

DISTRIBUTION, GROWTH AND REPRODUCTIVE ECOLOGY OF
THREE PIPEFISH FROM SEAGRASS BEDS

by

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The work contained in this thesis, except where acknowledged, is the result of my own investigations.

[Redaction]

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ABSTRACT

The composition of the fauna of seagrass beds in New South Wales has been studied extensively, but few species have been investigated in detail. The spatial and temporal distributions, recruitment, growth and the reproductive ecology of the pipefishes (Syngnathidae) *Stigmatopora argus*, *Stigmatopora nigra* and *Urocampus carinirostris* were studied in Botany Bay and Pittwater, two estuaries of the Sydney region. Samples were collected bimonthly from six sites (three in each bay) where beds of *Z. capricorni* and *P. australis* occurred adjacently. This was done with a small beam-trawl (1m x 0.5m) with 2mm meshes in the body and 1mm meshes at the cod-end.

Stigmatopora argus, the largest and most mobile of the three pipefishes, had a wide distribution and occurred in both *Z. capricorni* and *P. australis* at all sites. The smallest and most sedentary pipefish, *Urocampus carinirostris*, and the third species, *Stigmatopora nigra*, were found virtually only in *Z. capricorni* and also had a restricted distribution among sites. In Botany Bay, *S. argus* and *S. nigra* were most abundant at Kurnell where *Urocampus carinirostris* were rarely collected. On the other hand, *Urocampus* were present in greater numbers at Quibray Bay where *Stigmatopora* was seldom collected. Temporal variation in abundances of *S. argus*, *S. nigra* and *U. carinirostris* was great in *Z. capricorni* and differed for the three species. In contrast, the population of *S. argus* in *P. australis* fluctuated little. The interpretation of seasonal patterns was limited by the small frequency of sampling and the great variability in abundance.

The height of leaves and density of shoots were not reliable predictors of abundance; the three pipefishes responded differently to the same changes in seagrass and correlations for the same pipefish varied among sites and species of seagrass. The results do not support the model proposed by Heck and Orth (1980) to explain the structure of the populations of animals living in seagrasses.

Recruitment and growth explained only part of the seasonal variability. Patchiness, resulting probably from migrations within beds, is suggested as a major cause of the temporal fluctuations in abundance.

The reproductive seasons of the two genera differed. Brooding males of *Stigmatopora* were collected at all times. By contrast, male *U. carinirostris* bred only between November and March. Although *S. argus* recruited all the year round, the size-distribution of juveniles indicated that recruitment was more intense between March and July and occurred virtually only in *Z. capricorni*. Recruits more than doubled their sizes and were capable of breeding in less than a year. Young adults possibly migrate from *Z. capricorni* to *P. australis* in July-September. *S. argus* grew little in *P. australis*. The majority of *S. nigra* collected in this study were adults. Recruitment probably occurs in inshore areas of *Z. capricorni* (including the intertidal zone). Recruitment of *U. carinirostris* was between November and March and thus coincided with the reproductive season. These fish reached sexual maturity within a year.

Sex-ratios of *S. argus* in Botany Bay differed in the two seagrasses: females were more abundant in *Z. capricorni* but males were predominant in *P. australis*. In Pittwater, the sex-ratio of *S. argus* did not, in general, differ from 1:1 although there was a tendency for an overabundance of females. Male *S. nigra* outnumbered females at all times. The number of male and female *U. carinirostris* nearly equalled a 1:1 ratio at two sites (Towra Point in Botany Bay and Barrenjoey in Pittwater) but females were more abundant at the third site where this species was abundant (Quibray Bay in Botany Bay).

The results of this study do not conform to the 'stochastic settlement model' advanced by Bell and Westoby (1986c). Pipefishes do not apparently include in their life-history a 'planktonic phase' as a broadcasting mechanism. It is suggested, instead, that only a small proportion of the population (usually juveniles) is compelled into the plankton. Furthermore, those individuals that end up in the plankton (irrespective of numbers) are probably able to discriminate among beds. Recruitment is therefore not stochastic. Instead, it is influenced by factors such as the reproductive output of the local population and by characteristics of the seagrass bed such as its exposure to wave-action.

CHAPTER ONE

GENERAL INTRODUCTION

1. HISTORICAL BACKGROUND

The unusual morphology and reproductive biology of pipefishes (Syngnathidae) were recognized more than 2000 years ago. Writing in the third century B.C., Aristotle noted: 'That fish which is called *Belone*, at the season of reproduction, bursts asunder, and in this way the ova escape; for this fish has a division beneath the stomach and bowels like the serpents called typhlinae. When it has produced its ova it survives and the wound heals up again.' (Gudger, 1905). About three centuries later, Aristotle's accurate observations were confirmed by Pliny the Elder, in his 'Natural History'. Additional observations on the reproduction of pipefishes were made at about 200 A.D. by the Roman Claudius Aelianus. There are no further records on pipefishes until 1554, when Rondelet's 'De Piscibus Marinis' was published (Gudger, 1905). Rondelet's observations were mostly accurate and based on live fish. His single misconstrued idea that females brood the young would, however, endure for over two hundred years. John Walcott (cited in Gudger, 1905) in 1784-1785 was the first to correct this misconception and to show that only males bear the brood-pouch. The Swedish naturalist Eckstroem (1831; cited in Gudger, 1905), working independently, confirmed Walcott's observations. Eckstroem not only stated that males bear the

young, but also declared that copulation was repeated several times and that the embryos were nourished while in the pouch. These statements were not generally accepted for many years. They also incited a debate which lasted for forty years and focussed on whether males or females brood the young. The controversy was finally settled in 1872, when the work of Marcussen and his pupil Passentewitsch established beyond doubt that male pipefish have brood-pouches (Gudger, 1905). The settlement of the question as to whether males brood the young has had important repercussions on the direction of research on Syngnathids in this century: it has promoted interest in the biology of this group and has provided researchers with a particularly useful model with which to study the theory of sexual selection.

The literature on the reproductive biology of Syngnathids is extensive (e.g. Bayer, 1980; Breder, 1940; Breder and Rosen, 1966; Eastman, 1915; Fiedler, 1954; Gill, 1905; Graham, 1939; Gudger, 1905; Takai and Mizokami, 1961; Targett, 1984; Thevenin, 1936) and recent studies have used pipefishes to test the hypotheses related to the theory of sexual selection (e.g. Berglund *et al.*, 1986a, b, 1988; Gronell, 1984; Svensson, 1988).

Hypotheses dealing with the evolutionary ecology of reproduction predict that the sex which makes a greater investment into the production of offspring - among birds and mammals it is normally the females - should become a 'limiting resource' for the other sex. In males, selection should favour those characteristics that attract females (e.g. increased size and colour) and are

advantageous in intrasexual competition (Trivers, 1972; Williams, 1975). One way of testing these hypotheses is to look at those species where the 'usual' sex roles are reversed, i.e. the males invest more heavily into the production of offspring (e.g. by providing all or most of the parental care) and may therefore be a limiting resource for the reproductive success of females. The family Syngnathidae (seahorses and pipefishes) has often been indicated as a potential group for testing the above model (e.g. Trivers, 1972; Williams, 1975) because it is the only family of fish where most of its members have a specialized structure - the brood-pouch - for caring for the eggs or young. Parental care is therefore extensive and exclusive to males.

2. AN OVERVIEW OF THE ECOLOGY OF PIPEFISHES AND OTHER FAUNA FROM SEAGRASSES

Despite the interest in the reproductive biology of Syngnathids, knowledge of their ecology is scarce. The literature dealing specifically with the ecology of pipefishes consists, to my knowledge, of the unpublished thesis of Mercer (1973; cited in Howard and Koehn, 1984), and four studies on the feeding ecology of pipefishes (Ryer, 1988; Ryer and Boehlert, 1983; Ryer and Orth, 1987; Tipton and Bell, 1988), all from seagrass beds in the U.S.A. Howard and Koehn (1984) is the only published work in Australia that deals with the ecology of these fishes. This paucity of information is surprising for two reasons. First, knowledge of their distribution and abundance, growth and breeding biology is essential for designing and interpreting experiments to test the hypotheses generated by the sexual selection theory. Second, one would expect to find a larger body of literature on the ecology of pipefishes considering that they normally represent a major portion of the fish assemblages of seagrasses in Australia and elsewhere (see review by Pollard, 1984). Moreover, much research has been done in the last two decades with the objective of understanding the ecology of fishes living in these habitats. This apparent contradiction is due mainly to the fact that the great importance attributed to seagrasses is characteristically associated with their function as 'nursery areas' for species of economical importance.

Much of what is known about the distribution, abundance and feeding habits of pipefishes has come from studies on the whole communities living in seagrasses and the general trends set by this type of work have had a marked influence on the progression of more specific research on pipefishes. For this reason, a review of the literature on the ecology of the seagrass fauna is desirable. This review is not intended to be exhaustive. The concepts discussed here are mostly those which have been emphasized in the literature and which I consider to be relevant to those aspects of the ecology of pipefishes which are dealt with in the chapters that follow. First there is a brief summary of the development of research on seagrass habitats. Spatial and temporal patterns of abundance at different scales are reviewed next. I then consider the 'residence status' of fishes living in seagrasses and the role of these habitats as 'nursery areas'. A summary of the feeding ecology is then followed by an outline of the models that have been proposed to explain the distribution and abundance of the fauna of seagrasses.

THE EVOLUTION OF RESEARCH ON SEAGRASS HABITATS

The importance of seagrasses was made apparent at the end of the last century (1890-1920) by the pioneer work of Petersen and other investigators from the Danish Biological Station, Copenhagen, (Phillips and Lewis, 1987; Rasmussen, 1977). In 1970, a new thrust was given to research on the ecology of seagrasses and their fauna by the publication of den Hartog's 'The

Seagrasses of the World' (Pollard, 1984). Subsequently, the first 'International Seagrass Workshop' was held in Leiden (The Netherlands) in 1973. This meeting was of paramount importance because it fostered the publication of several volumes on the general ecology of seagrass beds (see Pollard, 1984) including several reviews on the consumer ecology and faunal relationships in these habitats (Kikuchi, 1974; Kikuchi and Peres, 1977; Kikuchi, 1980; Ogden, 1980). In 1984, Pollard summarized the literature on ecological studies with special emphasis on works done in Australia. Several regional review papers on the ecology of the fauna of seagrasses have been written more recently (e.g. Gilmore, 1987; Virnstein, 1987) including one on the ecology of seagrass-associated fishes in Australia (Bell and Pollard, 1988). It is evident from these reviews that research on the fauna of seagrasses has changed dramatically in the last few decades: whereas early work was mainly qualitatively descriptive, by late 70's there was a substantial number of quantitative and experimental studies, and in 1980 Heck and Orth proposed the first conceptual model to explain the relationship between seagrasses and their fauna.

SPATIAL PATTERNS OF ABUNDANCE

A major part of the literature on seagrasses is concerned with the characterization of the fauna. Pollard (1984) reviewed the relationships between 30 dominant fish assemblages occurring in a variety of seagrasses in seven geographical regions: the

Mediterranean, north-western Atlantic, Gulf of Mexico, Caribbean and north-western Pacific areas. Although the studies differed in many ways (including sampling intensity and methods), it became evident that the Syngnathidae was one of the ten most important families of fishes from seagrasses; it was mentioned in 24 of the 25 studies reviewed by Pollard (1984). Its predominance was also apparent when Australian studies on the fauna of seagrasses were analysed as a separate group.

The assemblages of fishes associated with seagrasses vary on a latitudinal basis. For example, tropical seagrasses have a greater diversity and/or abundance of species and this has been attributed to the presence of coral-reef associated species (e.g. Ogden, 1980; Ogden and Zieman, 1977; Weinstein and Heck, 1979). Despite these differences in the fauna, comparative studies on the fish fauna on a latitudinal scale in the U.S.A. (e.g. Orth and Heck, 1980; Gilmore, 1987; Weinstein and Heck, 1979) and other community studies at different latitudes in Australia (for example, Robertson, 1980; Young, 1981; Young and Wadley, 1979) have shown that Syngnathids, including pipefishes, are a regular component of seagrass assemblages in temperate, sub-tropical and tropical seagrasses.

There appears to be a scarcity of studies designed to compare the assemblages of fishes from seagrasses in different estuaries. Pollard (1973, unpublished data; cited in Pollard, 1984) noted that the assemblages of fishes from *Posidonia* in Jervis Bay, N.S.W., were very similar to those of Botany Bay and Port

Hacking. Burchmore *et al.* (1984) found that approximately 75% of the species collected from one *Posidonia* bed in Port Hacking were also present in a study done in Botany Bay (Middleton *et al.*, 1984) and represented a similar percentage of the fauna.

Bell *et al.* (1988) and Rigby (cited in Bell and Pollard, 1988) have also shown that, at least in some estuaries, composition and abundances of some species varied among 'zones', i.e. depending on the distance of the seagrass bed (and units of artificial seagrass in the case of Bell *et al.*, 1988) from the mouth of the estuary. Variation of the fauna among beds was found to differ also between arms within the same estuary (Bell *et al.*, 1988). Unfortunately, Syngnathids were not included in Bell *et al.*'s study. Although members of the family Syngnathidae are usually present at all sites within a bay, the relative abundance of the species vary significantly from site to site (e.g. FRI, 1987; Sogard *et al.*, 1987; Young and Wadley, 1979).

The diversity and abundance of assemblages of fishes vary among species of seagrass and this is also true for Syngnathids (e.g. Bell and Westoby, 1986b; Martin and Cooper, 1981; Middleton *et al.*, 1984; Virnstein and Howard, 1987a, b; Young, 1981). These dissimilarities in the composition and abundance of the fauna have been attributed to differences in such factors as in plant biomass (e.g. Stoner, 1983); because different resources offered by the two seagrass species can be used by different species (e.g. Young, 1981); habitat selectivity and differential survivorship (Middleton *et al.*, 1984; Virnstein and Howard,

1987a) or stochastic recruitment and the vertical location of larvae in the plankton (Bell and Westoby, 1986b).

At a much smaller scale, the fauna of seagrasses has often been classified according to the microhabitat (in a vertical gradient) where species are normally found and their mode of life. The initial classification proposed by Kikuchi (1966) was modified by Kikuchi and Peres (1977) and comprised four categories 1) on the leaves; 2) stem and rhizomes; 3) under the canopy; 4) in or on the sediment. The mode of life, as used by Kikuchi and Peres, referred mainly to the degree of motility (sessile, sedentary, etc) of the animals.

Similarly to the above classification system, Howard and Koehn (1984) suggested that species of pipefish can be categorized into 'functional ecological groupings' (or microhabitat use) based on 'behavioural and morphological attributes'. The first group comprises species that occupy the 'upper macrophyte canopy' whereas species in the second group are divided into those that live in the 'zone close to the substratum' and those which are associated with the canopy 'well above the substratum'.

The categories of microhabitat have often been defined according to different criteria. The main difference in the classification systems is the scale. For example, fishes within the seagrass canopy could be grouped together (e.g. according to Robertson and Howard, 1978) or be placed in smaller groups according to the part of the canopy they are found in (e.g. Kikuchi and Peres,

1977)). Similarly, the feeding modes range from a more general (e.g. Duka, 1978) to a more specific and more informative system (e.g. Bell and Westoby, 1986b; Livingston, 1982). For simplicity - and because pipefishes are found in different areas of the seagrass bed - the term microhabitat will not be used in this study.

TEMPORAL PATTERNS OF ABUNDANCE

There is only limited documentation of long-term changes in the abundances of organisms from seagrasses. Some studies suggest, nevertheless, that assemblages may be constant through time (Burchmore *et al.*, 1984; Robertson, 1980; Weinstein and Heck, 1979). Robertson (1980), over a period of 4½ years, found that despite the seasonal fluctuations in standing crops of individual species within a year, the relative abundance of each of ten species (Syngnathids were not included) from a *Zostera* bed in Victoria remained fairly constant from year to year.

In contrast to the above studies, Young (1981) found great variability in a 3½ years' study of the 'vagile epifauna' (including Syngnathids) from two seagrasses in Port Hacking, N.S.W. Although species were found more often, and in greater numbers, in summer than in winter of the same year, variability between years was such that some species occurred so frequently and in as great an abundance in the summers of one year as in the

winters of others. Young (1981) attributed the observed changes to differential recruitment.

Seasonal fluctuations in number of species, number of individuals (including pipefishes) and biomass are characteristic of fish in seagrasses. For example, abundance, number of species (Orth and Heck, 1980) and biomass (Adams, 1976a; Middleton *et al.*, 1984) have been reported to increase in spring and early summer and were significantly correlated with water temperature, plant biomass, and the arrival of seasonal residents. In Redfish Bay, Texas, Hoese and Jones (1963) found that the greatest densities of macroinvertebrates and fishes occurred in spring and autumn and correlated best with the amount of water in the bay.

The greater diversity, abundance, and biomass of fish recorded at night in seagrass beds have been attributed in some cases to the migration of fishes from nearby rocky-reefs (e.g. Bell and Harmelin-Vivien, 1982) and coral-reefs (e.g. Weinstein and Heck, 1979). Similar patterns have, however, been observed in isolated beds (Adams, 1976b; Leber and Greening, 1986; Orth and Heck, 1980; Stoner, 1983) and related to migrations out of the bed due to high water temperatures during the day (Adams, 1976b; Cameron, 1969; Hoese and Jones, 1963) and greater efficiency of gear at night (Gray and Bell, 1986; see also General Methods). Olney and Boehlert (1988) also found that densities of larvae were one order of magnitude greater at night and suggested that that may be due in part to predation since planktivores, including pipefishes (Ryer and Boehlert, 1983) typically feed during the

day. In contrast to these studies, there is evidence that abundance and/or diversity are not always greater at night (e.g. Gray and Bell, 1986; Rigby, 1984, cited in Bell and Pollard, 1988). Furthermore, in Victoria, Robertson (1980b) found that temperatures never reached lethal levels and concluded that the greater abundance of five species at night and four during the day were the result of at least 3 factors: differential availability of prey at day and night, changes in predation time, and avoidance of interspecific competition.

THE RESIDENCE STATUS OF FISHES FROM SEAGRASSES

Fishes living in seagrass beds show different degrees of association with these habitats. To account for this variability, Kikuchi (1966) developed a classification system which is based on the relative amount of time (or proportion of life-history) a species is associated with the seagrass bed. This system has been modified by some authors (e.g. Kikuchi and Peres, 1977; Middleton *et al.*, 1984) thus creating confusion. The original system and some of its variations are summarized below.

The four categories described by Kikuchi (1966) were:

- 1) Residents (Kikuchi, 1966), permanent residents (Kikuchi, 1974; Kikuchi, 1980; Kikuchi and Peres, 1977; Middleton *et al.*, 1984) - this group is well defined and comprises those species (usually small fishes) which breed and are present in

seagrass beds all year round. The most common examples are Syngnathids and Gobiids.

- 2) 'Seasonal' was the word used by Kikuchi (1966; 1974; 1980) and Kikuchi and Peres (1977) to describe those fishes residing in the seagrass bed for one season or stage of their life-history. Bell and Pollard (1988) noted that the word seasonal 'implies that a long-lived species may visit seagrass during a particular season each year'. None the less, 'seasonal residents' as defined by Kikuchi and Peres (1977; and Kikuchi, 1966) also includes 'residents [that] spend definite developmental stages in the seagrass bed; some species spend their spawning season and the others spend their juvenile or subadult stages'. Burchmore *et al.* (1984) and Middleton *et al.* (1984) called this category 'temporary residents'. Bell and Pollard (1988) suggested that in Australia, according to the classification adopted by Burchmore *et al.* (1984), a seasonal species (i.e. that returns to the bed each year in the same season) would be likely to be categorized as 'Transient'. It appears to me, however, that such species would be more appropriately classified as 'temporary'.

Which word is better? Neither term suffices here. Species that live in seagrass beds as juveniles and move out of the bed and never return are not truly 'seasonal'. 'Temporary', on the other hand, does not really apply to those species that return each

season either. For simplicity, it would be better to use the word 'seasonal' as defined by Kikuchi (1966) and Kikuchi and Peres (1977).

3) Transients (Kikuchi, 1966), temporary (Kikuchi, 1974) or temporal residents (Kikuchi, 1977) and visitors (Burchmore *et al.*, 1984; Kikuchi, 1980; Middleton *et al.*, 1984) are those species that forage over a wider area than the seagrass bed; thus, they carry out only part of their daily activities (usually feeding) in the seagrass bed. This can happen in a predictable manner, such as those species that 'often visit and feed in the seagrass bed at night' (Kikuchi and Peres, 1977), as well as those that show no apparent predictable patterns (e.g. sharks and rays). Bell and Pollard (1988) noted that Kikuchi's (1966) 'transients' category does not cater for species that move into the beds on a tidal or diel basis. Kikuchi and Peres's (1977) definition can, however, accomodate those species.

4) Casual species (Kikuchi, 1966; Kikuchi, 1980), occasional migrants (Kikuchi, 1974; Kikuchi and Peres, 1977) - these are species that appear only occasionally in the seagrass bed and are not therefore truly related to this habitat. Burchmore *et al.* (1984) did not include this category.

Thus, Kikuchi's (1966) original categories (permanent, seasonal, transients and casual) should be adequate provided that the second category 'seasonal' is interpreted as containing truly

'seasonal' species in addition to 'temporary' ones, i.e. those that spend only one stage of their life-history in seagrass beds. Studies on seagrass beds in the USA have not adopted this classification (Bell and Pollard ,1988). Nevertheless, in his recent review, Gilmore (1987) noted that this classification can be useful.

SEAGRASS BEDS AS NURSERY AREAS

Species of economic importance have been studied to a much greater extent than have the smaller inhabitants of seagrasses (e.g. SPCC 1981a, b, c; see review by Gilmore, 1987). The unpublished thesis of Brown (1972; cited in Howard and Koehn, 1984) in the U.S.A. appears to be the single major work on the life-history of pipefishes. There is a consensus in the literature that seagrass beds are relatively unimportant as spawning habitats for fishes (Bell and Pollard, 1988; Kikuchi, 1980; Olney and Boehlert, 1988; SPCC Report, 1981c). For instance, of the 47 species of economical importance collected in the environmental control study carried out in Botany Bay, only 2 are believed to spawn in seagrass beds (*Zostera*). The importance of seagrass beds as spawning sites is obviously relative to the spawning habits of the species. For example, Olney and Boehlert (1988) compared the abundance of eggs in three habitats (2 seagrasses and sand area) and concluded that the areas of submerged aquatic vegetation were not important for species with pelagic eggs, but were important for species with demersal eggs

(e.g. Atherinids) and those that brood the eggs (e.g. Syngnathids).

That seagrass beds are habitats for juvenile fish has been recognized for, at least, nearly 60 years (Pearson, 1929; cited in Gilmore, 1987). It is also established now that seagrass beds function as feeding grounds for both decapod crustacea (e.g. Leber, 1985) and juvenile fishes (e.g. Carr and Adams, 1973; Livingston, 1982). The extent to which juveniles depend on these habitats is, however, not usually known. A notable exception is the series of studies on the pinfish *Lagodon rhomboides* in the U.S.A. (Cameron, 1969; Stoner, 1980a, 1980b; Stoner and Livingston, 1984; Weinstein *et al.*, 1984).

A more strict approach to the 'nursery function' of seagrass beds was adopted by Virnstein (1987). He argued that for seagrass beds to show true nursery function, juveniles must not only be more abundant in these habitats, but also grow at a faster rate due to increased food supply and/or show greater survivorship due to the better degree of protection provided by the beds. The study of Peterson *et al.* (1984) seems to be the only one, however, to show that the growth rate of an organism (the bivalve *Mercenaria mercenaria*) is greater in seagrass beds than in bare-sand areas (Virnstein, 1987). There seems to be no similar studies for fishes.

There is now substantial evidence that certain seagrass beds hold greater densities of some juvenile fishes than unvegetated

substrata and that survivorship improves (in a step-function relationship rather than linearly) with density of seagrass (see references below). These pieces of evidence have been generally considered as sufficient to establish the characteristic of seagrass beds as a nursery area (Bell and Pollard, 1988; Kikuchi, 1966; Kikuchi and Peres, 1977; Kikuchi, 1980; Miller and Dunn, 1980; Pollard, 1981; Virnstein, 1987). It should be noted, nevertheless, that there is no direct evidence that improved survivorship of juveniles from vegetated areas has any influence on the adult populations that live elsewhere. Furthermore, the assumption that juvenile fish living in estuaries do not or cannot live in other, open habitats awaits confirmation.

Some seagrass beds do not function as nursery areas. This is because juveniles of species usually associated with seagrasses live in shallow sublittoral rocky-reefs (Bell and Harmelin-Vivien, 1982); or are as abundant in bare-sand areas (Heck and Thoman, 1981); or are found in adjacent seagrass-beds of different species (e.g. Bell, 1980; Middleton *et al.*, 1984) or mats of drift algae (e.g. Kingsford and Choat, 1985, 1986; Kulczycki *et al.*, 1981), with which juvenile of some species of pipefishes are many times associated. Finally, Olney and Boehlert (1988) questioned the function of seagrass as nursery area for early larvae. They suggested that, whereas later stages may benefit from reduced predation pressure, early larvae may suffer increased predation by planktivores.

FEEDING HABITS AND TROPHIC RELATIONSHIPS

The relationship between diet and feeding habits was identified in the 1973 Seagrass Workshop as one of the basic areas where research was much needed. Consequently, the literature on diet, feeding ecology and trophic relationships is vast.

Dietary lists usually accompany most of the papers on feeding ecology (e.g. Adams, 1976c; Bell *et al.*, 1978a, b; Burchmore *et al.*, 1984; Brook, 1977; Conacher *et al.*, 1979; Duka, 1978; Howard and Koehn, 1984; Livingston, 1982; Robertson, 1977, 1980).

Interpretation of feeding studies can be made difficult, however, by several methodological problems. Kikuchi and Peres, (1977) stressed the importance of knowing the availability of prey in the foraging site. Identification of prey to species is important because some species are eaten more often than others and in different proportions to their relative abundance (Virnstein, 1987). To be accurately identified, items in the diet have to be fresh - therefore sampling for analysis of contents of guts should be intensive (e.g. Ryer and Boehlert, 1983). Problems associated with caging experiments in seagrass beds have also been discussed at length in several reviews (e.g. Choat, 1982; Virnstein, 1978, 1980).

Despite the variability in the sampling methods, and in the processing of the contents of guts, a number of generalizations have been made so far as the diets of seagrass fishes are concerned (see also reviews by Bell and Pollard, 1988; Kikuchi,

1980; Kikuchi and Peres, 1977; Pollard, 1984). Free-living planktonic and epifaunal species, especially crustaceans, form the major part of the diet of most fishes (e.g. Adams, 1976b; Bell and Harmelin-Vivien, 1983; Brook, 1977; Burchmore *et al.*, 1984; Carr and Adams, 1973; Duka 1978; Howard and Koehn, 1984; Livingston, 1982; Robertson, 1978). Detritus and teleosts have only occasionally been reported as being part of the diet of fishes (Bell and Harmelin-Vivien, 1983; Kikuchi and Peres, 1977; Orth, 1975; Weinstein and Heck, 1979). Fish feeding on seagrasses has been considered as a 'Caribbean [or tropical] phenomenon' (Ogden, 1980). Several Australian Monacthantids include, nevertheless, not only algae but also seagrass in their diets (Thompson, 1959; Bell *et al.*, 1978b; Conacher *et al.*, 1979; Nichols *et al.*, 1985).

A number of studies has described the trophic ecology of fishes associated with seagrass meadows (e.g. Brook, 1977; Carr and Adams, 1973; Duka, 1979; Kikuchi, 1966; Livingston, 1982, 1984; Stoner, 1980a) and a few have actually quantified the energy flow through a whole fish community (e.g. Adams, 1976b, Robertson, 1984).

Ontogenic changes have been documented for many fishes (e.g. Adams, 1976c; Livingston, 1982, 1984; Robertson, 1977, 1982, 1984). Changes in the relative abundance of prey (e.g. Kikuchi, 1974; Robertson, 1977, 1982), body size (e.g. Adams, 1976c; Bell, 1980; Middleton *et al.*, 1984; Robertson, 1977) and mouth-gape of

the fishes (e.g. Robertson, 1977; Tipton and Bell, 1988), have been suggested as the primary cause of ontogenic changes in diet.

Syngnathids feed mainly on small crustaceans (e.g. Livingston, 1984; Howard and Koehn, 1984; Ryer and Orth, 1987; Tipton and Bell, 1988) and most species undergo ontogenic changes in diet (e.g. Adams, 1976c; Livingston, 1982; Ryer and Orth, 1987; Tipton and Bell, 1988). Recent experiments in aquaria have also shown that selection of prey by the pipefish *Syngnathus floridae* was a consequence of the accessibility of different prey rather than preference by the fishes. Visibility of prey appeared to be the most important factor and was the result of both size and motion (Main, 1985). Ryer (1988) investigated the effects of 2 levels of habitat 'complexity' (narrow and wide ^{leaves}) on pipefish *Syngnathus fuscus* of 2 different size-classes foraging on amphipods of 3 different size-classes. He concluded that 'pipefish appear able to judge prey accordingly, and adjust foraging tactics to match environmental constraints'. Furthermore, he cautioned to the fact that the effect of the physical structure of the seagrass on the prey/predator interactions should be considered in view of the relative size of prey, predator and the hiding place.

THE IMPORTANCE OF SEAGRASS BEDS AS VEGETATED HABITATS

Comparative studies have shown that most seagrass beds have a greater number of organisms and diversity of species than

adjacent unvegetated habitats (Briggs and O'Connor, 1971; Brook, 1978; Kikuchi, 1974; Orth and Heck, 1980; Stoner, 1983 ; SPCC, 1981a; Summerson and Peterson, 1984; Thayer *et al.*, 1975; Weinstein and Brooks, 1983; see Heck and Thoman, 1981 and Hanekom and Baird, 1984, for other results). The reasons often associated with these differences are that seagrass beds buffers the effects of currents and waves and hold sediments, and they also provide a shaded environment, food and protection from predation (e.g. Kikuchi and Peres, 1977). Some of these factors could, however, be the reason why seagrasses are found where they are, rather than be caused by the presence of seagrasses. Additionally, there is as much as 20 times more surface area for small sessile flora and fauna as compared to unvegetated areas (May *et al.*, 1978).

In the last decade much research on seagrass beds has concentrated on the relationship between the diversity and abundance of seagrass animals and the 'complexity' of seagrass beds. As observed by Virnstein (1987), the question of 'habitat structural complexity is not a simple one', and perhaps the term 'complexity' is not always appropriate. Many times (see examples below) complexity is measured as plant abundance, which is a measure of the amount of habitat space and not complexity. Thus, before I outline the models that have been proposed to explain the relationship between the 'complexity' of the seagrasses beds and the abundance of the fauna, I will summarize some of the different ways this term has been used in the literature.

1) Physical structure of the plants - 'complexity' in this sense has been measured as biomass (Orth, 1977; Stoner, 1980a); macrophyte biomass (irrespective of plant species (Heck and Wetstone, 1977)); shoot/blade density (Homziak *et al.*, 1982); shoot/blade density and height of blades (Gray and Bell 1986; Bell^{et al.} 1986a,b,c); width of blades (Ryer, 1988); surface area (Stoner and Lewis, 1985); leaf-surface-area per area of bottom substrate (Heck and Orth, 1980). I think in these cases the names of the features being measured would substitute well for the term complexity.

2) Different types of habitat - complexity has been appropriately used to indicate different species of seagrasses, association with drift algae and epiphytic algae, and spatial patchiness. For example, drift algae can be very abundant in seagrass beds, thus increasing the complexity of the structure of the beds. Drift algae have been shown to be a potential habitat for both invertebrates (Kulczycki *et al.*, 1981; Leber, 1985; Virnstein and Howard, 1987a) and fishes, especially small fishes such as Syngnathids and Gobiids (e.g. Kingsford, 1986; Kingsford and Choat, 1985, 1986; Kulczycki *et al.*, 1981). Attached green algae will also add to the structural complexity and can support large densities of macrocrustaceans (Stoner, 1985). Algal epiphytes attached to seagrass blades not only increase the structural complexity but are also a part of the diet of most mobile animals that live on seagrass blades (see review by Virnstein, 1987). Bell and Westoby (1987) have shown, however, that a decrease in abundance of some fish species occurred during a bloom of an

epiphytic alga. They suggested that the physical complexity of the habitat increased to such an extent that individuals were excluded from the canopy.

INTERACTIONS BETWEEN THE PHYSICAL STRUCTURE OF SEAGRASSES AND PREDATION

It has been shown that seagrass biomass is positively correlated with abundance and diversity of both invertebrates (Heck and Wetstone, 1977; Hooks *et al.*, 1976; Homziac *et al.*, 1982; Lewis and Stoner, 1983; Stoner, 1980a; Summerson and Peterson, 1984) and fishes (Adams, 1976b; Orth and Heck, 1980). Experimental studies indicate that denser vegetation or larger surface area can provide greater protection for potential prey because these factors reduce the ability of predators to search for (e.g. Nelson, 1979a; Ryer, 1988; Savino and Stein, 1982) and capture prey (e.g. Heck and Thoman, 1981; Ryer, 1988; Stoner, 1982; Minello and Zimmerman, 1983).

In 1980, Heck and Orth proposed a model to explain the interaction between the diversity and abundance of seagrass-associated animals and the amount of plant cover in a given area. They hypothesized that changes in the 'plant surface area per area of bottom substratum', i.e. leaf area index (LAI) will have such an effect on predation efficiency or intensity as to alter the diversity and abundance of invertebrates and juvenile fish. They suggested that as LAI increases, survivorship will also

increase, but only to a certain point (asymptote). Vegetation may become so dense as to cause unfavourable conditions for both invertebrates and juvenile fish (e.g. anoxic conditions) as well as for large fish (e.g. movement within the canopy becomes difficult). Heck and Orth's (1980) model was later expanded to account for variation in prey and predator characteristics (e.g. epifaunal or infaunal, tube-dwellers or non-tube dwellers) and several features of seagrasses which may interfere with predator-prey interactions (Orth *et al.*, 1984).

Although there is evidence that confirms in part the model proposed by Heck and Orth (see references above), it has become evident that their hypotheses cannot hold true for a whole community and generalizations should be considered with caution (Bell and Westoby, 1986b; Stoner, 1980^a; Young and Young, 1978). This became particularly obvious from the manipulative studies done by Bell and Westoby (1986b, c) in Australia. To investigate whether the patterns (but not whether they were caused by predation) of abundance and diversity predicted by Heck and Orth (1980) would occur at a small scale, they reduced leaf height and density within single beds of *Zostera capricorni* and *Posidonia australis* in Botany Bay, N.S.W. Their experiments showed conclusively that species richness and total abundance of assemblages of fish and decapods did not always respond to the manipulations. Furthermore, species responded differently to the same manipulations (Bell and Westoby, 1986b). Data from larger-scale studies (patterns between seagrass beds) have not confirmed

the predictions of Heck and Orth's model either (e.g. Bell and Westoby, 1986c; Bell *et al.*, 1988; Sogard *et al.*, 1987).

THE STOCHASTIC SETTLEMENT MODEL

A major focus in the study of mechanisms to explain the structure of assemblages of marine animals has been on the importance of stochastic processes associated with the settlement, metamorphosis and recruitment of individuals from the plankton (see reviews by Mapstone and Fowler, 1988, and Underwood and Denley, 1980).

The idea that density-independent factors such as stochastic recruitment might be important in organizing seagrass communities has also been considered for seagrass beds. For example, Young (1981) concluded that 'the differences in the fauna of the two seagrasses were controlled by external events leading to variable recruitment success'. It was only recently, however, that this concept was incorporated into a model. Bell and Westoby's stochastic settlement model as stated by Bell and Pollard (1988) predicts that: 1) Competent fish larvae are distributed patchily when ready to settle; 2) They do not discriminate among seagrass beds when ready to settle; and 3) They do not leave a bed soon after settling but redistribute within the bed to select microsites favouring survival.

