a large female of the same social unit resided at opposite ends of the male territory and, as a consequence, did not come into contact with one another. In three such situations, the social unit divided when both dominant female and large adult

Figure 46

Contraction of the territorial boundary of a male as a result of social unit division.

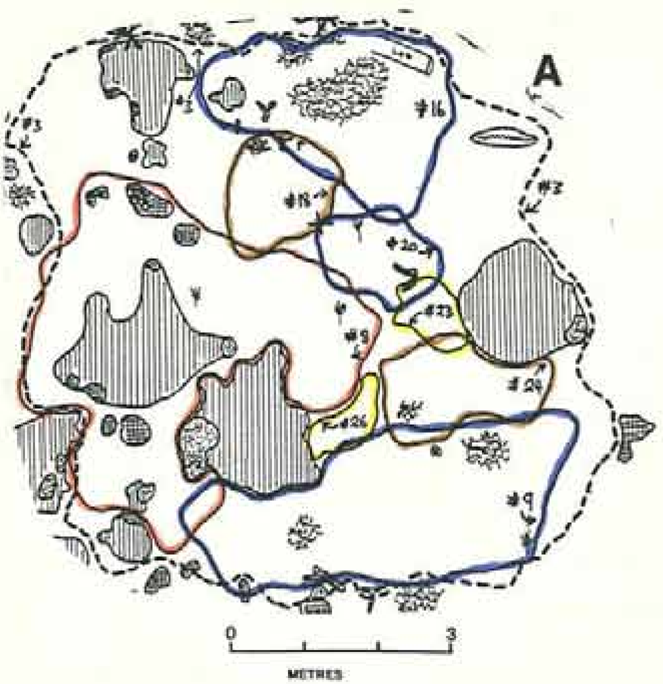
A. Social unit C, study period 8, study site G_{15} (A2-Map 40).

B. Social units C_1 & C_2 (formed through division of social unit C), study period 9, study site G_{15} (A2-Map 41); note contraction of male #3's territory and expansion of "new" male #8's territory.

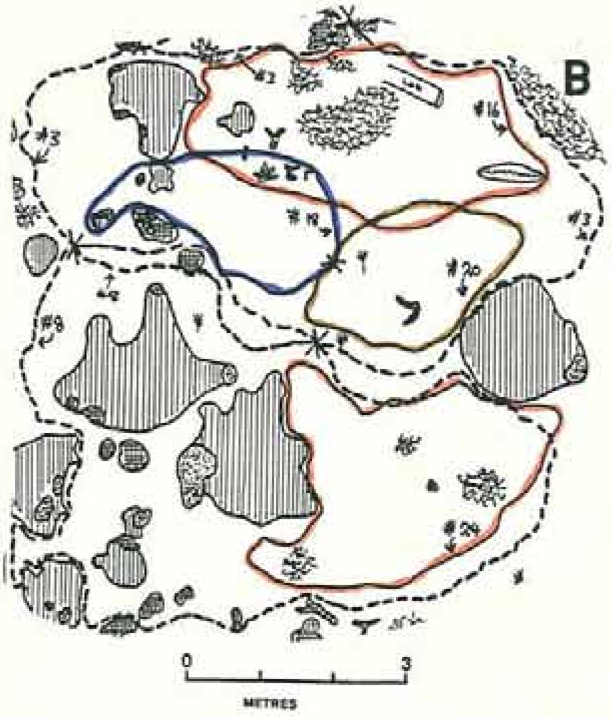
<u>Key</u>: As for Fig.37

TERRITORY MAP

DOMINANCE HIERARCHY



Social unitC: #3♂ (101TL)>#8A(88 TL)>#9A(78TL)≯#16A(67TL)≯#24A(63 TL)/#18A(62TL)≈#20A(61TL)>#23SA (53TL)≯#26SA(48TL)



Social unit C_1: #8♂ (92TL)>#24A (72TL)

Social unit C_2: #3♂ (101TL)>#16 A(75TL)>#18A(70TL)≈#20A(70TL)

Figure 47

Changes in territory boundaries and ownership following loss of a male from a social unit within study site G_{10}

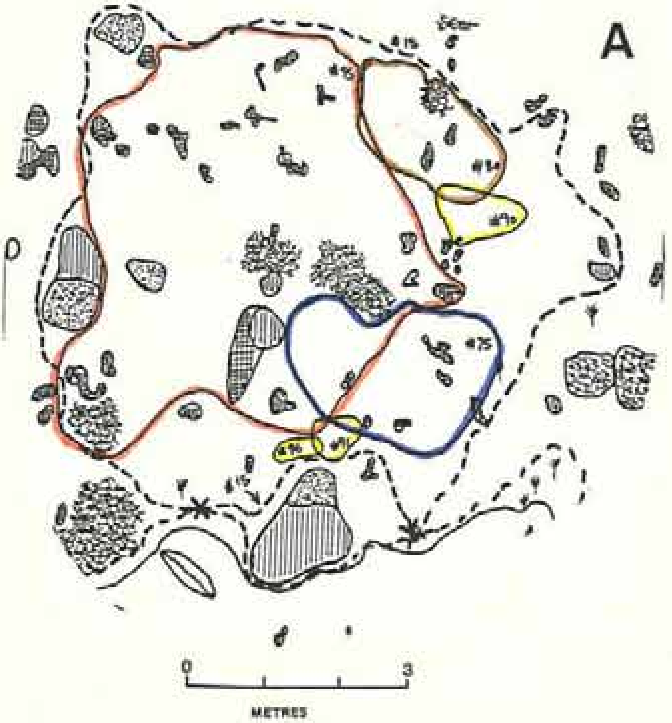
A. Social unit B, study site G_{10}, study period 8, before loss of #15 ♂; territory size #15♂ = $40.7m^2$, territory size #8 (dominant female) = $22.3m^2$ (A2-Map 19).

B. Social unit B, study site G_{10}, study period 9, after loss of #15♂ and #8 had assumed the male role; territory size #8♂ = $39.6m^2$ (A2-Map 20).

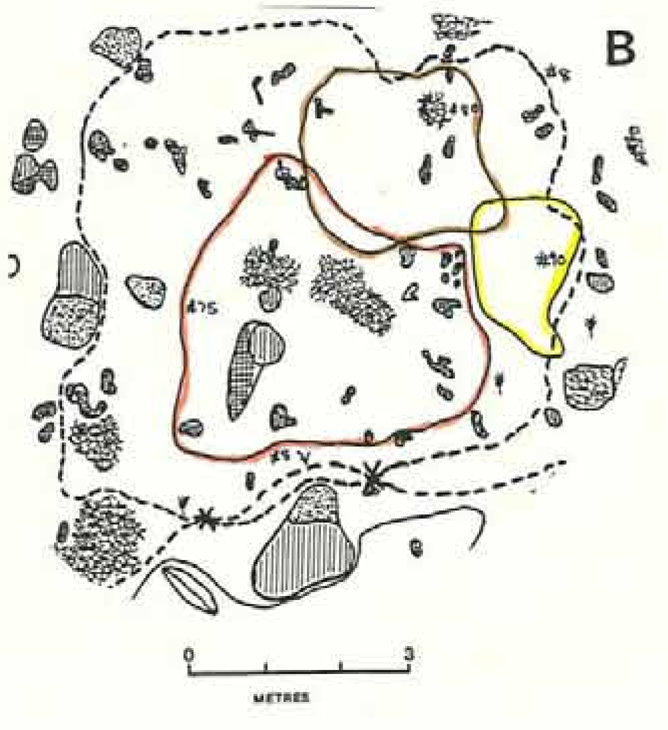
<u>Key</u>: As in Fig.37, except for substrata key from Fig.38.

TERRITORY MAP

DOMINANCE HIERARCHY



#15♂ (110TL)>#8A(94TL)>#75A(64TL)> #80A(61TL)>#90SA(42TL)>#91SA(38TL) >#96SA(29TL)



#8♂ (95TL)>#75A(70TL)>#80A(67TL)> #90SA(53TL)

Figure 48

Changes in territory boundaries and ownership following loss of the male from the social unit within study site G_{14}.

A. Study site G_{14}, study period 8, before loss of #12♂ ; territory size #12♂ = 52.4m^2, territory size #22 (dominant female) = 22.7m^2 (A2-Map 30).

B. Study site G_{14}, study period 9, after loss of #12♂ and #22 had assumed the male role; territory size #22♂ = 49.0m^2 (A2-Map 31).

Key: As in Fig. 47

TERRITORY MAP

DOMINANCE HIERARCHY

#12♂ (108TL)>#22A(85TL)>#24A(75 TL)≯#28A(65TL)≯#56SA(42TL)/#53SA (40TL)

#22♂ (87TL)>#24A(76TL)>#28A(69TL) ≯#56SA(50TL)/#53SA(49TL)

Figure 49

Changes in territory boundaries and ownership following loss of the male from the social unit within study site LHI

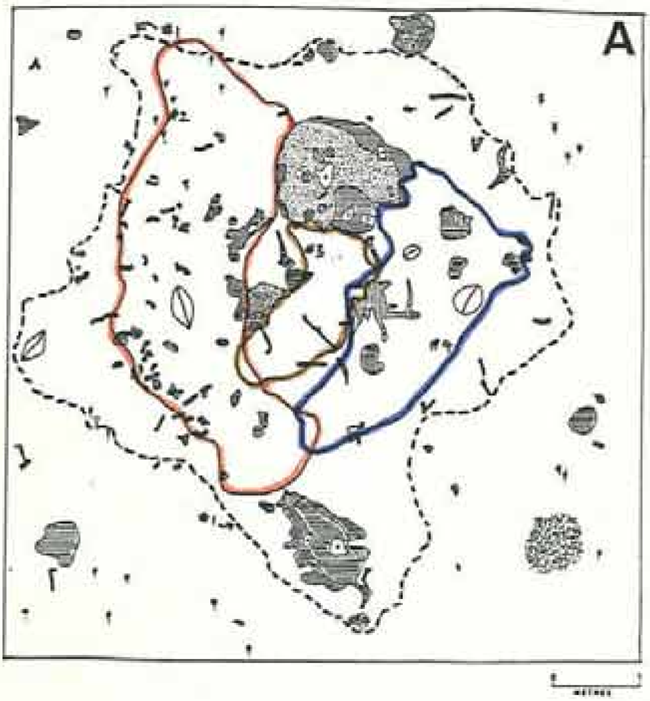
A. Study site LHI, 25/5/78, 1 day before removal of #1♂ ; territory size #1♂ = 25.9m^2, territory size #2 (dominant female) = 7.1m^2 (A2-Map 43).

B. Study site LHI, 25/6/78, 30 days after removal of #1♂ and #2 had assumed the male role; territory size #2♂ = 23.9m^2 (A2-Map 46).

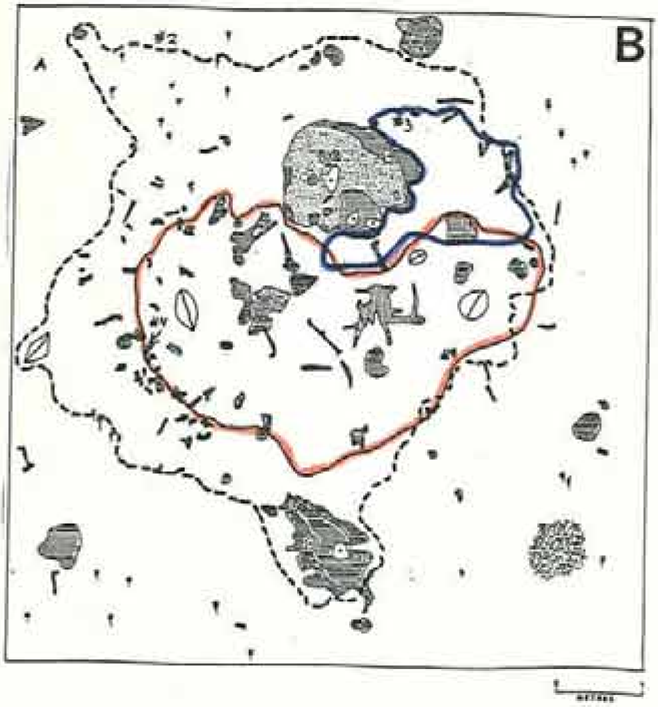
<u>Key</u>: As in Fig. 47

TERRITORY MAP

DOMINANCE HIERARCHY



#1♂ (115TL)>#2A(95TL)>#4A(75TL)
>#3A(65TL)



#2♂ (95TL)>#4A(77TL)>#3A(69TL)

Figure 50

Changes in territory boundaries of codominant females following loss of the male from the social unit within study site SBI.

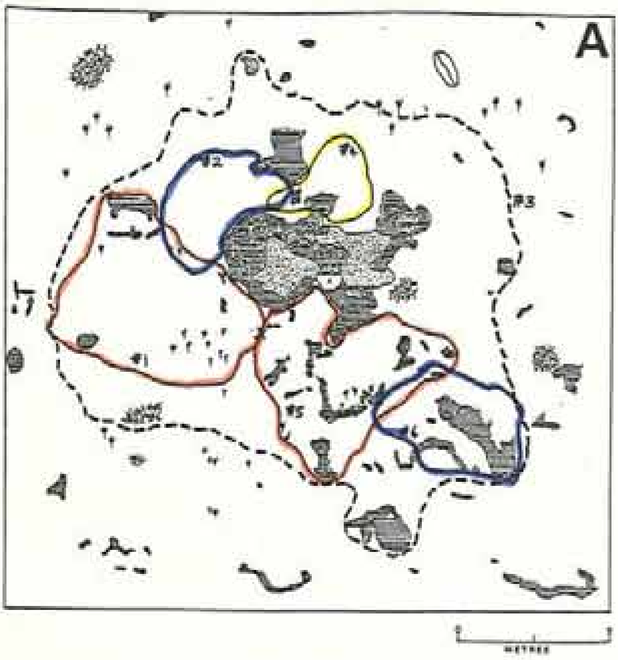
A. Study site SBI, 2/6/78, 1 day before removal of #3♂ ; territory size #3♂ = 25.8m^2, territory size #1 (codominant female) = 4.3m^2, territory size #5 (codominant female) = 3.4m^2
(A2-Map 47)

B. Study site SBI, 3/7/78, 30 days after removal of #3♂ and #1 and #5 had assumed male roles; territory size #1♂ = 10.9m^2, territory size #5♂ = 10.4m^2
(A2-Map 50).

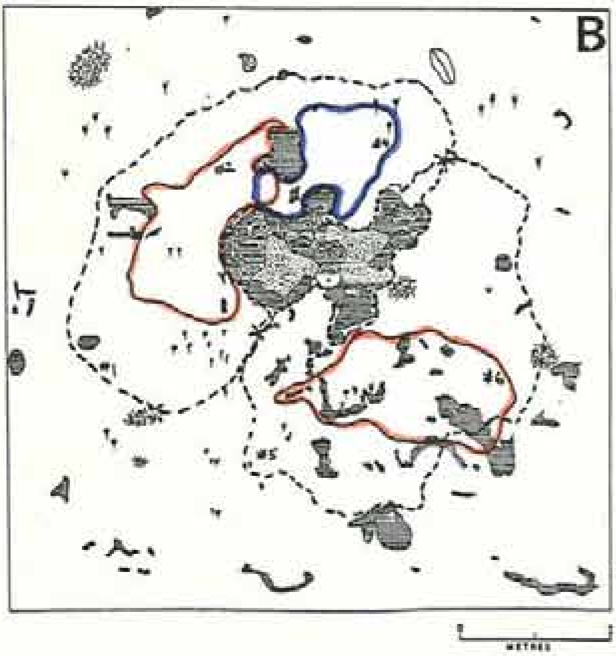
<u>Key</u>: As in Fig.47.

TERRITORY MAP

DOMINANCE HIERARCHY



#3♂ (88TL)>#1A(82TL)⋈#5A(81TL)>#6A (76TL)≥#2A(57TL)>#4SA(50TL)



Social unit A: #1♂ (83TL)>#2A(62TL) >#4A(56TL)

Social unit B: #5♂ (81TL)>#6A(78TL)

female changed sex following loss of the male from the social unit (Fig. 51).

The loss of the male from a social unit was quickly detected by the dominant female (or codominant females) of that social unit. Spatial re-organization within the social unit was noticeably underway five days after loss of the male. By this time, the dominant female had expanded her territory to incorporate at least some of the previous male's territory into her own territory; she still did not tolerate the presence of the other females of the social unit within her territory, thus territory expansions and boundary shifts by these individuals at this stage were, in most cases, limited and territory overlap values were low (<11%) (Figs. 52B & 53B, Tables 32 & 33). By day 15 (i.e. 15 days after disappearance of the male), the sex-reversing dominant female was clearly tolerating the presence of social unit members within its greatly expanded territory as evidenced by the high values of territory overlap (>40%) with other individuals; the future or "new" dominant female of the social unit had consequently begun to incorporate areas into her territory from which she had been previously excluded (Figs. 52C & 53C, Tables 32 & 33). By day 30, sexual transition was complete and the "new" male had extended its territory boundaries to encompass most, if not all, of the area originally held by the previous male; territory overlap between the "new" male and the other social unit members was in most cases 100% and the "new" dominant female had by this time incorporated much of the original dominant female's area into her own territory (Figs. 52D & 53D, Tables 32 & 33).

Sex reversal within the social unit did not always take place

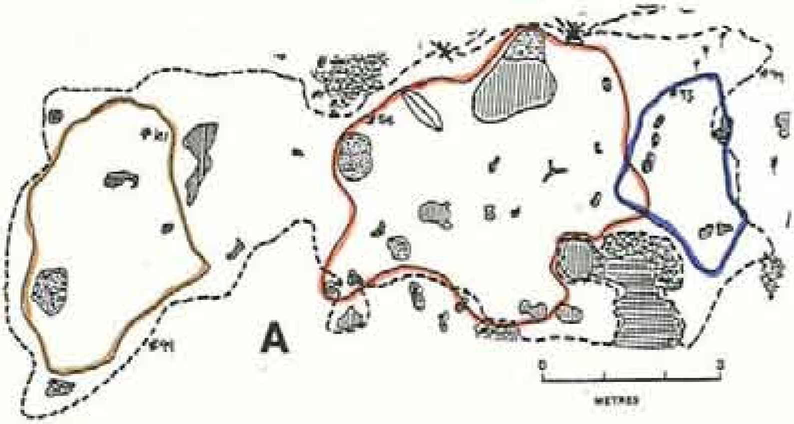
Figure 51

Social unit division following loss of the male from a social unit within study site G_{10}

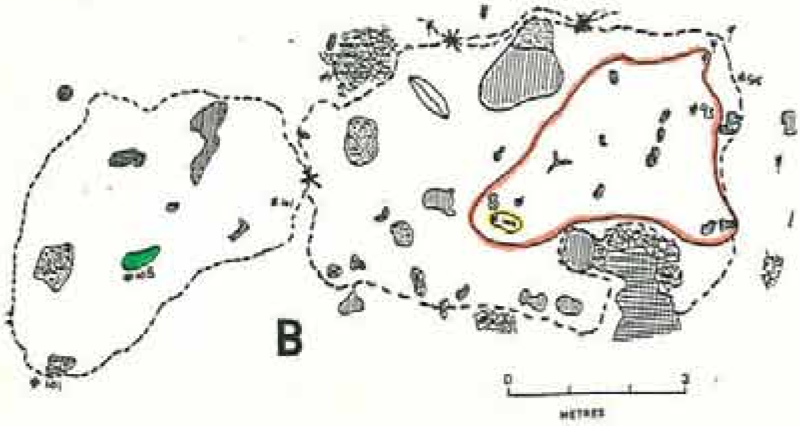
A. Social unit A, study site G_{10}, study period 10, before loss of #99♂ ; territory size #99♂ = 51.6m^2, territory size #58 (dominant female) = 18.4m^2, territory size #101, (large adult female) = 9.7m^2.
(A2-Map 21).

B. Social unit A_1 & A_2, study site G_{10}, study period 11, after loss of #99♂ and #58 and #101 had assumed male roles; territory size #58♂ = 30.1m^2, territory size #101♂ = 16.4m^2.
(A2-Map 22)

Key: As in Fig. 47.



DOM. HIER. : Social unit A : #99♂(110TL)>#58A(80TL)≯#101A (79TL)≯#93A(56TL)



DOM. HIER. : Social unit A_1 : #101♂(81TL)>#105J(24TL)
Social unit A_2 : #58♂(84TL)>#93A(69TL)>#100SA(30TL

Figure 52

Changes in territory boundaries and ownership following loss of the male from the social unit within study site LHI.

A. 1 day before removal of #1 ♂ from the social unit, 25/5/78, study stie LHI (A2-Map43)

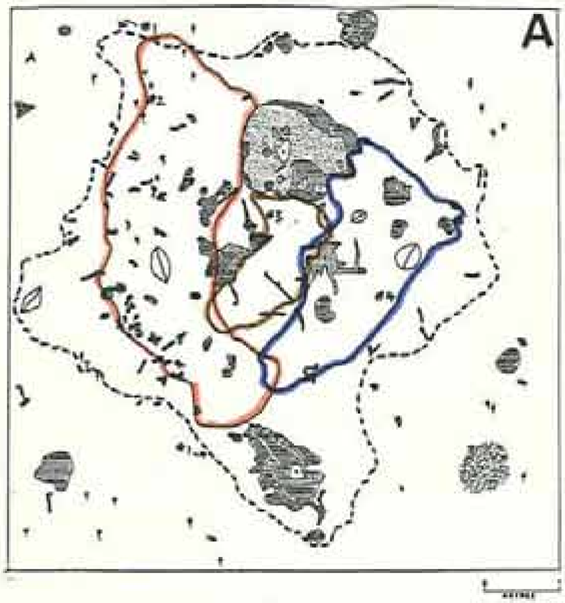
B. 5 days after removal of #1♂ , 31/5/78, study site LHI (A2-Map 44) - note territory expansion of #2.

C. 15 days after removal of #1♂ , 10/6/78, study site LHI (A2-Map 45) - note increased territory overlap between #2 and other indiviudals.

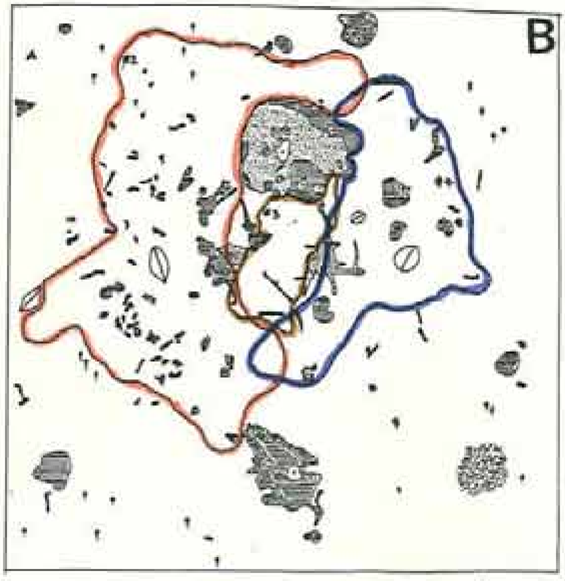
D. 30 days after removal of #1♂ , 25/6/78, study site LHI (A2-Map46) - note territory expansion of #2 to cover approximately the same area as that held by the original ♂ .

Key: As for Fig.47.

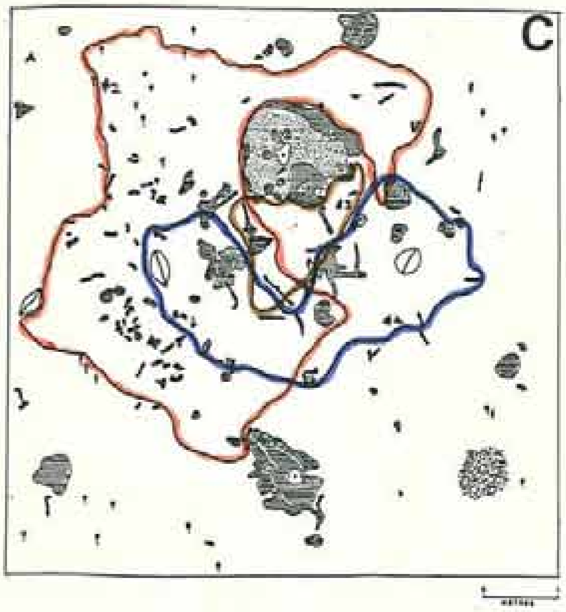
(see Table 32 for corresponding measurements of territory size and overlap).



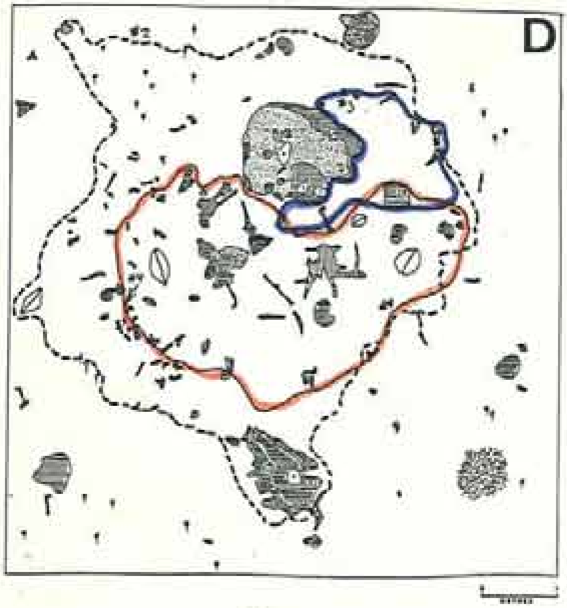
DOM. HIER. : #1♂ (115TL)>#2A(95TL)
>#4A(75TL)>#3A(65TL)



DOM. HIER. : #2♂/♀A(95TL)>#4A(75TL)
>#3A(65TL)



DOM. HIER. : #2♂/♀A(95TL)>#4A(76TL)
>#3A(67TL)



DOM. HIER. : #2♂(95TL)>#4A(77TL)>
#3A(69TL)

Figure 53

Changes in territorial boundaries and ownership following loss of the male from the social unit within study site BMI.

A. 1 day before removal of #6♂ from the social unit, 28/5/78, study site BMI, (A2-Map 51).

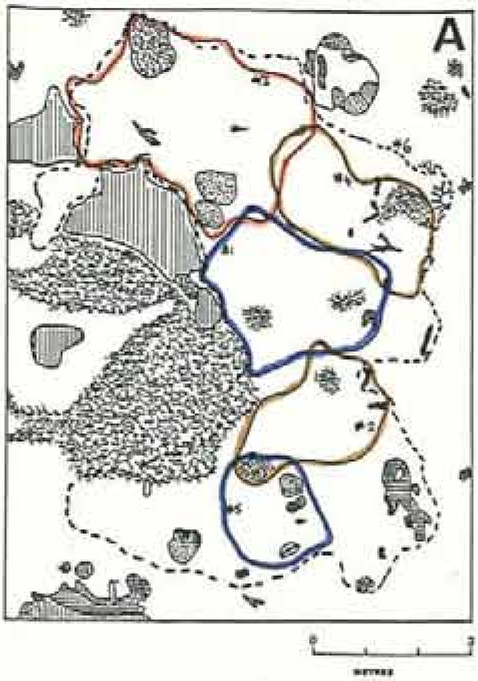
B. 5 days after removal of #6♂ , 3/6/78, study site BMI (A2-Map 52) - note territory expansion of #3.

C. 15 days after removal of #6♂ , 13/6/78, study site BMI (A2-Map 53) - note increased territory overlap between #3 and other individuals.

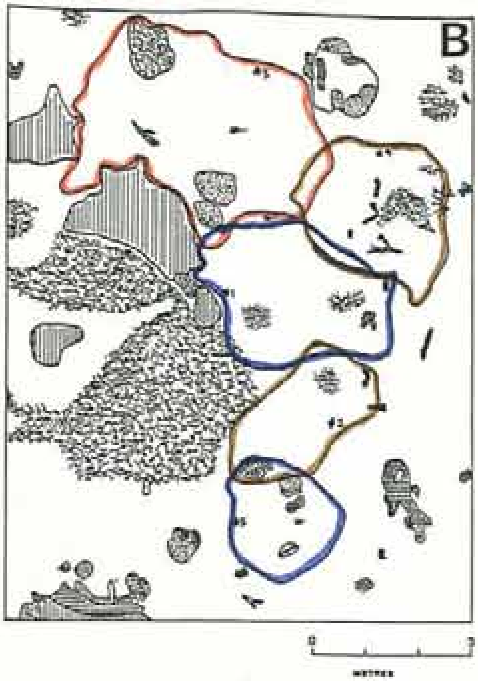
D. 30 days after removal of #6♂ , 28/6/78, study site BMI, (A2-Map 54) - note territory expansion of #3 to cover approximately the same area as that held by the original ♂ .

Key: As for Fig. 47

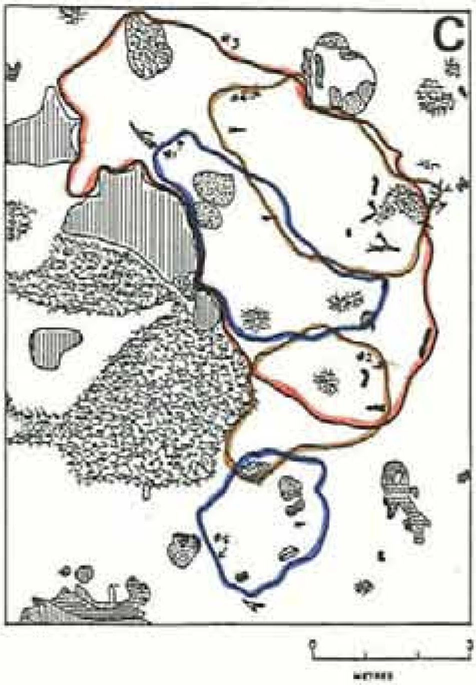
(see Table 33 for corresponding measurements of territory size and overlap).



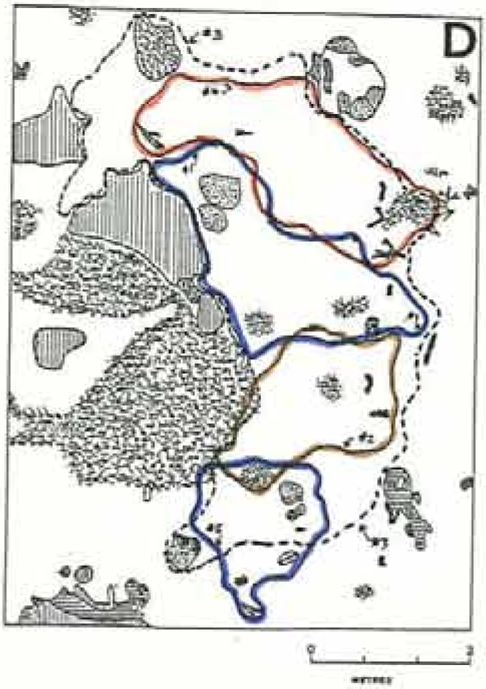
DOM. HIER. : #6♂ (96TL)>#3A(80 TL)>#4A(75TL)>#1A(71TL)>#2A(66TL) >#5A(60TL)



DOM. HIER. : #3♂/♀A(80TL)>#4A(75TL) >#1A(71TL)>#2A(66TL)>#5A(60TL)



DOM. HIER. : #3♂/♀A(80TL)>#4A(76TL) >#1A(72TL)>#2A(62TL)>#5A(61TL)



DOM. HIER. : #3♂(81TL)>#4A(77TL) >#1A(73TL)>#2A(69TL)>#5A(63TL)

Table 32. Changes in territory size and overlap upon loss of the male from the social unit within study site LHI (see Fig. 52 for corresponding territory maps).

Territory mapping time & social unit members[a]	Territory size (m^2)	Territory size relative to #1♂ territory[b] (%)	Territory overlap with #2[c] (m^2)
1 day before ♂ removal			
#1♂ (115TL)	25.9	100.0	6.8 (26.3)
#2A(95TL) (dominant ♀)	7.1	27.4	-
#4A(75TL)	3.9	15.1	<0.1 (1.3)
#3A(65TL)	1.6	6.2	<0.1 (5.2)
5 days after ♂ removal			
#2♂/♀A(95TL) (sex-reversing female)	11.1	42.9	-
#4A(75TL)	5.6	21.6	0.4 (7.1)
#3A(65TL)	1.5	5.8	<0.1 (5.3)
15 days after ♂ removal			
#2♂/♀A(95TL) (sex-reversing female)	14.8	57.1	-
#4A(76TL)	6.3	24.3	3.1 (49.2)
#3A(67TL)	1.6	6.2	0.7 (43.8)
30 days after ♂ removal			
#2♂ (95TL) ("new" ♂)	23.9	92.3	-
#4A(77TL) ("new" dominant ♀)	9.2	35.5	9.0 (97.8)
#3A(69TL)	2.2	8.5	2.1 (95.5)

[a] A = adult female; TL = estimated total length in mm.

[b] Territory size of the individual expressed as a percentage of the territory size of the original male, #1, 1 day before its removal.

[c] Territory overlap between the individual and #2 is given first in m^2 followed in parentheses expressed as a percentage of the total territory size of the individual.

Table 33. Changes in territory size and overlap upon loss of the male from the social unit within study site BMI (see Fig. 53 for corresponding territory maps)

Territory mapping time & social unit members[a]	Territory size (m^2)	Territory size relative to #6♂ territory[b] (%)	Territory overlap with #3[c] (m^2)
<u>1 day before ♂ removal</u>			
#6♂ (96TL)	51.6	100.0	11.8 (22.9)
#3A (80TL) (dominant ♀)	12.3	28.8	-
#4A (75TL)	5.6	10.9	0.6 (10.7)
#1A (71TL)	7.5	14.5	0.2 (2.7)
#2A (66TL)	4.9	9.5	-
#5A (60TL)	3.6	7.0	-
<u>5 days after ♂ removal</u>			
#3A♂ /♀A (80TL) (sex-reversing ♀)	15.4	29.8	-
#4A (75TL)	7.1	13.8	0.6 (8.5)
#1A (71TL)	8.4	16.3	0.2 (2.4)
#2A (66TL)	5.0	9.7	-
#5A (60TL)	4.2	8.1	-
<u>15 days after ♂ removal</u>			
#3♂ /♀A(80TL) (sex-reversing ♀)	33.4	64.7	-
#4A(76TL)	10.0	19.4	9.8 (98.0)
#1A (72TL)	8.6	16.7	8.5 (98.8)
#2A (67TL)	6.4	12.4	3.8 (59.4)
#5A(61TL)	5.1	9.9	-
<u>30 days after o removal</u>			
#3♂ (81TL) ("new" ♂)	40.4	78.3	-
#4A (77TL) ("new" dominant♀)	10.6	20.5	10.5 (99.1)
#1A (73TL)	10.2	19.8	10.2(100.0)
#2A (69TL)	7.0	13.6	6.9 (98.6)
#5A (63TL)	5.5	10.7	3.9 (70.9)

[a] A = adult female; TL = estimated total length in mm

[b] Territory size of the individual expressed as a percentage of the territory size of the original male, #6, 1 day before its removal.

[c] Territory overlap between the individual and #3 is given first in m^2 followed in parentheses expressed as a percentage of the total territory size of the individual.

following death of the male. In seven of the 35 recorded cases of male disappearance, males from adjacent social units invaded and took over the vacated territory and social unit of the deceased male (Table 34). The invading male usually extended his territory boundaries to incorporate most, if not all, of the area originally held by his deceased neighbour (Fig. 54). The invasion and takeover of #5♂'s social unit by #27♂ within study site G_{15} was, however, only partially successful since the latter individual was unable to incorporate more than about 50% of the deceased male's territory and three of the six remaining social unit members into his own social unit (Fig.55). Adult female #4, the dominant female of #5♂'s former social unit was only 7 mm TL smaller than the invading male (see Table 34) and, at the time of census, possessed a colour pattern transitional between that of a male and female; #27♂ (the invader) was unable to completely dominate this transitional individual as is evidenced by #4♂/♀'s successful defence and control of a sizeable portion of #5♂'s former territory and social unit (Fig. 55).

Available data suggest that the dominant female will change sex and assume control of the social unit unless the invading male is able to completely dominate her. Dominance relationships, except between males, are size-dependent, hence one might expect there to be greater likelihood of successful invasion and takeover if the invading male is larger than the dominant female of the social unit invaded. Table 34 shows the sizes of invading males and dominant females of social units that were taken over. The invading male was always larger than the dominant female of the social unit invaded, and in five of the seven cases, considerably larger, i.e. 20 mm TL. Twenty-one cases were observed in which a male disappeared from a social unit adjacent to another social unit. The distribution of

Table 34. Size differences between invading males and the largest females of invaded social units.

	Invading male		Largest female of invaded social unit		Size difference	Study	
	Identity	TL[a] (mm)	Identity	TL[a] (mm)	(mm)	Site	Reference Appendix
1.	#75	90	#4	89	+ 1	G_8	A1-p.365; A2-Maps 3-4
2.	#99	109	#51	81	+28	G_{10}	A1-p.367; A2-Maps 18-19
3.	#27[b]	95	#4	88	+ 7	G_{15}	A1-p.370; A2-Maps 38-39
4.	#3	101	#16	67	+34	G_{15}	A1-p.370; A2-Maps 39-40
5.	#16	92	#5	71	+21	SCI	unmapped
6.	#21	97	#9	72	+25	MBI	"
7.	#13	105	#6	75	+30	BII	"

[a] Estimated total length.

[b] Invasion and takeover only partially successful (see text p.273).

Figure 54

Invasions and takeovers by neighbouring males following the loss of the male from the social unit.

A. #75♂ invades and takes over after #3♂ 's death, study site G_8, study periods 3-4. (A2-Maps 3-4).

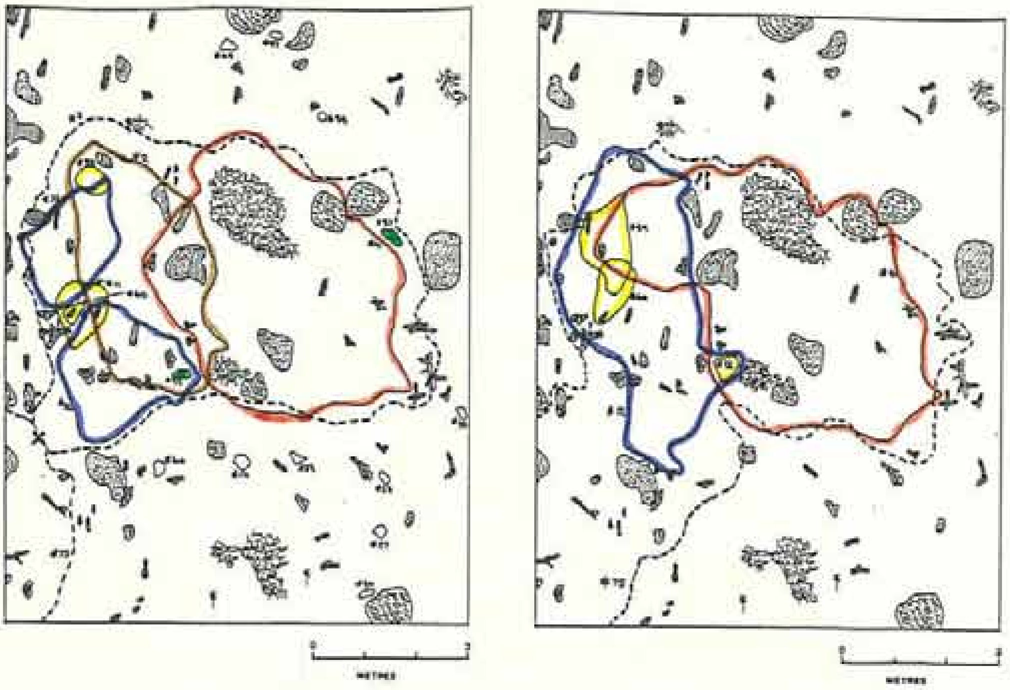
B. #99♂ invades and takes over after #4♂ 's death, study site G_{10}, study periods 7-8, (A2-Maps 18-19).

C. #3♂ invades and takes over after #4♂/♀ (transitional)'s death, study site G_{15}, study periods 7 - 8. (A2-Maps 39-40).

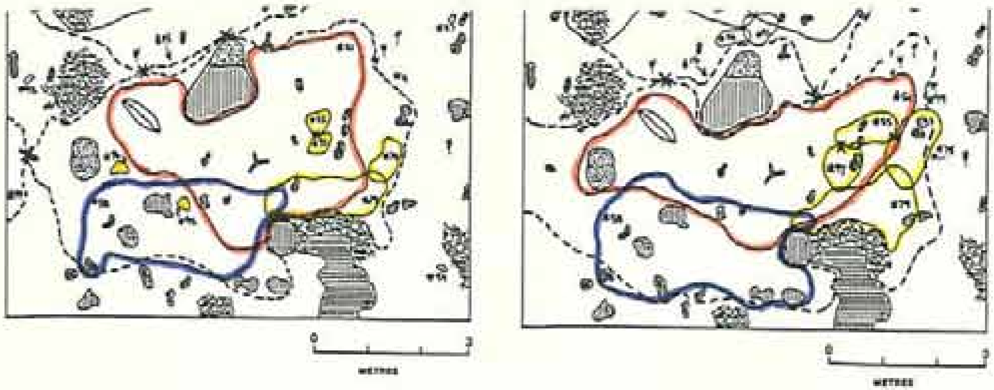
Key: As for Fig. 47

BEFORE INVASION AFTER INVASION

A



B



C

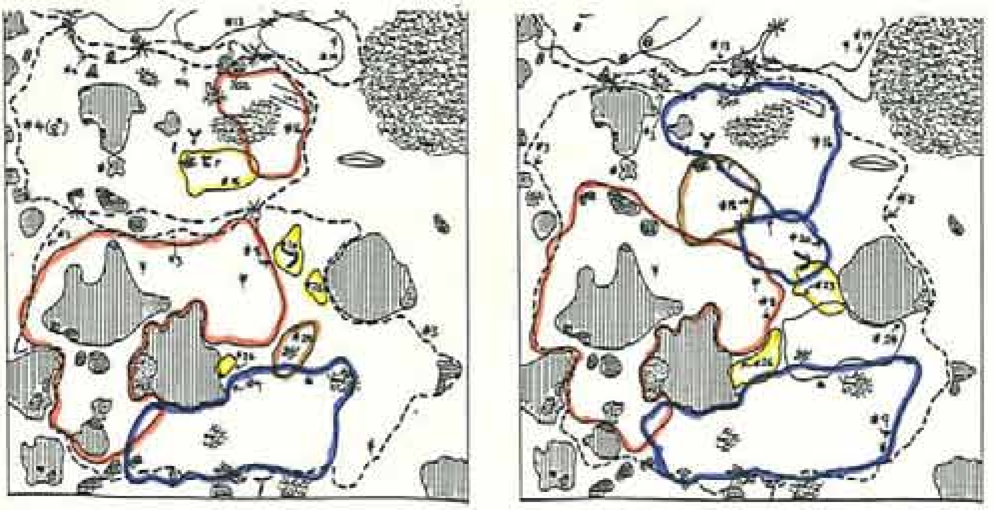


Figure 55

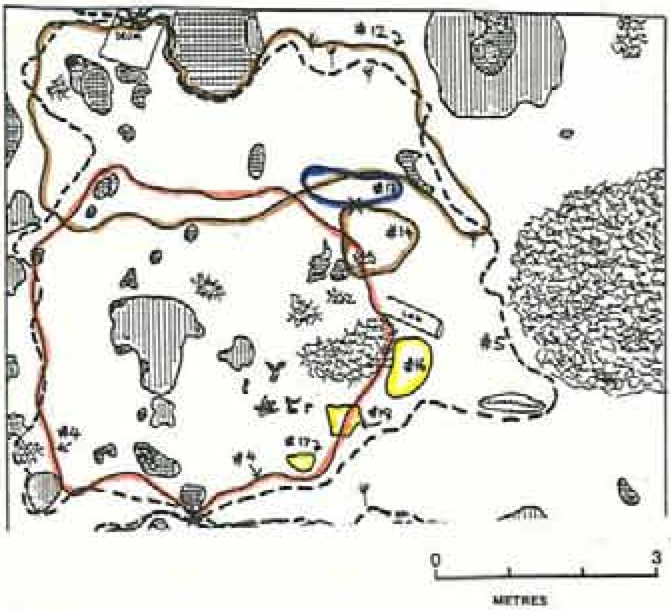
Invasion and partial takeover by a neighbouring male following the loss of the male from the social unit.

A. Social unit B, study site G_{15}, study period 6, before death of #5♂
(A2-Map 38).

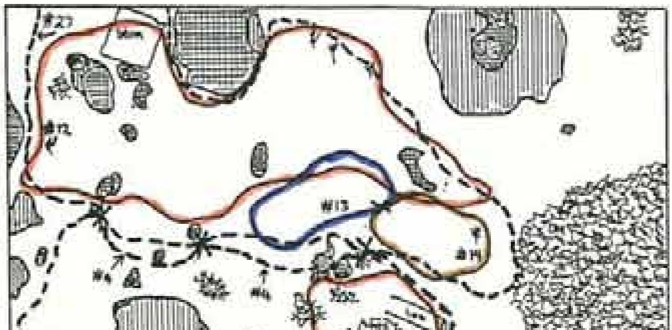
B. Social unit B, study site G_{15}, study period 7, after #5♂'s death - neighbouring #27♂ has invaded but only partially taken over the deceased male's social unit.
(A2-Map 39).

<u>Key</u>: As in Fig. 47

A



B



the resultant invasions and sex reversals, according to the relative size of the dominant female and neighbouring male is shown in Table 35. Each neighbouring male was assumed to have detected loss of the male from the adjacent social unit and, as such, was considered to be a potential invader of that social unit. A significantly greater proportion of invasions occurred in Case I situations (i.e. neighbouring male larger than dominant female of male-less social unit) than in Case II situations (i.e. neighbouring male smaller than dominant female of male-less social unit). (Fisher Exact Probability Test, $P < 0.01$ (Siegel, 1956)); this supports the idea that a male has greater likelihood of successfully invading an adjacent male-less social unit if he is larger than the dominant female of that social unit.

(ii) Adult females Each adult female occupied and defended a relatively fixed portion of the substratum until such time as she died or changed sex. The longest period of territorial occupancy by any one of the 34 adult females observed to be resident, at one time or another, over the four long term study sites was 16.8 months; this individual (#8, study site G_{10}, study periods 1-8, Appendix 2 - Maps 12-19) changed sex at the end of this time period. Excluding those adult females still present at the final census, the mean period of territorial occupancy was 7.0 months (SD = 4.8, n = 22) with the shortest period of occupancy by any one adult female being 2 days (#22, study site G_8, study period 3, Appendix 2 - Map 3). Table 36 shows the number of adult females that underwent particular fates i.e. changed sex, died, or were present at termination of the two year census period, along with the mean periods of territorial occupancy for each of these three categories. It can be seen that the number of adult females which died during the two year census period was

Table 35. Distribution of invasions and sex-reversals according to relative sizes of dominant females and potential male invaders

Size relationships	OUTCOME (following loss of male from social unit A)		Totals
	INVASION (neighbouring ♂ invades social unit A)	NO INVASION (dom. ♀ of social unit A changes sex)	
Case I[a]	7	4	11
Case II[b]	0	10	10
Totals	7	14	21

[a] Total length of neighbouring ♂ > total length of dominant ♀ of social unit A.

[b] Total length of neighbouring ♂ < total length of dominate ♀ of social unit A.

Fisher Exact Probability Test, significant, $P < 0.01$ (one-tailed); Siegel (1956).

Table 36. Periods of territorial occupancy by adult female *P.cylindrica* observed over long term study sites

Fate of individual	No. of individuals	Period of territorial occupancy (months)[a]
Changed sex	7	12.0 ± 3.8
Died	15	4.7 ± 3.3
Present at final census[b]	12	6.7 ± 2.9
Total adult females	34	

[a] Mean ± SD

[b] Individuals still present at termination of two year census period.

approximately twice the number of those which changed sex. In addition is is apparent that an individual spent a considerable period of time (12 months or so) defending a territory within a social unit as an adult female prior to its changing sex (Table 36).

Adult female territories generally underwent slight expansions through time as individuals grew in size (Fig.56). Major extensions in the territory boundaries of the dominant adult female occur with her sex reversal following loss of the male from the social unit, as has been previously demonstrated (see Figs. 47-49, 52-53; Tables 32 & 33). Death or sex reversal of the dominant female results in a vacant area much of which (generally 30-80%) is incorporated into the territory of the individual next highest in the dominance hierarchy of the social unit (Figs. 57-59; Table 37). Table 37 shows that the territory sizes of these individuals (i.e. "new" dominant females) increased significantly (Paired t-test, one-tailed hypothesis; $t_s = 5.17$, df = 9, $p < 0.01$), as did territory overlap with the original dominant female's territory (before death/sex reversal) (Paired t-test, one-tailed hypothesis; $t_s = 4.59$ df = 9, $p < 0.01$), following the death or sex reversal of the original dominant female. Concomitant with these changes in territory boundaries the "new" dominant female usually vacates a portion of her old territory; in some individuals the portion vacated was as much as 40% of the area of the old territory (Table 37).

When death or movement up the dominance hierarchy of more dominant individuals resulted in vacant territories or portions of territories, adult females of lower status were quick to incorporate these areas into their own territories, e.g. adult female #58 following adult female #51's rise in status to dominant female, study site G_{10} (Fig.58); adult female #3 following #4's rise in status to dominant female, study site LHI (Fig.59). Low-status adult females, like high-status adult

Figure 56

Changes in the size of four adult female territories through time.

A. #4 (70-89TL), study site G_8, Sept.1976-May 1977

B. #8 (70-94TL), study site G_{10}, Sept.1976-Feb.1978

C. #5 (80-96TL), study site G_{10}, Sept.1976-Sept.1977

D. #12 (59-89TL), study site G_{15}, Feb.1977-May 1978.

Dates refer to the period during which the individual, as an adult female, was present within a particular study site; figures in parentheses indicate total length of the individual in mm at the beginning and end of this period; adult females #4 and #5 disappeared and were presumed dead, #8 and #12 changed sex.

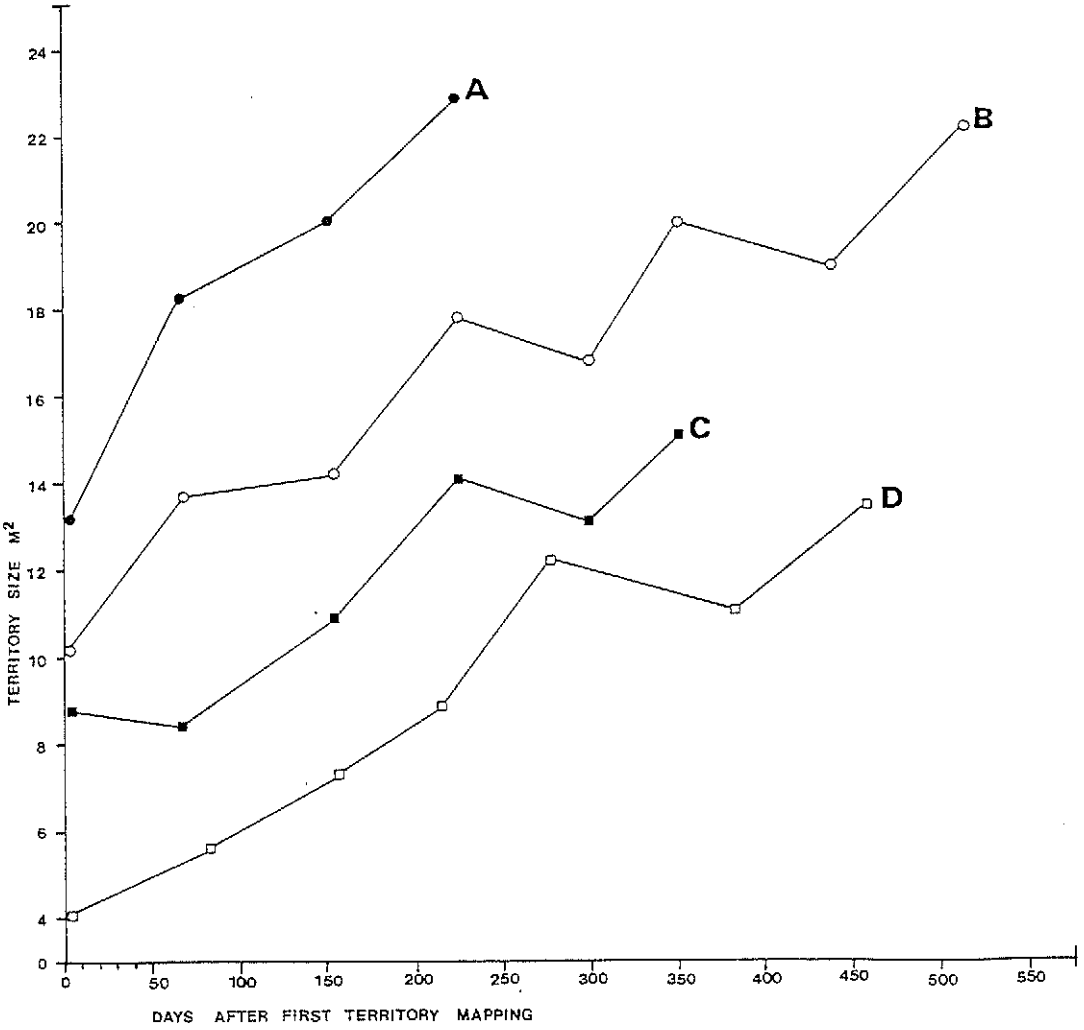

24
22
20
18
16
14
12
10
8
6
4
0
TERRITORY SIZE M²
0
50
100
150
200
250
300
350
400
450
500
550
DAYS AFTER FIRST TERRITORY MAPPING
A
B
C
D

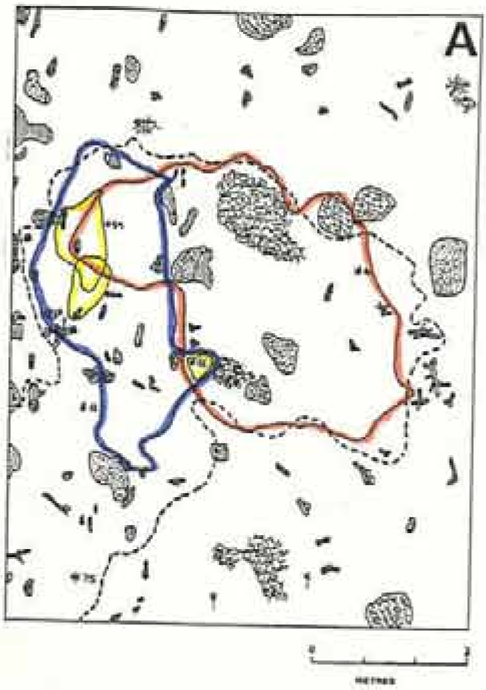
Figure 57

Changes in territory boundaries following death of the dominant female of the social unit within study site G_8.

