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THE FEEDING ECOLOGY OF RABBITFISH (SIGANIDAE) AT GREEN ISLAND REEF:

Ontogenetic and interspecific differences in diet, morphology and habitat utilisation

by

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"We need not marvel at extinction;
if we must marvel, let it be at our own presumption in imagining for a moment that we understand the many complex contingencies on which the existence of each species depends."

- Charles Darwin

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Joanna Maria Pitt
July 1997

ABSTRACT

The Siganidae are a taxonomically uniform yet behaviourally diverse family of herbivorous fishes. The intention of this study was to examine the interaction between diet, morphology and behaviour in this family by making ontogenetic and interspecific comparisons of species selected for their contrasting behavioural traits. The species chosen for the study were *Siganus doliatus*, *S. fuscescens*, *S. punctatus* and *S. lineatus*. *Siganus doliatus* and *S. punctatus* are considered pairing species, while *S. fuscescens* and *S. lineatus* are considered shoaling species.

Siganids showed significant dietary differentiation through ontogeny, and interspecific dietary differences in the adult phase. The juveniles fed selectively on turfing algae and animal material within the seagrass beds, but the diets of the adults were more representative of the relative abundances of items in their feeding areas. The diets of the juveniles and the adults of the pairing species can largely be explained in the context of the predictions that should apply to Type I herbivores based on algal chemistry and morphology and by the varying energetic requirements of different ontogenetic stages. The presence of chemically defended algae in the diets of the adults suggests that foods may be consumed on the basis of their nutritional value regardless of the effects of such defences, or that the adults of these species are minimally affected by the secondary chemistry of these algae. However, the dominance of seagrasses in the diets of adults of the shoaling species bears further investigation.

There are subtle morphological differences between the four species which have the potential to influence feeding ecology. The development of the alimentary tract in these species seems to be under the control of allometric growth functions, which persist after maturity. Relative gut length is consistent between species, and appears adapted to a general, rather than specific, herbivorous diet. There is the possibility that a functional threshold associated with size exists for bulk processing and / or absorption, and this may influence the ability of the larger species to maintain a positive energy balance from more refractory dietary items such as seagrass. The caeca are the only part of the gut where interspecific differences in relative absorptive area may be present, but this requires confirmation. Differences in stomach structure between the pairing and shoaling species are the most interesting aspect of this research, and may play a role in the digstion of seagrassses by the shoaling species. Aspects of the gape and head profile may affect the physical accessibility of food items to some species.

Juvenile siganids used microhabitats within the seagrass beds in a nonrandom fashion, and were often closely associated with large *Sargassum* plants. Strong behavioural patterns appear to have developed in association with these distributions, and distributions appear to be related to predator avoidance behaviours. The role of predation here seems to be as the indirect cause of preferences for structurally complex microhabitats. Differences in the distributions of new and older recruits suggest that settlement to seagrass beds operates in a non-selective manner, and that the observed habitat distributions occur because of microhabitat selection in the first month or so post-settlement. In siganids, this strategy appears to be mediated by the large size of recruitment shoals, which provides some protection from predators during this intermediate period.

Adult siganids at Green Island Reef exhibit spatial partitioning of resources. The greatest differences in resource use occur between the pairing and shoaling species, but differences are also evident between the two shoaling species. Feeding is partitioned on two scales: by habitat (coral versus seagrass) between pairing and shoaling species, and by site within the shoaling species. However, no partitioning is apparent between the two pairing species. Space utilisation in the coral areas appears to be determined at a finer scale, and is influenced by species-specific activity patterns and the characteristics of the individual sites. The occurrence of distinct forays and apparently extensive resting periods in *S. lineatus* is an unusual feature in an herbivorous fish, and bears further investigation. Although it is possible to make generalisations regarding the distributions of the four study species, the structural features of the different study sites mean that each site is utilised in a slightly different way in order to fulfill the requirements of the each species. There was no evidence of competitive interactions between species. Rather, it appears that predation-motivated behaviour, in the context of the different social habits of the four study species, has led to activity patterns which maximise access to food resources while minimising the risk of predation.

When all aspects of resource use by these species are taken into consideration, an interesting pattern emerges. In the juvenile phase, which is associated with the seagrass beds, resource utilisation patterns are very similar between species. As a result of the total habitat separation, there is no overlap in resource use between juveniles and the adults of the pairing species. Even between juveniles and the adults of the shoaling species, total resource overlap is very low. Among the adults, the only large overlap is between the two pairing species; these species also have moderate overlaps with *S. fuscescens*. Adult *S. lineatus* have low overlap with all other adults.

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TABLE OF CONTENTS

LIST OF TABLES, FIGURES AND PLATES

Chapter 4

Chapter 5

Chapter 6

Chapter 7

CHAPTER 1

INTRODUCTION

1.1 HERBIVORY IN FISHES

Herbivorous fishes are a conspicuous and integral part of coral reef ecosystems. They form a significant component of the total fish biomass and have a key role in the transfer of energy from primary production through to higher levels of the food chain (Russ, 1984a and b; Choat, 1991). The biology and ecology of these fishes are topics which have generated considerable current interest. Part of their mystique is their incontestable success in the face of the traditionally held view that the digestive systems of higher vertebrates are poorly equipped to facilitate the assimilation of plant material (e.g. Mattson, 1980).

Marine plants are chemically and structurally different from their terrestrial counterparts however (Percival, 1979; Littler *et al.*, 1983; Kloareg and Quatrano, 1988; see Chapter 3), and this may go some way towards explaining the success of herbivorous fishes. In addition, herbivorous fishes have evolved a diverse array of strategies with which to attack these plants. In Horn's (1989) review of the biology of herbivorous fishes, he described the alimentary canals associated with four types of digestive mechanisms. An updated summary (Horn, 1992) provides further examples of how various species fit into this scheme. These descriptions were further supported with quantitative 'chemical reactor' models which link gut structures to certain types of digestive processes (Horn and Messer, 1992). Adaptations for herbivory in fishes are primarily morphological, and it is widely recognised that (with a few exceptions) these adaptations are based around an elongated digestive tract (Horn, 1989).

The Type I digestive mechanism is dependent on acid based disturbance of the cell wall to gain access to cell contents. The alimentary canal is very similar to that of most carnivorous fishes, with little specialisation for herbivory other than the lengthening of the intestine, and it is not entirely clear how such a system might operate. Type II digestion is dependent on physical means to break open the cell wall. A thick-walled, gizzard-like stomach triturates plant material, which is often ingested with large amounts of sediment that act as additional abrasives; this is followed by a long intestine. Type III digestion is also dependent on mechanical breakdown of the cell wall. A pharyngeal mill, where the pharyngeal teeth have fused to form solid plates, is used to crush food before it reaches the alimentary tract. This digestive mechanism has no stomach and only a moderately long intestine. Type IV digestion centres around microbial fermentation in the hindgut, often in a modified chamber which is separated by valves from the rest of the long intestine. This aspect of herbivory in fishes has been reviewed by Clements and Choat (1995). It seems possible that some species, particularly many of the acanthurids, may operate combinations of the four methods (Choat, 1991).

There are other factors in this ecological equation however. On the side of the plants are numerous morphological and chemical defences which may help them escape predation (Littler *et al.*, 1983; Thayer *et al.*, 1984; Hay and Fenical, 1988; Steneck, 1988; Klumpp *et al.*, 1989; Hay, 1991a). On the side of fishes are further morphological adaptations to feeding on plants and hard substrata (Jones, 1968a; Bellwood and Choat, 1990; Choat, 1991), and a variety of behavioural strategies (Horn, 1989, 1992; Choat, 1991). Further factors affecting fishes include energy demands (Hughes, 1980; Targett and Targett, 1990) and the predation risks involved in acquiring food (Hughes, 1980; Werner *et al.*, 1983; Pulliam, 1989). Complicating the picture is the role of ontogeny in the development of many of the previously mentioned adaptations (Werner, 1984; Werner and Gilliam, 1984; Wainwright, 1996).

1.2 INTRODUCTION TO THE SIGANIDAE

Herbivorous fishes of the family Siganidae (Acanthuroidei: Pisces) occur in shallow waters throughout the tropical and subtropical Indo-West Pacific region (Woodland, 1983). Based on larval and general biology, they are considered most similar to the Luvaridae, Zanclidae and Acanthuridae (Leis and Richards, 1984; Woodland, 1990; Winterbottom and McLennan 1993). The taxonomy of the family was revised by Woodland in 1990, and it consists of a single genus, *Siganus* Forsskål, with two subgenera, *Siganus* and*Lo* Seale. The subgenus *Siganus* contains twenty-two species while the subgenus *Lo* contains five, the distinction being based on the strongly tubulate snouts of the latter. Despite this subdivision, the family is remarkably uniform with respect to general taxonomic characteristics (Woodland, 1990).

The Siganidae can be divided into species that form pairs as adults and species which shoal throughout life (Woodland, 1979, 1990). All species within the subgenus *Lo* are pairing species, while within the subgenus *Siganus* there are nine pairing species and thirteen shoaling species. It is rare for a taxonomically and morphologically uniform family to contain species which exhibit both pairing and shoaling behaviours, yet there have been no comparative studies of the two lifestyles.

Siganids are generally mature at a size of 160 - 200 mm standard length (SL) and one year of age, and the maximum size attained ranges between 200 and 450 mm SL depending on the species (Woodland 1990). As with many coral reef fishes, it is becoming apparent that siganids attain much greater ages than the three or four years predicted by population size structure alone (Woodland, 1990). An initial period of rapid growth followed by an extended period of asymptotic growth has masked the true age of such species in the past (Choat and Axe, 1996), but the situation is gradually becoming resolved since otolith ageing studies have been applied to tropical species. It appears that the various species of siganids in the Great Barrier Reef region may reach between 14 and 20 years of age (J.H. Choat, unpublished data; my own unpublished data).

Despite their largely tropical and sub-tropical distribution, siganids appear to have a definite spawning season, distributed around a peak in late spring / early summer (see review by Lam, 1974; Gundermann *et al.*, 1983; Al-Ghais, 1993). In some species an autumn peak may also be observed (Ntiba and Jaccarini, 1990). There are, however, reports of year-round spawning in some locations (Hara *et al.*, 1986). Spawning takes place with lunar periodicity, usually during the week after the new moon (Lam, 1974; Hasse *et al.*, 1977; Thresher, 1984; Juario *et al.*, 1985; Ntiba and Jaccarini, 1990). Larval durations of between 22 and 29 days have been reported (May *et al.*, 1974; Bryan and Madraisau, 1977; Hasse *et al.*, 1977; Gundermann *et al.*, 1983). Juveniles recruit to seagrass beds and other coastal areas at sizes between 20 mm and 30 mm standard length (SL) (May *et al.*, 1974; Bryan and Madraisau, 1977; Hasse *et al.*, 1977; Gunderman *et al.*, 1983).

The literature to date has largely focussed on the shoaling siganids because of their value as food fish. Wild fisheries for both adult and juvenile fish exist throughout most of their distribution (Ben-tuvia and Kissil, 1973; Lam, 1974; Kami and Ikehara, 1976; Woodland 1990; Al-Ghais, 1993), with the Australian coast being a notable exception (Woodland, 1979). In addition, the mariculture potential of Siganids has been widely investigated. More than thirty studies conducted in seventeen countries have examined eleven out of the thirteen shoaling species (see Lam, 1974; Von Westernhagen and Rosenthal, 1976; Woodland, 1990; Al-Ghais, 1993). Two pairing species, *S. virgatus* (Valenciennes) and *S. punctatus* (Schneider), were considered briefly in the study by von Westernhagen and Rosenthal (1976).

Background studies have been conducted to acquire relevant information on their diet and life cycles in the wild (Popper and Gundermann, 1975; Hasse *et al.*, 1977; Gundermann *et al.*, 1983). More specific research has centred around reproductive biology, early life history and growth rates in captivity. Natural gonad maturation cycles have been assessed (Hasse *et al.*, 1977; Hara *et al.*, 1986; Ntiba and Jaccarini, 1990; Al-Ghais, 1993) and spawning has also been artificially induced (Lam and Soh, 1975; Juario *et al.*, 1985). Larvae of several species have been successfully reared through metamorphosis (Ben-tuvia and Kissil, 1973; May *et al.*, 1974; Bryan and Madraisau, 1977; Hara *et al.*, 1986). Growth has been monitored under both wild and culture conditions (von Westernhagen and Rosenthal, 1976; Ntiba and Jaccarini, 1988; Al-Ghais, 1993). As a result of this economic interest, a reasonable amount of information is available about the biology of most shoaling species. Very little is known about the pairing species, either biologically or ecologically (Woodland, 1990), and there have been no biological studies in Australian waters.

Siganids are generally accepted as being herbivorous (Suyehiro, 1942) and are classified as browsers by most authors (Hiatt and Strasburg, 1960; Thresher, 1984; Horn, 1989, 1992), but they have been known to take bait and forage around dumps for scraps (Hiatt and Strasburg, 1960). Under Horn's (1989) classification, Siganids are Type I herbivores, with a thin-walled, acidic stomach and a long intestine, although the pH of their stomachs has never been measured (Horn, 1992). The general morphology of their digestive tract supports this conclusion and the Siganidae do not appear to have any morphological adaptations to suggest that they might employ Type II or Type III digestive mechanisms (Suyehiro, 1942; Bryan, 1975; Woodland, 1990). In addition, Clements (1991) and Clements and Choat (1995) found no evidence of endosymbiotic microbial fermentation (Type IV digestion), and the rapid gut transit times found by Bryan (1975) would almost certainly preclude this.

1.2.1 Siganids in the Great Barrier Reef region and at Green Island Reef

Like many groups of herbivorous fishes, siganids are widely distributed in the Great Barrier Reef region, however they are less abundant than other herbivorous families like the scarids, acanthurids and pomacentrids (Bouchon-Navaro and Harmelin-Vivien, 1981; Russ, 1984a and b). Although they have been included in community structure surveys (Russ, 1984a and b; Coles *et al.*, 1993; Hart *et al.*, 1996), their ecology has not really been studied before. This is particularly true of the pairing species. The herbivorous habits of this family generally restrict them to depths of less than 15 m (Woodland, 1990), and they are a potential, though currently underutilised, resource (Woodland, 1979).

Ten species of Siganidae are known from the northern area of the Great Barrier Reef (Woodland, 1990), and at Green Island Reef a total of nine species have been observed. Of these, four species were deemed to be common enough to be worth studying: *Siganus doliatus* Cuvier, *S. fuscescens* (Houttuyn), *S. lineatus* (Valenciennes) and *S. punctatus* (Schneider) (see Plate 1.1). Other species present were *S. argenteus* (Quoy and Gaimard), *S. corallinus* (Valenciennes), *S. puellus* (Schlegel), *S. spinus* (Linnaeus) and *S. (Lo) vulpinus* (Schlegel and Müller).

The identification of all of the above species was based on the descriptions given in Woodland's revision (1990), as this is the most recent publication in the peer-reviewed, scientific literature. Fortunately, siganids are generally readily identifiable, even as juveniles. The only species about which there may be some concern is *S. fuscescens*. A guide book in the popular literature (Kuiter, 1996) suggests that there may be as many as five similar species covering the range that Woodland (1990) has ascribed to *S. fuscescens* and *S. canaliculatus*. These conclusions are based largely on photographs of general appearance, and have not as yet been backed up by morphometric or other data that would allow the unequivocal allocation of my specimens to any one of the species. As such, there is the possibility of a change of nomenclature for this species, in this area, in the near future. The specimens referred to as *S. fuscescens* were collected and analysed as one species, and I am confident that this assumption is correct, regardless of the name to be applied to that species.

At Green Island Reef, the juveniles of *S. doliatus*, *S. fuscescens*, *S. lineatus* and *S. punctatus* are present, during the summer months, in shoals in the seagrass beds on the reef flat. In contrast, the adult fish are found primarily in the coral areas, where *S. doliatus* and *S. punctatus* form pairs, *S. fuscescens* form small shoals and *S. lineatus* form large shoals. Although the pairing species feed in these coral areas, the shoaling species have been observed feeding in the seagrass beds on the reef flat. Based on these observations it was hypothesised that there might be dietary differentiation both within and between species, that it might be influenced by ontogeny and behaviour, and that there might be corresponding differences in the morphology of feeding structures and the alimentary tract. In addition, if these differences are in fact present, then there is a case for presenting this situation as resource partitioning.

1.3 AIMS AND OBJECTIVES OF RESEARCH

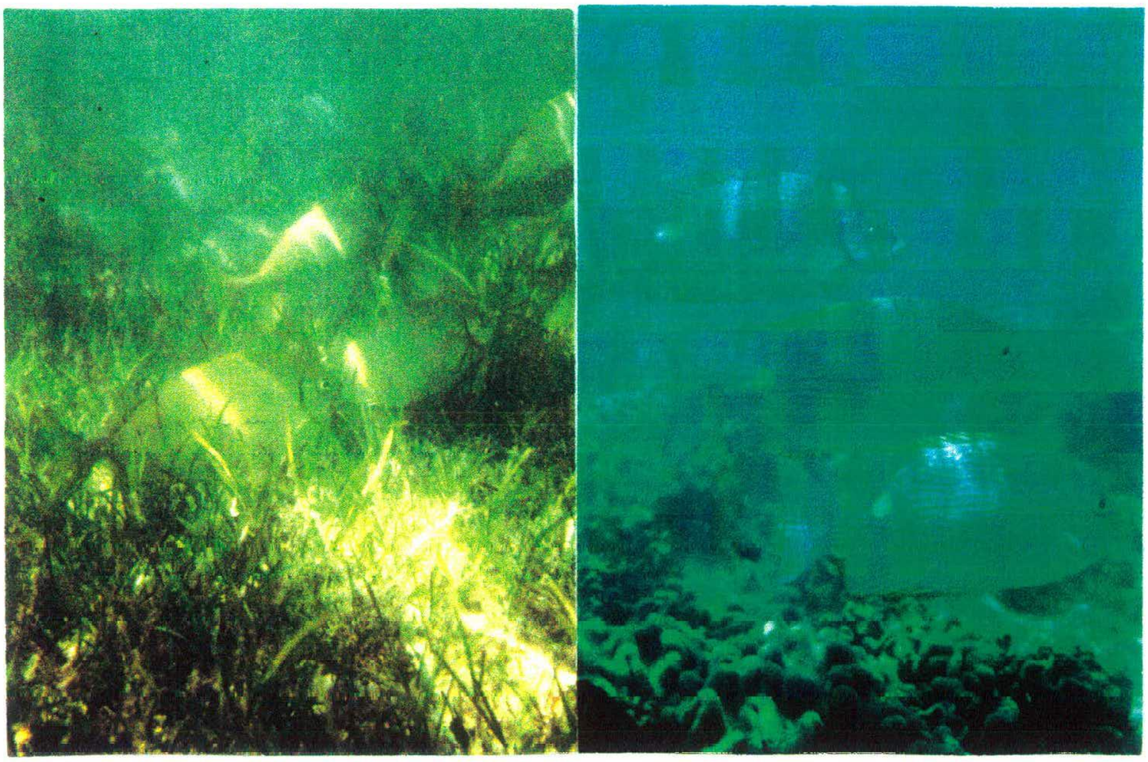
The Siganidae are a taxonomically uniform yet behaviourally diverse family of herbivorous fishes. The intention of this study was to examine various aspects of the biology and ecology of this family by making ontogenetic and interspecific comparisons of species selected for their contrasting behavioural traits. It was hoped that this would provide some insight into their place within the diverse array of marine herbivorous fishes. The focus of this study was the herbivorous habits of the Siganidae, and the interaction between diet, morphology and behaviour. The broad aim was to examine the feeding biology and ecology of the four common siganid species at Green Island Reef, and to make comparisons within species, through ontogeny, and between pairing and shoaling species. This can be divided into five more specific areas of study:

1. The quantification and comparison of diet and dietary development, and an evaluation of how siganids fit in with current theory regarding feeding and digestion in marine herbivorous fishes (Chapter 3).
2. A morphological description of the development of the head and alimentary tract, and an examination of the associations between these structures, diet and digestion (Chapter 4).
3. The description of the habitat utilisation patterns of juvenile siganids and an assessment of the role of structural protection at this stage in the life cycle (Chapter 5).
4. The description of the habitat utilisation patterns of adult siganids and an assessment of how behavioural adaptations may maximise access to both food and structural protection (Chapter 6).
5. An examination of the use of resources by the different species, and of the physiological and behavioural adaptations that mediate it, with the objective of testing for the occurrence of resource partitioning (Chapter 7).

Plate 1.1. Photographs of the four study species.