The patterns observed in the field studies by Bell and Westoby (1986b,c) are consistent with the above model. Manipulations of the density and height of seagrass leaves significantly affected the abundance of species of decapod crustaceans and small fishes within beds, which would be expected according to part (3) of the model. In addition, as predicted in (2), correlations were rare over a wide range of beds. These results do not, however, rule out the possibility that differential mortality may be the factor responsible for those patterns.

The second prediction regarding indiscriminate settlement has also been tested in the field by Bell *et al.* (1987) using 'artificial seagrass units' (ASU). Bell *et al.* (1987) concluded that 'abundances of juvenile fishes in isolated ASU's were not due to settlement preferences based on physical complexity of seagrass, or post-settlement predation. Rather, they were due to availability of larvae prepared to settle indiscriminately into any shelter'. Before I consider these results in view of the above model, it is necessary to define the term 'recruitment'.

For many organisms, there may be a phase after settlement into the habitat of the adult, in which the animal is unlikely to be detected and counted by an observer because of small size, cryptic behaviour, etc. This phase may last from hours to months (Scheltema, 1974) and it is the number of organisms passing through this phase that is termed recruitment, i.e. the number of larvae or juveniles that are seen to enter the benthic population (Keough and Downes, 1982). The relevant point here is that

factors affecting recruitment may take place before a census can be made by an observer.

Thus, although the patterns of abundance obtained by Bell *et al.* (1987), in relation to predation and presence or absence of vegetation, are consistent with their model, these patterns do not necessarily reflect indiscriminate settlement between ASU's with dense and sparse seagrass. Even though Bell *et al.* (1987) set limits as to what size of fishes were considered as 'settlers', the experiment ran for 5 weeks and provided no information on processes, apart from predation, that occurred between settlement and recruitment (or time of sampling). The assumption that recruitment reflects patterns of settlement is yet to be validated. Furthermore, although Bell *et al.* (1985, 1987, 1988) showed that ASU's 'attract assemblages of fish typical of real seagrass' (Bell *et al.*, 1987), their effect on larval behaviour is unknown, and the ASU's do not represent certain features of the seagrass (e.g. thickness) which might be important for settlers.

The hypothesis proposed by Bell and Westoby (1986b) to explain the correlations between abundance of fishes and decapods and the height and density of leaves within a bed (part 3 of the model) contrasts markedly with Heck and Orth's model. Bell and Westoby (1986b) proposed that predation is not the 'proximate' but the 'ultimate' cause of patterns of distribution and abundance of seagrass-associated animals. In other words, high correlations found within beds would be the result of 'habitat choice', and

not predation itself. Bell and Westoby suggested that because predation rates differ according to vegetation cover, natural selection would favour those individuals that, once settled in a bed, will seek better cover within that bed. The evidence for this comes from a study (Bell and Westoby, 1986a) where they demonstrated that the reduction in the abundance of some species, which was observed in their field manipulations (1986b), occurred again even when predators were excluded (1986a).

Bell and Westoby's model (1986b) accounts only for variation in abundance within and between beds. Bell *et al.* (1988) have, however, also hypothesized about mechanisms to explain the variation in diversity and abundance at larger spatial scales, i.e. of zones within an estuary and between estuaries. Other data that confirm or are not consistent with Bell and Westoby's model are reviewed by Bell and Pollard (1988) and will also be discussed later (General Discussion).

3. OBJECTIVES OF THE PRESENT STUDY

This study is on aspects of the ecology of three species of pipefishes: *S. argus* (Richardson 1840), *S. nigra* (Kaup 1853) and *U. carinirostris* (Castelnau 1872), which occur in beds of *Zostera capricorni* Aschers and *Posidonia australis* Hook f. in Botany Bay and Pittwater, two estuaries in the Sydney area.

Chapter 2 comprises General Methods and descriptions of the study sites and of the three pipefishes. The patterns of distribution, abundance and their relationship with the structure of the seagrass beds are dealt with in Chapter 3. Growth and aspects of the reproductive ecology of the pipefishes then follow in Chapter 4. Chapter 5 consists of a general discussion of factors which were not studied in this project, but which might explain the patterns discussed in Chapters 3 and 4; the results are then discussed in view of the models proposed to explain the structure of seagrass communities. This is followed by a summary and conclusions and recommendations for future research.

CHAPTER TWO

STUDY AREA, DESCRIPTION OF SPECIES AND SAMPLING METHOD

1. STUDY AREA

This study was done in Botany Bay and Pittwater, two estuaries of the Sydney Basin (Fig. 2.1). Botany Bay is a shallow semi-enclosed bay which experiences strong marine influences except during periods of heavy rainfall, when increased flow from the Georges River can bring about more estuarine conditions.

Pittwater forms the south-eastern arm of the Hawkesbury River-Broken Bay estuarine system. No major rivers flow into Pittwater and therefore, similarly to Botany Bay, conditions in the lower reaches of this estuary are predominantly marine (Roy, 1982).

In Botany Bay and Pittwater, *Zostera capricorni* Aschers and *Posidonia australis* Hook f. are the two major seagrasses and are found in the shallow sandy regions of these estuaries (West et al., 1985). *Posidonia australis* (hereafter *Posidonia*) dominates the sublittoral zone, occurring from a depth of 1.3m to 7m below mean spring high water (M.S.H.W.). *Zostera capricorni* (hereafter *Zostera*) is more tolerant to exposure to air and usually is predominant in the littoral zone, occurring to a depth of 1.3 to 1.5m (M.S.H.W.).

SYDNEY REGION
ESTUARIES AND LAGOONS

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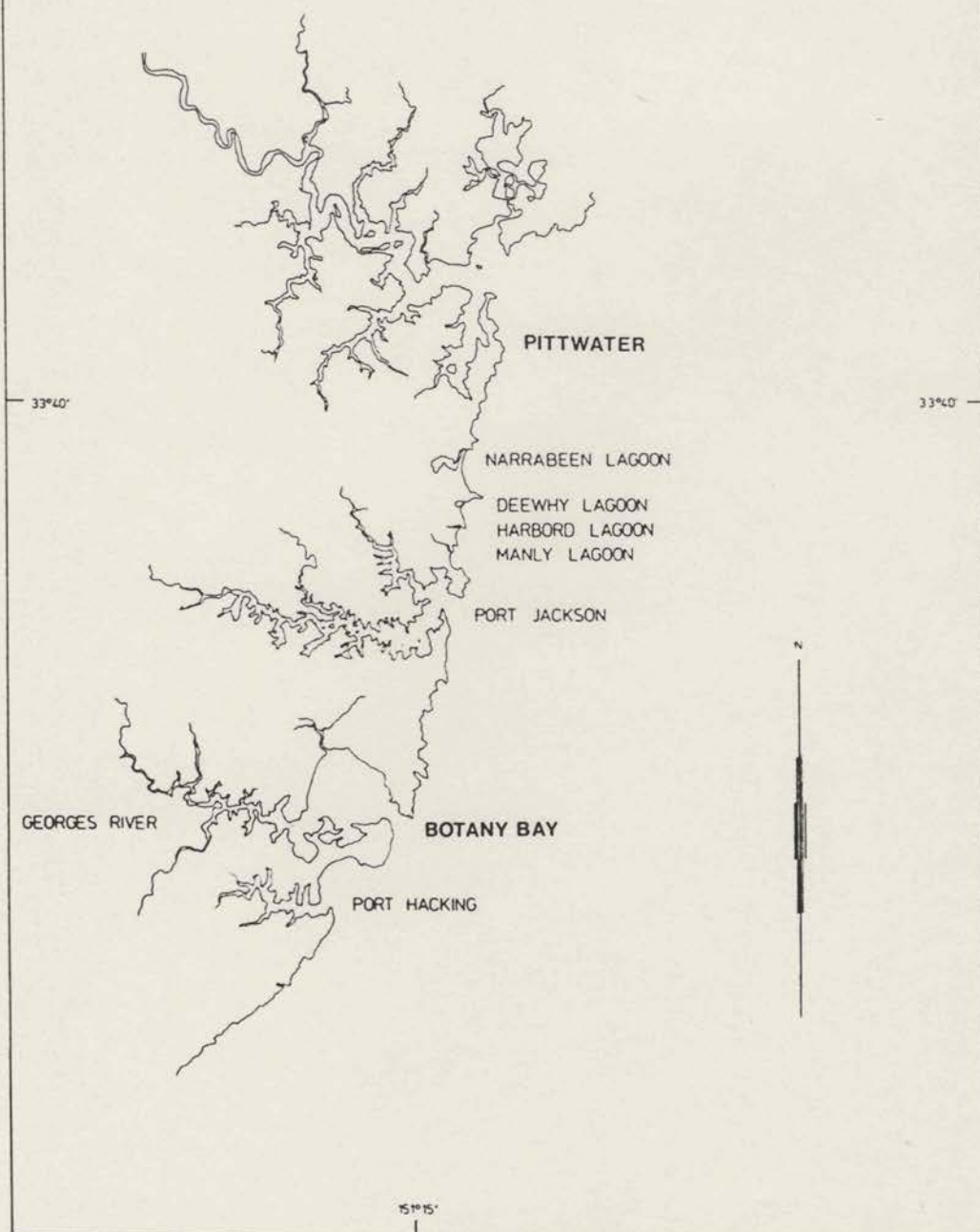


Fig. 2.1 - Estuaries and lagoons of the Sydney Region. (Taken from West *et al.*, 1986)

2. STUDY SITES

Three sites were chosen on the southern shores of Botany Bay, where most seagrass beds are found (Fig 2.2). They are located at Bona Point (hereafter referred to as KURNELL), on the east side of TOWRA POINT and on the west side of QUIBRAY BAY.

Two of the three study sites in Pittwater were located in Careel Bay, on the south-eastern shore of Pittwater (Fig. 2.3). Hereafter, the southern and northern sites in Careel Bay shall be referred to as CAREEL I and CAREEL II, respectively. The third site was located adjacent to Barrenjoey Head and hereafter will be called BARRENJOEY.

These sites were chosen at random from a number of sites in both estuaries where *Zostera* and *Posidonia* beds occurred adjacently.

Sampling areas were chosen within each seagrass bed, using reference points on shore to define their approximate boundaries. The sampling areas were all located in the subtidal zone and in such a way that none of the sides of the marked area was less than 5m from the boundary line between *Zostera* and *Posidonia* as well as from any edge of the bed. This was done to minimize possible edge effects (Orth, 1977).

All sampling areas, with the exception of the one *Zostera* bed at Barrenjoey, were in monospecific stands of seagrass (either *Zostera* or *Posidonia*). The sampling area in the *Zostera* bed at

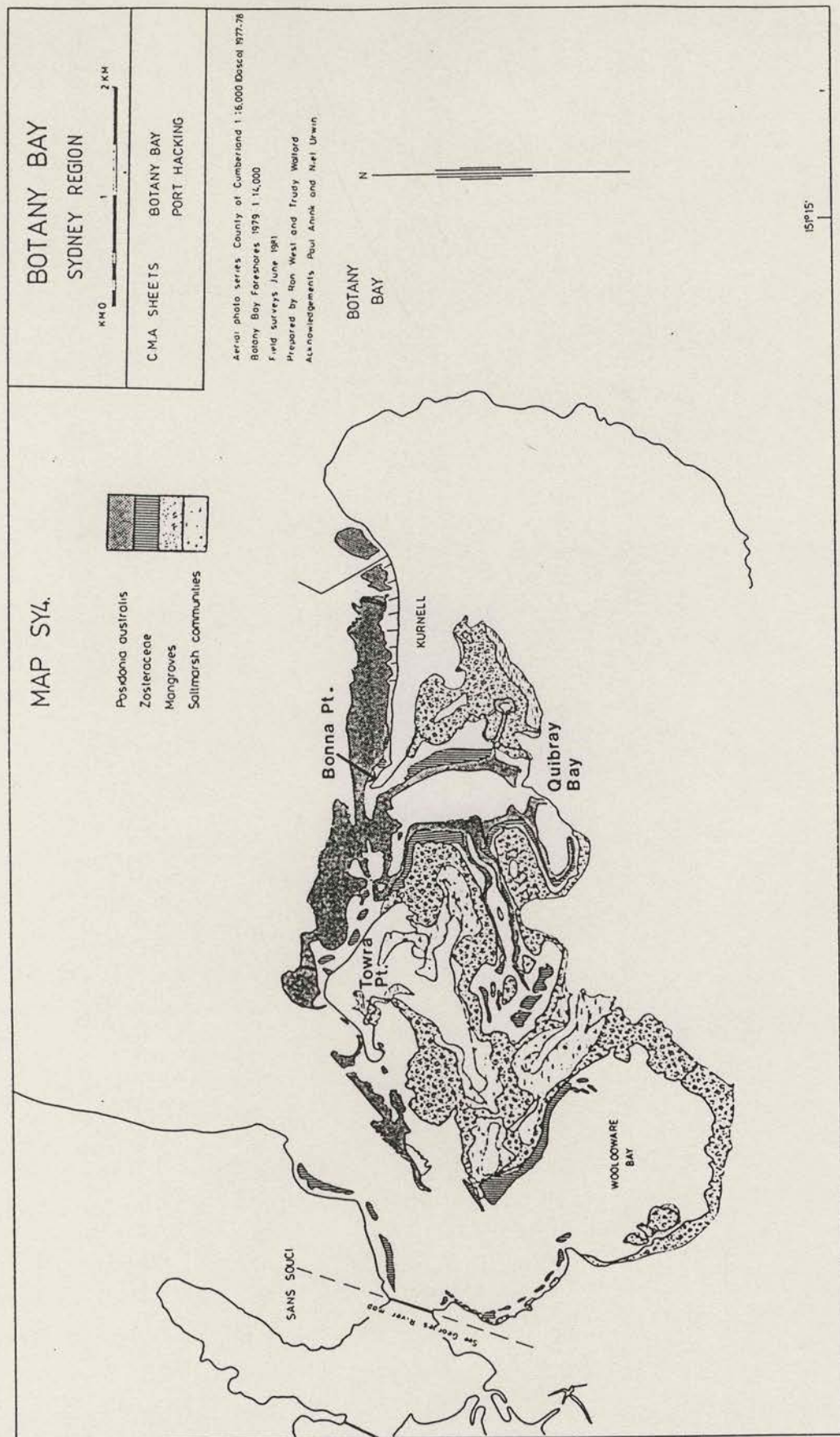


Fig. 2.2 – Distribution of seagrasses in Botany Bay.
(Taken from West *et al.*, 1986)

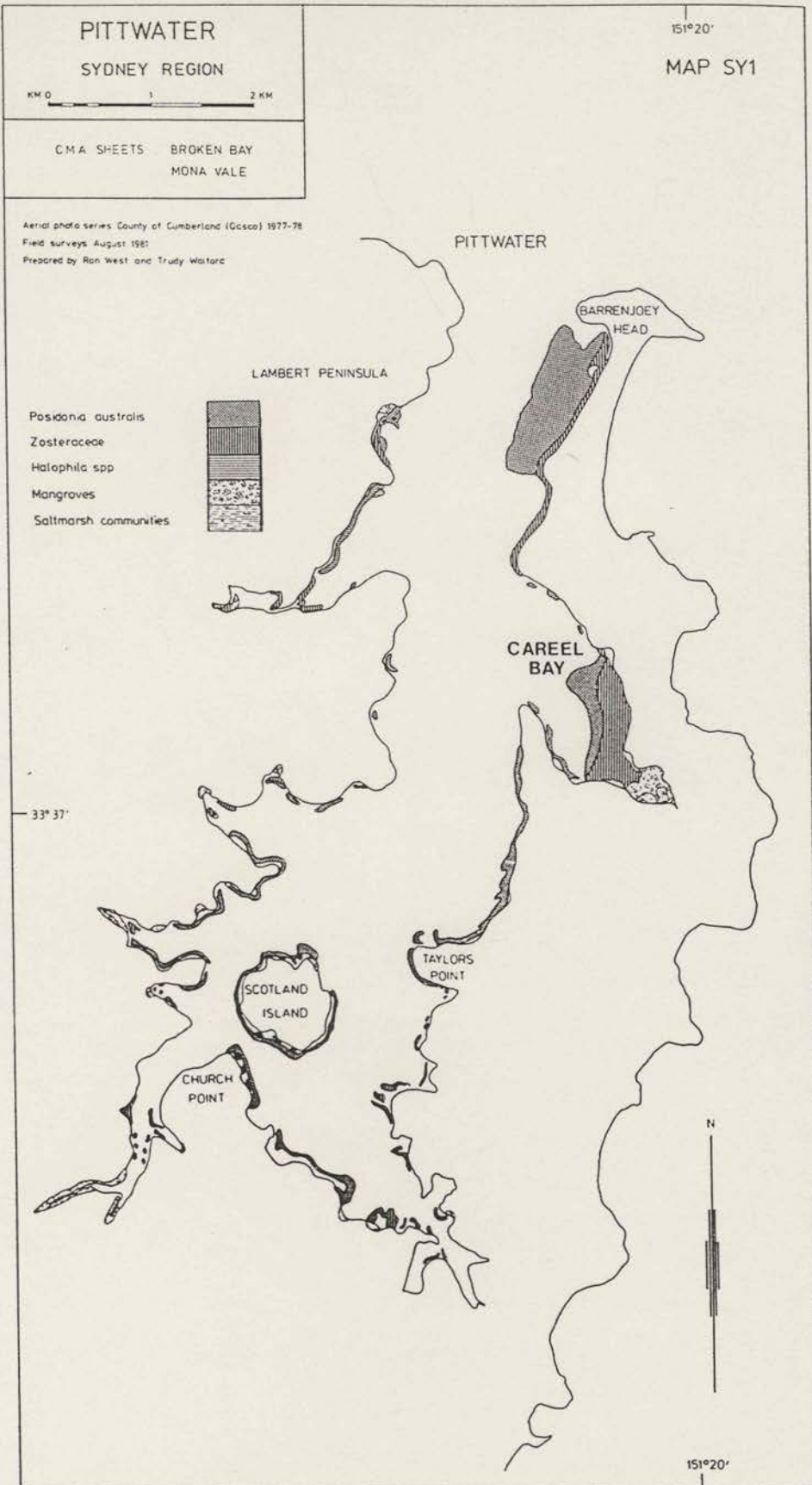


Fig. 2.3 – Distribution of seagrasses in Pittwater.
(Taken from West *et al.*, 1986)

Barrenjoey contained small pockets (about 2m²) of *Posidonia*. Because sampling was done at random, there were times when one part of a pocket of *Posidonia* was included in a sample. Barrenjoey also differed from the other sites in that between the monospecific beds of *Zostera* and *Posidonia* there was an intermediate zone approximately 5 metres wide (which was never sampled) where the two seagrasses intermingled.

3. DESCRIPTION OF PIPEFISHES

Urocampus carinirostris Castelnau 1872

This species is known only from Australia and New Guinea. In Australia, it has been collected from Narang, Queensland (ca. 24°53'S, 151°48'E) to Crawley Bay, Swan River, in Western Australia (ca. 32°01'S, 115°48'E), including Tasmania (Dawson, 1980). Its distribution appears to be restricted to the lower reaches of rivers, estuaries and other protected areas where it usually occurs among vegetation (Dawson, 1980).

This is a relatively small pipefish. Although individuals over 100mm total length (TL) were not abundant in samples collected by Howard and Koehn (1984) and in this study, Dawson (1980) examined much larger specimens (95mm standard length, SL).

Subadults and adults of this species have characteristic dermal flaps. In males they are well developed and can be simple or

irregularly branched distally; they can be present on the head and on trunk rings. Females typically have only head flaps which are usually small and simple. The anal fin is fairly well developed but caudal fin is rudimentary (Dawson, 1980). Dawson (1980) described the ground colour of this species as 'tan to dark brown'. Although animals thus coloured were common in this study, I have also collected light-green specimens which had white-silvery stripes and spots on the side (Fig. 2.4).

Males of *Urocampus carinirostris* brood the young in a pouch under the tail. The brood-pouch closure is usually of the semi-type (Herald, 1959), i.e. the free-margins often fail to meet on the ventral mid-line of the egg-filled pouch. Howard and Kohn (1984) found that males had a mean of 48 ± 3.3 (SE) eggs per brood. Dawson (1980) examined a specimen (76mm SL) with a total of 68 eggs. In the pouch, the larvae are coiled and carried inside open membranous compartments, which resemble a honeycomb, on the sides and dorsum of the pouch (Fig. 2.5).

U. carinirostris behaves like a sit-and-wait predator (Howard and Koehn 1984; pers. obs.). In aquaria, most of the time it has its prehensile tail attached to natural or artificial seagrass and is very reluctant to leave its hold of the seagrass blades.



Fig. 2.4



Fig. 2.5



Fig. 2.6

Fig. 2.4 - Female and juvenile *U. carinirostris*.

Fig. 2.5 - Brood-pouch (*S. argus*) showing membranous egg-compartments.

Fig. 2.6 - Females of *S. argus* (top), *S. nigra* (middle) and *U. carinirostris*.

This species is known from the southern half of Australia from the Hawkesbury River, N.S.W. (ca. $33^{\circ}30'S$, $151^{\circ}10'E$) to Rottnest Island and Shark Bay, Western Australia (ca. $25^{\circ}25'S$, $113^{\circ}35'E$), including Tasmania. It occurs among vegetation in estuaries and has also been collected from offshore waters (Dawson, 1984).

This is the largest of the three species studied here (Fig. 2.6). The fish from Tasmania and Western Australia appear to be larger (Dawson, 1984) usually measuring over 220mm TL compared with 200mm in New South Wales and South Australia.

The pouch of the males are rarely completely filled with eggs and the posterior part of the pouch is usually lacking egg compartments (Dawson 1984; Steffe *et al.*, in press; pers. obs.). Steffe *et al.* (in press) found that the mean clutch size in males with a full pouch was 20.7 ± 8.6 (SD, $n=9$). Dawson (1984) reported that a 230mm TL specimen carried 41 eggs. In aquaria a 140mm TL male gave birth to 15 young measuring 3.2 ± 0.1 (SD) (Fig 2.7).

Stigmatopora argus is the more active of the three species. Although its tail is not coiled as that of *U. carinirostris*, it wraps its tail around seagrass leaves and can remain in that position for long periods of time. *S. argus* will feed while attached to the leaves but, if for example food becomes scarce, it will swim freely among the blades while searching for the



Fig. 2.7

Fig. 2.7 - Young *S. argus* (approx. 10 days old).

Fig. 2.8 - Male *S. nigra*. Note eyes of larvae in the pouch.

Fig. 2.9 - Female *S. nigra*.



Fig. 2.8



Fig. 2.9

prey (see comparisons below for description of other features).

Stigmatopora nigra Kaup 1853

Stigmatopora nigra is known from Tangalooma Pt., South Queensland (ca. $27^{\circ}12'S$, $153^{\circ}22'E$) south and west to Rottnest I., Western Australia (ca. $32^{\circ}02'S$, $115^{\circ}36'E$), from Tasmania and New Zealand. This species is found among vegetation in shallow bays and estuaries as well as offshore waters (Dawson, 1984).

Males of *Stigmatopora nigra* usually carry a mean of 58.5 $\pm$ 14.8 (SD, n=11) eggs (Steffe et al., in press) which are also contained in membranous compartments in the pouch. In aquaria, a 100mm TL male gave birth to 23 young which measured 1.2 $\pm$ 0.1.

Although *S. nigra* does not have a prehensile tail, it also clings to the leaves similarly to *S. argus* (Fig. 2.8). In terms of motility, *S. nigra* is intermediate between *S. argus* and *U. carinirostris*: it is not as sedentary as *U. carinirostris* but much less active than *S. argus*.

Intergeneric and Interspecific Comparisons

The genus *Urocampus* Gunther 1870 can be distinguished from *Stigmatopora* Kaup 1853 based on the presence of the caudal fin and dermal flaps which are absent in *Stigmatopora*. Furthermore,

Stigmatopora has much longer and slender snouts (Fig. 2.6).

S. argus can be distinguished from *S. nigra* by the following features (Dawson, 1984):

- 1) *S. argus* have a longer lateral trunk ridge which reaches the 8th-20th tail ring versus the 1st tail ring in *S. nigra*;
- 2) the origin of the dorsal fin is more posterior in *S. argus* (on 9th-13th trunk ring versus 5th-7th in *S. nigra*);
- 3) *S. argus* never have the dark ventral stripes on the head which are usually present in *S. nigra* .
- 4) Only *S. argus* have lateral stripes on the pouch (not always) and this species reach a greater length (ca. 200mm TL) than *S. nigra* (ca. 160mm).

These differences are also apparent in the young fish.

Sexual dimorphism is also different between the two species. Mature females of *S. nigra* develop an exceptionally broad trunk (Fig. 2.9). This is true also for *S. argus* but is much less pronounced. On the other hand, female *S. argus* have in most cases a large number of dark spots on the dorsal surface which if present is not readily noticeable in either sexes of *S. nigra*. The ventral surface of *S. nigra* is, nevertheless, relatively much lighter than the dorsal surface and this difference is enhanced by the broadened abdomen.

4. SAMPLING EQUIPMENT AND PROCEDURES

SEINING

The first sampling method I explored was seining with a 10-metre-long seine (2mm mesh in the body and 1mm-mesh at the cod-end). This method was abandoned because although a relatively large area could be surrounded and sampled, the size of the area sampled could not be easily determined and fine sediments in several sites made seining extremely impractical.

TRAWLING

The main advantage of this technique over seining is that the area sampled can be estimated more accurately. A small beam-trawl is also easier to handle and can be pulled by boat or by hand.

(a) Description of the Sampling Equipment

The beam-trawl used was patterned on that of Young (1975) but instead of a roller at the foot it had a chain (Gray and Bell, 1986). The mouth of the net was 1m wide and 0.5m high, with 2mm mesh in the body and 1mm mesh at the cod-end. Also, I sewed onto the bottom of my net, just behind the chain, two 40 x 50cm pieces of nylon material for reinforcement for this seems to be the

first part of the net to wear out.

(b) Towing the Net

I initially examined the possibility of towing the trawl-net from a small (3m) aluminum boat for a fixed period of time. A pilot experiment was done to determine the duration of each transect. Three transects each of 2-and 4-minute duration (as suggested by Bell, pers. comm.) were taken at the *Posidonia* bed at Kurnell. The standard errors for the 2-and 4-minute trials (0.33 and 0.88 respectively) indicated that the 2-minute was as precise an estimate of the density of the population as that gained from the 4-minute transects.

Towing the trawl-net at a constant speed either for 2-minute transects or over a pre-measured transect of 35m proved to be more difficult than expected because of such factors as the wind force, swell, density and height of the seagrass bed, and type of sediment. These factors and the light nature of the boat available for the work made it difficult to take transects on a straight line and this could be another source of variation in the sampling procedure.

I then decided to pull the net by hand over a 35-metre transect (see pilot experiment above). The net was placed randomly within the sampling area (Fig.2.10; A) and a buoy was placed behind the net to mark the start of the transect. To minimize disturbance, I

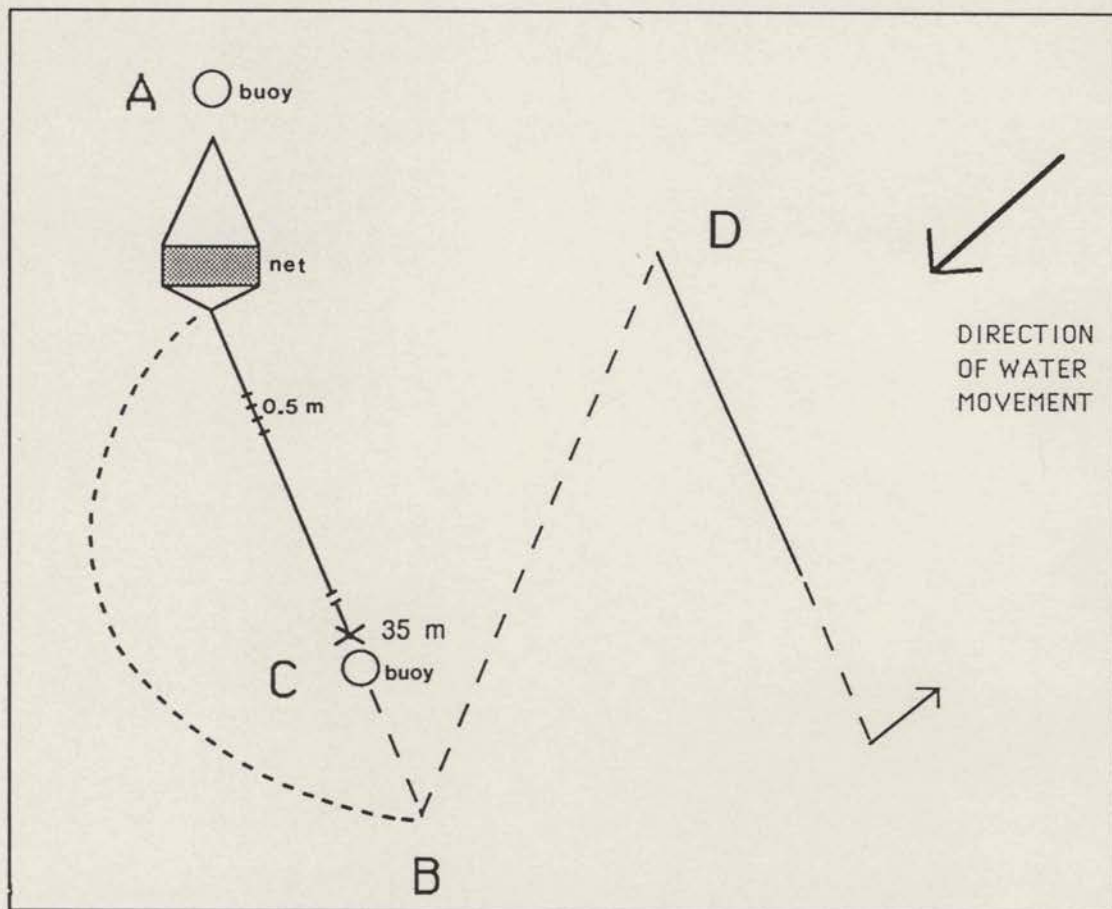


Fig. 2.10 - Diagram of sampling procedure (see text for description).

or an assistant walked with the rope in an arc from [A] to [B], thus avoiding stepping near the area to be sampled. The rope was then straightened and pulled in from the 35-metre mark [C]. A second buoy was placed at [C] to mark the end of the transect. The starting point of the next transect [D] and subsequent ones (not shown) were at least 5 metres apart to avoid overlapping. The order of the transects were taken in relation to the tidal water movement was such that the disturbance caused by one transect could not affect the next.

The pace at which the net was pulled was marked by an electronic device similar to a metronome beating at approximately 1 second intervals. To synchronize pulling the net with the timing device, knots were tied along the towing rope, at 0.5m intervals (Fig. 2.10) so that 0.5m of rope was pulled in approximately 1 second, thereby standardizing the speed of towing.

Each site, comprising one *Zostera* and one *Posidonia* bed, was sampled in one day and sampling was continued for the shortest number of days possible (weather permitting) on each sampling occasion. The order in which the sites were sampled was randomized to minimize possible effects of the inevitable varying weather, water turbidity, assistants, etc.

Samples were taken within 2 hours of low tide, which ranged in each sampling period from 0.3 to 0.6 of a metre. The depth of water at the time of sampling varied from 0.6 to 1.2 metre at all sites.

Pulling the net in *Zostera* beds could easily be done by one person. In *Posidonia* beds, however, the same operation was much more demanding because of the characteristics of this seagrass (e.g. longer leaves, more epiphytes). Therefore, in order to maintain the towing speed regular the help of an assistant was required.

(c) Bias associated with Trawling

There are two potential sources of bias when sampling fish by trawling: avoidance of and escapes from the net (see review by Kjelson and Colby, 1977). One way to minimize bias introduced by escapes is to discount any animals that are thought likely to be able to escape from the net (e.g. Young, 1981; Young and Wadley, 1979). In this study, the smallest pipefishes (young *U. carinirostris* and *S. nigra* which are at least 12mm TL) were much longer than the meshes of the net. Young pipefishes have, however, a very small diameter and it is feasible that some (up to 5mm TL, pers.obs.) were able to escape through the 2mm-mesh in the body of the net. Most of the net (cod-end) had 1mm meshes and these should be very efficient at catching even the smallest size-classes of pipefishes.

U. carinirostris are unlikely to avoid the net because this species is very sedentary and certainly not a strong swimmer. On the other extreme, *S. argus*, when disturbed, are able to make

quick evasive movements such as whirling of the body in a whip-like motion. I believe, however, that this sort of behaviour would be of little help in avoiding the net. The whip-like movement appears to be triggered only when something touches *S. argus* and although the whirling of the body makes it difficult to catch these fishes, it does not take them very far. Thus, by the time a fish is touched by the net, it is too late to avoid being caught by or to escape from it. My observations also showed that with the approach of the net, some fish try to swim away. But I have never seen a fish successfully avoiding the net although I have observed several attempting to do so. It is interesting to note that although *S. argus* is the most robust of the three species, it was the most abundant in the samples in this study. Finally, although trawling is supposed to introduce bias towards smaller fish because they are slow swimmers, this did not become apparent: the larger *S. argus* caught in this study had greater total lengths than those collected by Bell and Westoby (1986b)(Steffe et al., in press) and Burchmore et al. (1984) where the sampling technique used was poisoning.

Despite the above observations, there is evidence that suggests that trawling may be biased when sampling *S. argus* and *U. carinirostris*, at least in *Zostera* beds. Gray and Bell (1986) found that *S. argus* and *U. carinirostris* were caught in larger numbers when trawling at night than by trawling or poisoning during the day. The interpretation of their results for these two pipefishes was limited, however, by the fact that the SNK test of the mean abundances of *U. carinirostris* did not detect any

significant differences, and the number of *S. argus* collected was not sufficient for that species to be included in the overall analysis of variance. Furthermore, it seems unlikely that avoidance of the net could be responsible for these results considering that *U. carinirostris* is sedentary and a weak swimmer, and *S. argus* collected from *Zostera* are usually small juveniles; consequently, the net should be fairly efficient at catching them at any time. Also, escape from or avoidance of the net could not explain why the number of pipefishes collected by poisoning was smaller than that collected by trawling because the mesh-sizes used in all trials were very similar.

One explanation for the differences between trawling in the night and during the day is that the net was pulled at a speed that would allow the fishes to detect the approaching net and avoid it. If that happened, larger numbers would be expected to be caught at night. Unfortunately, it is not possible to make a comparison because Gray and Bell (1986) did not mention the speed the net was towed in their experiment. Towing speeds appear to vary considerably between studies. For example, the speed used in this study (0.5m s^{-1} or 30m min^{-1}) was faster by one order of magnitude than that (0.04m s^{-1} or 2.4m min^{-1}) used by Young (1981) and Young and Wadley (1979). The relatively small densities collected by poisoning could be due to the difficulty of seeing the small pipefishes during collection with a hand-net. Although I do not think that there was a significant bias in my sampling these pipefishes, caution is adviseable when considering the results regarding the very small and large size-classes.