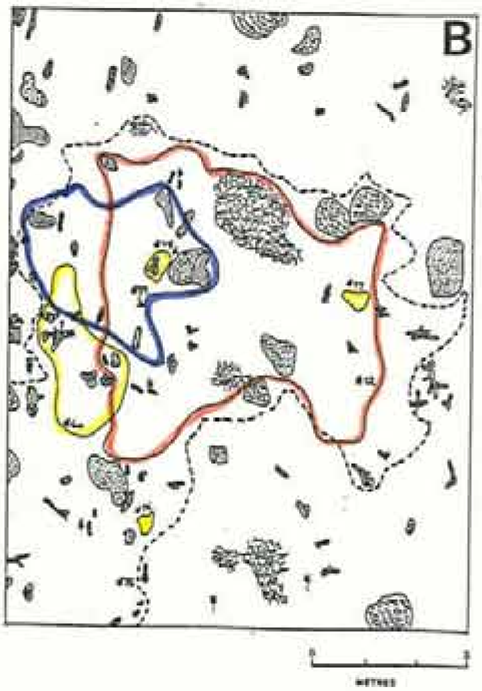
A. Study period 4, before loss of dominant female #4 from the social unit.
(A2-Map 4).

B. Study period 5, after loss of dominant female #4; note change in territory boundaries of adult female #12, i.e. the "new" dominant female.
(A2-Map 5).

Key: As for Fig. 47



DOM. HIER. : #75♂(90TL)>#4A(89TL)
>#12A(75TL)≯#21A(72TL)≯#59SA(55TL)
>#60SA(50TL)≯#55SA(35TL)



DOM. HIER. : #75♂(90TL)>#12A(80TL)
≯#21A(76TL)≯#59A(60TL)>#60SA(54TL)
≯#78SA(37TL)/#77SA(35TL)≯#76SA(30TL)

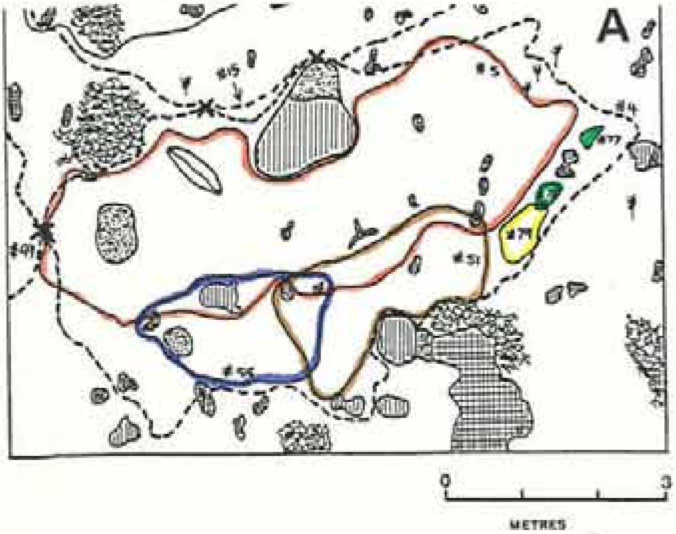
Figure 58

Changes in territory boundaries following death of the dominant female of a social unit within study site G_{10}.

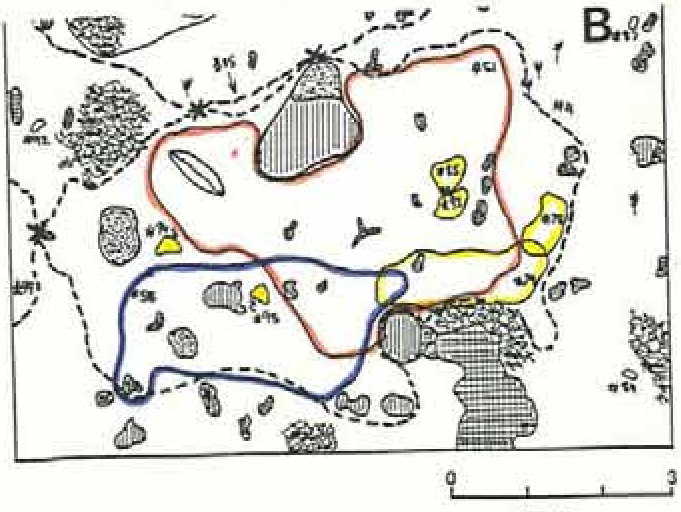
A. Study period 6, before loss of dominant female #5 from the social unit. (A2-Map 17).

B. Study period 7, after loss of dominant female #5; note changes in territory boundaries of adult female #51 (the "new" dominant female) and adult female #58. (A2-Map 18).

Key: As in Fig. 47



DOM. HIER. :#4♂(101TL)>#5A(96TL)>#51A(68TL)
>#58A(64TL)≯#79SA(36TL)>#78J(25TL)≯#77J(21TL)



DOM. HIER. : #4♂(102TL)>#51A(74TL)>#58A(69TL)
>#79SA(45TL)>#78SA(37TL)/#85SA(36TL)≸#93SA(36TL)
≯ #94SA(32TL)≯#95SA(29TL)

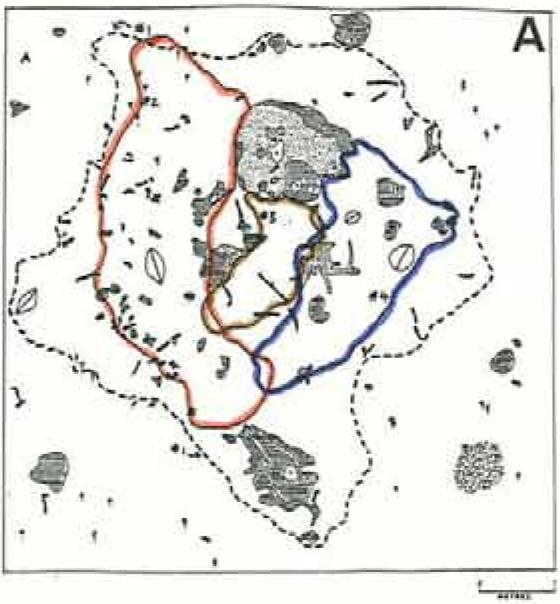
Figure 59

Changes in territory boundaries following sex reversal of the dominant female of the social unit within study site LHI.

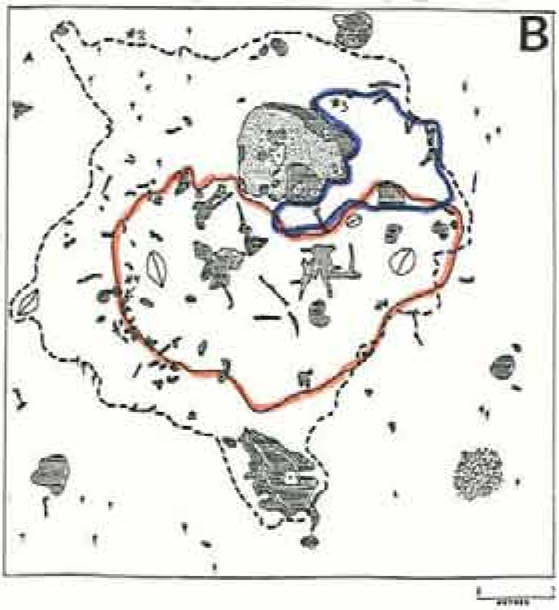
A. 25/5/78, before sex reversal of dominant female #2.
(A2-Map 43).

B. 25/6/78, after sex reversal of dominant female #2; note changes in territory boundaries of adult female #4 (the "new" dominant female) and adult female #3
(A2-Map 46).

Key: As in Fig. 47



DOM. HIER. : #1♂ (115TL)>#2A(95TL)>
#4A(75TL)>#3A(65TL)



DOM. HIER. : #2♂ (95TL)>#4A(77TL)>
#3A(69TL)

Table 37. Measurements of the territories of "new" dominant females both before and after death/sex reversal of the original dominant female.

Study site	Identity[a]	Territory size (m^2)[b]		Territory area vacated[c] upon boundary shift (m^2)	Percent overlap with original[d] dominant female		Fate of original dominant female	Appendix Reference
		Before event	After event		Before Event	After event		
G_{8}	#12	12.3	24.6	5.2(42.3)	16.7	77.7	Died	A2-Maps 4-5
G_{10}	#51	3.9	12.7	0.6(15.4)	8.1	74.8	Died	A2-Maps 17-18
G_{14}	#22	5.3	13.8	0.5(9.4)	1.3	47.2	Died	A2-Maps 24-25
G_{15}	#7	3.2	5.9	0.3(9.4)	2.7	20.1	Died	A2-Maps 35-36
G_{10}	#75	4.8	13.0	1.1(22.9)	8.1	43.0	Changed sex	A2-Maps 19-20
G_{14}	#24	9.3	16.3	0.4(4.3)	5.3	34.8	Changed sex	A2-Maps 30-31
LHI	#4	3.9	9.2	0.5(12.8)	0.7	47.9	Changed sex	A2-Maps 43 & 46
SBI	#6	2.0	3.0	0.5(25.0)	4.7	39.5	Changed sex	A2-Maps 47 & 50
SBI	#2	1.5	2.6	0.1(6.7)	2.9	35.3	Changed sex	A2-Maps 47 & 50
BMI	#4	5.6	10.6	1.5(28.8)	4.9	43.9	Changed sex	A2-Maps 51 & 54

[a] The individual next highest to the dominant female in the dominance hierarchy of the social unit i.e. the "new" dominant female following death/sex reversal of the original dominant female.

[b] Territory size of the individual the census before, and the census after, death/sex reversal of the original dominant female.

[c] Figure in parenthesis is area vacated expressed as percentage of territory size of individual before death/sex reversal of original dominant female.

[d] Area of overlap between the territories of the 'new" dominant female and the original dominant female before and after death/sex reversal of the latter; expressed as a percentage of the original dominant female's territory size.

females, did not usually abandon their territories for the vacated territories orginally held by more dominant individuals, but simply incorporated these areas by extending their territory boundaries.

(iii) Juvenile and subadult females There was considerable turnover of juveniles and subadults within study sites - individuals often disappeared between successive study periods after being present at a study site for only one study period. Of the 148 *Parapercis cylindrica* first sighted as juvenile or subadult females during the two year census over study sites G_8, G_{10}, G_{14} and G_{15}, only 28 (18.9%) "survived" (i.e. did not disappear from the study site) to adulthood. All evidence from observations and records suggests that emigration of juveniles from study sites was minimal and that most of these disappearances were the result of individual mortalities.

The numbers of young individuals (juveniles and subadults pooled) which (1) occupied areas within male territories compared with those which (2) occupied areas outside male territories are given in Table 38 along with the number of individuals of each category observed to survive to adulthood. Only 1.7% of those individuals which occupied areas outside male territories survived to adulthood compared with 30.0% for those individuals located within male territories (Table 38). Statistical treatment of the data shows there to be a highly significant association between survival (to adulthood) and the location of an individual i.e. within or outside a male territory (G-test of independence, $G_{adj.} = 11.53$, $p < 0.001$; Sokal and Rohlf, 1969).

Many juveniles which settled within male territories occupied areas which were also inside the territory boundaries of a subadult or adult female. These juveniles were vigorously attacked if they were observed by the subadult or adult female territory holder. When chased, the juvenile quickly retreated to a small crevice or hole

Table 38. Contingency table showing mortality/survival data for young individuals located within and outside male territories.[a]

	Died before adulthood	Survived to adulthood	Total
Within ♂ territories	63	27	90
Outside ♂ territories	57	1	58
Total	120	28	148

G-test of indpendence, $G_{adj} = 11.53$, $p<0.001$

[a] Juveniles and subadults pooled.

within its territory which was inaccessible to the much larger aggressor. The aggressor generally moved off shortly after the juvenile disappeared from sight. Juveniles were thus able to persist within subadult and adult female territories by virtue of their small size and use of the topographic features of the environment. Small subadult females utilized the topography in the same way to remain within the territories of adult females. As the juvenile or small subadult grew in size, its ability to utilize the topography in this way diminished. Increased exposure to the agonism of the larger and more dominant prior resident eventually forced the individual to abandon most, if not all, of its territory within that of the prior resident's; the individual generally took up a new territory at the edge of the prior resident's territory (Fig. 60).

Juvenile and subadult females, like adult females, gradually enlarged their territories through time i.e. as the individuals grew in size. The loss of a more, or equally, dominant individual from the social unit generated vacant space which resulted in further territory enlargement (Fig. 61). Vacant space generated through movement up the hierarchy of a more dominant individual also resulted in territory enlargement (Fig. 62). It can be seen that juvenile and subadult females, in the process of territory enlargement, did not usually abandon their original territory for the vacated territories or portions of territories originally held by more dominant individuals.

Figure 60

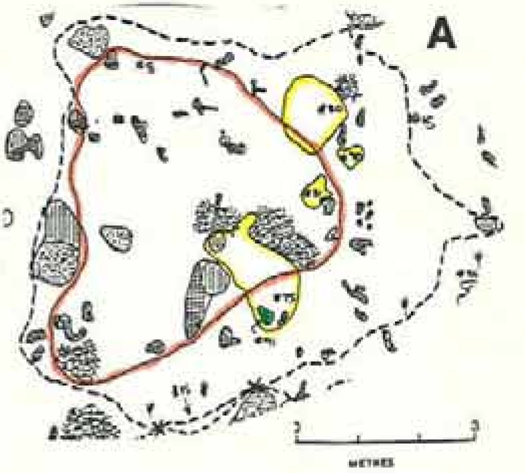
Changes in the location of territories of juveniles and small subadults due to agonistic behaviour of prior residents of higher status.

A. Social unit B, study site G_{10}, study period 7; note juvenile female #91 within subadult female #75's territory.
(A2-Map 18).

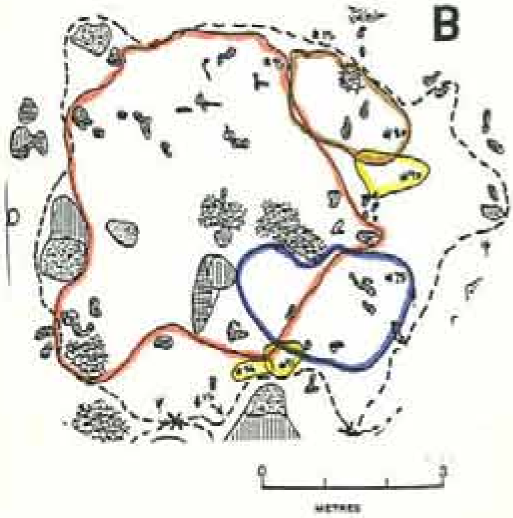
B. Social unit B, study site G_{10}, study period 8; note female #91 has grown into subadult size class and female #75 into adult size class and that #91 has vacated its original territory within #75's territory.
(A2-Map 19).

C. Social unit B, study site G_{15}, study period 4; note small subadult female #13 (33mm total length) within adult female #12's territory.
(A2-Map 36).

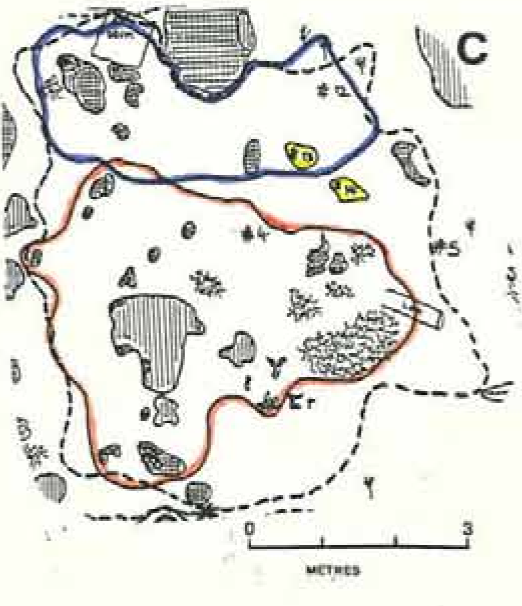
D. Social unit B, study site G_{15}, study period 5; note subadult female #13 (46 mm total length) has vacated its original territory within adult female #12's territory.
(A2-Map 37).



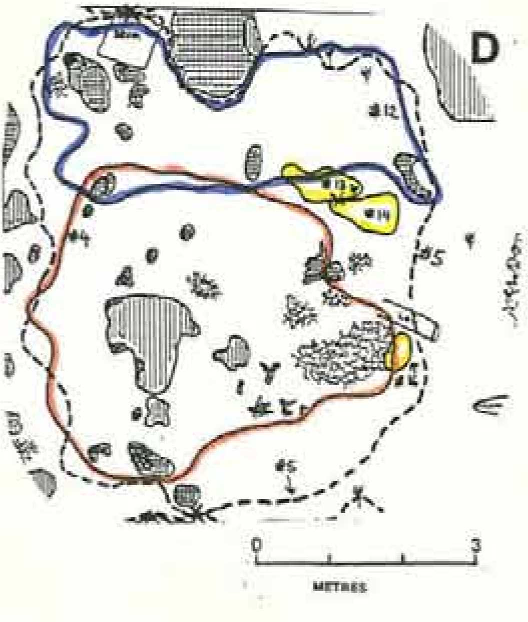
DOM. HIER. : #15♂(107TL)>#8A(92TL) >#75SA(55TL)≯#80SA(50TL)≯#81SA(38 TL)≯#90SA(30TL)≯#91J(24TL)



DOM. HIER. : #15♂(110TL)>#8A(94 TL)>#75A(64TL)≯#80A(61TL>#90SA (42TL)≯#91SA(38TL)>#96SA(29TL)



DOM. HIER. : #5♂(96TL)>#4A(80TL)> #12A(71TL)>#13SA(33TL)/#14SA(33TL)



DOM. HIER. : #5♂(96TL)>#4A(83TL) >#12A(76TL)>#13SA(46TL)≯#14SA(45 TL)≯#16SA(34TL)

Figure 61

Territory enlargement by juveniles and subadults following loss of more or equally dominant individuals from the social unit.

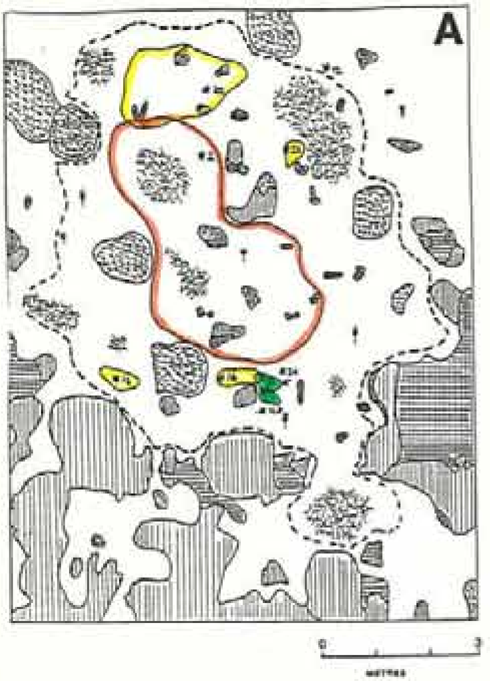
A. Social unit over study site G_{14}, study period 1 (3/12/76 - 5/12/76), before loss of subadult #16; note territory size (< $0.1m^2$) of juvenile #24 (A2 - Map 23).

B. Social unit over study Site G_{14}, study period 2 (16/2/77 - 19/2/77), after loss of subadult #16; note #24 has grown into subadult size class and has enlarged its territory (= $0.5m^2$) (A2 - Map 24).

C. Social unit B, study site G_{10}, study period 2 (29/11/76 - 2/12/76), before loss of subadult #7; note territory size (= $1.4m^2$) of subadult #9, an individual of equivalent status to #7 in dominance hierarchy (A2 - Map 13).

D. Social unit B, study site G_{10}, study period 3 (23/2/77 - 26/2/77), after loss of subadult #7, note #9 has grown into adult size class and has enlarged its territory (= $4.3m^2$) (A2 - Map 14).

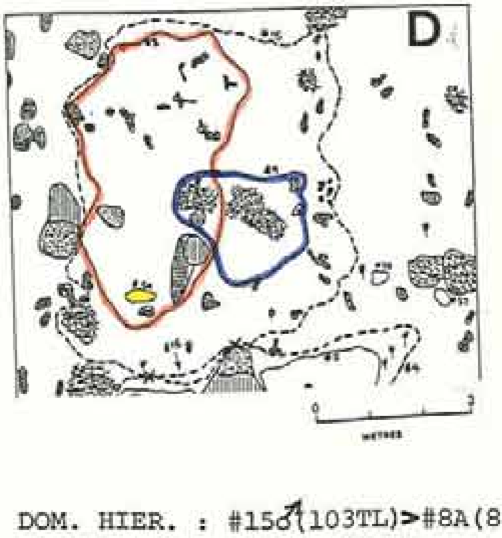
<u>Key</u>: As in Fig. 47



DOM. HIER. : #12♂(90TL)>#2A(69TL)>#22SA (50TL)≯#23SA(30TL)/#13SA(30TL)/#16SA (30TL)>#24J(25TL)>#11J(20TL)

DOM. HIER. : #12♂(95TL)>#2A(75TL) >#22A(60TL)≯#23SA(35TL)/#24SA(35 TL)

DOM. HIER. : #15♂(102TL)>#8A(77TL) >#9SA(45TL)≯#7SA(43TL)



DOM. HIER. : #15♂(103TL)>#8A(80 TL)>#9A(57TL)≯#54SA(30TL)

Figure 62

Territory enlargement by subadults following movement up the hierarchy of a more dominant individual.

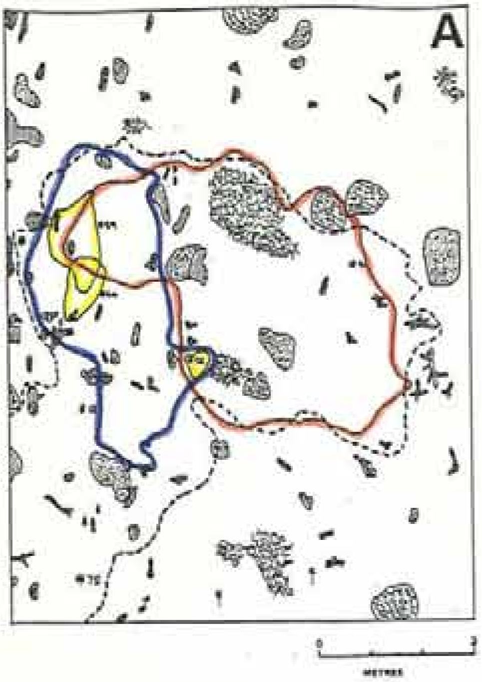
A. Social unit over study site G_8, study period 4 (30/4/77 - 1/5/77), prior to adult female #12's rise in status; note territory size (= $0.9m^2$) of subadult #60 (A2 - Map 4).

B. Social unit over study site G_8, study period 5 (12/7/77 - 14/7/77), after #12's rise in status to dominant female; note subadult #60 has enlarged its territory (= $3.3m^2$) (A2 - Map 5).

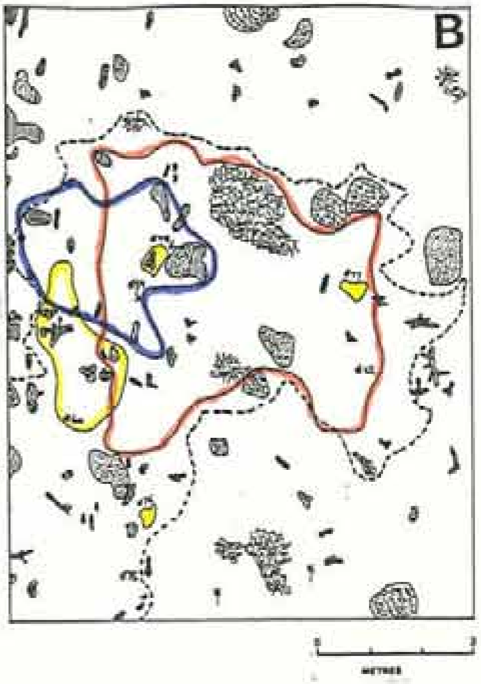
C. Social unit B, study site G_{15}, study period 6 (7/11/77 - 11/11/77), prior to adult female #4's rise in status; note territory size (= $0.5m^2$) of subadult #16 (A2 - Map 38).

D. Social unit B study site G_{15}, study period 7 (20/2/78 - 23/2/78); #4 has risen in status and begun to change sex (both ♂ and ♀ elements are present in colour pattern); note #16 has grown into adult size class and has enlarged its territory (= $2.7m^2$) (neighbouring #27 ♂ has invaded the social unit in a takeover bid consequently social unit B has split into two smaller social units, B_1 and B_2) (A2 - Map 39)

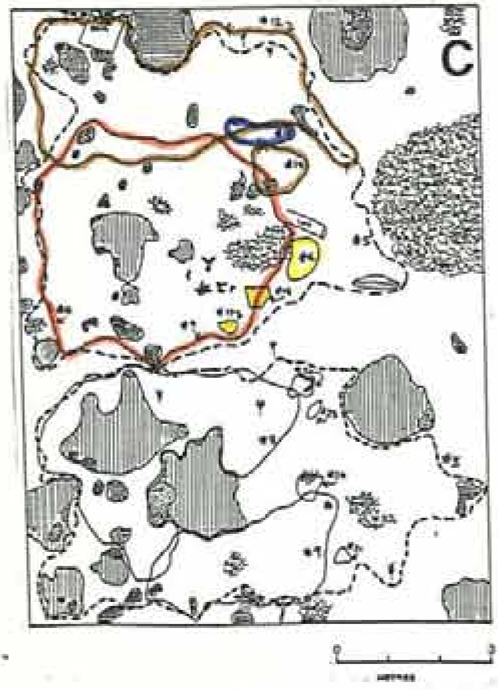
Key: As in Fig. 47



DOM. HIER. : #75♂(90TL)>#4A(89TL) >#12A(75TL)≯#21A(72TL)≯#59SA(55TL) >#60SA(50TL)≯#55SA(35TL)



DOM. HIER. : #75♂(90TL)>#12A(80TL) ≯#21A(76TL)≯#59A(60TL)>#60SA(54TL) ≯#78SA(37TL)/#77SA(35TL)≯#76SA(30 TL)



DOM. HIER. : #5♂(96TL)>#4A(85TL) >#12A(79TL)>#13A(56TL)⋈#14A(56TL) ≯ #16SA(47TL)≯#18SA(37TL)≯#17SA (30TL)

DOM. HIER. :B_1:#4♂/♀A(88TL)>#16A (60TL)>#18SA(52TL) ; B_2: #27♂(95TL) >#12A(84TL)≯#30A(80TL)≯#13A(66TL) ⋈#14A(66TL)

Subadults were sometimes "squeezed out" of part, or all of their original territories as a result of territory expansion by more dominant individuals (Fig. 63). As was discussed above, juveniles and subadults (as they grew in size) were also forced to abandon their original territories if these were within the territories of more dominant individuals.

5.3.5 Reproductive behaviour

5.3.5.1 *Diel reproductive periodicity* Field observations revealed daily periodicity in the reproductive activity of *Parapercis cylindrica* at Lizard Island. Reproductive activity occurred at no other time than around the evening crepuscular period. Courtship commenced about 40 minutes prior to sunset, became progressively more intense as daylight faded, and usually culminated in spawning shortly before complete darkness. The time of spawning, based on 465 observed spawnings, ranged from 18 minutes to 29 minutes (mean = 23 minutes) after sunset. During the breeding season (see 6.3.6) spawning occurred almost daily and showed no obvious relationship to moon phase or tidal rhythm. Daily courtship activity took place the year round.

5.3.5.2 *Mating system* *Parapercis cylindrica* has a polygynous mating system in that each male courts and often spawns with several females during the daily reproductive period. A male mates almost exclusively with females residing within his territory, i.e. the females of his social unit (98% of 465 spawnings, 20 males) and, by being permanently

Figure 63

Territory shift by a subadult as a result of territory expansion by individuals of higher status.

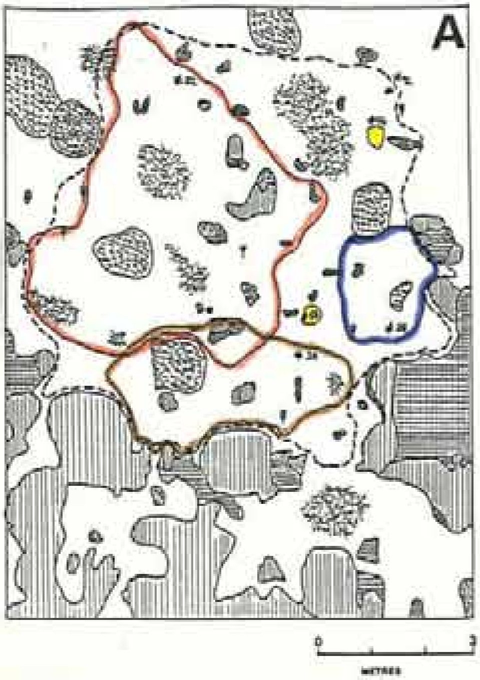
A. Social unit over study site G_{14}, study period 7 (12/2/78 - 14/2/78); note location and size of territories of adult females #24 and #28, and subadult #53 (A2 - Map 29).

B. Same social unit, study period 8 (1/5/78 - 2/5/78); note territory expansion by #24, #28, and #53 (A2 - Map 30).

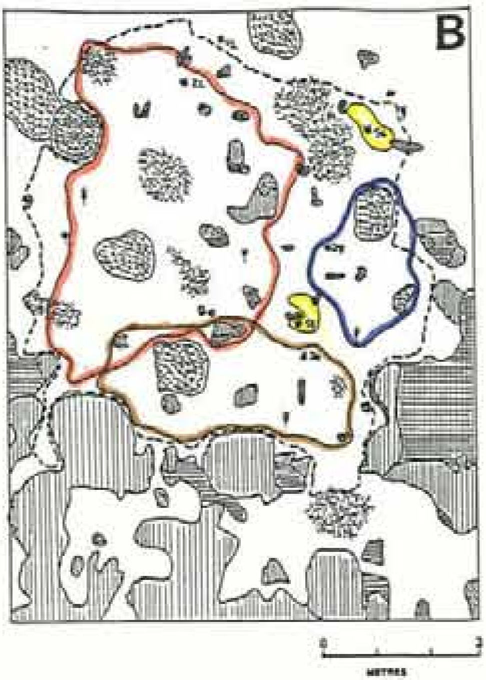
C. Same social unit, study period 9 (4/6/78 - 5/6/78); further territory expansion by #24 and #28 has apparently caused an upward shift in the location of #53's territory (#12♂ has disappeared, #22 has changed sex and taken control of the social unit) (A2 - Map 31).

D. Same social unit, study period 10 (8/9/78 - 9/9/78); note #53's territory is located even further away from its original site (A2 - Map 32)

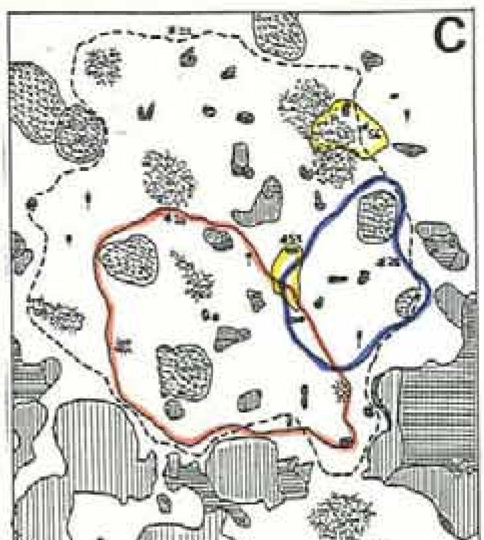
Key: As in Fig. 47



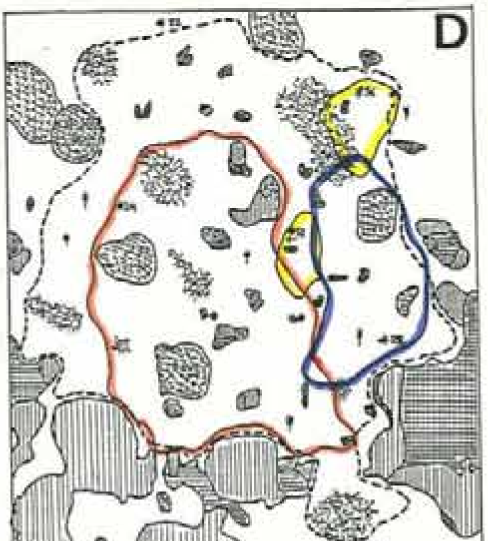
DOM. HIER. : #12♂(108TL)>#22A(80TL) >#24A(72TL)≯#28A(59TL)≯#56SA(33TL) /#53SA(32TL)



DOM. HIER. : #12♂(108TL≯#22A(85TL) >#24A(75TL)≯#28A(65TL)≯#56SA(42TL) /#53SA(40TL)



DOM. HIER. : #22♂(87TL)>#24A(76TL)>#28A(69TL)≯#56SA(50TL)/#53SA(49TL)



DOM. HIER. : #22♂(88TL)>#24A(78TL) >#28A(73TL)>#56SA(55TL)/#53SA(53TL) territorial, essentially prevents other males from mating with them. Consequently, *P. cylindrica* social units are considered to be harems.

Spawnings invariably occurred within the male's territory, each involving the male and a single female, i.e. pair spawning. No instances of interference to spawning pairs of individuals, by other males and females, were noted during the study.

5.3.5.3 *Motor patterns associated with courtship and spawning*

Reproductive behaviour in *P. cylindrica* was found to be characterized by five distinct motor patterns, each of which is described below.

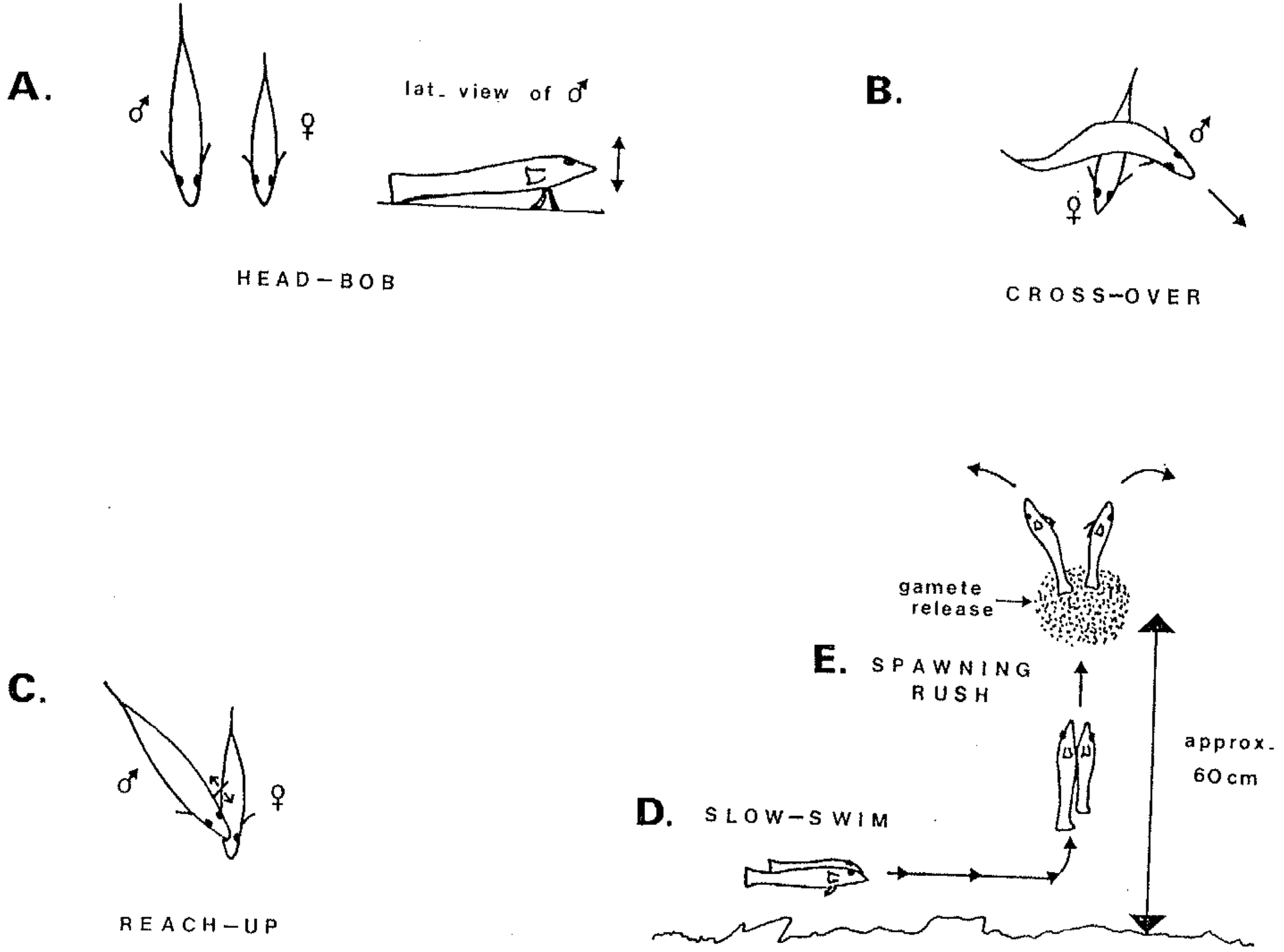
(i) Head-Bob: The anterior half of the body is slowly lowered and raised in the dorsal-ventral plane by a levering action of the ventral fins; the downward and upward movements together take approximately two seconds. This motor pattern was previously described in the section on agonistic behaviour (see 5.3.2), however the orientation and sex of the interactants in a reproductive context differs from that found in an agonistic context. In the former, the performer (male) adopts a position alongside, parallel to, and facing in the same direction as the receiver (female) (Fig. 64A); in the latter, the interactants are usually in a head-head formation, i.e. the performer (male) is in line with, and facing in the opposite direction to, the receiver (male) (see p.225).

(ii) Cross-Over: The performer (male) swims over the receiver at approximately a 90 degree angle, slightly touching the dorsal region of the receiver (female) with its abdomen in the process (Fig. 38B).

(iii) Reach-Up: The performer (male) takes up a position alongside the receiver (female) and, by a levering action of the ventral fins, raises the anterior half of its body to place its snout on the head of the receiver; at the same time, the performer fans the side of the receiver's

Figure 64

Motor patterns associated with courtship and spawning



A.
♂
♀
lat. view of ♂
HEAD-BOB
B.
♂
♀
CROSS-OVER
C.
♂
♀
REACH-UP
gamete release
E. SPAWNING RUSH
approx. 60 cm
D. SLOW-SWIM

body with one of its pectorals (Fig. 64C).

(iv) Slow-Swim: The interactants swim side-by-side along the bottom very slowly for a distance of about 30 centimetres (Fig. 64D); during this time the male's body is "rolled" slightly toward the female and he continually fans her abdominal region with one of his pectoral fins. Propulsion in both interactants is provided solely by adduction of the pectorals.

(v) Spawning-Rush: This consists of a rapid up-and-down dash by the male and female during which gamete release takes place. Male and female are abdomen to abdomen during the upward stage and usually so close together as to be almost touching. Gametes are released at the peak of this upward dash, approximately 60 centimetres off the bottom, and are visible as a white cloud that rapidly disperses (Fig. 64E). Immediately following gamete release male and female separate and dash to cover on the bottom. The complete up-and-down dash takes less than a second. Propulsion is provided predominantly by the caudal fin.

5.3.5.4 *The courtship and spawning sequence* A male visits each member of his harem with increased frequency during the late-afternoon (Table 39) and initiates courtship approximately 40 minutes prior to sunset. Courtship begins when the male, on one of these visits, performs two to five Head-Bobs in succession following his usual Spinous dorsal-Approach (see pp. 215, 223). The male then Crosses-Over the female and moves on to the territory of another of his females where he repeats the same sequence. The male continues this Head-Bob → Cross-Over sequence with the females of his harem, gradually moving faster and faster from one female to the next, as daylight fades. Approximately 20 minutes after sunset, the male begins to perform a Reach-Up after the Spinous

Table 39. Frequency of encounters between a single male *P. cylindrica* and members of his harem versus time of day[a]

Time of day	Harem member encountered	Frequency of encounter	Average time between each encounter (mins.)
Early morning (0600-0830 hrs) 120 mins[b]	♀ DF (89 mm TL)	14	8.6
	♀ DH (71 mm TL)	10	12.0
	♀ DG (70 mm TL)	12	10.0
	♀ DJ (45 mm TL)	7	17.1
	♀ DK (25 mm TL)	3	40.0
Mid-morning (0830-1100 hrs) 116 mins	♀ DF	12	9.7
	♀ DH	9	12.9
	♀ DG	11	10.5
	♀ DJ	10	11.6
	♀ DK	4	29.0
Mid-day (1100-1330 hrs) 125 mins	♀ DF	13	9.6
	♀ DH	12	10.4
	♀ DG	9	13.9
	♀ DJ	9	13.9
	♀ DK	3	41.6
Mid-afternoon (1330-1600 hrs) 120 mins	♀ DF	15	8.0
	♀ DH	11	10.9
	♀ DG	12	10.0
	♀ DJ	10	12.0
	♀ DK	4	30.0
Late-afternoon (1600-1830 hrs; includes daily reproductive period) 110 mins	♀ DF	29	3.7
	♀ DH	19	5.8
	♀ DG	16	6.9
	♀ DJ	15	7.3
	♀ DK	5	22.0

[a] ♂DI (105 mm TL) and his harem within study site DG-2; one encounter = Spinous dorsal-Approach only, by male; Spinous dorsal-Approach → Head-Bobbing, by male; or Spinous dorsal-Approach → Frontal Thrust(→ Butt → Bite) → Chase, by male.

[b] Sample observation time.

dorsal-Approach → Head Bob sequence, rather than a Cross-Over. The body contact involved in this motor pattern appears to disturb the female at first; her usual reaction is to move away from the male a few centimetres. The male usually persists in his advance and Head-Bobs several times before Reaching-Up once again. This Head-Bob → Reach-Up sequence is often repeated several times by the male since the female will frequently move away, again and again. Subsequent Head-Bob → Reach-Up sequences may or may not be preceded by the male Crossing-Over to the opposite side of the female. If the female still continues to move away, the male swims on to the territory of another of his females where he performs the same sequence of motor patterns. However, if the female holds her position and thus becomes receptive to the male, the two individuals go into a Slow-Swim followed by a Spawning-Rush. At the conclusion of the Spawning-Rush the male moves immediately to another female and, if she is receptive, repeats the same spawning sequence with her. Field observations also revealed that (1) a male generally spawns with each adult female of his harem each evening; (2) a female spawns only once per evening; (3) there is no fixed spawning order, e.g. the dominant female may or may not spawn first; and (3) spawnings within a harem generally take place in rapid succession (Table 40).

Table 40. Spawning orders and numbers for three *P. cylindrica* harems at Lizard Island

Date	Study site	Male identity	No. (and identity) of adult females in harem	No. (and spawning order) of adult females which spawned	Time difference between first and last spawning (mins:sec)
23/2/77	G_{10}	#4	3 (#5, #14, #25)	3 (#5, #25, #14)	4:03
24/2/77	G_{10}	#4	3 (#5, #14, #25)	3 (#5, #25, #14)	3:50
25/2/77	G_{10}	#4	3 (#5, #14, #25)	3 (#14, #5, #25)	3:31
2/9/77	G_8	#12	2 (#59, #60)	2 (#60, #59)	2:20
3/9/77	G_8	#12	2 (#59, #60)	2 (#60, #59)	3:10
4/9/77	G_8	#12	2 (#59, #60)	2 (#59, #60)	2:55
5/5/78	G_{15}	#3	6 (#8, #9, #16, #18, #20, #24)	5 (#8, #18, #9, #16, #20)	5:58
6/5/78	G_{15}	#3	6 (#8, #9, #16, #18, #20, #24)	6 (#8, #20, #18, #24, #16, #9)	7:13
7/5/78	G_{15}	#3	6 (#8, #9, #16, #18, #20, #24)	5 (#8, #18, #24, #20, #16)	7:23

5.4 Discussion

The results of the present study show the social organization of *Parapercis cylindrica* to be characterized by a combined territorial system and dominance order. The basic social unit is a harem consisting of a single male, two or three adult females, and a variable number of subadult and juvenile females. Within each harem, individuals are arranged into a linear, size-dependent, dominance hierarchy with the male always highest in status. Each female of the harem holds a relatively permanent territory which is defended against equivalent-sized or smaller females. The male maintains a permanent territory which encompasses all the territories of his females, and which he defends against other males. Nested territories, i.e. a territory maintained by an overlord male which is subdivided in turn by females (Wilson, 1975), have also been reported in the iguanid lizard *Anolis lineatopus* (Rand, 1967), the cichlid fish *Apistogramma trifasciatum* (Burchard, 1965), and the coral reef labrid fish *Labroides dimidiatus* (Robertson, 1972).

The male continually patrols his territory, concentrating his activities around certain localized areas within it. These areas of concentrated use ("activity sites") are usually located near the male's territory boundary or within the territories of his females and are interconnected by way of trails which the male frequently uses to travel from one activity site to another. This particular space-related behaviour indicates the presence of a good topographic memory in *Parapercis cylindrica*, as has been demonstrated for many other species of fishes (e.g. Aronson, 1951; Hasler, 1956; Rasa, 1969).

A male visits and aggressively interacts with each female of his harem at frequent, essentially regular intervals throughout the day. Hence, he is constantly advertising his presence to, and reinforcing his dominance over, the females of his harem. By making frequent visits to sites at his territory boundary the male also advertises his presence to neighbouring males. If the male dies, the dominant (largest) female of the harem changes sex and assumes control of the harem, provided she is large and aggressive enough to resist invasions of the harem by neighbouring males. Sexual transition is complete within a month after the death of the original male (see section 6.3.4); by this time, the "new" male has usually extended its territory boundary to encompass most, if not all, of the area originally held by the previous male. The other members of the harem, like the "old" dominant female, also advance one rank in the dominance hierarchy and undergo a certain amount of spatial re-organization. Vacant territories or portions of territories produced by high-status individuals moving up the dominance hierarchy are quickly incorporated into the territories of lower status individuals.

The most obvious functions of territorial defense in *Parapercis cylindrica* are the provision of food, shelter and requirements for reproduction. In males, most feeding activity and shelter use takes place at his "activity sites" together which make up only a small proportion of the total area of the territory. Theoretically then, males could probably maintain much smaller territories than they do and yet still obtain a sufficient amount of food and shelter. Taking this into account, it appears that maintenance of the male territory in *P. cylindrica* is concerned primarily with reproduction rather than with food or shelter.

From a male's point of view, the optimal strategy for reproductive success would be to mate with as many females as possible. One would expect this in turn to favour the development of larger territories and harems. This is supported by the fact that a male will readily invade the former harem and territory of a deceased neighbouring male and incorporate them into his own [assuming he detects the loss of the male and is of sufficient size to dominate the presumptive male (i.e. the dominant female) of the invaded harem - see p.273]. It is assumed this tendency toward mate accumulation and thus larger territory and harem size would not decrease until a point is reached where the energy cost of continued territorial defense against other males and maintenance of control over females exceeded the additional benefits gained (Emlen and Oring, 1977).

By defending his territory against other males, the male prevents other males from mating with the females residing within his territory; this, plus the fact that females rarely venture beyond the territorial limits of the male (and thus have little likelihood of mating with a strange male) would account for the high fidelity observed within harems of *P. cylindrica*. The male thus has continual, almost exclusive access to a large number of mates.

Foreign females caught intruding into another harem are notably repulsed by the resident females of that harem (even if the intruder is larger than the resident female it interacts with). Females such as these intruding into a harem theoretically threaten a resident female's hierarchical rank and may perhaps affect its ability ultimately to change sex (Robertson, 1974, 1981; Robertson and Hoffman, 1977). Consequently, female territoriality may be viewed as reinforcing dominance status within the harem.

Female territoriality is also probably functionally related to defense of food and shelter, particularly so in the case of juveniles and subadults. That the vacant territories or portions of territories produced by the death or movement up the dominance hierarchy of high-status individuals are quickly incorporated into the territories of low-status individuals suggests that the former might hold more preferred feeding and/or shelter sites than the latter.

Size, sex and prior residency are all factors which have been shown to affect, in one way or another, dominance relationships in fishes (see Braddock, 1949; Baerends and Baerends, 1950; Gibson, 1968; Phillips, 1971; Frey and Miller, 1972; Myrberg, 1972; Gorlick, 1976). In *Parapercis cylindrica*, size is the most important determinant of dominance within harems. The larger individual of a pair of interactants is always dominant over a smaller individual. Consequently, if the individuals of a harem are reasonably different in size to one another, as is usually the case, a linear rank order according to size results; this is maintained by way of spatially-dependent dominance relationships, i.e. one individual (in this case, the larger of the two interactants) is dominant over the other individual regardless of the locality of interaction. When two individuals of the same harem are of equivalent size (i.e. within 3 mm total length of each other), the dominance hierarchy becomes slightly more complicated since equivalent sized individuals hold the same overall rank and the dominance relationship between them is a spatially dependent one affected by prior residency, i.e. A is dominant over B in A's territory, but B is dominant over A in B's territory.

Separating the effect of sex from that of size, in the dominance relationships within harems of *Parapercis cylindrica* is difficult since the male is always the largest member of the harem. Some information is provided by the single observed case of a harem female changing sex whilst in the presence of its male (see pp. 258 & 261 ; Figure 46, p. 262). A considerable portion of the original male's territory was excised by the "new" male who was formerly the dominant female of the original male and consequently was the smaller of the two individuals. This suggests that the sex factor can override the size-dominance effect.

In *Parapercis cylindrica*, smaller males are able to successfully defend their territories against larger neighbouring males. Similarly, resident females of a harem are able to successfully repulse intruding females from their territories even if the resident is smaller than the intruder. Hence, the "prior residence effect" (Braddock, 1949) overrides size in determining the dominance relationships between individuals of different harems.

The dominance relationship between any pair of individuals in the hierarchy remains unchanged until such time as one of the individuals of the pair dies. As this is often a considerable period of time, dominance hierarchies are quite stable over the long term. When an individual dies, these individuals below it in status all advanced one position in rank whilst maintaining their respective dominance relationships; those individuals above it in status do not undergo a shift in rank or change in dominance relationships.

The present study also showed individuals to direct most of their aggression towards individuals closest in rank to themselves along with a consistent decrease in the amount of aggression towards those individuals further removed from a given rank (see Figs. 35 and 36). Myrberg (1972) has reported a similar pattern of aggression within dominance hierarchies of the damselfish *Eupomacentrus partitus*.

The hierarchical system in *P. cylindrica* can be designated as of the *nip-right* type (Masure and Allee, 1934; Schjelderup-Ebbe, 1935) since displays of overt aggression were performed only by the more dominant individual during an agonistic encounter.

Dominance hierarchies have been documented for only a few species of coral reef fishes to date, notably the pomacentrids *Dascyllus* *aruanus* (Sale, 1972; Fricke and Holzberg, 1974), *D. marginatus* (Fricke, 1980), *Amphiprion akallopisos, A. bicinctus* (Fricke and Fricke, 1977), *Eupomacentrus partitus* (Myrberg, 1972) and the labrid *Labroides dimidiatus* (Robertson, 1972). In common with *Parapercis cylindrica*, individuals of each of these species are strongly site attached and occur in relatively small, stable groups which show linear dominance hierarchies based upon relative difference in size of interacting individuals.

In *Parapercis cylindrica*, the individuals of a harem are able to distinguish other members of their harem from strange conspecifics. The experiments conducted during the present study suggest that colour pattern rather than size, location or behaviour of an individual is the cue upon which individual recognition in this species is based. Although widely assumed to occur in coral reef fishes, individual recognition of conspecifics has been demonstrated experimentally in only two other species, the anemonefish *Amphiprion bicinctus* (Fricke, 1973) and the damselfish *Eupomacentrus planifrons* (Thresher, 1979). In the former species, colour cues provide the information upon which individual recognition is based; in the latter, both location of the individual as well as its colour pattern appear to be important in the individual recognition of conspecfics. Individual recognition of conspecifics in *Parapercis cylindrica* would, amongst many other things, promote cohesiveness of the social group as well as stability in terms of maintenance of the dominance order.

The less frequently a male *P. cylindrica* patrols his territory, the greater the likelihood of territorial intrusion by other males and thus increased infidelity by the females of his harem. This, plus the fact that his presence with, and perhaps aggression towards, the mature females of his harem prevents them from changing sex and being lost from the harem, probably explains the high rate of movement of a male about his territory. This movement about the territory would require a considerable amount of energy on the part of the male. Since high-intensity aggression is energetically expensive, it is not surprising that males have reduced extended displays and fighting to only those times that either is absolutely necessary and show ritualized agonistic behaviour patterns, e.g. Spinous-dorsal Approach, Head-Bob. In addition, potential injury to interactants through intraspecific fighting would also favour the development of ritualized agonistic behaviour patterns (Eibl-Eibesfeldt, 1960; Lorenz, 1964), e.g. it would not be to a male's advantage to damage the females of his harem. Females show complementary appeasement behaviour [e.g. Spinous dorsal-Approach (♂) → Reverse Body-Sigmoid (♀)] which not only serves to reduce male aggression but also allows females of a harem to exist within the male's territory with little expenditure of energy.