S. doliatus

S. punctatus



S. fuscescens

S. lineatus

CHAPTER 2

GREEN ISLAND:

The study location and its role in the research program

2.1 INTRODUCTION: The Green Island environment

Green Island is a vegetated coral cay located at 16° 46'S and 145° 58'E, in the midshelf region of the Great Barrier Reef. It is 27 km northeast of Cairns, a major tourism centre for the area. The reef flat surrounding the island is approximately 3.5 km long, the majority of it extending 2.2 km from the southeast end of the island, and there is a lagoonal area to the northeast. There is a continuous coral ledge around the front (southeast or "weather" side) of the reef and the edge of the navigation channel, with large patch reefs on the sheltered side and smaller patch reefs in the lagoon (Plate 2.1). There are seagrass beds in the lagoonal area and on the reef flat (Plates 2.1 and 2.2).

2.1.1 The significance of the seagrass beds around Green Island

Green Island Reef was chosen for this study because it has extensive, well-developed seagrass beds in close proximity to coral areas. The availability of these two habitat types was considered an important feature as siganids are known to utilise coral reefs, seagrass beds, rocky shores and mangrove swamps, often moving between these different habitats (Bryan, 1975; Gundermann *et al.*, 1983; Woodland, 1990; Pinto and Punchihewa, 1996). Woodland (1990) specifically describes *S. lineatus* migrating between the lagoon and the reef flat at Heron Island, a coral cay similar in structure to Green Island but located at the southern end of the Great Barrier Reef.

Close associations between seagrass beds and coral reefs are relatively common in the Caribbean and sub-tropical Atlantic (Ogden and Zieman, 1977; Parrish, 1989) and there is considerable documentation of fishes moving between these habitats, particularly during foraging (reviewed in Bell and Pollard, 1989; Sogard *et al.*, 1989).

These associations have also been observed around islands in the equatorial Indo-Pacific (Ogden and Ogden, 1982; Gates, 1986). There are few major tracts of shallow seagrass in reefal waters of the Great Barrier Reef, as most seagrass beds in the region are coastal, while much of the reef is further offshore in deeper water (Coles *et al.*, 1987). Recently described deepwater seagrasses in the inter-reefal waters of the Great Barrier Reef do not appear to support animal populations to the same extent as their shallow counterparts (Lee Long and Coles, 1997). As such, areas where seagrass beds and coral reefs are in close enough proximity to provide interacting habitats for fishes are limited to the platforms of a few mid-shelf islands, notably Lizard Island and Green Island (Coles *et al.*, 1989; Lee Long *et al.*, 1993).

The significance of seagrass beds as nursery areas for juvenile reef fish is generally accepted, although it is acknowledged that it is not a universal phenomenon (Kikuchi, 1974; reviews by Pollard, 1984, Bell and Pollard, 1989 and Parrish, 1989). This nursery role has been widely studied in both tropical and temperate Atlantic waters and the Mediterranean Sea, but research in the Pacific has mainly centred on temperate-region seagrass habitats (see above reviews). Studies in the tropics are less numerous (Jones and Chase, 1975; Harmelin-Vivien, 1983; Blaber *et al.*, 1992) and those in the Great Barrier Reef region have focussed on prawns and fish species of interest to commercial and recreational fisheries (Coles *et al.*, 1993). The importance of the reef-platform seagrass beds as nursery areas is recognised (Lee Long *et al.*, 1993).

Accounts from the literature consistently report juvenile siganids recruiting to seagrass beds (see review in Chapter 5). For siganids and other families such as the Lutjanidae and Lethrinidae which recruit solely or primarily to seagrass beds (Mori, 1984; Wilson, in prep.), the availability of this habitat is very important. As suitable recruitment locations in reefal waters are fairly widely scattered (Coles *et al.*, 1989; Lee Long *et al.*, 1993), each one is therefore a potential source area for quite a large tract of reef. It is therefore imperative to learn as much as possible about the ecosystem dynamics of each of these areas. Although siganids may not necessarily migrate between reefs (some species can recruit to coral – Woodland, 1990), they are an important part of the community dynamics of juvenile fish in the seagrass beds, competing for food, space and refuge from predation.

2.1.2 The status of the coral areas around Green Island

In order to consider a location to be a genuine example of interacting habitats, the coral areas, as well as the other habitats, must be in a healthy state. In the summer of 1992-

1993, Green Island was classified as recovering from the Crown-of-Thorns Starfish (*Acanthaster planci*) outbreak which occurred in the early 1980's (Oliver *et al.*, 1995). A fine scale survey of benthic cover on the reef slope found that hard corals made up 10% of cover, soft corals 4 %, turf algae 67 %, and abiotic material 17 %, while other components (including dead coral) had a negligible presence (Christie *et al.*, 1995). Live hard coral cover of 10 % compares with a mean of 20 % on inner shelf reefs and a mean of 30 % in the Cairns region in the same study. Preliminary observations in August 1993 indicated a healthy reef, with no obvious dead coral and without the conspicuous algal blooms that have traditionally been considered a symptom of degradation (Hughes *et al.*, 1987; McCook and Price, 1996).

2.1.3 The balance between tourism and research activities

Its proximity to Cairns makes Green Island an important tourist destination, with large numbers of people visiting the island on a daily basis. The annual visitor turnover has been estimated at approximately 120,000 people (Anon. 1990). In such a situation there is the potential for conflict between researchers and recreational users of the reef, and the research permit granted by the Great Barrier Reef Marine Park Authority (GBRMPA) placed limitations on research activities. Specimen collection within the recreation precinct (the western end of the island and reef platform) was restricted to areas that were not utilised by tourists. In areas where collection activities would be visible, a further temporal restriction was imposed so that activities could not be carried out during day trip hours (09:15 to 16:30).

2.1.4 Aims and objectives

The aim of this work was to provide detailed and semi-quantitative descriptions of the community composition and physical structure at the individual study sites around Green Island reef, which could be utilised in conjunction with data on fish diet and behaviour.

2.2 MATERIALS AND METHODS

2.2.1 Selection criteria for sites

Preliminary observations were conducted to find appropriate sites for observation and sampling. The seagrass beds on the reef flat were examined for the presence of juvenile siganids in March 1993. Coral areas were examined for the presence of adult siganids in August, September and November of 1993. A number of criteria were taken into consideration when selecting sites for further study.

Sites had to be located and defined such that:

1. they encompassed the range of habitat types at Green Island reef which were occupied by juveniles and adults of the four study species.
2. they were large enough to accommodate the roving habits of the study species and thereby ensure their consistent presence during visual censuses.
3. they were large enough that the abundance of fish within a site would not be perceivably affected by the small amount of destructive sampling required.
4. they were not so extensive that covering the area during a visual census would be impractical.
5. they could be regularly and safely used throughout the year. (This eliminated the southeast section of the front reef and areas of heavy boat traffic.)
6. they could be worked under the spatial preferences and the temporal limitations inherent in the research permit granted by the GBRMPA.
7. their boundaries could make use of natural features or existing landmarks, due to the ban on semi-permanent substratum markers in the research permit.

Three shallow seagrass sites were chosen for the assessment and sampling of the juvenile population. One was on the north side of the island, while the other two were located on the south side (Plate 2.2). These areas were selected based on the consistent presence of significant numbers of juvenile siganids. Four coral sites were chosen for the assessment and sampling of the adult population (Plate 2.1). These sites represent the various types of coral habitats that are available on the island. The ledge is typical of the continuous coral cover on the weather side of the island. The channel edge site is similar to the ledge, but is in shallower water and is affected by the boating and associated dredging activities that take place in the channel itself. One group of patch reefs near the shore in the lagoon, and another group, further out towards the edge of the lagoon, were also selected. Although other sites were initially examined, these were the only workable areas where significant numbers of siganids were consistently found.

The total area of each site was calculated from aerial photographs, using ground truth measurements of the longest dimension of the site, or of each of the patch reefs comprising the site, as well as measurements of other features on the island such as the jetty and the helipad.

2.2.2 Habitat composition and structural complexity

2.2.2.1 Seagrass sites

In order to quantify the community composition of the seagrass sites, substrate cover was assessed. A 50 m transect tape was laid out haphazardly and five 30 cm by 30 cm quadrats were placed at 10 m intervals along the transect line. The quadrat was subdivided with string at 5 cm intervals to give 25 intercepts, and the percentage cover of vegetation and other substrata in each quadrat was recorded based on the 25 points immediately below the intercepts (Goldsmith, 1991; Levin, 1991). Seagrasses were identified to genus or species and macroalgae were identified to genus, but turfing algae were not identified further. For the purposes of analysis, cover was grouped into the following categories: Seagrass, *Sargassum spp.*, other macroalgae, turf algae, sponges, detritus, and sand.

From each quadrat, ten seagrass blades were chosen haphazardly, irrespective of species, and measured to the nearest millimetre using a ruler. The mean and maximum heights were used as an indication of general vertical complexity. Four transects per site were quantified in this manner. The quadrat was considered the unit of replication and the purpose of the transects was to distribute the twenty quadrats throughout the site.

As the transect tape was being rewound, the occurrence of structurally significant *Sargassum spp.* plants (Phaeophyta) within 1 m either side of the tape was recorded. Although holdfasts and stipes were assessed in the percentage cover survey, only plants with axial growth of greater than 10 cm were considered in this assessment. Plants were classified as single or as a large cluster (two or more individual *Sargassum spp.* plants growing close enough together that they effectively formed a contiguous shelter) or "*Sargassum* reef" (one or more *Sargassum spp.* plants growing attached to a rocky reef-like structure). Clusters and reefs were analysed as one category, on the basis that they both represented greater structural complexity than a single plant. The mean density of the two categories of *Sargassum spp.* plants per 100 m^2 was used as a measure of the three-dimensional structure available within the seagrass sites.

These surveys were repeated monthly during summer, which is the peak recruitment period for juvenile fishes, and in alternate months during winter. This gave a total of ten surveys between March 1994 and February 1995. The full year was completed in order to document the annual cycle of macrophytic growth and senescence and the resultant changes in community structure.

2.2.2.2 Coral sites

As an indication of the spatial complexity of the coral sites, the greatest dimensions of patch reefs were measured with a tape measure, while other sites were classified as continuous. Vertical relief was used as a measure of structural complexity, as it has been found to be highly correlated with rugosity, yet is easier and faster to measure, particularly in areas with greater relief (Luckhurst and Luckhurst, 1978). The heights of ten haphazardly chosen projections above the central reef matrix were measured to the nearest centimetre using a tape measure. This procedure was repeated for the heights of ten projections at the edge of the reef, with measurements taken relative to the base of the reef. The height of the central matrix above the seabed was found by subtracting its depth from the depth of the substrate adjacent to the reef. These measurements were made with both the tape measure and a decimetre depth gauge. The mean and the range of the two groups of projection heights were used as a measure of the vertical complexity at that site.

The substratum was assessed visually and cover was divided into the following structural categories: coral boulders; massive hard coral; plate / branching hard coral; soft coral; macroalgae; rubble or non-living reef matrix with algal turf, and sand. The dominant categories were ranked and the presence / absence of other categories was noted. This was done separately for the centre and the edge of each site.

The methods used provided a broad-scale description of community composition and physical structure, relevant to the utilisation of the habitat by highly mobile adult siganids. In the absence of a catastrophic event, this description was unlikely to change significantly during the course of this study, so a single assessment of each site was made.

2.2.2.3 The Habitat Complexity Scale

In order to provide a single, simple measure of the physical aspects of the habitats for comparative purposes, a semi-objective Habitat Complexity Scale was developed. The scale, ranging from 1 to 10, was based on an initial observation of the types and sizes of vegetation, corals and non-living substrata present in the different habitats, and the categories were further refined using the results from the habitat surveys. Height measurements were utilised to make structural distinctions between and within broad habitat types, with greater overall heights as well as a greater height range considered to be more complex. Within the types of coral habitat surveyed, where reefs were of varying sizes, increased sized was considered to provide a site with greater complexity.

2.3 SITE DESCRIPTIONS

2.3.1 Seagrass sites

2.3.1.1 North

Plate 2.2: Total area = 8110 m^2; Habitat Complexity rating = 1 to 6.

The northern site was on the leeward side of the island, so it was generally more protected than the other two reef flat sites. The site was 186 m long and 42 m to 63 m wide, the long edges being defined by the shoreward start and seaward cessation of seagrass growth. The area had a height 10 cm above chart datum and was exposed during extreme low spring tides.

This site had the tallest seagrass canopy, with an overall mean blade height which was generally greater than 80 mm (Figure 2.1). The mean height of the tallest blade measured in each quadrat was greater than 100 mm (Figure 2.1). There appears to be a peak in blade height in March, with a gradual build up during the December to February period.

The density of seagrass cover was also greatest here (Figure 2.2). Percentage cover ranged from 60 % to 94 %, with values generally greater than 70 %. The dominant seagrass species at this site was the wide-leaf morph of *Halodule uninervis,* which was responsible for 50 % to 84 % of total cover, followed by *Cymodocea spp.* and *Thalassia hemprichii.* After seagrass, bare sand was the next most important category (up to 19 %), followed by macroalgae (up to 15 %). The most important components of the macroalgal category at this site were *Dictyota spp.* (Phaeophyta) and *Halimeda spp.* (Chlorophyta). *Sargassum spp.* plants were shown separately from other macroalgae because of their greater height, and comprised up to 8 % of cover at times during this part of the survey. Detritus was a visible component of substratum cover in the early- to mid-summer period, but was largely absent during the rest of the survey period.

Density of structurally significant *Sargassum spp.* plants was low, (Figure 2.3), with mean occurrences of less than 5 single plants and less than 5 clusters / reefs per 100 m^2. There was free standing *Sargassum spp.*, as single plants and clusters, near the shore at the western end of the site. Raised rocky reefs were present further out from the shore, and these were covered by rhodophytic and phaeophytic macroalgae. At the eastern end of the site there were similar reefs with *Sargassum spp.* attached to them. This aggregation of *Sargassum spp.* plants at either end of the site was responsible for the large standard errors in Figure 2.3, as transects taken in aggregation areas would record high densities of plants, while those in the centre of the site would record none. This figure clearly shows the greater abundance of structurally significant plants in the summer months (November to May), and their virtual absence in winter. What is also apparent is that the few plants which retained any axial material in the middle of winter were those which were part of large clusters or "*Sargassum* reefs" - there were no single plants present in August.

2.3.1.2 South east reef flat

Plate 2.2: Total area = 8,000 m^2; Habitat complexity ratings = 1 to 5.

The southeast reef flat site was 160 m long and 50 m wide, and ran parallel to the beach rock 60 m out, at the eastern end of the island. It was the most weather-exposed site of the three, being to the southeast of the island, the direction from which the prevailing winds come. However, it was afforded some protection by the rocky rim of the reef flat. This side of the reef flat was approximately 60 cm above chart datum, and thus experienced longer and more frequent periods of exposure during low tides than the north site.

The seagrass on this side of the island was shorter and sparser than at the north site, and had a more varied species composition. Overall mean blade height at the southeastern site was always less than 80 mm, and the mean maximum heights were nearly always less than 100 mm (Figure 2.1). Blade heights were greatest in March of 1994, but remained relatively consistent during the rest of the survey period. Seagrass cover ranged from 46 % to 73 % during the study period(Figure 2.2). *T. hemprichii* was the dominant species, followed by *Cymodocea spp.* and the thin-leaf morph of *H. uninervis*. *Halophila ovalis* was present in negligible amounts. Cover was greatest in March and relatively consistent through the rest of the year. Bare sand was common here, with up to 26 % of the substrate having no cover. Macroalgae were also conspicuous at this site, comprising up to 13 % of cover. The large rhodophyte genera *Laurencia spp.* and *Acanthophora spp.* were the most important component, followed by *Halimeda spp.*. *Sargassum spp.* plants were not conspicuously present in this part of the survey. Detritus comprised up to 15 % of cover in early- to mid-summer, reaching a peak in January of 1995.

This site had the lowest overall mean density of *Sargassum spp.* plants (Figure 2.3), but density levels were the most consistent through the summer season. Only one cluster or reef per 100 m^2 remained during the winter months (Figure 2.3). Plants at this site were more evenly distributed compared to the northern site. They were frequently attached to small sunken reefs (dead coral heads from a period when the lagoon was deeper).

2.3.1.3 South west reef flat

Plate 2.2: Total area = 8,000 m^2; Habitat Complexity ratings = 1 to 5.

The southwest reef flat site was 200 m long and 40 m wide, and ran along the edge of the seagrass bed near the beach rock at the western end of the island. Apart from being closer to the shore, it was very similar to the eastern reef flat site. It was marginally less exposed to the wind but more cut off by the rocky rim. As a result, it did not receive the sideways water flow that the north site did, particularly at low tide.

In aspects of seagrass community structure and composition, this site was very similar to the southeastern site. Overall mean blade height was always less than 80 mm, and the mean maximum heights were nearly always less than 100 mm (Figure 2.1). Blade heights were greatest in March of 1994, but remained relatively consistent during the rest of the survey period. Seagrass cover ranged from 55 % to 77 % (Figure 2.2). *Cymodocea spp.* were dominant here, followed by *T. hemprichii* and the thin-leaf morph of *H. uninervis*. *Halophila ovalis* was present in negligible amounts. Again, cover was greatest in March and relatively consistent through the rest of the year. Bare sand was common, with up to 39 % of the substrate having no cover, while macroalgae comprised less than 4 % of cover.

This site exhibited the greatest variation in density of *Sargassum spp.* plants (Figure 2.3). Although density was generally low, mean total abundance (single plants plus clusters / reefs) exceeded 10 per 100 m^2 in April of 1994, influenced by the high numbers of single plants. This site was the only one which had more single plants than reefs. *Sargassum spp.* plants were not as evenly distributed here as at the southeastern site, but not as aggregated as at the northern site. Both single plants and *Sargassum* reefs were particularly abundant in a 10 m wide band along the shore edge of the site. As at the southeastern site, *Sargassum spp.* plants were commonly attached to small sunken reefs, and there were numerous rocks which were also used as attachment sites. As with the other sites, only a few *Sargassum* reefs were present in August.

2.3.2 Coral sites

A visual representation of the physical structure of the coral sites is provided by the vertical complexity data, which have been arranged to resemble a profile of each reef (Figure 2.4). The edge is to the left, and the right of the graph represents the central reef matrix with projections above it. Exposed areas of reef matrix usually formed the dominant substrate category and this is recorded in the dominance tables, but because the matrix usually has the same structural features as the live material creating it, only exceptional areas will be described further.

2.3.2.1 Front reef ledge

Plate 2.1: Total area = 15,000 m^2; Habitat Complexity rating = 10.

This site was 200 m long and 75 m wide, and was situated on the reef slope that runs continuously around the southeast (weather) side of the reef platform. It was subtidal, with depths of 1 m near the rim of the reef flat to 8 m near the edge of the reef platform. At the time of this study, it had good cover of live corals.

The edge of the reef platform was notable for the presence of large coral / matrix boulders, located on a sandy bottom (Figure 2.4 a top), a feature which did not occur at any of the other sites. Massive hard coral heads were common, and there were colonies of branching hard corals in the sandy areas. The height of these boulders and other structural features of the edge area ranged from 1.70 m to 2.90 m, giving the edge of this site the highest vertical structure of all the study sites. The central reef matrix sloped down from the rocky rim to the edge. Near the rim, there was a band of coral rubble with conspicuous macroalgal growth, primarily of calcareous *Halimeda spp.* (Chlorophyta). Moving down the slope, the next zone contained some small soft coral colonies. The most important structural components of the slope were plate, massive and branching hard corals, with turf-covered reef matrix between the colonies. In this area, vertical projections above the reef matrix ranged from 0.90 m to 1.90 m in height. This site had the greatest central vertical complexity .

2.3.2.2 Channel edge

Plate 2.1: Total area = 10,675 m^2; Habitat Complexity rating = 9.

This site ran along the edge of the dredged shipping channel, and was contiguous with the reef slope. There was an unbroken connection of similar habitat between it and the

Ledge site, and the southwestern end of the Channel was very similar in nature to the Ledge. Depth at this site varied from 2 m to 4 m.

The edge of this site was comprised mostly of massive hard corals (Figure 2.4 a middle), although there was a large soft coral component towards the northeastern end of the site, which was shallower and had higher levels of suspended sediment (due to boating activity). The height of these massive hard corals and other structural features ranged from 0.70 m to 2.00 m. When compared to the edges of other sites, the channel edge had the second greatest vertical complexity. In contrast, the central reef matrix was fairly uniform, with a height of 1.00 m and small, regular projections of 0.40 m to 0.80 m offering little vertical complexity. Near the rim of the reef flat, there was a considerable amount of exposed matrix, mostly covered in turf algae but with some macroalgal cover in the form of *Laurencia spp.* (Rhodophyta) and *Halimeda spp.*. There were numerous small soft coral colonies in this area and some small massive coral heads.