5. PROCESSING OF THE SAMPLES IN THE LABORATORY

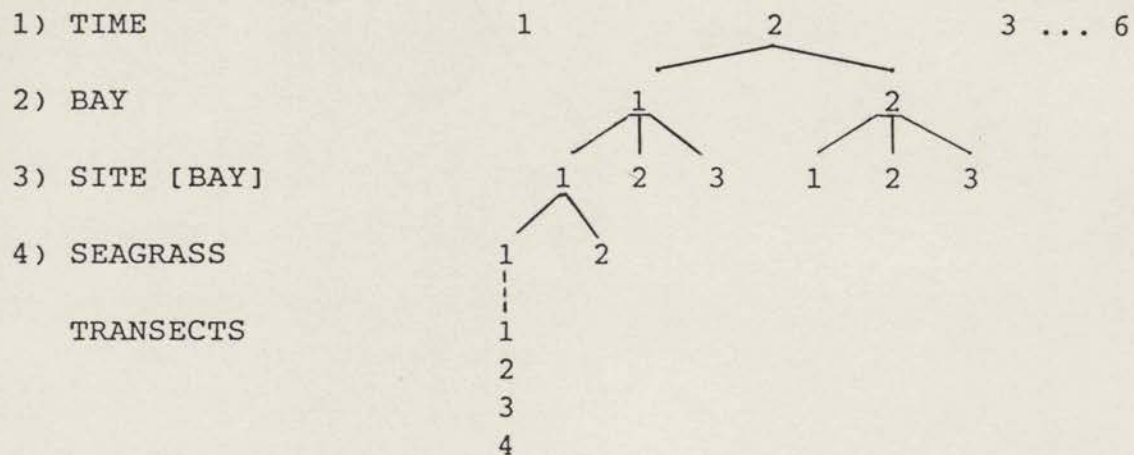
All samples were preserved in 10% formalin and sorted by hand in the laboratory. Sorting of the samples turned out to be very time-consuming because of the size of the fish and their cryptic nature in relation to the debris that accompanied the samples. Most samples required about 1 hour to sort out but approximately one quarter of them took over two hours.

6. SAMPLING PROGRAMME

Sampling was bimonthly from September 1986 to September 1987. Data from September 1986 were not included in the analysis of distribution and abundance (Chapter 3) because the samples were collected by boat. Those data were used, however, to construct size-frequency distributions of *S. argus* and *S. nigra* (Chapter 4).

The sampling effort was limited by the number of samples that could be collected within 2h of low tide. Four samples were collected during the day from each *Zostera* and *Posidonia* bed, at each of the three sites in Botany Bay and Pittwater (see Fig. 2.11)

Fig. 2.11 - Summary of Sampling Design



7. SOME DEFINITIONS

'Site' indicates the location of the seagrass meadows within the bay, e.g. Towra Point, Kurnell. The word 'bed' will refer to the sampling area marked within a seagrass meadow. For example, the *Zostera* bed at Kurnell refers to the sampling area within the *Zostera* meadow at that site.

'Population' will be used here in a biological sense (Caughley, 1977) and refers 'to the local assemblage of organisms being studied'.

The term 'recruitment' will be used according to the definition given in the General Introduction. Therefore, pipefishes surviving to a size collected by the net are considered recruited individuals. Note that according to this definition, recruits can be newly-born fish, juveniles or even adults.

Throughout this thesis (unless otherwise specified), * denotes the significance of the F-ratio; * * $p < 0.01$; * $p < 0.05$

CHAPTER THREE

PATTERNS OF ABUNDANCE OF *S. argus*, *S. nigra*, and *U. carinirostris* AND THEIR RELATIONSHIP TO THE HEIGHT AND DENSITY OF THE SEAGRASS BEDS

1. INTRODUCTION

Information on the distribution of fishes associated with *Zostera* and *Posidonia* in the Sydney area comes from community studies done mainly by two groups of researchers. The first group is composed of past and present researchers from the Fisheries Research Institute, NSW Department of Agriculture. They produced a series of early papers on community ecology (Burchmore *et al.*, 1984; Middleton *et al.*, 1984; Pollard, 1973; SPCC, 1981a; Young, 1981; see also Hutchings and Recher, 1974; and Wadley, 1980) and on the ecology of particular species of fishes from Botany Bay and Port Hacking (e.g. Bell, 1980; Bell *et al.*, 1978a, b; Conacher *et al.*, 1979; see also McDonald, 1981). The community studies provided information on the seasonal variation in the fauna, while the others focussed on aspects of feeding and reproduction. The importance of these studies cannot be overstressed as they have provided the backbone for the work that followed (e.g. Bell and Westoby 1986a,b,c; [redacted] and [redacted], 1986; and this study).

The second group at Macquarie University started their research on the fauna living in seagrasses in the 1980's. Their work reflected the ideas suggested in the late 70's to explain the great diversity and abundance of fauna in seagrass beds. The initial model stated that the greater densities of invertebrates in vegetated habitats, when compared with non-vegetated areas, was attributable to the cover provided by the vegetation against predation (e.g. Nelson, 1979^a; Heck and Thoman, 1981). Following this line of thought, Bell and colleagues undertook a series of comprehensive field studies (Bell, 1980; Bell and Westoby, 1986a, b, c; 1987; Bell *et al.*, 1985; 1987; 1988), mainly experimental, to investigate the relationship between the physical structure of seagrass and the abundance of the fauna.

Although pipefishes - as a major component of the fish assemblages living in *Zostera* and *Posidonia* - have been included in the community studies first mentioned, the information on their ecology is very restricted, because the emphasis of these studies was on the community as a whole. Information on individual species had to be sacrificed, and, moreover, except for Young (1981) and Wadley (1980), the focus of these papers was on economically important species. Finally, their conclusions are limited to seasonal patterns of abundance because the designs of these studies did not cater for analysis of spatial variation.

The main objective of this chapter is to provide information on the distribution of *S. argus*, *S. nigra* and *U. carinirostris* at

three different scales, and to investigate patterns of seasonal abundance. The following specific questions were asked:

- (1) Are the three pipefishes distributed equally between species of seagrass (*Zostera* and *Posidonia*), among sites within a bay, or between bays;
- (2) If any patterns become evident, are they common to the three species of pipefishes? Or to the two species of the genus *Stigmatopora*?
- (3) Do the densities of *S. argus*, *S. nigra* or *U. carinirostris* vary between seasons?
- (4) Is there a common seasonal pattern of abundance for the three species, or to *S. argus* and *S. nigra*? and,
- (5) Do any observed seasonal patterns vary consistently at any of the three spatial scales, i.e. in *Zostera* or *Posidonia*, among sites or bays?

The second objective is to examine the relationships between the abundance of pipefishes and the height and density of seagrasses at different sites. Bell and Westoby (1986c) have investigated how small fishes and decapods responded to changes in the physical structure of *Zostera* and *Posidonia* between beds of seagrass in Botany Bay, at a single time of the year. The major question considered here is whether the observed patterns in the

abundance of the three pipefishes, at different times and at different spatial scales, can be correlated directly with the height and density of the seagrass beds, without regard to other factors. This was examined by:

- (1) regressing the density of pipefish at different times of the year at a particular site (e.g. Kurnell) against the height and density of the beds; and
- (2) by regressing the density of pipefish at all sites at a particular time of the year (e.g. January) against the height and density of the seagrass.

2. METHODS

PROCEDURES FOR SAMPLING SEAGRASS

The height and density of the beds were monitored bimonthly from January to September 1987.

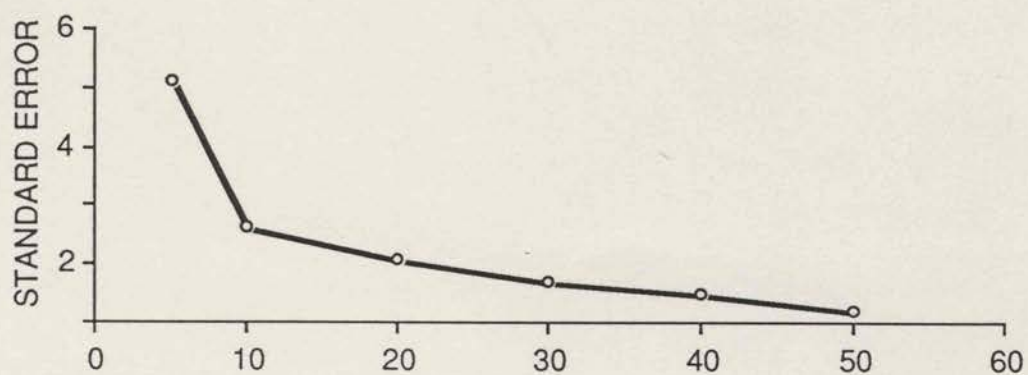
(a) Height of Seagrass Beds

To assess the variation in the height of the leaves in each *Zostera* and *Posidonia* bed, shoots were haphazardly collected from three of the four transects that had been used for the collection of fish. The exact position of each transect was marked by buoys (see Fig. 2.10). The tallest leaf of each shoot was then measured in the laboratory.

A pilot study was done to determine the sampling intensity required to minimize the variability associated with mean heights of replicate samples of the tallest leaf of each shoot (Fig. 3.1). This indicated that samples of 50 leaves should give a fairly precise estimate of the mean length of the tallest leaf.

This method of estimating the height of the seagrass beds is a modified version of that described by Bell and Westoby (1986b). It differs from their method in two ways. First, they used *Zostera* and *Posidonia* leaves of all sizes for their measurements. Here, only the tallest leaf of each shoot was used to indicate

(a)



(b)

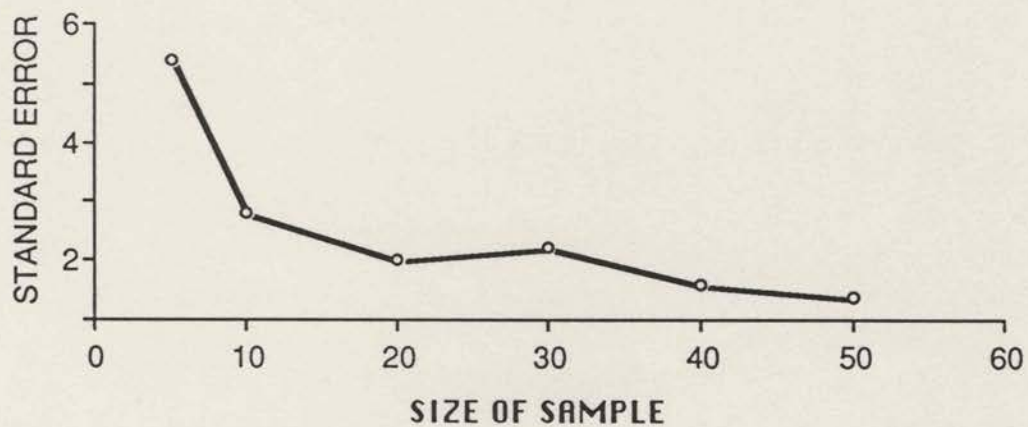


Fig. 3.1 - Standard errors associated with different sizes of samples of leaves of (a) *Zostera* and (b) *Posidonia*.

the general height of the whole plant and thus as an estimate of the relative height of the beds. One main advantage of measuring the tallest leaf was that it was less time-consuming. The second difference in the two methods was that Bell and Westoby (1986b) collected individual leaves of *Posidonia* in the field whereas here, whole shoots of *Posidonia* (and of *Zostera*) were collected in the field. This was done in an attempt to lessen the chance of introducing bias towards taller shoots/leaves. To collect individual leaves one needs to feel for the leaf before it can be picked up. The shoots, however, were collected from the base. It was not necessary for the collector to look at, or feel for, the leaves while collecting them. This, hopefully, decreased the chance of bias toward picking taller plants. This procedure was particularly important in this study because the leaves were collected by different people at different times of the year.

(b) Density of Seagrass Beds

The density of the seagrass beds was estimated by counting the number of shoots of *Zostera* and *Posidonia* within 0.063 m^2 and 0.125 m^2 quadrats (Bell and Westoby, 1986b), respectively. Two quadrats were thrown at random in three of the four transects where fish had been collected. The number of quadrats was limited by the amount of time that was available to work at each site.

Two different methods have been described to estimate the density of *Zostera* and *Posidonia* beds. Bell and Westoby (1986b) counted

the number of leaves while Gray and Bell (1986) counted the number of shoots. Counting the number of leaves *in situ* can be very difficult, especially for *Zostera* since its leaves are numerous and small. Turbidity due to the fine sediment present in *Zostera* beds can make this an even more difficult task. Based on that, and the fact that the number of leaves per shoot was known to be fairly constant among sites within a bay (J. Bell, pers. comm.), I decided to use the number of shoots as a means of estimating the density of the seagrass beds. None the less, because the number of leaves per shoot could vary between bays, I decided to do a pilot study in January 1987 to investigate this variability. The only significant source of variation was in the number of leaves per shoot between the two bays (Table 3.1): in Pittwater, the shoots of both *Zostera* and *Posidonia* on average had more leaves than in Botany Bay. This difference was, however very small, and not important for the regressions of density of fish against density of shoots at different times of the year because the analysis was done for each site separately. When the density of pipefishes at the six sites was regressed against leaf density for each time of the year separately, (e.g. January, March), the data was converted to 'density of leaves' using the mean number of leaves per shoot calculated for each bay.

STATISTICAL METHODS

The data used to investigate the relationship between the abundance of pipefishes and the height and density of the

TABLE 3.1

Two-factor ANOVA of number of leaves per shoot of (a) *Zostera* and (b) *Posidonia* in Botany Bay and Pittwater. Data was collected in January 1987. Both factors were random. Variances were homogeneous by Cochran's test, $p > .05$.

(a) *Zostera*

SOURCE	S.S.	d.f.	M.S.	F-ratio	P
Bay	1.18	1	1.18	43.50	**
Site (bay)	0.23	4	0.05	2.15	ns
Residual	0.33	12	0.03		
Total	1.74	17			

(b) *Posidonia*

SOURCE	S.S.	d.f.	M.S.	F-ratio	P
Bay	0.13	1	0.13	10.07	**
Site (bay)	0.05	4	0.01	0.85	ns
Residual	0.16	12	0.01		
Total	0.34	17			

seagrass beds were to be examined using an analysis of covariance where time, sites, and the species of seagrass were the main effects, and height and density of the seagrass beds the covariates. This was not possible because the data violated at least two important assumptions of this analysis. First, it became clear by plotting the data for each site that the slopes of the regressions differed significantly. Second, the data on the abundances of the three species did not comply with the assumption of homogeneity of variances around each regression, and had therefore to be transformed (Cochran's test was significant for all three species - Tables nos 3.2, 3.4 and 3.6) thus changing the relationship between the variables. Because of the large variability between sites, the data could not be analysed as a partial regression. Finally, in some sites there was a significant correlation between the density and height of the seagrass beds and therefore these two variables were not regressed in the same analysis.

The data on the abundance of *S. argus* were analysed by a 4-way ANOVA where time, bay, site (within each bay), and species of seagrass were the main factors (time and species of seagrass were fixed factors and bay and site were random). A 3-factor ANOVA was used for *S. nigra* and *U. carinirostris* because these species were sufficiently abundant for analysis only in *Zostera* and therefore the fourth main factor 'species of seagrass' was not included. An *a posteriori* Student-Newman-Kewls (SNK) test was done on those means that were significantly different.

3. RESULTS

PATTERNS IN THE ABUNDANCE OF *S. argus*

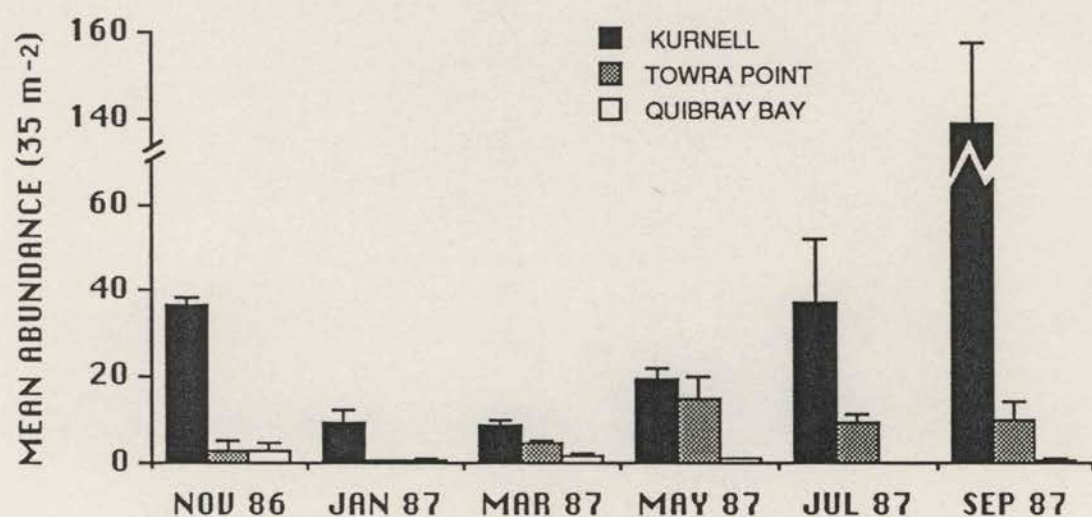
The patterns of abundance of *S. argus* varied significantly among seasons, sites and between types of seagrass (See Figs. 3.2 and 3.3 and ANOVA in Table 3.2 - note the significant Time x Site x Seagrass interaction).

(a) Spatial Variation

Zostera - There was a marked difference in the overall density of *S. argus* in the six sites (see means in Fig. 3.2 and SNK tests in Table 3.2). Kurnell and Barrenjoey had significantly greater densities of *S. argus* than Quibray and Careel II, at any time of the year, and than Towra Point and Careel I, at most times. The densities of *S. argus* at Towra Point and Careel I were very small from November to March and therefore not significantly different from Quibray and Careel II. From May to September, however, *S. argus* was consistently more abundant at Towra Point and Careel I than at Quibray and Careel II.

Posidonia - *S. argus* was generally more abundant at Kurnell, Barrenjoey and Towra Point (Means are shown in Fig. 3.3 and SNK

(a)



(b)

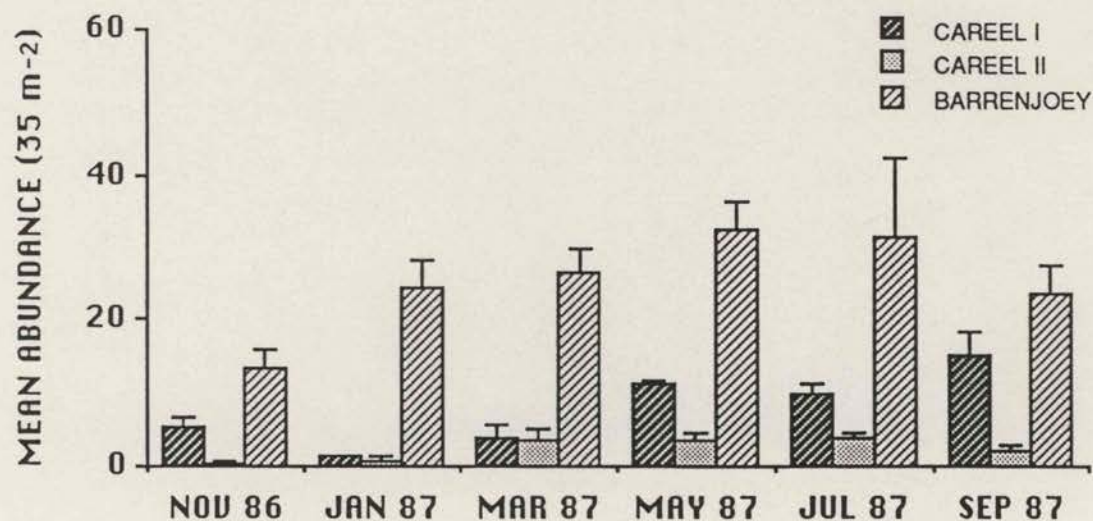
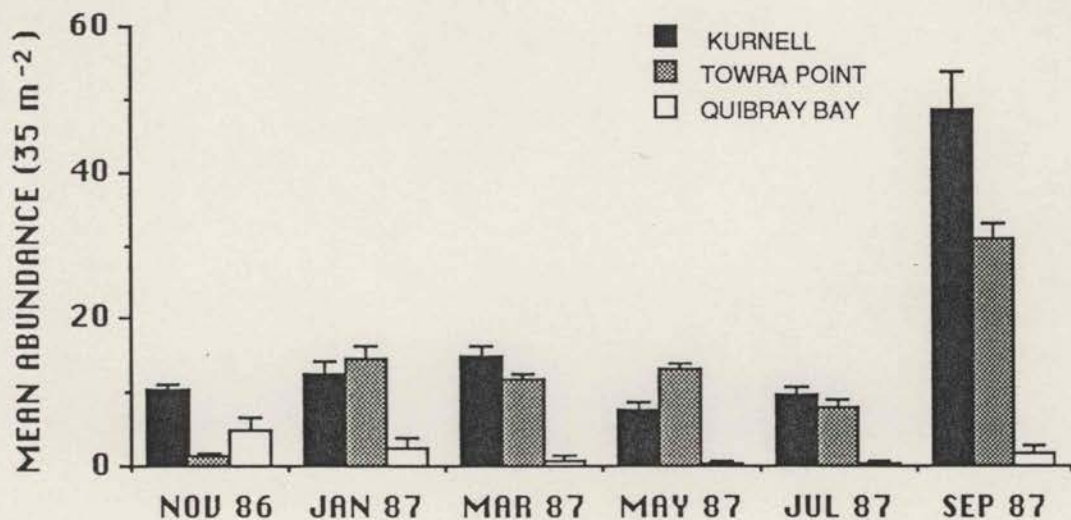


Fig. 3.2 - Mean abundances ($\pm$ SE) of *Stigmatopora argus* collected from *Zostera* beds in (a) Botany Bay and (b) Pittwater.

(a)



(b)

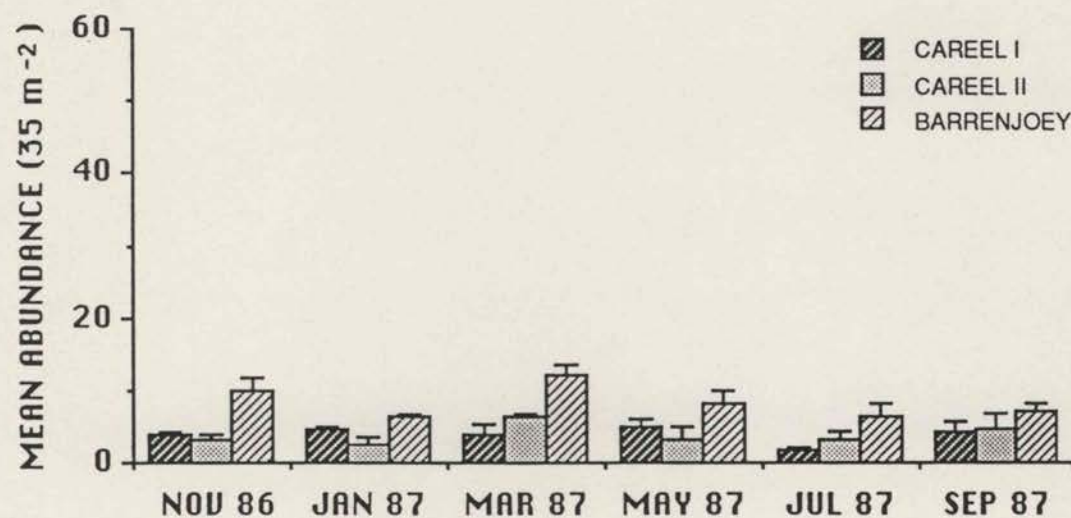


Fig. 3.3 - Mean abundances ($\pm$ SE) of *Stigmatopora argus* collected from *Posidonia* beds in (a) Botany Bay and (b) Pittwater.

TABLE 3.2

(a) Four-factor ANOVA and (b) SNK tests of the mean abundances of *S. argus* in Botany Bay and Pittwater over an 11-month period (Nov. 1986 - Sept. 1987).

(a) ANOVA

Cochran's test: significant, $p < 0.01$.

Transformation: $\log E_{[x+1]}$.

SOURCE	S.S.	d.f.	M.S.	F-ratio	P
Time of Sampling [T]	15.97	5	3.19	2.47	ns
Bay [B]	0.03	1	0.03	0.00	ns
Site (bay) [S]	182.52	4	45.62	205.50	**
Seagrass sp. [SS]	1.09	1	1.09	0.32	ns
T x B	6.45	5	1.29	0.67	ns
T x S	38.54	20	1.93	8.67	**
T x SS	13.93	5	2.79	2.55	ns
B x SS	3.42	1	3.42	0.60	ns
S x SS	22.60	4	5.65	25.44	**
T x B x SS	5.46	5	1.09	1.81	ns
T x S x SS	12.10	20	0.60	2.72	**
Residual	47.95	216	0.22		
Total	350.05	287			

TABLE 3.2 (cont'd)

(b) Student-Newman-Keuls Comparisons of the mean densities of *S. argus* in *Zostera* and *Posidonia* beds. Times and sites underlined were not significantly different.

	<i>Zostera</i>						<i>Posidonia</i>					
NOVEMBER	CII	<u>TP</u>	<u>QB</u>	<u>CI</u>	BJ	K	TP	<u>CII</u>	<u>CI</u>	<u>QB</u>	<u>BJ</u>	<u>K</u>
JANUARY	TP	<u>QB</u>	<u>CII</u>	<u>CI</u>	K	BJ	<u>QB</u>	<u>CII</u>	<u>CI</u>	<u>BJ</u>	<u>K</u>	<u>TP</u>
MARCH	<u>QB</u>	<u>CI</u>	<u>CII</u>	TP	K	BJ	<u>QB</u>	<u>CI</u>	<u>CII</u>	TP	BJ	K
MAY	QB	CII	<u>CI</u>	<u>TP</u>	K	BJ	QB	<u>CII</u>	<u>CI</u>	K	BJ	TP
JULY	QB	CII	<u>TP</u>	<u>CI</u>	<u>BJ</u>	<u>K</u>	QB	<u>CI</u>	<u>CII</u>	<u>BJ</u>	<u>TP</u>	<u>K</u>
SEPTEMBER	<u>QB</u>	<u>CII</u>	TP	<u>CI</u>	<u>BJ</u>	<u>K</u>	<u>QB</u>	<u>CI</u>	<u>CII</u>	<u>BJ</u>	<u>TP</u>	<u>K</u>
KURNELL	<u>Jan</u>	<u>Mar</u>	<u>May</u>	<u>Jul</u>	<u>Nov</u>	<u>Sep</u>	<u>May</u>	<u>Jul</u>	<u>Nov</u>	<u>Jan</u>	<u>Mar</u>	<u>Sep</u>
T. POINT	Jan	Nov	<u>Mar</u>	<u>Sep</u>	<u>Jul</u>	<u>May</u>	Nov	<u>Jul</u>	<u>Mar</u>	<u>May</u>	<u>Jan</u>	<u>Sep</u>
QUIBRAY	<u>Jul</u>	<u>Jan</u>	<u>Sep</u>	<u>May</u>	<u>Mar</u>	<u>Nov</u>	<u>Jul</u>	<u>May</u>	<u>Mar</u>	<u>Sep</u>	<u>Jan</u>	<u>Nov</u>
CAREEL I	Jan	Mar	<u>Nov</u>	<u>Jul</u>	<u>May</u>	<u>Sep</u>	<u>Jul</u>	<u>Mar</u>	<u>Sep</u>	<u>Nov</u>	<u>May</u>	<u>Nov</u>
CAREEL II	<u>Nov</u>	<u>Jan</u>	<u>Sep</u>	<u>Mar</u>	<u>May</u>	<u>Jul</u>	<u>Jan</u>	<u>May</u>	<u>Jul</u>	<u>Nov</u>	<u>Sep</u>	<u>Mar</u>
BARRENJOEY	<u>Nov</u>	<u>Sep</u>	<u>Jan</u>	<u>Mar</u>	<u>Jul</u>	<u>May</u>	<u>Jul</u>	<u>Jan</u>	<u>Sep</u>	<u>May</u>	<u>Nov</u>	<u>Mar</u>

In this and subsequent tables the following abbreviations will be used for sites: Botany Bay: K = Kurnell; TP = Towra Point; QB = Quibray Bay;

Pittwater : CI = Careel I; CII = Careel Bay II, and BJ = Barrenjoey.

tests in Table 3.2). The abundance of *S. argus* at the other three sites fluctuated at very low levels.

(b) Temporal Variation

Zostera - Marked seasonal differences were evident at Kurnell, Towra Point and Careel I (See means in Fig. 3.2 and SNK tests in Table 3.2). At these sites the largest densities occurred usually between May and September, and the smallest numbers of *S. argus* were collected in November and/or January and March. At Barrenjoey, where *S. argus* was also abundant, there was no marked seasonality in the density of this pipefish.

Posidonia - the variation in the abundance of *S. argus* was less pronounced in *Posidonia* beds (Means are shown in Fig. 3.3 and SNK tests in Table 3.2). The only significant change was the sudden increase in densities recorded at Kurnell and Towra Point in September.

(c) The Relationship between the Abundance of *S. argus* and the Height and Density of *Zostera* and *Posidonia* beds

Zostera - There was no significant correlation between the densities of *S. argus* and the height of the *Zostera* (means are shown in Fig. 3.4) at any site (Table 3.3).

(a) DENSITY OF *Zostera* SHOOTS

(b) LENGTH OF *Zostera* LEAVES

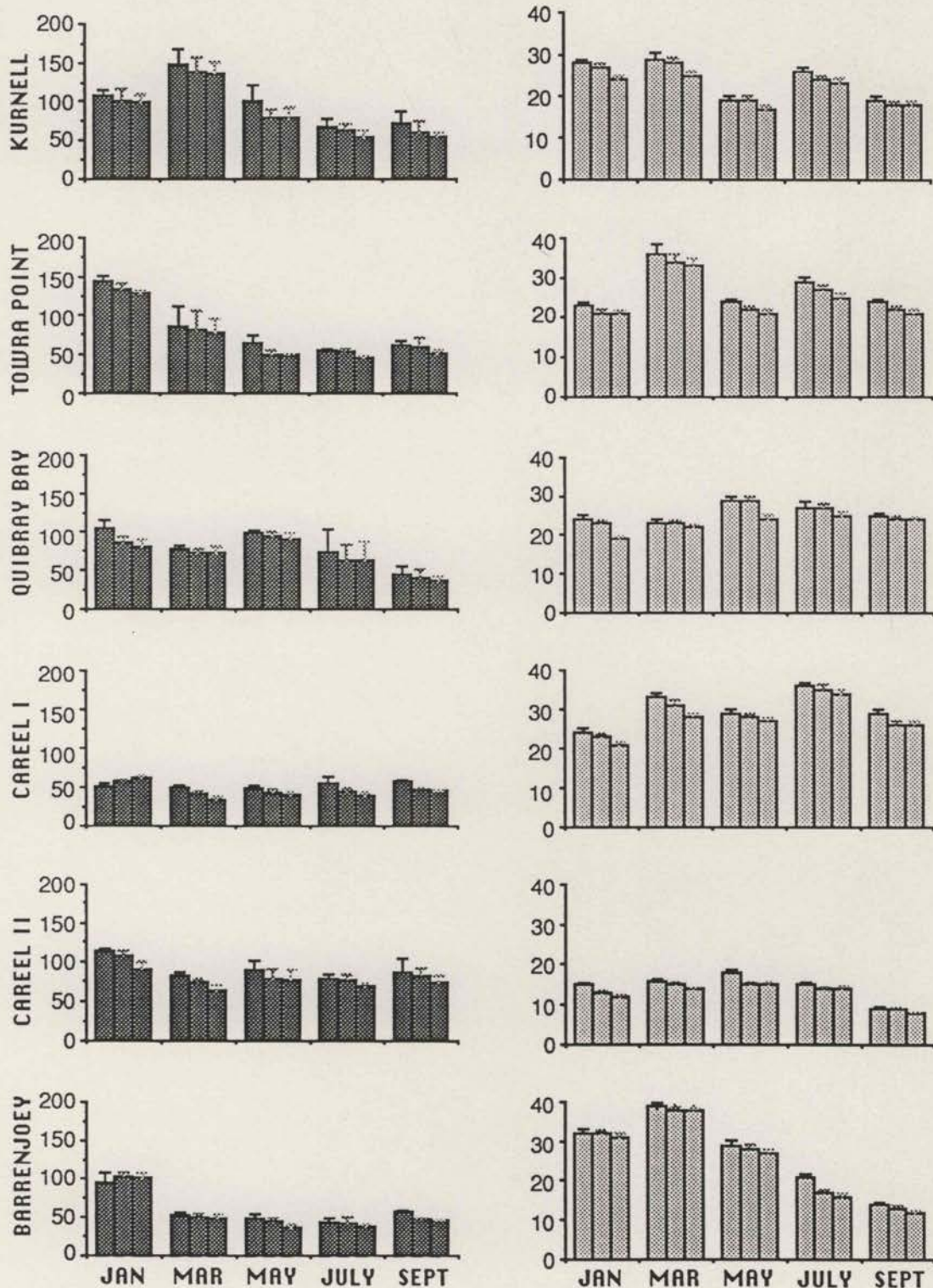


Fig. 3.4- (a) Mean density of *Zostera* shoots per 0.063 m² (+SE, n=2) and (b) Mean lengths of *Zostera* leaves (+SE, n=50), collected from each of three transects, from January to September 1987.

TABLE 3.3

Slopes of linear regressions of the mean abundance of *S. argus* on the mean density of shoots and height of leaves of (a) *Zostera* and (b) *Posidonia*. Data for each site were analysed separately.

(a)

	<i>Zostera</i> - HEIGHT			<i>Zostera</i> - DENSITY		
	r ²	b	p	r ²	b	p
KURNELL	0.24	-5.47	ns	0.39	-0.92	**
T. POINT	0.09	-0.49	ns	0.40	-0.13	**
QUIBRAY	0.07	-0.12	ns	0.00	-0.65	ns
CAREEL I	0.14	0.46	ns	0.05	-0.16	ns
CAREEL II	0.04	0.14	ns	0.36	-0.08	**
BARRENJOEY	0.49	0.20	ns	0.00	-0.02	ns

(b)

	<i>Posidonia</i> - HEIGHT			<i>Posidonia</i> - DENSITY		
	r ²	b	p	r ²	b	p
KURNELL	0.04	-1.10	ns	0.01	-0.40	ns
T. POINT	0.56	1.34	**	0.05	-0.32	ns
QUIBRAY	0.04	0.08	ns	0.02	-0.05	ns
CAREEL I	0.10	0.06	ns	0.08	-0.08	ns
CAREEL II	0.06	-0.07	ns	0.20	0.18	ns
BARRENJOEY	0.30	-0.42	*	0.02	-0.05	ns

There was a significant negative relationship between the density of *S. argus* and the density of *Zostera* (see means in Fig. 3.4) at three sites: Kurnell, Towra Point and Careel II (Table 3.3).

Posidonia - The relationship between the height of *Posidonia* leaves (means are shown in Fig. 3.5) and the abundance of *S. argus* contrasted in the two sites where a significant correlation occurred (Table 3.3). While the correlation between these two variables was positive at Towra Point, it was negative at Barrenjoey.

The density of the *Posidonia* beds (see means in Fig. 3.5) was not significantly related to the abundance of *S. argus* (Table 3.3).