Behaviour patterns similar to "Head-Bobbing" (see p. 215) in *Parapercis cylindrica* have been documented for several other groups of fishes which live in intimate contact with the substratum, e.g. blenniids (Wickler, 1963; Phillips, 1977), tripterygiids (Wirtz, 1978), chaenopsids (Robins et al., 1959) and gobiids (Kinzer, 1960). All are associated with threat behaviour and involve pronounced raising and lowering of the anterior portion of the body in the dorso-ventral plane, which may or may not, be repeated rhythmically. That this particular type of threat movement has not been observed in any non-benthic fish led Wirtz (1978) to hypothesize that raising the anterior part of the body when threatening represented a behavioural convergency of benthic fishes. In *P. cylindrica*, Head-Bobbing is used in threat behaviour between males, hence these observations agree with the above hypothesis. However, apparently unlike any other benthic fish, Head-

Bobbing is also used by the male in courtship albeit with the interactants in a different orientation. *Parapercis cylindrica*, in common with other benthic fishes, slightly raises the anterior portion of its body just prior to swimming. Consequently, Head-Bobbing as used in a threat context may have begun its evolutionary transformation as a simple intention movement to start swimming towards an opponent (Wickler, 1963; Wirtz, 1978). Head-Bobbing as used in courtship (i.e. with the interactants side-by-side) could have evolved the same way - support for this comes from the fact that side-by-side swimming (i.e. the Slow-Swim) is a prelude to spawning in this species.

The rapid, upward and downward dash associated with spawning (i.e. the Spawning-Rush) in *Parapercis cylindrica* is similar to that observed in various species of labrids (Randall and Randall, 1963; Warner et al., 1975; Robertson and Hoffman, 1977), scarids (Randall and Randall, 1963), acanthurids (Randall, 1961; Lobel, 1978) and mullids (Randall and Randall, 1963; Colin and Clavijo, 1978). Randall (1961) at first suggested this behaviour might have developed to confuse possible predators of the spawning participants but later decided that its primary function was to facilitate gamete release through expansion of the swimbladder at reduced hydrostatic pressure. Since *Parapercis cylindrica* does not possess a swimbladder, this hypothesis is unsatisfactory in explaining the functional significance of the spawning rush in this species.

The author tends to agree with Robertson and Hoffman (1977) and Johannes (1978) that the structure and rapidity of spawning rushes have evolved as the result of an attempt to reach the most favourable gamete release site without placing undue risk of predation on the spawning participants. In addition to being more favourable from the point of view of dispersal, releasing gametes higher up in the water column would result in less exposure to reef-based egg predators, e.g. corals, planktivorous fishes, etc. *Parapercis cylindrica* relies heavily on the substratum for shelter from its predators among which are the synodontid *Synodus englemani* (Sweatman, MS), the serranid *Plectropoma leopardus* (Choat, 1968), the lutjanid *Lutjanus carponotatus* (pers. obs.) and stingrays of the genus *Dasyatis* (Whitley, 1926). Consequently, the less time spent up in the water column, the less likelihood of predation on the spawning fishes. This would favour development of rapid ascent and descent.

At Enewetak Atoll, Hobson and Chess (1978) found that whilst pelagic fish eggs were an important part of the diets of diurnal planktivores, they were insignificant in the diets of nocturnal planktivores, even though there was a seven-fold increase in egg density at night. With the spawning activity of *Parapercis cylindrica* restricted to the evening crepuscular period, most diurnal planktivores are inactive when this species spawns. Hence, the timing of spawning in *P. cylindrica* would tend to minimize egg predation. Spawning is also limited to the evening crepuscular period in many other species of pelagic spawners (e.g. Lobel, 1978; Moyer and Nakazono, 1978a; Moyer, 1979; Bauer and Bauer, 1981).

In *Parapercis cylindrica* spawning, feeding and all day-to-day activities are carried out within the relatively small area comprising an individuals territory. Females are particularly sedentary in their habits unlike, for example, the females of various protogynous *Thalassoma* spp. which are considerably mobile and, to a certain degree, opportunistic wanderers (Robertson and Choat, 1974; Warner et al., 1975; Robertson and Hoffman, 1977). It is possible that the development of harems in *P. cylindrica* is the result of large males which have capitalized on the potential for mate molopolization created by the combination of strong site attachment, lack of mobility and clumped distributions of females. If this is the case, male territoriality would be based on the females themselves being a defended resource ("female resource polygyny" *sensu* Emlen and Oring, 1977) rather than primarily on food and/or shelter requirements. Limited support for such a view comes from two observations: (1) males do not defend their territories from the numerous potential interspecific competitors they encounter on the reef (see p. 227) many of which have similar, if not identical, food and/shelter requirements (Hiatt and Strasburg, 1960; Low, 1971; Sale, 1977); and (2) differential use of space within male territories suggests that males could probably maintain smaller territories than they do and yet still obtain a sufficient amount of food and shelter (see p. 301). However, only an experimental approach, such as removing all the females from a male territory and observing whether the male abandoned the territory, will determine how valid the concept of female resource polygyny is to harem formation in *Parapercis cylindrica*.

Chapter 6 REPRODUCTIVE BIOLOGY

6.1 Introduction

Little published information is available on the reproductive biology of mugiloidid fishes. Graham (1939, 1953) and Doak (1972) provided information on the spawning season of the temperate water mugiloidid *Parapercis colias*. Robertson (1973), in describing egg development and hatched larvae of this species, also commented on its spawning season. With respect to previous work on tropical and subtropical species, Marshall (1950) suggested, but gave limited evidence for, protogynous hermaphroditism in *Parapercis hexophtalma*; Nellen (1973) provided an illustration of a post-larval *Parapercis* species from the northern Persian Gulf; and Mito (1956, 1960, 1962), in describing egg development and hatched larvae of *Parapercis sexfasciata* and nine unidentified species of mugiloidids, also commented on the spawning season of *P. sexfasciata*.

This section of the study aimed to investigate and describe the basic reproductive biology of *Parapercis cylindrica*, and where practical other *Parapercis* species, with emphasis on the possible occurrence of sex reversal in these fishes.

6.2 Methods and Materials

6.2.1 Species studied Data were collected for the following species: *Parapercis cylindrica, P. hexophtalma, P. xanthozona, P. clathrata, P. nebulosa,* and an undescribed species, *P.* sp. 1 (see Part I).

6.2.2 Field procedures Specimens were collected by spear, ichthyocides, anaesthetics, nets or otter-trawl as outlined in Part I (see pp.7-8). Upon capture each individual was placed in a numbered polythene bag and locality, date, time, and depth recorded on an underwater slate. Gut cavities were syringe injected with Bouin's solution or concentrated formal dehyde within one hour of capture.

Experimental manipulations involving the removal of males from harems of *P. cylindrica* were conducted at seven study sites around Lizard Island (Fig. 65). Each harem was monitored daily for at least 20 days following male removal.

6.2.3 Laboratory procedures Fish were weighed and measured, after which the gonads were removed, weighed, and placed individually into numbered vials containing Bouin's solution. Later, the gonads were dehydrated with alcohol, embedded in paraffin, and transversely sectioned at 5-10 microns. Sections were taken in series from anterior, mid, and posterior portions of both lobes and were stained with haematoxylin and eosin. Measurements were made with an ocular micrometer.

Oogenesis was divided into four stages following the criteria used by Kraft and Peters (1963) in their study of the genus *Tilapia* and is based on the size, degree of maturity, and vitellogenic activity of the oocytes:

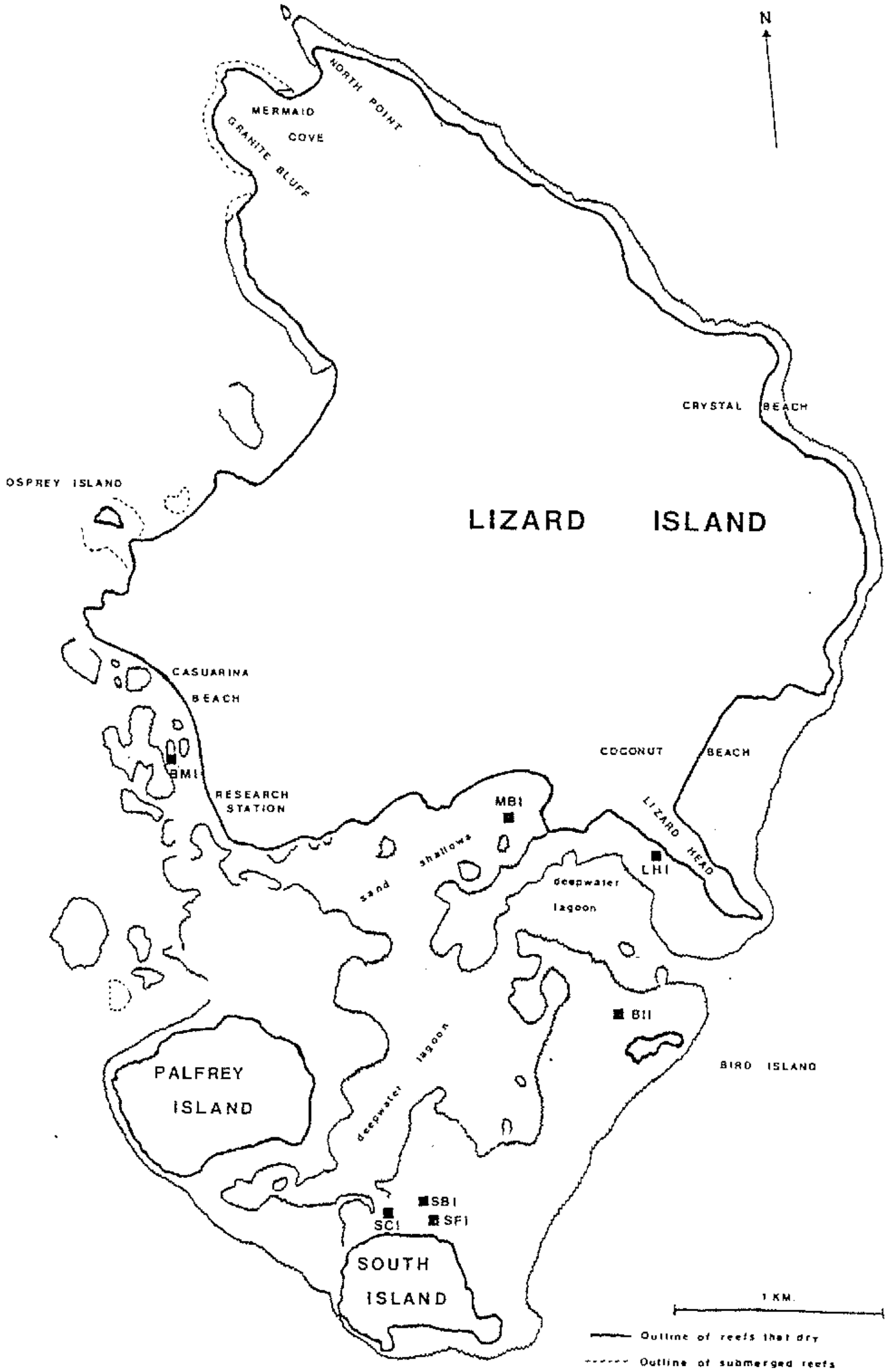
Stage 1. Very small (10-30 μ in diameter) oocytes with intensely basophilic cytoplasm surrounding a single nucleus containing a single nucleolus.

Stage 2. (25-100 μ) Previtellogenic oocytes with a strongly basophilic cytoplasm and a nucleus with many peripheral nucleoli.

Figure 65

Map of Lizard Island and its associated reefs and islands showing the location of study sites where experimental manipulations were conducted.

Key: ■ = study site


N
MERMAID COVE
NORTH POINT
GRANITE BLUFF
OSPREY ISLAND
LIZARD ISLAND
CRYSTAL BEACH
CASUARINA BEACH
BMI
RESEARCH STATION
COCONUT BEACH
LIZARD HEAD
MBI
LHI
sand shallows
deepwater lagoon
BII
BIRD ISLAND
PALFREY ISLAND
deepwater lagoon
SBI
SFI
SCI
SOUTH ISLAND
1 KM.
Outline of reefs that dry
Outline of submerged reefs

Stage 3. (90–210 μ) Vitellogenesis begins with the deposition of yolk vesicles in the less strongly basophilic cytoplasm. A thin outer membrane (zona radiata) can be seen in late Stage 3.

Stage 4. (200-500 μ) Well developed outer membrane; cytoplasm filled with yolk vesicles and globules.

Spermatogenesis was divided into three stages following those of Robertson (1974):

Spermatogonia. Nucleus present as a fine, lightly stained irregular network.

Spermatocytes. Nucleus large, dense, irregular and darkly stained.

Spermatids and sperm. Nucleus very small, rounded and intensely stained.

Gonads were classified as either male, female, or transitional. Transitional gonads were defined as those dominated by the early stages of spermatogenesis, but which also contained many oocytes and occasional atretic bodies (Moe, 1969; Warner, 1975a; Jones, 1980).

In dichromatic species, colour patterns were divided into three types: Initial phase (IP), Transitional phase, and Terminal Phase (TP). Transitional phase individuals possessed elements of both IP and TP colouration (see Part I for descriptions of IP and TP colour patterns).

Data on fecundity and on egg and larval development were obtained through enumeration and rearing of eggs collected from spawning individuals held in 100 litre aquaria at Lizard Island Research Station.

6.3 Results

6.3.1 Gonadal structure and sex reversal

The gonads of a total of 332 individuals, belonging to six species of *Parapercis*, were histologically examined during the study (Table 41).

Table 41. Number, size-range and species of individuals whose gonads were histologically examined

Species	No. individuals	Size-range (mm total length)
Parapercis cylindrica	158	40-123
Parapercis hexophtalma	65	73-239
Parapercis sp. 1	43	33-79
Parapercis xanthozona	37	62-155
Parapercis clathrata	15	83-162
Parapercis nebulosa	14	117-233
Total	332	

The ovaries in all six species were bilobate and situated in the postero-dorsal region of the pentoneal cavity. The two lobes joined at their posterior ends and then formed a common oviduct which carried the mature eggs to the exterior via the genital pore. Each ovary, bounded by a wall of muscle containing elastic fibres, is hollow, and its lumen is continuous with that of the oviduct. The internal surface is thrown into numerous folds or lamellae which project into the lumen (Plate 21A) and are lined with a germinal epithelium. Developing oocytes are embedded in a thin stroma of ovarian tissue. When the egg ripens, it breaks into the lumen and travels down the common oviduct. Oocytes interrupted in their development or not shed underwent resorption into

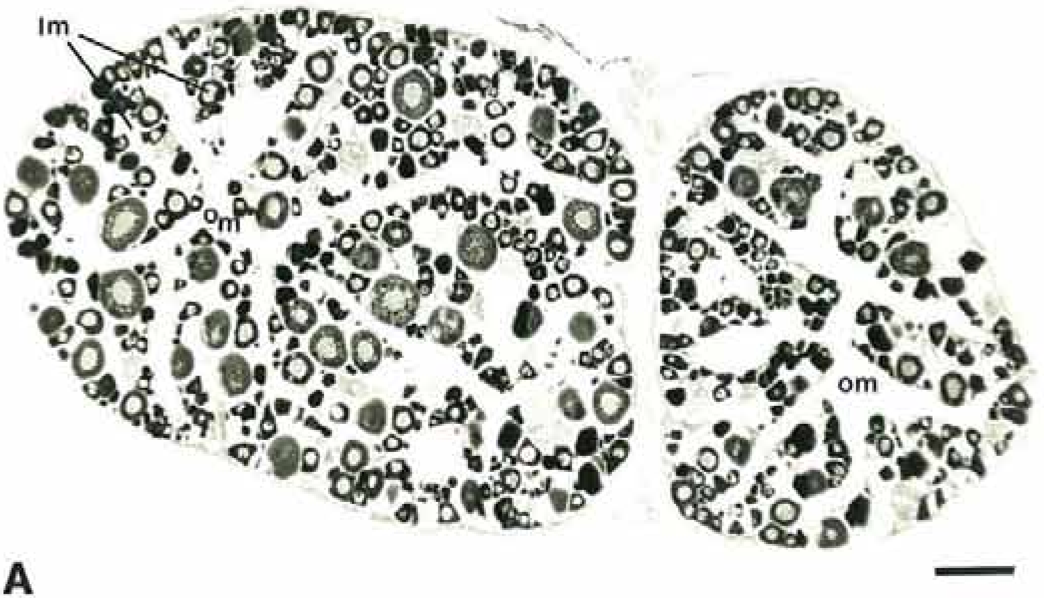
Plate 21

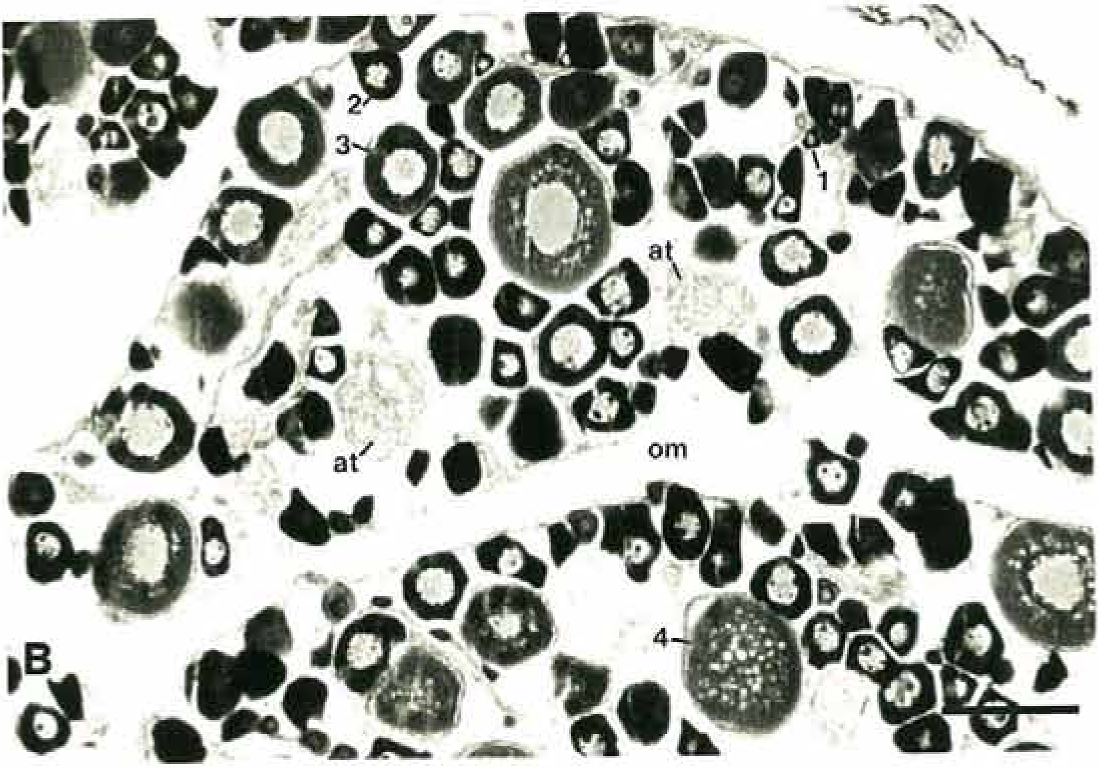
Medial transverse section of the ovaries from a 70 mm TL *Parapercis cylindrica* (specimen #729).

A. Low magnification showing ovarian lumen and lamellae. Scale 200 μ.

B. Higher magnification of ovary showing atretic bodies and developing oocytes. Scale 100 μ.

<u>Key</u>: om = lumen
lm = lamellae
at = atretic body
1 = stage 1 oocyte
2 = stage 2 oocyte
3 = stage 3 oocyte
4 = stage 4 oocyte


lm
om
om
A


2
3
1
at
at
om
4
B

atretic bodies (Plate 21B).

Fifty-two percent of *P. cylindrica* females exhibiting oogenesis had traces of testicular tissue in the form of isolated, enclosed seminiferous crypts in the ovarian lamellae (Plate 22). These seminiferous crypts were also found in females of *P. clathrata* (50% of females exhibiting oogenesis), *P. nebulosa* (20%), *P. hexophtalma* (17%) and *P.* sp. 1 (14.2%) (Plate 23).

Transitional gonads were found in *Parapercis cylindrica, P. hexophtalma, P. nebulosa,* and *P.* sp. 1 and were characterized by proliferating seminiferous crypts throughout the lamellae and numerous stage 1 and stage 2 oocytes (Plate 24). Gonads in this transitional stage were not functional testes since only the early stages of spermatogenesis were present. As transformation to the male phase occurs, the oocytes undergo resorption, the lamellae gradually coalesce, and the former ovarian lumen becomes less distinct (Plates 25 and 26). Sperm are not released into the lumen but collect in a series of sinuses on the periphery of the gonad which in turn feed ducts in the wall of the now redundant oviduct. In time, the lumen disappears completely so that the only clues to the gonad's ovarian origin are in the presence of peripheral sperm sinuses, and to a limited extent, atretic bodies (Plates 27-29) (atretic bodies may also be formed by the degeneration of unshed sperm). Males of all six species of *Parapercis* possessed gonads of this type. No male gonads of the type described by Reinboth (1962, 1968, 1970) as "primary" were found during the study.

6.3.2 The relationship between size and sex

6.3.2.1 *Parapercis cylindrica* The relative frequencies of each sexual type in successive 5 mm total length (TL) groupings for 158 individuals

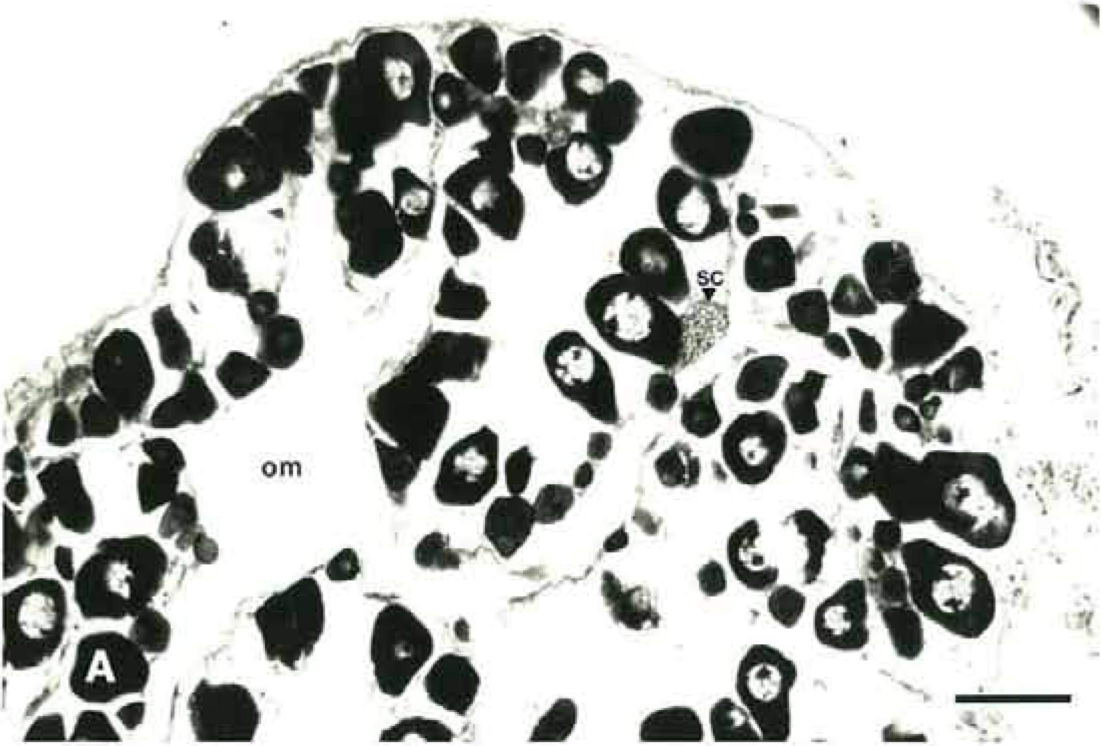
Plate 22

Seminiferous crypts in ovaries of *Parapercis cylindrica*

A. Medial transverse section of ovary from specimen #677, 63 mm TL. Scale 50 μ.

B. Medial transverse section of ovary from specimen #735, 68 mm TL. Scale 50 μ.

Key: om = lumen
lm = lamellae
sc = seminiferous crypt


sc
om
A

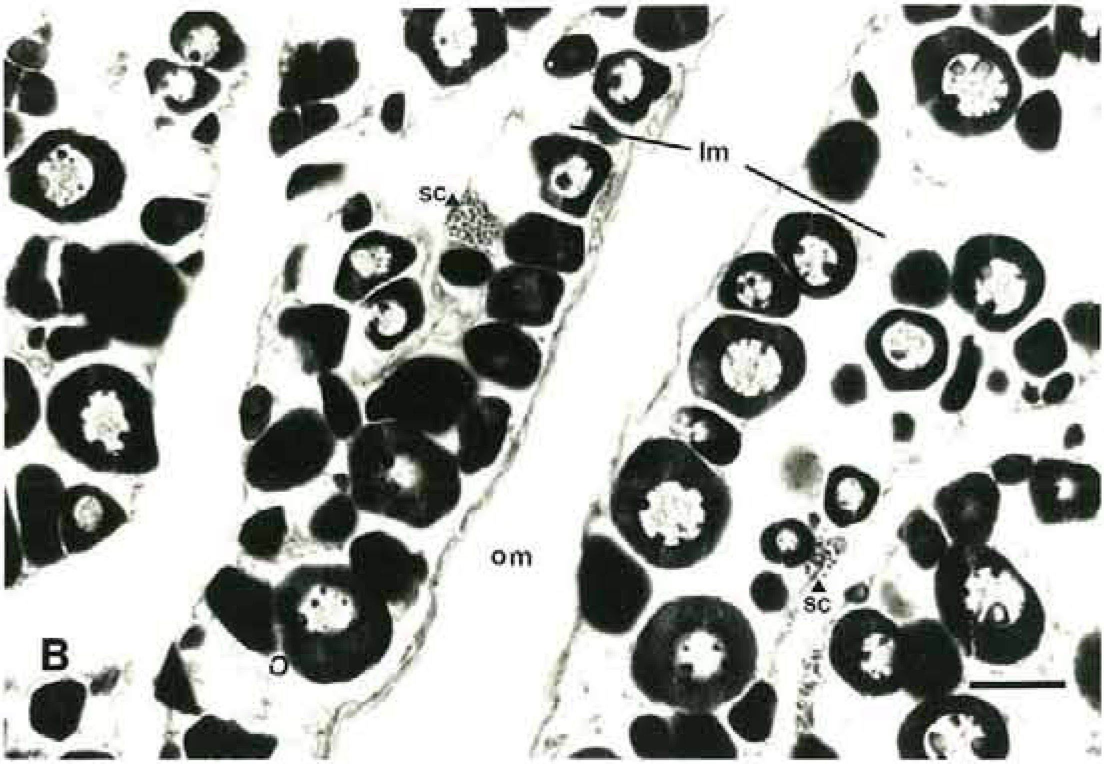

lm
sc
om
sc
B
o

Plate 23.

Seminiferous crypts in ovaries of *Parapercis clathrata* and *P.* sp. 1

A. Medial transverse section of *P. clathrata* ovary. Specimen #1043, 137 mm TL. Scale 200 μ.

B. Medial transverse section of *P.* sp. 1 ovary. Specimen #638, 63 mm TL. Scale 50 μ.

<u>Key</u>:

om	=	lumen
lm	=	lamellae
sc	=	seminiferous crypt
4	=	stage 4 oocyte

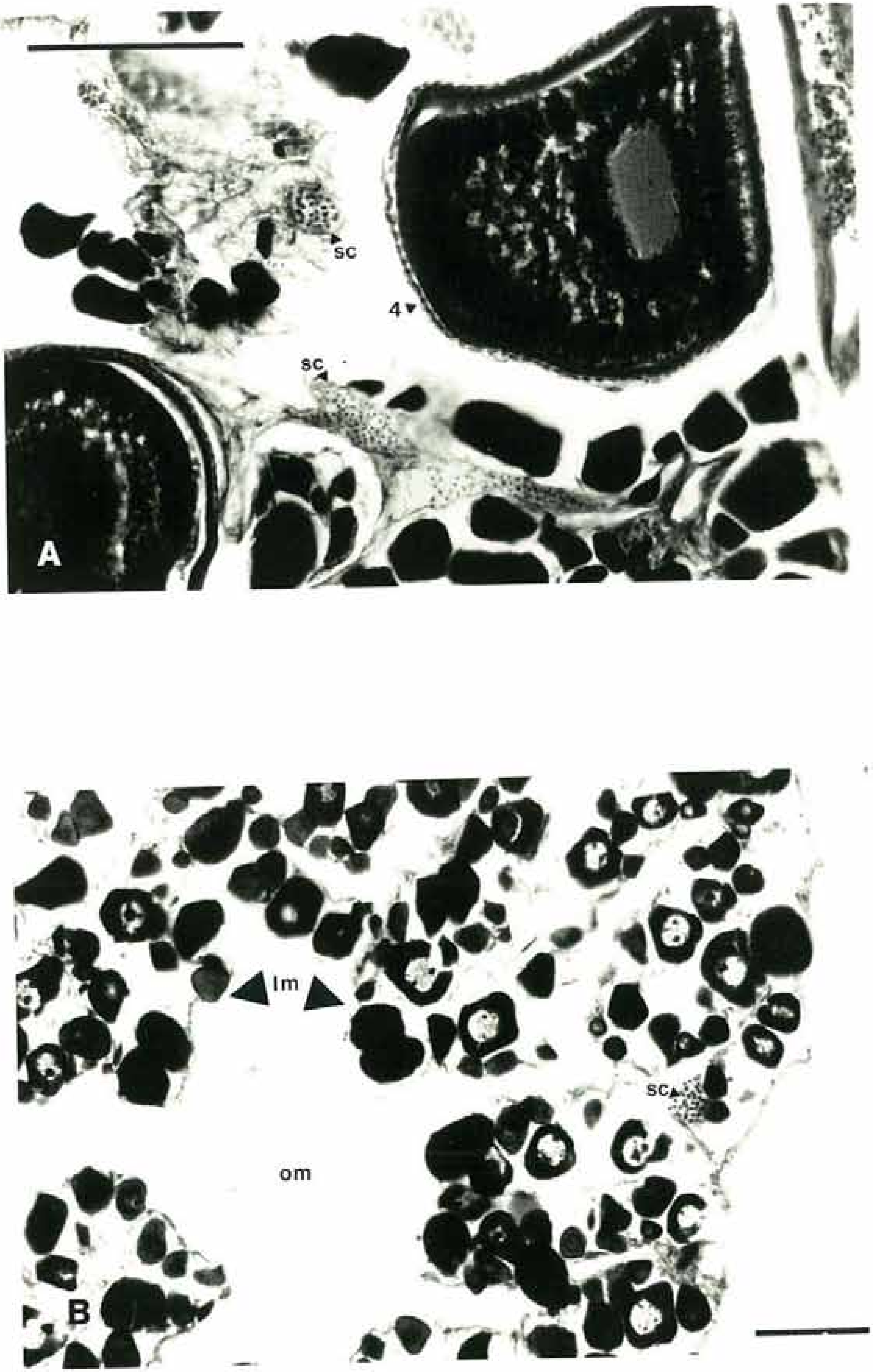

sc
4
sc
A
lm
sc
om
B

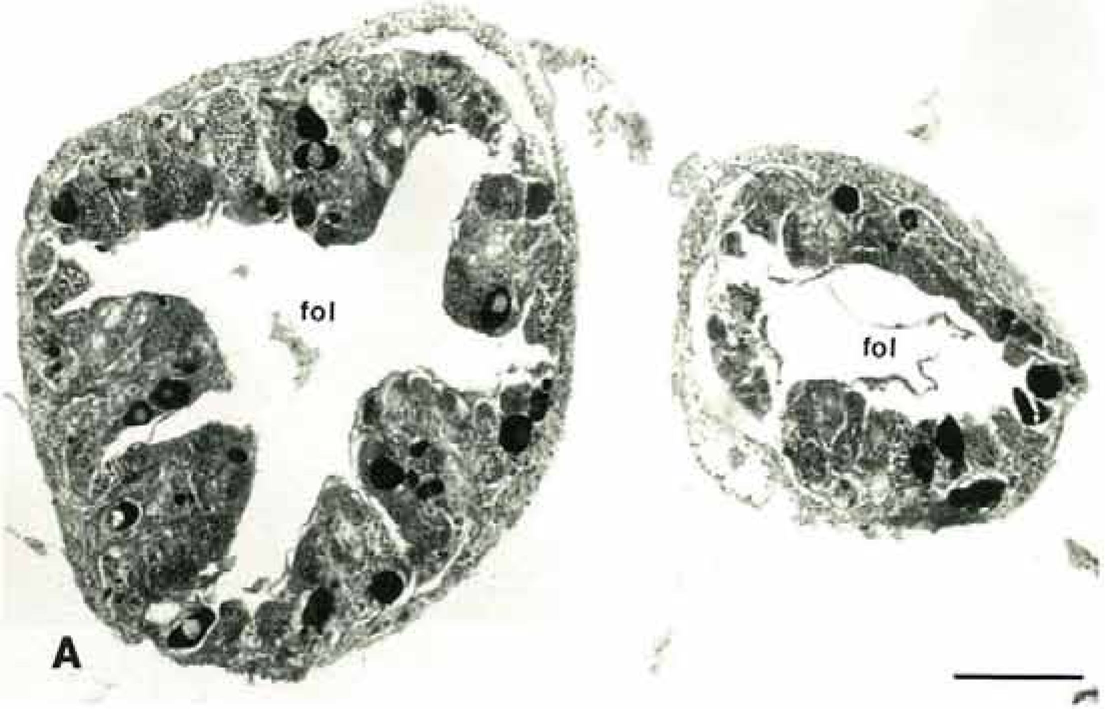
Plate 24

Medial transverse section of a transitional gonad of *Parapercis cylindrica*

A. Low magnification showing basic ovarian structure. Specimen #681, 68 mm TL. Scale 100 μ.

B. Higher magnification of same gonad. Scale 50 μ.

<u>Key</u>: fol = former ovarian lumen
spg = spermatogonia
spc = spermatocytes
1 = stage 1 oocyte
2 = stage 2 oocyte


fol
fol
A

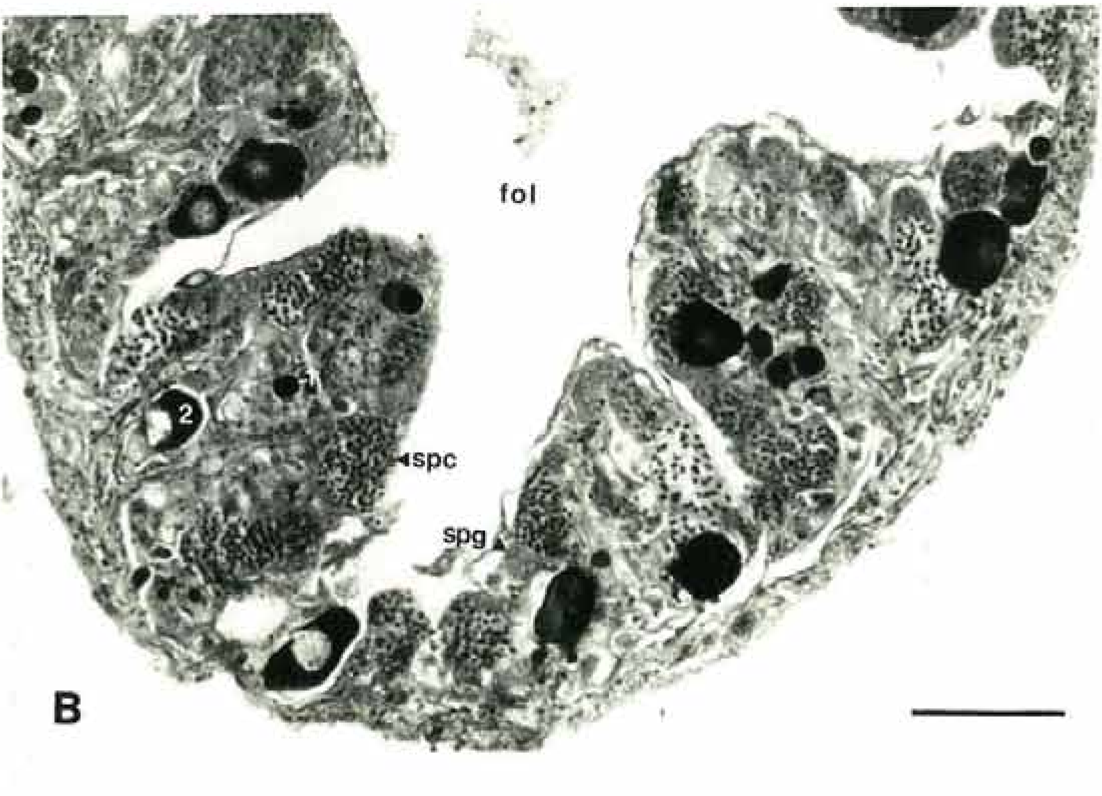

fol
1
2
spc
spg
B

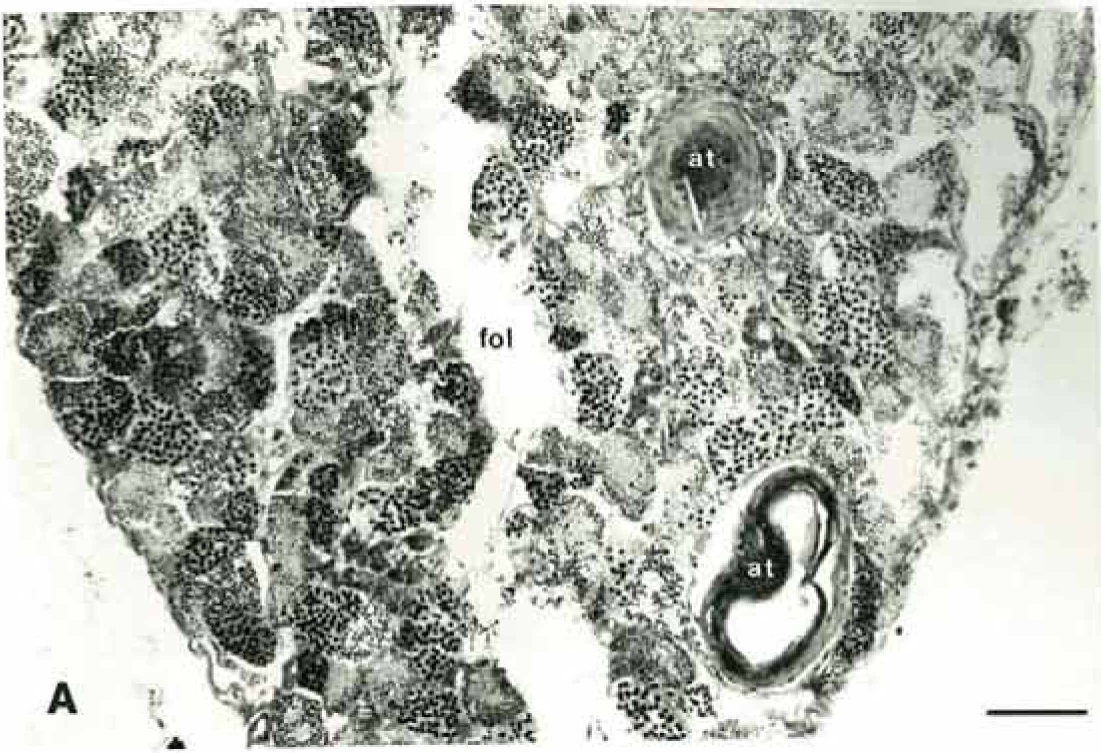
Plate 25

Medial transverse sections of testes of secondary males

A. *Parapercis cylindrica*. Specimen #739, 90 mm TL. Scale 50 µ.

B. *Parapercis cylindrica*. Specimen #789, 81 mm TL. 28 day old male. Scale 200 µ.

Key:
at = atretic body
fol = former ovarian lumen
ss = sperm sinus filled with sperm


at
fol
at
A

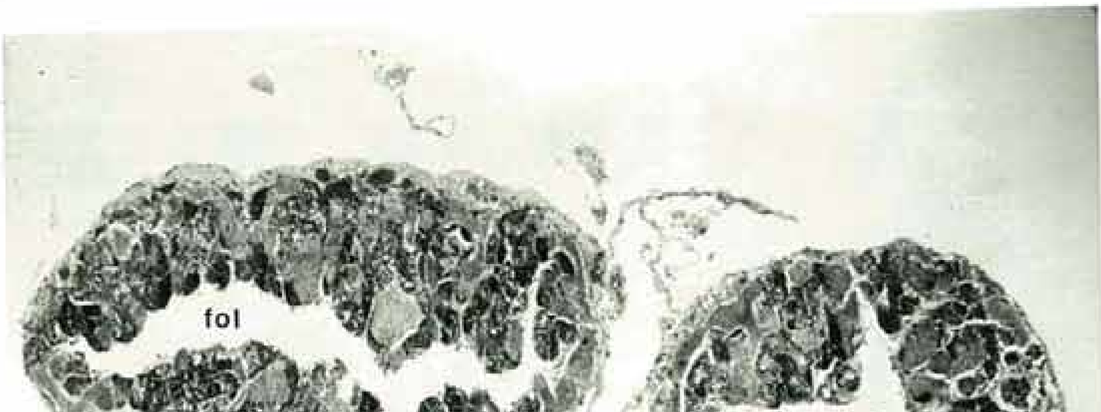

fol
fol
ss
ss
B

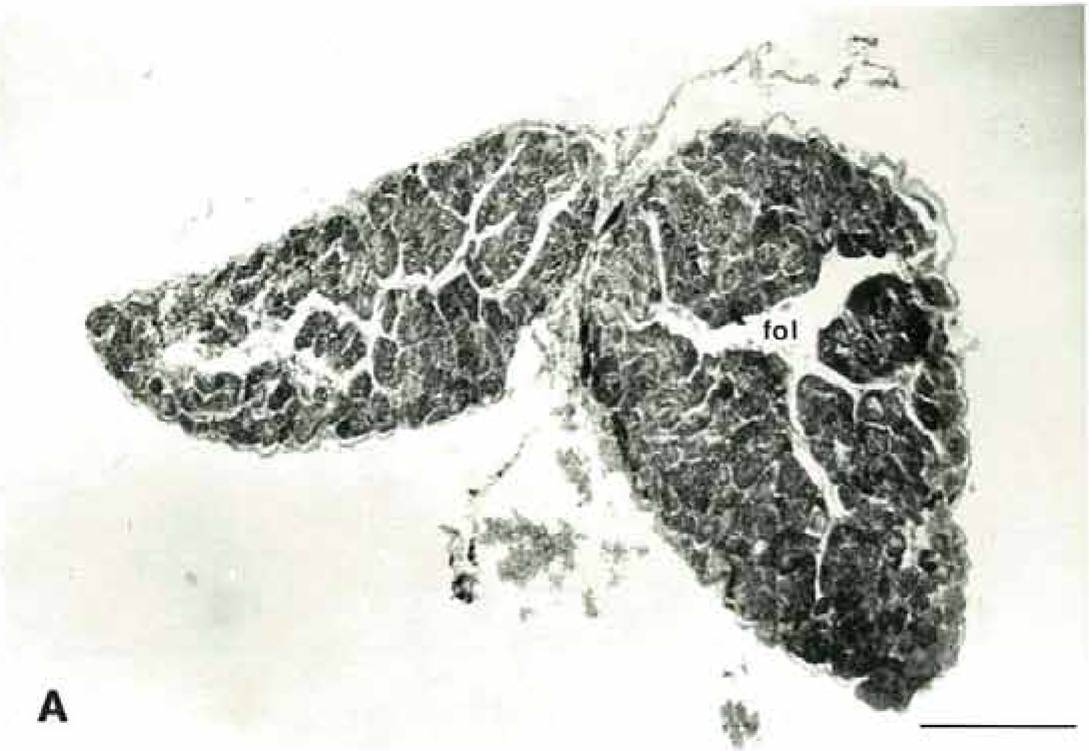
Plate 26

Medial transverse sections of testes of secondary males

A. *Parapercis cylindrica*. Specimen #737, 86 mm TL. Scale 200 µ.

B. *Parapercis cylindrica*. Specimen #679, 85 mm TL. Scale 200 µ.

<u>Key</u>:
do = degenerating oocyte
fol = former ovarian lumen


fol
A

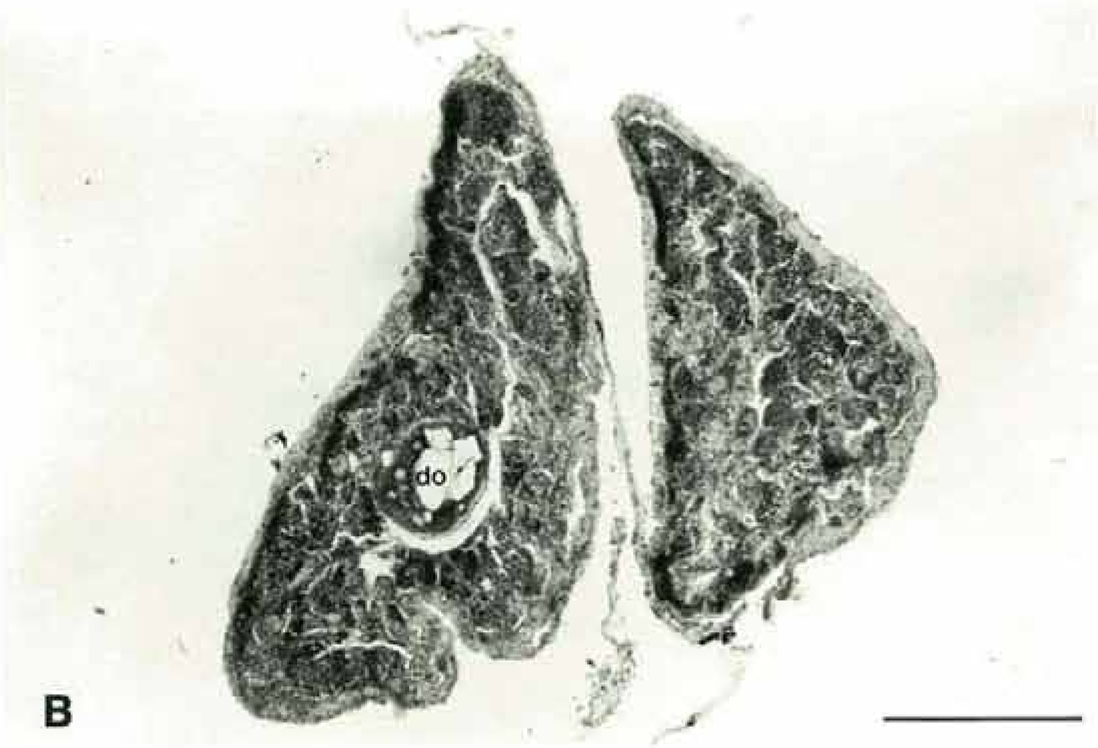

do
B

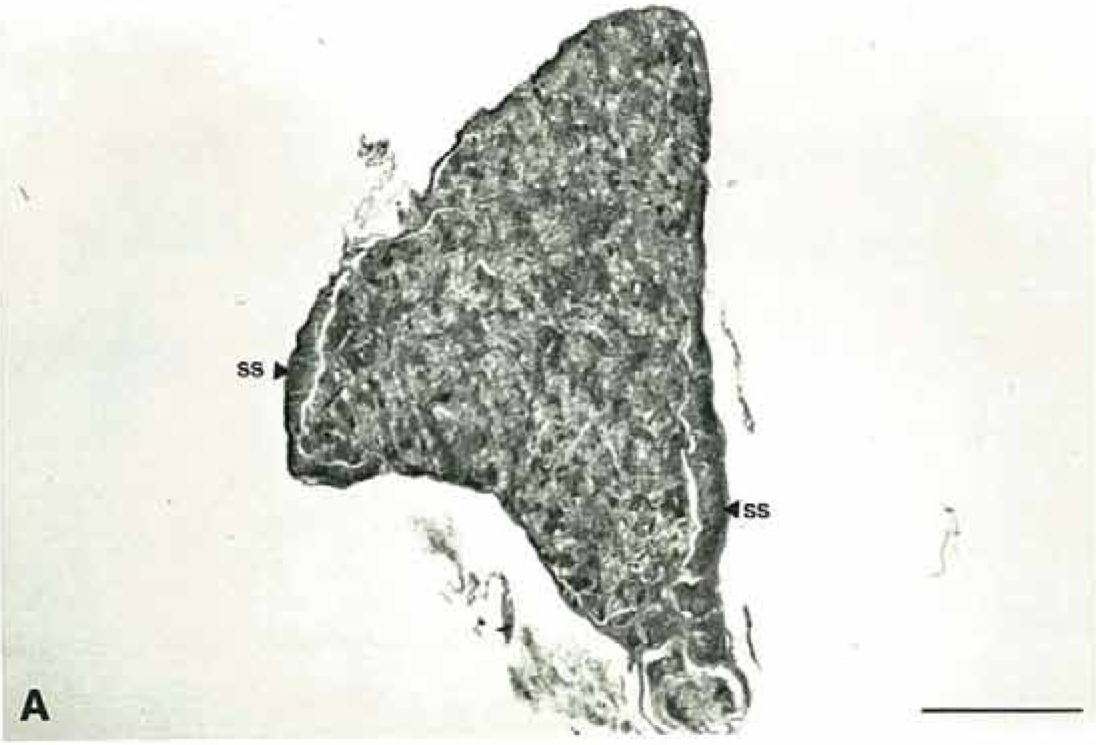
Plate 27

Medial transverse section of testis of a secondary male of *Parapercis cylindrica*

A. Low magnification showing peripheral sperm sinuses. Specimen #771, 103 mm TL. Scale 500 µ.

B. Higher magnification of same testis showing sperm in peripheral sperm sinus. Scale 50 µ.

Key:
ss = sperm sinus
spc = spermatocytes
spg = spermatogonia
sp = sperm and spermatids


ss
ss
A

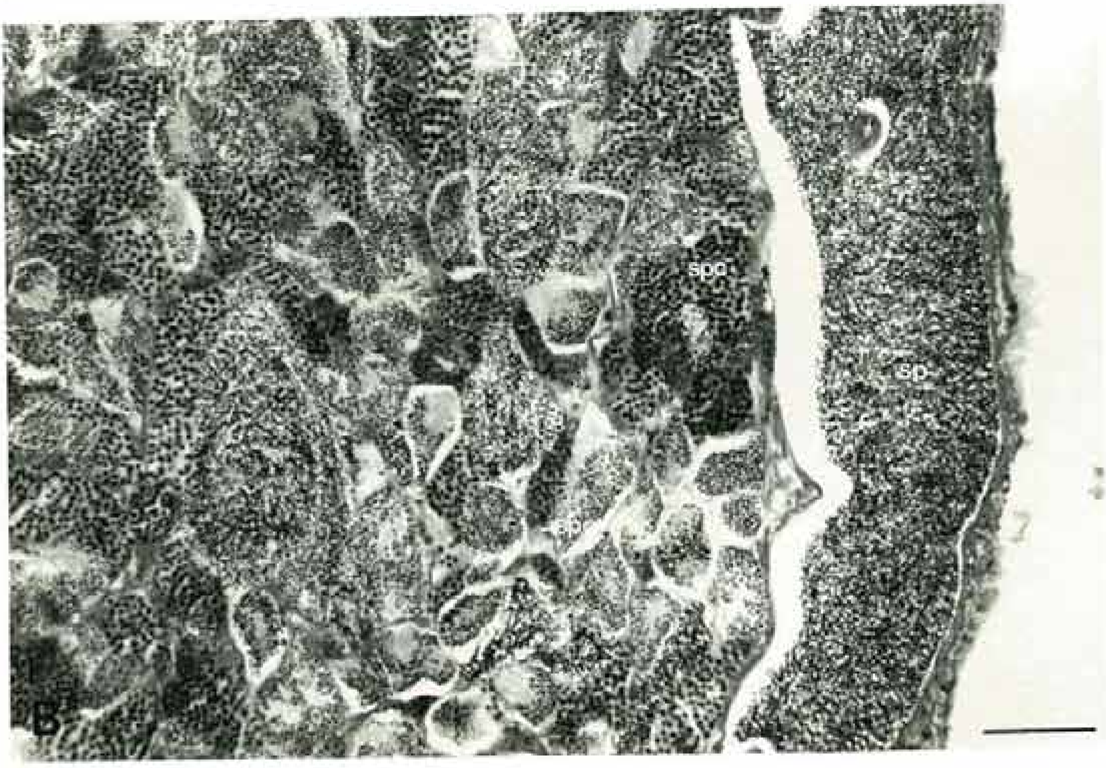

spc
sp
spc
B

Plate 28

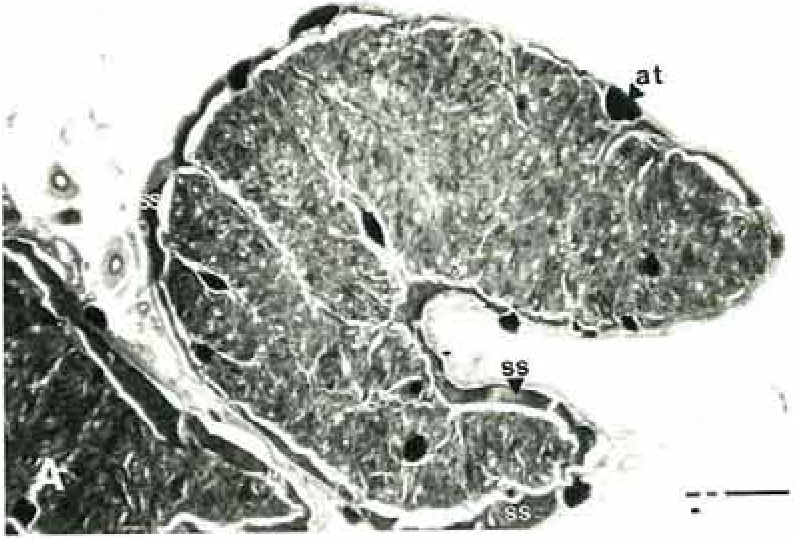
Transverse sections of testes of secondary males

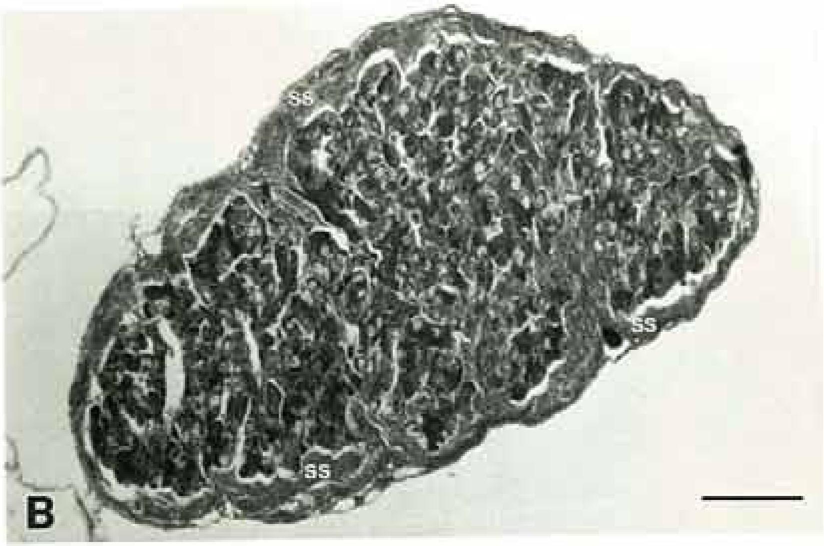
A. *Parapercis hexophtalma*. Specimen #698. 231 mm TL. Medial section. Scale 400 μ.