2.3.2.3 Near shore patch reefs

Plate 2.1: Total area = 645 m^2; Habitat Complexity rating = 7.

The near shore patch reefs site was much smaller than the others, and consisted of small adjoining patch reefs and coral heads close to the shore near the jetty, in an area which is approximately 1.25 m deep. The reef structure is contiguous and relatively consistent throughout the site, so the area was assessed as a whole, rather than distinguishing between patch reefs as at the lagoonal patch reefs site. The greatest dimension of this site was 58 m.

This site had little vertical complexity (Figure 2.4 a lower). The live cover on the edge of the reef was comprised mostly of soft corals and branching hard corals, although there were a few massive hard coral heads. The height of these structural features ranged from 0.30 m to 0.95 m. The central reef matrix at this site had a height of 0.30 m, which was slightly lower than the edge and resulted in a shallow bowl profile. There was a considerable amount of exposed reef matrix covered in turf algae, and there were also numerous small soft coral colonies. There were some massive hard corals in the central area, but they were generally small. The vertical projections in this area ranged from 0.20 m to 0.70 m in height, resulting in low vertical complexity.

2.3.2.4 Lagoonal patch reefs

Plate 2.1: Total area = 2953 m^2; Habitat Complexity ratings = 6 to 8.

This site consisted of a series of six patch reefs located in the deep seagrass meadow to the northwest of the island, at a depth of 4 m. The reefs could be divided into two categories: those with good coral cover (A, C, and F) and those with large quantities of algae, particularly *Halimeda spp.*, and poor coral cover (B, D, and E). This latter group were presumably reefs that were badly infested during the last Crown-of-Thorns Starfish outbreak in the 1980's (Oliver *et al.*, 1995). Four of the reefs were of approximately equal size, ranging from 422 m^2 to 506 m^2, with greatest dimensions of 27 m (reefs D and E), 30 m (reef F) and 33 m (reef B). Reef C was smaller than the others (207 m^2 with a greatest dimension of 16 m) and reef A was larger (822 m^2 with a greatest dimension of 35 m). When size, substrate composition and structural features were all taken into account, reefs A and F were designated Habitat Complexity ratings of 8, reefs B and C were rated 7 and reefs D and E were rated 6.

Branching hard corals were a major component of the edge structure of all six of these reefs, being the most important live cover at reefs A, C and F, and coming second after soft corals at reef B. At reefs A and F, massive hard corals were the next most dominant category, while at reef C soft corals filled this position. Reefs B and C both had massive hard corals as a fourth component, while reefs A and F had soft corals in this position. Reefs D and E had diffuse rather than consolidated edges, with soft corals located in open sand. This was the main difference in the composition of the reef edge communities.

It is the height of these features that is the key to the real differences between the edge areas of these patch reefs. Reefs A and F had the greatest relief, being similar in complexity to the channel edge site. These reefs had mean edge heights of 1.03 m and 1.29 m, and maxima of 1.60 m and 2.10 m respectively. Reefs D and E were the most similar and also had the lowest edge heights. Both had mean edge heights of 0.45 m, with maxima of 0.65 m and 0.75 m respectively. Reefs B and C fell in between these two quite distinct groups, both in substrate composition and structural height.

In the central areas of the reefs, the differences in substrate composition were more obvious. The central areas of reefs B, D and E were dominated by macroalgae, mainly *Halimeda spp.*, but where reefs D and E also had a large soft coral component in their centres, reef B had more hard coral. The live cover in the central areas of reefs A and F was dominated by massive hard corals, with numerous plate and branching hard corals as well. The main live cover in the centre of reef C was plate hard corals, with some massive hard corals, but there was a lot of exposed reef matrix covered in turf algae.

As with the edge areas, the height of structural features highlights the differences between reefs. Reefs A and F had the greatest vertical complexity, with maximum heights of 1.90 m and 2.45 m respectively. Although the central area of reef D was dominated by a single very large projection, reefs D and E still had the lowest profiles overall, with mean projection heights of 0.65 m and 0.67 m respectively. As before, reefs B and C fell between the other two groups, based on both substrate and structure. The height of the central reef matrix did not follow the same pattern however, but rather seemed to decrease along the line of reefs. Reefs A and B both had central matrix heights of 0.75 m, reefs C and D had matrix heights of 0.50 m and 0.55 m respectively, while reefs E and F had central matrix heights of 0.30 m and 0.25 m respectively. Despite this, the range of heights being considered is small enough that when the heights of the projections in the central area are added to their relevant bases the overall structural groupings remain the same.

2.3.3 The Habitat Complexity Scale

The Habitat Complexity Scale (Table 2.1) provides a "logarithmic scaling" of the available habitats. The two main habitat types were assessed with the size of the fishes using them in mind: the seagrass beds were examined at a fine scale relevant to the small sizes of the juvenile fish inhabiting them, while the coral areas were described on a much broader scale which was relevant to the adults. The values of this scale that apply to the seven individual study sites are listed in the site descriptions.

2.4 DISCUSSION

2.4.1 Seagrass bed summary

Descriptions of the community structure and composition of the reef flat seagrass beds compare well with those of Wilson (in prep.) who conducted similar surveys in 1993. The main distinction between the communities at the three sites was that the seagrass was taller and denser on the northern side of the island. This could be due to the greater depth, which results in shorter and less frequent periods of exposure during low tides, and therefore less heat and dehydration stress. The presence of the macroalgae *Dictyota spp.* and *Halimeda spp.*, both genera which are known to exhibit nutrient limited productivity patterns (LaPointe *et al.*, 1987), also suggests that increased nutrient levels could have been introduced to the area in the past. Given the shallow depth and the dominance of *H. uninervis*, an aggressive, late-pioneering species, this might be considered the climax community for this location (Birch and Birch, 1984; Clarke and Kirkman, 1989; Coles *et al.*, 1989). The lower standing crop at the southern sites may be related to thermal and desiccation stress received during exposure at low tides. The dominance of *T. hemprichii* and *Cymodocea spp.* on the reef platform concurs with the findings of Coles *et al.* (1987). Birch and Birch (1984) considered this a mid-successional community.

The apparent March peak in seagrass blade height and percentage cover was in contrast to the findings of Mellors *et al.* (1993), who detected an October to December peak in standing crop of seagrasses in the northwestern lagoon on Green Island. Of the three seagrass sites in this study, the northern site was the most similar to the seagrass beds in the lagoon. The differences in depth and other environmental variables between the sites were considerable however, and factors such as light availability and temperature, which Mellors found important, seem likely to be quite different. Despite disagreement on the exact timing of the peak, the occurrence of summer maxima in tropical seagrass biomass is generally accepted (Zieman, 1975; Wahbeh, 1988).

Unlike the high density '*Sargassum* zones' on inshore fringing reefs (Morrissey, 1980; Martin-Smith, 1993), the abundance and distribution of *Sargassum spp.* plants in the seagrass beds is restricted by the availability of stable attachment sites on the otherwise sandy substrate. At the northern site raised rocky reefs were the most common site of attachment, while at the southern sites this role was filled by single sunken dead coral heads. Although the large clusters appeared to be attached to the sand, they were usually attached to similar rocky substrates just below the surface. Standard errors were generally high, reflecting the patchy distribution of these plants within the seagrass beds.

Seasonality of axial growth, with summer maxima and winter minima, is in agreement with Martin-Smith (1993). This study found that axial material was lost from most plants, and suggested that some species appeared to be pseudoperennial, surviving the winter as holdfasts and producing new axes each year. This would account for the observation that *Sargassum spp.* plants were located in the same areas during each year of this study (pers. obs.). The slight differences in the length of the time for which structurally significant plants were abundant may be explained by the possibility of a slightly different species mix at the various sites. As different species have different periods of peak growth and biomass (Martin-Smith, 1993), the combination of species present could lead to either an extended or contracted period of high *Sargassum spp.* biomass.

2.4.2 Coral area summary

The front ledge had the greatest overall structural complexity, followed by the channel edge and reefs A and F of the lagoonal patch reefs. As a general rule, edge areas were more structurally complex than centres. The only exceptions to this were reefs A and F of the lagoonal patch reefs site, which had similar heights and substrate compositions at both the centre and the edge. It is my opinion that the coral cover at these study sites had improved slightly from the 10 % recorded in the 1992 - 1993 survey. Slight increases in numbers of *A. planci* were observed in the Cairns area between 1991 and 1993, but numbers were well below outbreak level (Oliver *et al.*, 1995). Numbers at Green Island increased between 1993 and 1996, starting with a single incidental sighting in August of 1994 and increasing to six incidental sightings in August 1996 (pers. obs.). The latest *A. planci* outbreak started in the northern sectors of the Great Barrier Reef in 1995 (Richard Stump, pers. comm.), and populations at Green Island had entered into an active outbreak phase by November 1996 (Michelle Rodrigo, pers. comm.). No effects on live coral cover were noticed prior to September 1996.

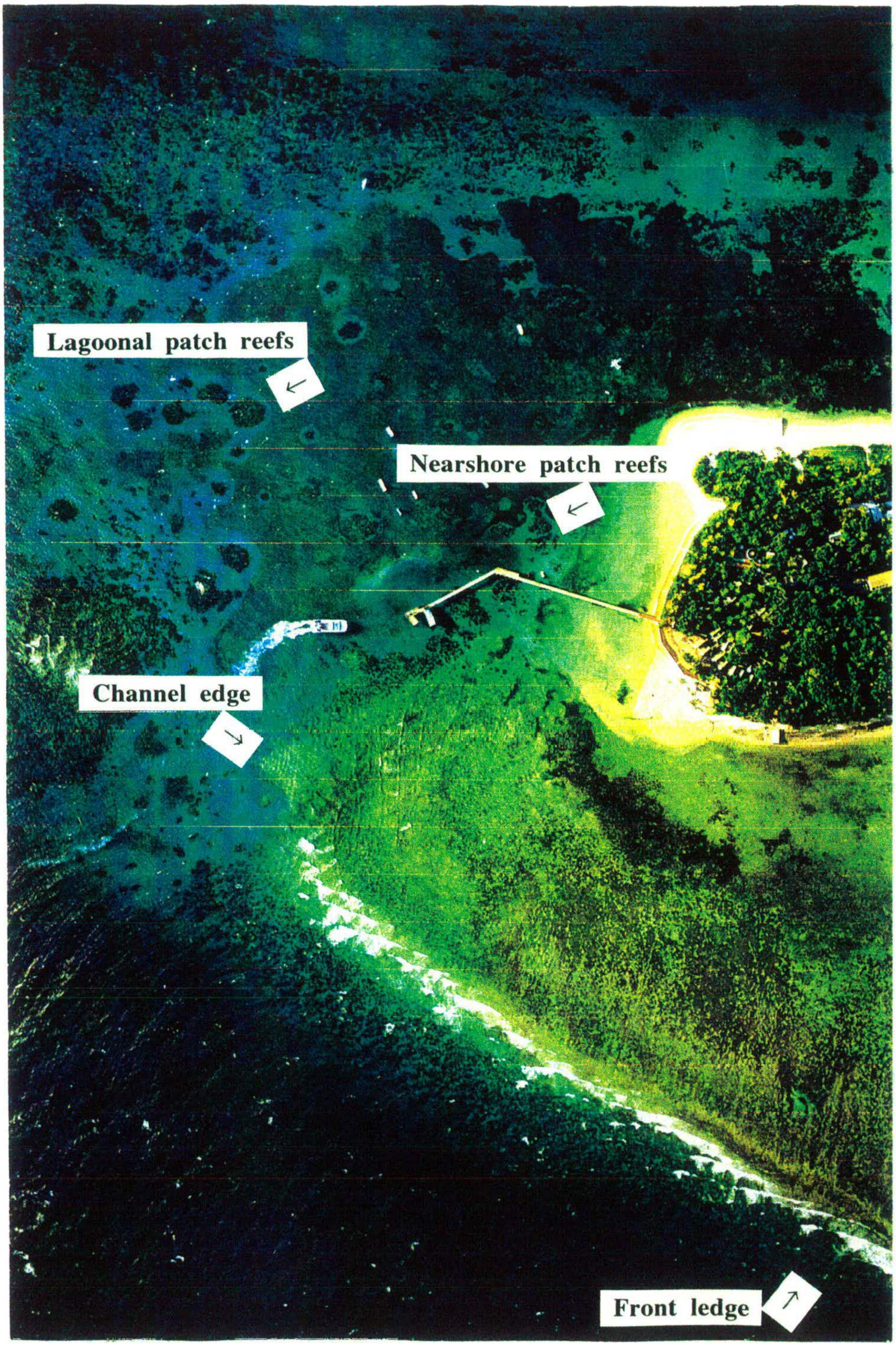
2.4.3 Implications of the location for the research program

In undertaking this study, it was understood that a number of features specific to Green Island Reef would have serious implications for the research program and the data that it generated. As is obvious from the site descriptions, the four adult sites are very different in their structural nature, their extent and their positions within the overall layout of the reef. Although the reef flat around Green Island is extensive, habitats with significant coral cover only occur in a restricted area around the edge of the reef flat. In addition, different positions around the perimeter result in habitats at a variety of depths and exposure levels. This had consequences for the selection of study sites, as well as the collection and interpretation of the data.

Due to the spatial requirements of the sites, each habitat type did not necessarily cover a large enough area to allow replication of sites within habitat types. This restricted the statistical tools available for data analysis, as parametric analyses based on distributions and error structures would have been inappropriate and meaningless. Even where apparently similar potential replicate sites were available, the sites chosen were the only ones actually utilised by siganids. In fact, the only area around Green Island known to have a relatively consistent siganid presence yet not included in this study was the area under the bend in the jetty and the small patch reefs just to the south of it. Use of this area for research was impossible because it was a very popular snorkelling area for the tourists, and even outside day trip hours it was affected by activities on the jetty. Destructive sampling was deemed inappropriate for such an area and visual observations could not be conducted due to the high numbers of users and their effects on fish behaviour.

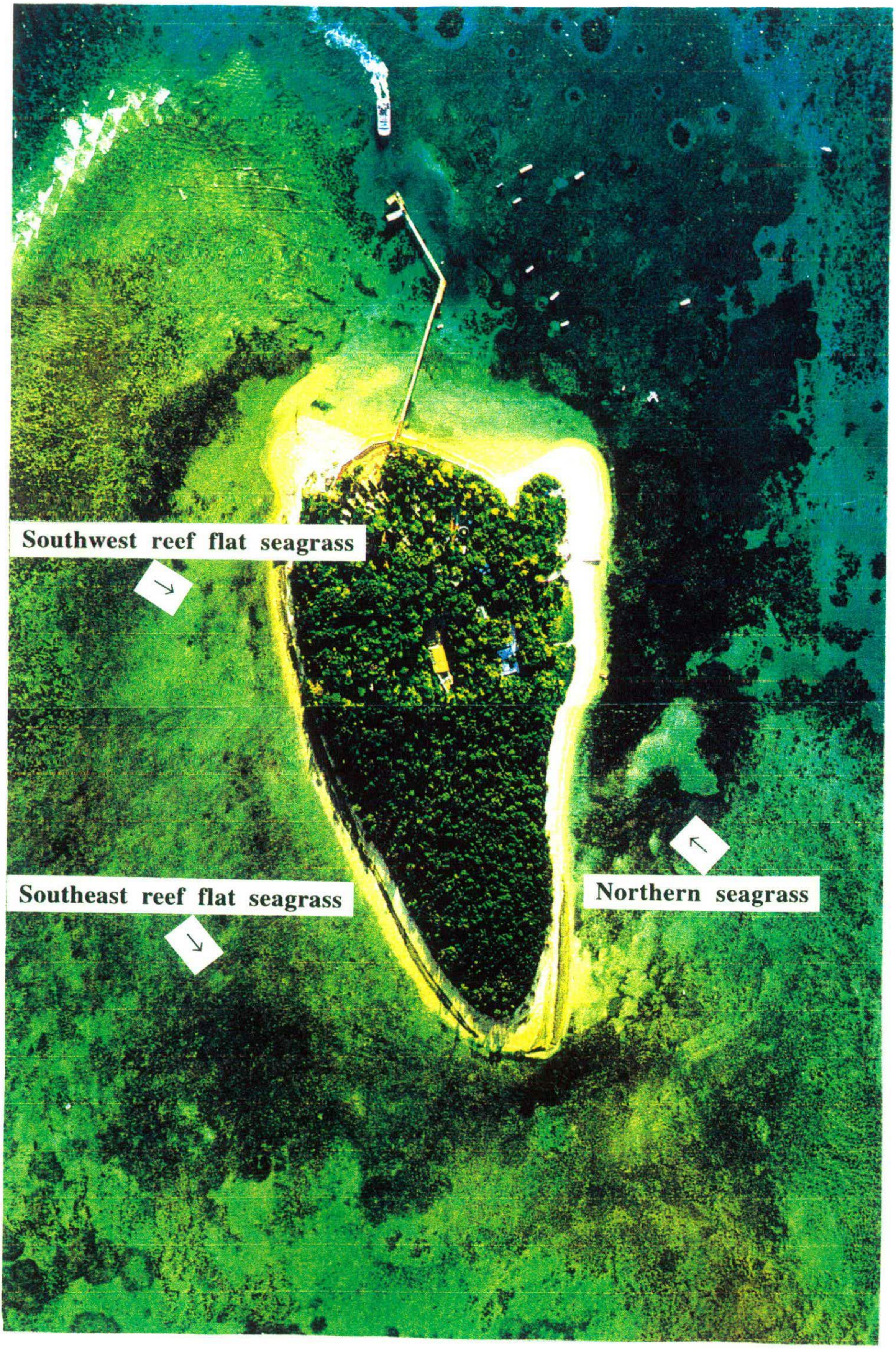
Another point that must be considered when interpreting the data collected from these sites is that any patterns found can only be ascribed to one site or another. The different positions of the sites on the reef platform mean that external factors, such as exposure level, depth and proximity to the reef flat, vary together with intrinsic factors, such as site structure and extent. As a result, no single driving factor can be separated from the rest. Nonetheless, it is still possible to speculate as to which of these factors are important. The site-specific nature of this study is acknowledged, and will be taken into consideration when discussing the results. Given the importance of Green Island in the region however, a knowledge of the interactions between the habitats present there is a useful tool.

Plate 2.1. Aerial photograph showing the four coral area (adult) sites.



Photograph reproduced with permission of the Department of Natural Resources, Queensland

Plate 2.2. Aerial photograph showing the three reef flat seagrass (juvenile) sites.



Photograph reproduced with permission of the Department of Natural Resources, Queensland

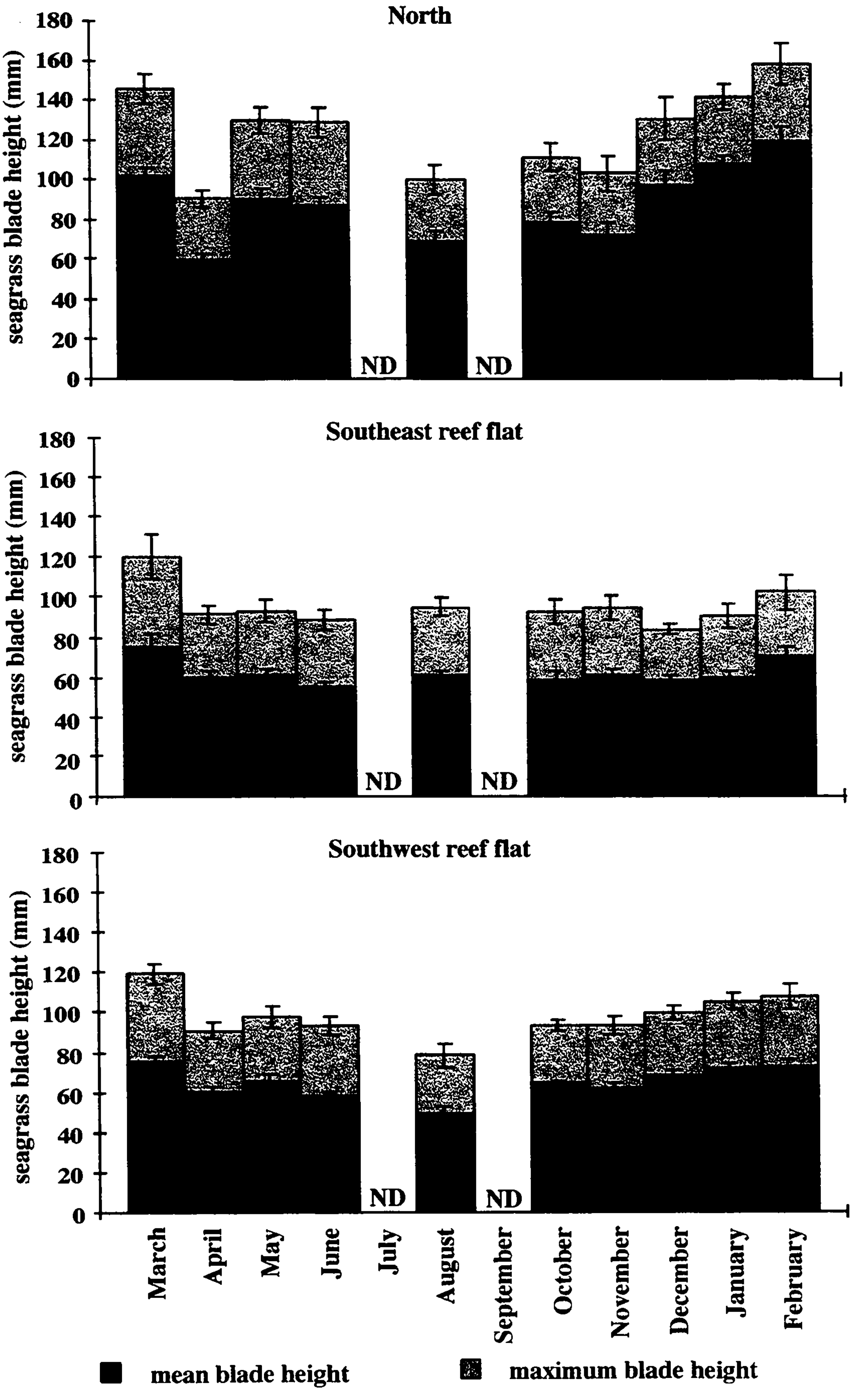


Figure 2.1. Monthly variation in mean and maximum seagrass height at the three seagrass bed study sites. Means are ± 1 S.E. (ND = No Data.)