PATTERNS IN THE ABUNDANCE OF *S. nigra*

(a) Spatial and Temporal Variation

S. nigra was not very abundant, occurring frequently only in *Zostera* at Kurnell and to a lesser extent at Barrenjoey (See means in Fig. 3.6, and ANOVA and SNK tests in Table 3.4)

The abundance of *S. nigra* varied seasonally and the seasonal patterns of abundance differed significantly among sites (See ANOVA, Table 3.4 - Note significant Time x Bay x Site

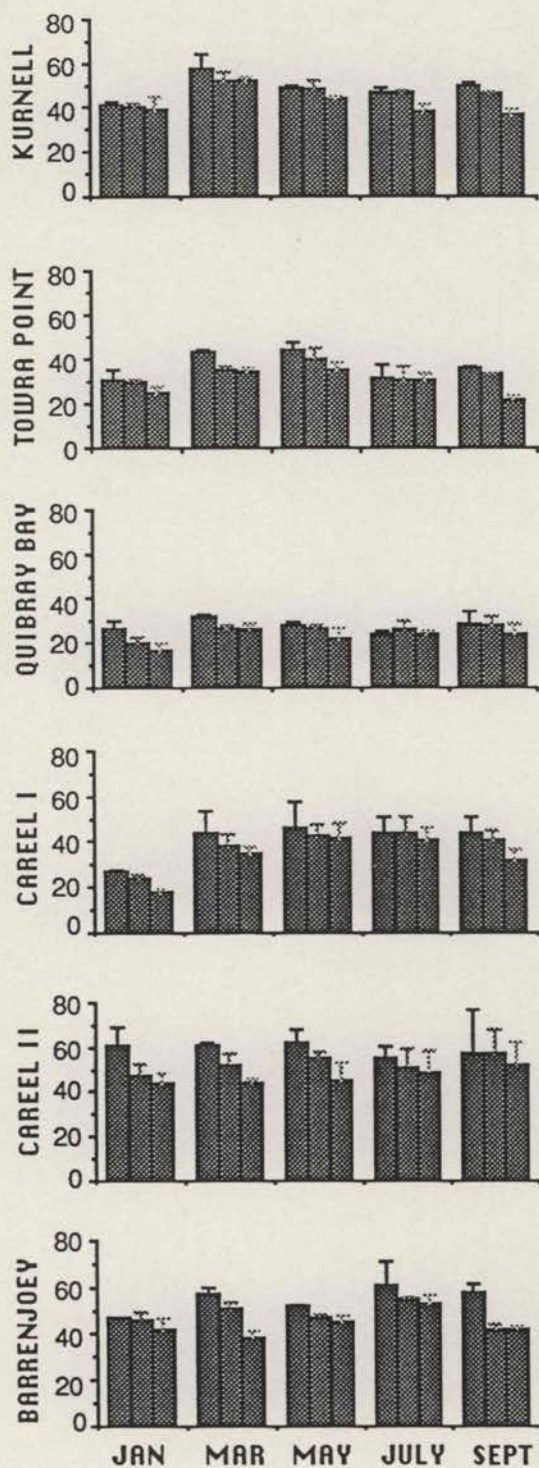
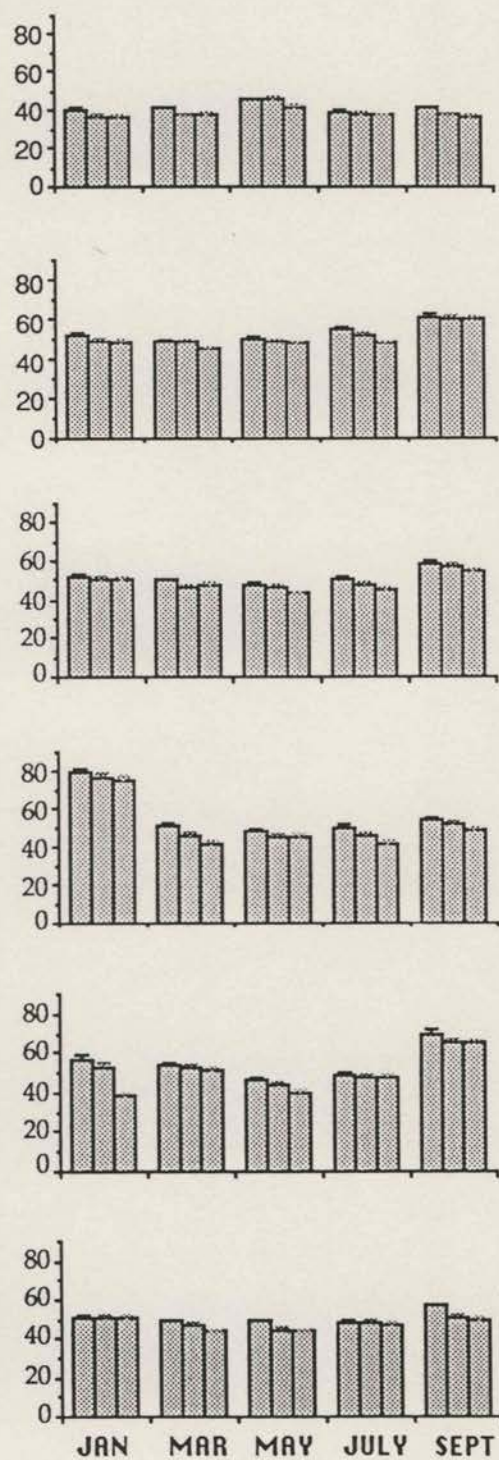
(a) DENSITY OF *Posidonia* SHOOTS**(b) LENGTH OF *Posidonia* LEAVES**

Fig. 3.5 - (a) Mean density of *Posidonia* shoots per 0.025 m² (+SE, n=2) and (b) Mean lengths of *Posidonia* leaves (+SE, n=50), collected from each of three transects, from January to September 1987,

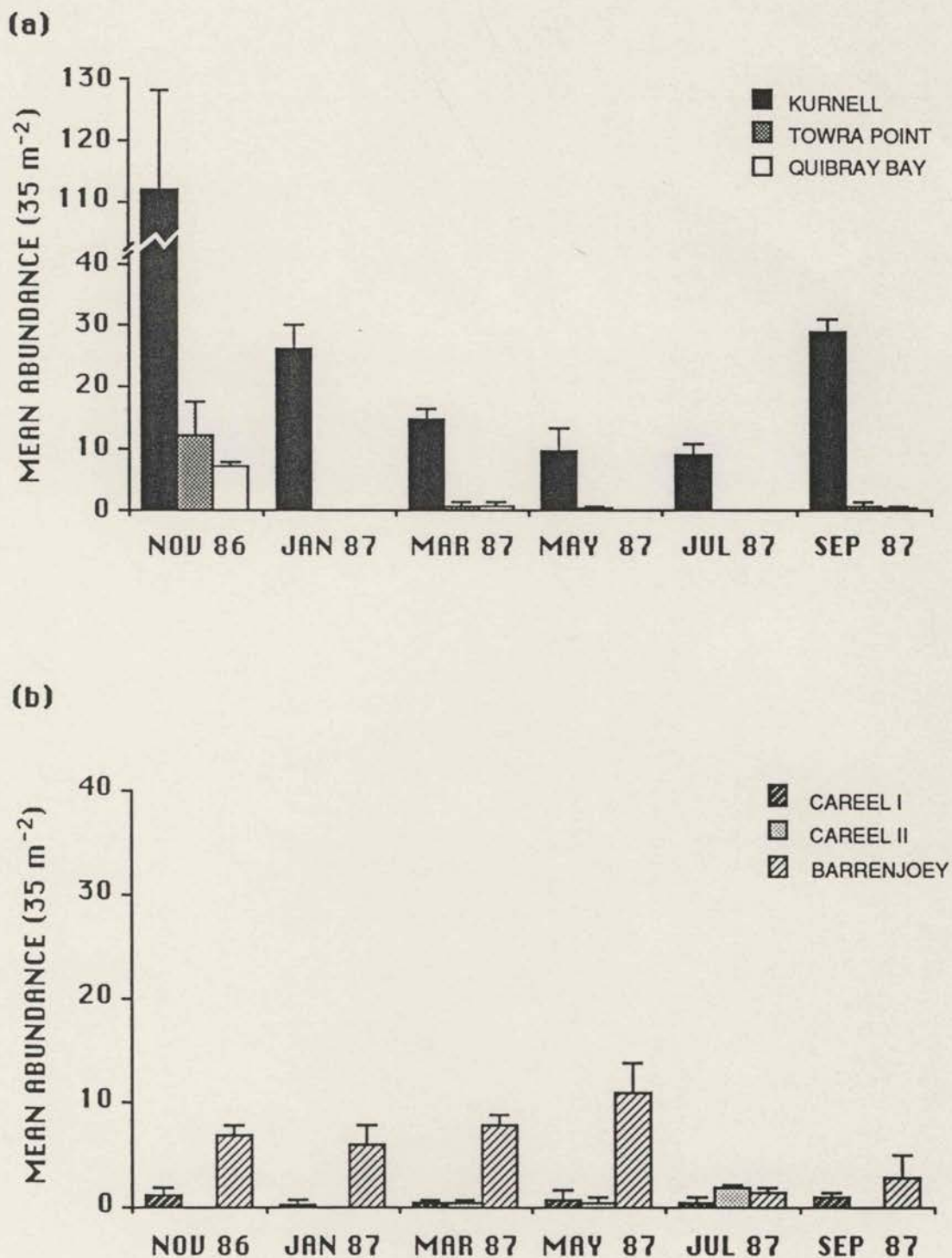


Fig. 3.6 - Mean abundances (+SE) of *Stigmatopora nigra* collected from *Zostera* beds in (a) Botany Bay and (b) Pittwater.

TABLE 3.4

(a) Three-factor ANOVA and (b) SNK tests of the mean abundances of *S. nigra* in *Zostera* beds in Botany Bay and Pittwater over an 11-month period (Nov. 1986 - Sept. 1987).

(a) ANOVA

Cochran's test: significant, $p < 0.01$

Transformation: $\log E_{[x+1]}$

SOURCE	S.S.	d.f.	M.S.	F-ratio	P
Time of Sampling [T]	23.86	5	4.77	5.77	*
Bay [B]	12.34	1	12.34	0.37	ns
Site (bay) [S]	133.85	4	33.46	173.38	**
A x B	20.67	5	4.13	6.19	**
A x C (B)	13.35	20	0.67	3.46	**
Residual	20.83	108	0.19		
Total	224.91	143			

TABLE 3.4 (cont'd)

(b) Student-Newman-Keuls Comparisons of the mean densities of *S. nigra* in *Zostera* beds. Times and sites underlined were not significantly different.

NOVEMBER	CII	CI	<u>BJ</u>	<u>QB</u>	<u>TP</u>	K
JANUARY	<u>CII</u>	<u>QB</u>	<u>TP</u>	<u>CI</u>	BJ	K
MARCH	<u>CII</u>	<u>CI</u>	<u>QB</u>	<u>TP</u>	<u>BJ</u>	<u>K</u>
MAY	<u>QB</u>	<u>CII</u>	<u>TP</u>	<u>CI</u>	<u>K</u>	<u>BJ</u>
JULY	<u>QB</u>	<u>TP</u>	<u>CI</u>	<u>BJ</u>	<u>CII</u>	K
SEPTEMBER	<u>CII</u>	<u>TP</u>	<u>QB</u>	<u>CI</u>	<u>BJ</u>	K

KURNELL	<u>May</u>	<u>Jul</u>	<u>Mar</u>	<u>Jan</u>	<u>Sep</u>	Nov
T. POINT	<u>Jan</u>	<u>Jul</u>	<u>May</u>	<u>Sep</u>	<u>Mar</u>	Nov
QUIBRAY	<u>Jan</u>	<u>May</u>	<u>Jul</u>	<u>Sep</u>	<u>Mar</u>	Nov
CAREEL I	<u>Jan</u>	<u>Jul</u>	<u>Mar</u>	<u>May</u>	<u>Sep</u>	Nov
CAREEL II	<u>Nov</u>	<u>Jan</u>	<u>Sep</u>	<u>May</u>	<u>Mar</u>	<u>Jul</u>
BARRENJOEY	<u>Jul</u>	<u>Sep</u>	<u>Jan</u>	<u>Nov</u>	<u>Mar</u>	<u>May</u>

interaction). At Kurnell, the largest number of *S. nigra* occurred in November (SNK tests in Table 3.4). The abundance of *S. nigra* declined drastically in the following months to increase again in September. At both other sites in Botany Bay (Towra Point and Quibray Bay), the density of *S. nigra* was also relatively larger in November. In contrast to the sites in Botany Bay, the abundance of *S. nigra* at Barrenjoey remained fairly constant from November to May. Only in July and September were the densities of *S. nigra* significantly smaller than at the other times of the year.

(b) The Relationship between the Abundance of *S. nigra* and the Height and Density of *Zostera* Beds

The height and density of the *Zostera* beds did not, in general, correlate significantly with the abundance of *S. nigra* (Table 3.5). In five of the six sites, the abundance of *S. nigra* tended to increase with the height of *Zostera*, but the only significant correlation occurred at Barrenjoey. There was no apparent pattern in the regressions of the mean density on the density of *Zostera*.

PATTERNS IN THE ABUNDANCE OF *U. carinirostris*

(a) Spatial and Temporal Variation

There was a great seasonal variability in the abundances of *U.*

TABLE 3.5

Slopes of linear regressions of the mean abundance of *S. nigra* on the mean density of shoots and height of *Zostera* leaves. Data for each site were analysed separately.

	<i>Zostera</i> - HEIGHT			<i>Zostera</i> - DENSITY		
	r ²	b	p	r ²	b	p
KURNELL	0.01	0.20	ns	0.00	0.01	ns
T. POINT	0.00	0.01	ns	0.05	-0.01	ns
QUIBRAY	0.05	-0.05	ns	0.12	-0.01	ns
CAREEL I	0.03	0.03	ns	0.01	0.01	ns
CAREEL II	0.07	0.07	ns	0.16	-0.02	ns
BARRENJOEY	0.23	0.26	*	0.03	0.04	ns

carinirostris and the seasonal patterns varied depending on the site (Means are shown in Fig. 3.7. See ANOVA, Table 3.6 - note the significant Time x Bay x Site interaction). For example, at Quibray Bay the density was relatively large from November to May, during which period there was a peak in abundance at Barrenjoey (See SNK tests in Table 3.6). The abundance of *U. carinirostris* then declined to reach its lowest level in July and September. At Towra Point, on the other hand, there were two peaks in the abundance of this pipefish, one in January and another in May. Abundance fluctuated at low levels at the remaining times of the year. Only a small number of *U. carinirostris* was collected at the other three sites.

In general, Quibray Bay, Barrenjoey and Towra Point had the largest densities of *U. carinirostris* (SNK tests in table 3.6).

(b) The Relationship between the Abundance of *U. carinirostris* and the Height and Density of *Zostera* Beds

There was a significant positive relationship between the abundance of *U. carinirostris* and the height of *Zostera* at Barrenjoey (Table 3.7). In contrast, a significant negative correlation occurred at Careel II; *U. carinirostris* was however seldom collected at this site.

The density of the *Zostera* beds was generally positively

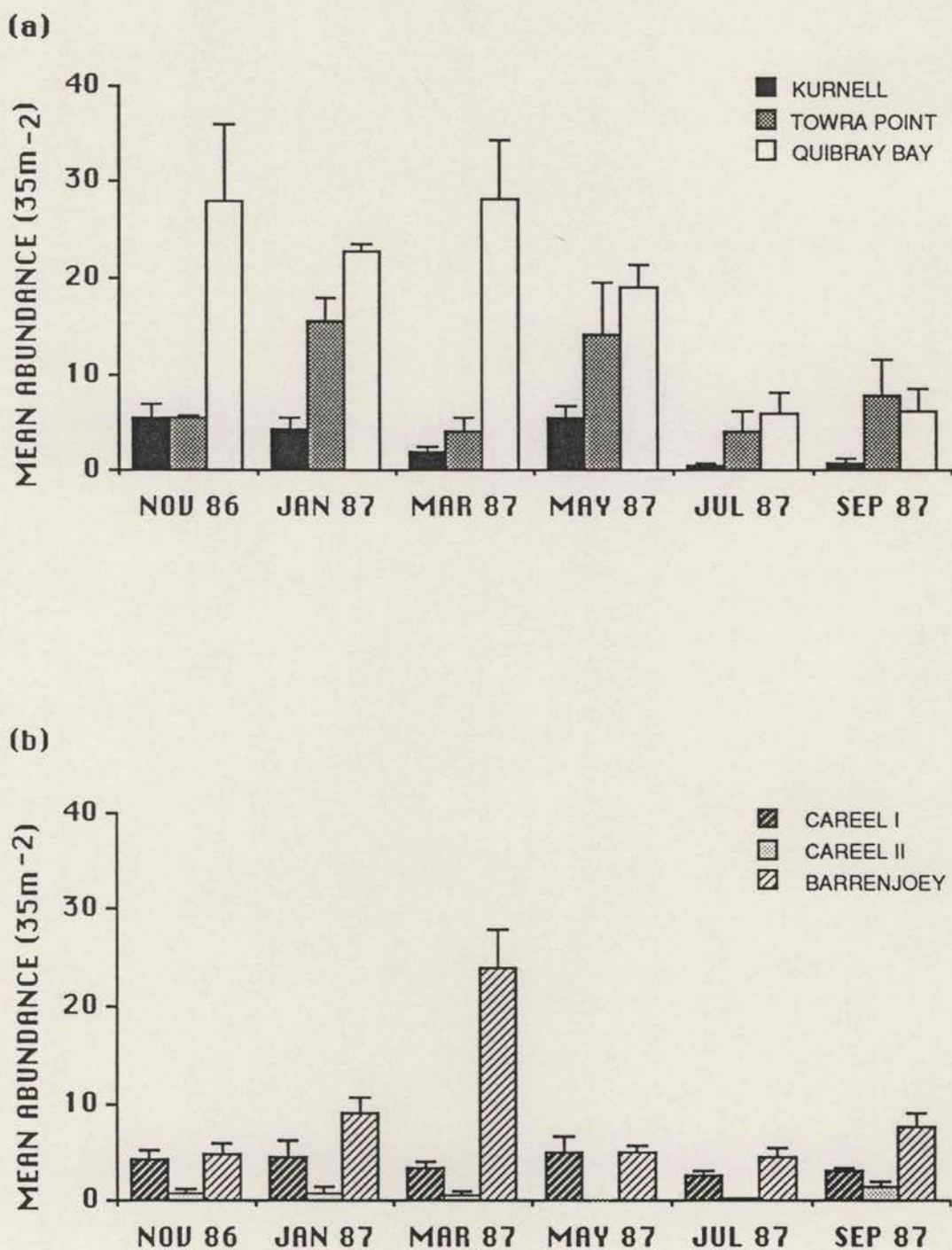


Fig. 3.7 - Mean abundances (+SE) of *Urocampus carinirostris* collected from *Zostera* beds in (a) Botany Bay and (b) Pittwater.

TABLE 3.6

(a) Three-factor ANOVA and (b) SNK tests of the mean abundances of *U. carinirostris* in *Zostera* beds in Botany Bay and Pittwater over an 11 month period (Nov. 1986 - Sept. 1987).

(a) ANOVA

Cochran's test: significant, $p < 0.01$

Transformation: $\log E_{[x+1]}$

SOURCE	S.S.	d.f.	M.S.	F-ratio	P
Time of Sampling [T]	12.77	5	2.55	1.48	ns
Bay [B]	14.24	1	14.24	0.85	ns
Site (bay) [S]	66.75	4	16.69	70.70	**
A x B	8.60	5	1.72	2.86	*
A x C (B)	12.02	20	0.60	2.55	**
Residual	25.54	108	0.24		
Total	139.91	143			

TABLE 3.6 (cont'd)

- (b) Student-Newman-Keuls Comparisons of the mean densities of *U. carinirostris* in *Zostera* beds. Times and sites underlined are not significantly different.

NOVEMBER	CII	<u>CI</u>	<u>K</u>	<u>BJ</u>	<u>TP</u>	<u>QB</u>
JANUARY	CII	<u>CI</u>	<u>K</u>	<u>BJ</u>	<u>TP</u>	<u>QB</u>
MARCH	CII	<u>K</u>	<u>CI</u>	<u>TP</u>	<u>BJ</u>	<u>QB</u>
MAY	CII	<u>CI</u>	<u>K</u>	<u>BJ</u>	<u>TP</u>	<u>QB</u>
JULY	<u>CII</u>	<u>K</u>	<u>CI</u>	<u>TP</u>	<u>BJ</u>	<u>QB</u>
SEPTEMBER	<u>K</u>	<u>CII</u>	<u>CI</u>	<u>QB</u>	<u>TP</u>	<u>BJ</u>
KURNELL	<u>Jul</u>	<u>Sep</u>	<u>Mar</u>	<u>Jan</u>	<u>Nov</u>	<u>May</u>
T. POINT	<u>Jul</u>	<u>Mar</u>	<u>Nov</u>	<u>Sep</u>	<u>May</u>	<u>Jan</u>
QUIBRAY	<u>Jul</u>	<u>Sep</u>	<u>May</u>	<u>Jan</u>	<u>Nov</u>	<u>Mar</u>
CAREEL I	<u>Jul</u>	<u>Sep</u>	<u>Mar</u>	<u>Jan</u>	<u>Nov</u>	<u>May</u>
CAREEL II	<u>May</u>	<u>Jul</u>	<u>Mar</u>	<u>Jan</u>	<u>Nov</u>	<u>Sep</u>
BARRENJOEY	<u>Jul</u>	<u>Nov</u>	<u>May</u>	<u>Sep</u>	<u>Jan</u>	<u>Mar</u>

TABLE 3.7

Slopes of linear regressions of the mean abundance of *U. carinirostris* on the mean density of shoots and height of *Zostera* leaves. Data for each site were analysed separately.

	<i>Zostera</i> - HEIGHT			<i>Zostera</i> - DENSITY		
	r ²	b	p	r ²	b	p
KURNELL	0.00	-0.02	ns	0.08	0.30	ns
T. POINT	0.22	-0.73	ns	0.29	0.11	*
QUIBRAY	0.10	-1.40	ns	0.33	0.32	*
CAREEL I	0.17	-0.23	ns	0.05	0.07	ns
CAREEL II	0.31	-0.19	*	0.02	0.01	ns
BARRENJOEY	0.42	0.61	**	0.00	-0.01	ns

correlated with the abundance of *U. carinirostris*. The only significant correlations occurred at Towra Point and Quibray Bay (Table 3.7).

4. DISCUSSION

SPATIAL VARIATION

This study indicated that each species of pipefish was more abundant at certain sites than others, and that the marked seasonal patterns of abundance, which were more evident in *Zostera* beds, varied among sites and according to the species of pipefish.

Although *S. argus*, *S. nigra* and *U. carinirostris* occurred in both bays, their distribution varied dramatically among sites, and types of seagrass. *S. argus* was, in general, the most abundant species and the most widely distributed, occurring at all sites, in both *Zostera* and *Posidonia* beds. Although the densities of *S. argus* differed significantly among sites, a common pattern became evident in the relative abundances of this pipefish in each of the two bays. In Botany Bay and Pittwater there was a site where *S. argus* was very abundant (Kurnell and Barrenjoey, respectively), one site where it was practically absent (Quibray and Careel II), and a site where the density of *S. argus* fluctuated at medium levels (Careel I and Towra Point). This pattern was more evident in *Zostera* beds (Fig. 3.2). In contrast to *S. argus*, *S. nigra*, had a very restricted distribution. It was abundant at only one site in each bay (Kurnell in Botany Bay and

Barrenjoey in Pittwater) and virtually occurred ^{only} in *Zostera* beds. *U. carinirostris* had a wider distribution than *S. nigra*, but, similarly to that species, it was restricted to *Zostera* beds. These results in general parallel the previous records for *S. nigra* and *U. carinirostris* in Botany Bay so far as their predominance in *Zostera* is concerned (Middleton *et al.*, 1984; Bell and Westoby 1986 b,c). The presence of *S. argus* in both *Zostera* and *Posidonia* has also been previously observed (Middleton *et al.*, 1984; Bell and Westoby 1986b,c). There are, however, discrepancies as regards the species of seagrass in which *S. argus* was more abundant. In this study, *S. argus* was more abundant in *Zostera* than in *Posidonia* beds. Bell and Westoby (1986b, Appendices 1 and 2), however, found that in their small-scale experiment the mean density of *S. argus* per 12.5 m² subplots (and the mean density when all treatments were combined) was significantly greater in *Posidonia* than in *Zostera*. This contrast in results on the relative abundance of *S. argus* in the two species of seagrasses could be attributed to many of the differences that exist between this study and that done by Bell and Westoby (1986b), such as site, area sampled and the nature of the two studies (theirs being experimental). It is not possible, given the available data, to assess how much each of these factors would contribute to this variation in the results. None the less, it is worthwhile to consider how the sampling techniques used in the two studies might have contributed to the observed differences. Poisoning, the technique employed by Bell and Westoby (1986a, b, c), relies on the collector seeing the dead fish. Considering that juveniles of *S. argus* are minute (=

30 mm) it is possible that the densities of small-sized pipefish are underestimated when the fauna is sampled by poisoning. Since juvenile *S. argus* are present almost exclusively in *Zostera*, it might be that the relatively small densities recorded by Bell and Westoby (1986b) for this pipefish in *Zostera* are partly due to the underestimation of the abundance of juveniles. The difference in relative abundances of *S. argus* in the two studies might also have been enhanced by limitations inherent to trawling as this method may underestimate the densities of larger, fast swimming fishes. This could explain the relatively smaller abundance of *S. argus* in *Posidonia* observed in this study because larger *S. argus* are predominant in this seagrass (see Figs 4.1 - 4.8). Pipefishes are, however, relatively slow swimmers and it is unlikely that a significant bias of this sort would occur with these species.

These three species of pipefishes have also been collected from Port Hacking, another estuary in the Sydney Region (Burchmore *et al.*, 1984; Young, 1981). The distributions of *S. nigra* and *U. carinirostris* in Port Hacking, as described by Young (1981), differ slightly from the results of this study. Young collected 108 samples over three years from one *Zostera* and one *Posidonia* bed. He found that *S. nigra* - which in this study was predominant in *Zostera* - was present more often in *Posidonia* (37 samples out of 108) than in *Zostera* samples (only 10 out of 108). It is not possible to tell the precision of that difference because the mean abundances of pipefishes per sample of *Zostera* and *Posidonia* did not differ much in Young's study (1.3 and 1.9 for *Zostera* and

Posidonia, respectively) and the standard errors associated with the means are not given. It is, nevertheless, accurate to say that in Young's study area, *S. nigra* was more frequent in *Posidonia* than in *Zostera*. Similarly to this study, Young collected *U. carinirostris* more often from *Zostera* (62 out of 108 samples, with a mean abundance per sample of 3.8) than in *Posidonia* (present in 48 samples; mean abundance of 2.4). The difference in the densities of *U. carinirostris* in *Zostera* and *Posidonia* was, however, very small in Young's study when compared with this study; as mentioned earlier, *U. carinirostris* was very seldom collected from *Posidonia* beds. Thus, in Port Hacking, *U. carinirostris* and *S. nigra* were collected more often from *Posidonia* in relation to *Zostera* than in this study (see General Discussion for possible reasons).

Small numbers of the third pipefish, *S. argus*, were recorded by Burchmore et al., (1984). It is interesting to note that only Burchmore (1984) recorded the presence of *S. argus* in *Posidonia* - this species was not collected by Young (1981) in either *Zostera* or *Posidonia*. On the other hand, although *U. carinirostris* was present in about half of the samples collected by Young (1981), neither this species nor *S. nigra* were included in the list of 39 species collected by Burchmore (1984). The sampling technique may again be partly responsible for these discrepancies. Burchmore used poisoning and the net used to enclose the area sampled (20 x 20 m) had meshes of 2.5cm, which is large enough for most pipefishes to pass through. The absence of *S. argus* from Young's sample cannot, however, be attributed to that because Young used

a trawl net very similar to the one used here, with a 1mm codend mesh. It could, nevertheless, have resulted from the small towing speed used in that study (see comparisons in General Methods).

Finally, an interesting pattern became evident in Botany Bay regarding the spatial distribution of the two genera of pipefish. Both species of *Stigmatopora* were most abundant at Kurnell and present in very small densities at Quibray Bay. In contrast, *U. carinirostris* was most abundant at Quibray Bay with smallest abundances being recorded at Kurnell. There was no such pattern in Pittwater - in this bay all three species were most abundant at Barrenjoey, followed by Careel I. The patterns described here for Botany Bay suggest that conditions at Kurnell may be more suitable for the two morphologically similar species (*S. argus* and *S. nigra*) than for *U. carinirostris*. Conversely, Quibray bay may be a more suitable site for *U. carinirostris*. Possible explanations for these differences in the distribution of the three species will be further examined in the General Discussion (Chapter 5).

TEMPORAL VARIATION

S. argus showed a marked seasonal variation in abundance at three of the four sites where this species was most abundant (Kurnell, Towra Point and Careel I). The greatest abundances in *Zostera* at Towra Point and Careel I (and to a lesser extent at Barrenjoey), occurred between May and September, but a little later in the

year at Kurnell (September and November). The smallest densities at Barrenjoey were recorded in November, and in January and March at the other sites. In contrast to the *Zostera* sites, where strong seasonal patterns were evident, the only significant seasonal variation in the density of *S. argus* was the marked increase in abundance in September 1987 at Kurnell and Towra Point.

Similarly to *S. argus*, the densities of *S. nigra* at Kurnell showed strong seasonal patterns with the largest numbers being recorded in November 1986 and September 1987. The lowest numbers were collected from March to July.

The seasonal patterns of *S. argus* - and, to a lesser extent, of *S. nigra* - contrasted markedly to the trends observed in the only study done in Botany Bay where the variation in abundance of the fish fauna was examined on a seasonal basis and included these species (Middleton *et al.*, 1984). Although the patterns of abundance of *S. argus* and *S. nigra* were not examined in detail in that study, the largest number of individuals was collected in February in the *Zostera* bed on the north side of the bay, where *S. argus* was most abundant (2.8 % total no. of individuals), and from December to June in the second *Zostera* bed (on the west side of the bay) where *S. nigra* was more abundant and represented 22.6 % of the total number of individuals collected. In their study, the largest density of *S. argus* in *Posidonia* was recorded in April, whereas, in this study, *S. argus* was most abundant in November 1986 and September 1987.

The distribution of *U. carinirostris* differed significantly from *S. argus* and *S. nigra* not only in space, but also in time. The largest densities of *U. carinirostris* were collected from November to May, and the smallest in July and September. This pattern is consistent with the seasonal trends observed for this species in Botany Bay (Middleton *et al.*, 1984), Port Hacking (Young, 1981) and, to a less extent, in South Australia, where the distribution of this species was studied in more detail by Howard and Kohen (1984). *U. carinirostris* and two other pipefishes, *Vacampus phillipi* and *Mitotichthys semistriatus* (plus a few *S. nigra*), were collected monthly over a 12-month period from intertidal mud flats containing 'dense' stands of the seagrass *Heterozostera tasmanica* in Western Port Bay, Victoria. In that study, the abundance of *U. carinirostris* increased after January to reach a peak in May-July, which is a little later than the time at which the greatest densities of this pipefish were recorded in this study. Also, in both studies there was a drastic reduction in densities right after the large abundance levels observed in late autumn.

The patterns of spatial distribution observed in this study were more conclusive than those regarding seasonal changes. This reflects well the major objective of the sampling programme which was designed to investigate differences in the distribution of these pipefishes at several spatial scales. The great seasonal variability among sites, and the limited sampling frequency (6 times in the year) restricted significantly the interpretation of

the temporal patterns of abundance.

The comparisons made between this study and the others (Burchmore *et al.*, 1984; Howard and Kohen, 1984; Middleton *et al.*, 1984) must be considered with caution. Apart from the differences already mentioned (e.g. between sites, area sampled, spatial scale, sampling technique), and the limitations of this sampling programme, the other studies are limited in that they lack replication of sites. Middleton *et al.* (1984) introduced a second *Zostera* site in the second year of the study period. These two sites cannot however be considered as proper replicates since the *Zostera* site on the north side of Botany Bay was seriously disturbed by the reclamation of 70% of this bed (Middleton *et al.*, 1984) at the beginning of the study (February 1978). The consequence of this common limitation in design is that one cannot tell whether the patterns described in those studies are of a general nature or inherent to the single sites where they took place.

THE RELATIONSHIP BETWEEN THE ABUNDANCE OF PIPEFISHES AND THE HEIGHT AND DENSITY OF SEAGRASS

Differences from time to time in the height and density of *Zostera* and *Posidonia*, as measured in this study, cannot adequately account for the marked seasonal variation in the abundances of *S. argus*, *S. nigra*, or *U. carinirostris*. If the height and density of the seagrass beds had a direct influence on

the abundance of the three species of pipefishes, some general trends would be expected. For example, the variation in density and height of seagrass was greater in *Zostera* beds (Fig 3.4) than in *Posidonia* (Fig. 3.5). One would expect, therefore, that significant correlations with the abundance of *S. argus* would be more widespread in *Zostera* than in *Posidonia* - this did not happen (Table 3.3). Also, some common seasonal trends observed in the physical structure of the beds had adverse effects at different sites and for different species. For example, a general decline in the density of *Zostera* occurred in winter/spring at several sites. This affected the abundance of *S. argus* (negatively) at two of the sites where this species was abundant (Kurnell and Towra Point), but not at the third, Barrenjoey, where a decline in density of *Zostera* also occurred. The density of *U. carinirostris* was positively correlated with the density of *Zostera* at Quibray Bay and Towra Point, but not at Barrenjoey, and *S. nigra* was not affected by the changes in *Zostera* density at all.

The effect of height and density of seagrass beds on the distribution of *S. argus* and *S. nigra* has been investigated in two other studies done in Botany Bay. Bell and Westoby (1986b) studied the changes in the abundance of small fishes (*U. carinirostris* was not sufficiently abundant for analysis) and decapods within single beds of *Zostera* and *Posidonia* when their height and density were manipulated at a small scale (25 m²-plots). In order to see whether the significant results obtained in the small scale experiment would reflect what happens at a

larger scale, a second study was done to sample several isolated beds of *Zostera* and *Posidonia* at different sites within Botany Bay (Bell and Westoby, 1986c). The results of those two studies (Bell and Westoby 1986b, c), and the results obtained in this study, are summarised in Table 3.8. It is important to note at this juncture one major difference regarding the nature of the correlative analyses used in this study and in Bell and Westoby (1986c). The interactions between pipefishes and the height and density of seagrass beds discussed earlier in this study are based on the seasonal variability in density of pipefishes and the height and density of seagrass for each site. A single regression was done for Kurnell, one for Towra Point, and so on. On the other hand, the larger-scale, correlative study by Bell and Westoby (1986c) - which was done at a similar spatial scale to the present study - investigated the relationship between the abundance of pipefishes and the physical structure of seagrass beds at several sites, at the same time of the year. Thus, for the sake of comparison, the data obtained in this study were also analysed in a similar manner, i.e. a single regression was done for January (using the mean densities from all sites at that time of the year), one for March and so on. These results are also summarized in Table 3.8. This new set of analyses did not reveal much. For example, Bell and Westoby (1986b, c) sampled *Zostera* and *Posidonia* in spring and autumn, respectively. The only correlation that occurred at a similar time in this study (negative correlation between *S. argus* and height of *Posidonia*) had an adverse effect from that recorded by Bell and Westoby (1986b, c). Nevertheless, these correlative analyses brought out

TABLE 3.8

(a) Summary of results of the relationships between the density of *S. argus* and the physical structure of seagrass beds.

	<i>Zostera</i>		<i>Posidonia</i>	
	H	D	H	D
THIS STUDY				
Correlations for each site	ns	(-) * * K-TP-CII	(+) (-) * * *	ns
Correlations for each time of the year	(+) * * Jan-Mar	(-) * * May	(-) * Mar	ns
Bell and Westoby 1986 (b) Small-scale manipulative study ¹	(+) < 0.10	(+) * *	(+) * * *	(+) *
Bell and Westoby 1986 (c) Large-scale correlative study ²	-	ns ³	(+) *	ns

The signs between brackets indicate the nature of the relationship. For studies by Bell and Westoby, * * * = $p < 0.001$; dash indicates that that species did not respond to that particular manipulation in the small-scale study and was not therefore included in the large-scale study.

¹ Extracted from Table III - Results of 3-way ANOVA. Data for *Zostera* was transformed to $\log_{10}[x+1]$

² Extracted from Table IV - Results of linear regression analysis.

³ Data was transformed to $\log_{10}[x+1]$

Note: in this study the height (H) and density (D) of seagrasses were estimated using a slightly different method from that used by Bell and Westoby (1986b, c) - for more details see Chapter 2.