B. *P. xanthozona*. Specimen #542, 135 mm TL. Medial section. Scale 300 μ.

C. *P. clathrata*. Specimen #5, 136 mm TL. Anterior section. Scale 350 μ.

<u>Key</u>: at = atretic body
ss = sperm sinus filled with sperm


at
ss
ss
ss
A


ss
ss
ss
B


ss
ss
ss
C

Plate 29

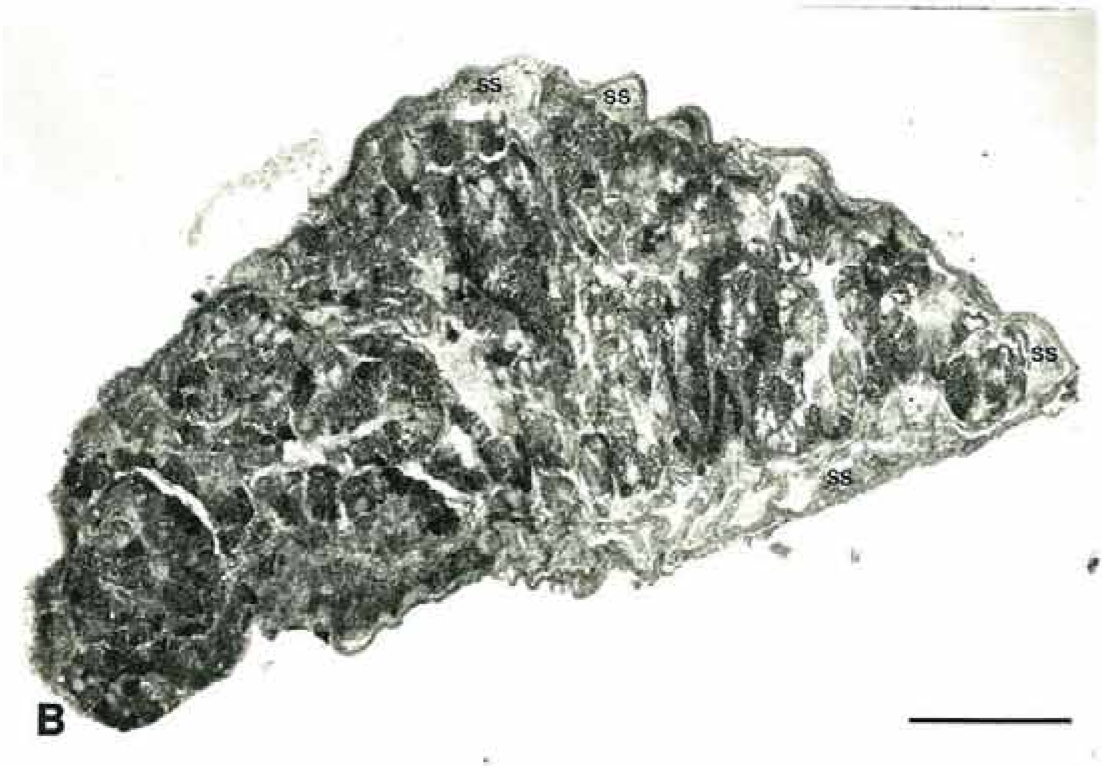
Medial transverse sections of testes of secondary males

A. *Parapercis nebulosa*. Specimen #750, 174 mm TL. Scale 200 µ.

B. *Parapercis* sp. 1. Specimen #700, 66 mm TL. Scale 200 µ.

Key: ss = sperm sinus filled with sperm


ss
ss
A


ss
ss
ss
ss
B

are presented graphically in Figure 66. It can be seen that the small size classes were made up exclusively of females. The smallest males were between 65 and 69 mm TL, and the largest females between 95 and 99 mm TL. Males though, predominated in the larger sizes. Transitionals were found in the region of overlap between males and females.

6.3.2.2 *Parapercis hexophtalma* The relative frequencies of each sexual type in successive 10 mm total length groupings for 65 individuals are shown graphically in Figure 67. Overlap between the sizes of males and females was minimal; the smallest males were in the 160-169 mm TL size-class whilst the largest females were recorded in the 180-189 mm TL size-class. Transitional individuals were restricted to the 180-189 mm TL size-class.

6.3.2.3 *Parapercis* sp. 1 The relative frequencies of each sexual type in successive 5 mm total length groupings for 43 individuals are presented in Figure 68. There was virtually no overlap in the sizes of males and females; both the smallest males and largest females were of lengths between 60 and 64 mm TL. Transitionals were restricted to the 65-69 mm size-class.

6.3.2.4 *Parapercis xanthozona* The relative frequencies of each sexual type in successive 10 mm total length groupings for 37 individuals are shown in Figure 69. It is apparent that the small size classes were made up exclusively of females. The largest females occurred in the 120-129 mm TL size-class and the smallest males, in the 110-119 mm TL size-class. No transitional gonads were found in this species.

Figure 66

Sexual composition of successive length classes of *Parapercis cylindrica*

<u>Key</u>: ■—■ = Female
△—△ = Transitional
▲—▲ = Male

TL = Total length

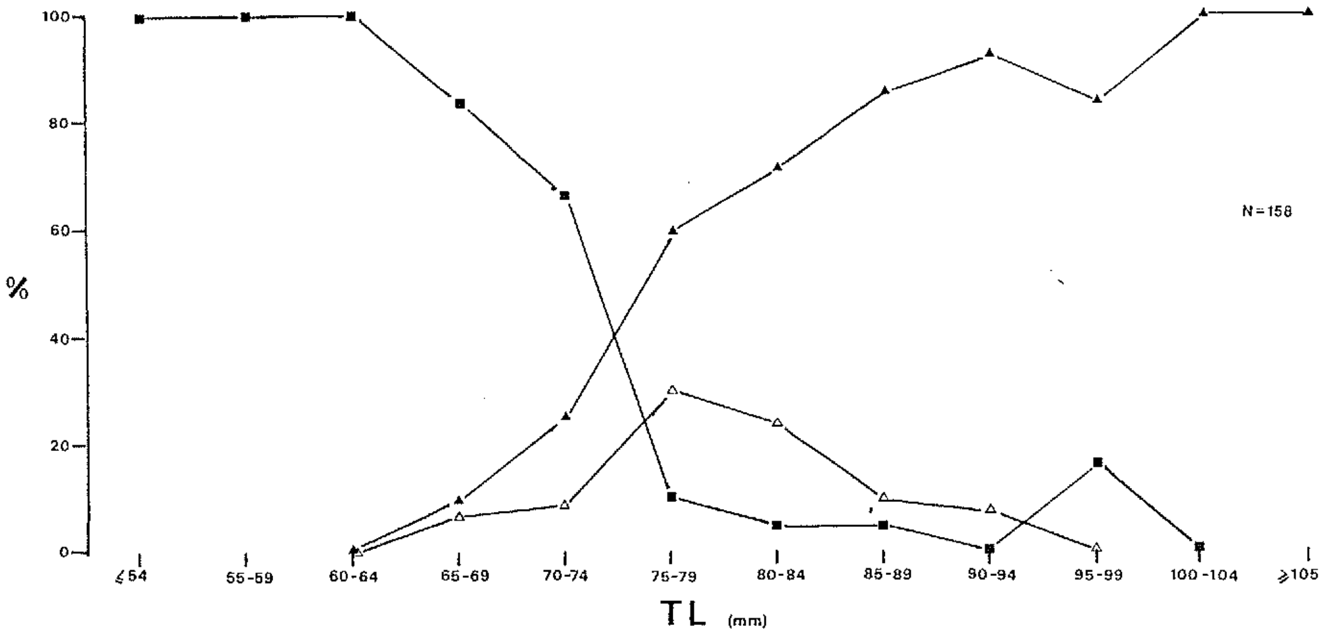

100
80
60
40
20
0
%
≤54
55-59
60-64
65-69
70-74
75-79
80-84
85-89
90-94
95-99
100-104
≥105
TL (mm)
N=158

Figure 67

Sexual composition of successive length classes of *Parapercis hexophtalma*

Key: ■—■ = Female
△—△ = Transitional
▲—▲ = Male

TL = Total length

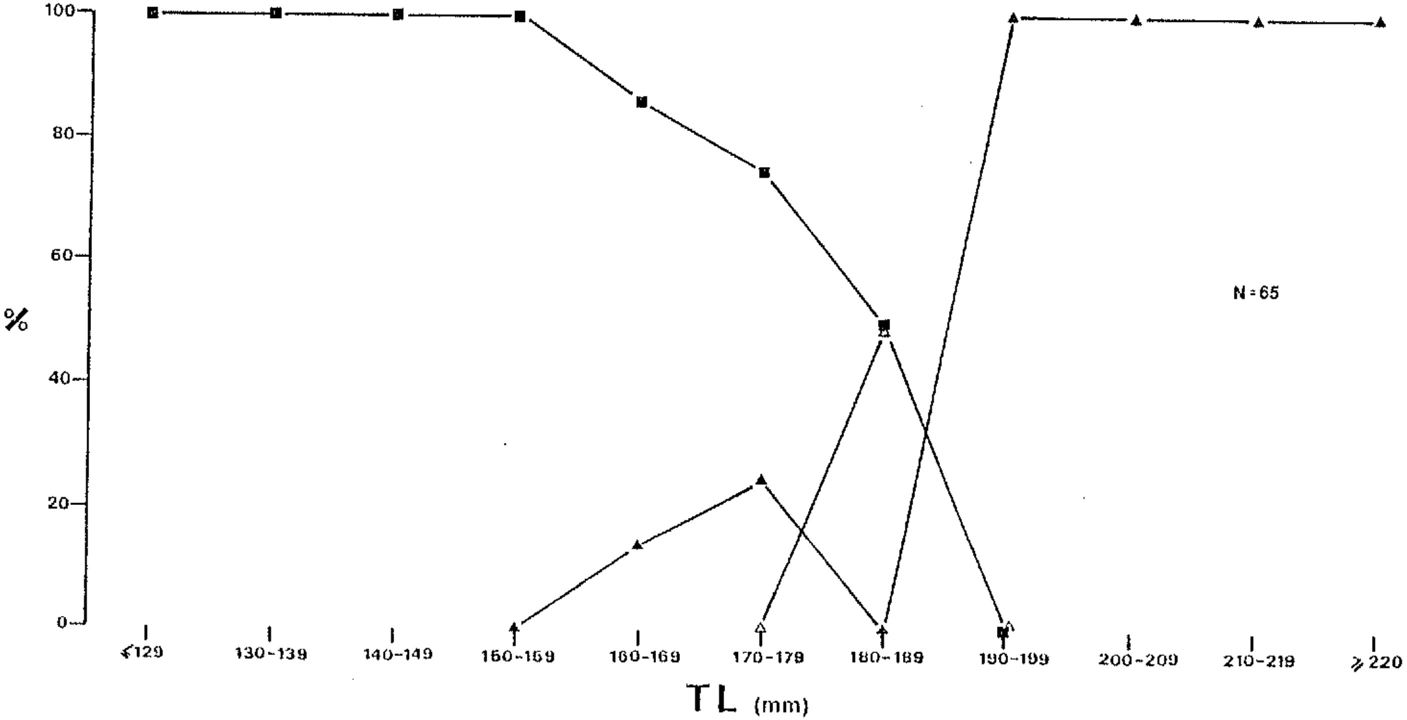

100
80
60
40
20
0
%
≤129
130–139
140–149
150–159
160–169
170–179
180–189
190–199
200–209
210–219
≥220
TL (mm)
N = 65

Figure 68

Sexual composition of successive length classes of *Parapercis* sp. 1

Key:
■—■ = Female
△—△ = Transitional
▲—▲ = Male

TL = Total length

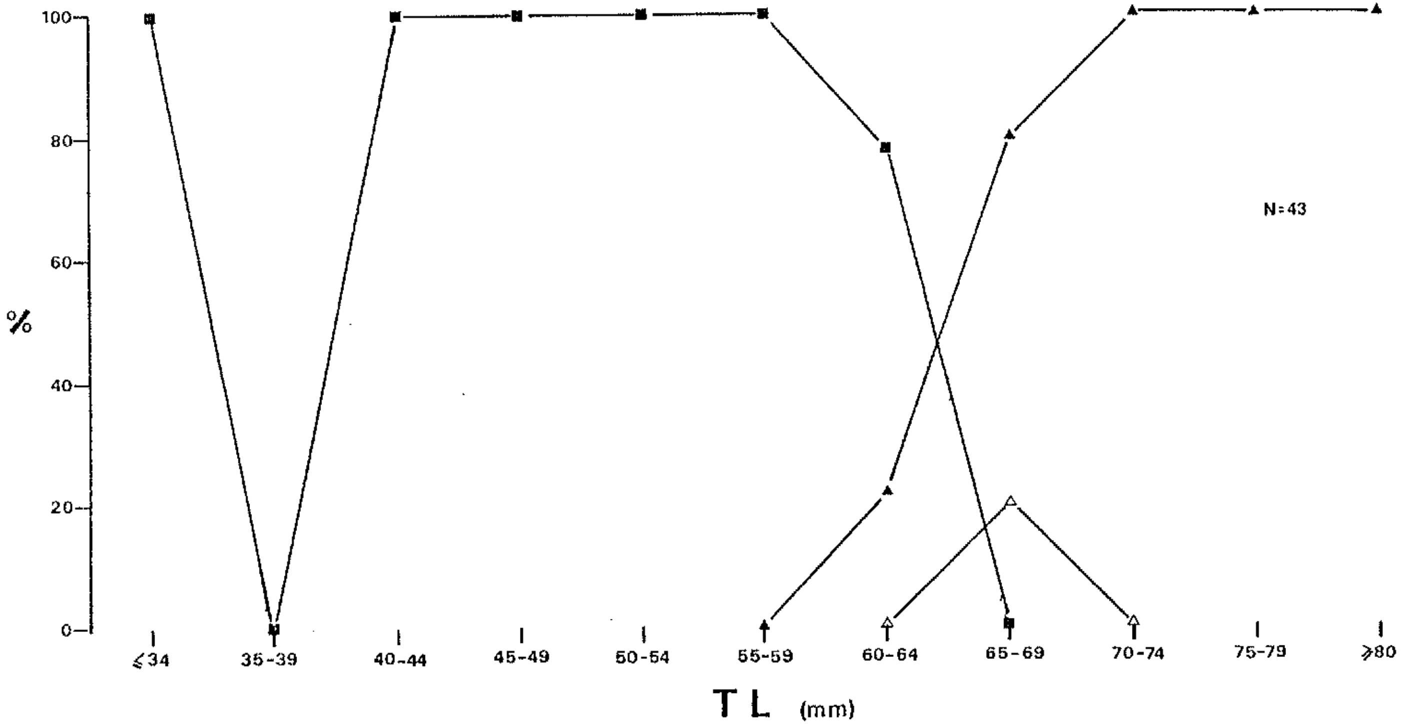

100
80
60
40
20
0
%
≤34
35-39
40-44
45-49
50-54
55-59
60-64
65-69
70-74
75-79
≥80
T L (mm)
N=43

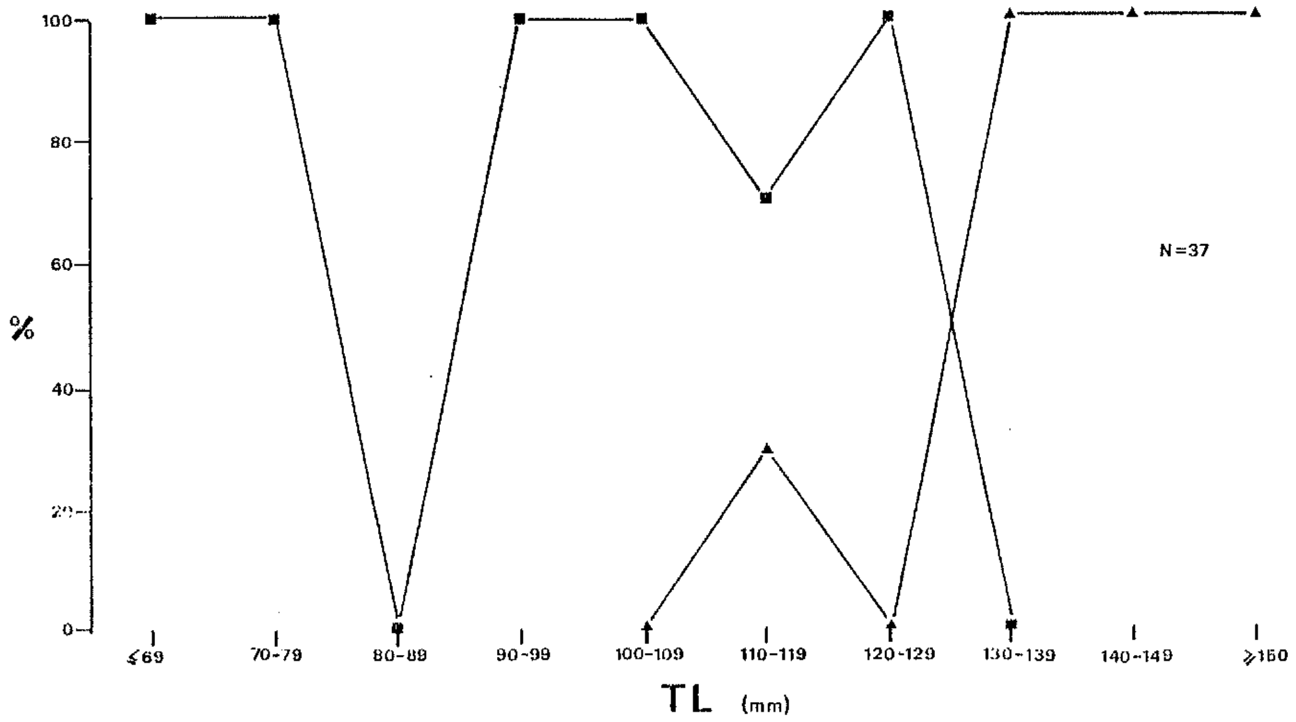
Figure 69

Sexual composition of successive length classes of *Parapercis xanthozona*

Key: ■—■ = Female

▲—▲ = Male

TL = Total length


100
80
60
40
20
0
%
N=37
≤69
70-79
80-89
90-99
100-109
110-119
120-129
130-139
140-149
≥150
TL (mm)

6.3.2.5 *Parapercis clathrata* The relative frequencies of each sexual type in successive 10 mm total length groupings for 15 individuals are presented in Figure 70. Although the data are limited, a bias towards females at the lower end of the size range and males toward the upper end of the size range, is apparent. The smallest males were in the 130-139 mm TL size-class whilst the largest females were in the 140-149 mm TL size-class. No transitional gonads were found in this species.

6.3.2.6 *Parapercis nebulosa* The relative frequencies of each sexual type in successive 10 mm total length groupings for 14 individuals are presented in Figure 71. Only females were found at sizes less than 170 mm TL; the largest females were in the 180-189 mm TL size-class. Transitionals were restricted to the 170-174 mm TL size-class.

6.3.3 The relationship between colour phase and sex

6.3.3.1 *Parapercis cylindrica* The numbers of *P. cylindrica* sampled in each colour phase (initial, transitional, terminal) and sexual type (female, transitional, male) are presented in Table 42. It can be seen that 91% of all males possessed TP colouration; 6% possessed transitional colouration; and 3%, IP colouration. All females had IP colouration, and 71% of individuals with transitional gonads also possessed transitional colouration.

Figure 70

Sexual composition of successive length classes of *Parapercis clathrata*

Key:

■—■ = Female

△—△ = Male

TL = Total length

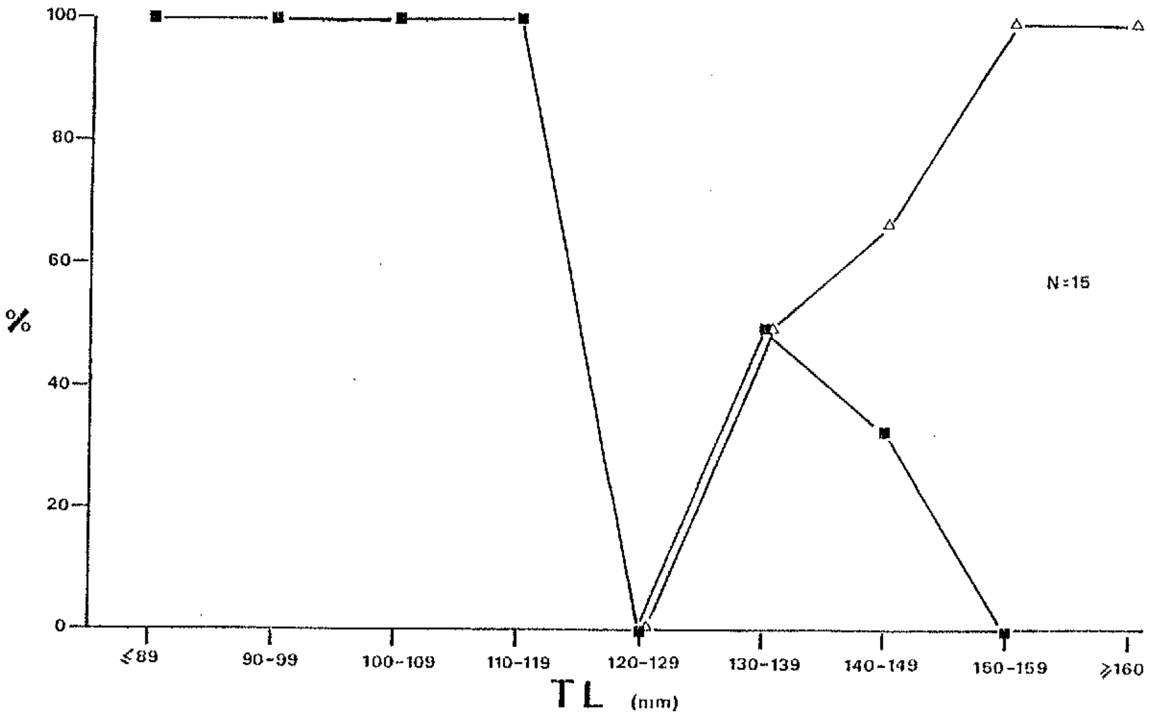
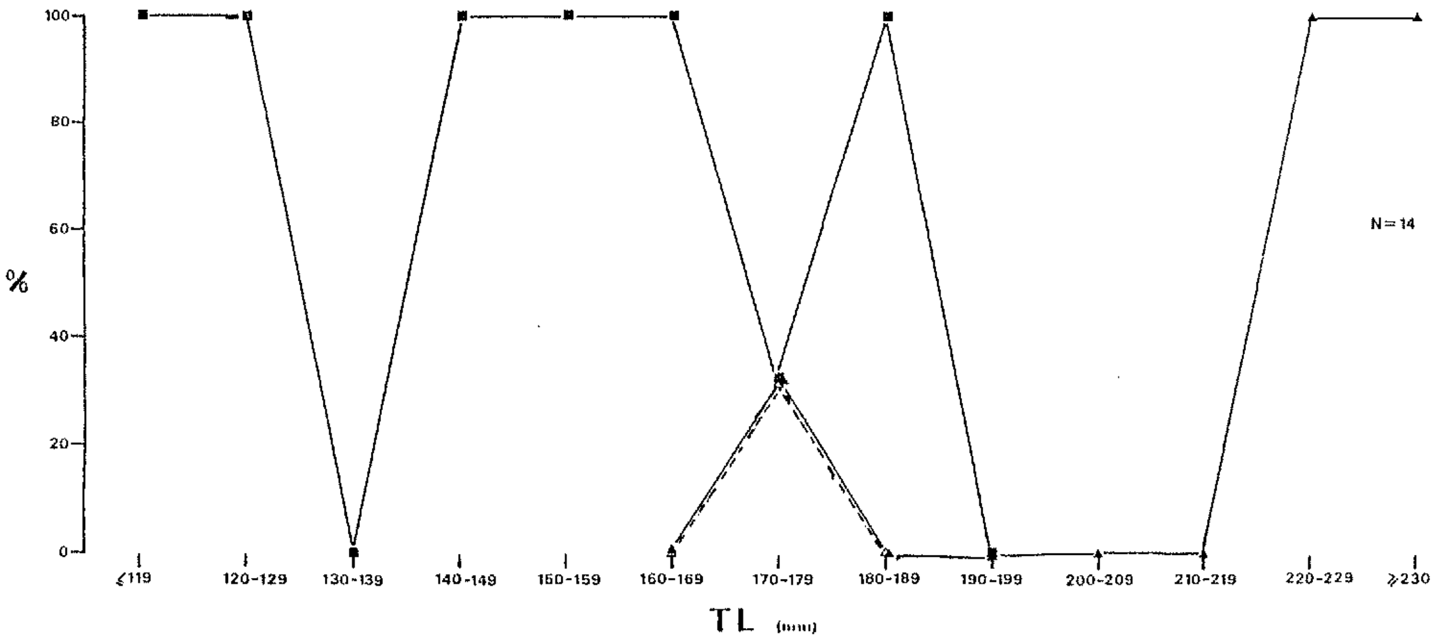

100
80
60
40
20
0
%
≤89
90-99
100-109
110-119
120-129
130-139
140-149
150-159
≥160
TL (mm)
N=15

Figure 71

Sexual composition of successive length classes of *Parapercis nebulosa*

Key: ■—■ = Female
△---△ = Transitional
▲—▲ = Male

TL = Total length



%
100
80
60
40
20
0
N=14
≤119
120-129
130-139
140-149
150-159
160-169
170-179
180-189
190-199
200-209
210-219
220-229
≥230
TL (mm)

Table 42. Colour phase-sex distribution in *P. cylindrica* at Lizard Island[a]

Sexual type	Colour Phase		
	IP	Transitional	TP
Female	76 (100)	--	--
Transitional	4 (29)	10 (71)	--
Male	--	6 (9)	62 (91)

[a] Numbers in parentheses refer to % of each sexual type.

6.3.3.2 *Parapercis hexophtalma* The numbers of *P. hexophtalma* sampled in each colour phase and sexual type are shown in Table 43. All females possessed IP colouration; the only other sexual type to possess IP colouration was a single transitional individual. Males possessed TP colouration exclusively.

Table 43. Colour phase-sex distribution in *P. hexophtalma* at Lizard Island[a]

Sexual type	Colour Phase		
	IP	Transitional	TP
Female	40 (100)	--	--
Transitional	1 (50)	1 (50)	--
Male	--	--	23 (100)

[a] Numbers in parentheses refer to % of each sexual type.

6.3.3.3 *Parapercis* sp. 1 The numbers of *P.* sp. 1 sampled in each colour phase and sexual type are presented in Table 44. Ninety percent of males were of TP colouration, the remaining 10%, of IP colouration. Only one transitional gonad was found, the individual that this was from showed transitional colouration. All females showed IP colouration.

Table 44. Colour phase-sex distribution in *P.* sp. 1 at Lizard Island[a]

Sexual type	Colour Phase		
	IP	Transitional	TP
Female	21 (100)	--	--
Transitional	--	1 (100)	--
Male	2 (10)	--	19 (90)

[a] Numbers in parentheses refer to % of each sexual type.

6.3.3.4 *Parapercis xanthozona* Table 45 shows the numbers of *P. xanthozona* sampled in each colour phase and sexual type. Sixty-nine percent of males possessed TP colouration, the remaining 31% had transitional colour patterns. Females were only found to possess IP colouration.

Table 45. Colour phase-sex distribution in *P. xanthozona* at Lizard Island[a]

Sexual type	Colour Phase		
	IP	Transitional	TP
Female	24 (100)	--	--
Transitional	--	--	--
Male	--	4 (31)	9 (69)

[a] Numbers in parentheses refer to % of each sexual type.

6.3.3.5 *Parapercis clathrata* The numbers of *P. clathrata* sampled in each colour phase and sexual type are shown in Table 46. All nine females examined had IP colouration. Conversely, all six males were of TP colouration. No transitional gonads or colour phases were found.

Table 46. Colour phase-sex distribution in *P. clathrata* at Lizard Island[a]

Sexual type	Colour Phase		
	IP	Transitional	TP
Female	9 (100)	--	--
Transitional	--	--	--
Male	--	--	6 (100)

[a] Numbers in parentheses refer to % of each sexual type.

6.3.3.6 *Parapercis nebulosa* This species, on the basis of specimens examined in the present study, is monochromatic. Colouration for *P. nebulosa* is described in Part I (pp.79-81).

6.3.4 Sequence and timing of behavioural and colouration changes during sex reversal in *P. cylindrica* In order to confirm social initiation of sex reversal in *P. cylindrica* and subsequently study the sequence and timing of behavioural and colouration changes associated with sex reversal, a series of male removal experiments were conducted on harems of this species.

Certain elements of the behavioural repertoire of males are absent from that of females, namely (1) the Spinous dorsal-Approach, and (2) the Head-Bob (see p.221, Table 21). Both motor patterns are performed by the male during interactions with his females; the Spinous dorsal-

Approach during agonistic encounters (see p.223), Head-Bobbing during courtship (see p.259). The times of onset of these male-specific behaviour patterns were examined in the above experiments.

The most important differences between terminal phase (TP) (i.e. male) colouration and initial phase (IP) (i.e. characteristically female) colouration are in the pigmentation of the eye, upper lip, and branchiostegal region (pp. 18-20, Fig. 2). The onset and completion of these elements of TP colouration were examined in the male removal experiments.

Experiments were conducted on 10 harems located within seven study sites (see Fig.65) during which a total of 14 males were experimentally removed (four harems underwent successive male removals, i.e. an individual which had changed sex following the removal of a male was, in time, removed from the harem - the time interval between successive removals from the same harem was never less than two months). All members of the harem were observed daily for changes in behaviour and/or colouration following removal of the male. At the completion of each experiment, the female(s) which assumed male colouration and behaviour were speared and their gonads examined histologically.

Experimental removal of 14 males resulted in a total of 17 females assuming male colouration and behaviour (11 dominant females in 11 "harems" and 6 codominant females in the remaining 3 "harems") (Table 47). These male removal experiments were controlled to the extent that eight undisturbed harems of *P. cylindrica* were monitored within study sites G_8, G_{10}, G_{14}, G_{15}, DG-1 and DG-2 over a 35-58 day period whilst the removal experiments were being conducted. In five of these eight "control" harems (1 harem each in G_8, DG-1, DG-2; 2 in G_{10}) there was no male disappearance and no sex reversals by females during this period. In two other harems (1 harem each in G_{14}, G_{15})

Table 47. Summary of *P. cylindrica* male removal field experiments conducted at Lizard Island.

Study Site	No. of harems in study site	No. of males removed	No. individuals changing sex	Status of sex-reversing individual(s)
BII	2	4†	4	all dominant ♀'s
BMI	1	1	1	dominant ♀
LHI	1	1	1	" "
MBI	2	2	3	1 dominant ♀; 2 codominant ♀'s
SBI	1	1	2	both codominant ♀'s
SCI	2	4†	4	" " "
SFI	1	1	2	all dominant ♀'s
Totals	10	14	17	

† Each harem in this study site underwent successive male removal i.e. an individual which had changed sex following removal of a male was itself removed from the harem - the time interval between successive removals was never less than two months.

†† Male removal and subsequent monitoring conducted from 25/5/78 - 1/7/78 except for the second male removals within study sites BII and SCI which were conducted from 2/9/78 - 22/9/78.

males were lost through natural disappearance and in both cases the dominant female of each harem changed sex. In the remaining "control" harem (2nd harem in G_{15}), sex-reversal of the dominant female occurred whilst in the presence of the male of the harem. However, just prior to sex-reversal of the dominant female, the male had extended his territory enormously as a result of invading a neighbouring harem - consequently there was some potential for social unit division. This was in fact the only case observed during the whole 2½ year study of *P. cylindrica* where sex-reversal took place that was not preceded by male disappearance (see p.261). Taking the observations from the "control" harems into account, it seems highly probable that the observed sex-reversals of females during the male removal experiments were not simply naturally occurring events coincidental with the removals but were actually a consequence of male removal.

The day of onset of male specific behaviour patterns in sex-reversing individuals following male removal are given in Table 48. Individuals began to perform Head-Bobs around Day 7 (days counted from the day of male removal) and Spinous dorsal-Approaches around Day 8.

Changes in the branchiostegal pigmentation were first noticed around Day 7 and were usually complete by about Day 9 (Table 49). The eye and upper lip pigmentation usually began to change around Day 10; the former was usually complete by about Day 17, the latter, Day 20 (Table 49). Thus, transition from initial to terminal phase was usually complete by the time the "new" male was about 20 days old, i.e. 20 days from the day of male removal. Since terminal phase individuals of this species are exclusively males (see 6.3.3), it can be assumed that the duration required for gonadal sex change is around 20 days or less from the day of male removal. Confirmation of this comes from histological examination of the gonads of the "new" males, all 17 of which were collected between Day 20 and Day 31. Each gonad showed sperm sinuses filled with sperm (e.g. see p.320, Plate 25).

Table48. Day of onset of male specific behaviour patterns in "new" males following male removal[a]

Behaviour pattern	Day of onset[b]	
	Median	Range
Head-Bob	7	5-11
Spinous dorsal-Approach	8	7-11

[a] Table based on daily observations of 17 "new" males following male removal.

[b] Days counted from the day of male removal.

Table49. Day of onset and completion of terminal phase colouration in "new" males following male removal[a]

Elements of TP colouration	Day of onset[b]		Day of completion	
	Median	Range	Median	Range
Eye pigmentation	10	8-13	17	15-18
Upper lip pigmentation	10	9-12	20	17-24
Branchiostegal pigmentation	7	6-8	9	8-11

[a] Table based on daily observations of 17 "new" males following male removal.

[b] Days counted from the day of male removal.

6.3.5 Sexual maturity Females were considered immature if their gonads contained oocytes at developmental stages no greater than Stage 2 and lacked atretic bodies; the gonads of mature females possessed oocytes of Stages 1, 2 and 3 and usually had atretic bodies. Table 50 shows the sizes of the largest immature female and the smallest mature female found in *Parapercis cylindrica, P. hexophtalma, P.* sp. 1 and *P. xanthozona*. *Parapercis cylindrica* apparently matures between 48 and 63 mm total length, *P. hexophtalma* between 95 and 106 mm total length, *P.* sp. 1 between 37 and 50 mm total length, and *P. xanthozona* between 94 and 110 mm total length.

Table 50. Size at maturity for four species of *Parapercis* at Lizard Island

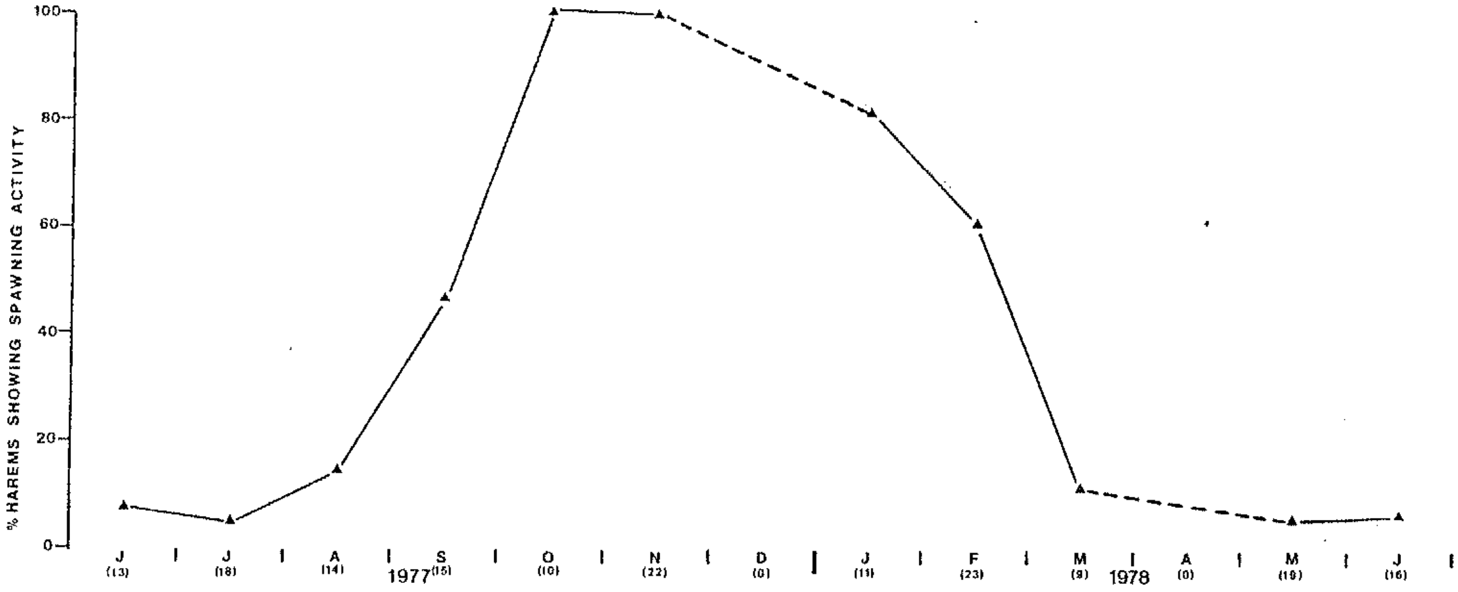
Species	Sample size		Largest immature female (mm TL)	Smallest mature female (mm TL)
	Immature ♀♀	Mature ♀♀		
P. cylindrica	29	47	63	48
P. hexophtalma	17	33	106	95
P. sp. 1	7	14	50	37
P. xanthozona	11	13	110	94

6.3.6 Breeding seasonality Figure 72 shows the number of *P. cylindrica* harems in which spawning activity was observed, expressed as a percentage of the total number of harems observed (i.e. during the daily reproductive period) per month for each month of the year. It can be seen that whilst spawning activity in a few harems occurred the year round, spawning activity in the majority of harems took place from August to March, i.e. approximately 8 months of the year.

Figure 72

Percentage of P. *cylindrica* harems showing spawning activity at different times of the year

Numbers in parentheses refer to the total number of harems observed per month during the daily reproductive period


% HAREMS SHOWING SPAWNING ACTIVITY
100
80
60
40
20
0
J (13)
J (18)
A (14)
1977
S (15)
O (10)
N (22)
D (0)
J (11)
F (23)
M (9)
1978
A (0)
M (19)
J (16)

6.3.7 Fecundity Fecundity estimates were obtained through enumeration of eggs spawned by individuals of *P. cylindrica* held in aquaria. Immediately following spawning, the eggs floated to the surface after which they were siphoned off and counted. The numbers of eggs spawned by five females in single spawning acts are presented in Table 51. It is apparent that there was considerable variation in the number of eggs released, the maximum being about 1100 eggs, the minimum 150 eggs. Assuming a female spawns every day of the 8 month long breeding season, she will release anything from 40,000 to 270,000 eggs during this time.

Table 51. Numbers of eggs spawned by females during single spawning acts

Date	Size of female (mm TL)	Number of eggs spawned
5/ 9/78	76	1106
5/ 9/78	74	890
7/11/78	81	155
7/11/78	79	586
11/11/78	75	262

6.3.8 Egg and larval development The eggs of *Parapercis cylindrica* are pelagic, spherical, smooth, non-adhesive and colourless and measure 0.75 to 0.84 mm (mean = 0.81, n = 29) in diameter. Each has a single colourless oil globule measuring 0.17 to 0.22 (mean = 0.19, n = 29) in diameter. Development of the egg is rapid, taking between 22 and 24 hours at 22.7 to 27°C.

Newly hatched larvae, ranging in total length from 1.58 to 1.64 mm, are elongate, with a large yolk sac, no fins, and a single oil droplet in the yolk sac near its posterior margin. There are six characteristic patches of xanthophores present - the first below the unpigmented eye, the second above the eye, the third on the myomeres over the middle of the yolk sac, the fourth and fifth on the myomeres just anterior to, and just posterior to the oil globule respectively, and the sixth near the end of the notochord. Sixty-two hours after fertilization the yolk is depleted and the post-larva is 2.02 to 2.15 mm in total length.

Since spawning activity rises sharply to a peak in October (see Fig. 72, p. 341), and there is a peak in juvenile recruitment in November (see Fig. 19, p.147), the duration of the planktonic larval stage is probably in the vicinity of a month. Newly settled juveniles range in size from about 12 to 17 mm in total length.

6.4 Discussion

There are three main types of intersexuality among fishes: (1) simultaneous hermaphroditism; (2) protandrous hermaphroditism; and (3) protogynous hermaphroditism (Reinboth, 1970). In simultaneous or synchronous (Atz, 1964) hermaphroditism, an individual is capable of functioning as a male and a female at the same time. The sexes in protandrous and protogynous hermaphrodites are, on the other hand, functionally separate, i.e. hermaphroditism is sequential rather than simultaneous. Choat (1969) defined protandrous hermaphroditism as the process whereby individuals whose initial identity is male undergo sex reversal to become female, and protogynous hermaphroditism as the process whereby individuals whose initial identity is female undergo sex reversal to become males.

Protogynous hermaphrodites can be subdivided into two main categories: (1) *diandric* species in which both primary males (i.e. males "born" as males) and secondary males (i.e. males derived from females through sex reversal) are present, and (2) *monandric* species in which all males are of the secondary type (Reinboth, 1967, 1970). Primary males can be distinguished from secondary males on the basis of gonadal structure. In secondary males, the former ovarian cavity usually persists and there is development of a series of sperm sinuses on the periphery of the gonad which are used in sperm transport; in primary males sperm transport is achieved by way of a single, simple tube (Reinboth, 1962; Smith, 1965). Ovarian remnants such as atretic bodies and small oocytes in the testis also point to the ovarian origin of the gonads of secondary males (Moe, 1969).

Gonad structure in males of all six *Parapercis* species examined in the present study was secondary in nature. The presence of secondary males plus the finding of transitional gonads in four of the six species supports the thesis that the *Parapercis* species examined in the present study are monandric protogynous hermaphrodites. Further support comes from the sex-separated size distributions found in these species (see Figs. 66-71 , which are a standard feature of the populations of protogynous species (e.g. McErlean and Smith, 1964; Choat, 1969; Roede, 1972; Choat and Robertson, 1975; Warner, 1975a).

Sex and colour pattern were closely linked in the species of *Parapercis* examined, with colouration change essentially occurring at the same time as sex change. This is not unlike that found in several species of labroid fishes (Choat, 1969; Warner and Downs, 1977; Robertson and Warner, 1978; Warner and Robertson, 1978). Terminal phase individuals were exclusively males in all *Parapercis* species examined. In all species except *Parapercis* sp. 1, individuals exhibiting initial phase colouration were either female or transitional in gonad state, though predominantly the former. About 10% of initial phase individuals of *Parapercis* sp. 1 were males. This sex/colouration combination could be attributable to the individuals being collected immediately following sex reversal but just prior to colour change. Alternatively, these fishes may have changed sex a considerable time before and have been functioning as males whilst possessing initial phase colouration. Such initial phase males have been described for the temperate labrid *Pseudolabrus celidotus* (Jones, 1980). However, the presence of many degenerating oocytes and a very distinct lumen in the gonads of initial phase males of *Parapercis* sp. 1 indicates these individuals had just undergone sex change.

The results of the male removal experiments with *Parapercis cylindrica* confirmed that social initiation of sex reversal occurs in this species. The presence of the male prevents the largest female(s) of his harem from changing sex. Without exception, removal of the male resulted in sex reversal by the dominant female or codominant females of the harem. Social initiation of sex reversal has also been demonstrated in *Anthias squamipinnis* (Fishelson, 1970; Shapiro, 1979, 1981), *Centropyge interruptus* (Moyer and Nakazono, 1978a), *Amphiprion akallopisos, A. bicintus* (Fricke and Fricke, 1977), and *Labroides dimidiatus* (Robertson, 1972, 1973, 1974) and probably also occurs in *Paragobiodon echinocephalus, P. xanthosoma* (Lassig, 1977), *Amphiprion frenatus, A. clarkii, A. polymnus, A. perideraion, A. sandracinos, A. ocellaris* (Moyer and Nakazona, 1978b), *A. melanopus* (Ross, 1978) and *Thalassoma bifasciatum* (Warner et al., 1975). Dominance has been suggested as the social factor controlling sex reversal in a large number of these species (Robertson, 1972, 1973, 1974; Fricke and Fricke, 1977; Moyer and Nakazono, 1978a, 1978b; Robertson and Warner, 1978). This also appears to be the case in *Parapercis cylindrica*. The hierarchical organization within a harem of *P. cylindrica* results in the dominant female being subordinate to, and receiving aggression from, only the male. Females of lower status on the other hand are subordinate to, and receive aggression from, both the male and one or more females. Loss of the male results in an increase in dominance rank by one rank for all individuals of the harem. The previous dominant female is now totally dominant and thus receives no aggression from other members of the harem; however, the other females are still subordinate to, and thus receive aggression from, one or more individuals of the harem. The previous dominant female's release from aggressive dominance (by the male) apparently initiates the process of sex reversal within that individual.

Exactly how release from dominance is translated into the endogenous processes which affect the gonads themselves, and whether the physiological mechanism involved is one of disinhibition (Robertson, 1972, 1973, 1974; Fricke and Fricke, 1977) or stimulation (Shapiro, 1979, 1981) is not known. Reinboth (1980:57) hypothesized that "either continuous dominance or inferiority could be paralleled by different levels of circulating hormones, specifically of hormones which affect the functional conditions of the gonad." Such a mechanism appears conceivable, especially in the light of recent work by Harding and Follett (1979) who found that concentrations of hormones in the plasma of blackbirds during agonistic encounters were significantly different from those found in individuals not recently involved in agonistic encounters.

Sex reversal and its associated behavioural and colouration changes is quite rapid in *Parapercis cylindrica*. Male behaviour was first observed about 7 days after male removal as were changes in the branchiosiegal pigmentation. The eye and upper lip pigmentation began to change about 10 days after male removal and overall, the transition from initial phase colouration to terminal phase colouration took approximately 20 days. Gonads of individuals collected 20 days or more from the time of male removal were all fully functional males. Estimates of the duration of gonadal sex change following male removal in other species include 14 days for *Anthias squamipinnis* (Shapiro, 1979) and *Labroides dimidiatus* (Robertson, 1974), and 20 days for *Centropyge interruptus* (Moyer and Nakazono, 1978a). The faster an individual *P. cylindrica* is able to change sex and thus consolidate its new position within the harem, the less likelihood there is of invasions and takeovers of the harem. Consequently, development of rapid sex reversal would be favoured.

Ghiselin (1969) presented three different models to explain the origin of hermaphroditism in animals. The *low density model* is applicable to those populations where the density of individuals is so low that males and females have difficulty in finding each other in order to mate, whilst the *gene dispersal model* explains hermaphroditism in situations where loss of genetic variability due to inbreeding or reproduction in isolated groups is a problem. The third model, the *size advantage model*, appears the most applicable in explaining the evolution of protogynous sex reversal in *Parapercis cylindrica*. This model, which has been subsequently expanded and formalized (Robertson and Choat, 1974; Ghiselin, 1974; Warner, 1975; Warner et al., 1975), asserts that sequential hermaphroditism would be adaptive in those cases "where it was more advantageous for the individual to be of one sex at a particular age or size and the other sex when larger or older" (Warner, 1978:85), i.e. sequential hermaphroditism is adaptive when male and female fertility are differentially distributed with age. Thus, where male fertility is higher than the female's in later ages, as in many polygynous species, protogynous hermaphroditism would be selected for. The polygynous mating system in *Parapercis cylindrica*, like in several other reef fish species has led to high fertilities in old, large and aggressively dominant males (Robertson, 1972; Roede, 1972; Robertson and Choat, 1974; Choat and Robertson, 1975; Warner et al., 1975; Warner, 1978). Since each male has a mean of 2.32 mature females in his harem (see p.212) with whom he mates daily, his fertility is over twice that of the females. Consequently, there would be strong selection for sex reversal from female to male at later ages. In addition, there are secondary advantages to be gained by such a sex change system as that observed in *P. cylindrica*. Since the male is derived from the oldest female of the harem, his is the genotype best adapted to the environment and, because of the polygynous mating system, his is the one most widely spread (Robertson, 1972, 1973). Hence genetic advantages are accrued to the species by this system of favouring the fittest genotypes.

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APPENDIX 1

Compendium of dominance hierarchies within *P. cylindrica* social units

The dominance relationships presented below are based on the observed outcomes of agonistic interactions between social unit members in addition to the sizes of individuals comprising the social unit. Dominance hierarchies in each regularly mapped social unit during each study period are given along with the number of the Composite Map (Appendix 2) showing the spatial relationships within the social unit at that particular time.

KEY:

(i) #1, 2, 3, ... #n = identity number of an individual within a particular study site.

(ii) ♂ = male, A = adult female, SA = subadult female, J = juvenile female.

(iii) (10, 11, 12, ... n TL) = estimated total length in mm.

(iv) #x > #y = #x is dominant over #y regardless of the locality of the interaction, i.e. a spatially independent dominance relationship.

(v) #x $\gtrless$ #y = #x is dominant over #y in #x's territory, but #y is dominant over #x in #y's territory, i.e. a spatially dependent dominance relationship.

(vi) #x / #y = no pair contact was observed between #x and #y, but, due to the small size difference between them, their dominance relationship would probably be a spatially dependent one as in (v).

(vii) #x $\not>$ #y = no pair contact was observed between #x and #y, but, due to the large size difference between them, #x would almost certainly be dominant over #y.

(viii) Hierarchies are essentially linear with the highest ranking individual given first followed by lower ranking individuals, e.g. #3 ♂ (100 TL) > #2 (85 TL) > #5 A (80 TL) > #1 SA (53TL) indicates that fish #3 is dominant over #2, #5 and #1; fish #2 is dominant over #5 and #1; fish #5 is dominant over #1 only.

1. Long term observational sites

(a) Study site G_8

(i) Study period 1 (21/9/76 - 23/9/76) - Composite Map 1:
#3 ♂ (90 TL) > #4 A (70 TL) > #2 A (60 TL) > #22 SA (49 TL) / #12 SA (48 TL) > #11 SA (42 TL).

(ii) Study period 2 (26/11/76 - 28/11/76) - Composite Map 2:
#3 ♂ (92 TL) > #4 A (72 TL) > #2 A (61 TL) > #22 SA (50 TL) / #12 SA (50 TL) > #11 SA (45 TL) ≯ #43 J (20 TL).

(iii) Study period 3 (20/2/77 - 22/2/77) - Composite Map 3:
#3 ♂ (95 TL) > #4 A (85 TL) > #2 A (75 TL) > #22 A (65 TL) / #12 A (65 TL) > #11 SA (55 TL) ≯ #59 SA (40 TL) ≯ #60 SA (35 TL) ≯ #55 J (20 TL) / #57 J (20 TL).

(iv) Study period 4 (30/4/77 - 1/5/77) - Composite Map 4:
#3 ♂ has disappeared; neighbouring #75 ♂ has invaded and successfully taken over the social unit:-
#75 ♂ (90 TL) > #4 A (89 TL) > #12 A (75 TL) ≯ #21 A (71 TL) ≯ #59 SA (55 TL) > #60 SA (50 TL) ≯ #55 SA (35 TL).

(v) Study period 5 (12/7/77 - 14/7/77) - Composite Map 5:
#75 ♂ (90 TL) > #12 A (80 TL) ≯ #21 A (76 TL) ≯ #59 A (60 TL) > #60 SA (54 TL) ≯ #78 SA (37 TL) / #77 SA (35 TL) ≯ #76 SA (30 TL).

(vi) Study period 6 (2/9/77 - 4/9/77) - Composite Map 6:
#75 ♂ has disappeared; #12 has changed sex (♀ → ♂) and taken control of

the social unit:

#12 ♂ (84 TL) > #59 A (63 TL) > #60 A (57 TL) ≯ #78 SA (43 TL) ≯ #81 SA (35 TL) ≯ #80 J (25 TL).

(vii) Study period 7 (24/11/77 - 26/11/77) - Composite Map 7:

#12 ♂ (86 TL) > #59 A (70 TL) > #78 SA (59 TL) ≯ #81 SA (41 TL) ≯ #80 SA (31 TL) / #87 SA (30 TL) ≯ #88 J (25 TL) / #89 J (25 TL) / #90 J (25 TL).

(viii) Study period 8 (2/2/78 - 4/2/78) - Composite Map 8:

#12 ♂ (89 TL) > #59 A (73 TL) > #78 SA (54 TL) > #81 SA (45 TL) ≯ #87 SA (36 TL) ≯ #89 SA (30 TL) > #101 J (25 TL) / #100 J (25 TL).

(ix) Study period 9 (3/5/78 - 4/5/78) - Composite Map 9:

#12 ♂ (91 TL) > #78 A (60 TL) > #81 SA (52 TL).

(x) Study period 10 (26/6/78 - 27/6/78) - Composite Map 10:

#12 ♂ (92 TL) > #78 A (63 TL) > #81 A (56 TL).