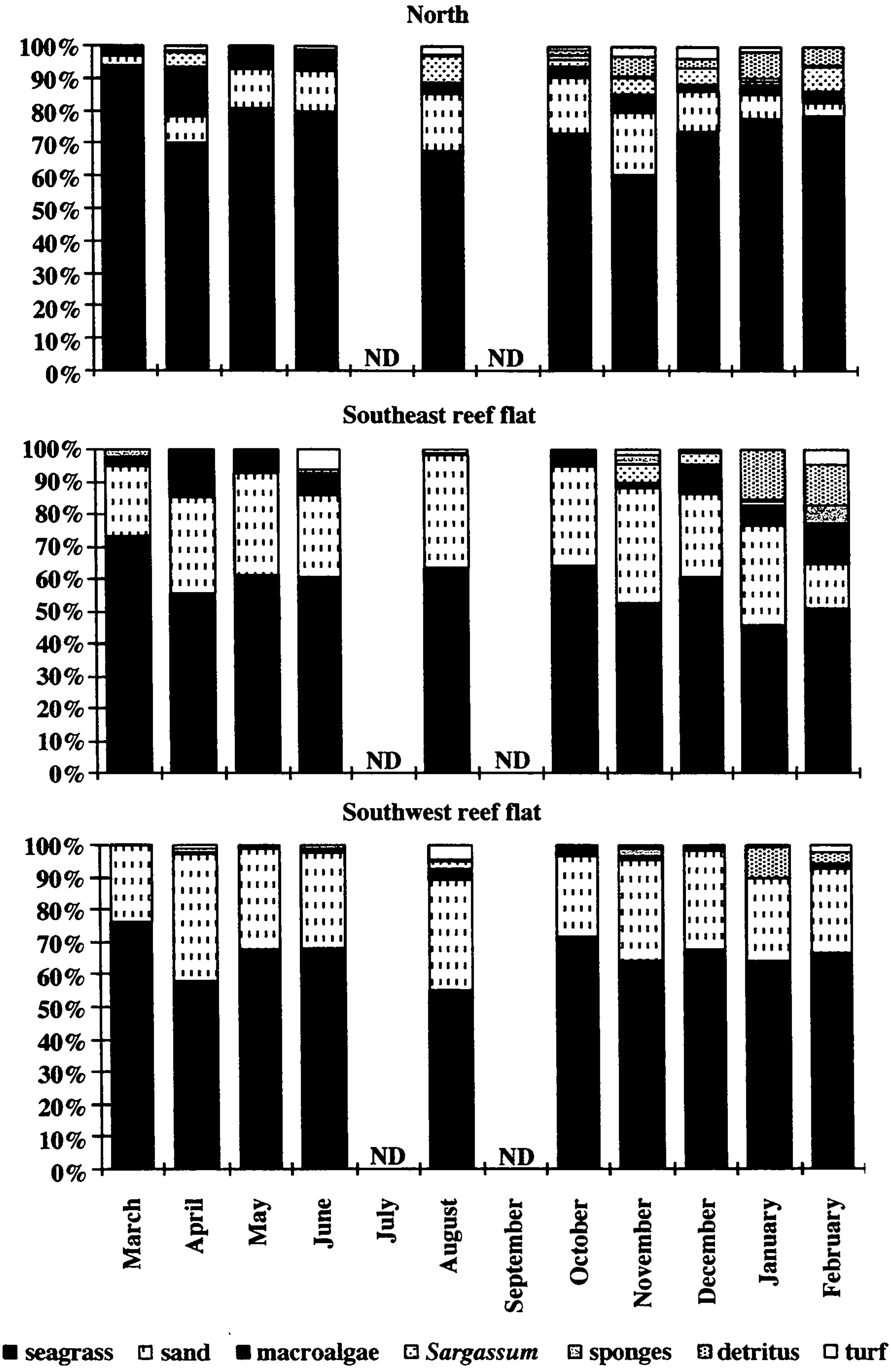


Figure 2.2. Monthly variation in percentage cover at the three seagrass bed study sites. (ND = No Data.)

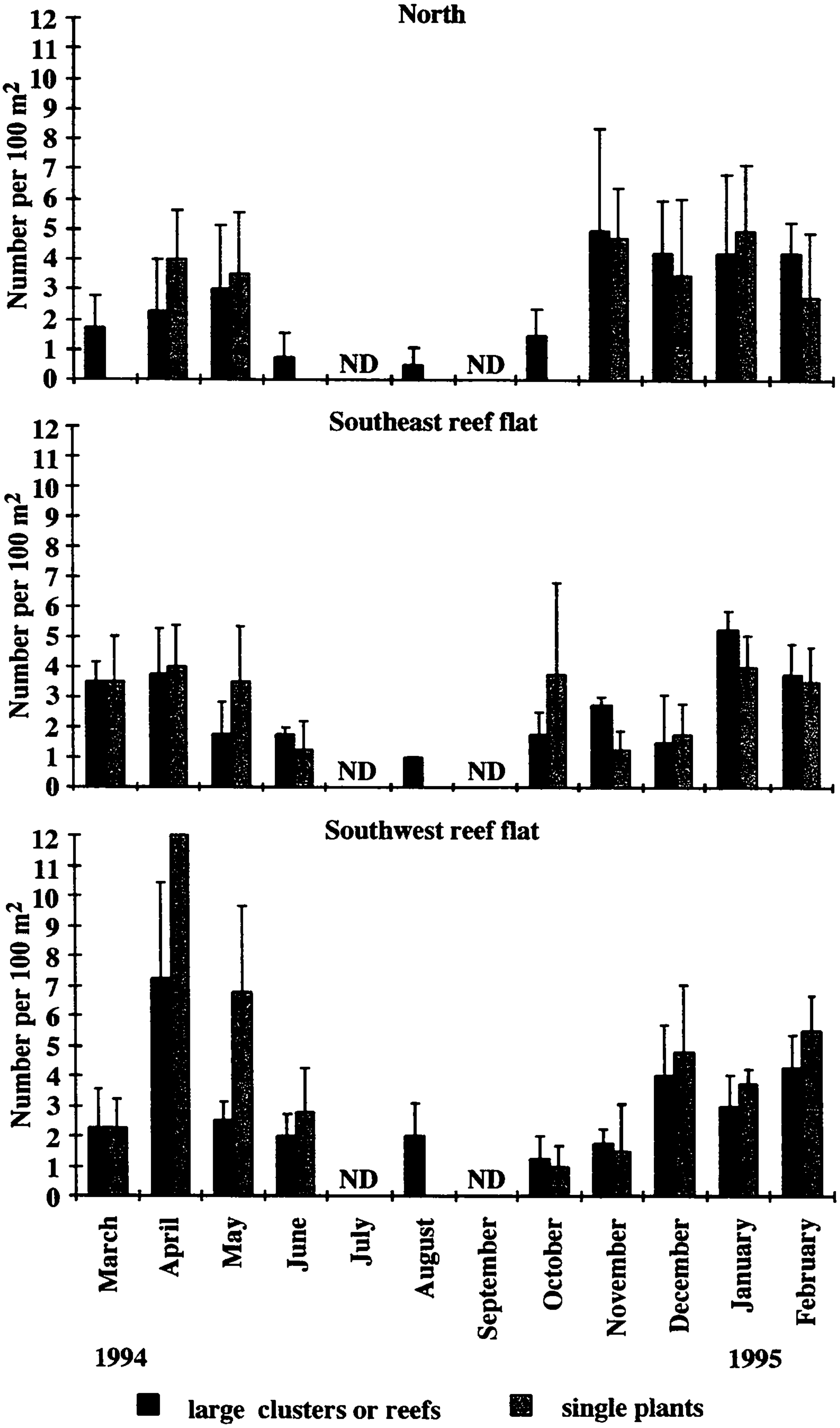
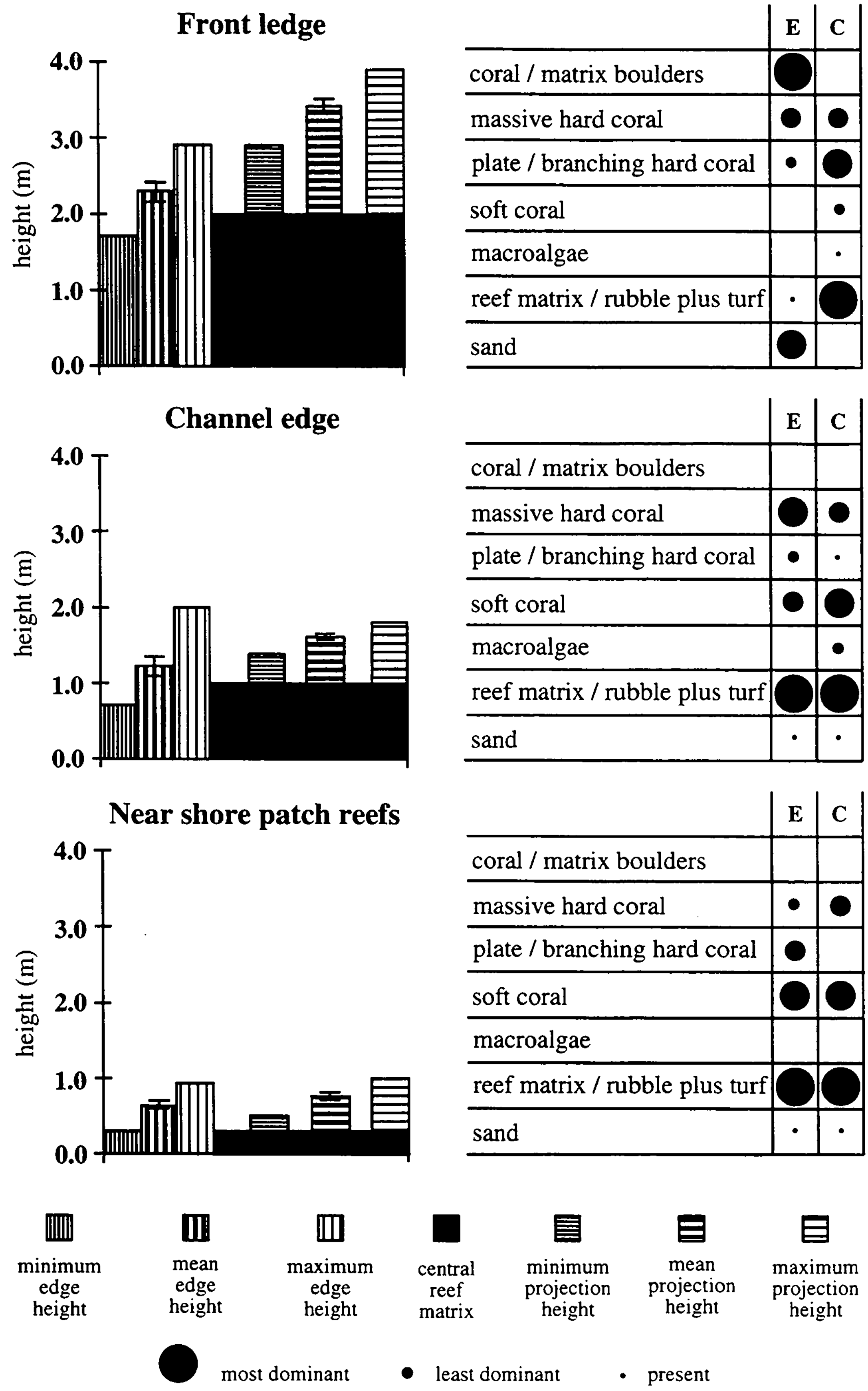


Figure 2.3 Monthly variation in density of different sized groups of *Sargassum spp.* plants at the three seagrass bed study sites. Means are ± 1 S.E. (ND = No Data.)



Front ledge

	E	C
coral / matrix boulders	⬤	
massive hard coral	●	●
plate / branching hard coral	•	⬤
soft coral		•
macroalgae		·
reef matrix / rubble plus turf	·	⬤
sand	⬤	

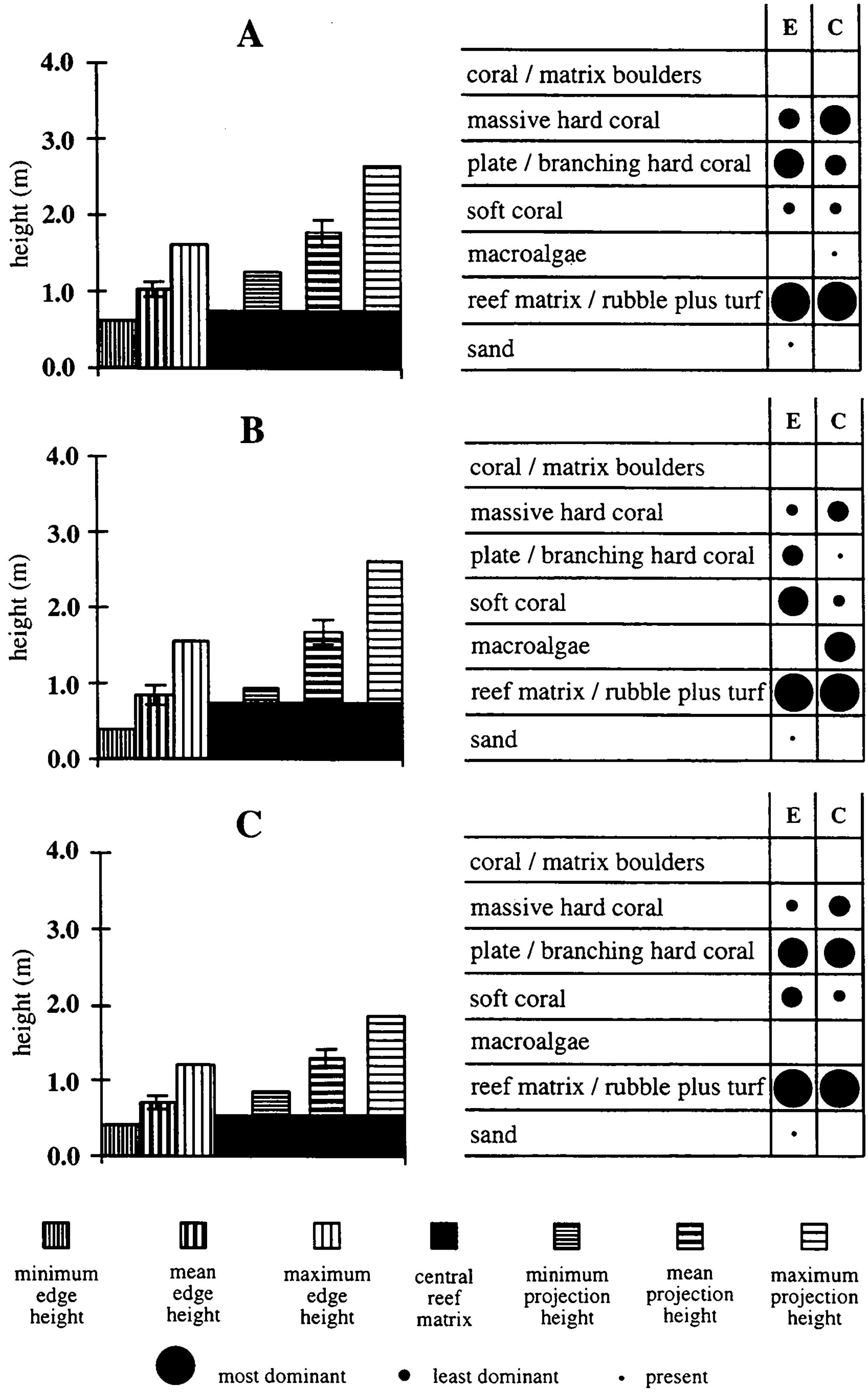
Channel edge

	E	C
coral / matrix boulders		
massive hard coral	⬤	●
plate / branching hard coral	•	·
soft coral	●	⬤
macroalgae		•
reef matrix / rubble plus turf	⬤	⬤
sand	·	·

Near shore patch reefs

	E	C
coral / matrix boulders		
massive hard coral	•	●
plate / branching hard coral	●	
soft coral	⬤	⬤
macroalgae		
reef matrix / rubble plus turf	⬤	⬤
sand	·	·

Figure 2.4 a. Vertical complexity and habitat composition characteristics of both the edge (E) and the centre (C) of the Front ledge, Channel edge and Near shore patch reefs sites. Mean heights are ± S.E.



A

	E	C
coral / matrix boulders		
massive hard coral	●	⬤
plate / branching hard coral	⬤	●
soft coral	●	●
macroalgae		•
reef matrix / rubble plus turf	⬤	⬤
sand	•	

B

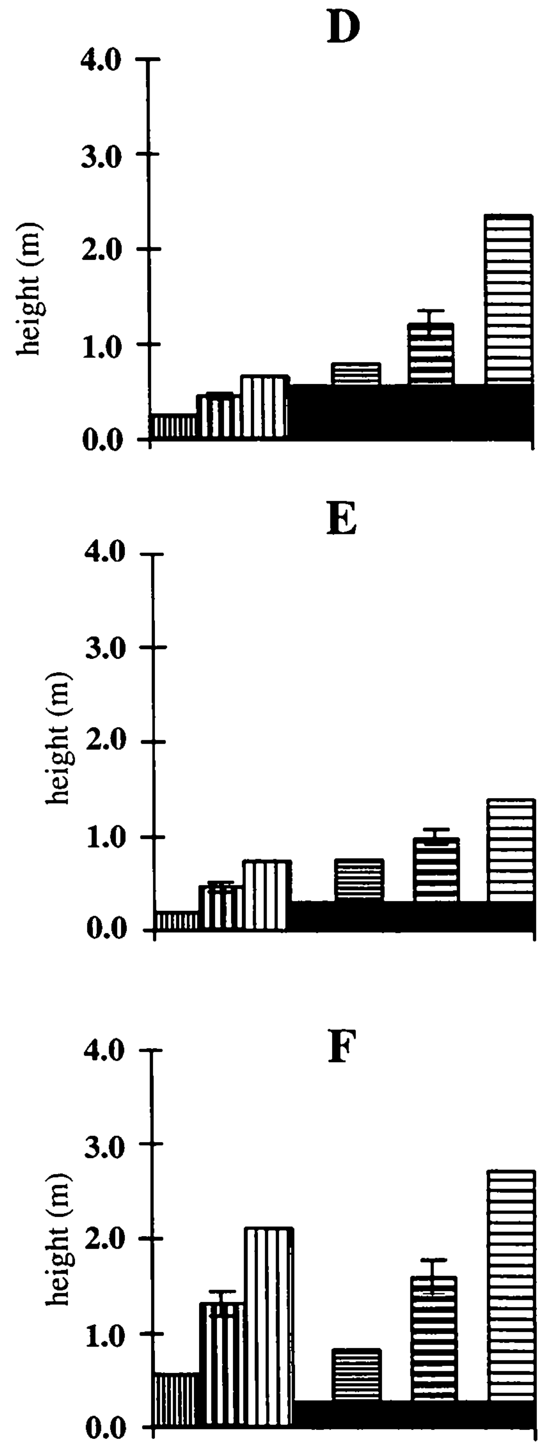
	E	C
coral / matrix boulders		
massive hard coral	●	⬤
plate / branching hard coral	⬤	•
soft coral	⬤	●
macroalgae		⬤
reef matrix / rubble plus turf	⬤	⬤
sand	•	

C

	E	C
coral / matrix boulders		
massive hard coral	●	⬤
plate / branching hard coral	⬤	⬤
soft coral	⬤	●
macroalgae		
reef matrix / rubble plus turf	⬤	⬤
sand	•	

⬤ most dominant ● least dominant • present

Figure 2.4 b. Vertical complexity and habitat composition characteristics of both the edge (E) and the centre (C) of reefs A, B and C of the lagoonal patch reefs site. Mean heights are ± S.E.