TABLE 3.8 (cont'd)

(b) Summary of the relationships between the density of *S. nigra* and the physical structure of the *Zostera* beds. (Definitions as for Table 3.8a)

	H	D
THIS STUDY		
Correlations for each site	(+) * BJ	ns
Correlations for each time of the year	(+) * * Jan	(+) * * Mar
Bell and Westoby 1986 (b) Small-scale manipulative study ¹	(+) * * *	ns
Bell and Westoby 1986 (c) Large-scale correlative study ²	(+) * *	-

two interactions that had not been detected before: the positive correlation of *S. argus* with height of *Zostera* in January and March, and the positive relationship between *S. nigra* and density of *Zostera* in May. The negative correlation between *S. argus* and the density of *Zostera* was also present in the new series of analyses as was the negative correlation between *S. argus* and height of *Posidonia*.

With regard to the studies undertaken by Bell and Westoby (1986b, c), only two out of four responses to the physical structure of seagrass recorded for *S. argus* and *S. nigra* in their manipulative experiment (1986b) were repeated at a larger scale (1986c), suggesting that the height and density of leaves affect the density of these species more significantly at a smaller scale. The spatial scale is probably not, however, the only factor responsible for the decrease in responses of *S. argus* and *S. nigra* in their larger-scale study. An indication of this is the fact that despite the similarity in the scale of this study and the larger-scale study done by Bell and Westoby (1986c), many contrasts in the results became evident. For instance, the relationship between *S. argus* and the density of *Zostera*, and to a certain extent, with the height of *Posidonia*. On the other hand, there were several differences between these studies which must be kept in mind when comparisons between results are made. For example, the area sampled by Bell and Westoby (1986c) was square in shape (25 m^2 plots) whereas the area sampled in this study was a strip of $35 \times 1\text{ m}$ of seagrass - although the total area is not much different, this $35 \times 1\text{ m}$ strip was more likely

to include zones of the seagrass beds which had different features and were therefore more patchy than the small-sided square area sampled by Bell and Westoby. Also, whereas the regressions done in their study were much more powerful (d.f. for *Zostera* = 1,27, and 1,30 for *Posidonia*) than in this study (d.f. for regressions per site = 1,13, and 1,16 for regressions per time), here the relationship between the pipefishes and the height and density of seagrasses were examined at six different times, and at 5 times of the year, thus giving a broader view of these interactions.

Finally, it is interesting to further consider whether differences described earlier could be associated with limitations in the sampling technique used in this study. For example, could the negative correlations found in this study reflect the fact that denser or taller beds are more difficult to sample? This is unlikely. Sampling *Zostera* never offered any difficulties and in January and March, more pipefishes were collected in taller and denser beds of this seagrass. On the other hand, sampling *Posidonia* was more difficult. Nevertheless, the speed at which the net was towed was kept fairly constant (see General Methods). Furthermore, some of the largest densities of *S. argus* in *Posidonia* beds were collected at Towra Point, one of the tallest, and probably most difficult, sites to sample.

CHAPTER FOUR

GROWTH AND BREEDING BIOLOGY

1. INTRODUCTION

Much of the research on seagrass beds has been motivated by the importance of this habitat for juveniles of economically important species (e.g. Bell *et al.*, 1978a, b; Bell, 1980; FRI, 1988; SPCC, 1981c). It is not surprising, therefore, that information on aspects of the life-history of smaller fishes - such as Syngnathids and Gobiids - from seagrass beds in the Sydney area is scarce (e.g. McDonald, 1981) even though these fishes are abundant and spend most of their lives in these habitats (Middleton *et al.*, 1984; Pollard, 1984).

Information on the recruitment and growth of *S. argus* and *S. nigra* is non-existent. Dawson (1984) and Steffe *et al.* (in press) have provided some basic information on aspects of the life-history and breeding biology of these two pipefishes. These topics were, however, not the main objectives of their works and consequently their observations in this regard are limited. Aspects of the life-history of *U. carinirostris* were investigated in some detail by Howard and Koehn (1984) in Victoria, but very little is known about the populations of this pipefish elsewhere. Thus, this part of the present study has three main objectives concerning the life-history and breeding ecology of *S. argus*, *S.*

nigra and *U. carinirostris*:

- 1) to provide information on recruitment and growth;
- 2) to study the breeding regime of each of the three species by examining the seasonal patterns of abundance of brooding males; and
- 3) to determine the male:female ratio of the adults.

2. METHODS

PROCEDURES

(a) Length Measurements

The total lengths of *S. argus* and *S. nigra* [collected from September 1986 to September 1987], and of *U. carinirostris* [from November 1986 to September 1987], were recorded using a measuring-board graduated to the nearest 1mm.

Some large specimens of *S. argus* and *S. nigra* (<10% of adult population) were missing several tail rings. To avoid having to exclude these specimens from the size-distributions, which would underestimate the relative abundance of the large-sized fish, their total lengths (TL) were extrapolated from their standard lengths (SL) using the following regression equations: for *S. argus*: $2.30 \text{ [SL]} + 5.32$, $r^2 = 99\%$, $p < 0.001$; and for *S. nigra*: $2.13 \text{ [SL]} + 9.39$, $r^2 = 94\%$, $p < 0.001$. These analyses were based on measurements from 24 specimens of each of *S. argus* and *S. nigra* that were larger than 100mm and 75mm, respectively, and appeared not to have any missing tail rings. Specimens of *U. carinirostris* never had rings missing in the tail.

Although all pipefishes collected were measured, results are presented only for those sites where each species was sufficiently abundant for a meaningful analysis. The sites chosen

were: for *S. argus* - Kurnell, Towra Point, Careel I and Barrenjoey; *S. nigra* - Kurnell and Barrenjoey; *U. carinirostris* - Quibray, Towra Point and Barrenjoey.

(b) Sexing Pipefishes

Males of the three species of pipefishes can be easily identified because of the presence of a ventral brood-pouch. Young females, however, cannot be distinguished from juveniles on external morphological characteristics. To solve this problem, Steffe *et al.* (in press) used the 'minimum length at which a brood pouch was present (minimum male total length) as an arbitrary point for the onset of sexual maturity for both sexes'. Thus, any fish larger than the 'minimum male total length' that did not have a pouch were classified as a female, and the others as juveniles. I used a modified version of this method. I adopted the total length of the smallest male that was brooding at a particular time of the year as the point for the onset of sexual maturity. This had to be done because at some times of the year the pouch of the smallest male was only rudimentary and it was apparent that that male could not yet hold any eggs. An additional criterion had to be devised for the few times of the year when there were no brooding males in the sample to be used as a reference point, or when the total length of the 'smallest brooding male' was much greater than the size at which a male would be expected to start brooding. For those cases, I used a conservative estimate of the size at which males of each species

could be expected to have fully developed pouches (and therefore be able to brood). This estimate was based on the results of this study (which showed that variation in the length at which males of a particular species start brooding is small), on the validation study described below, and other sources (Dawson, 1980, 1984; Howard and Kohen, 1984; Steffe *et al.*, in press). The total lengths were 55, 65 and 120mm for *U. carinirostris*, *S. nigra* and *S. argus*, respectively.

(c) Validation of the Method for Sexing Pipefishes

The validation was done to confirm whether fishes that had no male external morphological characteristics (e.g. brood-pouch) were indeed females. This was achieved by examining the gross morphology of the gonads. Female gonads were identified by the presence of eggs. Although the eggs could be seen even in the smallest fishes examined here, this method could not be used to sex all pipefishes because young adults have small and delicate gonads which are difficult to dissect. The gonads of 5 small males whose pouches were just forming were used as a reference for confirmation of the results. *S. argus* was used in the validation study because of the three species this was the one that showed the greatest range of sizes.

Six samples, each of 10 specimens of *S. argus*, were taken from each time of the year. The fish ranged from 74 to 141mm; 50% of these measured between 100 and 120mm. The samples were taken from

those *Zostera* beds which had a large number of fish in the 'size-transition zone', that is the size range when external male characteristics are most likely to appear. The samples were chosen from Kurnell (July, November and September 1987); from Careel I (May); and from Barrenjoey (January and March).

Of the 60 fish examined, one (114mm) was a male. This specimen had only a very small fold in the skin, which was probably the origin of the pouch. Apart from that, this fish could not be readily identified as a male. Gonads of five fish measuring 86, 86, 87, 97 and 107mm could not be satisfactorily identified, probably because of poor preservation. All the other fishes were females.

(d) Determination of Breeding Patterns

The breeding patterns of *S. argus*, *S. nigra* and *U. carinirostris* were determined from the abundance of brooding males and their relative abundance in the total male population.

Males were classified into two main categories. BROODING MALES carried eggs, larvae or young in their pouches at the time they were collected. NON-BROODING males comprised two groups. First were those males which had brood-pouches with egg compartmentation. Given that egg-compartmentation lasts for at least a week (but probably longer) after the young have been released (pers. obs.) its presence was indicative that a male had

been brooding recently before collection. In fact, in many males, bits of egg cases could still be seen in the empty egg cups in the pouch. The second group were males without egg-compartmentation: these males had either not been brooding for some time before they were collected, or were nulliparous.

STATISTICAL ANALYSIS

The size-frequency data were originally collected so that cohorts could be extracted, and the abundance of individuals in - and mean size of - each cohort could then be calculated, using Underwood's (1975) probit modification of Cassie's (1954) graphical method. This was not possible, however, because of the small size of some samples. Instead, size classes were defined on a visual basis and the mode of the distribution used as an indicator of the predominant size-class in a particular cohort.

Comparisons of size-distributions - The Kolmogorov-Smirnov (KS), non-parametric two-sample test (Siegel, 1956) was used to compare two size-frequency distributions. Most K-S tests were done in a MacIntosh 'Statview' program, which should be used with caution because it will calculate probabilities for K-S tests on two samples of any size, and whether or not they have the same number of individuals. Siegel (1956), the major work on which 'Statview' is based, did not, however, provide tables with the probabilities associated with ' D ' when two samples n_1 and n_2 are of different sizes and have between 20 and 40 individuals, i.e. for those

cases where $20 < n_1 \neq n_2 < 40$. Therefore, when this was the case in this study, the larger sample was randomly sub-sampled to make $n_1 = n_2$. These cases are indicated in the tables. The K-S test was used only to test hypotheses generated by the patterns shown in the graphical representation of the size-distributions. For instance, it became apparent that *S. argus* from *Posidonia* beds had greater lengths than those collected from *Zostera*.

Kolmogorov-Smirnov tests were then used to test whether the two samples were sufficiently different to suggest that they had indeed come from two populations with different size-structures. Kolmogorov-Smirnov tests were also used to examine whether the size-structure of the populations of *S. argus* from *Zostera* and *Posidonia* at different sites were similar.

Pooling Data for K-S Tests - The graphical representation of the size-structure of *S. argus* from the two bays suggested that the fish collected from Pittwater had greater total lengths than those from Botany Bay. To test this hypothesis, the data from the two *Zostera* and two *Posidonia* beds in each bay were pooled and their size-distributions compared using a K-S test.

The above hypotheses were tested using a series of K-S tests (Tables 4.1, 4.2 and 4.3). To keep the probability of making a Type I error at the 0.05 level, p had to be adjusted for each individual test (Underwood, 1981a). For a series of seven tests, p was estimated to be 0.01 (approximated to two decimals).

Sex-ratios were examined by χ^2 tests.

3. RESULTS

SIZE-FREQUENCY DISTRIBUTIONS

(a) *S. argus*

a.1 *Zostera*

Botany Bay - The first time the population of *S. argus* at Kurnell was sampled, in September 1986, the distribution was bimodal (Fig. 4.1). The major component of the population (mode: 50-60mm) consisted of juveniles while the smaller component was formed by adults (mode: 120-130mm). From November to May, the total lengths of the juvenile fish increased steadily, so that by July the population had one major adult cohort (mode: 130-140mm). In September 1987 the size-distribution of *S. argus* was again bimodal, with a major component of juveniles and a smaller one formed by adults. In May and July, a second group of small *S. argus* (20-40mm) also became evident.

The population of *S. argus* in the *Zostera* bed at Towra Point (Fig. 4.2) differed significantly from that of Kurnell only in September 1987 (See K-S tests in Table 4.1). The most outstanding difference in the distributions of the two sites in September 1987 was the fact that the adult component at Towra Point formed a separate cohort from that of the juveniles, thus contrasting to Kurnell.

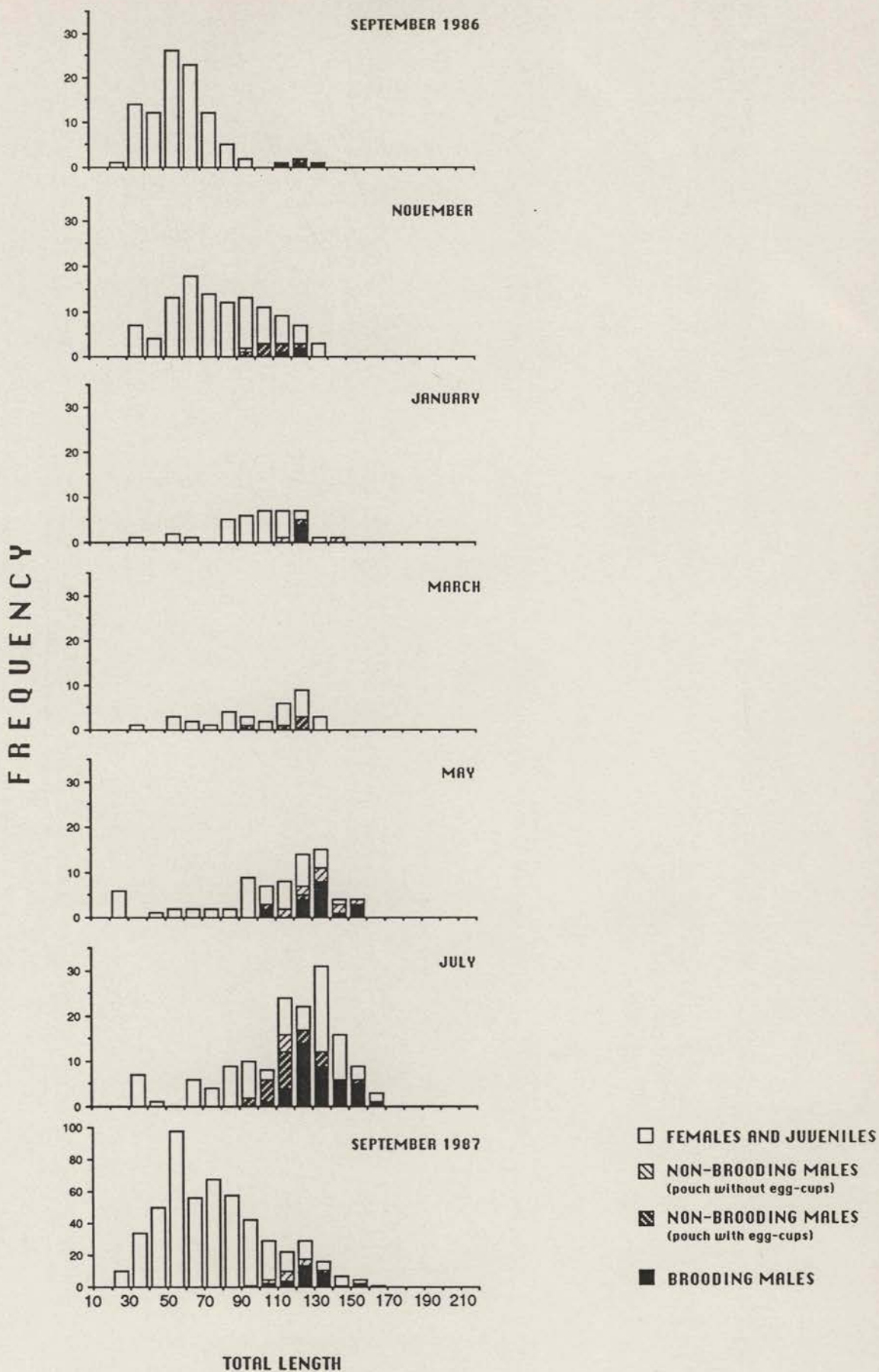


Fig. 4.1 - Size-frequency distributions of *S. argus* collected from *Zostera* at Kurnell (all samples combined). (Note different scale on the Y-axis in Sept. 1987.)

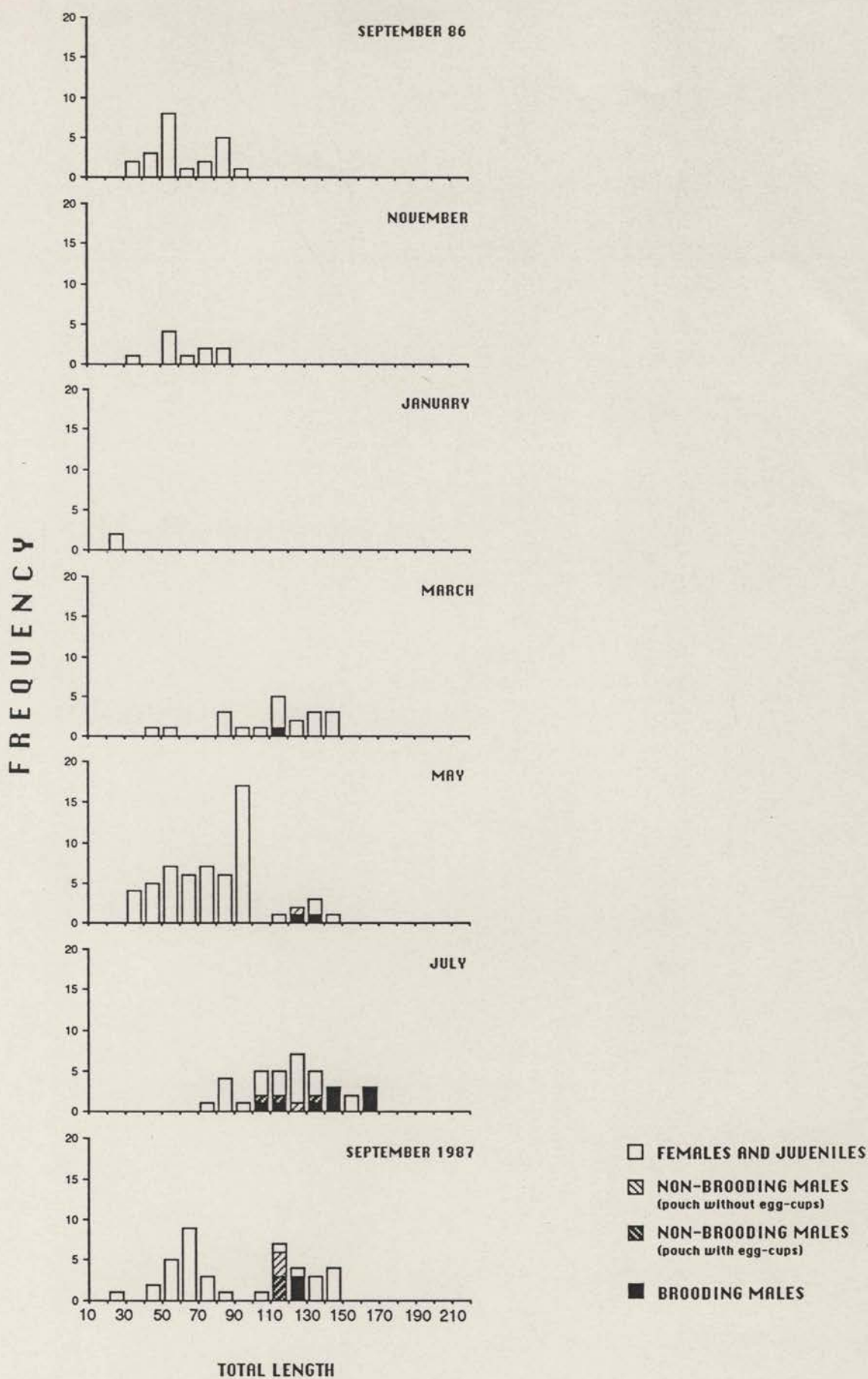


Fig. 4.2 - Size-frequency distributions of *S. argus* collected from *Zostera* at Towra Point (all samples combined).

TABLE 4.1

Comparisons (Kolmogorov-Smirnov Tests) of the size-distributions of the populations of *S. argus* from *Zostera* and *Posidonia* beds. 'N' indicates those cases where the larger size-distribution was randomly sub-sampled to make $n_1 = n_2$ (see text for further explanation). A test was done only in those cases where each sample was equal to or larger than 20.

Zostera

	Sep	Nov	Jan	Mar	May	Jul	Sep
Kurnell = n_1	99	-	-	35	76	150	526
Towra Point = n_2	22	-	-	20	59	41	40
N ($n_1=n_2$)	22			20			
p	ns			ns	ns	ns	* *

	Sep	Nov	Jan	Mar	May	Jul	Sep
Careel I = n_1	84	-	-	-	45	40	57
Barrenjoey = n_2	24	-	-	-	141	125	102
N ($n_1=n_2$)	24						
p	ns				* *	ns	ns

Posidonia

	Sep	Nov	Jan	Mar	May	Jul	Sep
Kurnell = n_1	47	-	50	59	30	39	168
Towra Point = n_2	29	-	58	47	53	32	123
N ($n_1=n_2$)	29				30	32	
p	*		ns	ns	* *	ns	ns

N.B. All samples of *S. argus* collected from *Posidonia* at Careel I were smaller than 20. Therefore, comparisons between the size-distribution of *S. argus* from *Posidonia* beds at Careel I and Barrenjoey could not be made.

Pittwater - At Barrenjoey, the size-distribution of *S. argus* in September 1986 was unimodal (mode: 60-70mm)(Fig. 4.3). Most fish were juveniles, although large fish (110-120mm) were also present. After September, the size of the juvenile fish increased markedly so that by March there were mainly adults in the population. By May, these adult fish had reached their maximal length (mode:150-170). From May to September 1987, there was a steady decrease in the mode of the large-sized *S. argus*. Small juveniles (mode: 30-40mm) formed a separate cohort in the size-distributions of *S. argus* in March and July. In September 1987, this cohort formed by juveniles became - as in September 1986 - the predominant component of the population.

The size-distributions of *S. argus* from Careel I (Fig. 4.4) showed similar trends to those of Barrenjoey (K-S tests in Table 4.1). The size-distributions of these two sites differed significantly only in May when the mode of the distribution from Barrenjoey (150-170mm) was greater than that of Careel I (120-140mm).

a.2 *Posidonia*

Botany Bay - Few changes were noticeable in the size-frequency distributions of *S. argus* from *Posidonia* beds in this Bay (Figs. 4.5 and 4.6). At Kurnell, the distribution was initially bimodal (September 1986) but the juvenile cohort had already disappeared

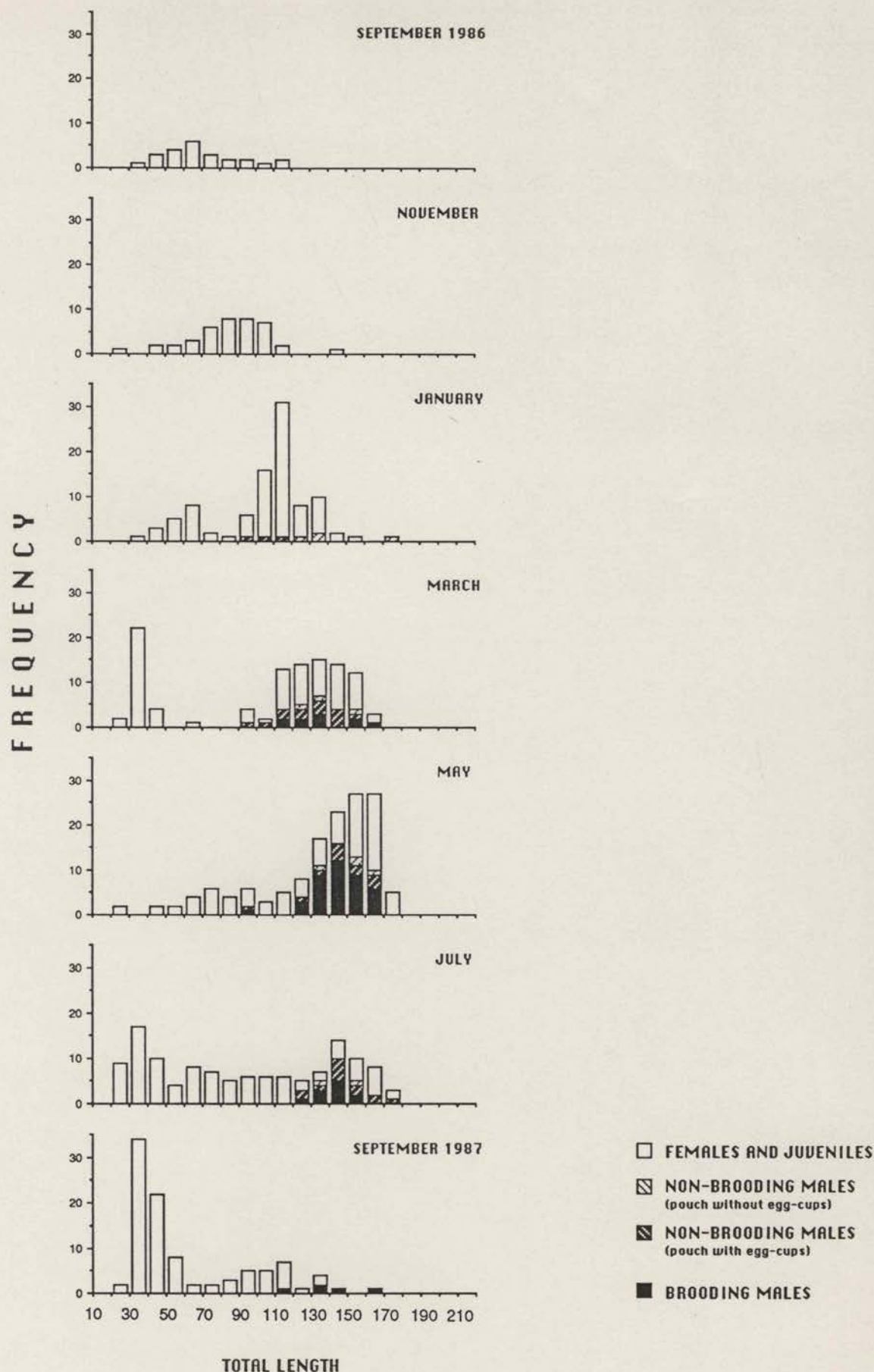


Fig. 4.3 - Size-frequency distributions of *S. argus* collected from *Zostera* at Barrenjoey (all samples combined).

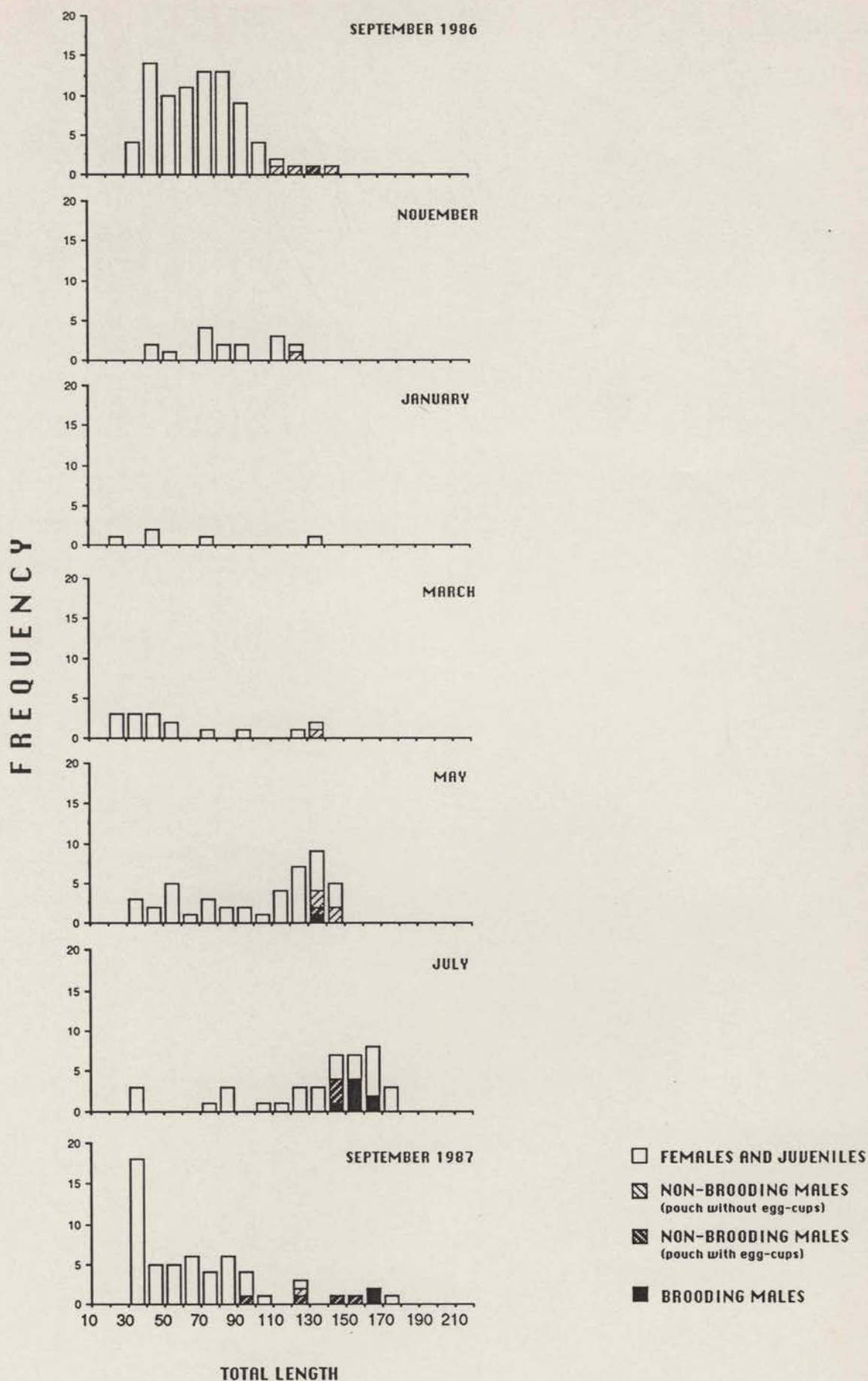


Fig. 4.4 - Size-frequency distributions of *S. argus* collected from *Zostera* at Careel Bay I (all samples combined).

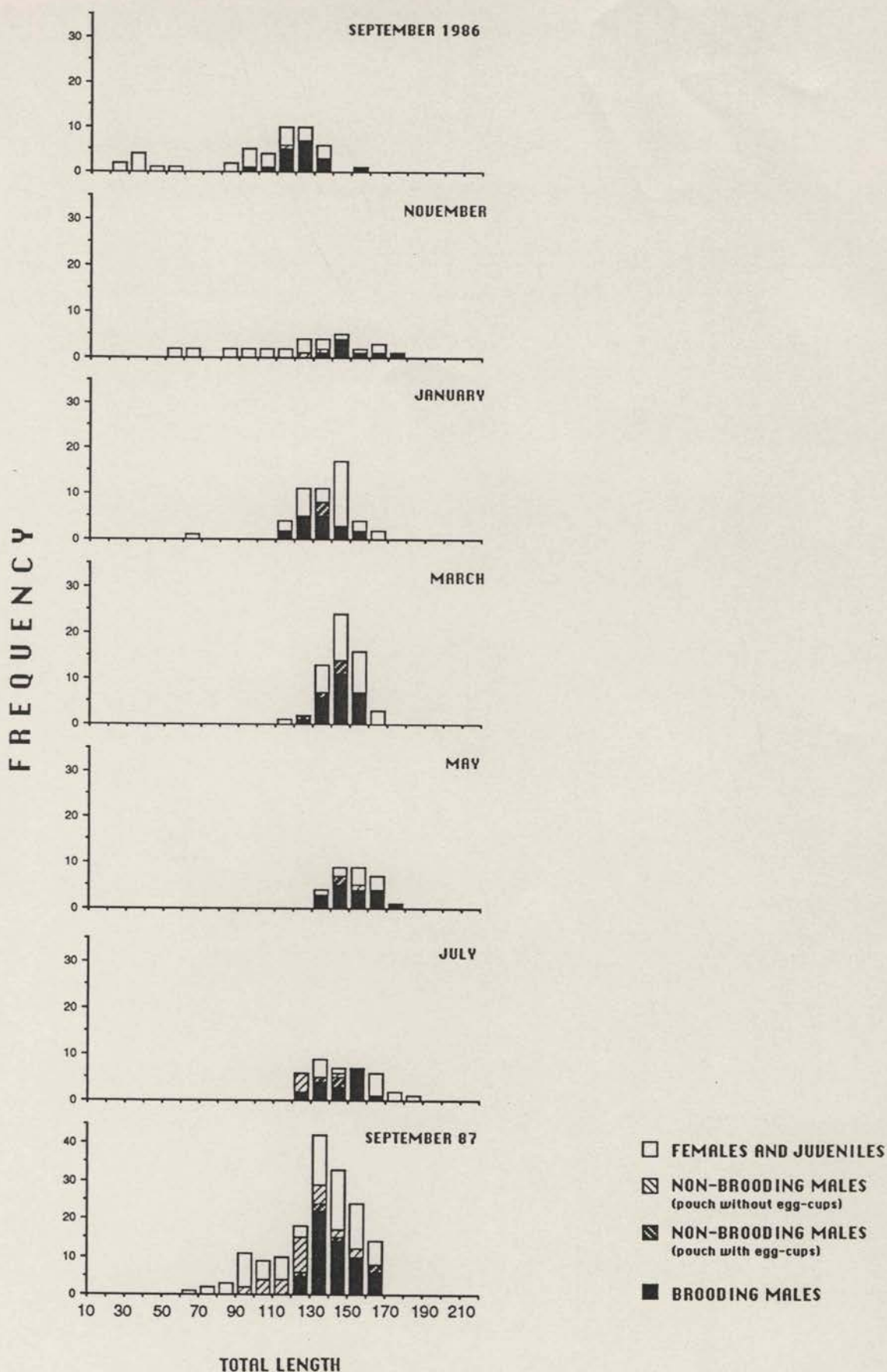


Fig. 4.5 - Size-frequency distributions of *S. argus* collected from *Posidonia* at Kurnell (all samples combined). (Note different scale on Y-axis in September 1987).

by March 1987. The major component of the distribution in September 1986 had a mode in the 140-150mm interval and this did not change significantly until July 1987 when the population of *S. argus* was formed by a small number of large fish. It was at this time of the year that the largest fish were collected at this site (180-190mm). By September 1987 the size-distribution had regained a definite mode (130-140mm) and was formed mainly by medium-sized adults.

The size-distributions of *S. argus* at Towra Point (Fig. 4.6) were generally similar to those at Kurnell (Table 4.5). The only significant differences between the size-distributions of *S. argus* at these sites occurred in September 1986 and May (Table 4.1). In September 1986, a group of juvenile fish (40-80mm) was present at Kurnell but not at Towra Point. In May, although the distributions at the two sites had a cohort with a mode in the 130-140mm interval, at Towra Point, in contrast to Kurnell, this cohort represented a very small proportion of the whole population.