(xi) Study period 11 (10/9/78 - 11/9/78) - Composite Map 11:

#12 ♂ (94 TL) > #78 A (66 TL) > #81 A (60 TL).

(b) Study site G_{10}

(i) Study period 1 (23/9/76 - 25/9/76) - Composite Map 12:

Social unit A: #4 ♂ (85 TL) > #5 A (80 TL) > #14 A (62 TL) ≯ #25 SA (32 TL) ≯ #13 J (23 TL).

Social unit B: #15 ♂ (100 TL) > #8 A (70 TL) ≯ #9 SA (30 TL) ≭ #7 SA (30 TL) ≯ #12 J (25 TL).

(ii) Study period 2 (29/11/76 - 2/12/76) - Composite Map 13:

Social unit A: #4 ♂ (92 TL) > #5 A (85 TL) > #14 A (70 TL) ≯ #25 SA (45 TL) ≯ #13 SA (38 TL) ≯ #22 SA (34 TL) ≯ #26 SA (31 TL) ≯ #48 J (20 TL) / #49 J (20 TL) / #33 J (19 TL) ≯ #34 J (16 TL) / #36 J (15 TL) / #50 J (15 TL).

Social unit B: #15 ♂ (102 TL) > #8 A (77 TL) > #9 SA (45 TL) ≭ #7 SA (43 TL).

(iii) Study period 3 (23/2/77 - 26/2/77) - Composite Map 14: Social unit A: #4 ♂ (95 TL) > #5 A (89 TL) > #14 A (77 TL) ≯ #25 A (56 TL) ≯ #22 SA (45 TL) > #26 SA (42 TL) ≯ #33 SA (39 TL) / #51 SA (38 TL) ≯ #58 SA (35 TL) ≯ #55 SA (32 TL) ≯ #61 J (20 TL).

Social unit B: #15 ♂ (103 TL) > #8 A (80 TL) > #9 A (57 TL) ≯ #54 SA (30 TL).

(iv) Study period 4 (2/5/77 - 4/5/77) - Composite Map 15: Social unit A: #4 ♂ (97 TL) > #5 A (91 TL) > #51 SA (50 TL) ≯ #58 SA (46 TL) > #74 SA (32 TL) > #73 J (25 TL).

Social unit B: #15 ♂ (103 TL) > #8 A (85 TL) > #9 A (68 TL).

(v) Study period 5 (15/7/77 - 17/7/77) - Composite Map 16: Social unit A: #4 ♂ (100 TL) > #5 A (93 TL) > #51 A (61 TL) > #58 A (58 TL).

Social unit B: #15 ♂ (105 TL) > #8 A (89 TL) > #75 SA (35 TL).

(vi) Study period 6 (5/9/77 - 7/9/77) - Composite Map 17: Social unit A: #4 ♂ (101 TL) > #5 A (96 TL) > #51 A (68 TL) > #58 A (64 TL) ≯ #79 SA (36 TL) > #78 J (25 TL) ≯ #77 J (21 TL).

Social unit B: #15 ♂ (105 TL) > #8 A (91 TL) > #75 SA (45 TL) ≯ #80 SA (39 TL) ≯ #81 J (24 TL).

(vii) Study period 7 (1/12/77 - 4/12/77) - Composite Map 18: Social unit A: #4 ♂ (102 TL) > #51 A (74 TL) > #58 A (69 TL) > # 79 SA (45 TL) > #78 SA(37 TL) / #85 SA (36 TL) ≸ #93 SA (36 TL) ≯ #94 SA (32 TL) ≯ #95 SA (29 TL).

Social unit B: #15 ♂ (107 TL) > #8 A (92 TL) > #75 SA (55 TL) ≯ #80 SA (59 TL) ≯ #81 SA (38 TL) ≯ #90 SA (30 TL) ≯ #91 J (24 TL).

(viii) Study period 8 (15/2/78 - 18/2/78) - Composite Map 19: Social unit A: #4 ♂ has disappeared; neighbouring #99 ♂ has invaded and successfully taken over the social unit:-

#99 ♂ (109 TL) > #51 A (81 TL) > #58 A (75 TL) ≯ 101 A (71 TL) ≯ #79 SA

(54 TL) > #78 SA (47 TL) ≹ #85 SA (47 TL) ≹ #93 SA (47 TL).

Social unit B: #15 ♂ (110 TL) > #8 A (94 TL) > #75 A (64 TL) ≯ #80 A (61 TL) > #90 SA (42 TL) ≯ #91 SA (38 TL) > #96 SA (29 TL).

(ix) Study period 9 (6/5/78 - 8/5/78) - Composite Map 20:

Social unit A: #99 ♂ (110 TL) > #58 A (80 TL) ≯ 101 A (75 TL) ≯ #93 A (56 TL).

Social unit B: #15 ♂ has disappeared; #8 has changed sex (♀ → ♂) and taken control of the social unit:-

#8 ♂ (95 TL) > #75 A (70 TL) > #80 A (67 TL) > #90 SA (53 TL).

(x) Study period 10 (28/6/78 - 30/6/78) - Composite Map 21:

Social unit A: #99 ♂ (110 TL) > #58 A (83 TL) ≯ 101 A (79 TL) ≯ #93 A (62 TL).

Social unit B: #8 ♂ (96 TL) > #75 A (74 TL) > #80 A (70 TL) > #90 A (59 TL).

(xi) Study period 11 (12/9/78 - 14/9/78) - Composite Map 22:

Social unit A: #99 ♂ has disappeared: #58 has changed sex (♀ → ♂) and taken control of the social unit:-

#58 ♂ (84 TL) > #93 A (69 TL) > #100 SA (30 TL).

Social unit B: #8 ♂ (96 TL) > #75 A (79 TL) > #80 A (76 TL) > #90 A (66 TL).

(c) Study site G_{14}

(i) Study period 1 (3/12/76 - 5/12/76) - Composite Map 23:

#12 ♂ (90 TL) > #2 A (69 TL) > #22 SA (50 TL) ≯ #23 SA (30 TL) / #13 SA (30 TL) / #16 A (30 TL) > #24 J (25 TL) > #11 J (20 TL).

(ii) Study period 2 (16/2/77 - 19/2/77) - Composite Map 24:

#12 ♂ (95 TL) > #2 A (75 TL) > #22 A (60 TL) ≯ #23 SA (35 TL) / #24 SA (35 TL).

(iii) Study period 3 (5/5/77 - 7/5/77) - Composite Map 25:

#12 ♂ (100 TL) > #22 A (70 TL) > #23 SA (44 TL) / #24 SA (45 TL).

(iv) Study period 4 (18/7/77 - 19/7/77) - Composite Map 26: #12 ♂ (103 TL) > #22 A (73 TL) > #24 SA (53 TL) ≯ #28 SA (34 TL).

(v) Study period 5 (11/9/77 - 12/9/77) - Composite Map 27: #12 ♂ (105 TL) > #22 A (75 TL) > #24 A (60 TL) ≯ #28 SA (43 TL).

(vi) Study period 6 (22/11/77 - 23/11/77) - Composite Map 28: #12 ♂ (106 TL) > #22 A (77 TL) > #24 A (65 TL) ≯ #28 SA (50 TL) ≯ #50 SA (32 TL) > #49 J (24 TL) ≯ #48 J (19 TL).

(vii) Study period 7 (12/2/78 - 14/2/78) - Composite Map 29: #12 ♂ (108 TL) > #22 A (80 TL) > #24 A (72 TL) ≯ #28 A (59 TL) ≯ #56 SA (33 TL) / #53 SA (32 TL).

(viii) Study period 8 (1/5/78 - 2/5/78) - Composite Map 30: #12 ♂ (108 TL) > #22 A (85 TL) > #24 A (75 TL) ≯ #28 A (65 TL) ≯ #56 SA (42 TL) / #53 SA (40 TL).

(ix) Study period 9 (4/6/78 - 5/6/78) - Composite Map 31: #12 ♂ has disappeared; #22 has changed sex (♀ → ♂) and taken control of the social unit :-

#22 ♂ (87 TL) > #24 A (76 TL) > #28 A (69 TL) ≯ #56 SA (50 TL) / #53 SA (49 TL).

(x) Study period 10 (8/9/78 - 9/9/78) - Composite Map 32: #22 ♂ (88 TL) > #24 A (78 TL) > #28 A (73 TL) > #56 SA (55 TL) / #53 SA (53 TL).

(d) Study site G_{15}

(i) Study period 1 (17/11/76 - 20/11/76) - Composite Map 33:

Social unit A: #3 ♂ (85 TL) > #2 A (75 TL) ≯ #7 SA (50 TL) ≯ #8 SA (45 TL).

Social unit B: #5 ♂ (90 TL) > #4 A (58 TL) > #12 SA (50 TL).

(ii) Study period 2 (8/2/77 - 10/2/77) - Composite Map 34:

Social unit A: #3 ♂ (86 TL) > #2 A (80 TL) > #7 A (60 TL) > #8 SA (54 TL)

≯ #9 SA (33 TL) ≯ #10 J (20 TL).

Social unit B: #5 ♂ (92 TL) > #4 A (68 TL) > #12 A (59 TL).

(iii) Study period 3 (28/4/77 - 29/4/77) - Composite Map 35:

Social unit A: #3 ♂ (90 TL) > #2 A (85 TL) > #7 A (69 TL) > #8A (62 TL) ≯ #9 SA (42 TL).

Social unit B: #5 ♂ (95 TL) > #4 A (74 TL) > #12 A (66 TL).

(iv) Study period 4 (9/7/77 - 10/7/77) - Composite Map 36:

Social unit A: #3 ♂ (94 TL) > #7 A (75 TL) > #8 A (70 TL) > #9 SA (51 TL).

Social unit B: #5 ♂ (96 TL) > #4 A (80 TL) > #12 A (71 TL) > #13 SA (33 TL) / #14 SA (33 TL).

(v) Study period 5 (6/9/77 - 8/9/77) - Composite Map 37:

Social unit A: #3 ♂ (95 TL) > #8 A (74 TL) > #9 A (56 TL).

Social unit B: #5 ♂ (96 TL) > #4 A (83 TL) > #12 A (76 TL) > #13 SA (46 TL) ≭ #14 SA (45 TL) ≯ #16 SA (34 TL).

(vi) Study period 6 (7/11/77 - 11/11/77) - Composite Map 38:

Social unit A: #3 ♂ (96 TL) > #8 A (80 TL) > #9 A (64 TL) > #24 SA (36 TL) / #20 SA (36 TL) ≯ #21 SA (30 TL) ≯ #23 J (25 TL) ≯ #22 J (19 TL).

Social unit B: #5 ♂ (96 TL) > #4 A (85 TL) > #12 A (79 TL) > #13 A (56 TL) ≭ #14 A (56 TL) ≯ #16 SA (47 TL) ≯ #18 SA (37 TL) ≯ #17 SA (30 TL).

(vii) Study period 7 (20/2/78 - 23/2/78) - Composite Map 39:

Social unit A: #3 ♂ (100 TL) > #8 A (85 TL) > #9 A (72 TL) > #24 A (56 TL) ≯ #20 SA (50 TL) ≯ #23 SA (40 TL) ≯ #26 SA (34 TL).

Social unit B: #5 ♂ has disappeared; #4 has begun to change sex (both ♂ and ♀ elements are present in colour pattern) whilst neighbouring #27 ♂ has invaded the social unit in a takeover bid; as a result social unit B has split into two smaller social units, B$_1$ and B$_2$:-

Social unit B$_1$: #4 ♂/♀ A (88 TL) > #16 A (60 TL) > #18 SA (52 TL).

Social unit B_2: #27 ♂ (95 TL) > #12 A (84 TL) ≯ #30 A (80 TL) ≯ #13 A (66 TL) ≷ #14 A (66 TL).

(viii) <u>Study period 8</u> (5/5/78 - 8/5/78) - <u>Composite Map 40</u>:

Social units A and B_1: #4 ♂/♀ A has disappeared from social unit B_1; #3 ♂ from social unit A has invaded and taken over social unit B, thus forming social unit C (= A + B_1):-

Social unit C: #3 ♂ (101 TL) > #8 A (88 TL) > #9 A (78 TL) ≯ #16 A (67 TL) ≯ #24 A (63 TL) / #18 A (62 TL) ≷ #20 A (61 TL) > #23 SA (53 TL) ≯ #26 SA (48 TL).

Social unit B_2: #27 ♂ (97 TL) > #12 A (89 TL) ≯ #30 A (85 TL) ≯ #13 A (74 TL) ≷ #14 A (73 TL).

(ix) <u>Study period 9</u> (1/7/78 - 3/7.78) - <u>Composite Map 41</u>:

Social unit C: #8 has changed sex (♀ → ♂) which has resulted in the social unit splitting into two smaller social units, C_1 and C_2:-

Social unit C_1: #8 ♂ (92 TL) > #24 A (72 TL).

Social unit C_2: #3 ♂ (101 TL) > #16 A (75 TL) > #18 A (70 TL) ≷ #20 A (70 TL).

Social unit B_2: #27 ♂ has disappeared; #12 has changed sex (♀ → ♂) and taken over control of the social unit:-

#12 ♂ (92 TL) > #13 A (78 TL) ≷ #14 A (78 TL).

(x) <u>Study period 10</u> (15/9/78 - 17.9.78) - <u>Composite Map 42</u>:

Social unit C_1: #8 ♂ (94 TL) > #24 A (80 TL).

Social unit C_2: #3 ♂ (102 TL) > #18 A (77 TL) ≷ #20 A (76 TL).

Social unit B_2: #12 ♂ (95 TL) > #13 A (84 TL) ≷ #14 A (84 TL).

2. <u>Experimental sites (male removal)</u>

(a) <u>Study site LHI</u>

(i) <u>1 day before removal</u> of #1 ♂ (25/5/78) - <u>Composite Map 43</u>:

#1 ♂ (115 TL) > #2 A (95 TL) > #4 A (75 TL) > #3 A (65 TL).

(ii) 5 days after removal of #1 ♂ (31/3/78) - Composite Map 44: #2 ♂/♀ A (95 TL) > #4 A (75 TL) > #3 A (65 TL).

(iii) 15 days after removal of #1 ♂ (10/6/78) - Composite Map 45: #2 ♂/♀ A (95 TL) > #4 A (76 TL) > #3 A (67 TL).

(iv) 30 days after removal of #1 ♂ (25/6/78) - Composite Map 46: #2 ♂ (95 TL) > #4 A (77 TL) > #3 A (69 TL).

(b) Study site SBI

(i) 1 day before removal of #3 ♂ (2/6/78) - Composite Map 47: #3 ♂ (88 TL) > #1 A (82 TL) ≹ #5 A (81 TL) > #6 A (76 TL) ≯ #2 A (57 TL) > #4 SA (50 TL).

(ii) 5 days after removal of #3 ♂ (8/6/78) - Composite Map 48: #1 ♂/♀ A (82 TL) ≹ #5 ♂/♀ A (81 TL) > #6 A (76 TL) ≯ #2 A (57 TL) > #4 SA (51 TL).

(iii) 15 days after removal of #3 ♂ (18/6/78) - Composite Map 49: The social unit has divided into two small social units, A and B -

Social unit A: #1 ♂/♀ A (83 TL) > #2 A (60 TL) > #4 SA (53 TL).

Social unit B: #5 ♂/♀ A (81 TL) > #6 A (77 TL).

(iv) 30 days after removal of #3 ♂ (3/7/78) - Composite Map 50:

Social unit A: #1 ♂ (83 TL) > #2 A (62 TL) > #4 A (56 TL).

Social unit B: #5 ♂ (81 TL) > #6 A (78 TL).

(c) Study site BMI

(i) 1 day before removal of #6 ♂ (28/5/78) - Composite Map 51: #6 ♂ (96 TL) > #3 A (80 TL) > #4 A (75 TL) > #1 A (71 TL) > #2 A (66 TL) > #5 A (60 TL).

(ii) 5 days after removal of #6 ♂ (3/6/78) - Composite Map 52: #3 ♂/♀ A (80 TL) > #4 A (75 TL) > #1 A (71 TL) > #2 A (66 TL) > #5 A

(60 TL).

(iii) 15 days after removal of #6 ♂ (13/6/78) - Composite Map 53: #3 ♂/♀ A (80 TL) > #4 A (76 TL) > #1 A (72 TL) > #2 A (67 TL) > #5 A (61 TL).

(iv) 30 days after removal of #6 ♂ (28/6/78) - Composite Map 54: #3 ♂ (81 TL) > #4 A (77 TL) > #1 A (73 TL) > #2 A (69 TL) > #5 A (63 TL).

APPENDIX 2

Composite territory maps of regularly mapped *P. cylindrica* social units

KEY:

(i) #1, 2, 3, ... #n = identity number of an individual within a particular study site (refer to Appendix 1 for data on size and status).

(ii) ✖ = Border dispute site.

(iii) Territory boundaries:

- - - - = Males

▬ = Dominant or Codominant adult females

▬ or ▬ = Other adult females

▬ = Subadult females

▬ = Juvenile females

(iv) Substrata:

▥ = Living hard coral - massive or encrusting

▩ = Living hard coral - staghorn *Acropora* spp.

▦ = Dead hard coral

▒ = Soft coral (Alcyonaria)