D	E	C
coral / matrix boulders		
massive hard coral		•
plate / branching hard coral	⬤	●
soft coral	⬤	⬤
macroalgae		⬤
reef matrix / rubble plus turf		●
sand	●	

E	E	C
coral / matrix boulders		
massive hard coral		
plate / branching hard coral	⬤	●
soft coral	⬤	⬤
macroalgae		⬤
reef matrix / rubble plus turf		●
sand	●	

F	E	C
coral / matrix boulders		
massive hard coral	●	⬤
plate / branching hard coral	⬤	●
soft coral	●	●
macroalgae		•
reef matrix / rubble plus turf	⬤	⬤
sand	•	

⬤ most dominant ● least dominant • present

Figure 2.4 c. Vertical complexity and habitat composition characteristics of both the edge (E) and the centre (C) of reefs D, E and F of the lagoonal patch reefs site. Mean heights are ± S.E.

Table 2.1. The Habitat Complexity Scale.

Scale value	Description
1	Open sand and beach rock
2	Short, sparse seagrass blade height < 10 cm, < 70 % cover
3	Tall, dense seagrass blade height ≥ 10 cm, > 70 % cover
4	Sargassum clumps, diameter <50 cm / low rocky reefs average height <50 cm
5	Sargassum reefs (several large clumps or including rocky reef) average height >50 cm
6	Low algae / soft coral patch reef average height <1 m
7	Small mixed hard and soft coral bommies average height <1 m
8	Mixed hard and soft coral patch reef average height >1 m
9	Continuous mixed hard and soft coral significant soft coral component
10	Continuous hard coral minimal soft coral presence

CHAPTER 3

DIETARY DIFFERENTIATION IN SIGANIDS:

Ontogenetic and interspecific comparisons

3.1 INTRODUCTION

It is a general assumption that diet should reflect feeding patterns aimed at maximising the rate of net energy gain (Pyke *et al.*, 1977; Hughes, 1980; Horn, 1983). However, the low nitrogen levels in plant tissues (Mattson, 1980; Atkinson and Smith, 1983) have important implications for herbivorous fishes. Given low levels of available protein, carbohydrates are the main energy source for these fishes and, compared to carnivores, herbivores have high activity levels of carbohydrases in their gut and moderate to high assimilation rates for carbohydrates (Kapoor *et al.*, 1975; Fänge and Grove, 1979; Horn, 1989; Sabapathy and Teo, 1993). In addition, maximising protein intake might be more important consideration than maximising energy in the dietary choices of herbivores (Montgomery and Gerking, 1980; Horn, 1983; Horn *et al.*, 1986). Maximising energy gain and protein intake by consuming the most nutritious food items may seem an obvious dietary strategy (Horn, 1983; Targett and Targett, 1990), but it is not as simple as it sounds. There are many factors which influence dietary composition in herbivorous fishes (Horn, 1989), and these may be viewed as positive and negative influences, promoting or discouraging the consumption of a particular item. Dietary choice should reflect a trade-off between these influences.

Although chemical analyses may assess the potential food quality of plants based on total protein, lipid, carbohydrate and ash proportions (Montgomery and Gerking, 1980; Neighbors and Horn, 1991), the assimilation efficiency for a given plant will vary between consumers depending on the susceptibility of the plant to the digestive mechanisms employed by that consumer (Lobel, 1981; Galetto and Bellwood, 1994). The nutritional value of marine plants needs to be considered in terms of the cell contents and the cell wall, the latter being traditionally considered unavailable for assimilation by fishes without microbial aids to digestion (Lobel, 1981; Horn, 1989; but see Anderson, 1987). The Siganidae are considered Type I herbivores (Horn, 1989, 1992), with an acid-based digestive mechanism. This classification is largely based on the absence of the morphological adaptations (pharyngeal mill or gizzard) or microbial endosymbionts which define the other digestive types.

There has, however, been little discussion in the literature of how an acid-based digestive system might operate. Commonly referred to as acid lysis (Lobel, 1981; Horn, 1989, 1992), this name suggests a rupturing of the cell wall in the acidic medium and, while permitting access to the cell contents, would preclude assimilation of the cell wall. The weakening of hydrogen bonds between the cell wall components (Wilkins, 1984) has been suggested as a means by which cell contents could be leached out (Horn, 1989; Montgomery and Targett, 1992). Alternatively, the extractive action of acid on the polysaccharides of the cell wall matrix (Percival, 1979; Ting, 1982; Kloareg and Quatrano, 1988) could effectively dissolve portions of the cell wall. This could conceivably result in the assimilation of the extracted polysaccharides, and has important implications for potential food value. Lastly, despite a failure thus far to detect endogenous cellulolytic enzymes in herbivorous fishes (Horn, 1989), the possibility of a novel enzymatic process utilising the digestive enzymes known to occur in herbivorous fishes cannot be completely ruled out (Kendall Clements, pers. comm.). However, in keeping with the current literature, the following review of the potential nutritional values of marine plants is tailored to Horn's (1989, 1992) assessment that siganids have an acid based digestive system.

3.1.1 Marine algae as a food source

The first obstacle to successful digestion of plants is the cell wall. Marine algae generally present less of a problem in this respect than higher plants, as their cell walls have a greater relative proportion of mucilaginous matrix components to skeletal elements (cellulose) (Kloareg and Quatrano, 1988). In phaeophytes and rhodophytes, cellulose typically comprises only 1 - 8 % of thallus dry weight, while in chlorophytes and higher plants the proportion is frequently 30 % or more (Kloareg and Quatrano, 1988). Depending on whether gastric acid merely weakens the structure of plant cell walls (Wilkins, 1984) or actually extracts portions of the matrix polysaccharides (Percival, 1979; Kloareg and Quatrano, 1988), the proportion of matrix material to skeletal material could affect the efficiency of cell wall disruption and the amount of wall material that is made available for assimilation.

In rhodophytes and phaeophytes, the sulphated polysaccharides of the cell wall and extracellular matrix are agars or carageenans and alginates or fucans respectively (Percival, 1979; Kloareg and and Quatrano, 1988). The presence of α-bonds in these polymers makes them susceptible to hydrolysis by amylase, an enzyme with high activity in the guts of herbivorous fishes (Kapoor *et al.*, 1975; Fänge and Grove, 1979; Montgomery and Gerking, 1980; Sabapathy and Teo, 1993). Agars, carageenans and alginates should be at least partly assimilated, but the complexity of fucans makes their assimilation unlikely (Percival, 1979; Kloareg and Quatrano, 1988). The sulphated polysaccharides and complex proteoglycans in chlorophytes do not contain α-bonds (Percival, 1979), and are unlikely to be assimilated. The cell covering of the prokaryotic cyanophytes is composed of the proteoglycan murein (Delaney 1990; Price, 1990), and appears to be readily disrupted by acid (Lobel, 1981), but the susceptibility of this compound to enzyme hydrolysis is not known.

The intracellular material consists of proteins, lipids and energy storage compounds. The chief storage products of algal cells are polysaccharides (Price, 1990), and these are known to vary considerably between taxa. Chlorophytes produce starch very like that of terrestrial plants (Phillips, 1990); rhodophytes produce Floridean starch, which has a structure like amylopectin and glycogen (Kraft and Woelkerling, 1990); phaeophytes use mannitol and laminaran as food reserves (Percival, 1979; Clayton, 1990); cyanophytes produce myxophycean starch, similar to Floridean starch (Delaney, 1990; Price, 1990). The digestibility of the three types of starch is similar, and all are hydrolysed by amylase (Percival, 1979; Price, 1990; Sabapathy and Teo, 1993). Laminaran is hydrolysed by the enzyme laminarinase, which is present in the alimentary tracts of siganids (Sabapathy and Teo, 1993). Given the apparently equal digestibility of energy storage compounds between taxa, it seems possible that, for siganids, nutritional preference might be based on variations in the relative proportions of matrix and skeletal elements in the cell wall, and the digestibility of the wall matrix and extracellular polysaccharides. In this scenario, rhodophytes would be the most desirable dietary items, followed by phaeophytes then chlorophytes. While cyanophytes appear to be susceptible to disruption by acid (Lobel, 1981), their place in this scenario is unclear due to limited knowledge of their biology.

Data on the calorific and nutrient content of benthic marine algae are limited, and most studies have been conducted on species that are relevant to the diets of temperate herbivores. Montgomery and Gerking (1980) found that chlorophytes had higher calorific values and protein content than rhodophytes and phaeophytes, but other studies have found that, while values are similar within genera, the ranges of the major divisions are largely overlapping (Paine and Vadas, 1969; Horn and Neighbors, 1984;

Neighbors and Horn, 1991). Ambient nutrient levels influence the calorific values of marine algae (Paine and Vadas 1969), and Atkinson and Smith (1983) found that nitrogen levels in algae from North Queensland and other oligotrophic waters were significantly lower than the levels in specimens found in more eutrophic conditions. Thus, at Green Island Reef, any algal species or genera with higher than average nitrogen content should be eaten preferentially by herbivorous fishes.

Beyond the basic nutritional attributes of a potential food item, there are other factors which influence the likelihood of consumption and digestion. Although not necessarily a true example of coevolution (Hay, 1991b; Steneck, 1992), the extensive variation in morphology and chemical composition presented by marine algae is a testimony to the selection pressures exerted upon them by herbivorous fishes (Hay, 1991a). Selected traits can be roughly divided into morphological defenses, chemical defenses and the use of refuges (Lubchenco and Gaines, 1981; Steneck, 1988; Duffy and Hay, 1990). Morphological defenses of marine algae were summarised by Littler *et al.* (1983), who developed a 'functional-form' hypothesis that correlated thallus structure with shear stress and predation resistance. In accordance with the model, filamentous algae were easiest to break and most heavily grazed. Calcified crustose algae were not grazed. The gradation between these extremes placed membranous forms after filamentous algae, followed by coarsely branching fleshy algae, jointed calcareous algae and thick leathery forms. This functional group approach was supported and expanded by Steneck (1988), who proposed additional subdivisions.

The potential for secondary metabolites of marine algae to act as deterrents against herbivore feeding has been established (see reviews by Hay and Fenical, 1988; Van Alstyne and Paul, 1988). The compounds act by reducing the digestibility or palatability of the alga concerned (e.g. Targett *et al.*, 1986; Paul, 1987; Wylie and Paul, 1988), but assigning compounds to these categories based on broad chemical structure is now discouraged (Hay, 1991a and b). Contributing to this view is the increasing evidence that polyphenolics, traditionally thought to reduce digestibility, do not seem to have the same role in tropical waters as they do in temperate waters or in terrestrial ecosystems (Steinberg *et al.*, 1991; Targett *et al.*, 1995). Reducing palatability through the production of lipophilic compounds such as terpenoids seems to be a more important strategy in the tropics (Steinberg and Paul, 1990). Some of the more heavily defended tropical algae in this respect include *Lyngbya spp.* (filamentous cyanophytes), *Dictyota spp.* and some related membranous phaeophytes, numerous chlorophyte genera and *Laurencia spp.* (fleshy rhodophytes) (Paul and Fenical 1987; Faulkner, 1990, 1992; Hay, 1991a). Based on this aspect of their biochemistry, these algae should be avoided by herbivorous fishes.

3.1.2 Seagrasses as a food source

The potential of seagrasses as a food source for larger herbivores was reviewed by Thayer *et al.* (1984) and Klumpp *et al.* (1989). Cellulose and other structural components make up a high percentage of the organic matter of seagrasses (30 % to 80 %) and lignin content increases with the age of the blade, reducing digestibility even further. Both reviews concluded that, in the absence of cellulases or microbial aids to digestion, most macroconsumers of seagrasses would need to disrupt the cell wall mechanically to gain access to cell contents. This assertion was based on the complex structure and resistant bonds of cellulose, and the observation that seagrasses appeared undigested by acidic gastric secretions (Bell *et al.*, 1978; Bjorndal, 1980).

A study by Conacher *et al.* (1979) found that although microscopic examination of seagrass pieces from the rectum of omnivorous monacanthids revealed little apparent structural damage caused by digestion, a subsequent experiment using ^{14}C-labelled seagrass showed that digestion removed significant proportions of labile carbon compounds from the plant. Montgomery and Targett (1992) also reported assimilation of seagrass by an omnivorous sparid, although a later study found evidence of cellulolytic microbes in the intestine of the same species (Luczkovich and Stellwag, 1993). Nonetheless, it seems plausible that herbivorous fishes with an acid-based digestive system may gain access to the cell contents of seagrasses, possibly through the weakening of hydrogen bonds between cellulose strands under acidic conditions (Wilkins, 1984) or the extractive action of protons on pectin molecules in the cell wall (Ting, 1982).

Some studies have found that the protein content of seagrasses can be greater than or equal to that of algae from the same location (Table 13.1 in Klumpp *et al.*, 1989). The nutrient content of a seagrass leaf is a function of the age of the leaf and the degree of epiphytism. The protein content is highest in new, green leaves and declines with age (Zieman *et al.*, 1984), while epiphyte load increases with the age of the leaf (Heijs, 1985; Borowitzka and Lethbridge, 1989). This results in a trade-off between the nutrients available from the seagrass itself and nutrients available from the epiphytes. Herbivores may consume newer, less lignified leaves to supply protein, and older leaves with more epiphytes to supplement carbohydrate intake. Like most higher plants, seagrasses produce phenols as secondary metabolites (McMillan *et al.*, 1980), but these compounds are similar to those in phaeophytes that Steinberg *et al.* (1991) and Targett *et al.* (1995) found have little effect on tropical herbivores.

3.1.3 Energetics

There are other factors affecting diet which are external to the food item itself. Implicit in maximising net energy gain is an evaluation of the cost of procuring different food items (Hughes, 1980; Putman and Wratten, 1984). When feeding rate is taken into account, a trade-off is possible such that items of low nutritional value may be eaten in large quantities to compensate for poor quality (Targett and Targett, 1990). Another trade-off in the food procurement equation is the predation risk involved (Werner *et al.*, 1983; Pulliam, 1989). Energy expediture during prey capture will be less significant for herbivores than carnivores, but the risk of predation is of greater concern. An evaluation of these factors would include the area searched to find adequate quantities of a food item, consumption effort, the predation risk in habitats with differing food availabilities and the cost of travelling between feeding and refuge areas.

3.1.4 Ontogenetic changes in diet

Diet rarely remains constant through ontogeny and most species exhibit some differences between the juvenile and adult phases (Helfman, 1978; Livingston, 1982; Hickley *et al.*, 1994). Given the obvious physical differences in size and strength between juvenile and adult fish this is hardly surprising and, in general, larger dietary items are taken as the fish increases in size (Grossman, 1980; Clements and Choat, 1993; Hickley *et al.*, 1994). In addition, dietary differences may be a reflection of different food availabilities in the different habitats occupied by juvenile and adult fish (Clements and Choat, 1993), especially where juveniles recruit to distinct nursery grounds.

Many herbivorous fishes are known to be wholly or partly carnivorous during their early life history, becoming herbivorous later in life (Carr and Adams, 1973; Montgomery, 1977; Horn *et al.*, 1982; Lassuy, 1984; Stoner and Livingston, 1984; Rimmer, 1986; Bellwood, 1988). Even when the herbivorous habit is dominant during the juvenile stage, there is often a change in the relative importance of different types of dietary items (Clements and Choat, 1993). These observations are consistent with a need for greater amounts of both energy and protein during the juvenile phase, a consequence of both metabolic scaling (Peters, 1983) and the rapid growth rates exhibited at this time. These requirements cannot be fulfilled by increasing intake while fish are so small. Less obvious differences related to the digestive process, such as retention time and its effect on the assimilation of different food items (Benevides *et al.*, 1994), may also play a role. Even after reaching maturity, fish may have varying nutritional requirements at different times of the year (Horn *et al.*, 1986), and Fishelson *et al.* (1987) suggested that a dietary change in winter allowed adult acanthurids to build-up reserves for gametogenesis in spring.

3.1.5 Availability and accessibility

When considering dietary selectivity, the availability of food items is usually taken into account. There is evidence that despite distinct preferences for certain foods under laboratory conditions, the natural diets of animals will, to a certain extent, reflect the relative abundance of food items available to them (Ivlev, 1961; Bryan, 1975; Lundberg and Lipkin, 1979; Horn *et al.*, 1982; Horn, 1983). Johnson (1980) argued that presence in the habitat does not necessarily make an item available. Here, "availability" will refer to the presence or absence of a food item in the habitat, and "accessibility" will indicate whether the individual is capable of utilising an item when it is present. Accessibility may be affected by physical restrictions on consumption or limitations associated with digestion. While availability should be consistent in a given habitat over a short time period, accessibility may change through ontogeny.

3.1.6 Previous research on the diet of siganids

A number of studies have trialed siganid feeding preferences under culture or experimental conditions, and there have also been several studies of their diets in the wild. Juveniles eat seagrasses and filamentous algae (von Westernhagen, 1973; Pinto and Punchihewa, 1996), especially *Enteromorpha spp.* and rhodophytes, and can consume most marine plants (von Westernhagen, 1974; Bryan, 1975). Adult diets are varied and include seagrass, all three major algal divisions, and occasionally cyanophytes (von Westernhagen, 1973; Lundberg and Lipkin, 1979). The response to algal secondary metabolites was unpredictable (Hay *et al.*, 1988; Paul *et al.*, 1990), but tough and calcareous species were avoided (von Westernhagen, 1974; Lundberg and Lipkin, 1979; Schupp and Paul, 1994). Lundberg and Lipkin (1979) suggested that wide-ranging shoaling species would have greater dietary diversity than site-attached species. The study by Lundberg and Lipkin (1979) is the only one to have provided mean relative abundance estimates, rather than pooling samples or using frequency data, and there is room for studies that provide quantitative estimates of dietary composition with an indication of variability. With the exception of Hay *et al.* (1988), all studies have involved shoaling species in areas other than the Great Barrier Reef. As with most aspects of siganid biology, little is known about the pairing species in the field, and no comparative studies of shoaling and pairing species have been made.

3.1.7 Predictions for dietary composition

Based on algal chemistry, rhodophytes and then phaeophytes should be consumed in preference to chlorophytes to maximise digestibility and energy gain. Seagrasses should be avoided on the basis that their cell walls are less vulnerable to acid lysis. Unpalatable, chemically defended genera should be avoided. In cases where foods with low nutritional value are consumed, these items should be eaten in large quantities to compensate for poor quality. Based on algal morphology, the consumption of delicate growth forms (filamentous, then membranous, then fleshy algae) should minimise consumption effort and maximise the cell disruption achieved in biting. The high surface area to volume ratio of these groups would also maximise the effects of gastric acid. Heavily calcified items should be avoided due to physical constraints and to prevent the neutralisation of stomach pH. Juveniles should consume easily digestible items with higher energy and nutrient content than those eaten by adults, due to their greater metabolic requirements and developing digestive system. They may even include animal material in their diet. It is possible that the wide-ranging shoaling species might have a more varied diet than the pairing species. It is expected that diet should reflect the relative availabilities of the various types of marine plants within the constraints of overall preference patterns.

3.1.8 Aims and objectives

The aim of this research was to quantify the diets of juveniles and adults of *Siganus doliatus*, *S. fuscescens*, *S. lineatus* and *S. punctatus* at Green Island, looking at ontogenetic changes within species and comparing the pairing and shoaling species. The primary objective was to assess the extent to which diet is related to the nutritional composition of algae and their defensive strategies, in accordance with the predictions made in section 3.1.7. This would allow an evaluation of the assumed status of siganids as Type I herbivores and of how they conform with current theory on digestive mechanisms. The second objective was to determine whether there were differences in diet between any of the species / age groups. Two methods for the quantification of stomach contents were investigated: the intercept method (Jones, 1968b) and the transect method (Choat and Clements, 1993).

3.2 MATERIALS AND METHODS

3.2.1 Specimen collection and initial processing

Specimens of *Siganus doliatus*, *S. fuscescens*, *S. lineatus* and *S. punctatus* were collected from the seven study sites around Green Island Reef between November 1993 and August 1996. Adults were sampled during both summer and winter periods, while juveniles were only available during the summer recruitment period (see Chapter 1).