Pittwater - In September 1986, the size-distribution of *S. argus* at Barrenjoey (Fig. 4.7) consisted only of very large fish (mode: 170-180). In November, a second group of small adults (110-120mm) also became apparent. The size-distribution of *S. argus* in January had a much greater dispersion than that of November 1986 suggesting that the two cohorts from November had merged. The single mode of the January size-distribution increased from March to May (170-180) and then remained virtually unchanged until

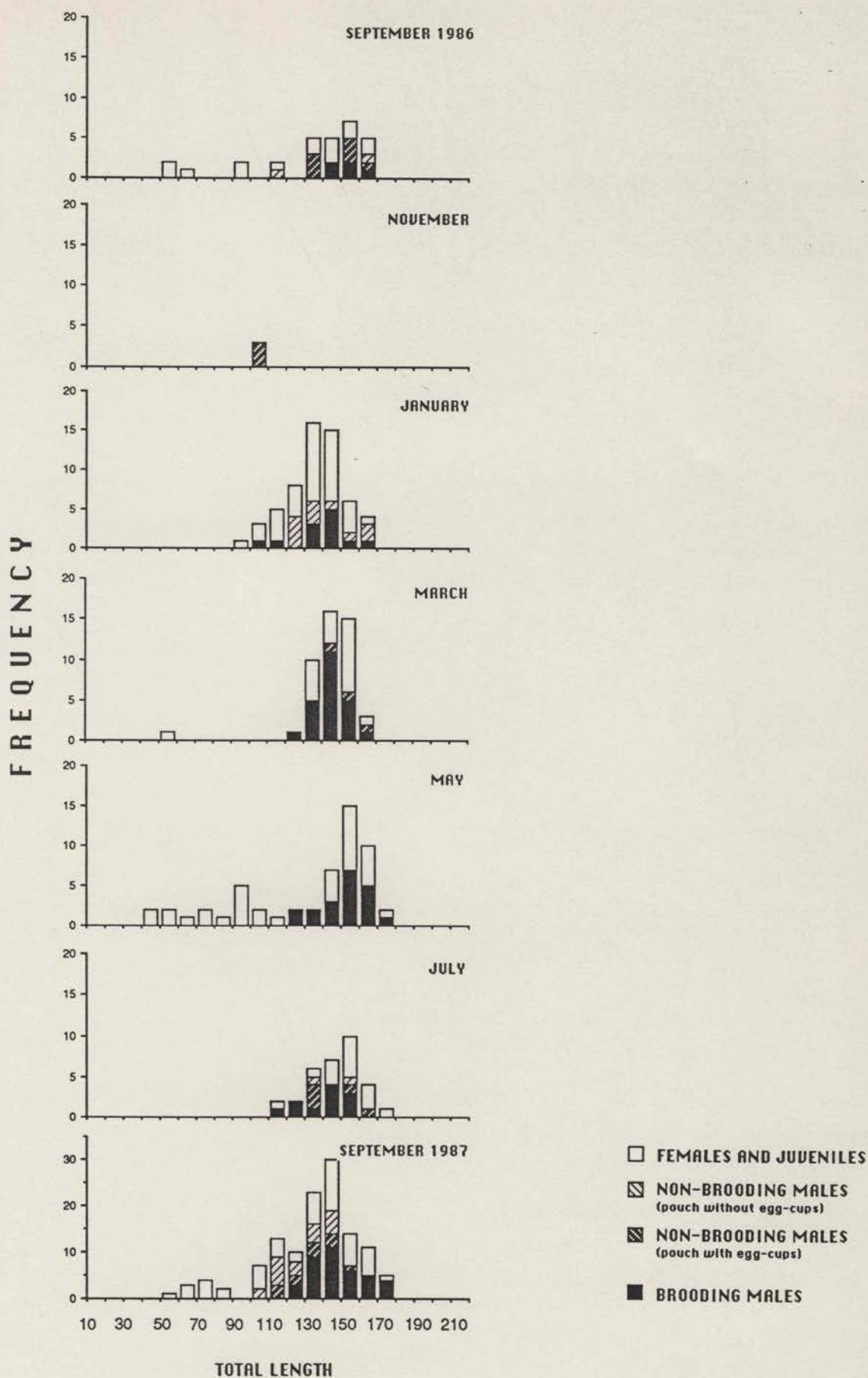


Fig. 4.6 - Size-frequency distributions of *S. argus* collected from *Posidonia* at Towra Point (all samples combined). (Note different scale on Y-axis in September 1987).

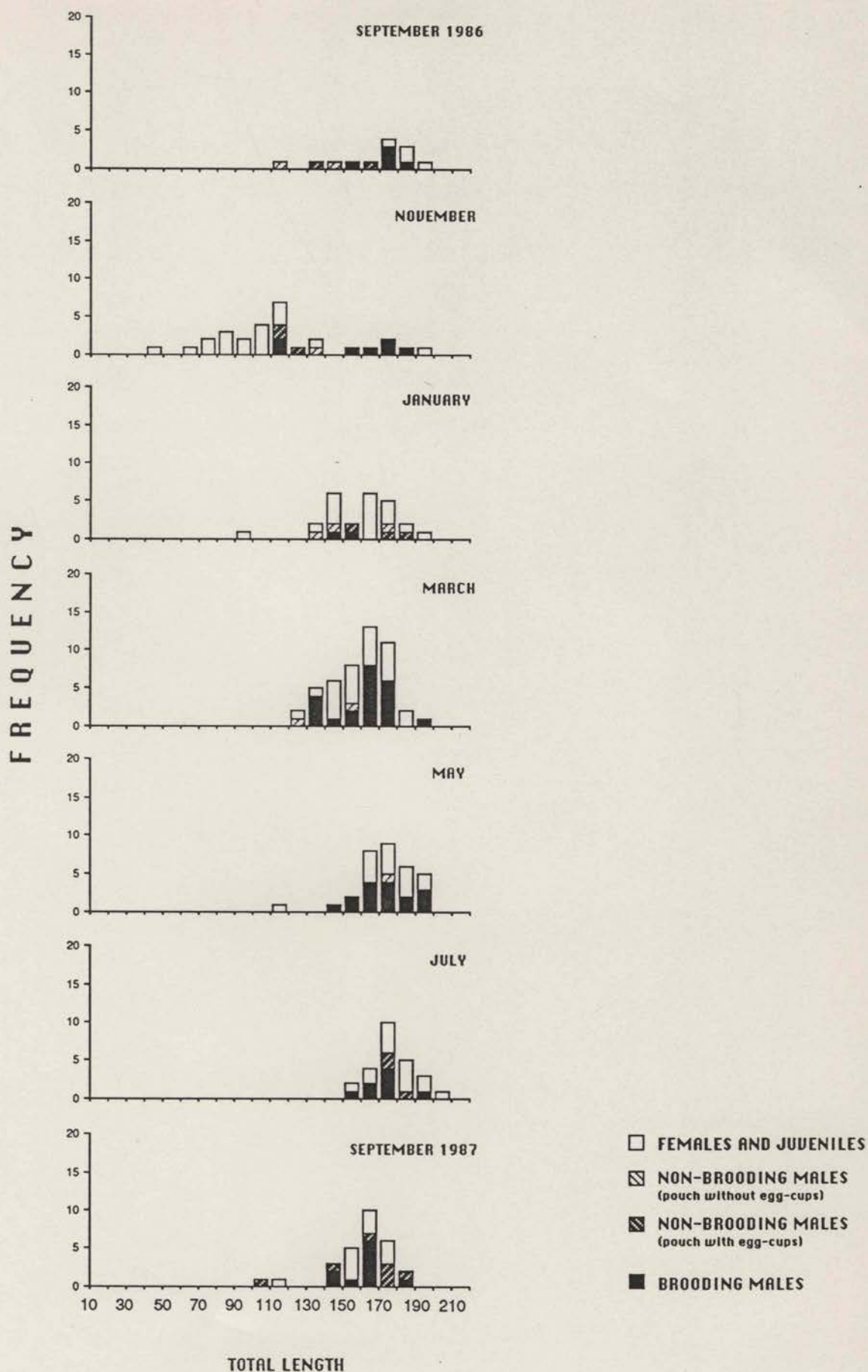


Fig. 4.7 - Size-frequency distributions of *S. argus* collected from *Posidonia* at Barrenjoey (all samples combined).

September 1987. Also note that after March there was a small but steady decline in the range of the size-distributions of *S. argus*.

The small size of the samples at Careel I made the break-down of the size-distributions difficult (Fig. 4.8). Nevertheless, there was a similar trend to that of Barrenjoey in that two groups of different sizes appeared to have merged in January. Also, as at Barrenjoey, in July the distributions had a noticeably narrow range of size-classes in comparison to the previous times.

a.3 Variation in the Size-Distributions from *Zostera* and *Posidonia*

The size-distributions of *S. argus* collected from *Zostera* and *Posidonia* beds differed significantly (K-S tests in Table 4.2) at any time of the year at the three sites (Kurnell, Towra Point and Barrenjoey) where samples were adequate (> 20) for analysis. The size-distributions of *S. argus* in *Zostera* and *Posidonia* generally differed in two ways. The fish collected from *Posidonia* were on average larger than those from *Zostera* and the range of size-classes was smaller in *Posidonia* than in *Zostera*. These trends were also apparent at Careel I (Figs. 4.4 and 4.8) even though the *Posidonia* samples at this site were not sufficiently large for analysis.

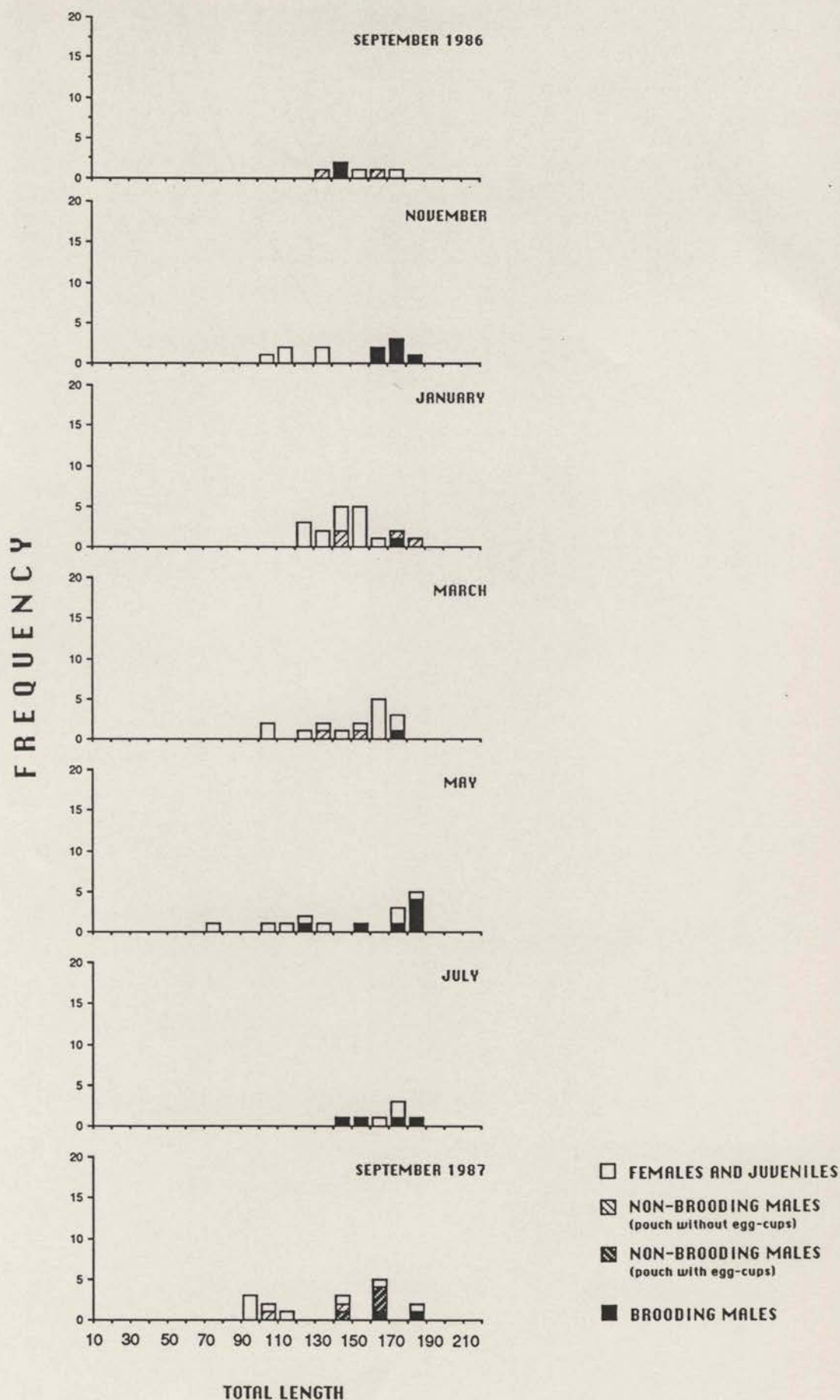


Fig. 4.8 - Size-frequency distributions of *S. argus* collected from *Posidonia* at Careel Bay I (all samples combined).

TABLE 4.2

Comparisons (Kolmogorov-Smirnov Tests) of the size-distributions of the populations of *S. argus* from *Zostera* and *Posidonia* beds at three sites. 'N' indicates those cases where the larger size-distribution was randomly sub-sampled to make $n_1 = n_2$ (see text for further explanation). A test was done only in those cases where both samples were equal to or larger than 20.

KURNELL							
	Sep	Nov	Jan	Mar	May	Jul	Sep
<i>Zostera</i> = n_1	99	111	38	35	76	39	526
<i>Posidonia</i> = n_2	47	31	50	59	30	150	168
N ($n_1=n_2$)		31	38	35	30	39	
p	**	**	**	**	**	**	**
TOWRA POINT							
	Sep	Nov	Jan	Mar	May	Jul	Sep
<i>Zostera</i> = n_1	22	-	-	20	59	37	40
<i>Posidonia</i> = n_2	29	-	-	47	54	32	123
N ($n_1=n_2$)	22			20		32	
p	**			**	**	**	**
BARRENJOEY							
	Sep	Nov	Jan	Mar	May	Jul	Sep
<i>Zostera</i> = n_1	-	40	95	106	141	125	102
<i>Posidonia</i> = n_2	-	30	25	48	32	25	28
N ($n_1=n_2$)		30	25		32	25	28
p		**	**	**	**	**	**

N.B. All samples of *S. argus* collected from *Posidonia* at Careel I were smaller than 20.

a.4 Variation in the Size-Distributions from Botany Bay and Pittwater

In general, the most noticeable difference between the populations of *S. argus* from Botany Bay (pooled data from Kurnell and Towra Point) and Pittwater (Barrenjoey and Careel I) was that the fish from Pittwater were on average larger than the fish collected from Botany Bay at the same time of the year. This trend was more apparent for the populations of *S. argus* from *Posidonia* beds (Table 4.3). Note, for example, that although the dispersions of the size-distributions of fish collected from *Posidonia* beds in Botany Bay and Pittwater were very similar, their modes differed noticeably. Also, although no significant difference was detected in November 1986 between the populations from the *Posidonia* beds in the two bays, the large-sized fish present in Pittwater were not represented in the size-distribution for Botany Bay.

(b) *S. nigra*

The size-structure of the populations of *S. nigra* from the *Zostera* beds at Kurnell and Barrenjoey (the two sites where *S. nigra* was most abundant) did not change much through time (Figs. 4.9 and 4.10). All samples contained mainly adults (95-110mm). A few juveniles (< 50mm) were collected in September 1986 at each site, and, in May 1987, at Barrenjoey and September 1987 at Kurnell.

TABLE 4.3

Comparisons (Kolmogorov-Smirnov Tests) of the size-distributions of *S. argus* collected from Botany Bay (data pooled for Kurnell and Towra Point) and Pittwater (data pooled for Careel I and Barrenjoey). 'N' indicates those cases where the larger size-distribution was randomly sub-sampled to make $n_1 = n_2$ (see text for further explanation). A test was done only in those cases where both samples were equal to or larger than 20.

Zostera

	Sep	Nov	Jan	Mar	May	Jul	Sep
Botany Bay = n_1	121	122	40	55	81	187	566
Pittwater = n_2	108	55	100	121	186	165	159
p	* *	*	ns	* *	*	*	ns

Posidonia

	Sep	Nov	Jan	Mar	May	Jul	Sep
Botany Bay = n_1	-	35	108	106	84	71	291
Pittwater = n_2	-	41	43	64	47	32	44
N ($n_1=n_2$)		35				32	
p		ns	* *	* *	* *	* *	* *

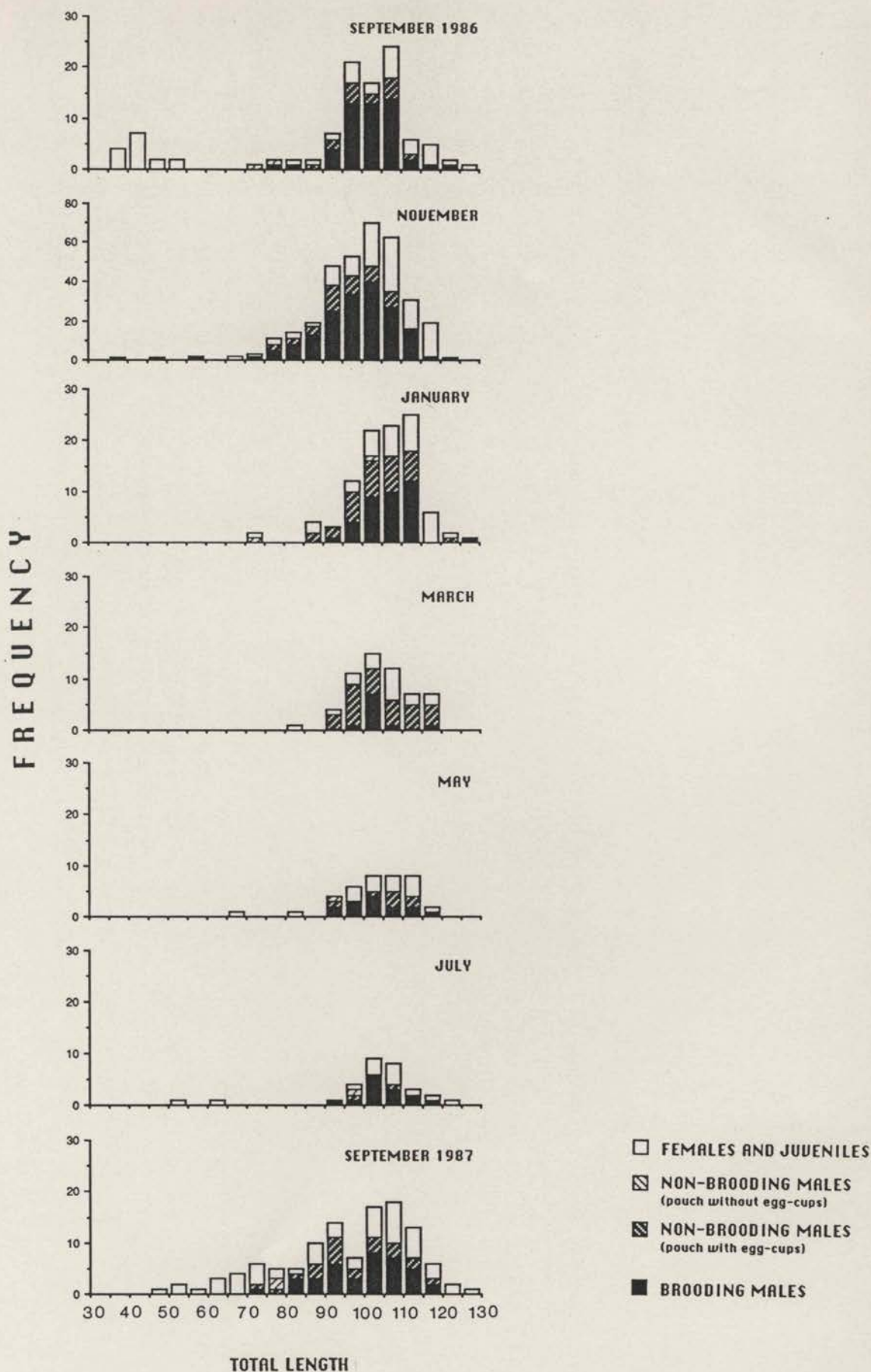


Fig. 4.9 - Size-frequency distributions of *S. nigra* collected from *Zostera* at Kurnell (all samples combined). (Note different scale on Y-axis in Nov. 1986).

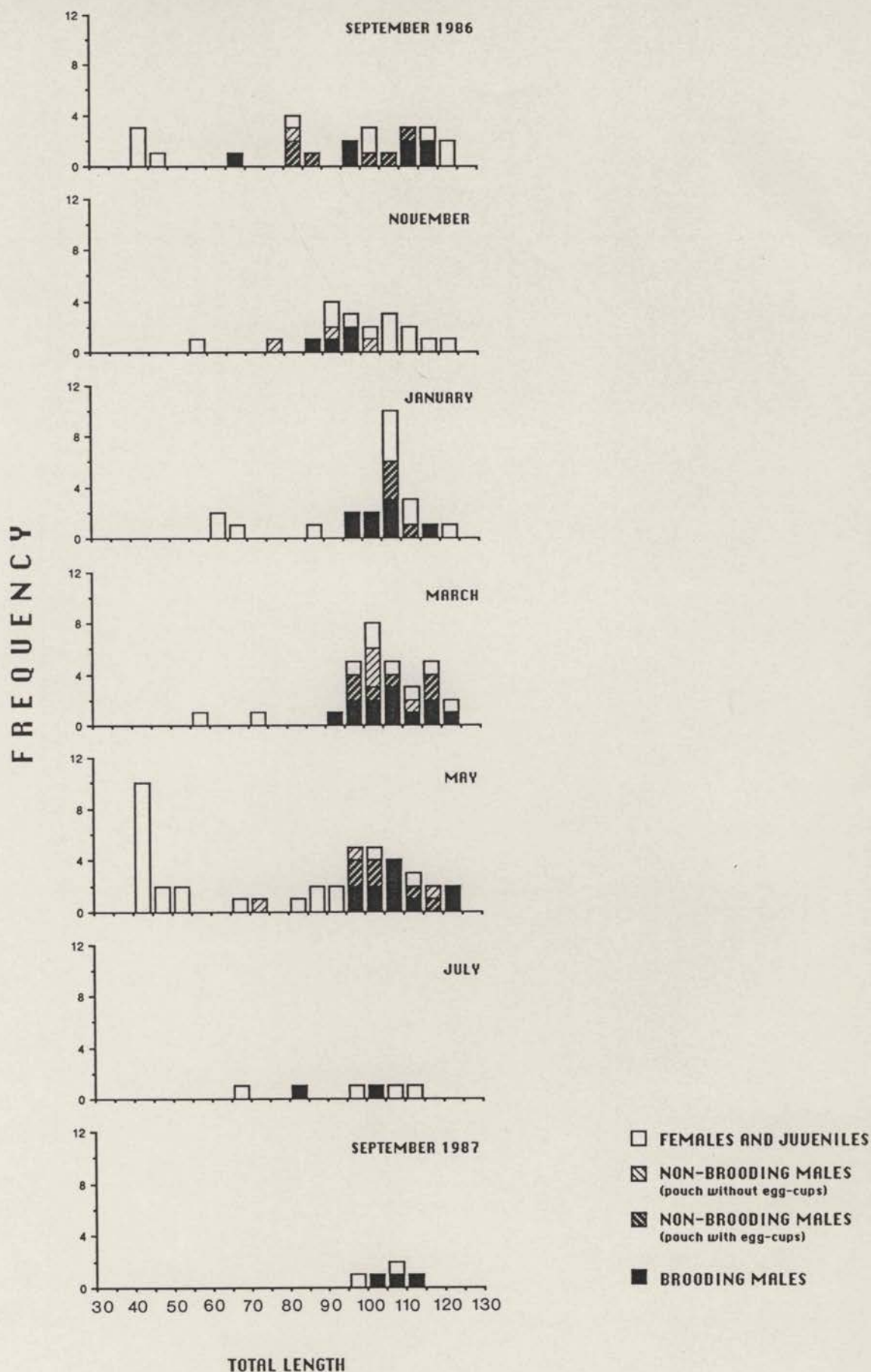


Fig. 4.10 - Size-frequency distributions of *S. nigra* collected from *Zostera* at Barrenjoey (all samples combined).

(c) *U. carinirostris*

The size-distribution of *U. carinirostris* at Quibray Bay in November 1986 (Fig. 4.11) had one major component formed by large fish (mode: 75-80mm). After November, however, the frequency of the size-classes in this major cohort declined steadily and, by May, the large fish had practically disappeared from the population. As the abundance of large fish declined, a second cohort formed by medium-sized adults became apparent. Although this group of fish was present in November 1986 (60-65mm), it was only in January that it became the major component of the population. The fish in this cohort did not change much in size from March to September 1987 although the proportion of larger fish (65-75mm) increased in this period. The size-structures of the populations of *U. carinirostris* at Towra Point and Barrenjoey (Figs. 4.12 and 4.13) were very similar to that at Quibray Bay. Furthermore, at the three sites, juveniles (< 40mm) were present in the samples mainly from November to March. At Towra Point, as at Quibray Bay, larger fish tended to disappear after March.

SEASONAL BREEDING PATTERNS

(a) *S. argus*

The breeding patterns of *S. argus* from *Zostera* beds at Kurnell, Towra Point, Careel I and Barrenjoey were similar in that brooding males were more abundant in May-July (Table 4.4; Figs.

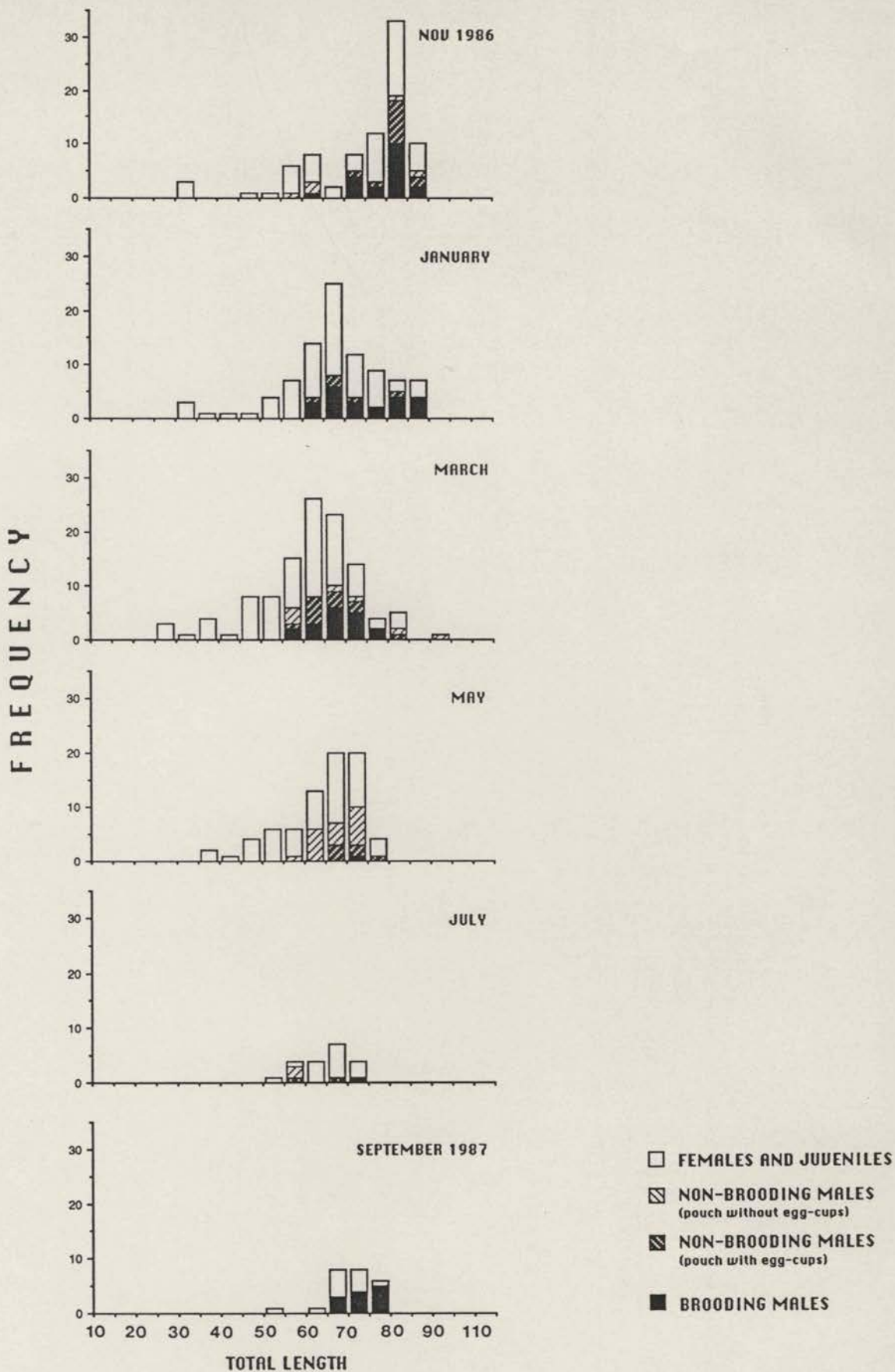


Fig. 4.11 - Size-frequency distributions of *U. carinirostris* collected from *Zostera* at Quibray Bay (all samples combined).

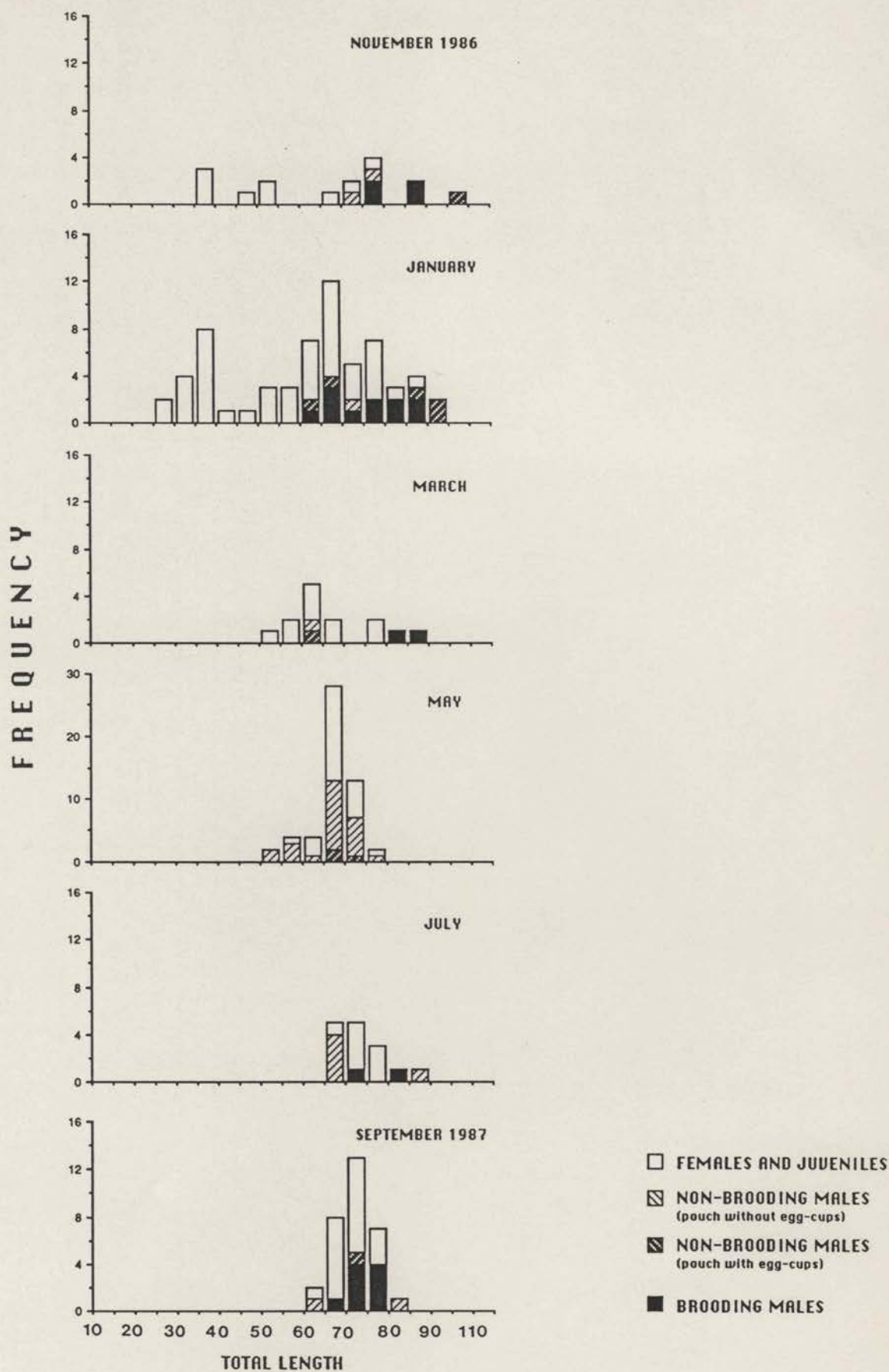


Fig. 4.12 - Size-frequency distributions of *U. carinirostris* collected from *Zostera* at Towra Point (all samples combined). (Note different scale on Y-axis in May 1987).

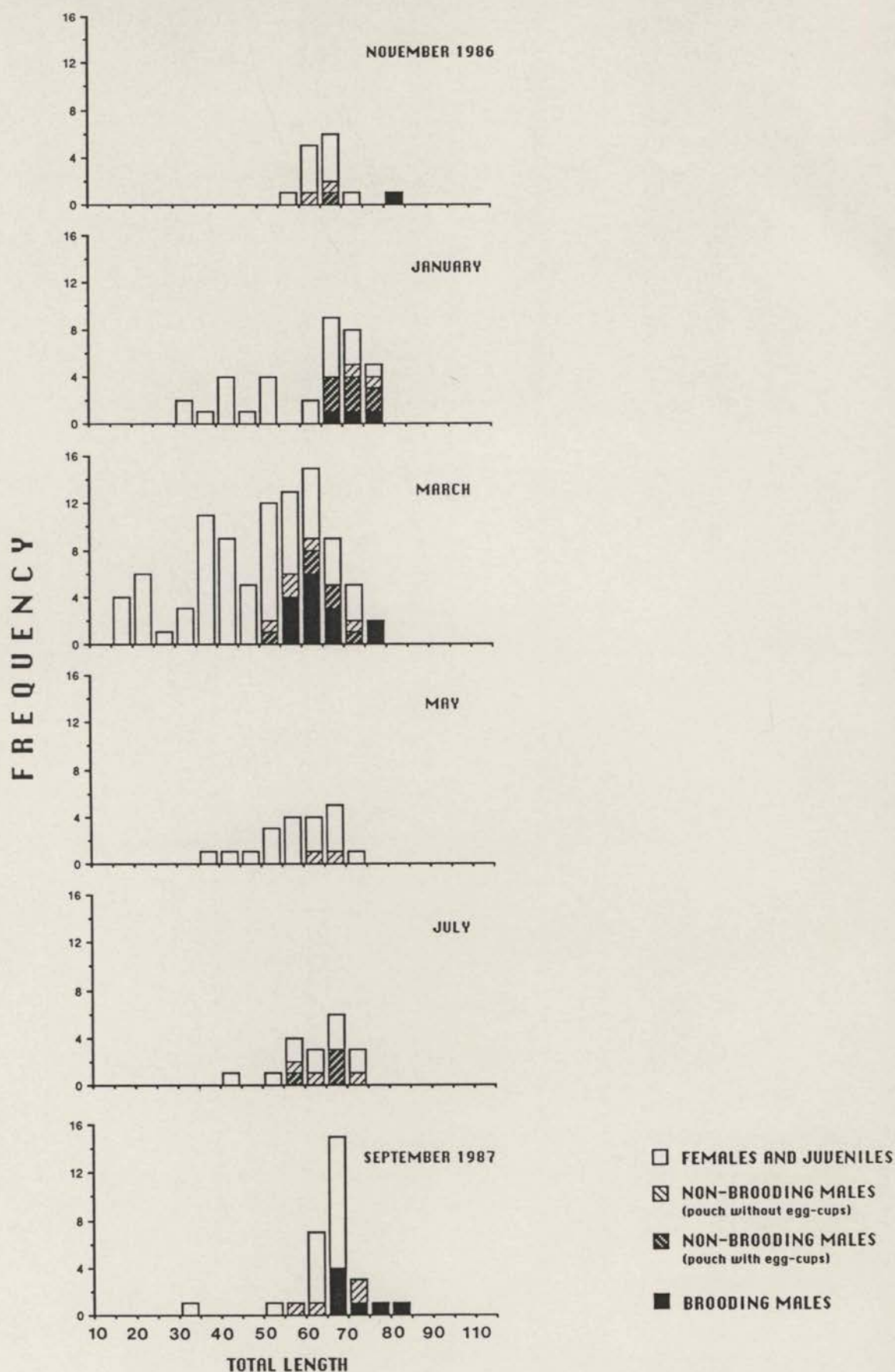


Fig. 4.13 - Size-frequency distributions of *U. carinirostris* collected from *Zostera* at Barrenjoey (all samples combined). (Note different scale on Y-axis in March 1987).