⚘ = Macroscopic algal clump

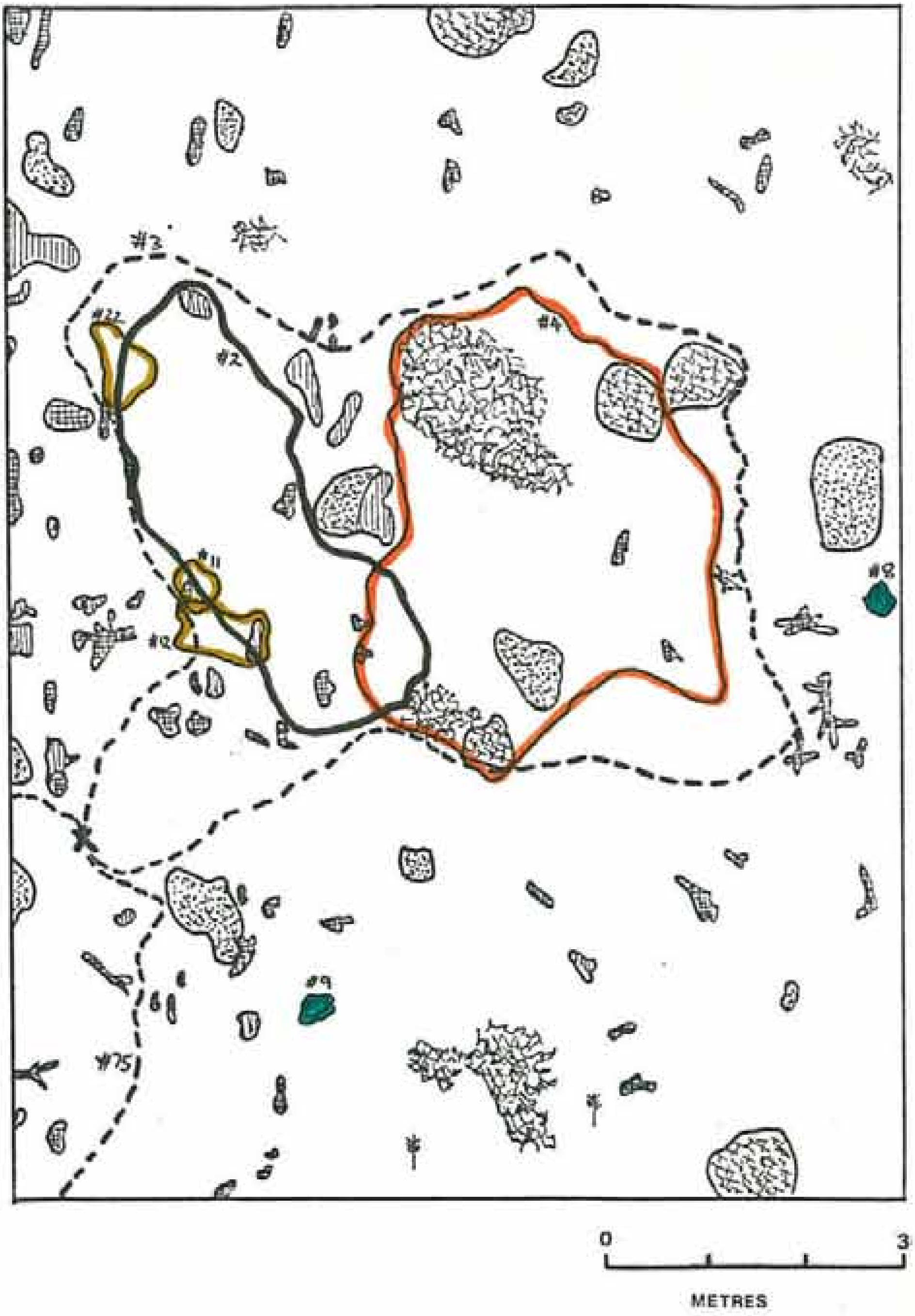
Ⓐ = Sea anemone

⬯ = *Tridacna* clam

Y = Sponge

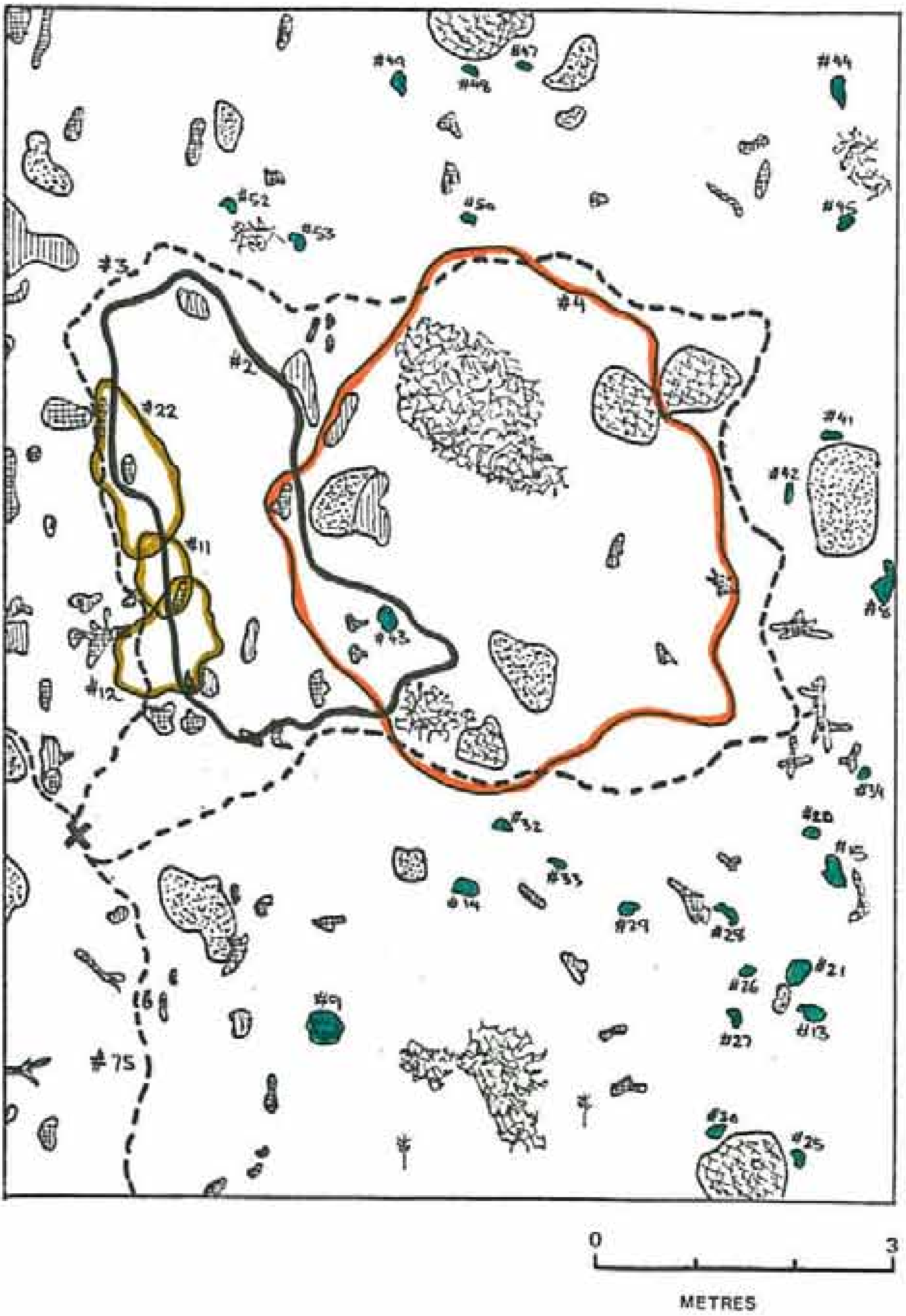
COMPOSITE MAP 1

STUDY SITE G_8 : STUDY PEROD 1



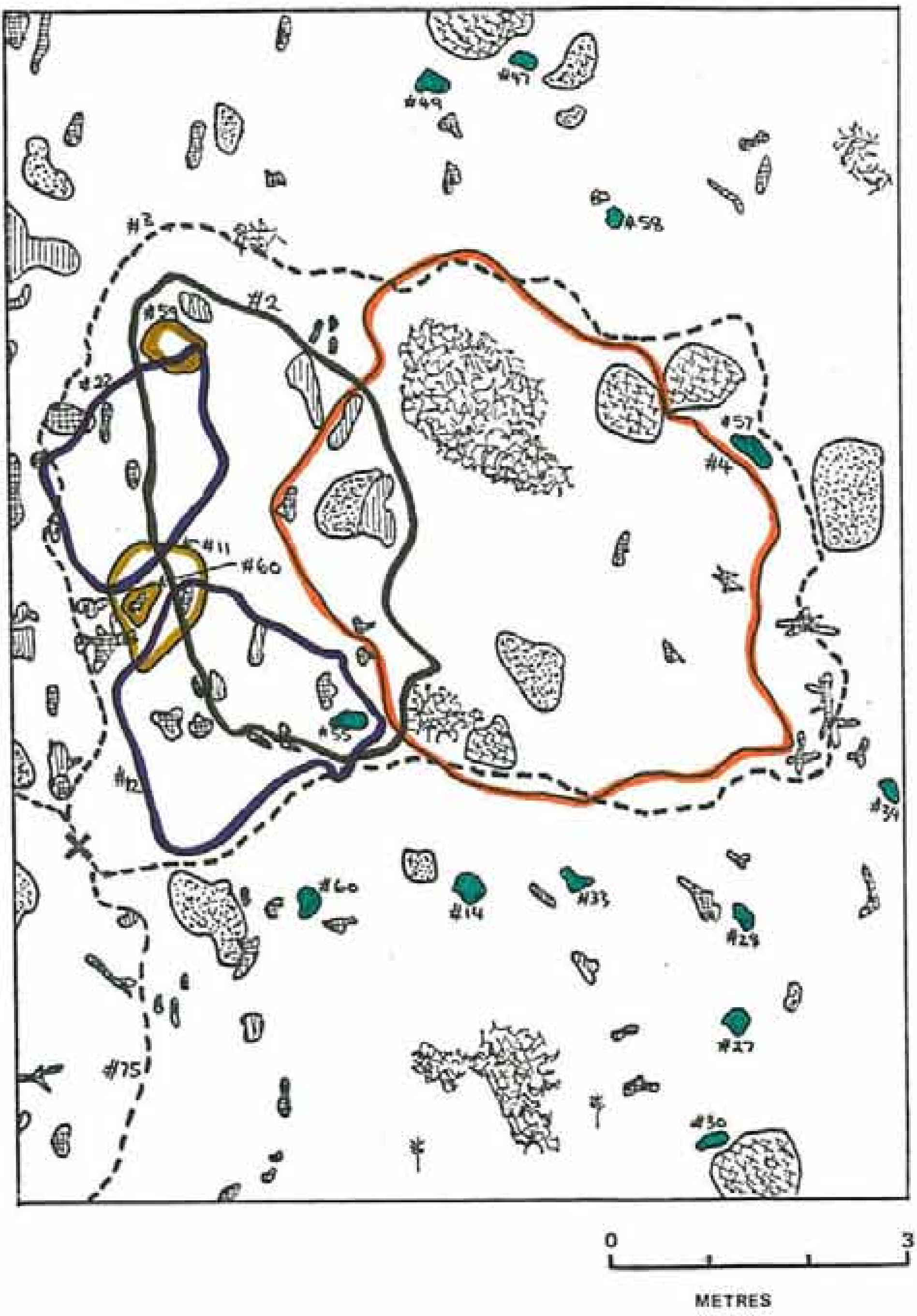
COMPOSITE MAP 2

STUDY SITE G_8 : STUDY PERIOD 2



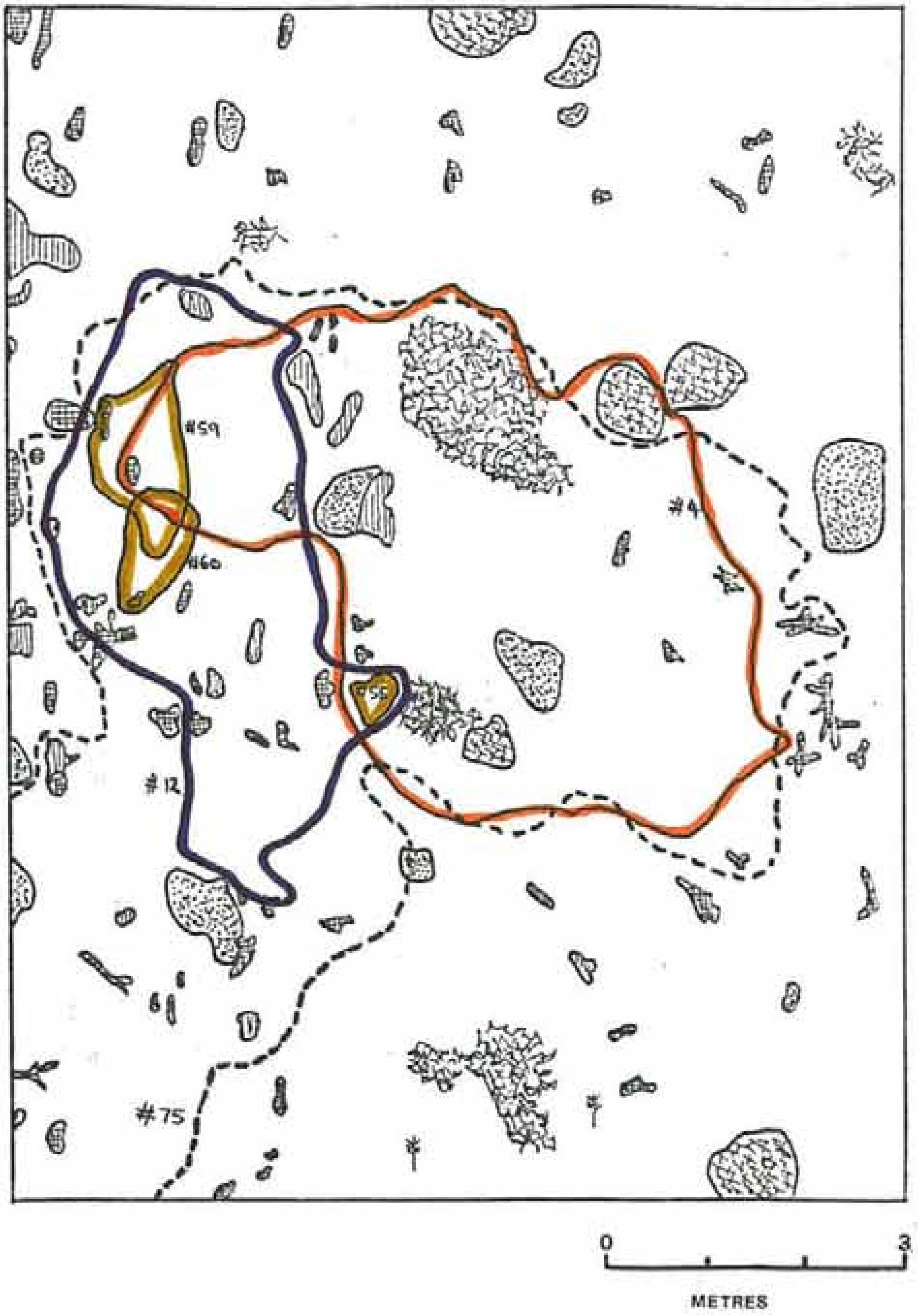
COMPOSITE MAP 3

STUDY SITE G$_8$: STUDY PERIOD 3



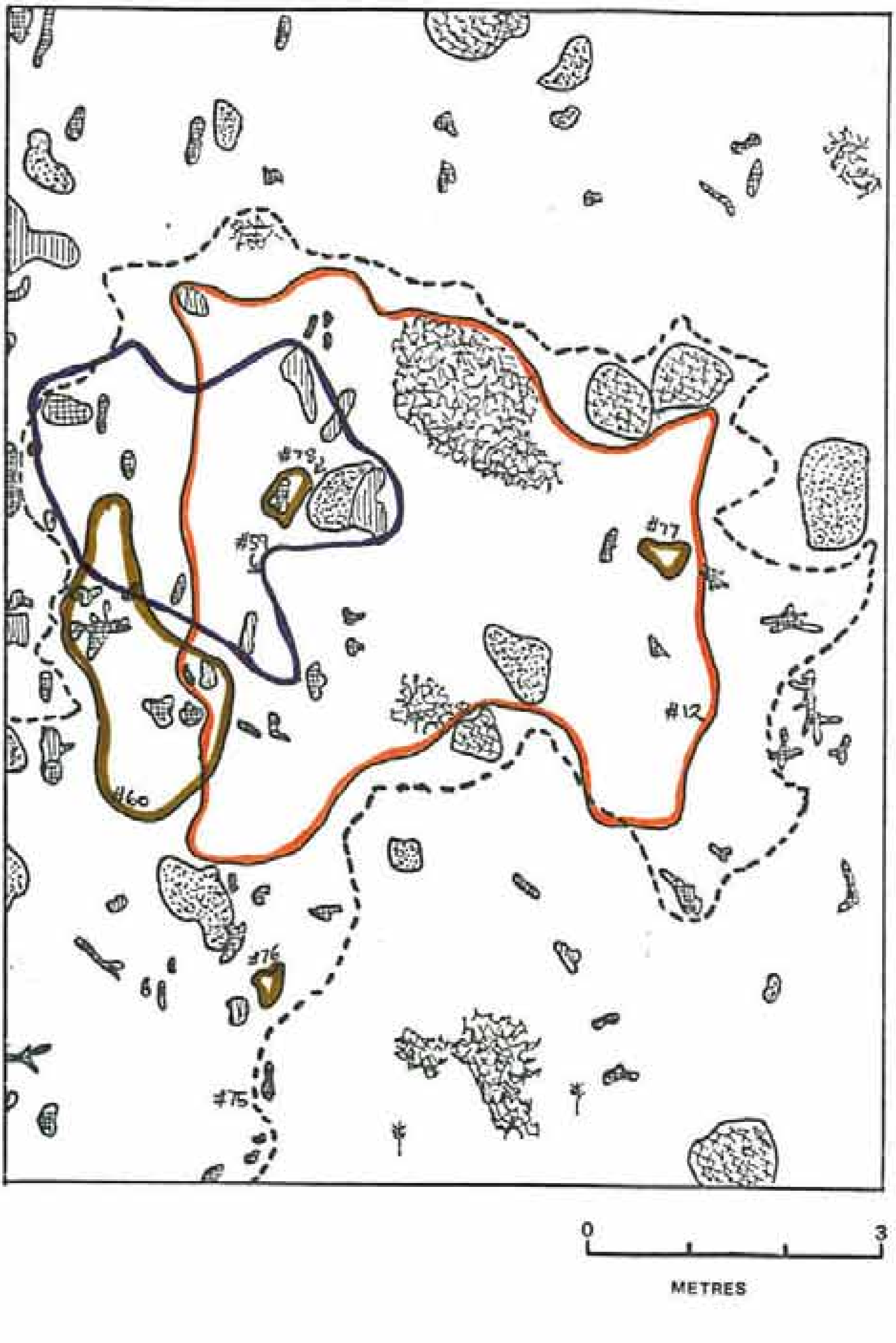
COMPOSITE MAP 4

STUDY SITE G_8 : STUDY PERIOD 4



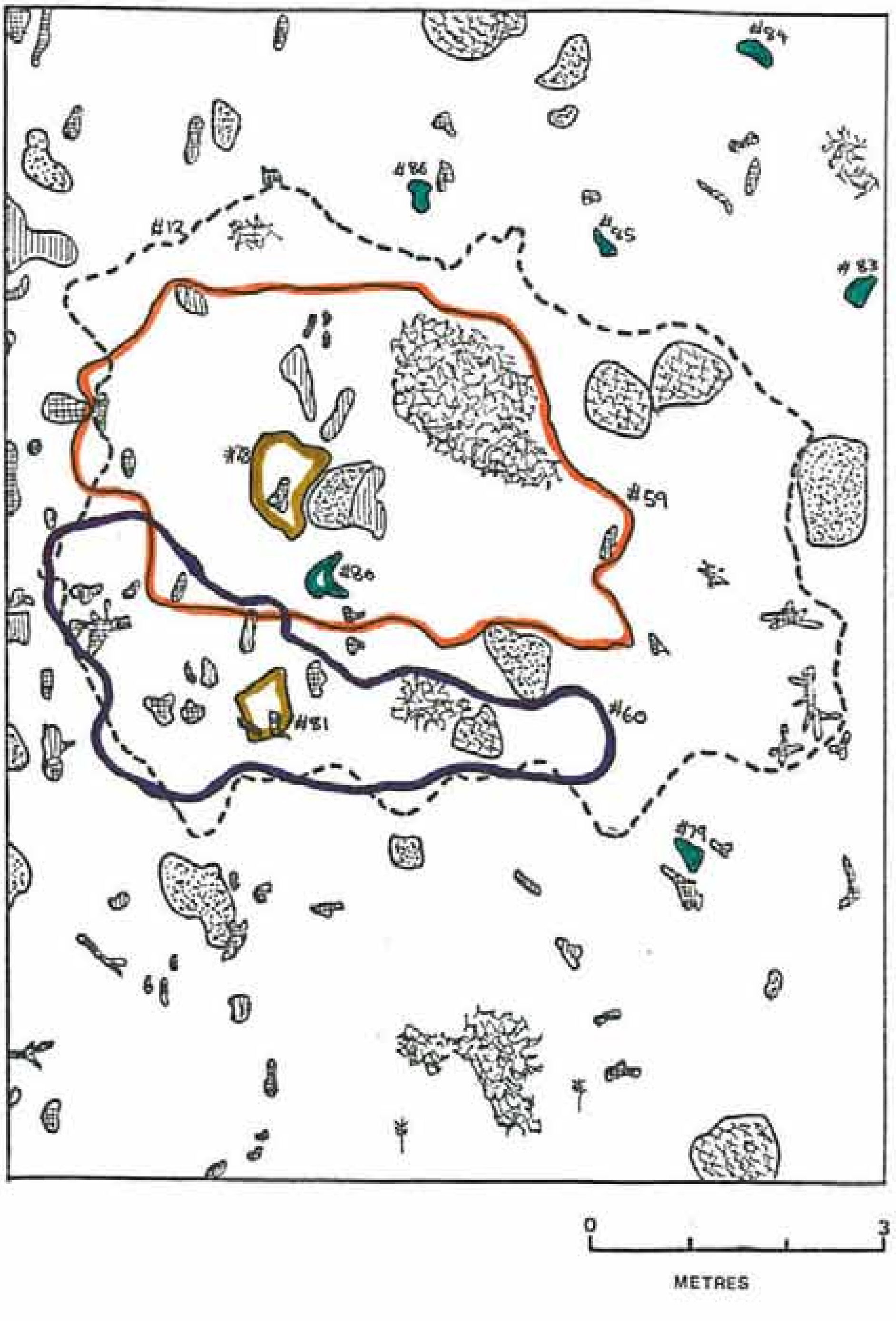
COMPOSITE MAP 5

STUDY SITE G_8 : STUDY PERIOD. 5



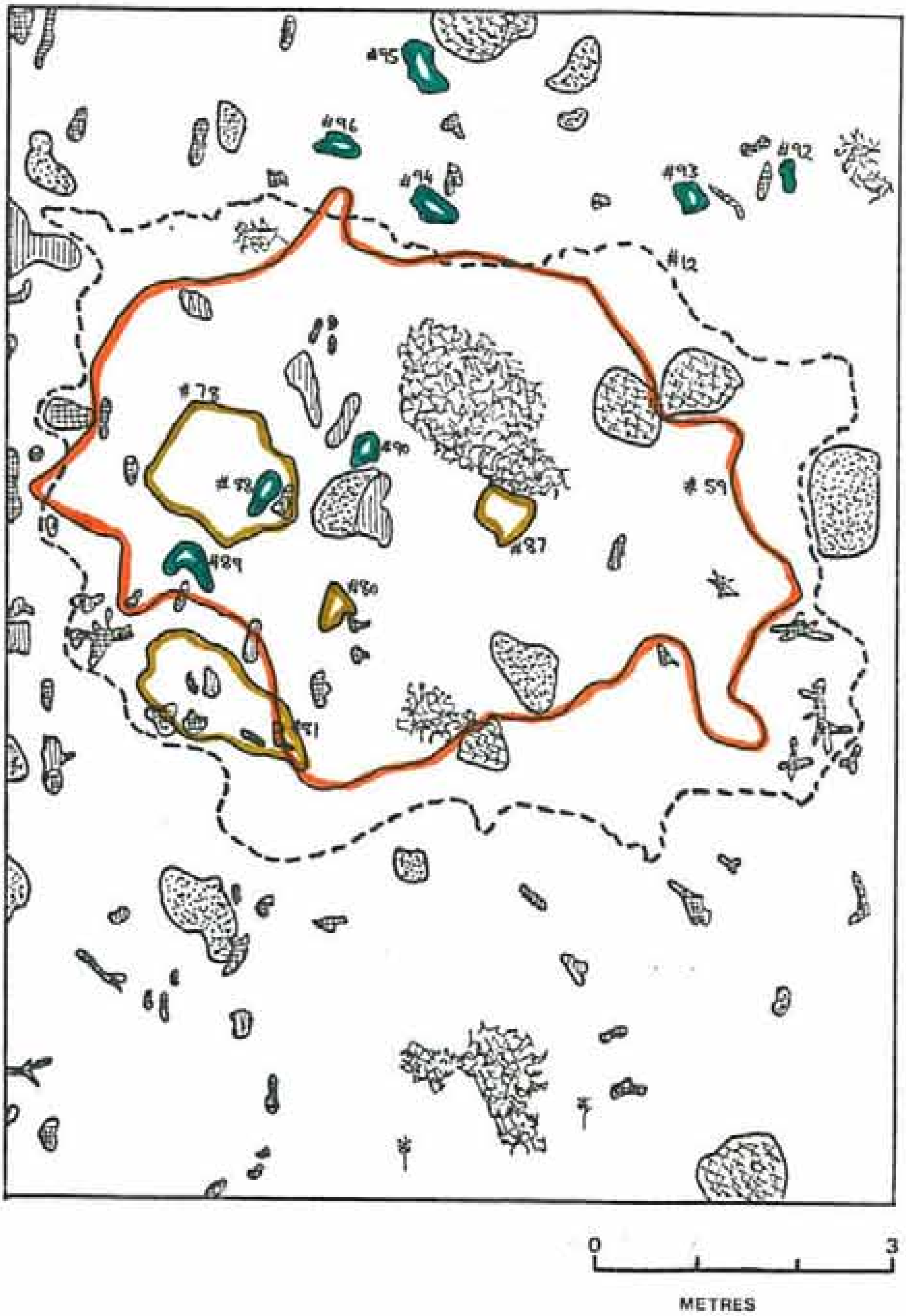
COMPOSITE MAP 6

STUDY SITE G_8 : STUDY PERIOD. 6



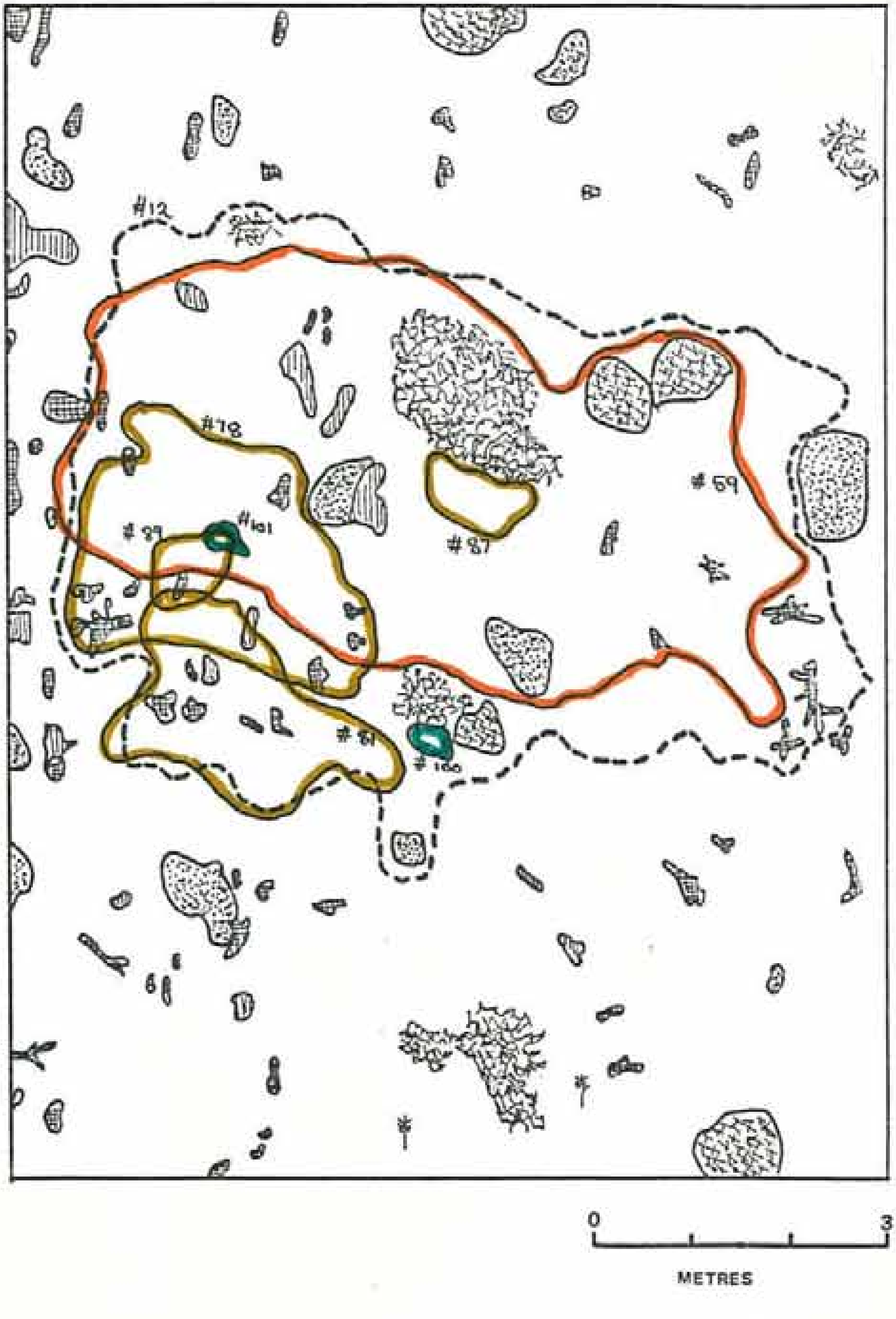
COMPOSITE MAP 7

STUDY SITE G_8 : STUDY PERIOD. 7



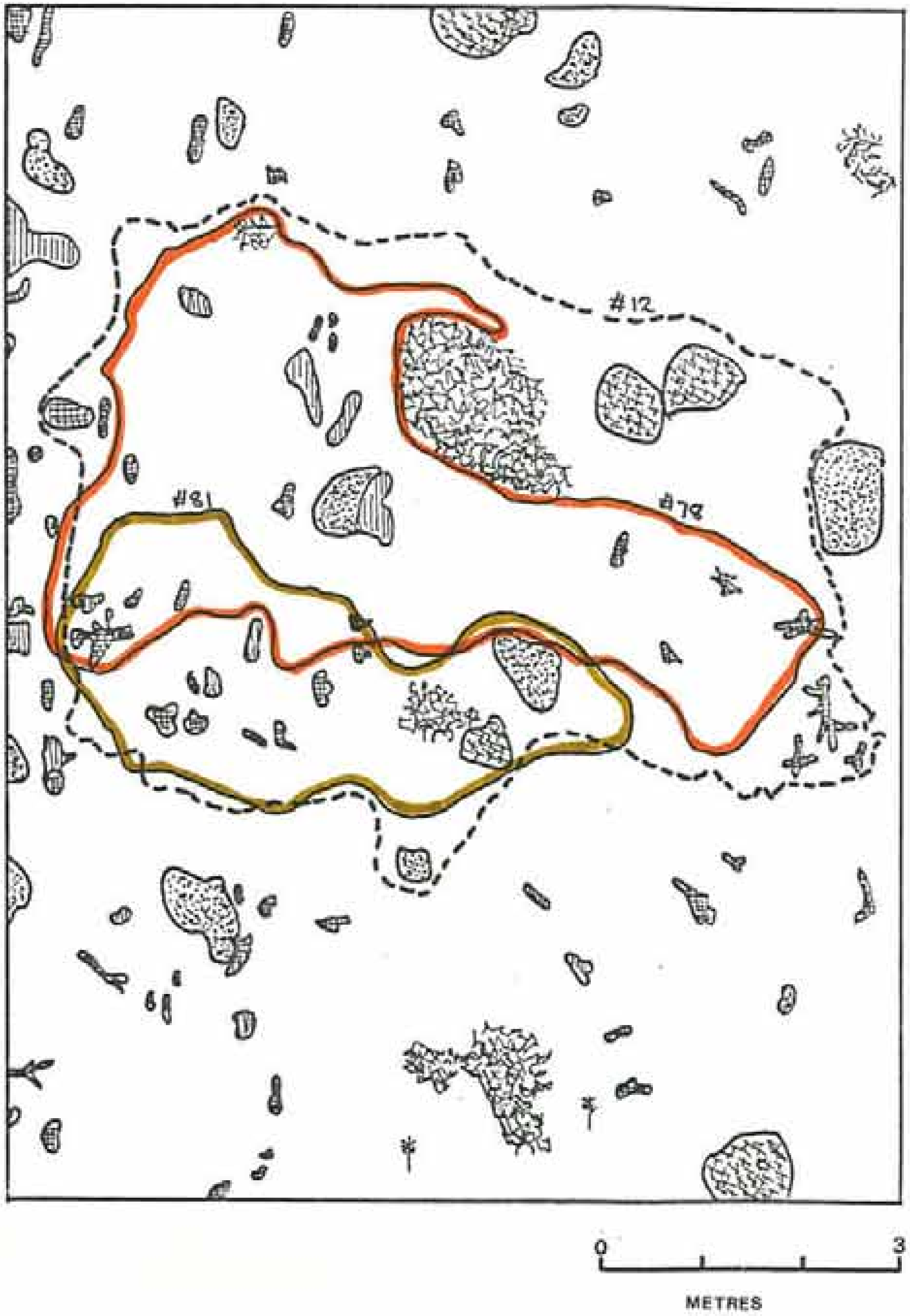
COMPOSITE MAP 8

STUDY SITE G8 : STUDY PERIOD 8



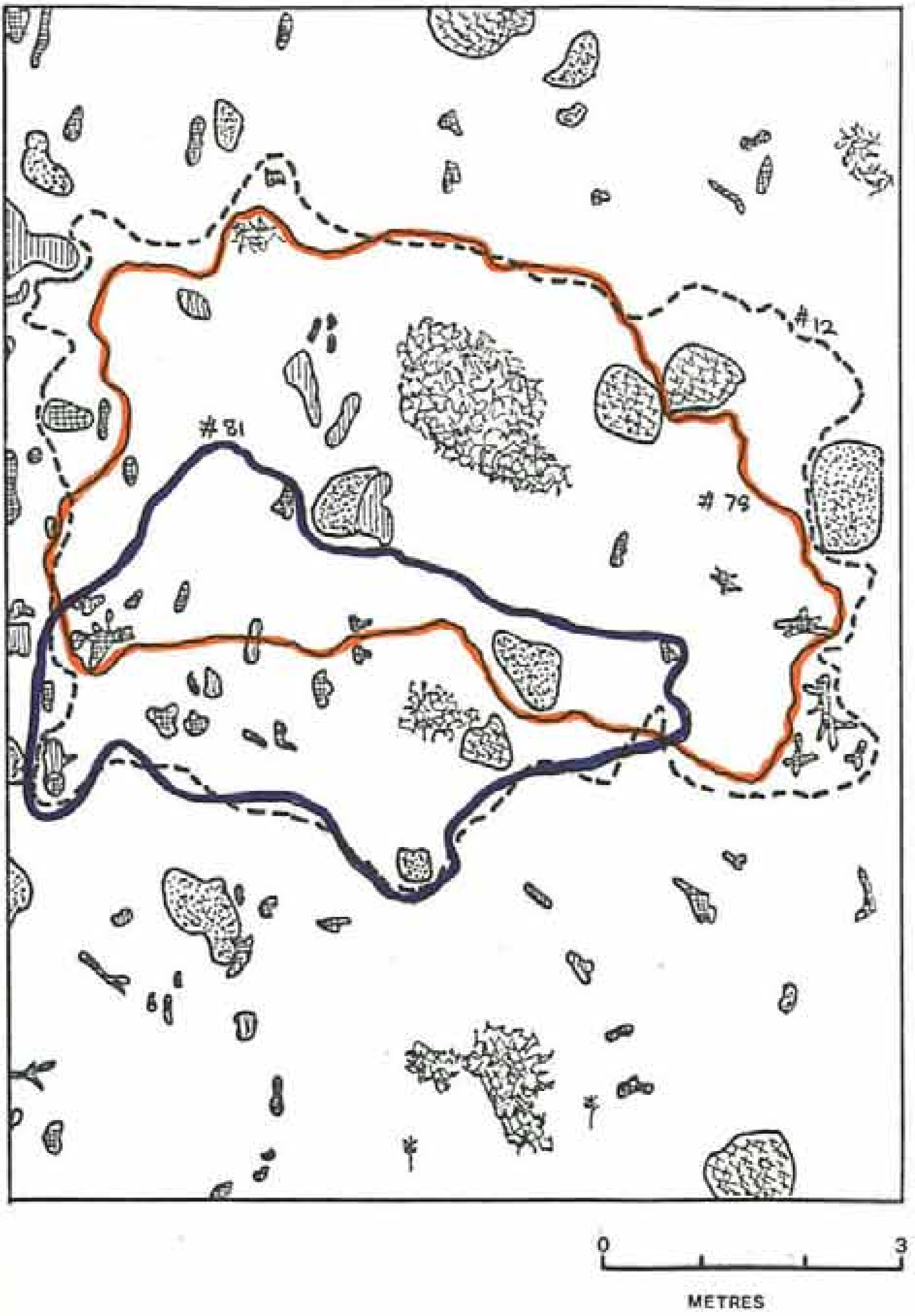
COMPOSITE MAP 9

STUDY SITE G_8 : STUDY PERIOD 9



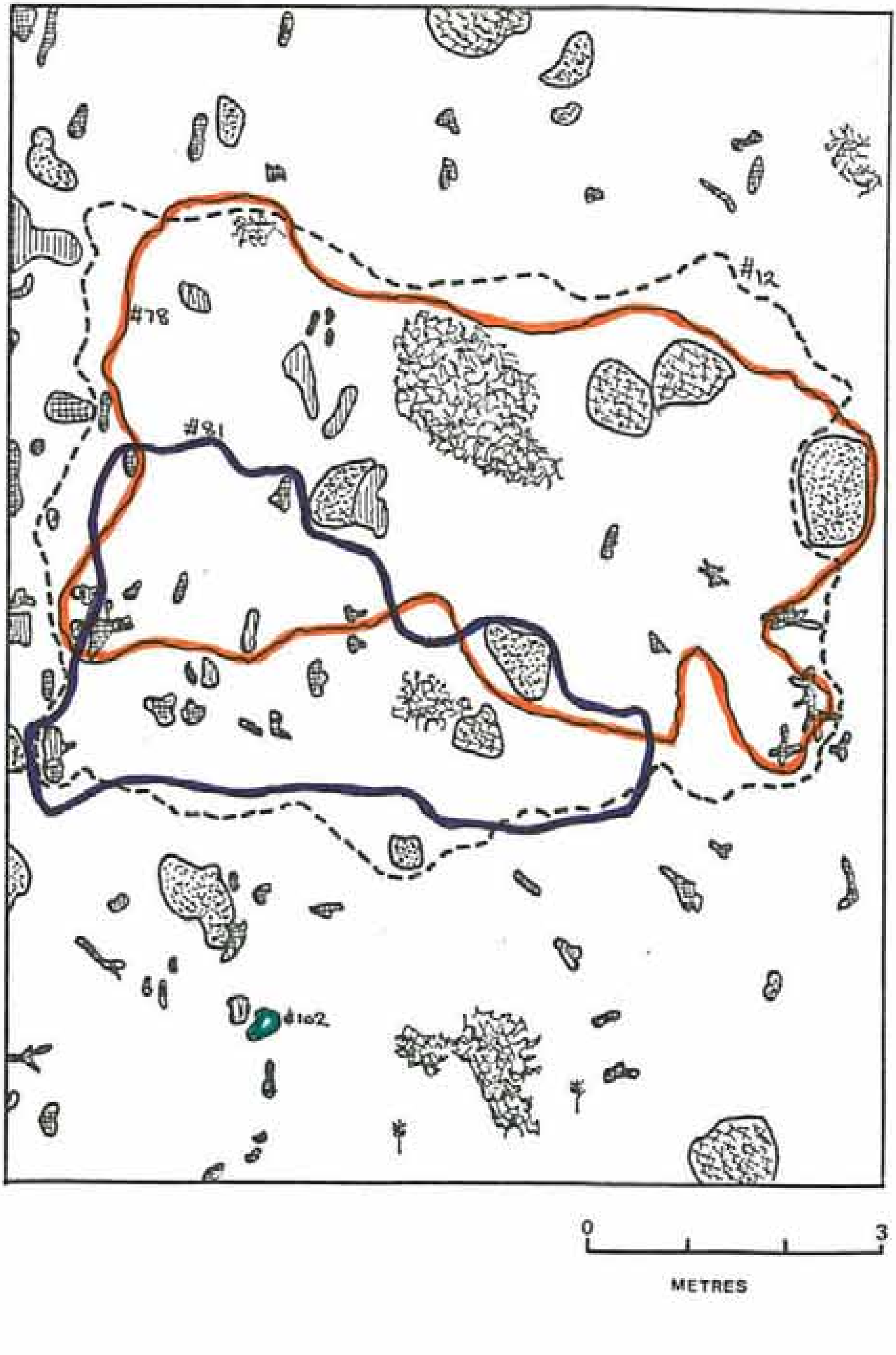
COMPOSITE MAP 10

STUDY SITE G_8 : STUDY PERIOD 10



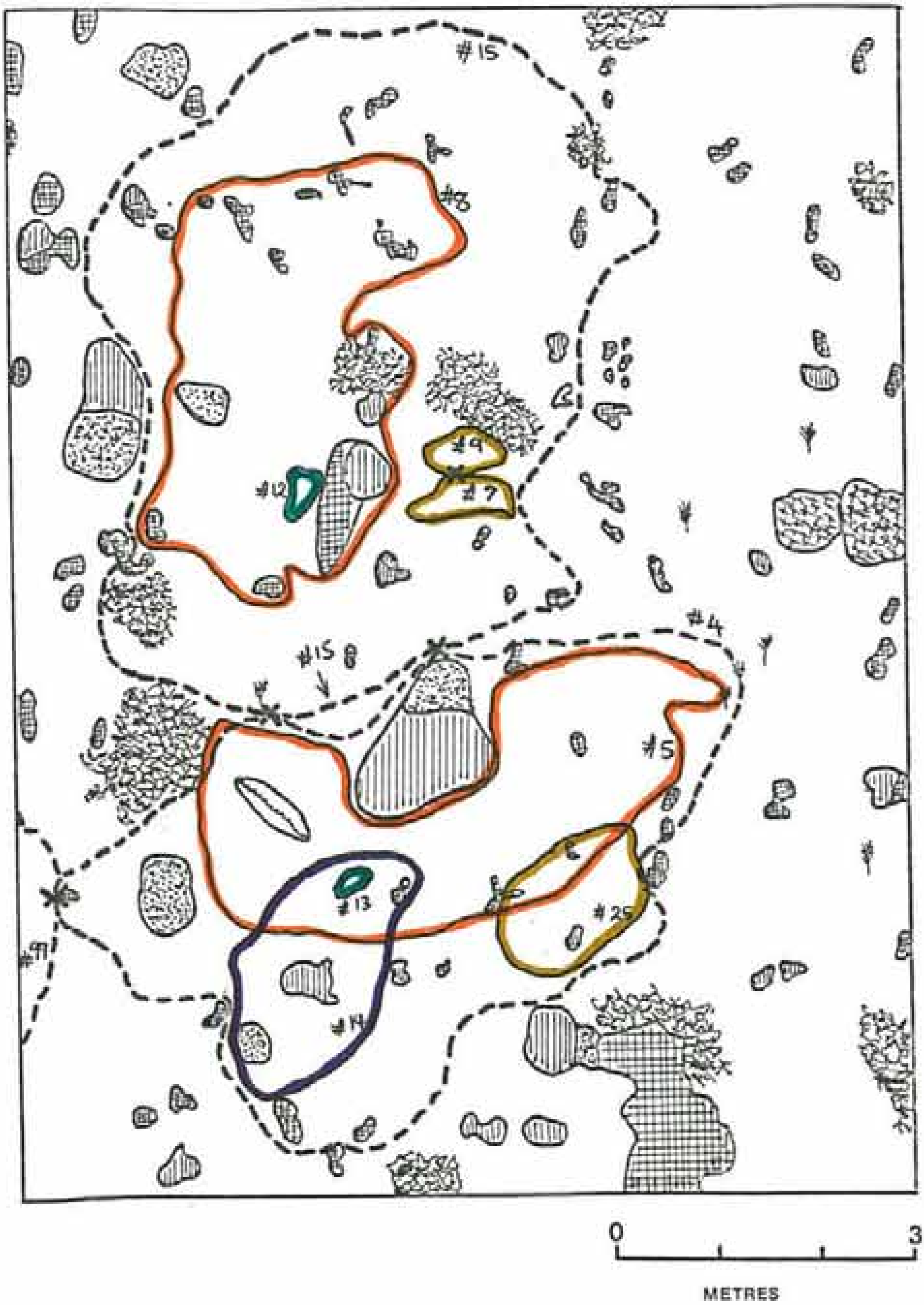
COMPOSITE MAP 11

STUDY SITE G_8 : STUDY PERIOD 11



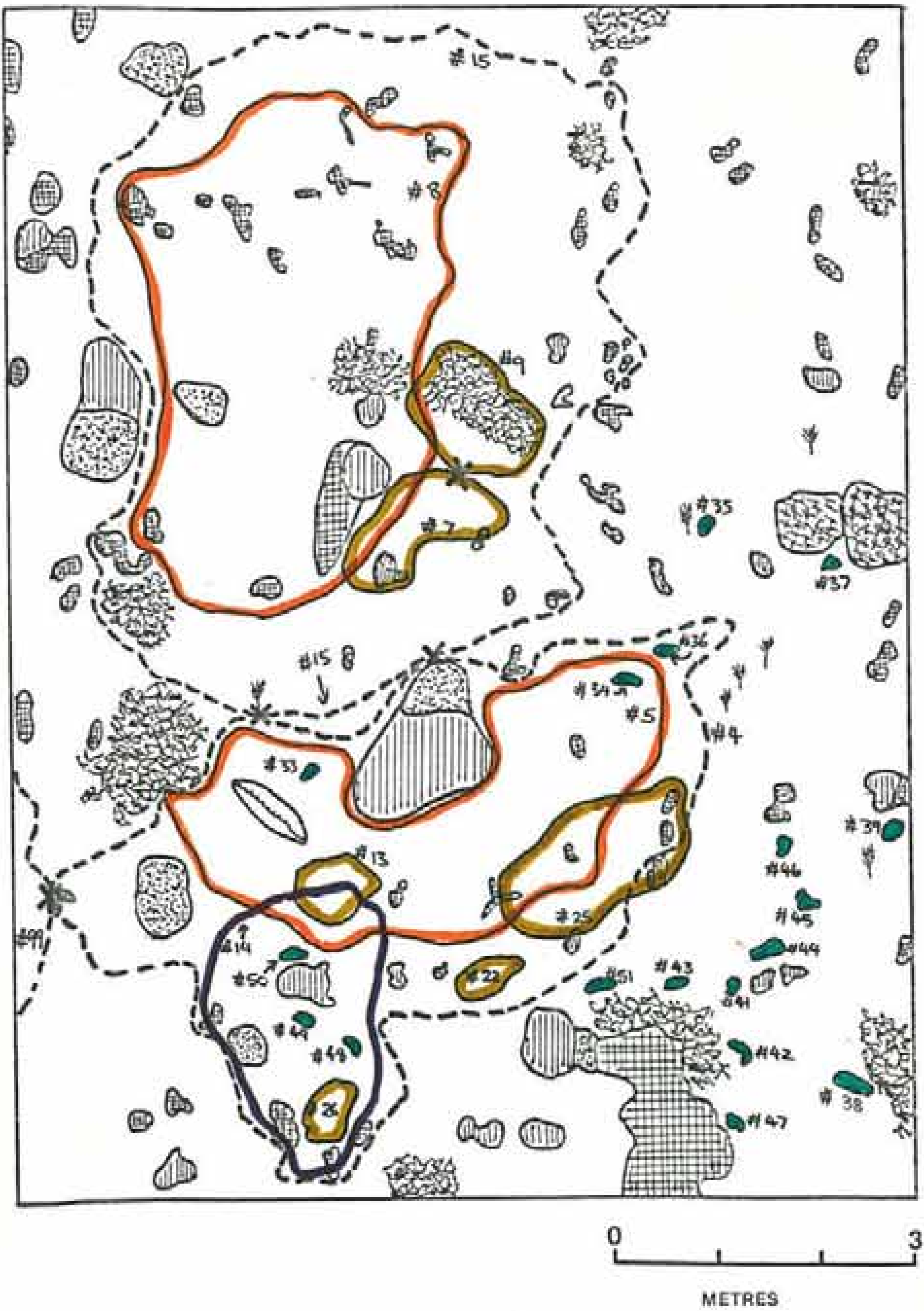
COMPOSITE MAP 12

STUDY SITE G_{10} : STUDY PERIOD 1



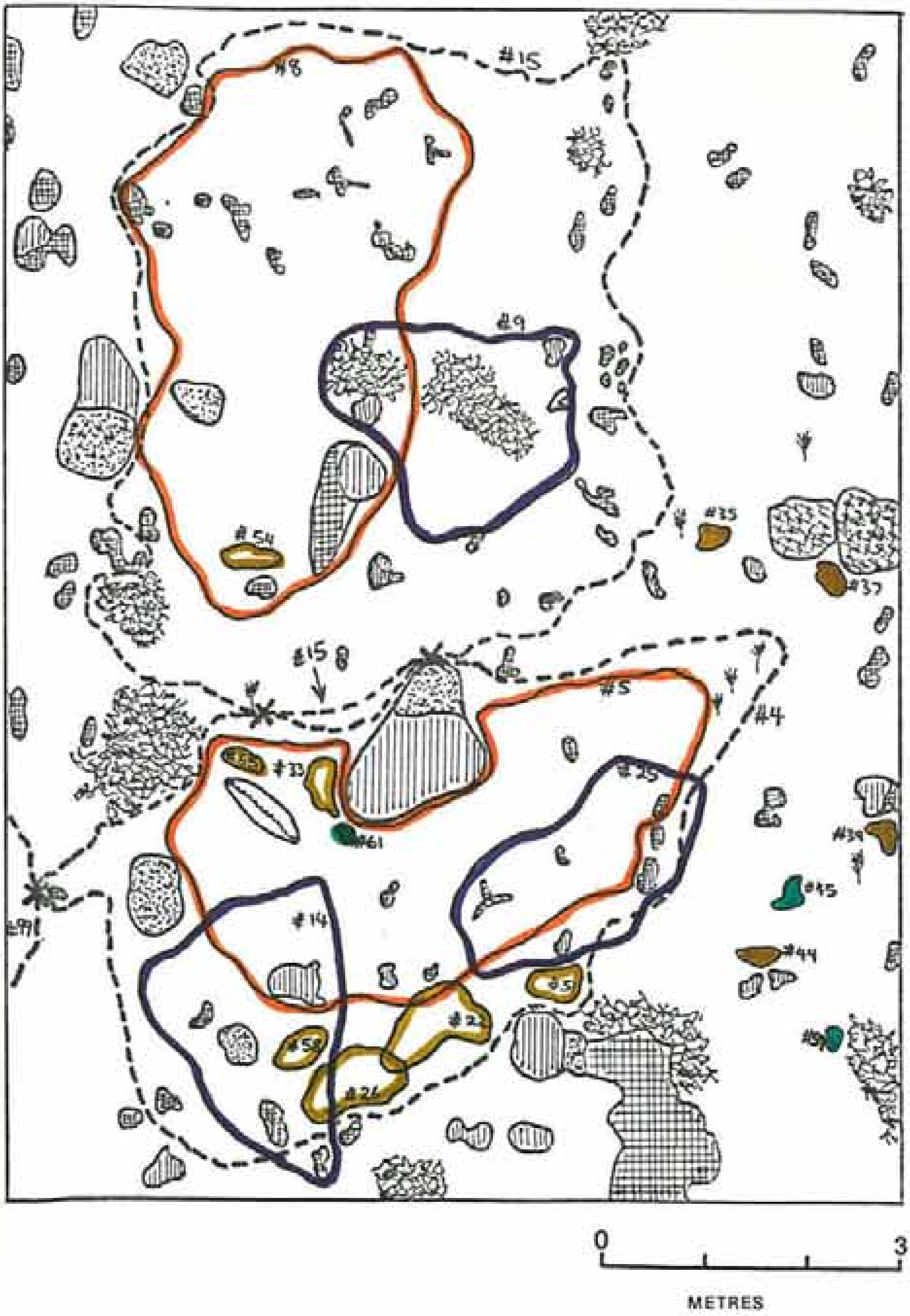
COMPOSITE MAP 13

STUDY SITE G_{10} : STUDY PERIOD 2



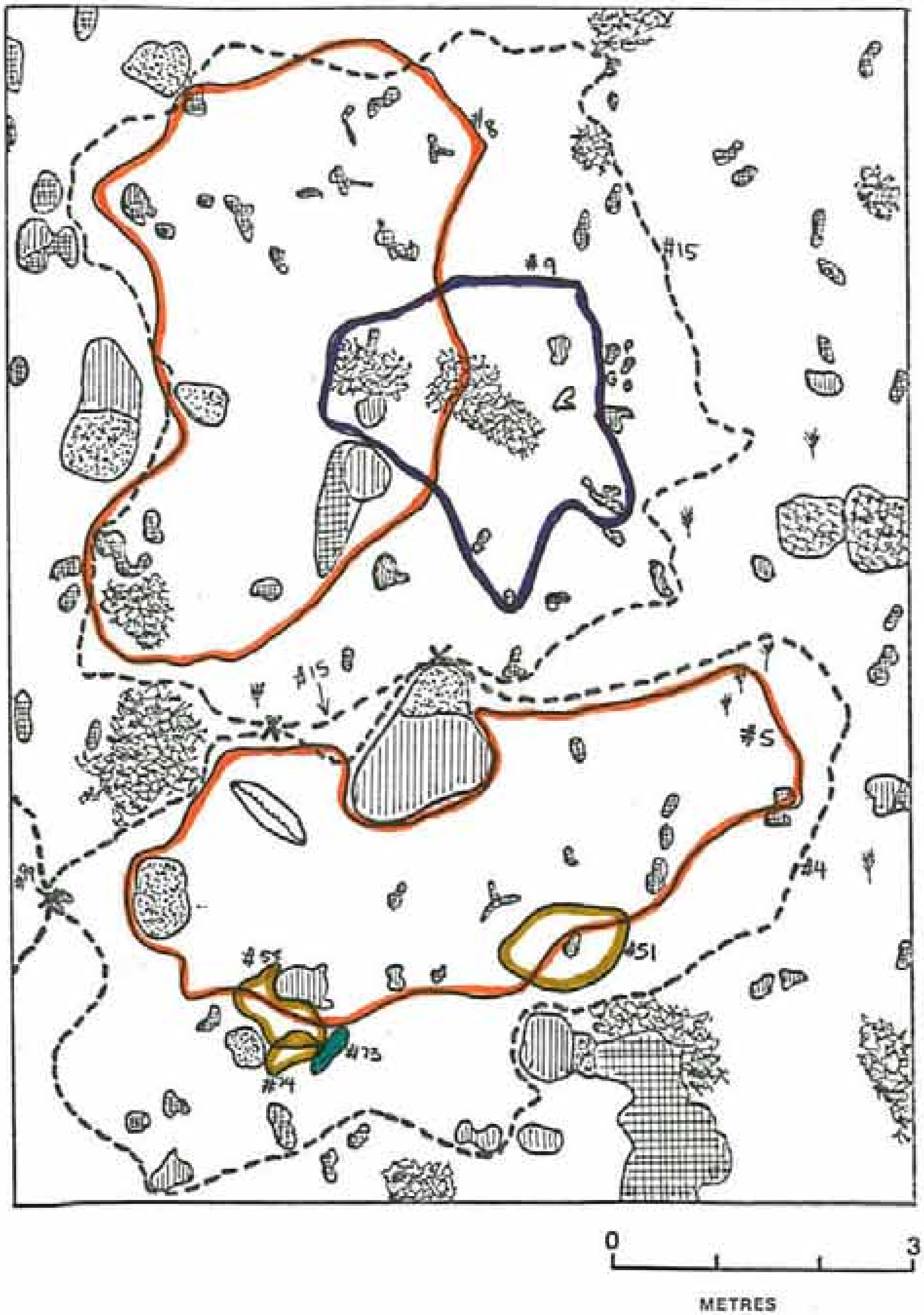
COMPOSITE MAP 14

STUDY SITE G_{10} : STUDY PERIOD 3



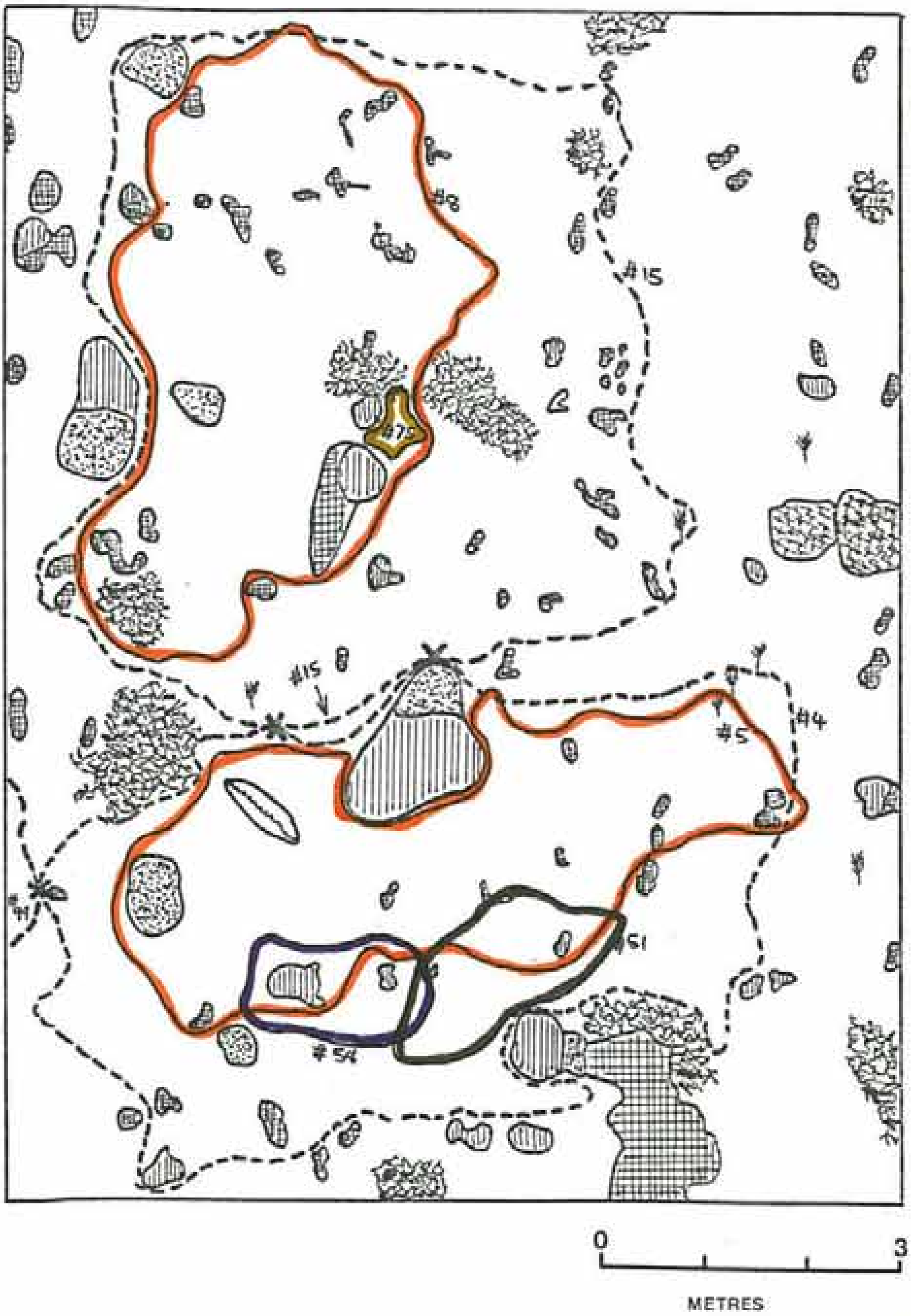
COMPOSITE MAP 15

STUDY SITE G_{10} : STUDY PERIOD 4



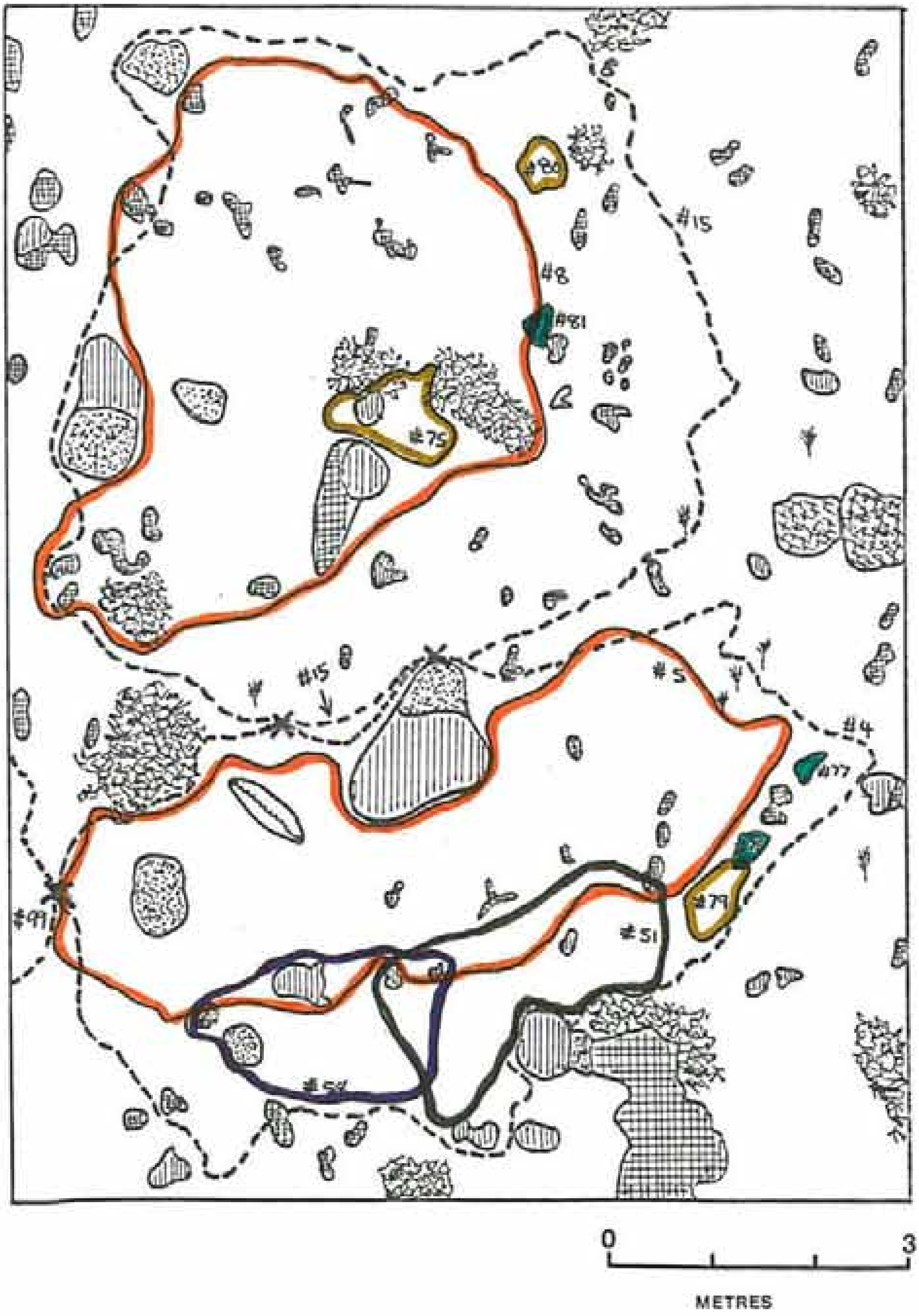
COMPOSITE MAP 16

STUDY SITE G_{10} : STUDY PERIOD 5



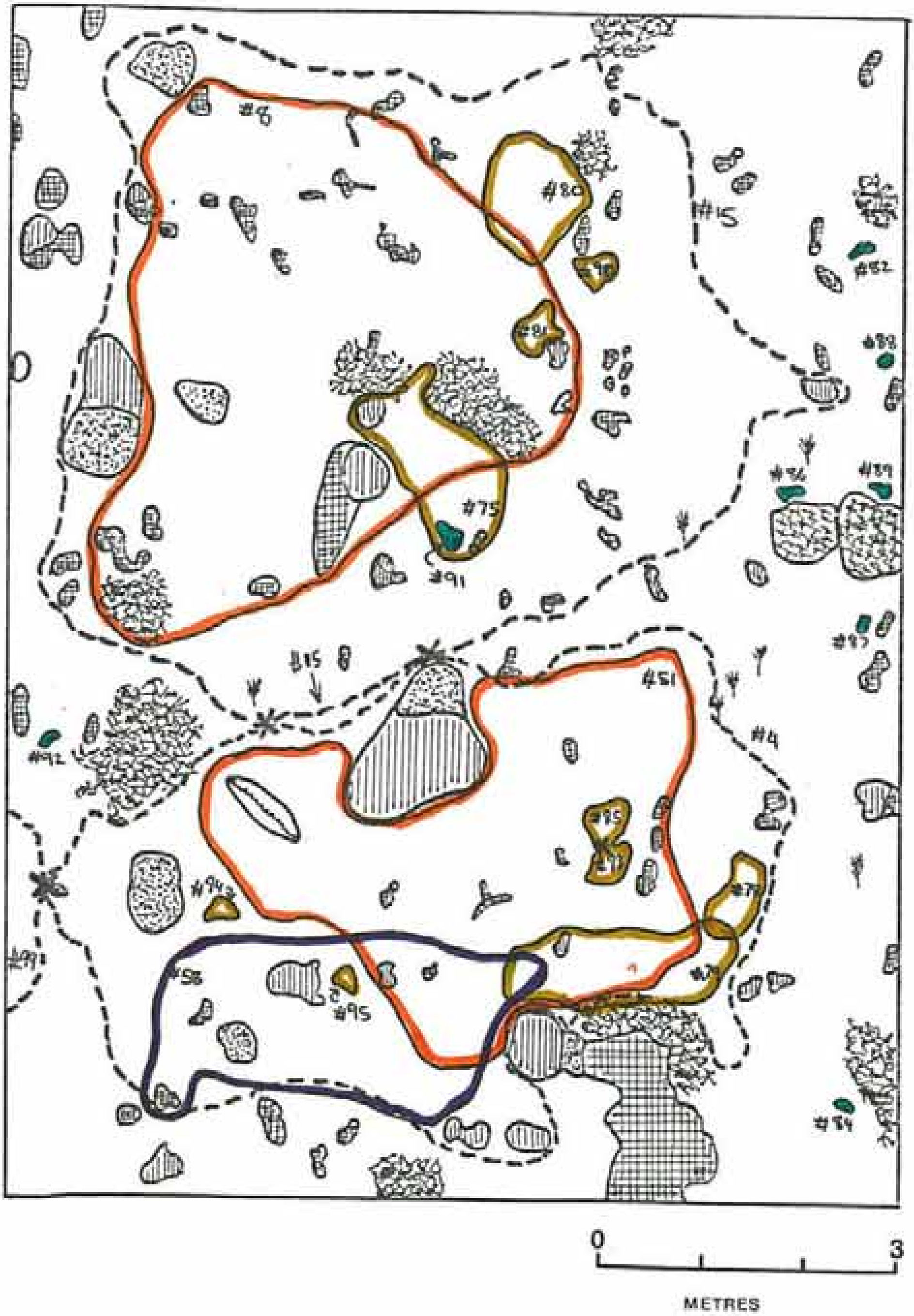
COMPOSITE MAP 17

STUDY SITE G_{10} : STUDY PERIOD 6



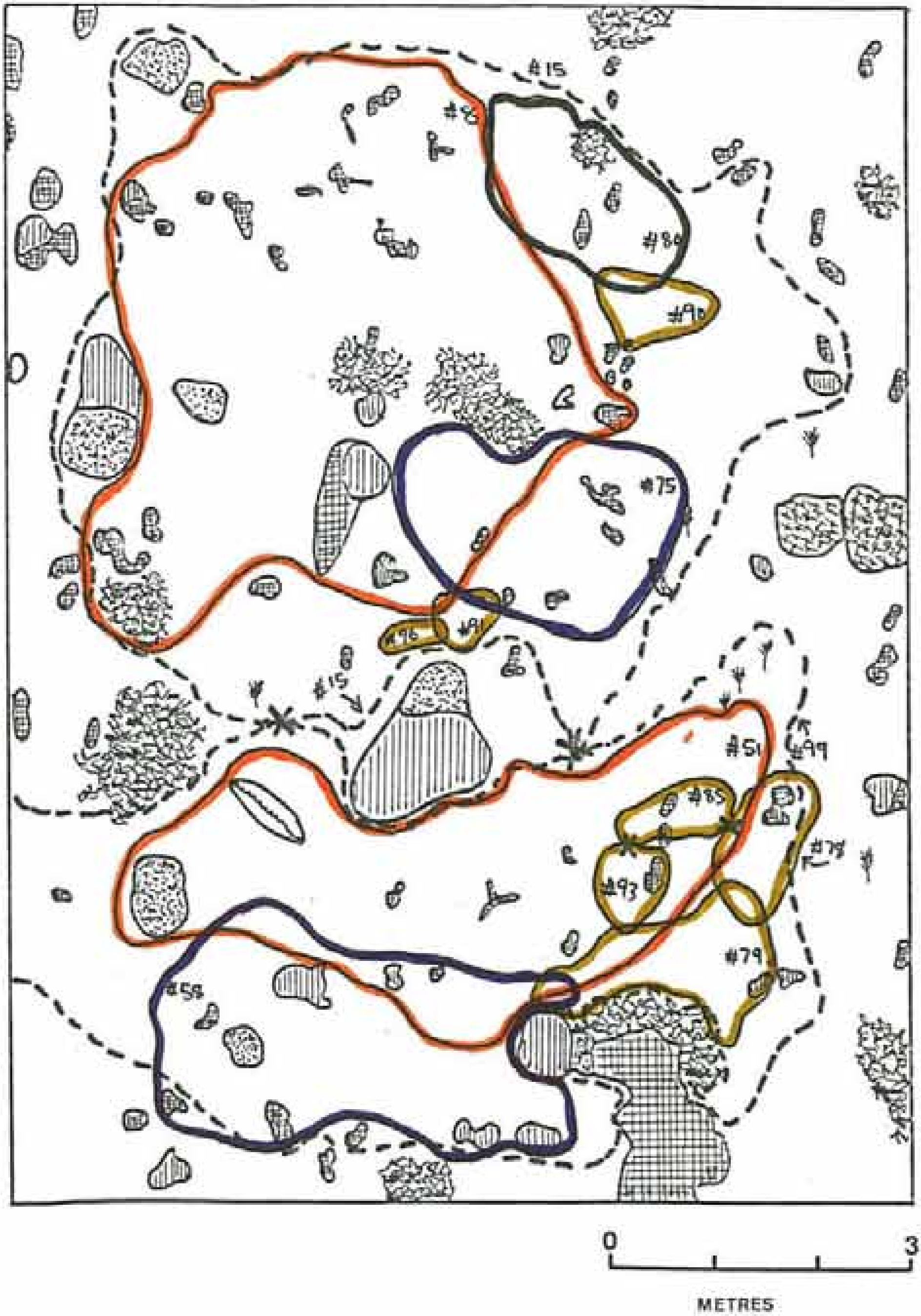