Adult fish (defined by a standard length of greater than 110 mm, and by possessing gonads) were captured with a speargun while using SCUBA. They were taken to the boat and pithed immediately, and placed on ice to prevent deterioration. Juvenile fish (defined by a standard length of less than 110 mm and by the absence of gonads) were collected using a 15 m long beach seine net with a cod end (mesh size: 9 mm stretch) which was walked through the seagrass beds on the reef flat at mid-tide. On removal from the net, fish were placed in a bucket of seawater, which was put in the freezer as soon as possible. The same specimens were used for both dietary and morphological analyses, but the details of the morphometric measurements will be given in Chapter 4.

In the laboratory on the island, adult specimens were weighed to the nearest gram and standard length was measured to the nearest millimetre. The contents of the gut cavity were dissected out, and the gonads and other viscera were removed. The alimentary tract was unravelled and morphometric measurements were taken, then it was preserved whole, with the contents inside, in 10 % formalin in seawater. The rest of the fish was frozen to allow further morphometric measurements at a later date.

Frozen juveniles were returned whole to the laboratory at James Cook University (J.C.U.) where they were weighed to the nearest 0.1 g and measured to the nearest 0.1 mm. The alimentary tract was dissected out with the aid of a microscope, then unravelled, and measured. Other morphometric measurements were also made at this time. Following this, the stomach was put aside for immediate analysis of its contents and the rest of the gut was preserved in 10% formalin in seawater.

3.2.2 Stomach contents analysis

Proportional occurrence, numerically or by weight or volume, is the most common measure of dietary composition (see review by Hyslop, 1980). For herbivorous fishes, two-dimensional estimates of percentage cover similar to those used to assess vegetation cover are becoming more commonly used (e.g. Jones, 1968b; Bryan, 1975; Montgomery *et al.*, 1989; Axe, 1990; Choat and Clements, 1993; Clements and Choat, 1993).

The decision to use a two-dimensional quantification technique for this study, rather than calculating proportions by weight or volume (e.g. Horn *et al.*, 1982; Horn, 1983), was based on the nature of the plant fragments, which were generally small and flat. Flat surface area was therefore considered a reasonable measure on which to base an estimate of proportional composition. Physical separation of such small items for weighing would have been very time consuming, and the juveniles had only small quantities of material in their stomachs which would have been very difficult to weigh accurately.

In a pilot study to select the most appropriate means of dietary analysis for these fish, the stomach contents of the first sixteen adult specimens of *S. doliatus* and *S. lineatus* and all thirteen adult specimens of *S. fuscescens* were analysed using two percentage cover methods: a modification of the intercept method proposed by Jones (1968b), and the transect method, proposed by Lucas and Seber (1977) and modified by Choat and Clements (1993). The intercept method was modified to allow a single sample to be quantified using both methods.

Five transect lines were marked on a piece of 1 mm graph paper: each transect was 5 cm long, and the lines were drawn 1 cm apart. The paper was secured to a glass petri dish (9 cm in diameter) so that the grid was visible through the base. The stomach was slit open and the contents scraped into the petri dish with the aid of a dissecting microscope to ensure all material was extracted. The contents of the stomach were spread out evenly in a single layer, covering as much of the grid as possible. In the few cases where there was too much material to permit easy identification, the sample was thinned by haphazardly removing small amounts of material and spreading out the rest.

The stomach contents were quantified using a dissecting microscope with a 1 cm cross-hair micrometer eyepiece. For the intercept method, the 17 intersections of the millimetre marks and the cross-hairs were used as intercept points (Figure 3.1), and the food item below each point was recorded. The grid was positioned by aligning the centre of the cross-hairs with the centimetre marks on the transect lines (Figure 3.1). There were thirty such marks on the transect lines, but the original method (Jones, 1968b) required only 27 grids, therefore three randomly selected marks were omitted. At a magnification of x 16, the length of the cross-hairs covered 6.25 mm of the graph paper. This magnification was used in order to impose a gap between adjacent grids. Since the outer intercepts were 5 mm apart, this method sampled 6.75 cm^2 or 27 linear cm of the petri dish. A total of 459 intercept points were examined, but proportional composition was calculated based on the number of points for which a food item had been recorded.

For the transect method, the vertical line of the cross-hair micrometer was aligned with the transect lines on the graph paper (Figure 3.1). At a magnification of x 10, the micrometer covered 10 mm of the graph paper and superimposed a scale that was subdivided to 0.1 mm. The length of the transect covered by a given food item was then measured to the nearest 0.1 mm. For very small items, the magnification could be increased to x 40 and items could then be measured to the nearest 0.025 mm. This method sampled a total of 25 linear cm of the petri dish. Proportional composition was calculated based on the total length of recorded items.

Plant material was identified to the lowest possible taxonomic category using keys, descriptions and illustrations provided in Cribb (1983), Lanyon (1986), Clayton (1990), Delaney (1990), Kraft and Woelkerling (1990), Phillips (1990) and Price (1991). The identification levels varied from species to family, depending on the distinctiveness and size of the fragment. Any animal material present was identified to a broader level, usually between order and phylum.

To reduce the number of variables, items were assigned to 18 taxonomic and structural categories (Table 3.1) based on the major algal divisions and the functional form groups of Littler *et al.* (1983). Several algal genera were maintained as separate categories because of their secondary metabolite chemistry. Large and small fleshy rhodophytes were divided at 300 μm because most genera fitted well into one category or the other. The decision was also based on the fact that the species in the "large" category have slightly bulkier thallus forms and are visible with the naked human eye.

Table 3.1. Categories of items from stomach contents analysis, with definitions and / or lists of main components.

Category	Definition / Main Components
Seagrasses	*Cymodocea spp., Halodule uninervis, Halophila ovalis Syringodium isoetifolium, Thalassia hemprichii*
Filamentous cyanophytes	primarily *Lyngbya spp.*
Filamentous phaeophytes	mostly Ectocarpaceae plus others
Membranous phaeophytes	*Padina spp., Lobophora variegata*
Fleshy phaeophytes	*Sargassum spp., Colpomenia sp.* and others
Dictyota spp.	membranous phaeophytes known to possess anti-herbivore secondary metabolites
Filamentous chlorophytes	*Cladophora spp., Bryopsis sp.* and others
Membranous chlorophytes	*Anadyomene sp., Ulva sp.*
Fleshy chlorophytes	*Caulerpa spp.*
Halimeda spp.	calcareous macroalgal chlorophytes
Filamentous rhodophytes	*Ceramium spp., Griffithsia spp., Tolypiocladia sp., Aglaothamnion spp.* and others
Membranous rhodophytes	*Amansia glomerata, Hypoglossum spathulum, Leveillea jungermannioides*
Small fleshy rhodophytes	fleshy rhodophytes where the main axis had a diameter < 300 μm, e.g. *Caulacanthus indicus, Gelidiopsis spp., Lomentaria spp., Gelidiella spp., Pterocladia caloglossoides* and others
Large fleshy rhodophytes	fleshy rhodophytes where the main axis had a diameter >300 μm, e.g. *Hypnea spp., Gracilaria spp., Champia spp., Gelidiella acerosa, Chondria spp., Coelarthrum spp., Pterocladia caerulescens, Scinaia sp.* and others
Calcareous rhodophytes	*Jania spp., Amphiroa spp.* (only geniculate forms were eaten)
Laurencia spp.	large fleshy rhodophytes known for their powerful secondary metabolites
Animal material	all taxa - Foraminiferida, Porifera, Alcyonaria, Nematoda, Crustacea, Ascidiacea
Detritus and other material	dead and decaying material, usually of phytal origin

Based on the results of the pilot study (see Results section 3.3.1), the modified intercept method was chosen as the better method for estimating proportional composition of diet components. The remainder of the specimens were assessed using this method alone.

3.2.3 Data analysis

Fleshy and membranous chlorophyte algae were both infrequent components of siganid diets so the two categories were amalgamated under the heading of chlorophytes for analysis. Calcareous rhodophytes were also uncommon, and because they were small and usually co-occurred with other small rhodophytes, they were included in that category for analysis. This reduced the number of categories to 16.

For each species, the results from the two pilot methods were compared using a paired Hotelling's T^2 - test, the multivariate equivalent of a paired Student's t - test (Johnson and Wichern, 1983). A difference matrix was calculated by subtracting the values generated by the transect method from those generated by the intercept method. This difference matrix was tested to determine whether it was significantly different from a null matrix (all values = 0). The test statistic generated, T^2, was compared to the critical distance, c^2, which was calculated from the variance-ratio (F) distribution using the following equation (from Johnson and Wichern, 1983):

$$c^2 = \frac{(n_1 + n_2 - 2)p}{(n_1 + n_2 - p - 1)} F_{p, n_1 + n_2 - p - 1}(\alpha)$$

where n_1 and n_2 are the sizes of the paired samples, p is the number of categories being compared and F is the value of the F – distribution for the given degrees of freedom and α - level. The null hypothesis should be rejected if T^2 is greater than c^2 (Johnson and Wichern, 1983).

The dietary composition data were analysed using Canonical Discriminant Analysis (CDA) to demonstrate the separation between the group centroids. CDA has been recommended for stomach contents analysis (Crow, 1978; Ellison 1978) and is considered a robust technique (McArdle, 1994). The analysis standardises groups (juveniles and adults of the four species) to unit within-sample variance, and the calculations are weighted by sample size. The structure coefficients were used to portray the relationships between the original variables and the new canonical axes, as they are considered more appropriate for describing a response-type situation (McArdle, 1994).

3.3 RESULTS

3.3.1 Pilot study

The results of the comparison between the intercept method and the transect method are summarised in Figure 3.2 and Table 3.2. For each of the three species considered, Figure 3.2 illustrates the mean differences in the proportional composition estimates produced by the two methods. The greatest mean difference for any one category was 0.031, and the 95% confidence intervals overlapped 0 in all but two instances. The greatest differences detected between the methods occurred in the seagrass and filamentous cyanophytes categories for *Siganus fuscescens* and in the seagrass category for *S. lineatus*. The actual mean proportions of these categories in the diets of those two species were 0.53, 0.24 and 0.47 respectively (see Figures 3.4 b and 3.5 b), so a difference in the order of 0.03 was inconsequential. In addition, the differences in the estimates of seagrass proportions in the diets of *S. fuscescens* and *S. lineatus* occurred in opposite directions (Figure 3.2), indicating that there is no systematic bias which causes one method to overestimate this type of food item.

The results of the paired Hotelling's T^2 - test showed that, for the three species tested, there were no significant differences between the results produced by the two quantification methods (Table 3.2). The level of α was set at 0.05. There were not enough samples of *S. punctatus* available to allow this species to be evaluated in the pilot study.

Table 3.2. Results of the paired Hotelling's T^2 – test, where T^2 is the test statistic and c^2 is the critical distance against which it is compared. F is the value of the F – distribution, with the given degrees of freedom and an α level of 0.05, which was used to calculate c^2. H_0 is retained when $T^2 < c^2$.

Species	T^2	$F_{p,\, n_1+n_2-p-1}$ (0.05)	c^2(0.05)	significance
S. doliatus	4.86	2.40	67.5	not significant
S. fuscescens	10.12	2.69	59.6	not significant
S. lineatus	3.83	2.46	65.1	not significant

The choice of methodology must also take practicality into account. The main factor affecting the time taken to quantify stomach contents was the heterogeneity of the sample but, although exact sample processing times were not recorded, it became clear that the intercept method was consistently less time consuming. *S. fuscescens* and *S. lineatus* samples, which were dominated by seagrass and filamentous cyanophytes, were usually quantified in less than 45 minutes using either method. In contrast, *S. doliatus* samples, which were more heterogeneous, took longer to quantify and the time differences were more noticeable: the intercept method usually took 1 to 2 hours, while the transect method took 3 to 5 hours.

Another advantage of the intercept method is that the primary magnification is not restricted by the need to fit in with the units on the transect line, but can be set at a level appropriate to the size of the dietary components. The use of a magnification of x 16 for the intercept method was convenient for the spacing of the grids, and most food items could be readily identified at that degree of magnification. When using a magnification of x 10 for the transect method, it was constantly necessary to increase the degree of magnification in order to positively identify or accurately measure items.

A final consideration in the decision was the extent to which the two methods covered the sample material. The intercept method covered a greater linear area than the transect method - a total of 27 cm as opposed to 25 cm - although that coverage was less intensive. In addition, the spread of the intercept grids meant that a greater proportion of the sample was assessed, as it is a more truly 2-dimensional method.

In the absence of a significant difference between proportional composition estimates provided by the two pilot study methods, or of any evidence of bias, the intercept method was chosen as the most appropriate means of quantifying stomach contents for the remainder of this study because of its processing advantages.

3.3.2 Dietary composition

Rhodophytes and animal material were the main dietary items of both juvenile *S. doliatus* (Figure 3.3 a, n = 25) and juvenile *S. fuscescens* (Figure 3.4 a, n = 20). Filamentous rhodophytes contributed 19.1 (± 4.6) % and 11.7 (± 3.6) %, large rhodophytes 14.5 (± 3.7) % and 15.4 (± 4.0) %, and small rhodophytes 13.3 (± 2.9) % and 9.1 (± 2.3) % to their respective diets. In addition, membranous rhodophytes contributed 18.4 (± 6.1) % of the diet of juvenile *S. fuscescens* and fleshy phaeophytes comprised 11.1 (± 2.8) % of the diet of juvenile *S. doliatus*. Animal material comprised 13.1 % of the diet in both groups, ± 3.9 % and 5.0 % respectively. Referring to Figure 3.7, it can be seen that the groups had similar dietary diversity, consuming items from a mean of 7.2 ± 0.6 and 7.3 ± 0.7 of the 18 food categories respectively. The maximum number of categories consumed by a single individual was 13 in both species.

Filamentous algae were the most important food items for juvenile *S. lineatus*, with phaeophytes comprising 30.2 (± 6.5) % of their diet, chlorophytes 15.4 (± 3.8) %, and rhodophytes 12.8 (± 6.1) % (Figure 3.5 a, n = 14). Animal material was 11.1 (± 5.1) % of dietary intake. The mean number of food categories consumed by this group was 4.3 ± 0.6, while the maximum number was 8 (Figure 3.7).

Animal material was the most important category in the diet of juvenile *S. punctatus*, comprising 32.0 (± 7.7) % of the total intake (Figure 3.6 a, n = 18). Fleshy and filamentous phaeophytes contributed a further 15.7 (± 7.3) % and 15.0 (± 4.9) % respectively, while filamentous and large fleshy rhodophytes contributed 9.3 (± 4.8) %. When the animal material was examined in more detail, most of it was found to be from sessile invertebrates. Sponges were the main component, followed by colonial ascidians. Other items such as foraminiferans, small worms and microcrustaceans were infrequent. The mean number of dietary categories eaten by this group was 4.7 ± 0.6, while the maximum number was 11 (Figure 3.7).

Adult *S. doliatus* were the only group which consumed a significant amount of *Dictyota spp.*: 26.4 (± 3.0) % (Figure 3.3 b, n = 34). Other membranous phaeophyte genera from the same order comprised a further 9.5 (± 1.3) % of the diet. The next most preferred items were all types of rhodophytes, with small and large fleshy genera comprising 15.1 (± 2.0) % and 12.9 (± 1.6) % of the diet respectively, followed by membranous and filamentous genera. As Figure 3.7 illustrates, adult *S. doliatus* had the most diverse diet of all the groups, consuming items from an average of 10.6 ± 0.3 food categories, with a maximum of 14. This implies an expansion of dietary range through ontogeny for this species. There was a shift in emphasis away from animal material and towards species from the order Dictyotales, although rhodophytes played an important role in the diets of both juveniles and adults.

The diets of both adult *S. fuscescens* (Figure 3.4 b, n = 13) and adult *S. lineatus* (Figure 3.5 b, n = 31) were clearly dominated by seagrasses, which comprised 53.1 (± 9.0) % and 44.5 (± 6.7) % of their respective diets. Filamentous cyanophytes, which were avoided by juveniles and adult *S. doliatus*, comprised 24.2 (± 7.7) % and 13.0 (4.2) % respectively. Large fleshy rhodophytes were the only other significant contributor to the diet of species, comprising 12.1 (± 5.7) % and 17.3 (± 5.1) % respectively. When the seagrass data were examined in more detail, *Halodule uninervis* and *Cymodocea spp.* were found to be the most abundant species, while *Syringodium isoetifolium* and

Halophila ovalis occurred less frequently. The presence of different seagrass species may reflect feeding in different areas of the seagrass beds.

The dominance of seagrass in the diet of these fish is illustrated in Figure 3.7. Adult *S. fuscescens* consumed items from an average of 5.1 ± 0.7 food categories, with 10 being the greatest number of categories consumed. Similarly, adult *S. lineatus* consumed items from and average of 3.4 ± 0.4 categories, with a maximum of 11. When the dietary diversity of juveniles and adults of these species was compared, a contraction of the dietary range through ontogeny became apparent. More importantly, these species underwent an extreme shift in dietary composition, changing from a more general diet with an emphasis on rhodophytes and animal material to a highly restricted diet of seagrass with filamentous cyanophytes and large fleshy rhodophytes.

Membranous rhodophytes were the most important dietary component of adult *S. punctatus*, contributing 32.8 (± 14.0) % of their diet (Figure 3.6 b, n = 5). Unlike any of the other species, *S. punctatus* retained a significant proportion of animal material (19.9 (± 5.0) %) in their diet as adults. Seagrass and filamentous cyanophytes were also important contributing 19.0 (± 12.4) % and 12.6 (10.5) % respectively. As with the juveniles, the animal material was comprised mostly of sessile invertebrates, mainly colonial ascidians and sponges. Figure 3.7 shows that the mean number of categories from which items had been consumed was 7.4 ± 2.3, but one individual had eaten items from 16 out of the 18 categories. As with *S. doliatus*, there was an expansion in the dietary range of this species through ontogeny. Although the animal material component was maintained, there was a shift away from filamentous algae of the major divisions towards membranous rhodophytes, seagrass and filamentous cyanophytes.

Animal material was consistently present in the juvenile diets and preferences for delicate growth forms and rhodophytes were apparent. Fleshy phaeophytes were only eaten by juvenile *S. doliatus* and *S. punctatus*. Calcified algae, filamentous cyanophytes, membranous phaeophytes and larger chlorophytes were not eaten by any of the juveniles, while *Dictyota spp.* and *Laurencia spp.* were eaten in insignificant amounts. Despite their living in the seagrass beds, seagrass never comprised more than 5 % of the diet of juvenile siganids.

In contrast, seagrasses were the dominant component in the diets of the shoaling adults. Filamentous cyanophytes were eaten by three of the four species, and *Dictyota spp.* were consumed in large quantities by adult *S. doliatus*. Calcified algae and chlorophytes were still avoided, and consumption of *Laurencia spp.* was still negligible.

In addition, detritus was no longer consumed, and consumption of animal material was restricted to *S. punctatus*.

Figure 3.8 shows the first two discriminant axes of the CDA, which summarises the previous data with an emphasis on the differences between the groups. These first two axes account for 81.8 % of the total variation in the data set. Discriminant axis 1 (on the horizontal) accounts for 45.9 % of the variation, and acts to separate the juvenile groups from the adults. The trend plot shows that positive values on this axis are associated with the consumption of filamentous phaeophytes and chlorophytes, animal material and detritus. The centroids of all four juvenile groups are tightly clustered on this half of the axis (Plot A). When the spread of the data is examined (Plot B), it is obvious that the juveniles of all species have very similar diets as the individual data points from all four groups are intermingled throughout this area. Negative values on axis 1 are associated with the consumption of seagrass, *Dictyota spp.*, other membranous phaeophytes and filamentous cyanophytes, all of which are important components of the adult diets.

Discriminant axis 2 (on the vertical) accounts for a further 35.9 % of the variation in the data, and acts to separate the adults of the pairing species from those of the shoaling species. The trend plot shows that positive values on this axis are associated with the consumption of *Dictyota spp.*, other membranous phaeophytes and small rhodophytes. Adult *S. doliatus* are clearly isolated in the upper left quadrant of both plots. Negative values on this axis are associated with the consumption of seagrass and filamentous cyanophytes. The group centroids for the adults of the two shoaling species, *S. fuscescens* and *S. lineatus*, are positioned together in the lower left quadrant, and the data points for individuals of these groups were intermingled within that space. Adult *S. punctatus* retain dietary characteristics similar to those of the juveniles through their consumption of animal material, but they also consume rhodophytes, seagrass and blue-green algae. Their central position on Plot A and the wide spread of their data points of Plot B reflect their generalist / opportunist tendencies.