4.1-4.4). Before May, the few males present in samples were usually not brooding (e.g. at Kurnell and Barrenjoey).

In *Posidonia*, brooding males were collected from all four sites at all times of the year (Figs. 4.5-4.8) except November at Towra Point. Although the percentage of brooding males did not vary much in time (Table 4.4), it was generally greater in March and May at Kurnell, Towra Point and Barrenjoey. The absolute number of brooding males was greater between March and September.

Size of Males at First Brooding - The smallest brooding male measured 106mm and the largest male - which was also brooding - was 185mm long. The largest *S. argus* collected was a 210mm-long female.

The smallest fish to show signs of the formation of a brood-pouch measured 96mm but the length at which the pouch formed varied. For example, while a 97mm male had a well-developed pouch, three males measuring 112, 115 and 116mm had only rudimentary pouches (folds were just beginning to form). Despite this variation, results indicated that brood-pouches in general formed when fishes were between 100 and 120mm long.

(b) *S. nigra*

Males of *S. nigra* were brooding at all times at both sites (Kurnell and Barrenjoey. See Table 4.5 and Figs. 4.9 and 4.10).

TABLE 4.4

Percentage of brooding males of *S. argus* collected from September 1986 to September 1987. Results are given only for those times of the year when the total number of males equalled or was greater than ten.

	KURNELL		TOWRA POINT		CAREEL I		BARRENJOEY	
	Zos	Pos	Zos	Pos	Zos	Pos	Zos	Pos
Sep	-	95	-	35	-	-	-	-
Nov	19	80	-	-	-	-	-	58
Jan	-	85	-	48	-	-	-	-
Mar	-	83	-	88	-	-	37	92
May	60	85	-	100	-	-	71	94
Jul	59	65	52	55	-	58	43	73
Sep	48	62	-	55	-	-	-	77

TABLE 4.5

Percentage of brooding males of *S. nigra* collected from *Zostera* beds between September 1986 and September 1987. Results are given only for those times of the year when the total number of males equalled or was greater than ten.

	KURNELL	BARRENJOEY
Sep	76	50
Nov	76	-
Jan	52	66
Mar	21	54
May	63	55
Jul	82	-
Sep	61	-

TABLE 4.6

Percentage of brooding males of *U. carinirostris* collected from *Zostera* beds between November 1986 and September 1987. Results are given only for those times of the year when the total number of males equalled or was greater than ten.

	TOWRA POINT	QUIBRAY BAY	BARRENJOEY
Nov	-	50	-
Jan	65	81	25
Mar	-	48	58
May	0	4	-
Jul	-	-	-
Sep	75	100	64

At Kurnell, the smallest percentages of brooding males occurred in January and March. The greatest numbers of brooding males were collected in September, November and January. At Barrenjoey, the greatest abundances of males were in September, January and May but only about 50% of these were brooding.

Size of Males at First Brooding - The smallest brooding male was 68mm long and the largest (also brooding) 127mm. The largest female measured 123mm. The smallest fish with a brood-pouch measured 52mm. Males generally developed a pouch between 60 and 65mm.

(c) *U. carinirostris*

The breeding patterns of *U. carinirostris* at Quibray Bay, Towra Point and Barrenjoey showed similar trends. The greatest percentages of brooding males were recorded at the three sites in November 1986, January, March and September 1987. It was also during this period that the greatest numbers of brooding males were collected (TABLE 4.6).

Size of Males at First Brooding - The smallest brooding male measured 55mm. A 45mm-long specimen was the smallest fish with a brood-pouch. The greatest total length recorded for a male was 97mm (it was not brooding) and 84mm for a female. It is interesting to note that the largest male and female specimens were collected at each of the three sites either in November or

January, and the smallest brooding male was collected from the three sites in January or March.

PATTERNS OF SEX-RATIO

(a) *S. argus*

Zostera - Females were in general the most abundant sex in the *Zostera* beds of Botany Bay (Table 4.7). At Towra Point, females were significantly more abundant than males at all times of the year (total: 45:27). The ratio between males and females at Kurnell changed through time (in both *Zostera* and *Posidonia*), with an overabundance of females from November to March and of males from May to September. The only significant departure from the 1:1 ratio, however, occurred in March, when females outnumbered males. Overall, more females (185) were collected from the *Zostera* bed at Kurnell than males (169).

In Pittwater, the number of females exceeded that of males at both *Zostera* beds although Barrenjoey was the only site where the ratio differed significantly from 1:1 (204:120)(Table 4.7). Note that in this case the significant heterogeneity of the overall χ^2 was not due to opposing trends in the individual sex-ratios. Rather it reflected the disproportionally large number of females collected in January (63:7).

TABLE 4.7

Sex-ratios of *S. argus* collected from *Zostera* and *Posidonia* beds, from September 1986 to September 1987 (p is outcome of X^2 tests of equality of proportions of the two genders).

		Sep	Nov	Jan	Mar	May	Jul	Sep	TOTAL
KURNELL									
<i>Zostera</i>	Males	4	11	7	5	30	66	50	169
	Females	0	21	16	17	22	49	60	185
	<i>p</i>	-	ns	ns	* *	ns	ns	ns	ns
$X^2_{\text{het}} = 17.1, 6 \text{ d.f.}, p < 0.01$									
<i>Posidonia</i>	Males	12	10	21	29	20	26	91	209
	Females	7	13	28	30	10	13	51	152
	<i>p</i>	ns	ns	ns	ns	ns	*	*	*
$X^2_{\text{het}} = 13.9, 6 \text{ d.f.}, p < 0.05$									
TOWRA POINT									
<i>Zostera</i>	Males	0	0	0	1	3	14	9	24
	Females	0	0	0	13	5	17	10	40
	<i>p</i>	-	-	-	* *	-	ns	ns	*
$X^2_{\text{het}} = 3.2, 2 \text{ d.f.}, \text{n.s.}$									
<i>Posidonia</i>	Males	14	1	23	27	20	20	70	174
	Females	10	0	34	19	21	12	43	139
	<i>p</i>	ns	-	ns	ns	ns	ns	*	*
$X^2_{\text{het}} = 7.1, 5 \text{ d.f.}, \text{ns.}$									

TABLE 4.7 (continued)

		Sep	Nov	Jan	Mar	May	Jul	Sep	TOTAL
CAREEL BAY I									
<i>Zostera</i>	Males	4	1	1	0	7	12	7	26
	Females	1	4	2	0	15	19	3	37
	<i>p</i>	-	-	-	-	ns	ns	ns	ns
$\chi^2_{\text{het}} = 5.7, 2 \text{ d.f.}, \text{ns.}$									
<i>Posidonia</i>	Males	4	6	4	3	7	5	8	28
	Females	2	2	14	11	7	2	2	36
	<i>p</i>	-	ns	*	*	ns	-	ns	ns
$\chi^2_{\text{het}} = 8.9, 4 \text{ d.f.}, \text{ns.}$									
BARRENJOEY									
<i>Zostera</i>	Males	4	0	7	27	55	26	5	120
	Females	2	1	63	45	62	27	7	204
	<i>p</i>	-	-	**	*	ns	ns	ns	**
$\chi^2_{\text{het}} = 33.6, 4 \text{ d.f.}, p < 0.01$									
<i>Posidonia</i>	Males	9	12	8	24	17	11	13	94
	Females	4	5	16	24	14	14	13	90
	<i>p</i>	ns	ns	ns	ns	ns	ns	ns	ns
$\chi^2_{\text{het}} = 5.51, 6 \text{ d.f.}, \text{ns.}$									

Posidonia - In contrast to *Zostera* beds, there was an overabundance of males at both *Posidonia* sites in Botany Bay. At Towra Point, the sex-ratio departed significantly from 1:1 in favour of males (174:139). At Kurnell - similarly to the patterns observed in *Zostera* - females were more abundant (though by only a small margin) from November to March, while males outnumbered females at the other times. A significant bias towards males occurred in July and September 1987 and, overall, more males (209:152) were collected from this *Posidonia* bed.

In Pittwater, there were almost equal numbers of males and females in the *Posidonia* beds, although at CI, a significantly larger number of females were collected in January and March.

(b) *S. nigra*

Males were significantly more abundant than females in *Zostera* beds at Kurnell and Barrenjoey, at all times except November at Barrenjoey (see Table 4.8).

(c) *U. carinirostris*

At Towra Point and Barrenjoey, the total number of males almost equalled the total number of females. At Quibray Bay, the total numbers of females was significantly greater than the number of males (184:143)(Table 4.9).

TABLE 4.8

Sex-ratios of *S. nigra* collected from *Zostera* beds between September 1986 and September 1987. (p is outcome of X^2 tests of equality of proportions of the two genders).

[illegible]

TABLE 4.9

Sex-ratios of *U. carinirostris* collected from *Zostera* beds between November 1986 and September 1987 (p is outcome of χ^2 tests of equality of proportions of the two genders).

	Nov	Jan	Mar	May	Jul	Sep	TOTAL
TOWRA POINT							
Males	7	17	3	29	7	12	75
Females	4	23	8	26	8	19	88
p	ns	ns	ns	ns	ns	ns	ns
$\chi^2_{\text{het}} = 4.84, 5 \text{ d.f.}, \text{ns.}$							
QUIBRAY BAY							
Males	37	27	37	25	5	12	143
Females	34	47	43	36	13	11	184
p	ns	*	ns	ns	ns	ns	*
$\chi^2_{\text{het}} = 6.3, 5 \text{ d.f.}, \text{ns.}$							
BARRENJOEY							
Males	4	13	26	2	7	9	61
Females	6	11	19	10	9	17	72
p	ns	ns	ns	*	ns	ns	ns
$\chi^2_{\text{het}} = 11.2, 5 \text{ d.f.}, \text{ns.}$							

4. DISCUSSION

S. argus

(a) Growth and Breeding

The size-distributions of *S. argus* indicate that this species inhabits *Zostera* and *Posidonia* successively: whereas juveniles (<100mm) were present almost exclusively in *Zostera*, adults were predominant and reached a greater length in *Posidonia* (Figs 4.1 to 4.8). Although the use of different habitats by juveniles and adults has been reported for several fishes in Botany Bay (e.g. Bell^{etal.}, 1978; 1980; Middleton *et al.*, 1984), this is the first time this has been shown in detail for Syngnathids.

In general, the patterns of recruitment of *S. argus* were consistent with the observed breeding patterns. Small juveniles (20-40mm) were present at all times of the year in *Zostera*, which was expected considering that at least some males were able to breed all the year round (Figs. 4.1 to 4.4). Several facts indicated that recruitment was more intense from autumn to early spring. First, the abundance of small recruits (<40mm) was greater at this time of the year. This was probably related to the fact that brooding males - especially in *Zostera* - were more abundant during this time. Second, although there was no apparent 'peak of recruitment' that could be followed through the early stages of growth, the size-distribution of *S. argus* in September

at Kurnell and Towra Point (but a little later at Barrenjoey) had a fairly discrete mode and consisted mainly of medium-sized juveniles (50-70mm) suggesting therefore that most of the fish in these cohorts had been born within the previous 4 months.

The fact that recruitment of *S. argus* occurred only in *Zostera* does not necessarily exclude the possibility of young being born in *Posidonia*. The absence of recruits from this seagrass could be interpreted in at least two ways. First, the young born in that seagrass quickly die or, second, that the young migrate to a *Zostera* bed either by floating on the surface or by moving within the canopy (see 'General Discussion' for further considerations on these topics).

The changes in the size-distributions of *S. argus* from *Zostera* beds at Kurnell and Barrenjoey, where *S. argus* were more abundant, showed that this pipefish more than doubled its length from September 1986 to May 1987. By this time, the young recruited in the previous year had reached sexual maturity and had started to breed. Assuming that *S. argus* did indeed migrate from *Zostera* to *Posidonia*, it was between the months of May and July that this was most likely to happen. This conclusion is based on the following changes observed in the population of *S. argus* in *Zostera* beds in Botany Bay (Figs. 4.1 and 4.2) and concomitant events in the population of *S. argus* from *Posidonia* (Figs. 4.5 and 4.6). First, in *Zostera*, after May 1987, the young adults of *S. argus* started to disappear from the samples so that, by September 1987, the number of large fish had declined

dramatically and the samples were mainly of juveniles. Second, in contrast to the decrease in the abundance of young adults in *Zostera* (after May), in *Posidonia* in September 1987, there was a marked increase in the number of young adults suggesting that these had come from the population of *S. argus* from the *Zostera* bed. Furthermore, it is very unlikely that the fish collected in the *Posidonia* bed in September 1987 had come from the same population that was sampled in that same seagrass in the previous times. This is because adults of *S. argus* in *Posidonia* had reached a maximal length in May-July and could not therefore have 'decreased in size' and originated the size-distribution of September 1987. The patterns in the size-distribution of *S. argus* at Towra Point were very similar to those described above and are thus consistent with this model.

The size-distribution of *S. argus* in *Zostera* and *Posidonia* beds at Barrenjoey differed from the sites in Botany Bay in two ways. First, at Barrenjoey, young adults of *S. argus* remained in the *Zostera* bed for a longer period of time (until July) and attained a greater length than the adults from the *Zostera* beds in Botany Bay. Second, although the slow growth rate of *S. argus* observed in *Posidonia* in Botany Bay also occurred at Barrenjoey, the fish collected there in September 1987 were on average larger than those collected in July, suggesting that the two samples (July and September) had come from the same population. In other words, although the number of adults in the *Zostera* bed at Barrenjoey declined (as happened in Botany Bay), there were no apparent changes in the population of *S. argus* in *Posidonia* in September

1987 that indicated that adults had migrated to this seagrass from *Zostera*. Rather, the fish collected from the *Posidonia* bed at Barrenjoey in the period from May to September seemed to have come from the same population.

The inconsistency in the growth patterns of *S. argus* at Barrenjoey in relation to the 'migration model' described for Botany Bay does not necessarily exclude the possibility that at Pittwater *S. argus* migrate between the two beds. Migration might take place later in the year. For example, the cohort of young adults (110-120mm mode) present in November 1986 at Careel I and Barrenjoey could have originated from the population in *Zostera*. Furthermore, considering that at Barrenjoey *S. argus* on average reached a greater length in *Posidonia*, it is possible that some large individuals change habitats, but do so only after they reach a certain length. If this idea is correct, at Barrenjoey the 'critical size' at which *S. argus* switch habitats is greater than that at the sites in Botany Bay.

Another possible explanation for the divergent patterns observed at Barrenjoey is the distinctive configuration of the seagrass beds at this site. Whereas at other sites the two seagrasses form a fairly clear-cut border, at Barrenjoey there is an intermediate zone (5m wide) where the two species of seagrass intermingle. It is therefore possible that on leaving *Zostera* after July, the fish move to this area, either temporarily or permanently.

The results reported here do not show unequivocally that juveniles and adults of *S. argus* inhabit *Zostera* and *Posidonia*, respectively. There are at least two other mechanisms by which the same patterns could be produced. First, daily tidal migrations might occur. The samples were collected during low tide and it is possible that during this period the larger fish migrate to *Posidonia* but move back to *Zostera* at high tide. This is an unlikely hypothesis because large *S. argus* are present in *Posidonia* during high tides (pers. obs.). The second possibility is differential mortality in the two types of seagrass (as mentioned earlier). The absence of recruits and juveniles from *Posidonia* could be due to greater mortality of the newly-born fish in this seagrass, where the young would be more conspicuous than in the short-leaved *Zostera*. Nevertheless, differential mortality alone could not account for all the patterns described here.

(b) Sex-ratio

The patterns of sex-ratio observed in this study suggest that female mortality increases as the fish increase in size and/or migrate from *Zostera* to *Posidonia*. For example, whereas in the *Zostera* beds in Botany Bay females were generally more abundant, in *Posidonia* there was an overabundance of males. In Pittwater, at least at Barrenjoey, the shift in the sex-ratio from an overabundance of females in *Zostera* to a nearly equal number of males and females in *Posidonia* also suggests an increase

mortality of females as the fish change habitats and/or increase in length. I have no favoured explanation for the different patterns of sex-ratio observed in the *Posidonia* beds of the two bays. The greater density of *S. argus* per unit area in Botany Bay, different species and abundances of potential predators are two of the many possible factors that could have contributed to these patterns.

The overabundance of male *S. argus* in *Posidonia* beds in Botany Bay has also been observed by Steffe *et al.* (in press). They investigated the differences in habitat choice of males and females of *S. argus* and *S. nigra* in that estuary. The data used in this part of their study were originally collected for the small-scale field experiment done by Bell and Westoby (1986b), where they manipulated the height and density of the seagrass leaves. In this same study, Steffe and colleagues also determined the sex-ratio for *S. argus* and *S. nigra*. The analysis of the sex-ratios was based on data collected by Bell and Westoby for the study mentioned above (1986b) as well as on the collection of specimens from their large-scale study (1986c). It is important to note that the 'minimum male total lengths' for *S. argus* and *S. nigra* used by Steffe *et al.* was very similar (5mm) to the 'average minimum male total lengths' described earlier in this chapter (Methods).

Given the limited information on the general behaviour of *S. argus*, it would be foolish to try to explain the sex-ratios described here. It is, however, worthwhile, to examine these

results in view of the hypothesis advanced by Steffe *et al.* (in press) to explain the observed male-biased sex-ratio of *S. argus*. Of particular relevance here are their results on habitat choice and feeding. Steffe *et al.* found that males and females of this species strongly preferred long over short seagrass. With regard to density of the leaves, however, males strongly preferred dense seagrass while females were equally abundant in dense and in experimentally thinned *Posidonia*. The presence of females in thinned areas of seagrass, where they are more conspicuous, was unexpected. Steffe *et al.* then examined the possibility that the presence of female *S. argus* in thinned *Posidonia* could be associated with 'improved feeding'. Fish collected from dense *Posidonia*, were, however, found to contain more food in their guts than were those from thinned areas. The explanation favoured by Steffe *et al.* for these results was that females were using the thinned patches 'to engage in sexual display either towards males or towards each other'. The smaller density of seagrass leaves would presumably allow females to be more easily seen by their conspecifics. But, because under these conditions females would also be more conspicuous to predators than males, they might be under a greater predation pressure, thus producing the male-biased ratio observed in their study.

The sex-ratios obtained in this study are consistent with the model hypothesized by Steffe *et al.* (in press). This model is also a reasonable explanation for the differences observed in the sex-ratio of *S. argus* from *Zostera* and *Posidonia*. Considering that the females from *Zostera* were on average smaller than those from

Posidonia, it is conceivable that because they were smaller and/or younger, they would display less often and thus be less conspicuous than the larger females. In other words, as a female becomes larger and/or older, it may increase its mating frequency thus increasing its susceptibility to predation.

The explanations for the patterns of sex-ratio that were discussed here rely on several assumptions. The most important of these is that, during courtship, females are more active than males. Although the brighter colouration and broadening of the females in both *S. argus* and *S. nigra* support this idea (Steffe *et al.*, in press) there is no evidence that this happens. Active courtship of males and defense of the spawning territory by females is known to happen in at least one family of reef fishes (Apogonidae; Fishelson, 1970) where the male incubates the eggs in the mouth. Extensive parental care by the male does not necessarily mean that females will be more active in courtship. For instance, in Opistognathids, another family of reef fishes where males also undertake oral incubation, courtship is limited only to males (Leong, 1967; Colin, 1972 cited in Tresher, 1984). The limited data on the courtship behaviour of Syngnathids show that the intensity with which females participate in courtship displaying varies from species to species. For instance, Gronell (1984) studied in detail the social organization of the tropical pipefish *C. intestinalis* and found that females participate extensively in courtship although their performance does not overdo that of males. Males and females of *Syngnathus typhle*, a pipefish found in *Zostera marina* meadows on the Swedish coast,

participate equally in courtship displaying. It is interesting to note that this species shows no sexual dimorphism (Berglund *et al.*, 1986b). *Nerophis ophidion*, which occurs in the same habitat as *S. thyphle*, seems to be the only pipefish where females have been observed to be more active in courtship (Fiedler, 1954). *N. ophidion* is similar to *S. argus* and *S. nigra*. Like *Stigmatopora*, *N. ophidion* has marked sexual dimorphism in that females are larger and more colourful than males. *N. ophidion*, however, differs from *S. argus* and *S. nigra*, in that its young are reared on the male's ventral abdomen rather than in a brood-pouch. Unfortunately, the role of females of *N. ophidion* in courtship is rather unclear because Berglund *et al.* (1986b), in contrast to the study by Fiedler (1954), did not notice anything in the behaviour of females that suggested that one female was dominant over another, nor that females were more active in courtship. On the contrary, they reported that 'the male actively followed one female during courtship'. In a later study, however, one of the authors (Svensson, 1988) describes again the female *N. ophidion* as being more active in courtship. Berglund and colleagues did not comment on this discrepancy between Fiedler's and their own observations.

S. nigra

(a) Growth and Breeding

The size-distribution of *S. nigra* was unique in that it consisted mainly of adults. Although some small juveniles (<50mm) were

collected in September of both years at Kurnell, and September 1986 at Barrenjoey, medium-sized fishes (50-90mm) were rarely present in the samples.

There are at least four explanations for these results.

1) Some small fish (<35mm) could have escaped through the 2mm-meshes in the front part of the net, but this is unlikely (See General Methods). Even if the very small fish had been able to escape, this could not explain the absence of medium-sized fishes.

2) Juveniles of *S. nigra* remained in the plankton and recruited only as adults. Although there is no evidence to contradict this idea, I find it very implausible. Moreover, this would have only happened if a major part of the juvenile population were in the plankton (See further considerations on recruitment in General Discussion).

3) The young *S. nigra* were somewhere outside the sampling area. If this had happened in a different *Zostera* bed, medium-sized *S. nigra* would consequently have had to migrate from one area to another. On the other hand, given that the *Zostera* bed where these samples were collected was adjacent to a *Posidonia* bed, it might be that initial growth occurred in the latter. In this case, the *S. nigra* collected in this study would have migrated from *Posidonia* to *Zostera*. *S. nigra* was, however, rarely collected from *Posidonia* thus making this last option very

improbable. Also, because of its relatively short tail, *S. nigra* would probably have found it difficult to keep itself attached to the wide *Posidonia* leaves.

4) The last explanation, and the one I favour, is that the young of this species spend the early stages of their life-history in the more inshore, shallower zones of *Zostera* including intertidal areas. Thus, assuming that brooding was more intense in September-November, when the greatest number of brooding males occurred, the young born at this time of the year in shallower waters would have reached maturity (=65mm) within twelve months, and then have migrated to the more 'offshore' areas of *Zostera*, where the sampling areas were located.

Finally, a possible 'variation' of this hypothesis is that initial growth takes place at the same depth, but in another part of the bed, not necessarily nearer the shore. In this case, young adults of *S. nigra* would migrate from adjacent areas (located at a similar depth) to the sampling area rather than from areas located closer to the shore. The seasonal distributional patterns of *S. nigra* at Barrenjoey were rather scattered as compared to Kurnell suggesting that the population of *S. nigra* was distributed more patchily at Barrenjoey. The broader range of sizes collected at Barrenjoey, particularly the relatively greater abundance of medium-sized fish, suggests that some patterns could be related to the configuration of the *Zostera* bed at this site. The *Zostera* bed at Barrenjoey was much narrower (30%) than that at Kurnell. Thus, if the above hypothetical

pattern of distribution of *S. nigra* in *Zostera* beds is correct, the different size-classes would be more concentrated in a smaller area at Barrenjoey and thus be more likely to be represented in the samples.

(b) Sex-ratio

The overabundance of male *S. nigra* at the two sites was unequivocal and confirms the results of Steffe *et al.* (in press). Unfortunately, it was not possible to determine whether the overabundance of male *S. nigra* was the result of a decline in the abundance of females as was observed for *S. argus* in Botany Bay. This could not be done because the smaller adult size-classes (65-90mm) of *S. nigra* were under-represented in the samples. The hypothesis advanced by Steffe *et al.*, i.e. that females may be more susceptible to predation than males, is nevertheless still applicable to *S. nigra*. Female *S. nigra* are significantly more conspicuous in colouration and shape than are the males. This prominence would be augmented if females are more active in courtship displaying. The only problem with this idea is that whereas female *S. argus* were found as often in thinned and dense *Posidonia*, both males and females of *S. nigra* preferred long dense *Zostera*. Therefore, the differential mortality of females, if it happens, cannot in the case of *S. nigra* be attributed to differences in habitat choice by the two sexes (Steffe *et al.*, in press). One possible reason suggested by Steffe and co-workers to explain the differences in the distributions of males and females

of *S. argus* and *S. nigra* is the way the adults of the two pipefishes are affected by *Zostera* and *Posidonia* leaves. I not only find this idea reasonable but will also elaborate on it later. Before I do that, however, it is necessary to consider briefly the differences in sexual dimorphism in *S. argus* and *S. nigra* and also to qualify further the statement made by Steffe *et al.* that 'female *S. nigra* do not have the conspicuous colour pattern seen in female *S. argus*, but only the broadening of the body'. First, I think that the colouration of female *S. nigra*, in contrast to male, differs by at least as much as the difference between the two sexes of *S. argus*. Indeed, female *S. nigra* do not have the spots that are present on the dorsal surface of the female *S. argus*. But *S. nigra* do have a much lighter colouration (light brown to orange) on the ventral surface of the abdomen (Fig. 2.9) which contrasts strikingly with the dorsal part of the body. Furthermore, this difference in colouration is enhanced by the broadening of the body, which is unquestionably much more pronounced in *S. nigra* than in *S. argus*. Thus, I think that the combination of these two features would make female *S. nigra* more noticeable in *Zostera* than are female *S. argus* in *Posidonia*. I also think that this could explain why female *S. nigra* may not need to use thinner patches of *Zostera* in order to be seen while displaying. The broadened abdomen of *S. nigra* is wider than any *Zostera* leaf; its brownish-orange abdomen contrasts well with the green (or brown when covered with sediment) leaves of *Zostera*. The body of the female *S. argus*, on the other hand, is not wider than any *Posidonia* leaf and its colouration, in my opinion, harmonizes well with the green leaves thus making it more

cryptic. Therefore it may be necessary for the females of this species to move to thinner patches of *Posidonia* if it is to be seen by other fish. Obviously, this would make it more visible also to predators. In conclusion, although females of *S. nigra* preferred dense *Zostera*, they may still be more conspicuous than male *S. nigra* because of their broadened abdomen and colouration in relation to *Zostera* leaves.

U. carinirostris

(a) Growth and Breeding

The seasonal breeding patterns observed in this study are very similar to those described for *U. carinirostris* by Howard and Koehn (1984) in Victoria. Brooding males were abundant in spring and summer (September 1986 to March 1987); Howard and Koehn (1984) found that brooding males were most abundant from October to March. Also, in both studies, recruitment of fish (<40mm) occurred from January to March, suggesting that breeding began in early summer. Although the growth of the young born from September 1986 to March 1987 could not be followed, it is likely that the newly-born young would reach adult size in less than a year as concluded by Howard and Koehn (1984). There are other factors that also support this idea. For instance, in aquaria, this species grows at a very fast rate at least in the first eight weeks (pers. obs.). Also, the disappearance of the large adults from the samples after the breeding season (May 1987) suggest that the few small brooding males present later in the

year (September 1987) had been born during the previous breeding season. If the above model is correct, the fish in the predominant size-class in January at the three sites (60-65mm) would also have been born in the previous year, but perhaps later in the season (March-May).

Although the data from this study and that by Howard and Kohen (1984) are consistent with their conclusion that the population of *U. carinirostris* is annual, there is at least one other plausible interpretation for the patterns described in the two studies. Rather than dying, larger and/or older fish could be migrating to deeper areas of the bed.

(b) Sex-ratio

The sex-ratios of *U. carinirostris* at Barrenjoey and Towra Point were close to 1:1. At Quibray Bay, however, there was a significant overabundance of females, which largely reflected the great number of females collected in January.

Although these patterns in the sex-ratio of *U. carinirostris* contrast markedly with the overabundance of males observed for *S. argus* in Botany Bay and *S. nigra*, they do by no means render invalid the hypothesis that greater female mortality may be the major cause for the relative larger abundance of males of the two species of *Stigmatopora*. The dissimilarities in the male:female ratios of the two genera can be explained in light of the their

differences in morphology and behaviour. *U. carinirostris* is the most sedentary and cryptic of the three species. If predation is a major factor affecting the male:female ratio, it should affect *U. carinirostris* the least. Finally, but not less importantly, is the fact that the sexual dimorphism in *U. carinirostris* is much less marked than in *Stigmatopora*. Thus one would expect predation - assuming that this species has predators that are visually oriented - to affect both sexes with a similar intensity. The lack of a brighter colouration and broadened abdomen in females further suggests that in this species the sexes contribute similarly to courtship, or perhaps that displaying is significantly reduced.

CHAPTER FIVE

GENERAL DISCUSSION

1. INTRODUCTION

This study investigated only one of the many factors that might influence the distribution and abundance of *S. argus*, *S. nigra* and *U. carinirostris* - the relationship between physical structure of the seagrass beds and the patterns of abundance of the three species of pipefishes (Chapter 3). Whenever it was relevant, patterns of growth and breeding were also related to the observed abundance (Chapter 4). I also hypothesized that the local distribution of pipefishes may be in part due to migrations. In this chapter, I will first characterize these patterns of movement according to the spatial scale at which they are thought to occur (2). This will lead to the discussion of additional factors which I believe - or which are mentioned in the literature - have a significant influence on the distribution of pipefishes. Physical factors are considered first (3) and are followed by feeding patterns (4). The importance of predation (5) and stochastic recruitment (6) are discussed in view of the models proposed by Heck and Orth (1980) and Bell and Westoby (1986c), respectively. Competitive interactions (7) are then briefly discussed and are followed by an overall summary and conclusions (8) and recommendations for future research (9)

2. PATTERNS OF MOVEMENT

Between Patches within the Sampling Area

Local patchiness in the distribution of seagrass fishes has been related to small-scale migrations (Choat, 1982). I suggest that this may be the explanation for the 'unexpected' short-term fluctuations in abundance that were observed here. An example of this situation was the pattern described for *S. argus* at Kurnell. In the *Zostera* bed at this site (Fig. 4.1), the abundance of *S. argus* declined significantly in January and March, but increased again in May, and by July *S. argus* were as abundant as in November. Although the decline observed in January could be due to mortality, the increased density in May and July could not be explained in terms of a recruitment pulse since the majority of the fishes in May and July were adults. Also, the fact that continued growth was observed even when the density was fluctuating at lower levels suggests that the samples were coming from the same population. Thus, although the fish within the sampling area were on average at a similar growth stage, their abundance varied between patches of seagrass (within the sampling area).

Between Zones within a Single Bed

The term 'zone' as used here refers to horizontal 'bands' of the seagrass bed. For instance, the intertidal area of a *Zostera* bed would be a zone and the subtidal portion of the bed may have a couple of zones, depending on the width of the bed; the sampling areas in *Zostera* were always located in the zone closest to *Posidonia*. An example of a migration 'between-zones' is the hypothetical movement of young *S. nigra* from the more inshore areas of *Zostera* to the sampling area as these fish reach sexual maturity. It should be noted that in this case - in contrast to the examples given in the previous section - the changes in abundance which suggested that migration might be occurring, took place in a gradual manner. Thus, young *S. nigra* would recruit to shallower zones of *Zostera* and in Spring, as they reach adult size (>65mm) they would migrate to more offshore areas of the *Zostera* beds, closer to *Posidonia*, where the sampling areas were located. Migration between zones of the same bed is also my favoured explanation (in preference to mortality) for the 'disappearance' of the large *S. argus* from the *Posidonia* samples in July/September. I believe that *S. argus* will move to deeper zones in the *Posidonia* beds. This conclusion is based on the fact that *S. argus* occur in deeper areas of *Posidonia* in Botany Bay (pers. obs .) as well as in Jervis Bay (FRI, 1987).

Between Adjacent Beds

An example of this type of migration was discussed in some detail for *S. argus* in Chapter 4, where it was showed that juveniles and young adults of *S. argus* live predominantly in *Zostera* and probably migrate to adjacent *Posidonia* beds in late winter/spring, after they reach adulthood.

Large-scale (within estuary) Migrations

Migrations between isolated beds or different habitats (e.g. seagrass beds and rocky reefs) have been reported for other species of fishes in Botany Bay (Bell, 1980; Bell *et al.*, 1978b; SPCC, 1981c; Middleton *et al.*, 1984; see also Kikuchi, 1974 and Pollard, 1984 for other locations). There is evidence that *S. argus*, *S. nigra* and *U. carinirostris* move between isolated beds: they have been found in plankton samples in Botany Bay (Steffe and Pease, 1988; Steffe, pers. comm.) and have been seen attached to floating objects (personal observations by Bell, Steffe and myself). The importance of these migrations in organizing the populations of these pipefishes will be considered later (8) in view of the model proposed by Bell and Westoby (1986c).

The distribution of two other pipefishes have been associated to large-scale migrations. The northern pipefish, *Syngnathus fuscus*, an abundant inhabitant of *Zostera marina* in Chesapeake Bay, Virginia, apparently moves into the shallow, vegetated areas

during spring where it remains until late autumn (Orth and Heck, 1980) when 'migration back to deeper channel areas occurs' (Ryer and Orth, 1987; also Wicklund et al., 1968). The phrase 'migration back' suggests that these pipefish undertake this migration at least twice in a life-time. Although it is quite likely that *S. argus* live longer than a year, the data presented here do not give any indication that *S. argus* move to deeper *Posidonia* only for a particular time of the year to return to shallower zones (or even to *Zostera*) in the following season.

The largest migration is attributed to the bay pipefish, *Syngnathus leptorhynchus*, in the Yakima estuary in Oregon. Bayer (1980) suggested that in summer, because salinity increases in the lower estuary (to more than 30‰), this pipefish migrates to the upper estuary (about 13.5 km from the Yakima estuary mouth).

3. PHYSICAL FACTORS

Fluctuations in abiotic features of a habitat (such as water temperature and salinity), can affect the abundance of species in two ways: directly, as a causative mechanism, and indirectly. An example of the first would be the effect of salinity in restricting the distribution of a particular species due to physiological constraints (e.g. Gunter, 1956; 1961). An indirect effect would be the influence of salinity, for example, on the distribution of an important prey or predator of that species (e.g. Miller and Dunn, 1980).

Physical variables need not be and usually are not independent of each other, nor independent of other variables such as the physical structure of the seagrass (e.g. Kirkman *et al.*, 1982; Larkum *et al.*, 1984). This interaction of mechanisms is reflected, in the literature, in the relatively small correlations between the variation in density and diversity of species and the measured physical characteristics of the seagrass beds (e.g. Brook, 1978,; Livingston, 1982; Nelson, 1980; Stoner, 1983; Virnstein *et al.*, 1984; Weinstein and Heck, 1979; Young, 1981; but see also Adams 1976a). Further complications in dealing with indirect relationships arise from the fact that species respond differently to changes in the environment (e.g. Bell and Westoby, 1986c; Livingston, 1982; Young, 1981) and are generally capable of changing their behaviour to cope with marked seasonal changes (Livingston, 1982; Hoss and Peters, 1976). Also, there is usually a time-lag between the time a physical factor will have an effect on a population and the time when this variable will be measured (Sogard *et al.*, 1987), and variables may affect only part of the life-history of a species (e.g. recruitment) and that phase may not be considered in the study (Young, 1981).