COMPOSITE MAP 18

STUDY SITE G_{10} : STUDY PERIOD 7



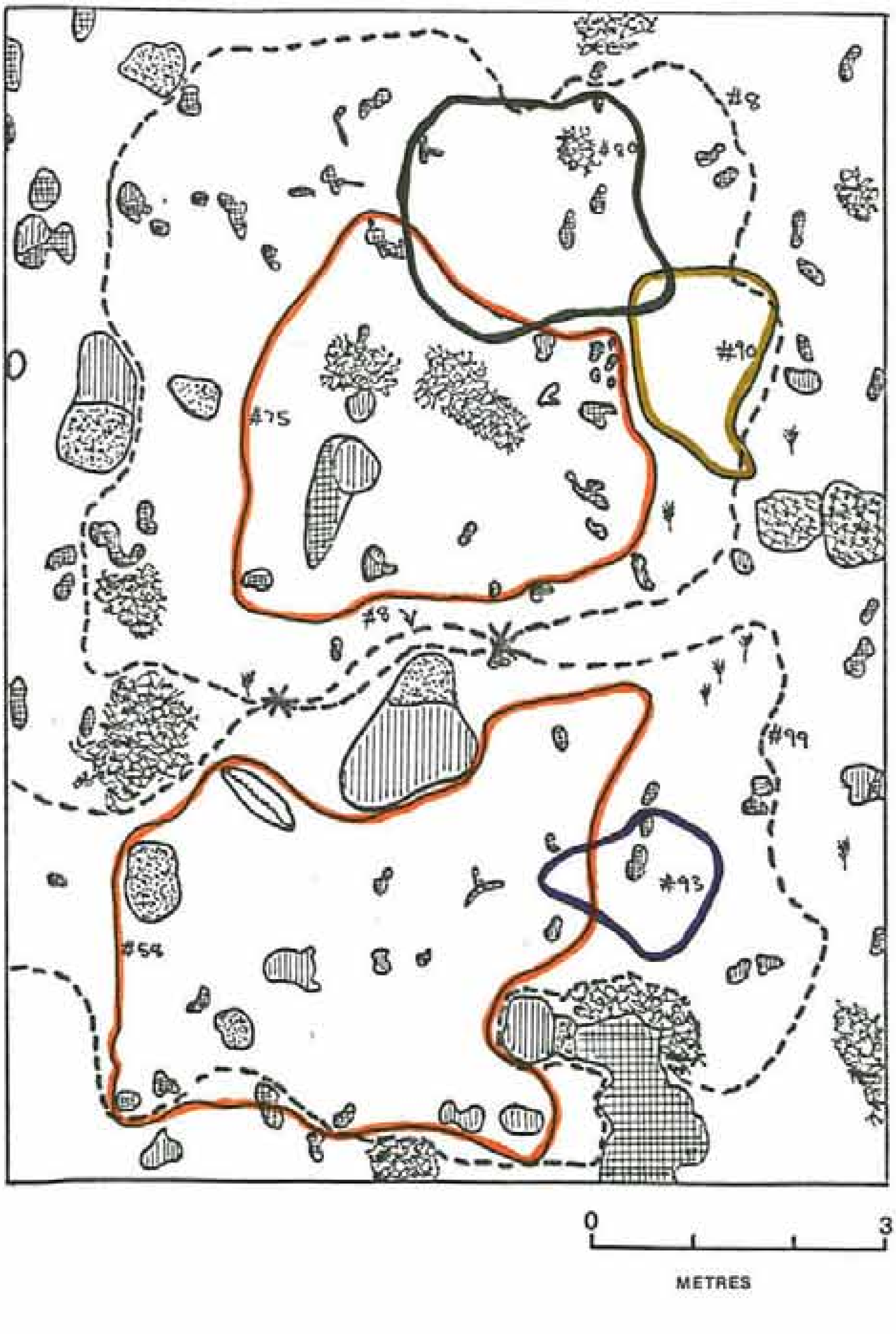
COMPOSITE MAP 19

STUDY SITE G_{10} : STUDY PERIOD 8



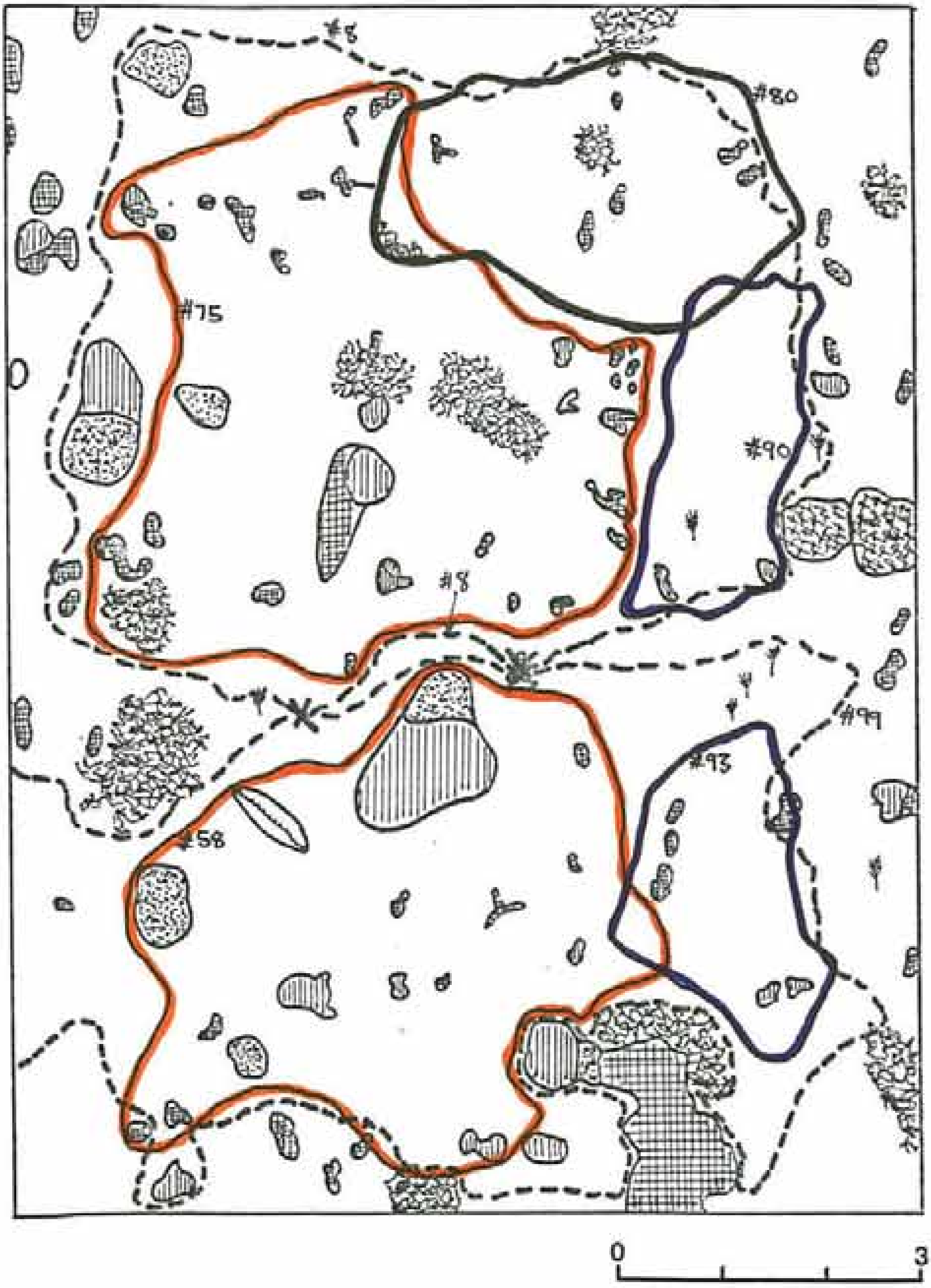
COMPOSITE MAP 20

STUDY SITE G_{10} : STUDY PERIOD 9



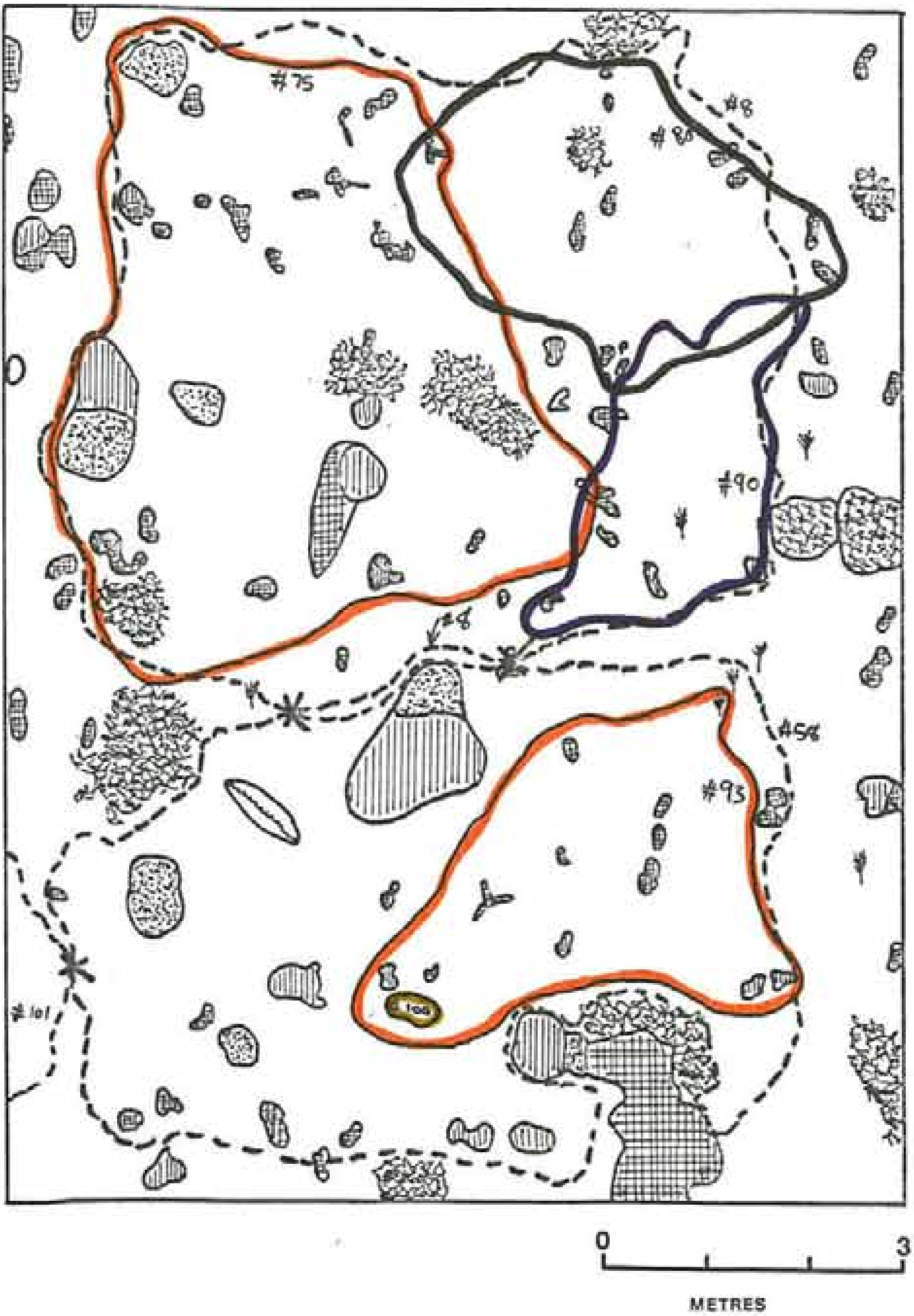
COMPOSITE MAP 21

STUDY SITE G_{10} : STUDY PERIOD 10



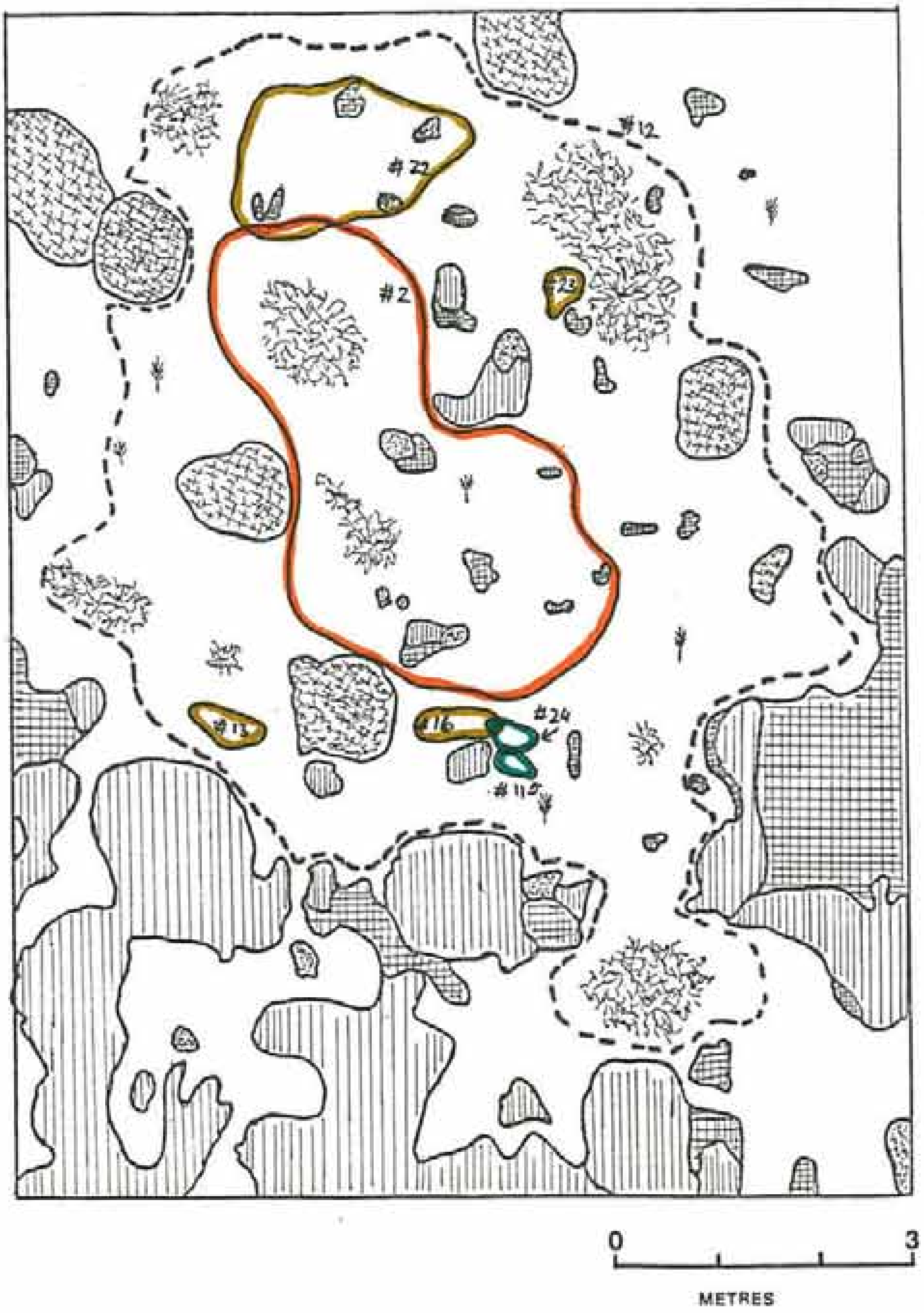
COMPOSITE MAP 22

STUDY SITE G_{10} : STUDY PERIOD II



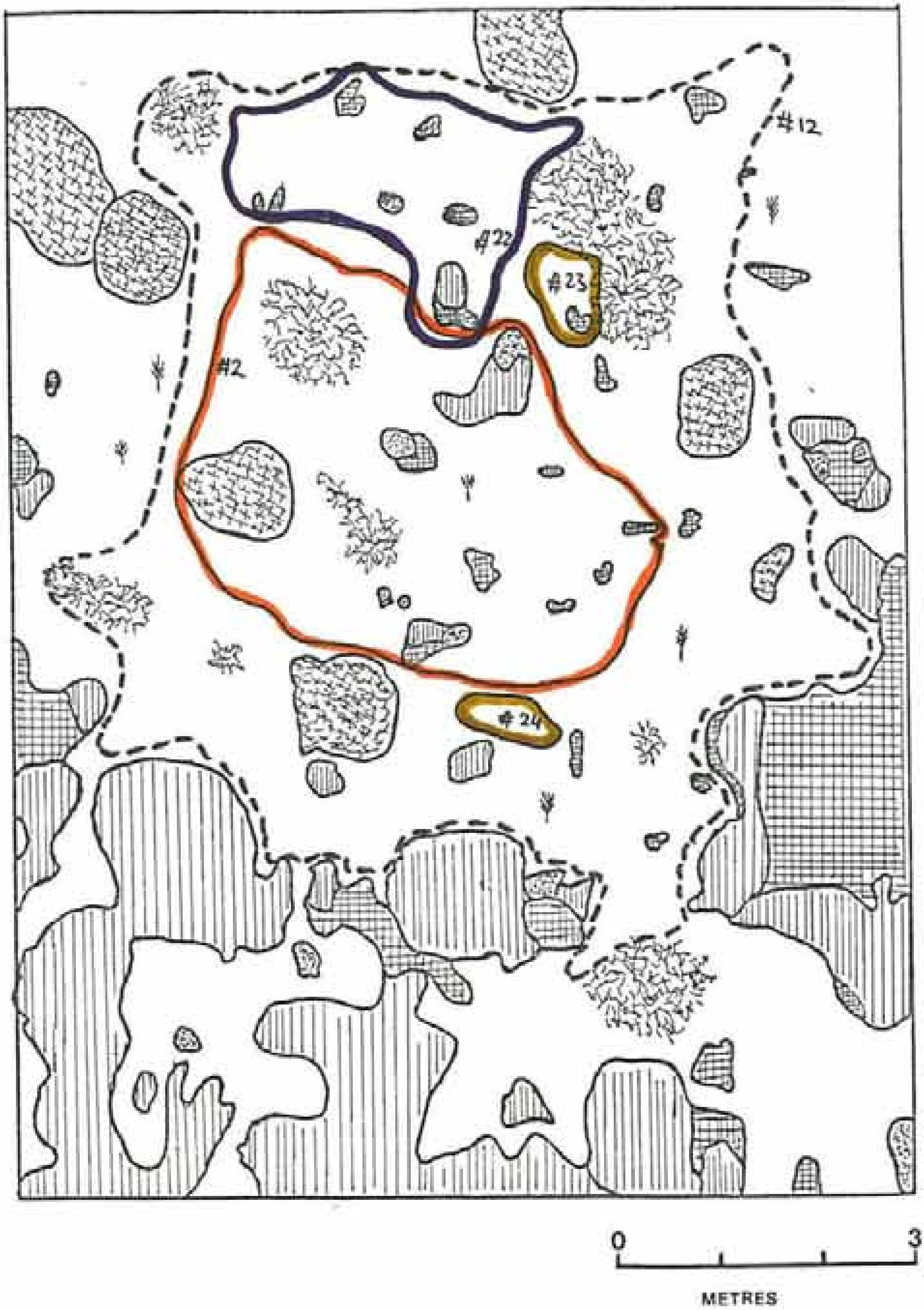
COMPOSITE MAP 23

STUDY SITE G_{14} : STUDY PERIOD 1



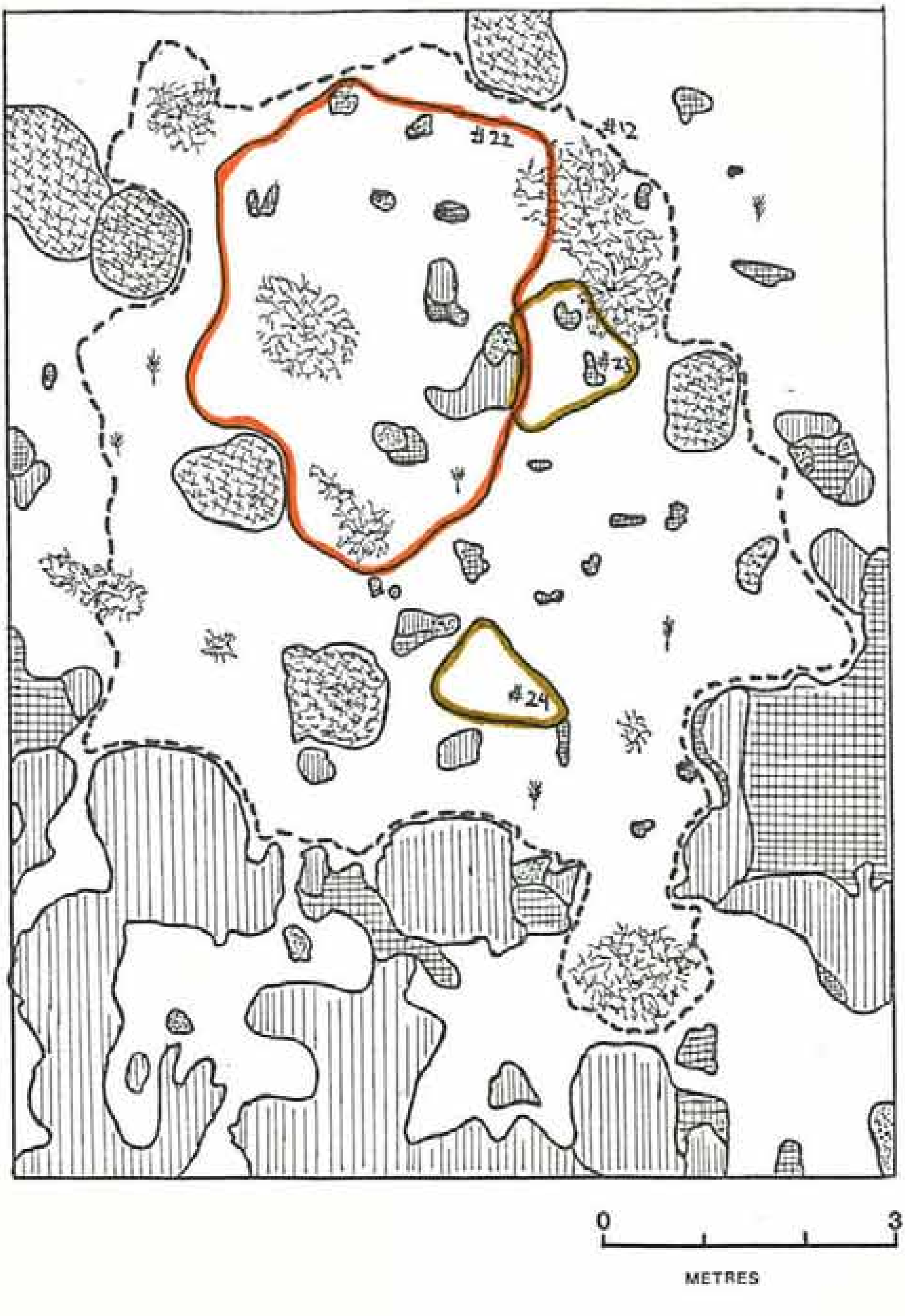
COMPOSITE MAP 24

STUDY SITE G_{14} : STUDY PERIOD 2



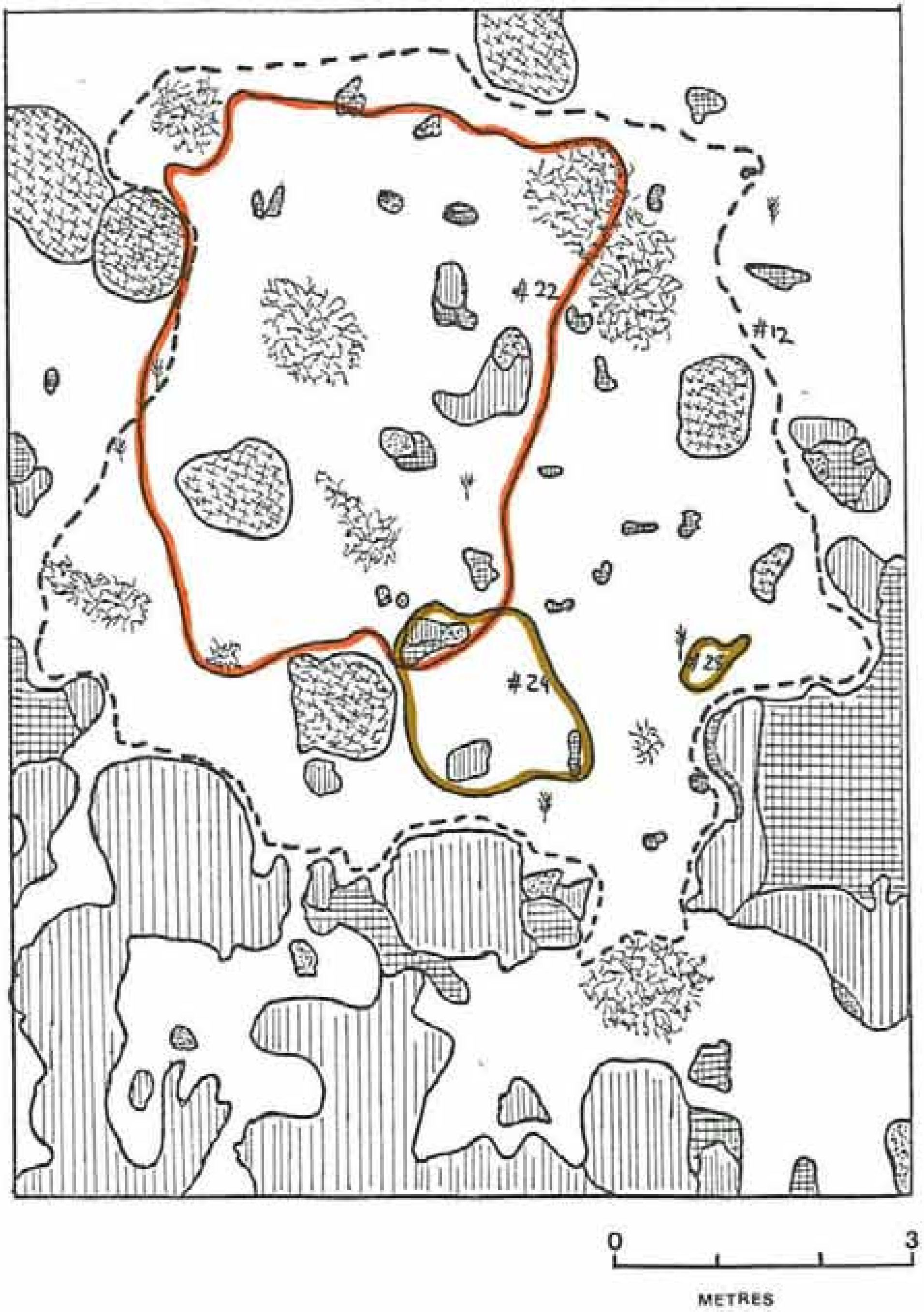
COMPOSITE MAP 25

STUDY SITE G_{14} : STUDY PERIOD 3



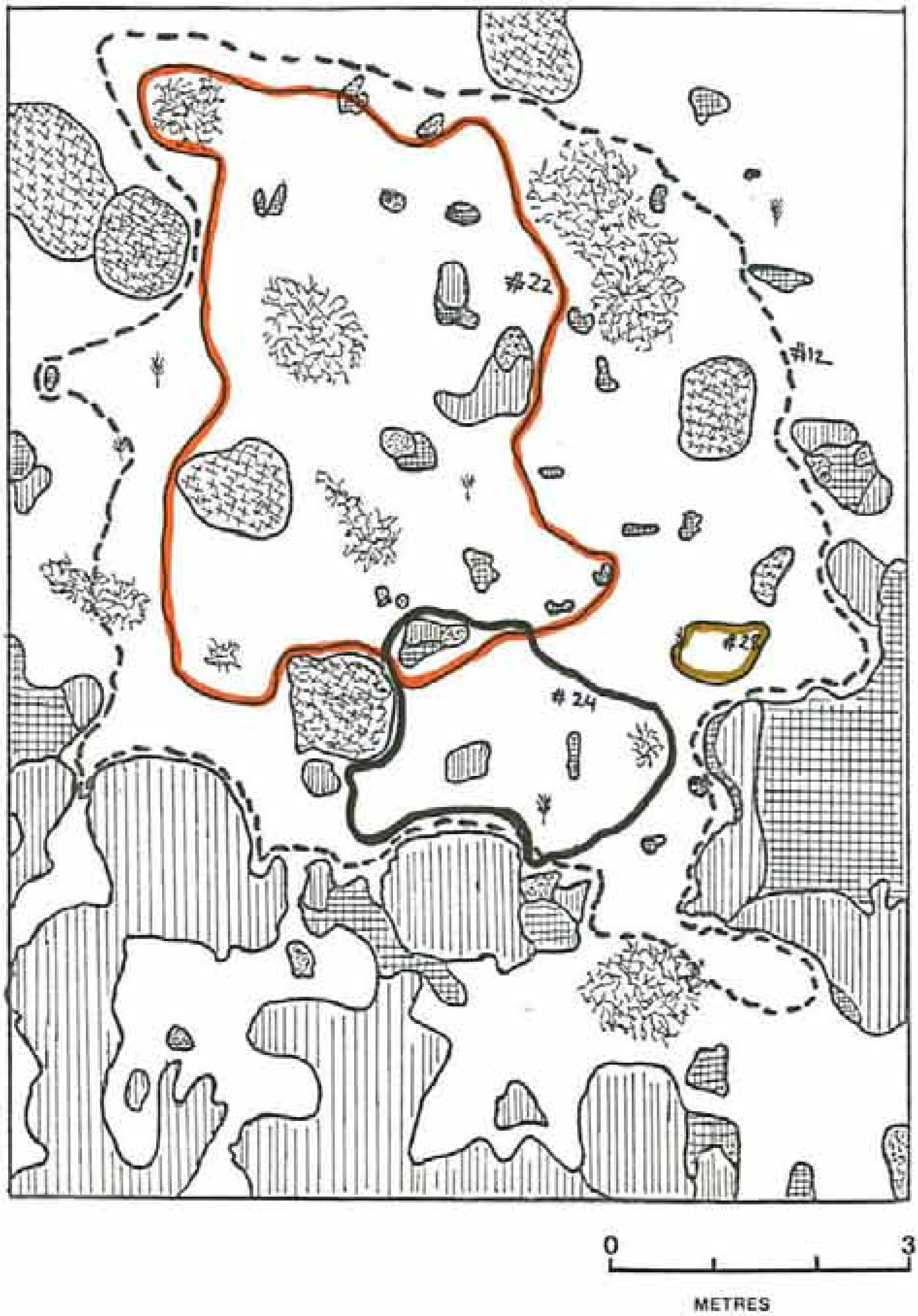
COMPOSITE MAP 26

STUDY SITE G_{14} : STUDY PERIOD 4



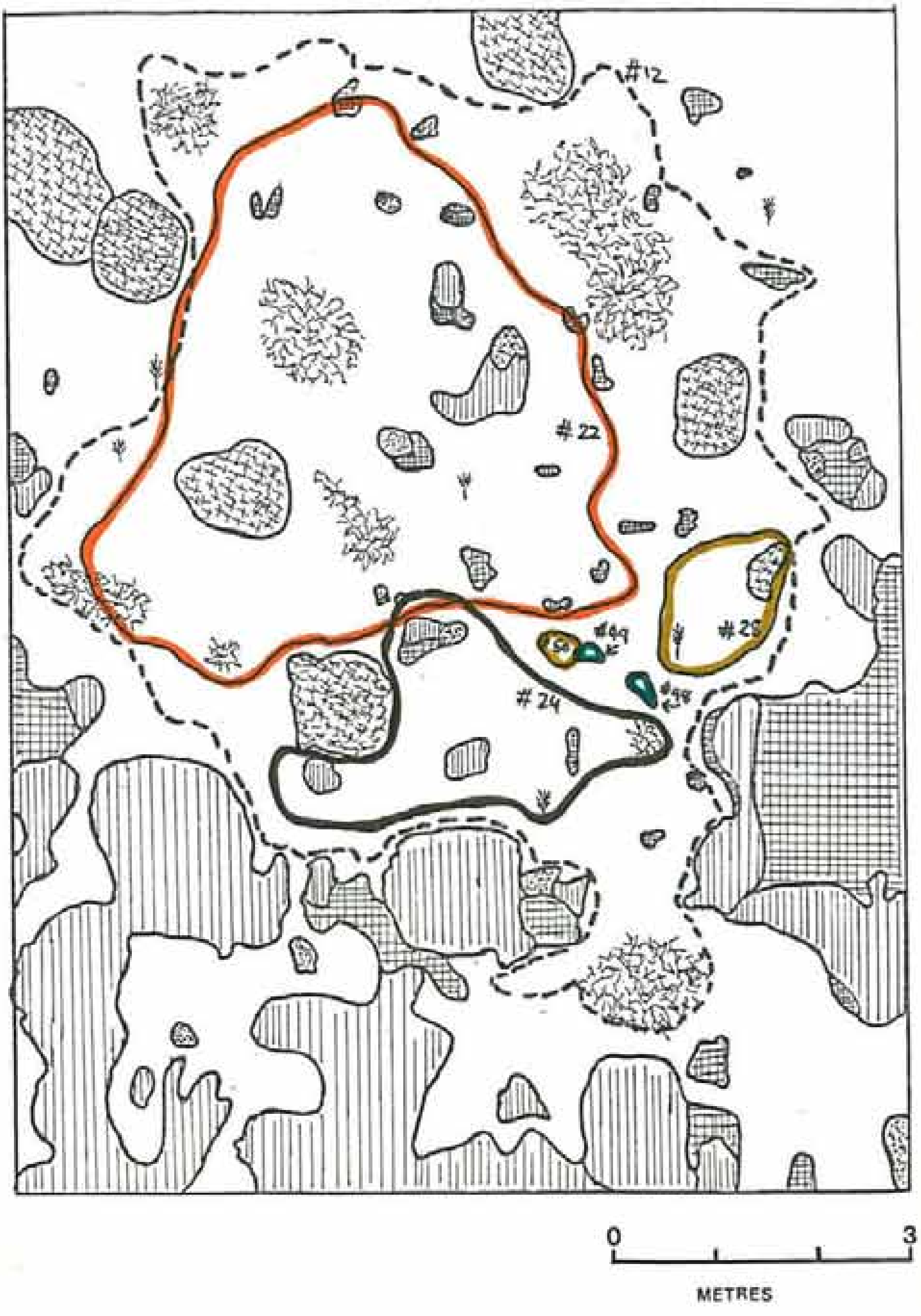
COMPOSITE MAP 27

STUDY SITE G_{14} : STUDY PERIOD 5



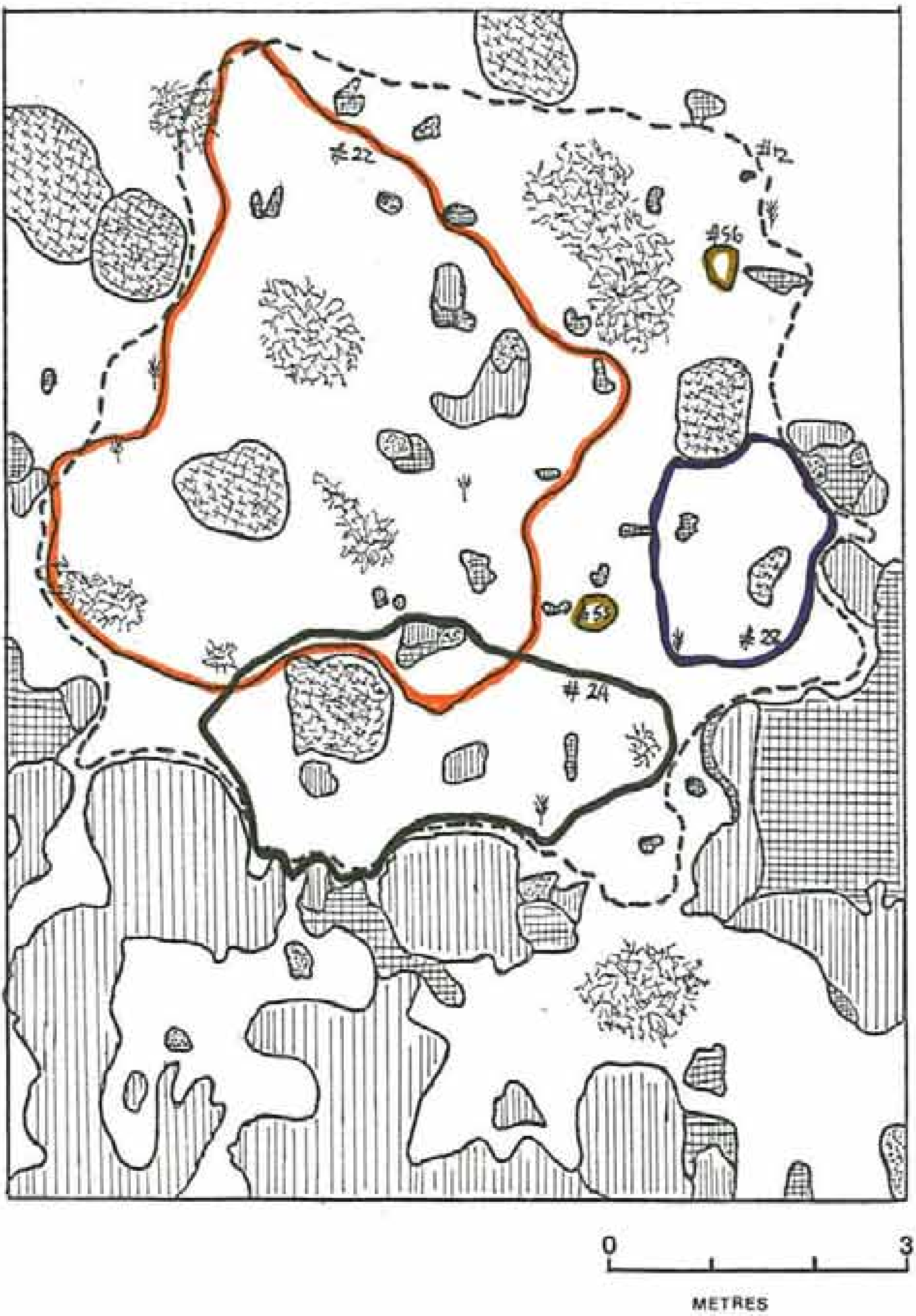
COMPOSITE MAP 28

STUDY SITE G_{14} : STUDY PERIOD 6



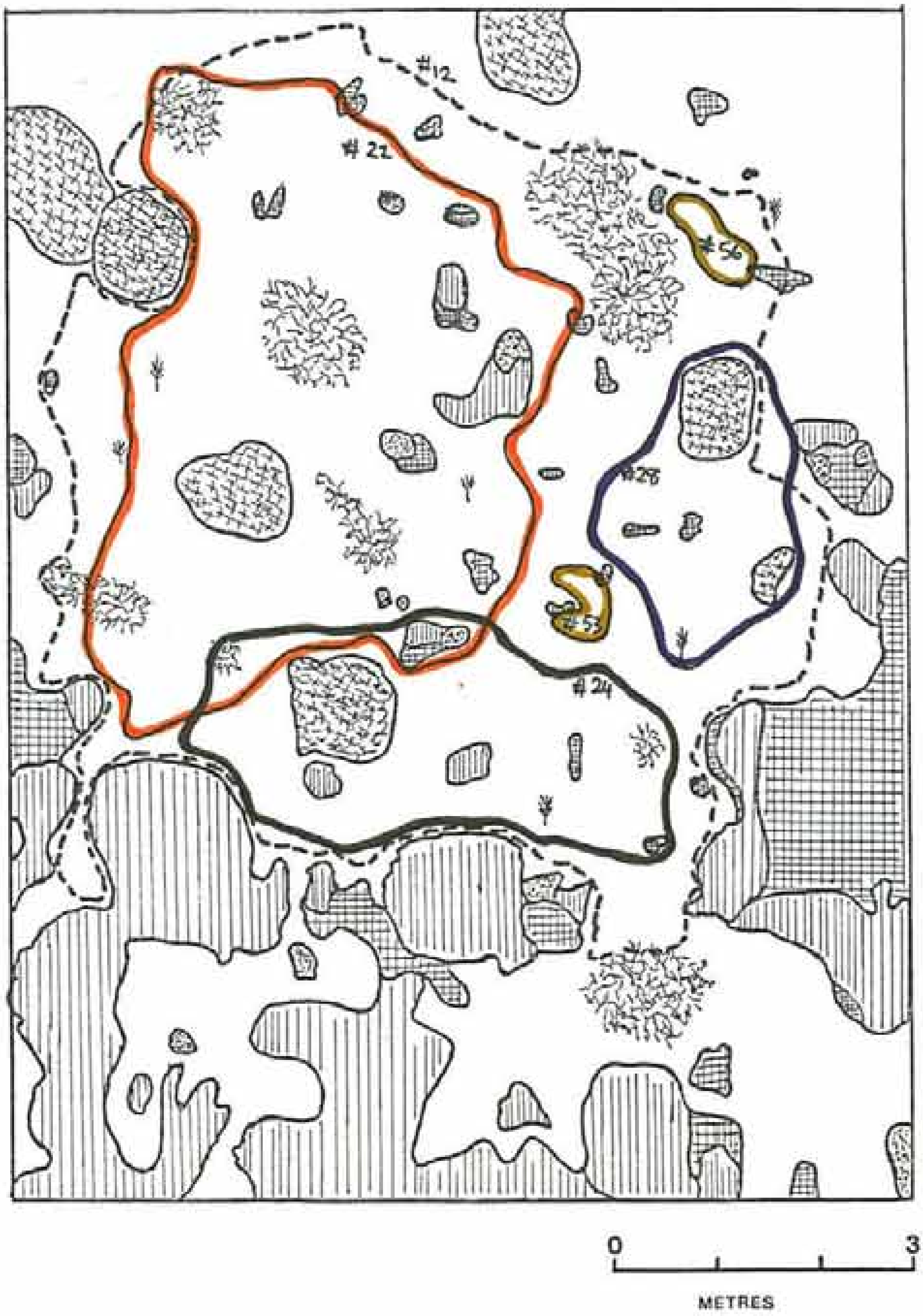
COMPOSITE MAP 29

STUDY SITE G_{14} : STUDY PERIOD 7



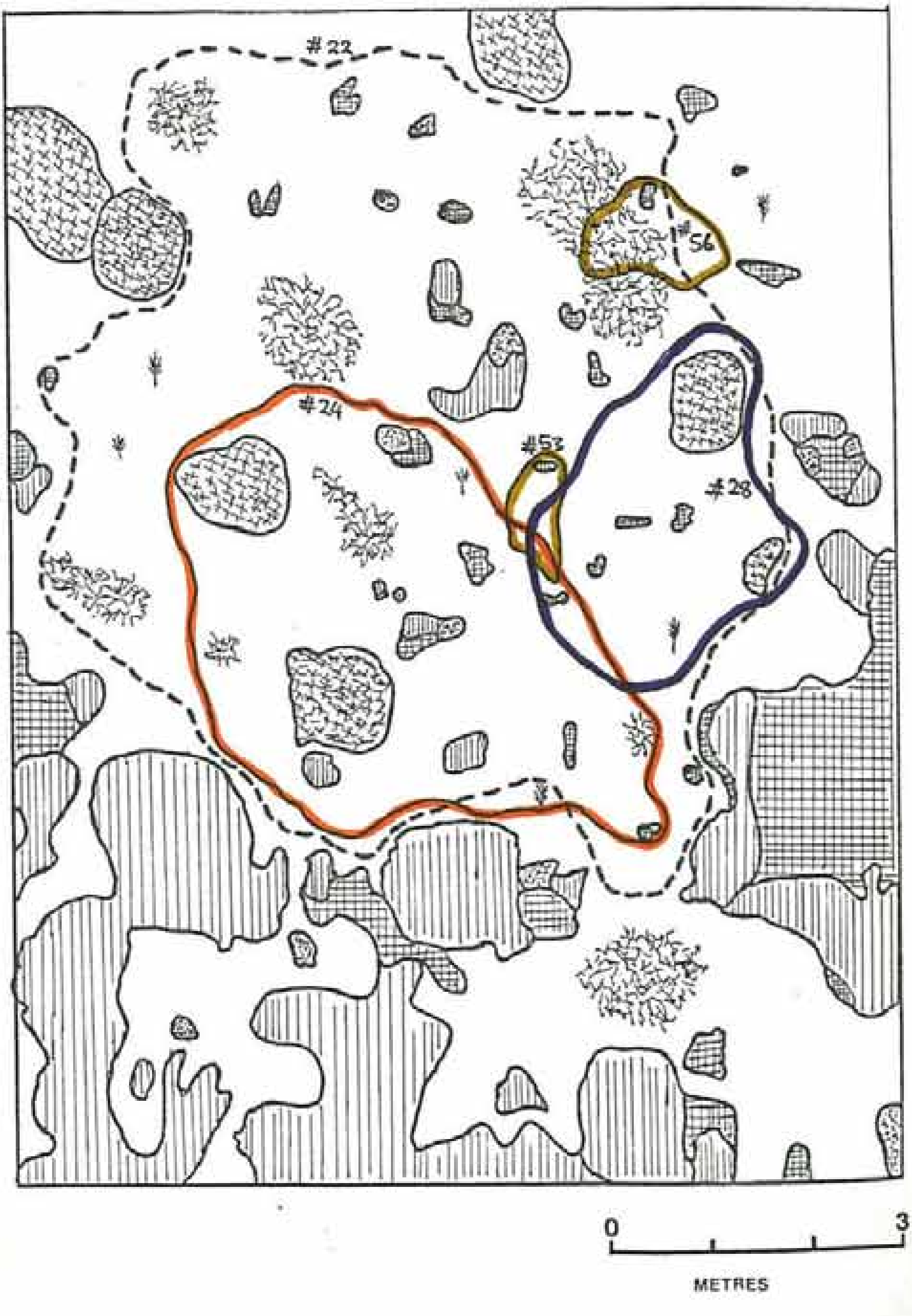
COMPOSITE MAP 30

STUDY SITE G_{14} : STUDY PERIOD 8



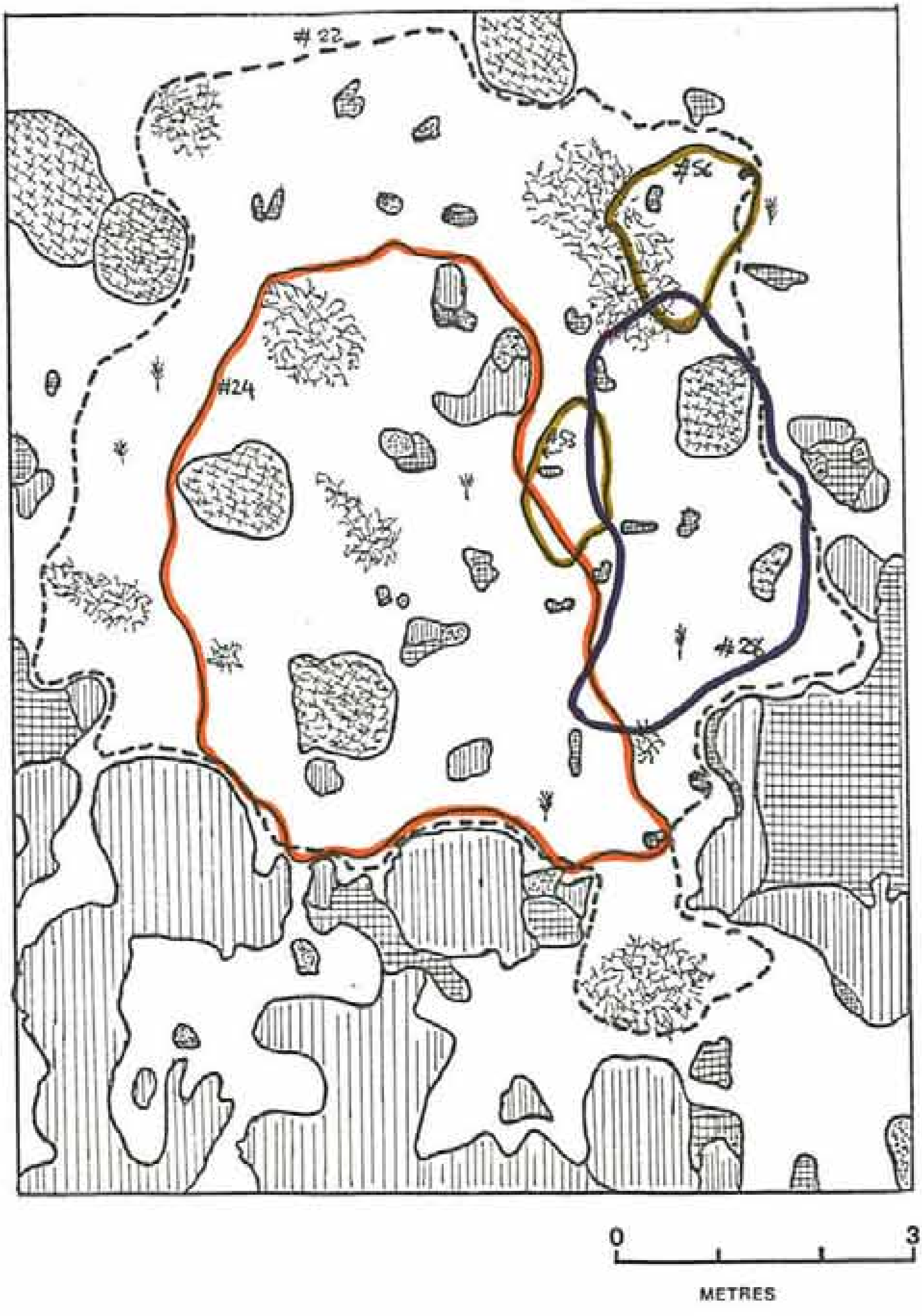
COMPOSITE MAP 31

STUDY SITE G_{14} : STUDY PERIOD 9



COMPOSITE MAP 32

STUDY SITE G_{14} : STUDY PERIOD 10

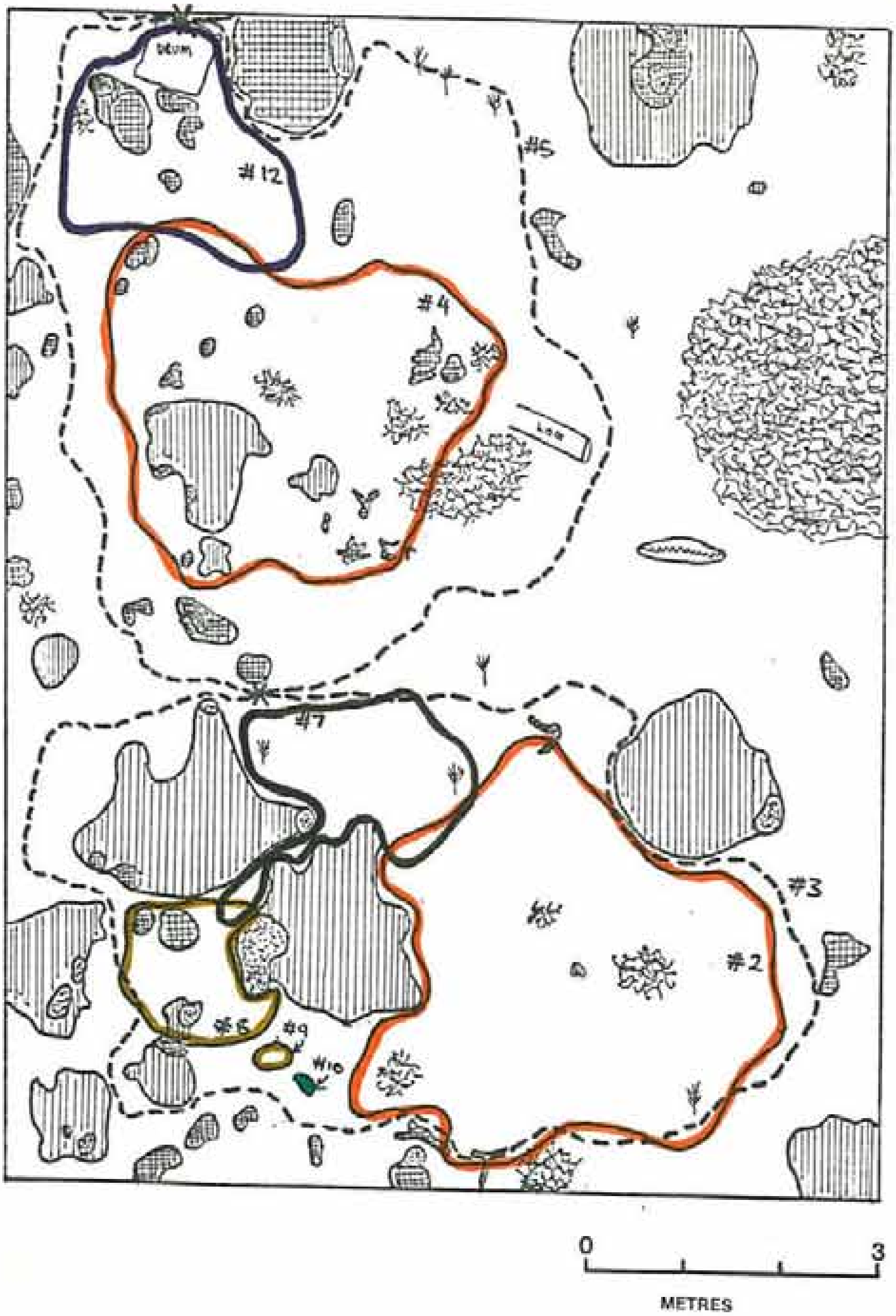


COMPOSITE MAP 33

STUDY SITE G_{15} : STUDY PERIOD 1

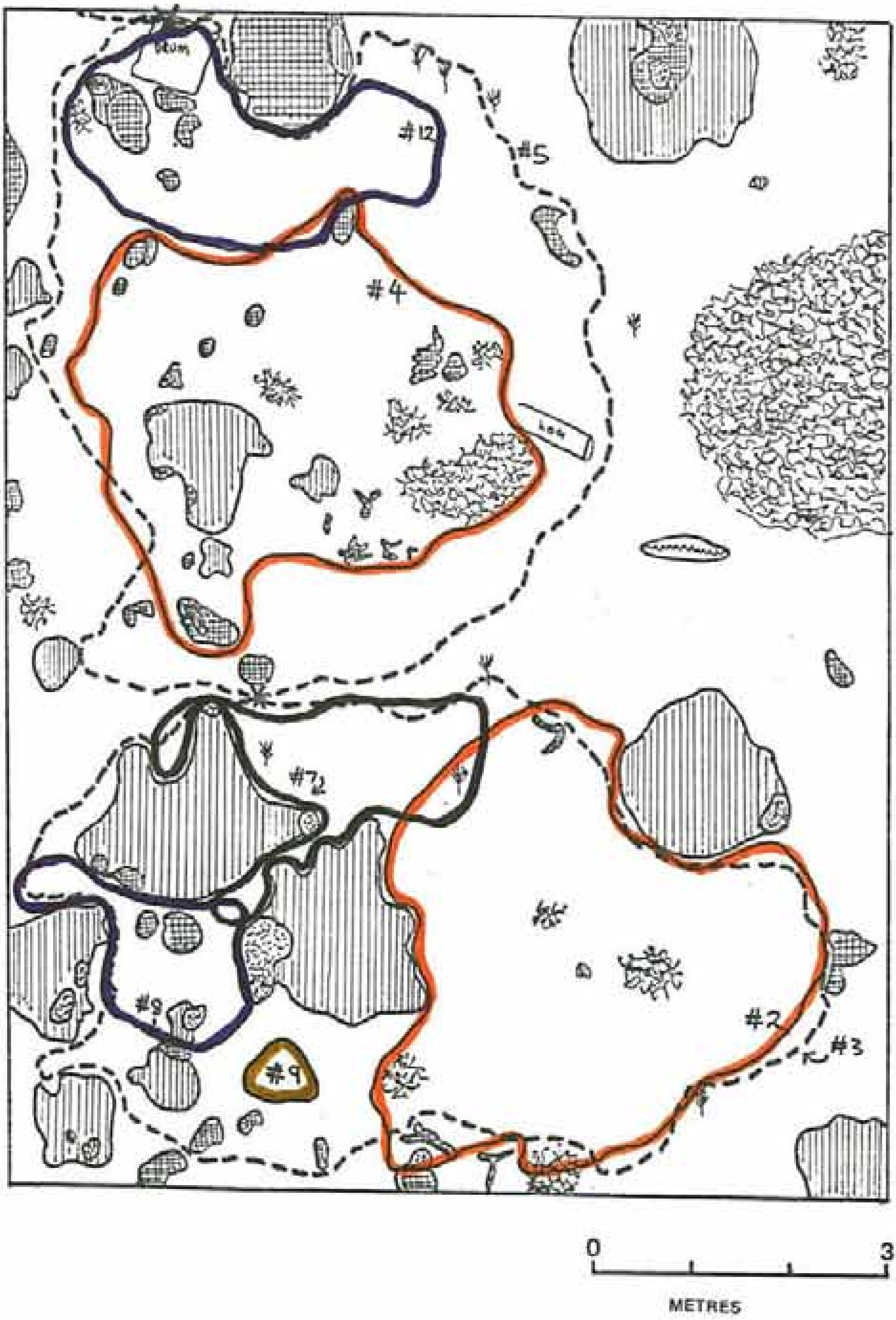
COMPOSITE MAP 34

STUDY SITE G_{15} : STUDY PERIOD 2



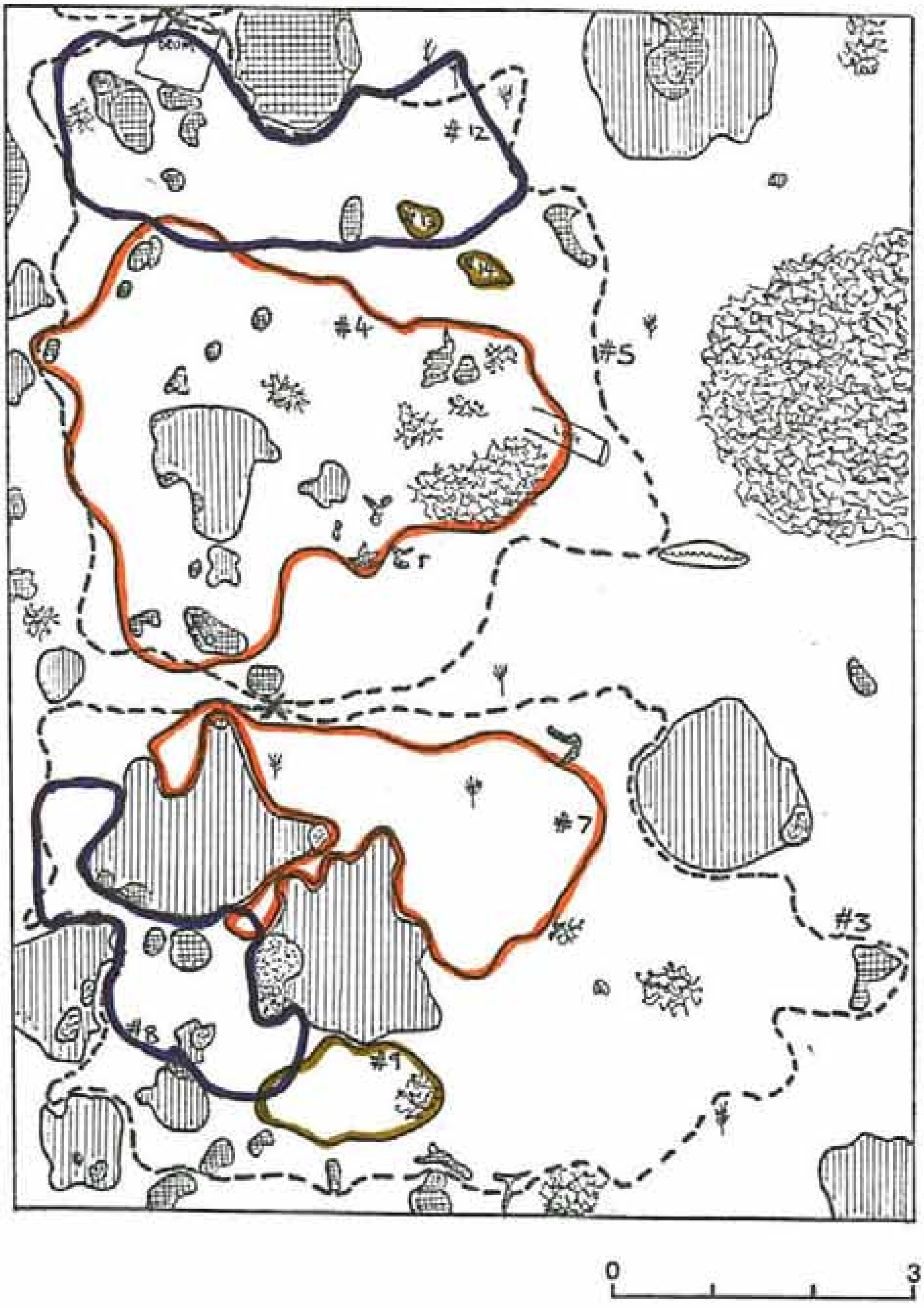
COMPOSITE MAP 35

STUDY SITE G_{15} : STUDY PERIOD 3



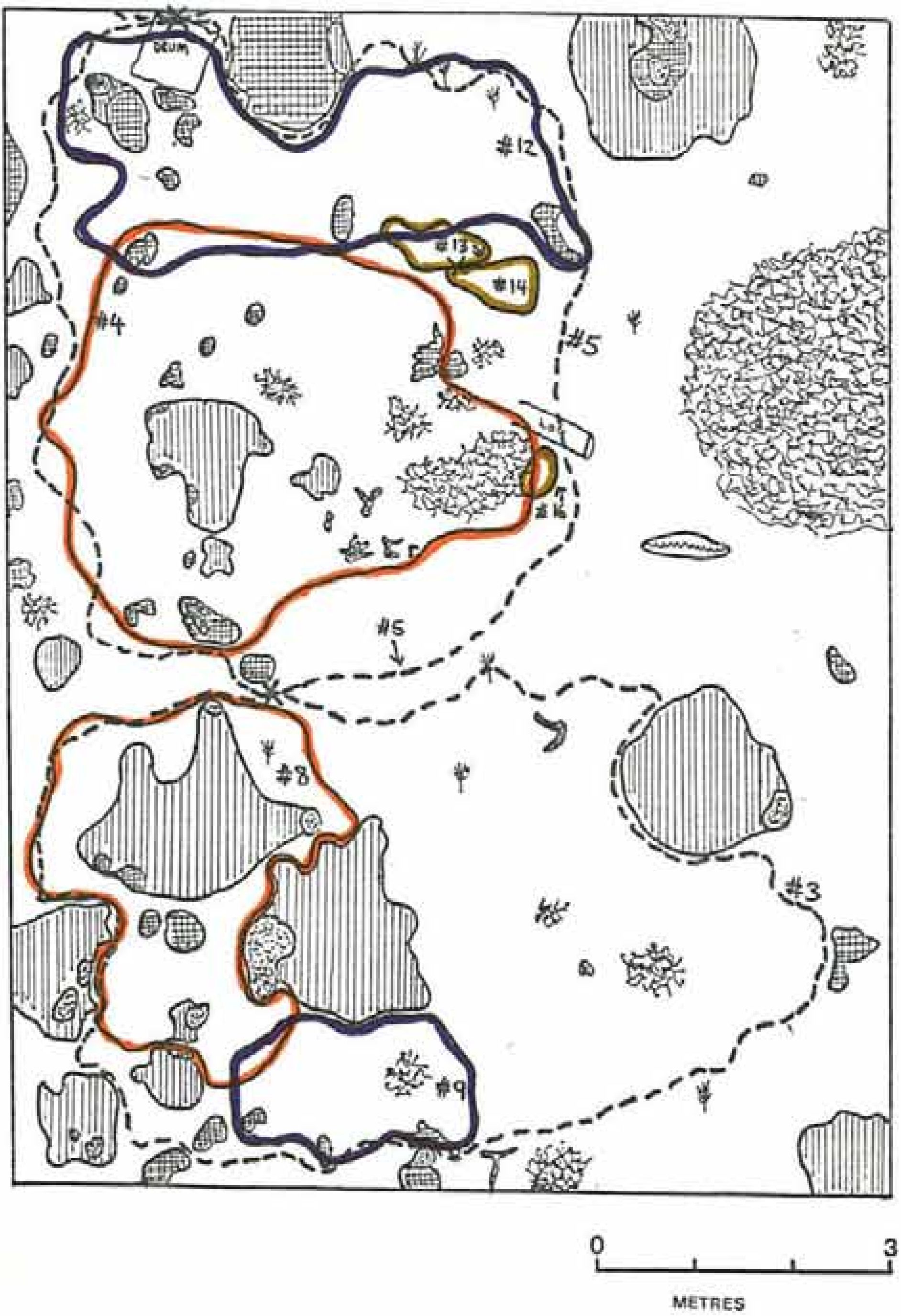
COMPOSITE MAP 36

STUDY SITE G_{15} : STUDY PERIOD 4