3.4 DISCUSSION

The results of this study indicate a number of general and specific features of siganid diets, not all of which are in line with the predictions for dietary composition in section 3.1.7. The Canonical Discriminant Analysis (CDA) shows that there are dietary differences within a species, through ontogeny, and between adults of the different species. Juveniles of all species have very similar diets. *Siganus doliatus* expands its dietary range through ontogeny, with a change in emphasis on target categories. *S. fuscescens* and *S. lineatus*, the shoaling species, exhibit a radical shift in diet, away from both the juveniles and the adult *S. doliatus*, and they undergo a contraction in dietary range. These groups form three very distinct clusters on the canonical graph, while the adult *S. punctatus* are located in the middle of them. Although there is some overlap in the diets of the different species / age groups, a reasonable degree of differentiation is present based on both age and species.

Rhodophytes of various structural forms were consumed in varying quantities by all groups, hence their notable presence in the univariate graphs and their lack of influence in the CDA. When considered as a whole, uncalcified rhodophytes comprised between 23.4 % and 54.6 % of juveniles diets, and between 16.1 % and 44.5 % of adult diets. *S. doliatus* was a consistent consumer of high proportions of rhodophytes, while *S. fuscescens* reduced their intake through ontogeny. Both *S. lineatus* and *S. punctatus* consistently ate moderate amounts of rhodophytes.

Phaeophytes comprised between 11.2 % and 33.0 % of juveniles diets, largely because of their high consumption of filamentous species, although *S. doliatus* and *S. punctatus* juveniles did eat significant amounts of fleshy phaeophytes. Of the adults, *S. doliatus* was the only species where phaeophytes comprised a significant proportion diet. Their consumption of *Dictyota spp.* and other membranous species nearly equalled their consumption of rhodophytes. The only group that consumed a significant amount of chlorophytes were juvenile *S. lineatus*, where filamentous species comprised 15.4 % of their diet.

These findings conform with the general prediction that, based on the biochemistry of the three major taxa (Percival, 1979; Kloareg and Quatrano, 1988), rhodophytes should present the most readily digestible food source to Type I herbivores, followed by phaeophytes, with chlorophytes the least digestible. Tropical chlorophytes possess a wide range of chemical defenses however (Paul and Fenical, 1987), and secondary metabolite chemistry may offer an alternative explanation, beyond digestive chemistry, for the fact that larger chlorophytes (membranous and fleshy forms) were not generally eaten. It is not possible to distinguish between reasons for avoidance, but this alternative rationale still conforms to the selection predictions.

The presence of a number of chemically defended algal genera in the diets of these fish was in contradiction to the prediction that such items should generally be avoided. *Laurencia spp.* were eaten in small amounts by all groups (except adult *S. punctatus*) despite the fact that Hay *et al.* (1988) found that their secondary metabolites deterred feeding by adult *S. doliatus*. More significantly, large quantities of *Dictyota spp.* were eaten by adult *S. doliatus*, and filamentous cyanophytes were a major component in the diets of the other adults. Yet Hay *et al.* (1988) found that *Dictyota spp.* metabolites significantly reduced feeding by *S. doliatus* and Thacker *et al.* (1997) found that metabolites from the cyanophyte *Lyngbya majuscula* deterred feeding by *S. spinus*, although in the second experiment deterrent effects were reduced when fish were hungrier (see also Cronin and Hay, 1996). In contrast, feeding trials with *S. argenteus* (Paul *et al.*, 1990) and *S. spinus* (Paul *et al.*, 1993) found that secondary metabolite chemistry could not explain the feeding preferences of these fish. Interestingly, this experiment was the only one to combine trials using actual plant pieces with trials using palatable algae coated with extracts from the defended plants; the other experiments used extract trials only.

The most likely explanation for these apparent contradictions is that the current data simply reflect the relative abundance of these algae at Green Island reef, away from the manipulations of feeding trials. The finding by Thacker *et al.* (1997) that deterrent effects were reduced when fish were hungry supports this. A consideration of the nutritive value of these food items suggests a further explanation. *Lyngbya spp.* had the highest nitrogen levels found in tropical algae from oligotrophic waters, and *Dictyota spp.* had the third highest (Atkinson and Smith, 1983). The former could be influenced by the protein in the cell coverings of cyanophytes (Price, 1990; Delaney, 1990). Comparatively high nutrient values (2 % to 3 % nitrogen, as opposed to the mean value of 1.3 %: Atkinson and Smith, 1983), might explain the willingness of siganids to consume these unpalatable algae under natural conditions (Horn *et al.*, 1986).

An important prediction based on marine plant chemistry - that siganids, as Type I herbivores, should not eat seagrasses - has been contradicted. Although the presence of an item in the diet does not guarantee that it is being assimilated, the abundance of seagrass in the diets of three adult groups implies a need to re-examine the assumptions that all siganids utilise a solely acid-based digestive strategy and that seagrasses are only minimally susceptible to this type of digestive system. Seagrass is the most abundant vegetation at Green Island reef (see Chapter 2), and it dominates the diet of the shoaling adults. These data may represent a quantity versus quality trade-off (Targett and Targett, 1990), where diet has adapted to availability. The situation may be mediated by the selection of specific plant parts in order to maximise nutritional value. Observations of siganids feeding on seagrass noted fish taking bites from the base of the leaves, the site where new leaf material is produced (Fry, 1983; Zieman, 1984; Lanyon, 1986). This new growth has the highest protein content of the various plant parts (Zieman *et al.*, 1984), and levels may even be higher than those available in co-occurring algae (Lowe and Lawrence, 1976; Dawes *et al.*, 1979). It should also provide the best opportunities for successful acid-based digestion due to the lower lignin concentrations (Bjorndal, 1980; Vincente *et al.*, 1980).

Work by Lobel and Ogden (1981) on Caribbean congenerics of *Halodule*, *Syringodium* and *Thalassia* suggest that parrotfish may assimilate the first two seagrass genera more efficiently than the last, although this is dependent on cell wall disruption by the pharyngeal mill of the scarids. The abundance of these potentially more digestible genera in the diets of siganids (along with a genus not included in the Caribbean study) lends credence to the above interpretation. It is possible that the seagrasses were consumed as a means of rapidly consuming large quantities of epiphytic material, but selection of leaf bases implies that the prime reason for eating seagrass was not to gain access to epiphytes, which are more common on the older parts of the plant (Heijs, 1985; Borowitzka and Lethbridge, 1989). The surfaces of leaves examined during stomach contents analysis did not appear to have heavy epiphyte loads.

It seems likely that acidic secretions in the stomach can weaken the cell wall by affecting pectin molecules and / or hydrogen bonds between the cellulose strands (Ting, 1982; Wilkins, 1984), and this would at least allow a slow leaching of the cell contents. It is also possible that there are features peculiar to, or more developed in, the digestive systems of the shoaling siganids that may enhance the effectiveness of acid-based digestion on seagrass. Contrary to most other authors, Lam (1974) describes siganid stomachs as "rather thick-walled", and reference material is cited (Suyehiro, 1942; Hiatt and Strasburg, 1960). These three studies examined shoaling rather than pairing siganids. An examination of gut morphology in all four study species should therefore be considered.

Further predictions regarding dietary composition were based on algal functional form groups. Filamentous algae of the major taxa comprised between 21.1 % and 58.4 % of the diets of juvenile siganids. In contrast, filamentous algae comprised less than 30 % of the diets of adults, and these values were strongly influenced by the consumption of filamentous cyanophytes, which were not consumed by the juveniles. Membranous algae were not common in the diets of the juveniles, with only *S. fuscescens* consuming significant amounts. They were the most abundant functional group in the diets of adult *S. doliatus* and *S. punctatus*, but were not significant in the diets of the other adults. Fleshy algae comprised similar proportions of juvenile and adult diets.

Calcified algae were generally avoided, as predicted (Schupp and Paul, 1994). Adult *S. lineatus* and *S. punctatus* consumed negligible amounts of *Halimeda spp.*, and adult *S. fuscescens* and *S. punctatus* had an incidental intake of small calcified rhodophytes which were epiphytic on the seagrass they had consumed. Heavily calcified rhodophytes such as *Galaxaura spp.* and *Liagora spp.* were abundant in the seagrass beds (pers. obs.) but never eaten. It is not possible to isolate the reason behind this avoidance. It can be interpreted either as a rejection of an item which provides very low nutritional return for costly acquisition, or as avoidance of carbonate material which would act as a buffer in an acidic stomach and reduce its effectiveness.

The large amounts of filamentous algae in the diets of the juveniles conform with the predictions that Type I herbivores, particularly juveniles, should consume more delicate growth forms (Littler *et al.*, 1983; Lobel, 1981). The greater representation of fleshy over membranous algae implies that the former structural group is more accessible to juveniles. It is more likely to be a result of the unexpected toughness of tropical membranous rhodophytes such as *Amansia glomerata* (pers. obs.). The only truly delicate membranous species is *Leveillea jungermannoides*, the species eaten by juvenile *S. fuscescens*. The adult diets generally conformed with the predictions based on algal functional morphology.

Aside from rhodophytes, animal material, filamentous algae from the other major divisions and detritus were important components in the diets of the juveniles of all species. This indicates a tendency amongst the juveniles towards more labile dietary items, appropriate for their developing morphology and physiology (Lassuy, 1984; Clements and Choat, 1993; Benevides *et al.*, 1994). Animal material generally comprised 11.1 % to 13.1 % of juvenile diets. It can be considered as supplementary protein for this period of high metabolic requirements and rapid growth (Benevides *et al.*, 1994) in a family that is essentially herbivorous from settlement (Bryan and Madraisau, 1977; Bellwood, 1988). *S. punctatus* present an exception to this rule, and it is interesting that the elevated levels of animal material found in their diet were sustained through maturity. In general however, the juvenile diets conform with the predictions regarding their digestive and nutritional needs.

From the group maxima in Figure 3.7, it is clear that individuals from most species are capable of eating food items from at least half of the dietary categories, and often more, including seagrass. These items are obviously available in their habitat and at least physically accessible to them. This leads on to the issue of feeding preference. For juveniles inhabiting the seagrass beds on the Green Island reef flat, consumption of any food items besides seagrass constitutes preferential feeding simply because of its dominance in their habitat (Figure 2.2 in Chapter 2). The minor presence of seagrass in the diets of juveniles shows that it is physically accessible to them. The fact that they do not consume more of it suggests that it may be inaccessible to them physiologically.

The turf algae that comprise the bulk of siganid diets appeared to be only a minor component of the seagrass bed habitat (see Chapter 2). The majority of the small algal genera found in the stomachs of the juveniles (as listed in the category definitions in Table 3.1) have been recorded growing epiphytically on seagrass blades (May *et al.*, 1978; Heijs, 1985), and presumably also grow on the larger macroalgae such as *Sargassum spp.* and *Halimeda spp.*. As a result, these algae are more abundant than they appear based on the survey of substrate cover alone. Juvenile siganids have been observed feeding on epiphytic material on seagrasses and large macroalgae (Popper and Gundermann, 1975; pers. obs.). A more detailed study of the relative abundance of algal species within the epiphytic communities on benthic plants would be required to determine whether selectivity for various types of turfing algae is occurring.

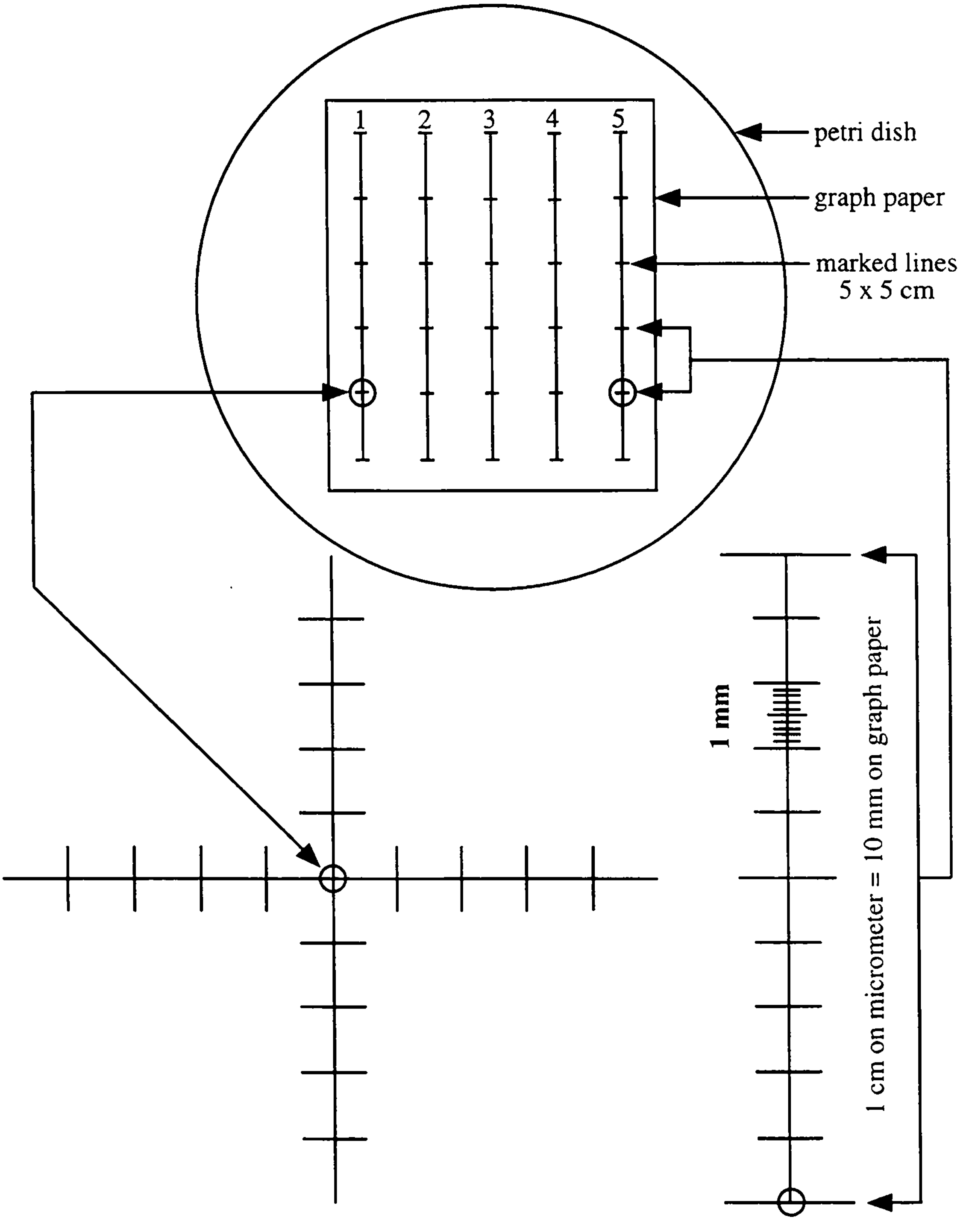
Although turf-covered reef matrix is the dominant benthic cover in the coral areas of Green Island reef (see Chapter 2), preferential feeding by adults of the pairing species cannot be addressed specifically without a detailed study of the epilithic turf algal communities. This is beyond the scope of this study. The dominance of seagrass in the diets of the shoaling species suggests that there is no preferential mechanism operating in the diets of these fish. The dietary patterns of adult siganids reflect the availability of generalised food types (turf or seagrass) in their feeding habitat, but preferential feeding almost certainly operates within these broader categories (Ivlev, 1960; von Westernhagen, 1973; Lundberg and Lipkin, 1979).

The prediction that the shoaling species might have greater dietary diversity than the pairing species because of their wide-ranging habits (Lundberg and Lipkin, 1979) obviously does not apply to this situation. It is even possible that shoaling behaviour may be responsible for the dominance of seagrasses in the diets of *S. fuscescens* and *S. lineatus*. Shoaling in fishes is considered to have a variety of foraging and anti-predator functions (Pitcher and Parrish, 1993), and it is possible that the security of the school might allow more intense or prolonged feeding episodes in a single spot. This implies a tendency for pairing species to move on after shorter, less intense feeding bouts. Stationary videotape evidence (S.W. Purcell, unpubl. data) has shown *S. doliatus* and *S. punctatus* (and other pairing siganids) feeding for prolonged periods in one spot, looking up approximately once every ten bites, then continuing feeding. The dominance of seagrasses in the diets of the shoaling species can thus only be ascribed to the dominance of this item in their feeding areas.

Although small sample sizes may be considered a limitation of this study, the differences in diet between the species / age groups in this study have clearly been demonstrated, regardless. The diet of adult *S. punctatus* showed some interesting features, epitomised by their central position of the CDA plot. A greater number of samples is required to determine whether this species is a true generalist (the source of dietary diversity is the individual), or an opportunist (the source of dietary diversity is the group). The information here is equivocal, with individuals consuming items from between 3 and 16 of the 18 dietary categories, but the large standard errors on the proportional composition graph (Figure 3.6) suggest an opportunistic feeding mode. Although *S. punctatus* was mainly used for comparative purposes in this study, further research should prove worthwhile.

3.5 CONCLUSIONS

Siganids at Green Island Reef show significant dietary changes through ontogeny, and there are distinct dietary differences between adults of the pairing and shoaling species. The diets of the juveniles, and of the adults of the pairing species, can largely be explained in the context of the predictions that should apply to Type I herbivores based on algal chemistry and morphology, and by the varying energetic requirements of different ontogenetic stages. The dominance of seagrasses in the diets of adults of the two shoaling species is in contradiction to these predictions, and this bears further investigation. Enzyme and assimilation studies are the next step on the way to determining the true role of seagrasses in fulfilling the nutritional requirements of these fishes. The presence of chemically defended algae in the diets of the adults might be explained by the relative abundance or the high nutritional value of the genera consumed. The juveniles feed selectively on turfing algae and animal material within the seagrass beds, but the diets of the adults are more representative of the relative abundance of items in their feeding areas. The driving forces behind these dietary differences remain unclear. Variable accessibility to or preference for different food items may be the result of a number of physical, physiological or behavioural attributes of the species / age groups concerned.



1 cm on micrometer = 6.25 mm on graph paper

magnification x 16

Intercept method
(Jones, 1968)

Items under the 17 intercept points are recorded. This is repeated for 27 grids, giving a total of 459 points.

magnification x 10

Transect method
(Lucas and Seber, 1977)

The length of the transect covered by each item is measured to the nearest 0.1 mm. Total length = 25 cm.

Figure 3.1 Illustration comparing the Intercept and Transect methods used for stomach contents analysis.

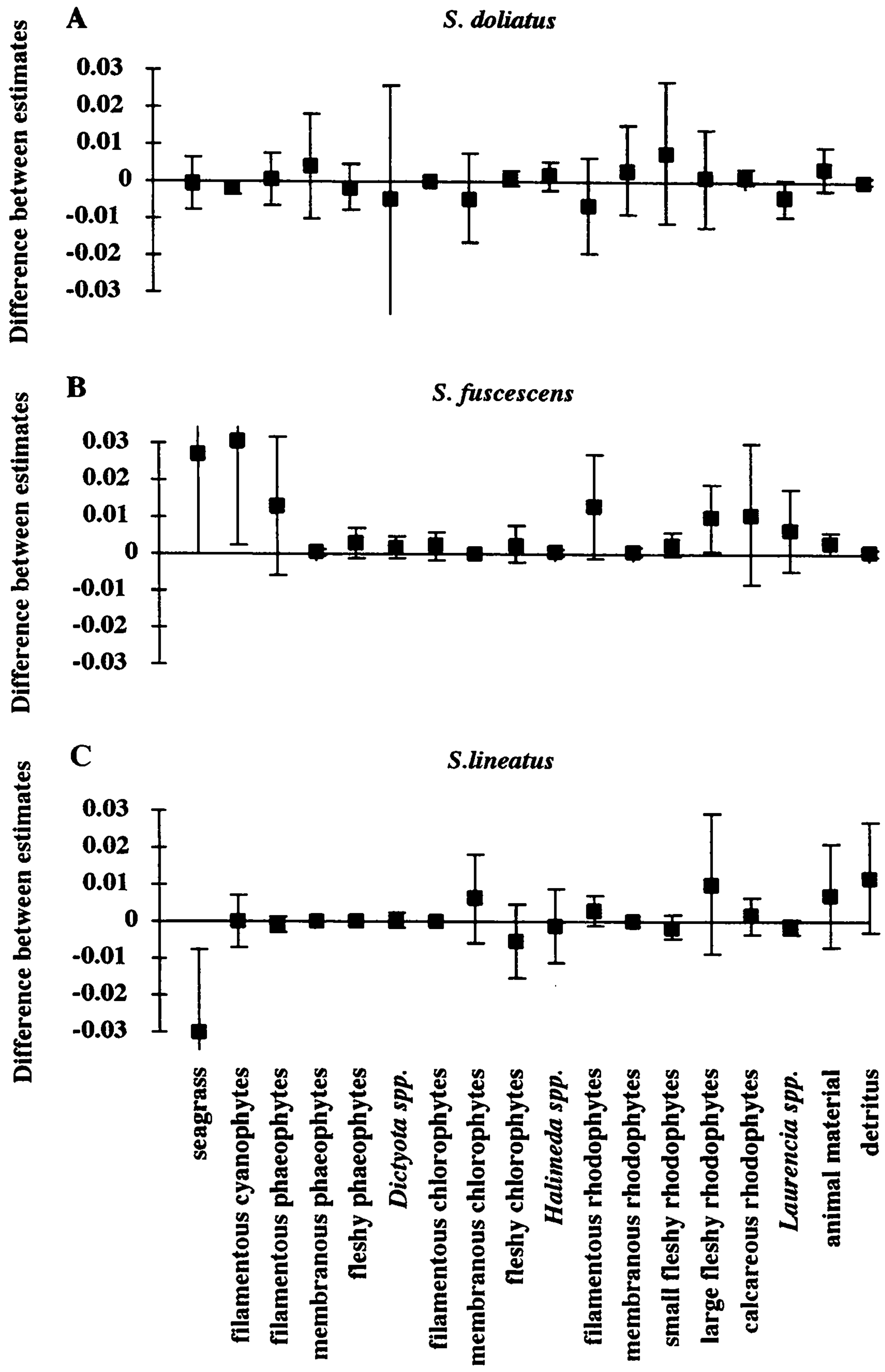


Figure 3.2 a, b and c. Differences in proportional composition estimates produced by the two pilot study methods, with 95 % confidence intervals.