Temperature and salinity of the water are probably the most often studied environmental variables (e.g. Adams, 1976b; Livingston, 1982; Orth and Heck, 1980; Robertson, 1980; Sogard *et al.*, 1987; Young and Young, 1978; Young *et al.*, 1976; Young, 1981; Young and Wadley, 1979) in seagrass communities, and although there is circumstantial evidence that temperature (e.g. Adams, 1976^a; Orth

and Heck, 1980) and salinity (Young and Young, 1978; Young *et al.*, 1976; Young and Wadley, 1979) influence the distribution and abundance of the seagrass-associated fauna, the effects of these variables are in most cases confounded with at least one other factor such as the distance of the site from the mouth of the estuary (e.g. Young and Wadley, 1978) or plant biomass of the seagrass bed (e.g. Adams, 1976a; Orth and Heck, 1980).

Migrations of pipefishes within an estuary have been, nevertheless, related to seasonal changes in water temperature (e.g. Orth and Heck, 1980; Wicklund *et al.*, 1968) and salinity (e.g. Bayer, 1980). Although some of the patterns observed here were seasonal, I could not identify any pattern of correlation with temperature or salinity.

Low concentration of O_2 is a possible limiting factor in the distribution of estuarine fish (Miller and Dunn, 1980), yet it is rarely mentioned in the literature (Dunn and Miller, 1980; Heck and Orth, 1980; Hoss and Peters, 1976). Anoxic conditions may affect the distribution of fishes in seagrasses when plant cover becomes too great. Heck and Orth (1980) suggested that some species decline in abundance if vegetation is too dense either because movement is impeded or because anoxic conditions may occur over night. This could explain the decrease in abundance of *U. carinirostris* at Quibray Bay in May and July 1987, when this site was nearly covered by the epiphytic brown alga *Giffordia mitchelliae*. Bell and Westoby (1987) showed that a bloom of this alga had a negative effect on the abundance of several species in

Zostera, although it had no effect on the abundances of *S. argus* and *S. nigra*. Unfortunately, *U. carinirostris* were not included in the study. The results for *S. argus* and *S. nigra* suggest that *U. carinirostris*, being a canopy dweller like the two other pipefishes, would not be affected by the bloom of *Giffordia*. On the other hand, Quibray Bay was the only site where *Giffordia* was very abundant and it was also the only site where a drastic decline in abundance of *U. carinirostris* occurred. It should be noted, however, that a similar decline of density of *U. carinirostris* at other sites could have been masked by the large fluctuations in abundance throughout the study.

Depth has also often been related to the distribution of at least some species associated with seagrass beds (e.g. Hoese and Jones, 1963; Sogard et al., 1987). For example, Sogard et al. (1987) found that the goldspotted killifish *Floridichthys carpio* was limited to the shallow areas (top) of the banks in Florida Bay. This negative relationship with depth explained 25.7% of the spatial variation in density of this species. The distributions of at least two pipefishes from Virginia also appear to be influenced by depth. Mercer (1973, cited in Orth and Heck, 1980) found that the pipefish *Syngnathus floridae* was significantly more abundant in deeper areas of eelgrass (*Zostera marina*) while *Syngnathus fuscus* inhabited shallow areas of the bed. In Florida Bay, Sogard et al. (1987) found, however, that depth had little effect on the distribution of *S. floridae*.

There is circumstantial evidence that the greater depth of

Posidonia beds may be limiting the distribution of *S. nigra* and *U. carinirostris*. As mentioned earlier (Chapter 3), in the sites used in this study, where *Posidonia* occurred at a greater depth than *Zostera*, *S. nigra* and *U. carinirostris* were rarely collected from *Posidonia*. In contrast, at Young's (1981) site, where the two seagrasses occurred at similar depths, *S. nigra* were collected more frequently from *Posidonia* and *U. carinirostris* almost as frequently in both seagrasses. The densities of these two species were, nevertheless, generally small and, unfortunately, Young (1981) had no replication for sites.

Three other physical variables associated with seagrass beds in Botany Bay have been found to be correlated with the abundance of *S. argus*. Once it became apparent that height and density of seagrass could not explain the significant variance in abundance of certain species in their wide-scale study, Bell and Westoby (1986c) examined whether properties of sediments, distance of the bed from the ocean, and area of the bed could explain any further variance in abundance. This analysis included only those species which had shown an inconsistent response in their manipulative study (Bell and Westoby, 1986b) and the wider scale study (Bell and Westoby, 1986c). Therefore, only *S. argus* was included in the analysis. Responses of *S. argus* to these variables differed in the two seagrasses; abundance was negatively correlated with the distance of the *Zostera* bed from the ocean, but correlated (presumably positively, but they did not say) in *Posidonia* with the percentage of phi 2 particles in the sediment and positively with the area of the *Posidonia* bed. Although these variables

cannot be considered as generally important in explaining the observed patterns of *S. argus* (Bell and Westoby, 1986c), I think that this 'inconsistency' in the results from the two types of seagrass may reflect to a certain extent the way that *S. argus* are distributed in the two seagrasses. In Chapter 4, it was shown that juvenile *S. argus* were more abundant in *Zostera* and adults in *Posidonia*. Thus, for example, the distance of the *Zostera* bed from the ocean may be correlated with the amount of turbulence in the bed and may influence the distribution of the smaller fish, but may not be important for the adults in *Posidonia*. On the other hand, the abundance of adults in *Posidonia* could be related to biological interactions and processes (e.g. courtship) which are characteristic of sexually mature animals. The physical stability of the sediment has been shown to influence the abundance and diversity of the infaunal community (e.g. Orth, 1977) but its influence on the epifauna may be limited (Bell and Westoby, 1986c). There does not appear to be any direct link between sediment properties and abundance of pipefishes.

The exposure to wave-action of a site can be very important in determining the distribution of species in other estuarine habitats such as rocky shores (Ballantine, 1961; Underwood, 1981b). Yet, virtually nothing is known of its effect on the seagrass fauna. This factor should be particularly important for the more sedentary epifauna, and the epiflora. For example, Weinstein and Heck (1979) suggested that a decline in abundance of individuals in an exposed site in Panama could be due to wave-shock. Waves generated by trade winds may in this area reach

sufficient force to dislodge sessile species of invertebrates (Glynn, 1972) and to uproot plants. The distribution of species such as pipefishes, which rely to varying degrees on the blades for temporary anchorage, may be affected by the degree of exposure of the bed to currents and wave action. For example, protection from wind has been identified as a major determinant in the distribution of the fringed pipefish (*Anarchopterus criniger*). Sogard et al. (1987) found that this species was more abundant on leeward transects of four banks in Florida Bay than in transects collected from the top of the banks, from the windward sides, or from a deeper site in the windward sides.

I believe that the spatial distribution of *U. carinirostris* is significantly influenced by the degree of exposure of the *Zostera* beds because this is a small and less robust pipefish which relies heavily on its anchorage to the plants. In this context, it is worth noting that *U. carinirostris* were most abundant at Quibray Bay, which is certainly the most protected site in Botany Bay, but was very rare at Kurnell, the most exposed site.

Thus, although some physical factors have a significant influence on the distribution and abundance of the fishes in seagrass, including some Syngnathids, the nature (direct or indirect) and intensity of these relationships is still unclear due to the many confounding interactions between the variables. Furthermore, whenever a significant correlation is found, the mechanism by which the variable is affecting the distribution of the species is usually not known.

4. FEEDING PATTERNS

As a Cause of Local Patchiness

Distribution of prey has been identified as a major cause of local patchiness for fishes associated with vegetated soft-substrata. Pipefishes rely heavily on visual cues for foraging. It is therefore to be expected that their distribution at a local scale will be, to some extent, influenced by the distribution of their prey. *S. argus*, *S. nigra* and *U. carinirostris* feed mainly on motile meiofauna (e.g. harpacticoid copepods) although macrofauna are also part of their diet (Steffe *et al.*, in press; Howard and Koehn, 1984). The distribution and abundance of the motile species of these groups of crustaceans in Botany Bay and Pittwater is unknown. Studies on the members of this taxa from seagrass beds in the U.S.A. (mainly Florida and Texas) indicate that they can be extremely motile (Bell and Devlin, 1983; Virnstein and Curran, 1986) and their distribution can vary dramatically between seasons and sites (e.g. Brook, 1978; Sheridan and Livingston, 1983; Hugh and Kitting, 1985; Nelson *et al.*, 1982) and on a diel basis (e.g. Howard, 1987; Walters, 1988). Data on the distribution of these organisms at a local scale, i.e. between patches within a seagrass bed, are nevertheless rare. Howard (1985) developed an *in situ* staining technique to measure the degree of mobility of epifauna within a bed of the seagrass *Halodule wrightii* in Florida. His results suggested that crustaceans (including amphipods and isopods) may

show complete turnover of individuals in 0.56 m^2 areas of substratum in less than 1 day.

Scarcity of prey may also be a potential cause of local patchiness in the distribution of pipefishes. The local density of the species eaten by pipefishes is thought to be affected not only by pipefishes (Ryer and Orth, 1987; Tipton and Bell, 1988) but also by other more agile predators such as the pinfish *Lagodon rhomboides* (Stoner, 1982). Selectivity of prey by pipefishes and factors that affect visibility of prey (e.g. size and behaviour) may also limit the number of individuals that can actually be captured and eaten by pipefishes (Main, 1985; Ryer, 1988; Ryer and Orth, 1987; Tipton and Bell, 1988) within a patch of seagrass thus probably increasing their need to move between patches.

Ontogenic Changes in Diet

The patterns of movement hypothesised for *S. nigra* (from inshore to more offshore zones of *Zostera*) and *S. argus* (from *Zostera* to *Posidonia*) not only happened at a similar spatial scale (20-30 metres) but are obviously related to the growth of the fish. The question is whether these growth-associated patterns could (among other factors) be related to ontogenic changes in diet.

The literature reporting the ontogenic changes in diets of estuarine fishes is extensive (see General Introduction).

Pipefishes also change their diet as they grow. This has been described for the pipefish *S. scovelli* in two localities in Florida (Livingston, 1982, 1984; and Tipton and Bell, 1988) and for *S. fuscus* in North Carolina (Adams, 1976c) and Chesapeake Bay, in Virginia (Ryer and Orth, 1987) and suggests that ontogenic change in diet is widespread among pipefishes.

The available data on foraging patterns and diet of *S. argus*, *S. nigra* and *U. carinirostris* (Howard and Koehn, 1984; Steffe *et al.*, in press) are insufficient to determine whether their diets change as they increase in size. Nevertheless, one observation made by Steffe, Bell and Westoby suggests that the prey items eaten by juvenile *S. argus* in *Zostera* may be on average smaller than those consumed by adults of that pipefish in *Posidonia*. Steffe and colleagues found that *S. argus* and *S. nigra* feed mainly on copepods (>90% volume). The diet of *S. argus* (adults > 125mm) was estimated by weighing the food components. This could not be done for *S. nigra*, however, because the prey items eaten by this pipefish were too small to be weighed, and had therefore to be counted. Considering that the adult *S. nigra* examined by Steffe *et al.* were of similar size and probably had a similar mouth-gape to juvenile *S. argus*, it is possible that the latter feed also on small prey, i.e. on prey of similar size to those eaten by *S. nigra*.

It does not necessarily follow that as fish grow they change their diet. Ontogenic changes in diet appear to be influenced, in Syngnathids at least, by the size range of the species and its

behaviour. A study by Tipton and Bell (1988) on the foraging patterns of two Syngnathids illustrates this well. Tipton and Bell's results are of particular relevance to this study because of the similarities between the two species in his study and those studied here. The smaller Syngnathid studied by Tipton and Bell (1988), the seahorse *Heterocampus zosterae* resembles *U. carinirostris* in size and in that it has limited motility when feeding. *Syngnathus scovelli*, the other Syngnathid studied by Tipton and Bell, is larger and more motile, and thus more similar to *S. argus*. Tipton and Bell found that although prey selectivity by the two fishes was similar in intensity, there were notable differences in their diets. Whereas the diet of the pipefish changed ontogenically to include larger and more motile prey such as amphipods and shrimps, seahorses of all sizes fed mainly on smaller prey (harpacticoid copepods). Tipton and Bell attributed these differences in diet to differences in feeding behaviour and the relative size of the two Syngnathids. A similar explanation was suggested by Howard and Koehn (1984) for the differences in diets of *U. carinirostris* and the two larger pipefishes in their study. Thus, of the three species studied here, *U. carinirostris* is the one less likely to undergo ontogenic changes in diet. Because of its small size and restricted motility, this species may be less effective in capturing the larger and more motile prey such as amphipods and shrimps. *S. argus*, at the other extreme, not only is a larger species, but also has a much larger size-range. With its larger mouth-gape and its greater motility, it would be expected that this species undergoes a dietary shift as it grows. Whether the change of habitats observed for *S.*

argus, and hypothetized for *S. nigra*, is influenced by ontogenic progressions in diet can only be established by careful observations and experimental work. This is dealt with later (Section 9).

5. HECK AND ORTH'S MODEL AND THE IMPORTANCE OF PREDATION

Heck and Orth (1980) proposed that predation is a primary factor influencing the structure of seagrass communities. Furthermore, they maintained that the abundance and diversity of the fauna would be related to the physical structure of the seagrass beds which can be described by 'the plant surface area per area of bottom substrate'. The model predicts that as vegetation cover increases (up to an asymptote), there should be an initial increase in abundance (and diversity) of invertebrates, juvenile fish, and adults. Where cover is too great, conditions will no longer be favourable for the prey, e.g. because of anoxic conditions, or for the predators because their 'effective hunting success would be reduced to a point equal to or lower than that realized in surrounding habitats', and therefore abundances would decline.

Do pipefishes have predators? The most basic assumption of Heck and Orth's (1980) model is that predation is the most significant factor influencing the distribution and abundance of a species. It is logical, therefore, to examine first the available evidence

of predation on pipefishes.

That pipefishes are a palatable prey is unquestionable. I have seen a female *S. nigra* eat almost her whole litter. 'Aquarists' learn quickly that pipefishes should not be kept with other seagrass fishes such as leatherjackets. The potential of pipefishes as prey has also been confirmed for other species (Howard and Koehn, 1984; Svensson, 1988).

Are pipefishes preyed upon under natural conditions? The evidence that pipefishes have natural predators is inconclusive. The only indication of predation in the field that I have seen is the missing tail rings in *S. argus* and *S. nigra*. A large portion of the tail was missing in several specimens and it was obvious that they could not have been just broken off (during sampling, for example). Howard and Koehn (1984) also reported that two specimens of *S. argus* were found in the contents of the stomach of a heron that had been feeding over eelgrass beds in Victoria (K.W.Lowe, cited in Howard and Koehn, 1984). On the other hand, limited information on stomach contents of other seagrass fishes and wading birds indicate that pipefish may not be a common prey. For instance, Howard (1984) found that only two specimens of the pipefish *Vacampus phillipi* had been eaten by 283 predatory benthic fish he examined. Wading birds, the other known predators of fishes in seagrass beds do not appear to eat many pipefish (Lowe, 1982, 1984; cited in Howard and Koehn, 1984). Furthermore, analysis of stomach contents should be considered with caution, particularly regarding pipefishes as prey. In a liquid medium

their bodies appear to soften and deteriorate much more quickly than the bodies of other fishes and this would make their identification in the analysis of stomach contents difficult. Furthermore, it has been shown that large piscivorous fishes may have a significant influence on populations of smaller fishes (Holt *et al.*, 1983). Predation at that level is, however, still largely undocumented for fishes from seagrass beds (Gilmore, 1987).

Heck and Orth (1980) advanced the above model (i.e. that predation has a major effect on the distribution of animal assemblages in seagrasses) to explain the composition of a whole community. The data presented here are by no means sufficient to test their model at that level. Nevertheless, if the model were to hold true for a whole community, it should be true for individual species in the same family, i.e. changes in the 'plant surface area per area of bottom surface' should influence the densities of pipefishes in a similar manner. The data presented in Chapter 3 showed that the abundances of the three species of pipefishes were affected differently by the same differences in the physical structure of seagrass. For instance, the density of *Zostera* at Towra Point was negatively correlated with the abundance of *S. argus*, positively correlated with *S. nigra* and had no significant relationship with the abundance of *U. carinirostris* (see Tables 3.3, 3.5 and 3.7). These results suggest that the predictions made by Heck and Orth (1980) cannot be expected to hold even for a family or genus. For that to happen, *S. argus*, *S. nigra* and *U. carinirostris* would have to respond

similarly to the same variations in the physical structure of the seagrass beds.

Other researchers have reached a similar conclusion (e.g. Bell and Westoby, 1986b; Heck and Orth, 1984; Sogard *et al.*, 1987; Young and Young, 1978) and there is now a consensus that the complex interactions between the physical structure of the seagrass, predation rates and abundance of the fauna have to be considered at the level of species.

The lack of a significant interaction between the 'leaf surface area per unit area' and abundance of the fauna does not necessarily mean that morphological features of seagrasses are unimportant in structuring communities. Whereas measuring the physical structure of the habitat with a single variable, as suggested by Heck and Orth (1980), has the advantage of being comparable among different species of seagrass, it does not take into consideration which feature of the morphology of the plant (e.g. height or density of blades) is contributing most to the observed changes in the 'leaf surface area per unit area'. For example, Bell and Westoby (1986b) showed that halving the 'leaf surface area per unit area' by reducing leaf density or by shortening leaves had adverse effects on abundances of different species. One particular feature of the morphology of seagrass that has often been overlooked (including this study) and that may be important for pipefishes is the width of the leaves. I have outlined in Chapter 4 how the widths of *Zostera* and *Posidonia* may affect the conspicuousness (and probably

susceptibility to predation) of *S. argus* and *S. nigra*. The width of leaves probably has an effect also on the distribution of prey of pipefishes. This has been suggested for the isopod *Erichsonella attenuata* (Lewis, 1984; Virnstein and Howard, 1987b) and recently Ryer (1988) showed that the capture of prey by pipefishes can be significantly affected by the width of the blades of seagrass.

6. THE STOCHASTIC 'SETTLEMENT' MODEL (Bell and Westoby, 1986c)

The model proposed by Bell and Westoby (1986c) is based on the fact that decapods and most fishes associated with seagrass beds are planktonic as larvae or are found in the plankton as juveniles (in the case of pipefishes), and that these larvae or juveniles are patchily distributed, as is typical for fish plankton (see refs in Bell and Westoby, 1986c). The model predicts that the observed patterns of distribution and abundance of seagrass-associated animals should, in general, reflect the composition in the plankton of those larvae or juveniles that are competent to 'settle'. I will now consider the processes associated with this model in view of the data presented here and the information available for other pipefishes living in seagrass beds.

- 1) Patchily distributed individuals settle into the first seagrass bed they encounter, once competent to do so, irrespective of the bed's physical complexity.

I have avoided using the term 'settlement' because it invokes associations with 'the termination of a pelagic, larval existence' (Scheltema, 1974). Even though in their model Bell and Westoby (1986c) do not use the term 'larva' for pipefishes, their model assumes that pipefishes have a 'pelagic phase' in their life-history; but this may not be so (see discussion below). This term also implies that during settlement the organism will adopt behaviours and activities which are indicative of their new life-history (Butman, 1987). This would not apply to pipefishes because those individuals found in the plankton are already juveniles and should resemble closely in morphology and behaviour the juveniles collected in the canopy.

That at least some individuals from the populations of pipefish spend some time in the plankton is unequivocal. *S. argus*, *S. nigra* and *U. carinirostris* have been collected in plankton samples (Steffe and Pease, 1988; Steffe, pers. comm.) and have been seen attached to floating seagrass leaves or drift algae (pers. obs.). There is also similar evidence for other pipefishes from different geographical regions (Jenkins, 1986; Kingsford, 1986; Kingsford and Choat, 1986; Olney and Boehlert, 1988) suggesting that this might be a common trend in the group.

Despite the above evidence, I do not think that pipefishes have a 'pelagic' phase in their life-history. Rather, those individuals collected from the plankton arrived there by accident; in other

words, the presence of pipefish in the plankton is not the result of 'broadcasting' as a dispersal mechanism. I suggest that those young that are able to remain in the bed where they were born will do so (in aquaria they would many times attach to the father's tail or the air tubing); if food and cover in a particular bed is adequate for a male to brood, that bed should also adequately provide for the newly born young. There are, however, circumstances in which the young (and adults to a lesser extent) will have no choice but to leave the canopy for the plankton. One of the factors that would affect the fate of the newly-born juveniles is the conditions of the sea at the time of birth. For instance, a litter born when water conditions are rough are likely to be swept out of the canopy before they can anchor themselves. The morphology of the seagrass could be another important factor. Young born in *Posidonia* would have to anchor to objects with a small diameter, such as epiphytic algae, because their tails are not sufficiently long to wrap around the wide blades of *Posidonia*. Furthermore, the morphologies of fishes collected and observed in the plankton are not unique to those individuals. Juvenile *S. argus*, *S. nigra* and *U. carinirostris* do not have any special adaptations for planktonic life and, in aquaria, they feed and behave in a very similar manner to adults. It is interesting to note that smaller fish had more difficulty staying anchored to the artificial seagrass if the current created by the filter was too strong.

Will pipefish 'settle into the first seagrass bed they encounter, once competent to do so'?

It is reasonable to assume that all juveniles in the plankton are capable of living among the seagrass canopy. I do not think, however, that those individuals that are in the plankton will leave it for the first bed they encounter, but will do so only when a 'suitable' bed comes by. For example, this study (and that by Middleton *et al.*, 1984) showed that only adult *S. argus* was abundant in *Posidonia* and this pattern was consistent for all sites. If the distribution of juvenile pipefishes in the plankton were an important process influencing the abundance of these species, recruits should be expected in both *Zostera* and *Posidonia*. My favoured explanation for these patterns is that juveniles of any of the three pipefishes may not usually settle in *Posidonia* beds because they are either a) responding to some visual cue such as the size of the blades - juveniles of *S. argus*, *S. nigra* and *U. carinirostris*, similarly to adults, rely on visual cues (pers. obs.), and may therefore be able to discriminate, for example, between different amounts of light in beds; or b) because they cannot anchor and stay in that bed. If these speculations are correct, the correlations found by Bell and Westoby (1986c) could be the result of choice of substratum or/and incapacity of the juveniles to anchor themselves.

Bell and Westoby (1986c) acknowledged inconsistencies between the results obtained by Middleton *et al.* (1984) and their model. They suggested that, considering that *Zostera* usually occurs in shallower waters, the differences in the *Zostera* and *Posidonia* were not 'due to discrimination by larvae but arise because *Zostera* received recruits from a suite of species with larvae

that ride surface waters (c.f. Grosberg, 1982) and "gravitate" towards the foreshore before settling'. If this is correct, juveniles of *U. carinirostris* and *S. nigra* should be 'surface-riders' whereas *S. argus* juveniles would be found at the surface and deeper layers of the water column. This seems unlikely because, although individuals of the three species of pipefishes have been collected 'loose' in the plankton (Steffe, pers. comm.), the great majority is usually associated with floating objects (e.g. seagrass leaves) and are therefore riding on the surface, yet *S. argus* is also found in isolated *Posidonia* beds (e.g. Middleton *et al.*, 1984). Furthermore, if the suite of species recruiting to a particular habitat can be determined by the depth they are found in the water column, recruitment to these beds should be predictable, at least within a vertical gradient, and not stochastic.

Finally, Bell and Westoby (1986c) argued that natural selection should not favour those larvae and juveniles that make a fine discrimination between the habitats because mortality in the plankton is known to be very high (Doherty, 1983; Mileikovsky, 1971; Purcell, 1985; Thorson, 1950). Later on they suggest, however, that 'mobile species with mechanisms for protection' should be able to move between beds. If drifting algae and leaves offer sufficient protection for pipefishes to move from bed to bed, it should also protect those that are compelled to the plankton after they are born. In other words, if pipefishes have good cover while in the plankton, there should be no predation pressure and they may be able to discriminate between beds. On

the other hand, if predation in the plankton is great for juvenile pipefishes, then movement between beds should not be a successful mechanism.

- 2) Individuals do not leave the seagrass bed once they have settled. This remains true for sedentary species but does not hold throughout life for mobile species with protective mechanisms enabling "safe" movement from shelter.

Thus, those individuals in the plankton would be expected to move from beds where they first arrived from the plankton to beds which offer better cover. The question of interest here is whether the percentage of the population that end up in the plankton would be sufficient to produce the correlations observed by Bell and Westoby (1986c). Although the number of juveniles of *S. argus*, *S. nigra* and *U. carinirostris* in the plankton is apparently fairly constant (Steffe, pers. comm.), as mentioned before, this may represent only a small proportion of the population. Another factor that suggests that movement of pipefish may not be very intensive is the relatively small recruitment rate of pipefish to artificial seagrass units (e.g. Bell *et al.*, 1985, 1987) in relation to natural seagrass (see Bell *et al.*, 1987, for other possible reasons).

Finally, it should be noted that, assuming that the percentage of individual pipefishes in the plankton is really important, the correlations observed by Bell and Westoby (1986c) could be explained by density-dependent factors such as differential

survival due to predation, rather than migration between isolated beds after 'settlement'. Although Bell and Westoby (1986a) provided evidence that some species of fishes and decapods (see also Leber, 1985) search for better cover within a bed, this has not been shown for *S. argus*, *S. nigra* or *U. carinirostris*.

Apart from the considerations made so far, the data presented in Chapter 3 did not conform to their prediction that the abundance of pipefishes will correlate well with the physical structure of seagrass at a larger scale (see discussion in that chapter for possible reasons for differences in results).

- 3) Individuals move around within seagrass beds to select the type of cover favouring survival.

This study provides no evidence that is relevant to this part of their model. Substantial evidence for this hypothesis can be found in Bell and Westoby, 1986b.

The data presented in this study are by no means a test of the model proposed by Bell and Westoby (1986c). The above considerations may, nevertheless, point to aspects of the life-history of Syngnathids that should be considered when tests of the model are designed.

7. COMPETITIVE INTERACTIONS

Although competition is often invoked as a major density-dependent factor in the organization of marine communities (e.g. Anderson *et al.*, 1981; Luckhurst and Luckhurst, 1979; Robertson, 1980; Sale, 1977 and 1979), it has rarely been related to the organization of seagrass-associated fauna (Heck and Orth, 1980; Pollard, 1984). This results in part from the concept that food appears to be abundant in seagrass beds (e.g. Adams, 1976a; Jackson, 1972; Nelson, 1979) and is probably not a limiting resource. Rather, competition for refuge from predation has been often considered as a potential factor. Heck and Orth (1980) suggested that it is interference and not exploitation which is important among seagrass-associated epifauna. Although there is evidence that is consistent with this hypothesis (Nagle, 1968; Thorp, 1976), the only attempt to test it experimentally appears to be that by Coen *et al.*, (1981). They showed that in the laboratory one species of palaemonid shrimp actively displaced another from vegetation, suggesting that cover might be a potentially limiting resource. Furthermore, they found that the predation on the displaced individuals was significantly greater and therefore mortality might be density-dependent. There seems to be not even anecdotal evidence that pipefishes compete either for food or cover. There is circumstantial evidence, nevertheless, that competition for mates may be important for the local distribution of pipefishes (Gronell, 1984; Svensson, 1988).

8. SUMMARY AND CONCLUSIONS

- 1) The abundance of the three species of pipefishes varied significantly among sites within each bay. *S. argus* had the broadest distribution and occurred in both *Zostera* and *Posidonia* beds at all sites. This pipefish was most abundant at Kurnell (Botany Bay) and Barrenjoey (Pittwater). *S. nigra* and *U. carinirostris* were restricted to *Zostera* beds. *S. nigra* was abundant at Kurnell only. *U. carinirostris* was most abundant at Quibray Bay (Botany Bay), followed by Barrenjoey and Towra Point.
- 2) The abundance of *S. argus*, *S. nigra* and *U. carinirostris* varied significantly from time to time; these temporal differences also varied among sites. The great variability in the results and the small frequency of sampling restricted the interpretation of seasonal patterns of abundance of these pipefishes.
- 3) The physical structure (height of leaves and density of shoots) of the seagrass beds did not explain the patterns of abundance in a consistent manner. The relationship varied for the three species of pipefishes, among sites and species of seagrass and from time to time (Chapter 3). These results do not conform to the model proposed by Heck and Orth (1980). Other features of the morphology of seagrasses might be important for these pipefishes. Recruitment and growth of the fish (see 4 below) could explain only part of the seasonal variability. It was suggested that patchiness, caused by migrations within beds of

seagrass, might be an important factor affecting the distributions of pipefishes at this small scale.

4) The two species of *Stigmatopora* showed a weak seasonal breeding pattern; at least some males were able to breed throughout the year.

Juveniles of *S. argus* virtually only occurred in *Zostera*. Although some recruitment was observed at all times of the year, the size-distributions of this pipefish indicated that it was probably more intense between March and July. In *Zostera*, recruits more than doubled their size and were breeding in less than a year. Changes in the size-distribution of *S. argus* in *Zostera* and *Posidonia* in Botany Bay indicated that young adults migrated from *Zostera* to *Posidonia* around July-September. These patterns were not evident at the sites in Pittwater. This inconsistency could be related to the relatively small sizes of the samples at Careel I and the configuration of the seagrass beds at Barrenjoey. The growth of *S. argus* in *Posidonia* was relatively slow. Adults reached their maximum length around July-September, when the largest fish disappeared from the samples.

Samples of *S. nigra* consisted mainly of adults. This pattern was probably due to recruitment which, it was suggested, occurs in inshore areas of *Zostera*. Once juveniles reach adult size (probably in Spring), they migrate to the offshore zones of the bed, where the sampling areas were located.

The breeding season of *U. carinirostris* was clearly defined: brooding males occurred from November to March and coincided with recruitment. Young of this species, as described for *S. argus*, reached sexual maturity in less than a year.

The patterns observed in this study do not lend support to the 'stochastic settlement' model proposed by Bell and Westoby (1986c). It was hypothesized here that pipefishes have no 'planktonic phase' as a broadcasting mechanism in their life-history. Rather, small juveniles (and some adults) are accidentally forced into the plankton. Because only a small proportion of the population will reach, and recruit from, the plankton, this mechanism is not the most important factor influencing the distribution and abundance of pipefishes. Furthermore, I proposed that those individuals that reach the plankton (irrespective of their numbers) do not 'settle' into the first bed they encounter, as suggested by Bell and Westoby (1986c), but discriminate among beds. Consequently, irrespective of numbers, recruitment from the plankton should not be stochastic.

5) The patterns of sex-ratios of *S. argus* differed in *Zostera* and *Posidonia*, and in the two bays. In the Botany Bay sites (Kurnell and Towra Point), females were more abundant in *Zostera* but males outnumbered females in *Posidonia*. It was concluded that this shift in sex-ratio was growth/age-related. A similar trend was also evident at Barrenjoey, in Pittwater, but not at Careel I. The sex-ratio of *S. nigra* was biased towards males at both

Kurnell and Barrenjoey. The number of males and females *U. carinirostris* almost equalled to 1:1, although at Quibray Bay there was an overabundance of females. It was speculated that the male bias in the sex-ratios of *S. argus* and *S. nigra* is, as suggested by Steffe *et al.* (in prep.), related to the differences in choice of habitat by males and females (*S. argus*) and the role played by the two sexes (*S. argus* and *S. nigra*) during courtship. The different patterns in the sex-ratios of the three species may be explained in view of differences in the morphology and sexual dimorphism.

6) In summary, the temporal and spatial abundances of *S. argus*, *S. nigra* and *U. carinirostris* may not be directly determined by density-independent recruitment. Rather, recruitment to a particular bed may be primarily influenced by density-dependent factors such as reproductive output, and physical factors such as exposure of the site to wave-action.

9. RECOMMENDATIONS FOR FUTURE RESEARCH

STOCHASTIC RECRUITMENT

Information is needed on the composition and variability of the plankton. Variability (and stability) must be clearly defined in terms of time and space before the data are collected. Steffe (pers. comm.) has been studying some of these aspects of planktonic life in Botany Bay.

If recruitment were stochastic (as proposed by Bell and Westoby, 1986c), distribution of recruits among beds should be random. Monitoring of initial recruitment will be difficult. Knowledge of the life-history of the species is necessary to differentiate between settlers and recruits of different ages. Before 'older' recruits can be considered as indicators of settlement patterns, it must be shown that post-settlement mortality is not significant or is not density-dependent. Recolonization experiments would be one way to achieve this, but if early recruits can be identified, sampling could also be used. If stochastic recruitment were responsible for the structure of assemblages of fish in seagrasses, correlations between number of recruits and adults should be large. A poor correlation would be indicative that density-dependent factors have a greater influence on the population than does recruitment.

SELECTION OF HABITAT

Recruits (and juveniles) could be detecting at least two types of cue. First, there are the physical features of the bed. It would be impossible to design experiments with all factors that have been suggested to be important for recruitment and find proper replicates for each of them. There are three options to solve this problem. 1) Use simpler models, e.g. classify beds as having good or bad cover based on leaf-surface area. 2) Identify the most important factors and test each separately. The effects of the other factors could be randomized provided there is enough replication; and 3) Use artificial seagrass units (ASU)(e.g. Bell *et al.*, 1985). Further validation of the suitability of ASU's is needed with regard to its effect on recruitment. It must be shown not only that the same suite of species will recruit to ASU's but also they will do so at similar densities.

To test the effect of depth on recruitment would require either transplanting natural seagrass (which is obviously impractical) or use ASU's.

Second, recruitment may be influenced by the abundance of adult conspecifics. Manipulations of the density of adults would be required to test their effect on recruitment. Invertebrates and some sedentary fish species would make more suitable models.

MIGRATIONS

Direct evidence of the patterns of movement at any scale can be obtained only by mark and recapture techniques. There are several logistic problems that must be overcome before that can be successfully used.

1) Control for the effects of predation which could cause a low rate of recapture. Caging would be feasible only for small-scale experiments and if it is shown that predation itself is not one of the causes of the migrations.

2) Defaunation of beds (or use of ASU's) would also remove prey. Consequently only planktivores could be used in these experiments (Bell, 1986).

3) It will be difficult to investigate migrations between isolated beds because, for example, fishes placed in a bed with poor cover could migrate to any bed in the bay offering better cover. Bell (1986) suggested placing a ring of ASU's with dense grass around a bed with poor cover. This could solve some problems but the effect of predation during migration would still be unknown.

4) A large number of small animals (recruits) would have to be marked.

Thus, it seems that comparative sampling is still the most suitable way to study patterns of migration at larger scales.

FORAGING

If changes in diet are a major cause of change of habitat by pipefishes (e.g. from *Zostera* to *Posidonia*), certain patterns would be expected. For example, there should be a significant difference in the size and/or abundance of prey in the two habitats and that should be reflected in the diet. There should also be selectivity by the predator. This could be tested in experiments in aquaria. Other factors that should be considered are the size and species of the prey, size of the predator its efficiency in capturing, handling, etc. the prey and the physical structure of the plants.

PREDATION

Evidence of predation on pipefishes can only be obtained with further knowledge of the diet of piscivorous fishes. Pipefish⁵_L and smaller species may be preyed upon but not detected in dietary studies.

Caging experiments (see Choat, 1982 and Virnstein, 1987) are required to establish whether predation influences the distribution and abundance of species directly (as a proximate factor, Heck and Orth, 1980) or indirectly (as an ultimate factor, Bell and Westoby, 1986a). If larger abundances in patches of seagrass with denser or taller leaves are the result of selective behaviour (but not predation directly), these patterns should happen also when predators are excluded. The identity of the predators must be known so that proper caging can be built.

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