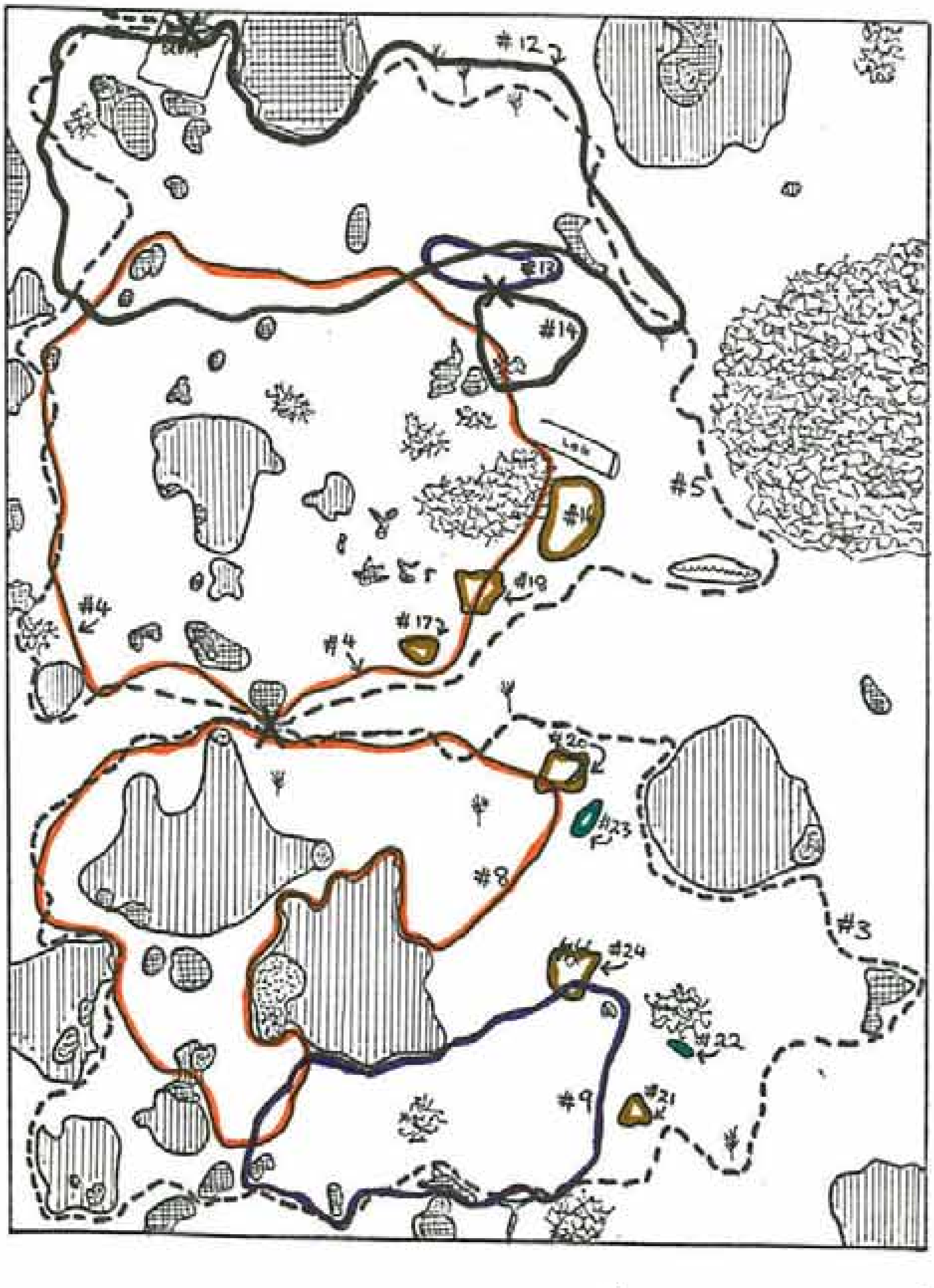
COMPOSITE MAP 37

STUDY SITE G_{15} : STUDY PERIOD 5



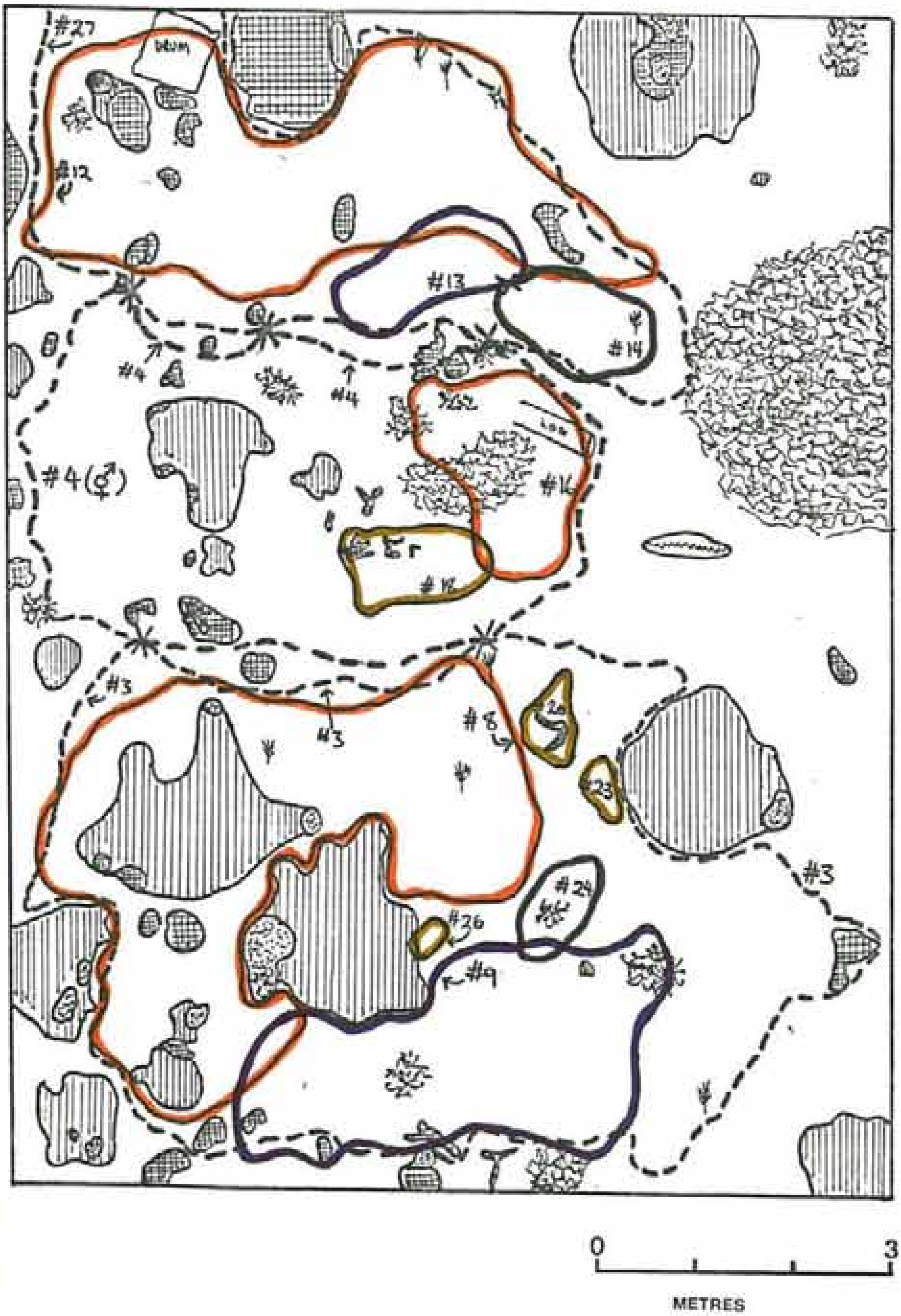
COMPOSITE MAP 38

STUDY SITE G_{15} : STUDY PERIOD 6



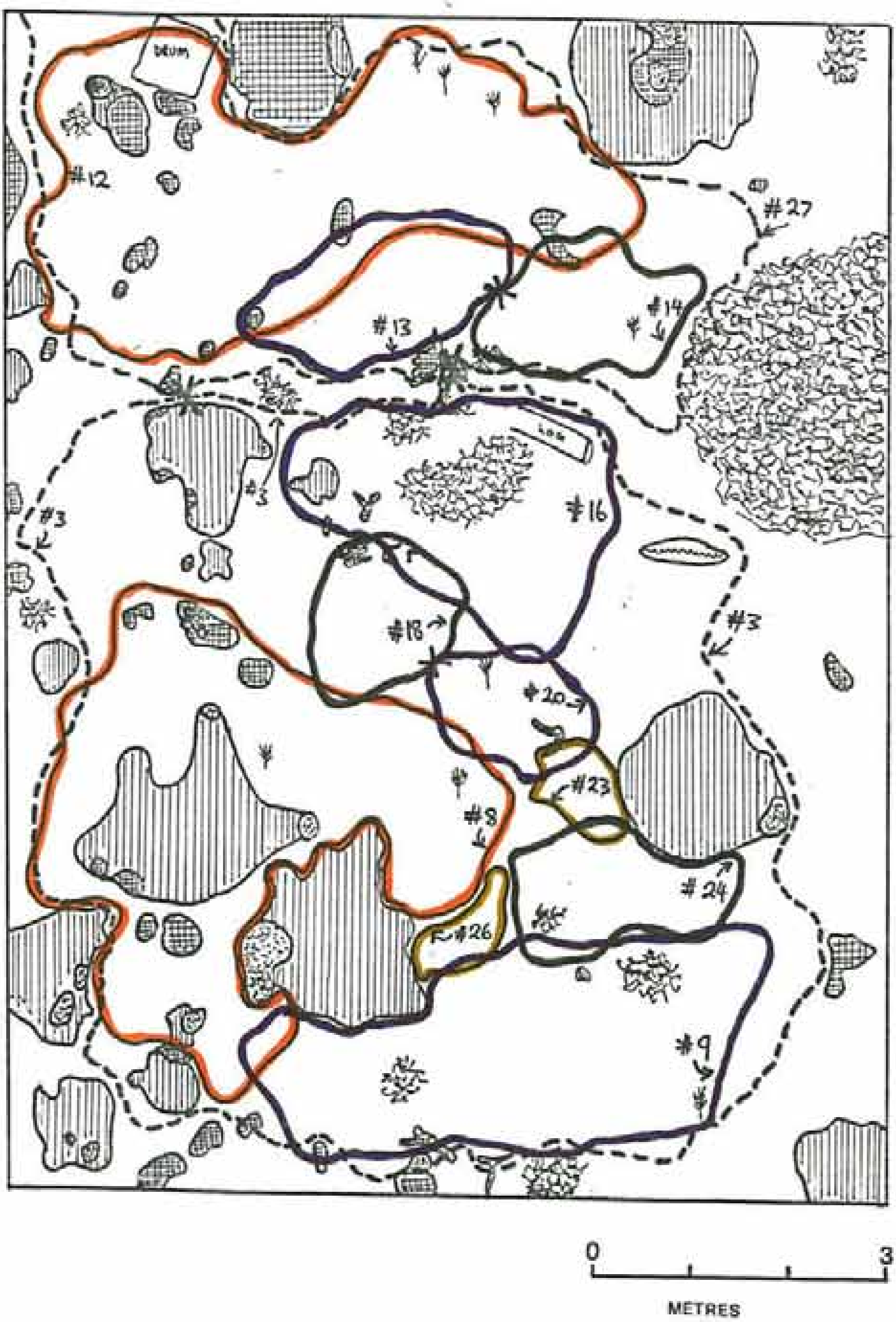
COMPOSITE MAP 39

STUDY SITE G_{15} : STUDY PERIOD 7



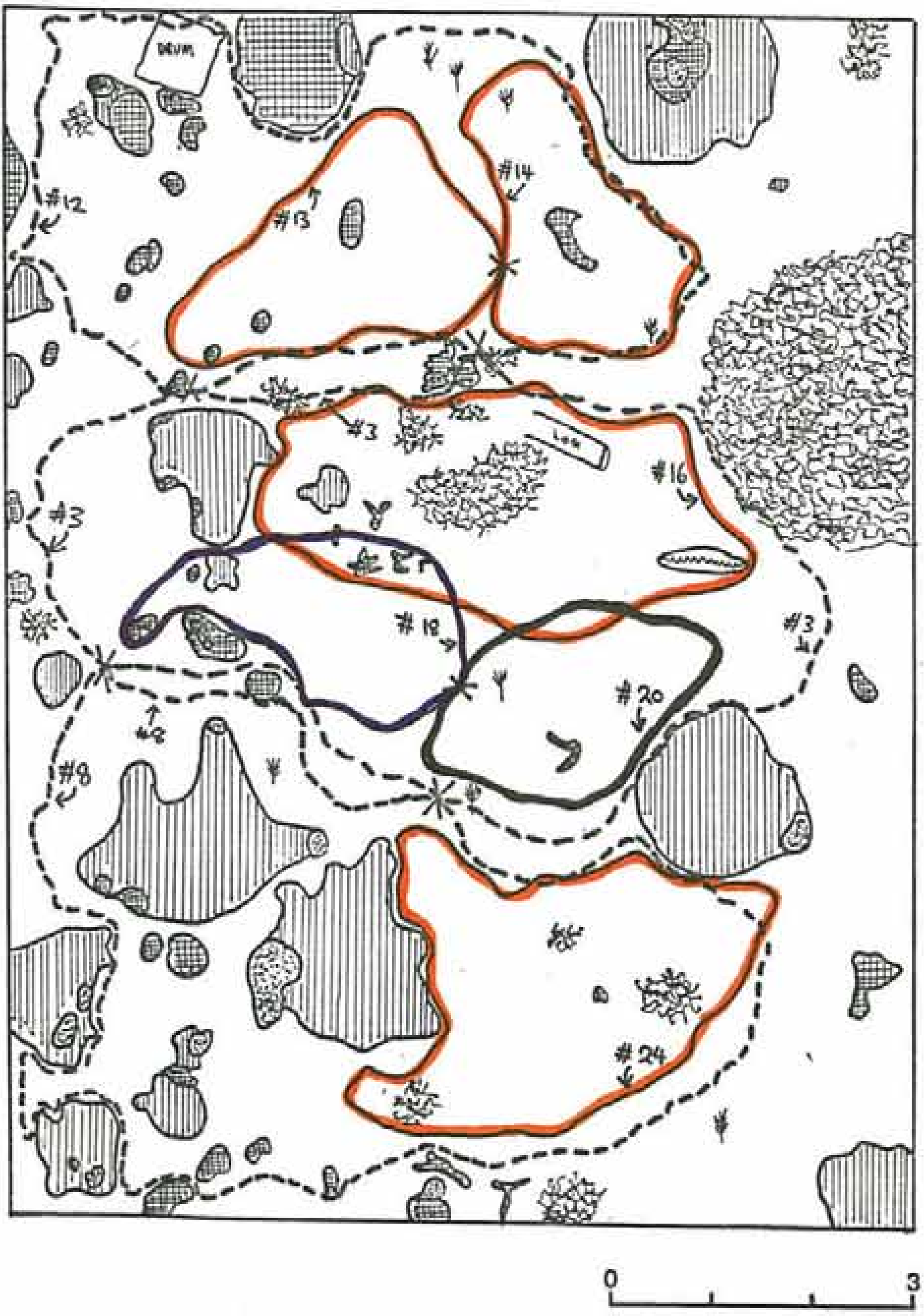
COMPOSITE MAP 40

STUDY SITE G_{15} : STUDY PERIOD 8



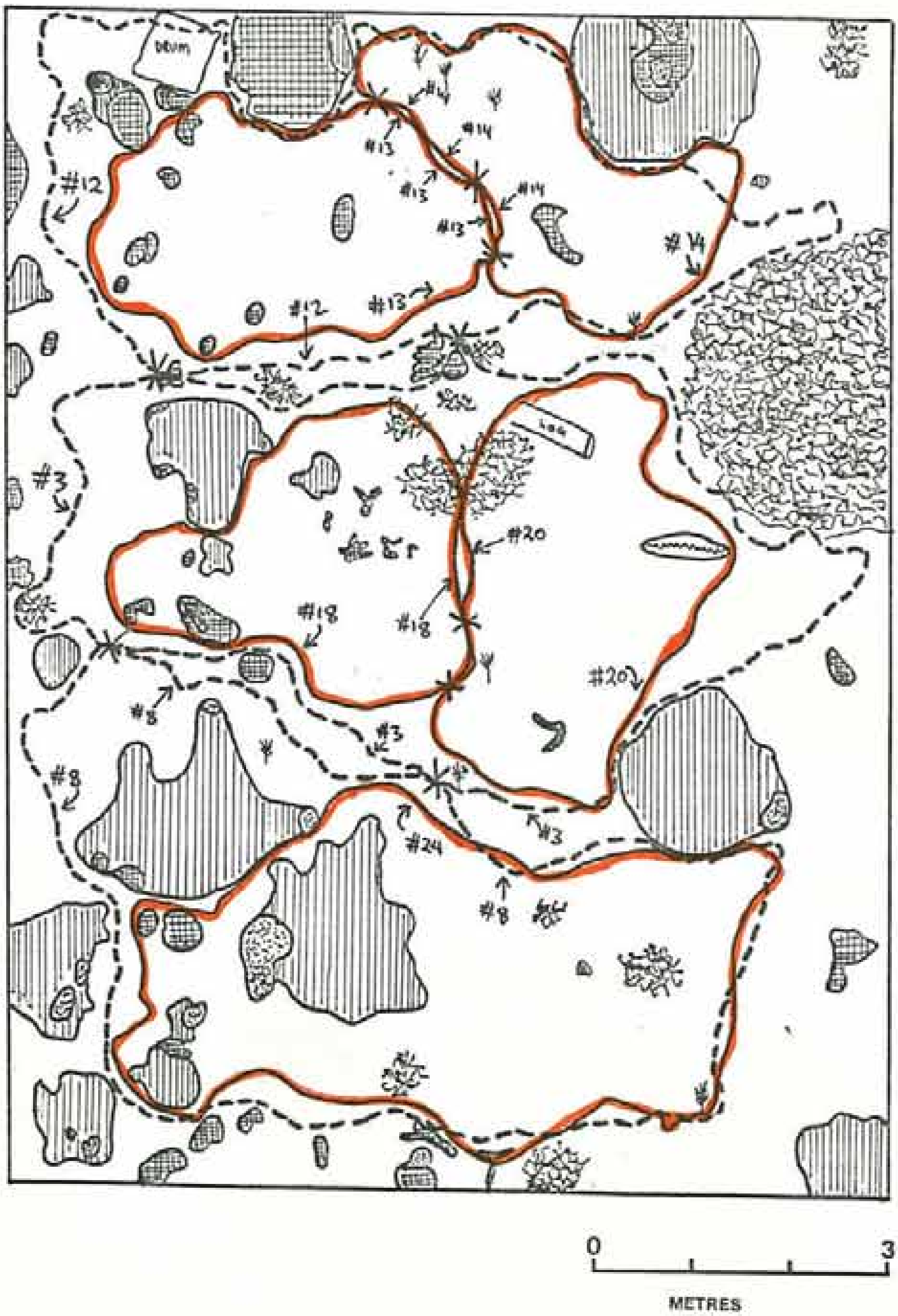
COMPOSITE MAP 41

STUDY SITE G_{15} : STUDY PERIOD 9



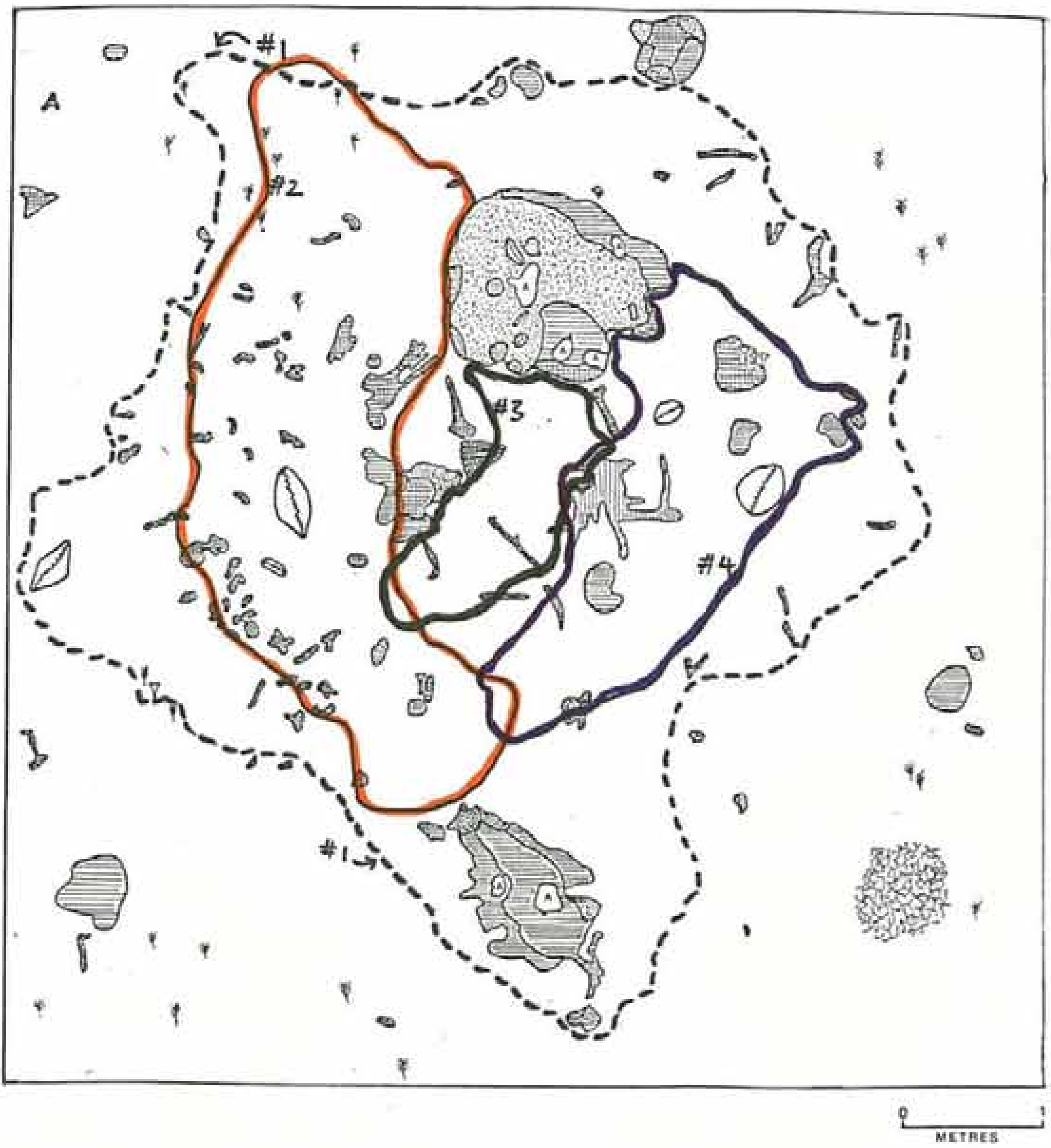
COMPOSITE MAP 42

STUDY SITE G_{15} : STUDY PERIOD 10



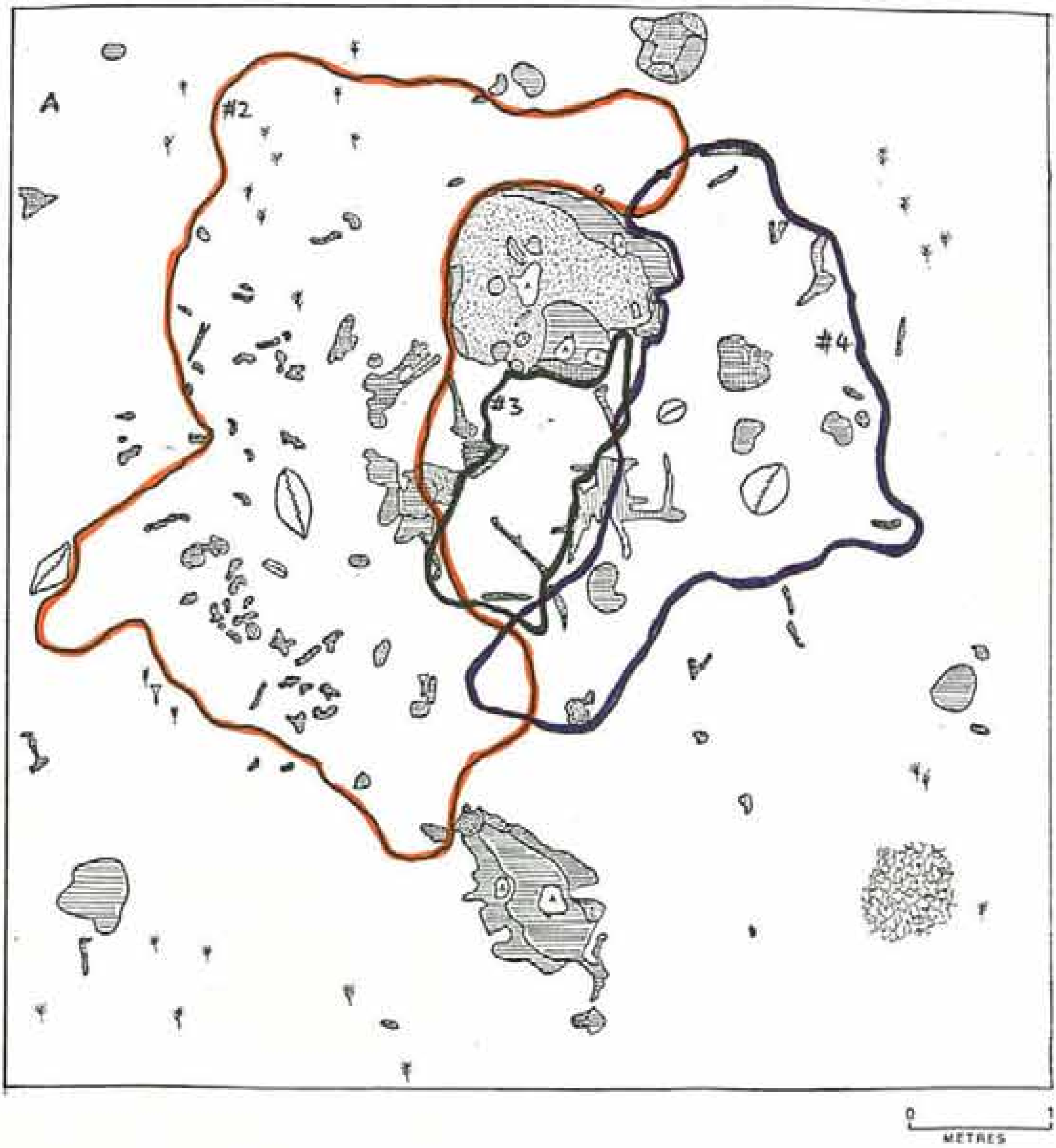
COMPOSITE MAP 43

STUDY SITE LHI : 1 day before removal of #1 ♂



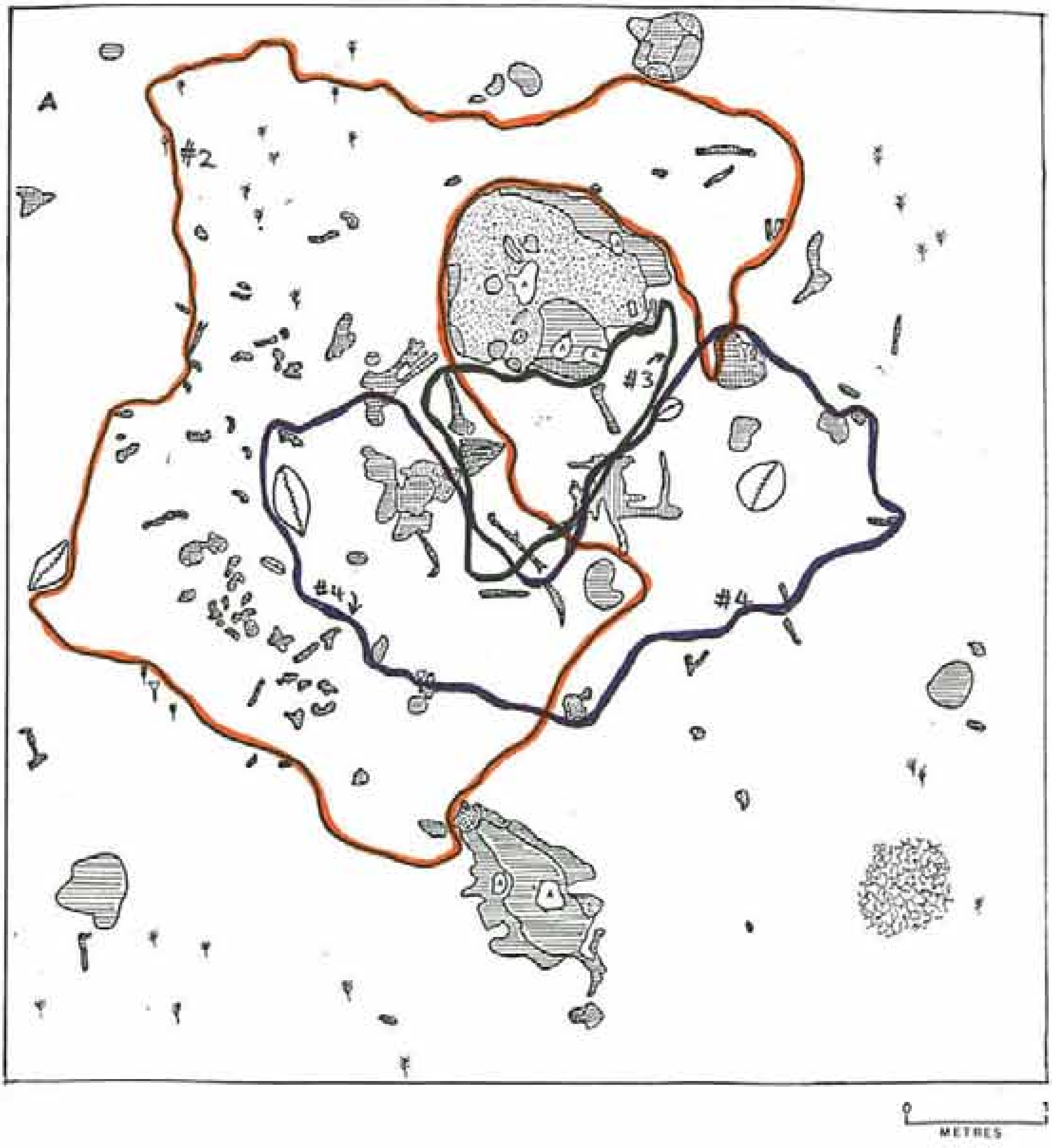
COMPOSITE MAP 44

STUDY SITE LHI : 5 days after removal of #1 ♂



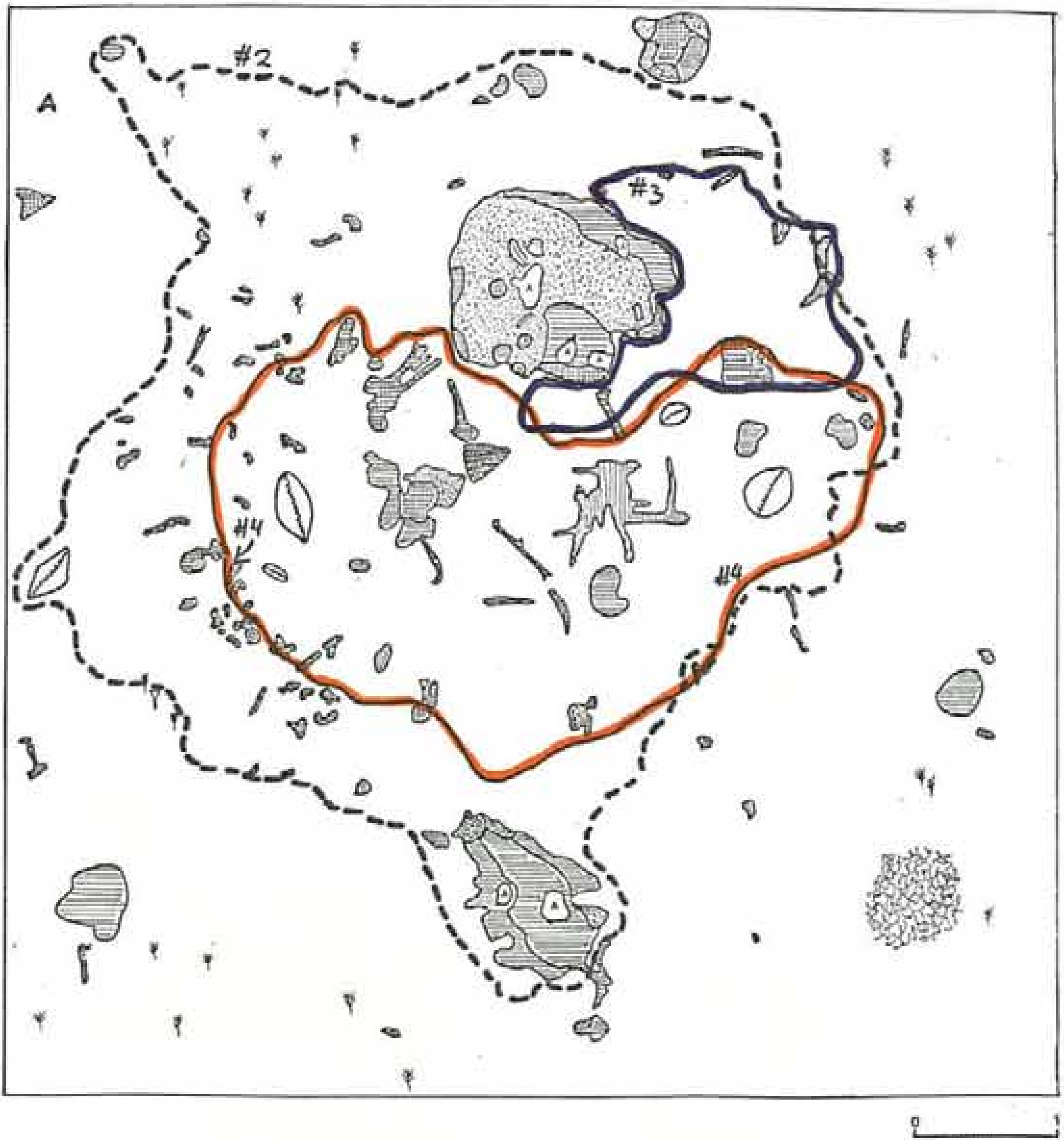
COMPOSITE MAP 45

STUDY SITE LHI : 15 days after removal of #1 ♂



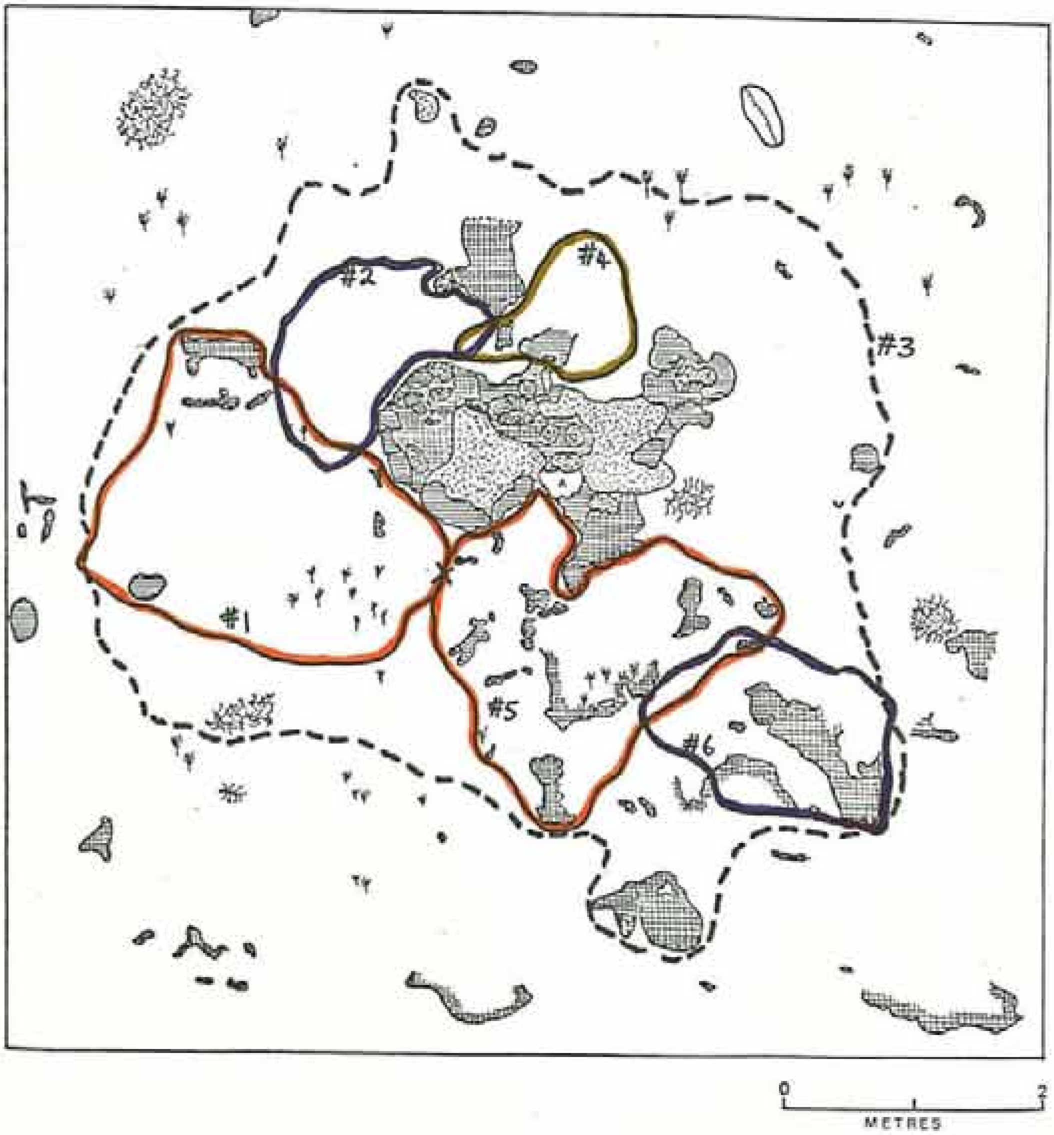
COMPOSITE MAP 46

STUDY SITE LHI : 30 days after removal of #1 ♂



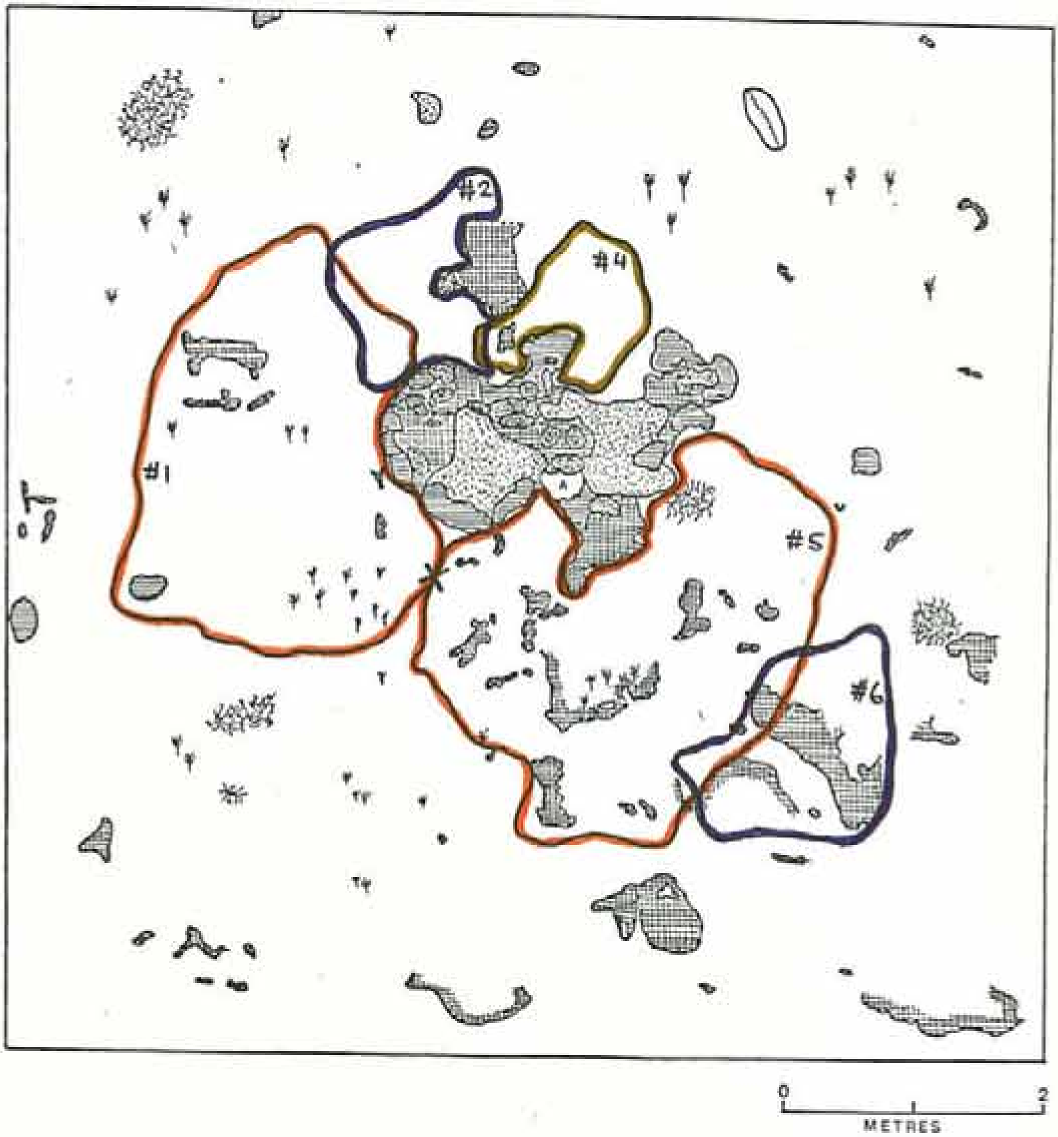
COMPOSITE MAP 47

STUDY SITE SB1 : 1 day before removal of #3 ♂



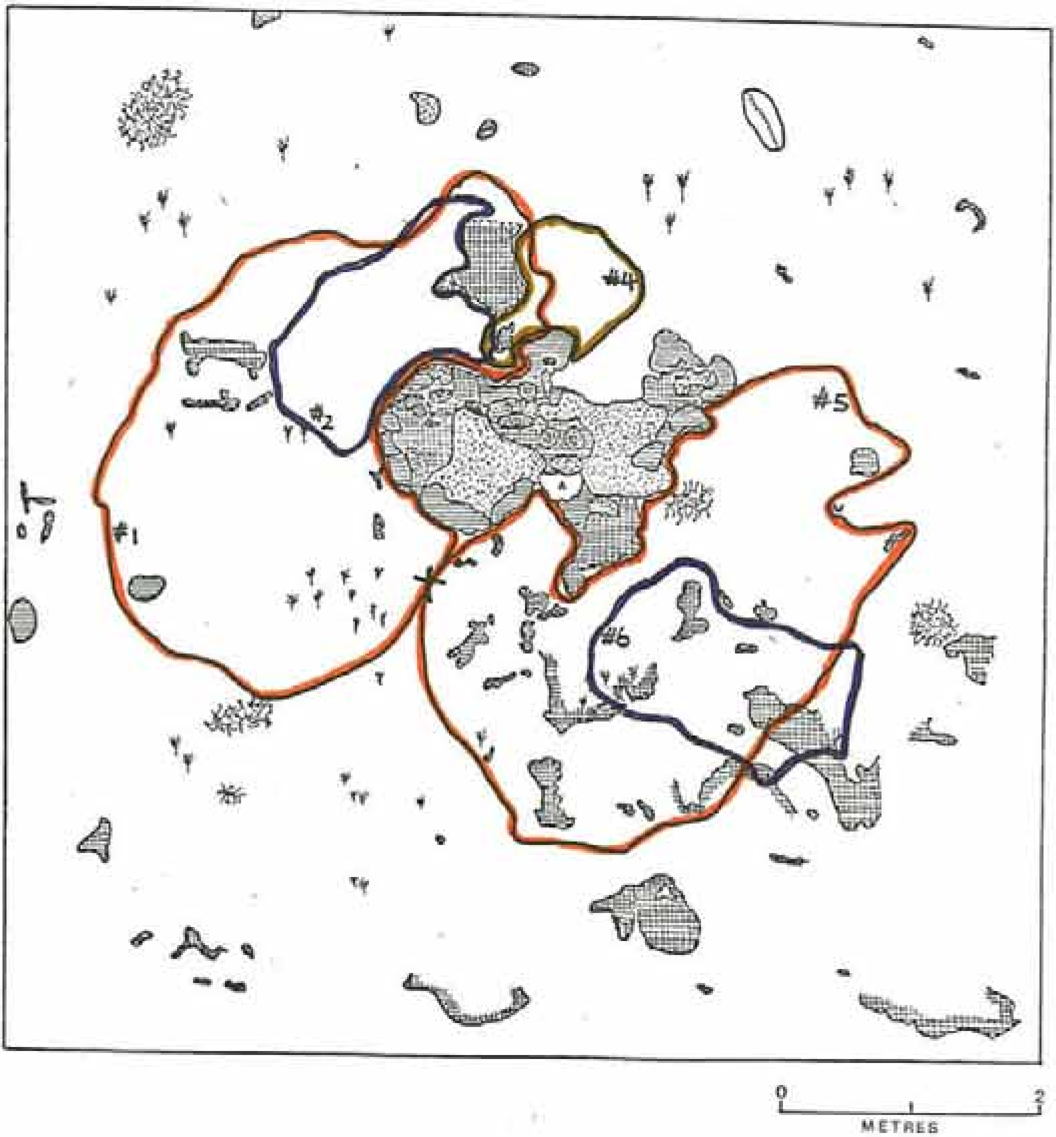
COMPOSITE MAP 49

STUDY SITE SBI : 5 days after removal of #3 ♂



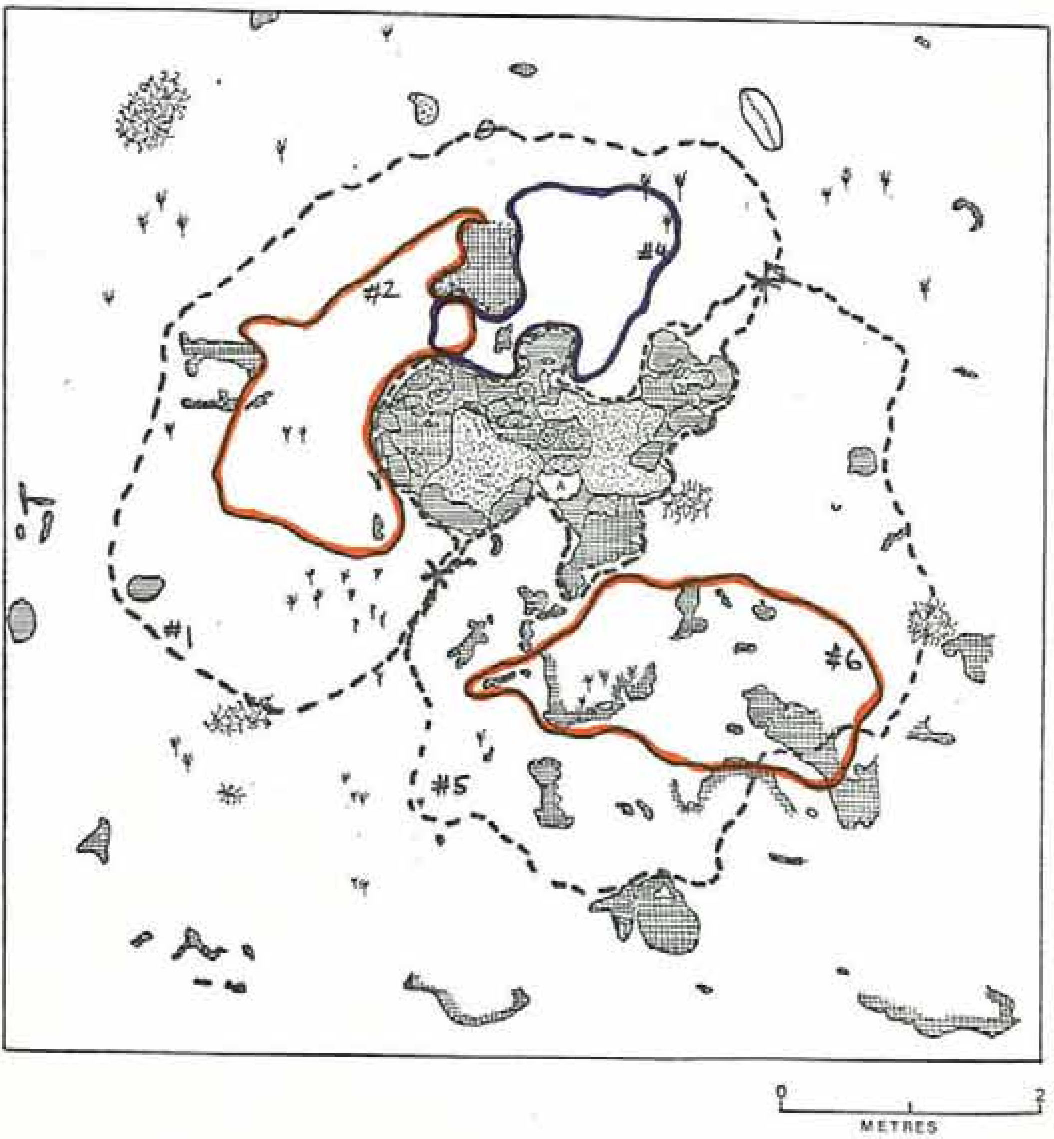
COMPOSITE MAP 49

STUDY SITE SB1 : 15 days after removal of #3 ♂



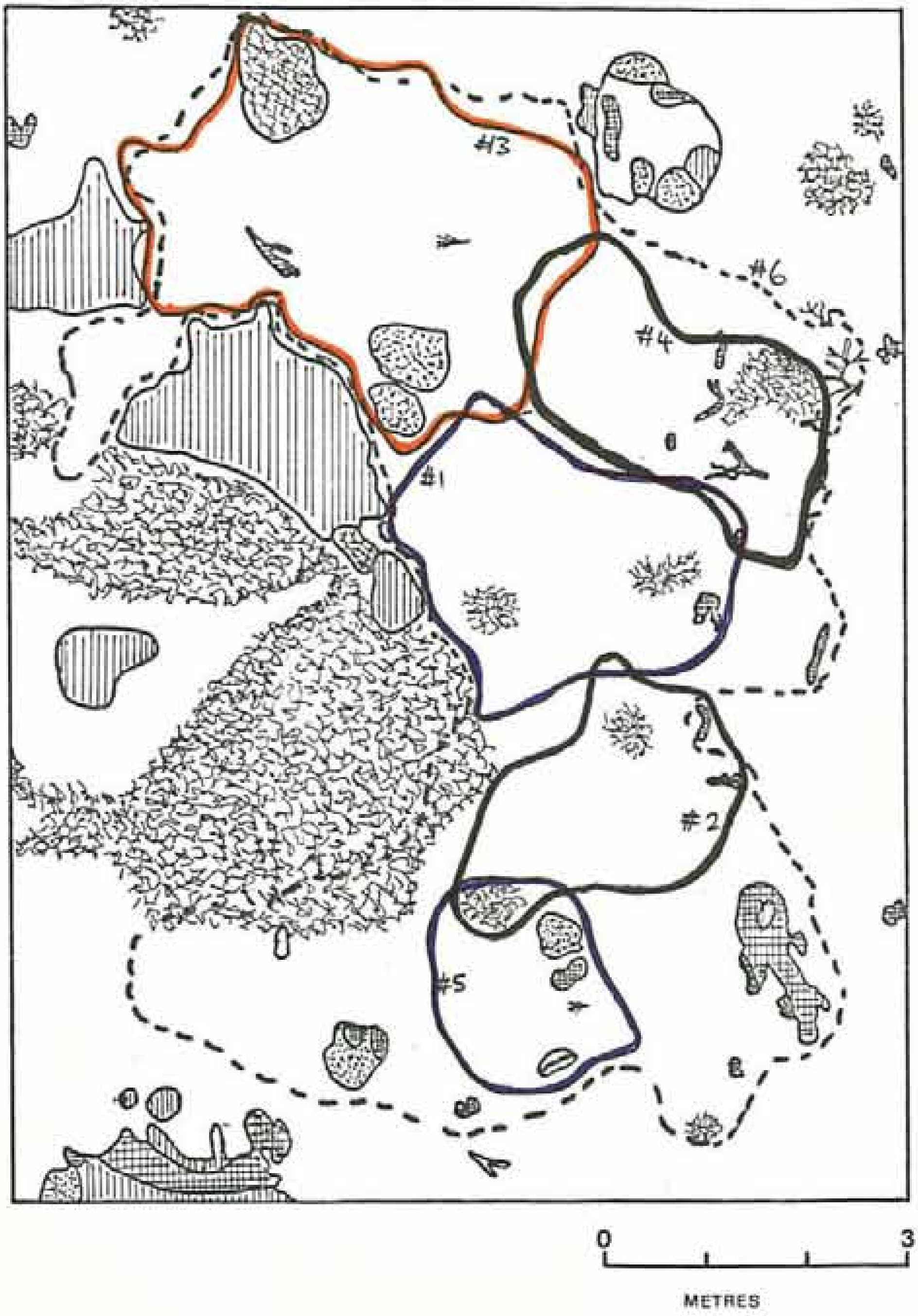
COMPOSITE MAP 50

STUDY SITE SBI : 30 days after removal of #3♂



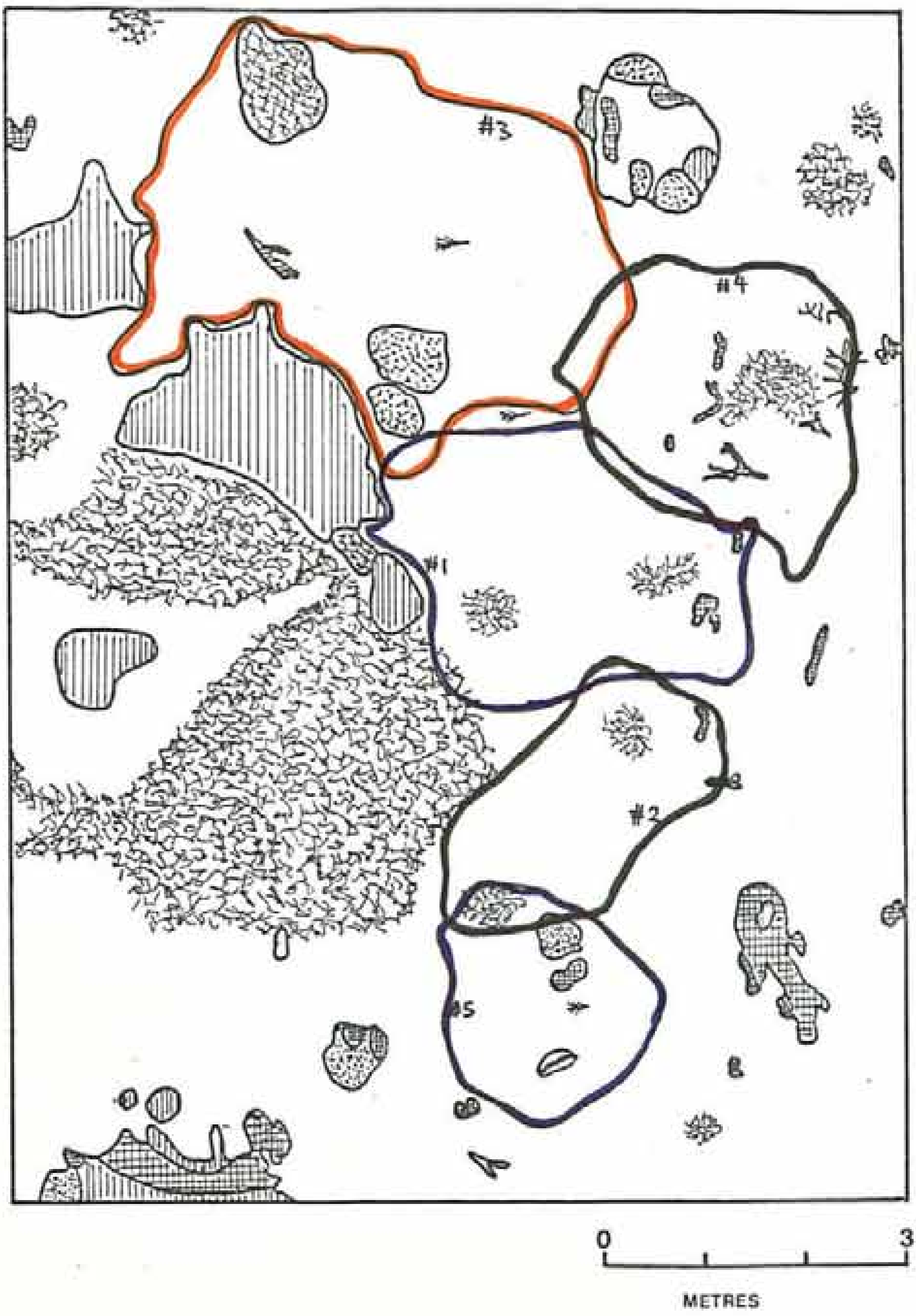
COMPOSITE MAP 51

STUDY SITE BMI: 1 day before removal of #6 ♂



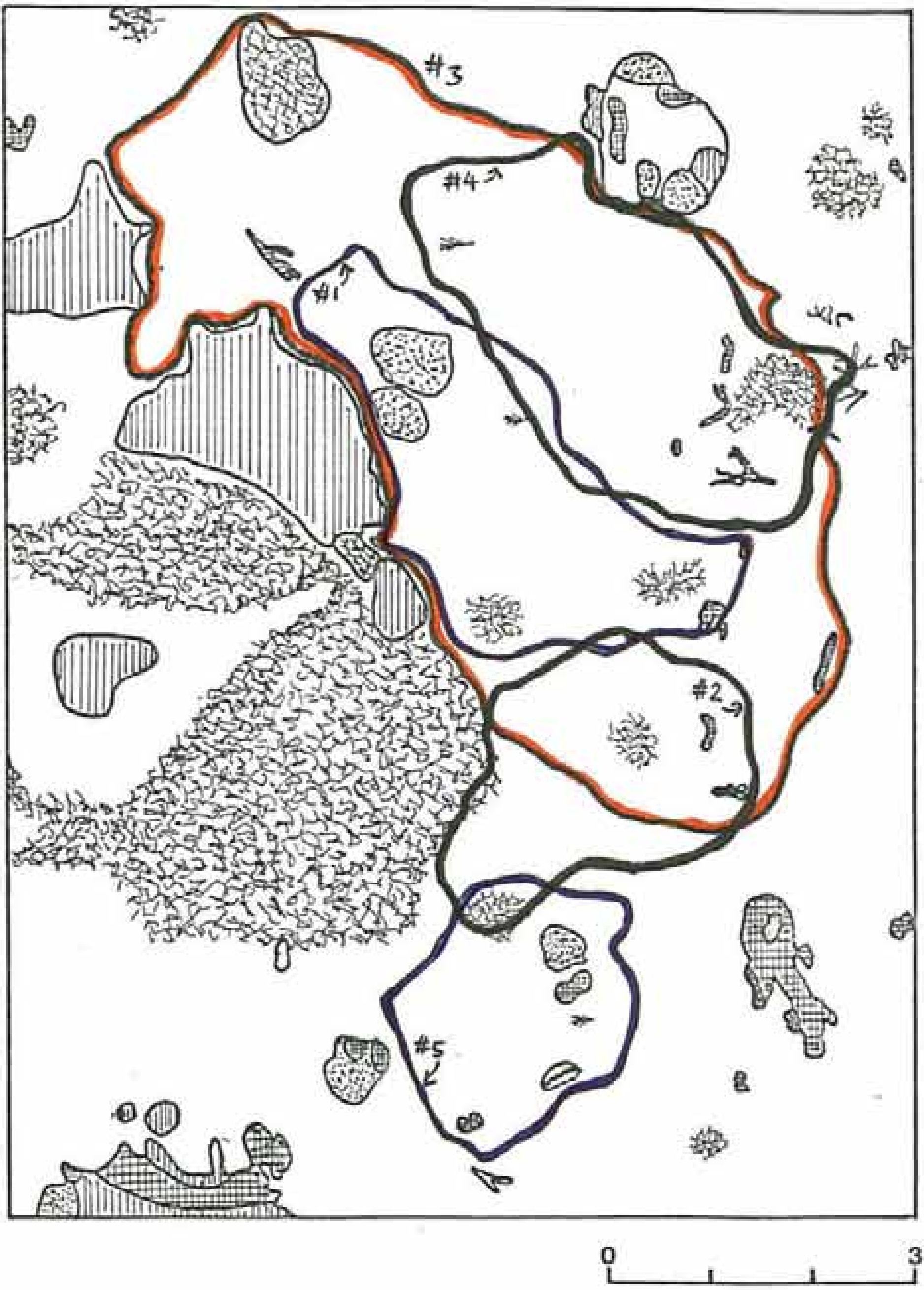
COMPOSITE MAP 52

STUDY SITE BMI: 5 days after removal of #6 ♂



COMPOSITE MAP 53

STUDY SITE BMI: 15 days after removal of #6♂



COMPOSITE MAP 54

STUDY SITE BMI: 30 days after removal of #6♂