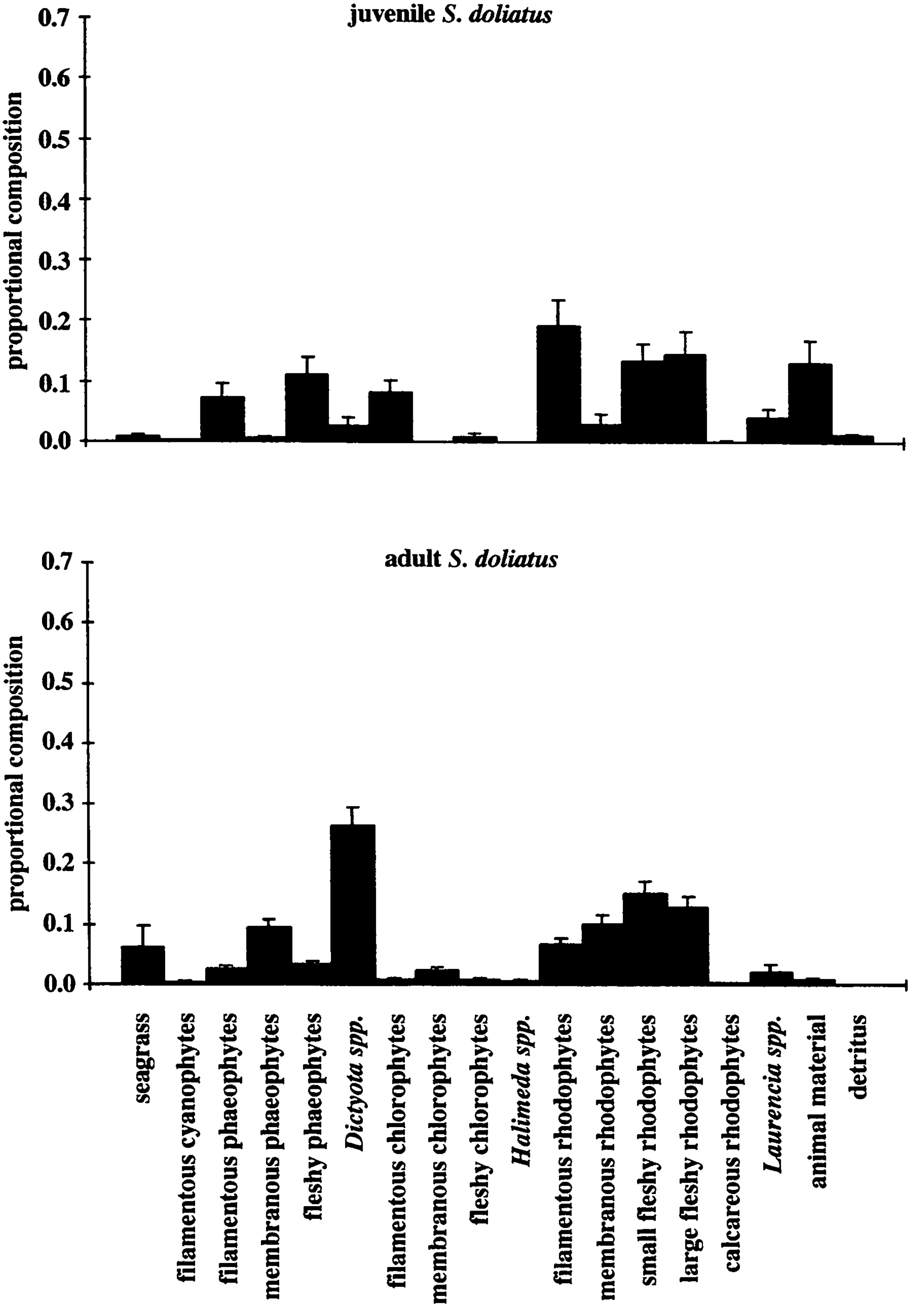


Figure 3.3 a and b. Mean proportional composition of the diets of juvenile and adult *Siganus doliatus* (± 1 S.E.).

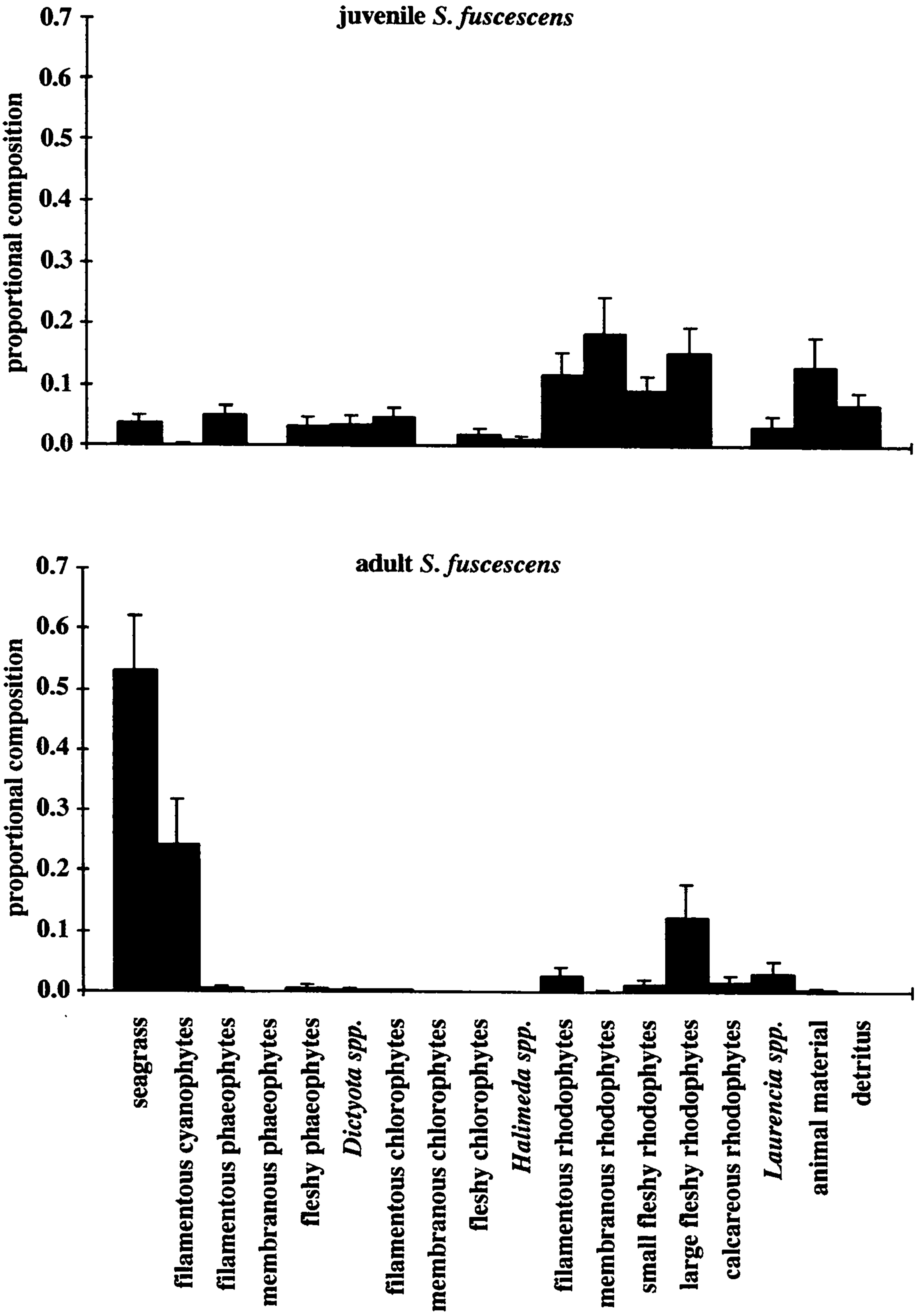


Figure 3.4 a and b. Mean proportional composition of the diets of juvenile and adult *Siganus fuscescens* (± 1 S.E.).

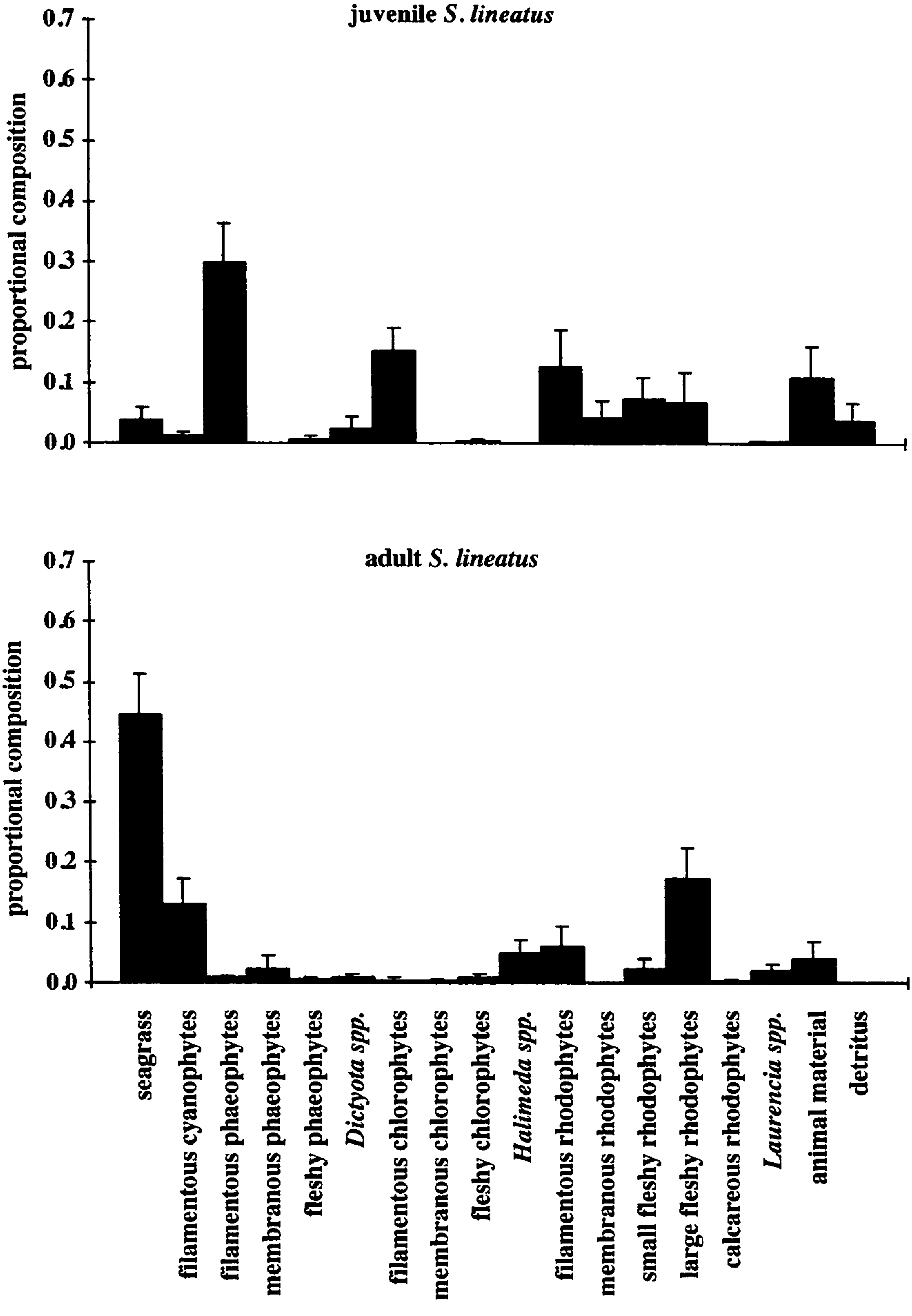


Figure 3.5 a and b. Mean proportional composition of the diets of juvenile and adult *Siganus lineatus* (± 1 S.E.).

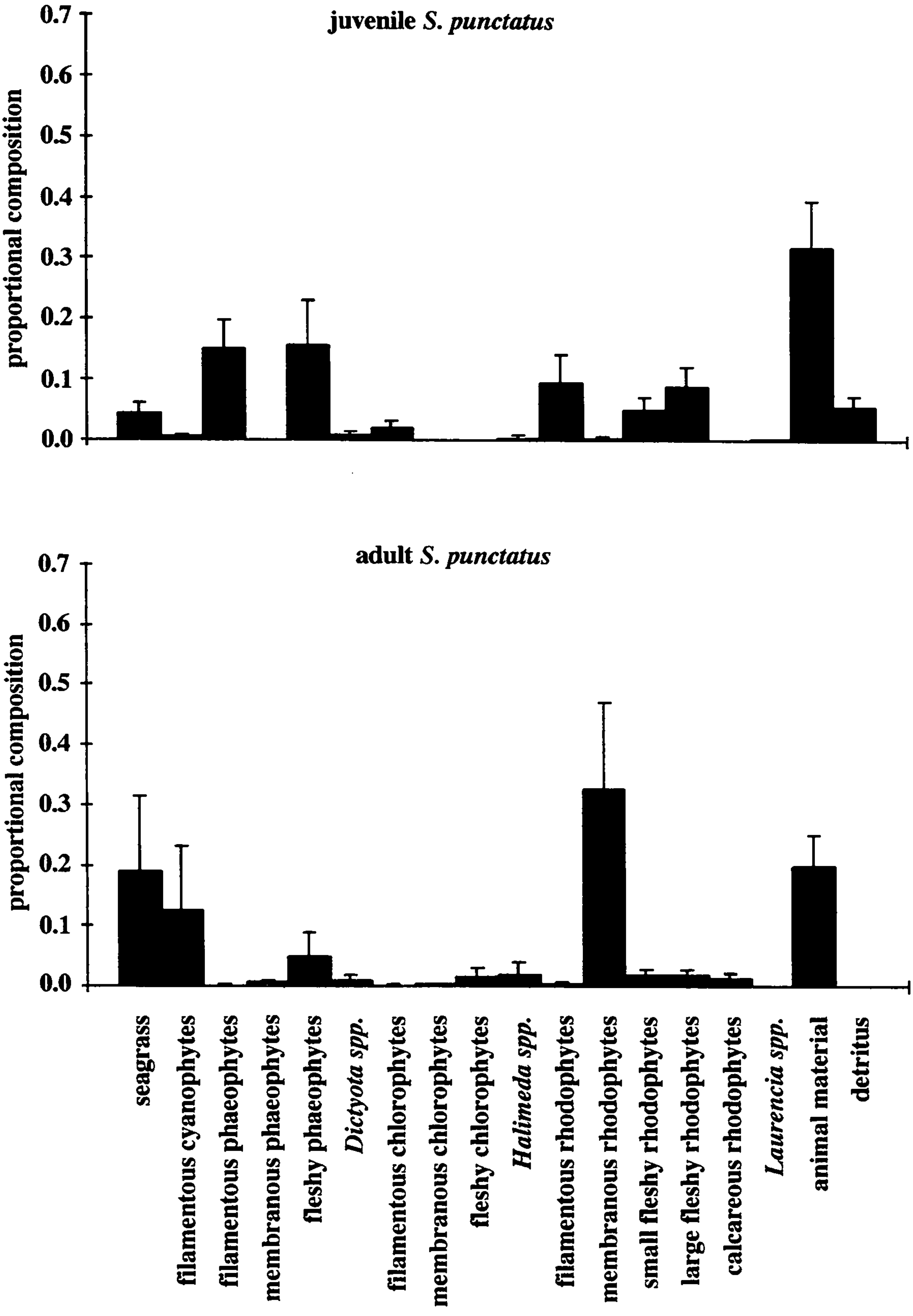


Figure 3.6 a and b. Mean proportional composition of the diets of juvenile and adult *Siganus punctatus* (± 1 S.E.).

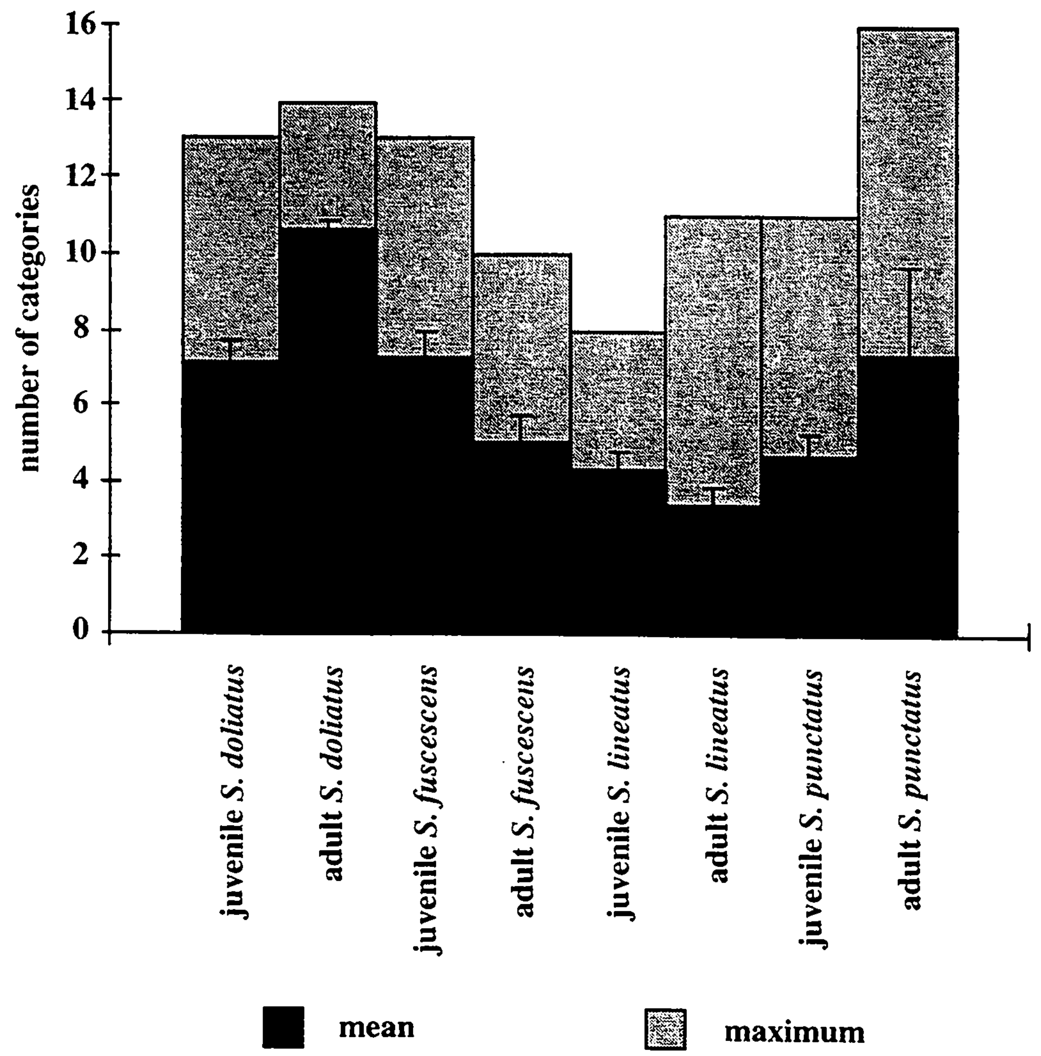


Figure 3.7. Mean and maximum number of food categories consumed by individuals from each species / age group. (Means are ± S.E.)

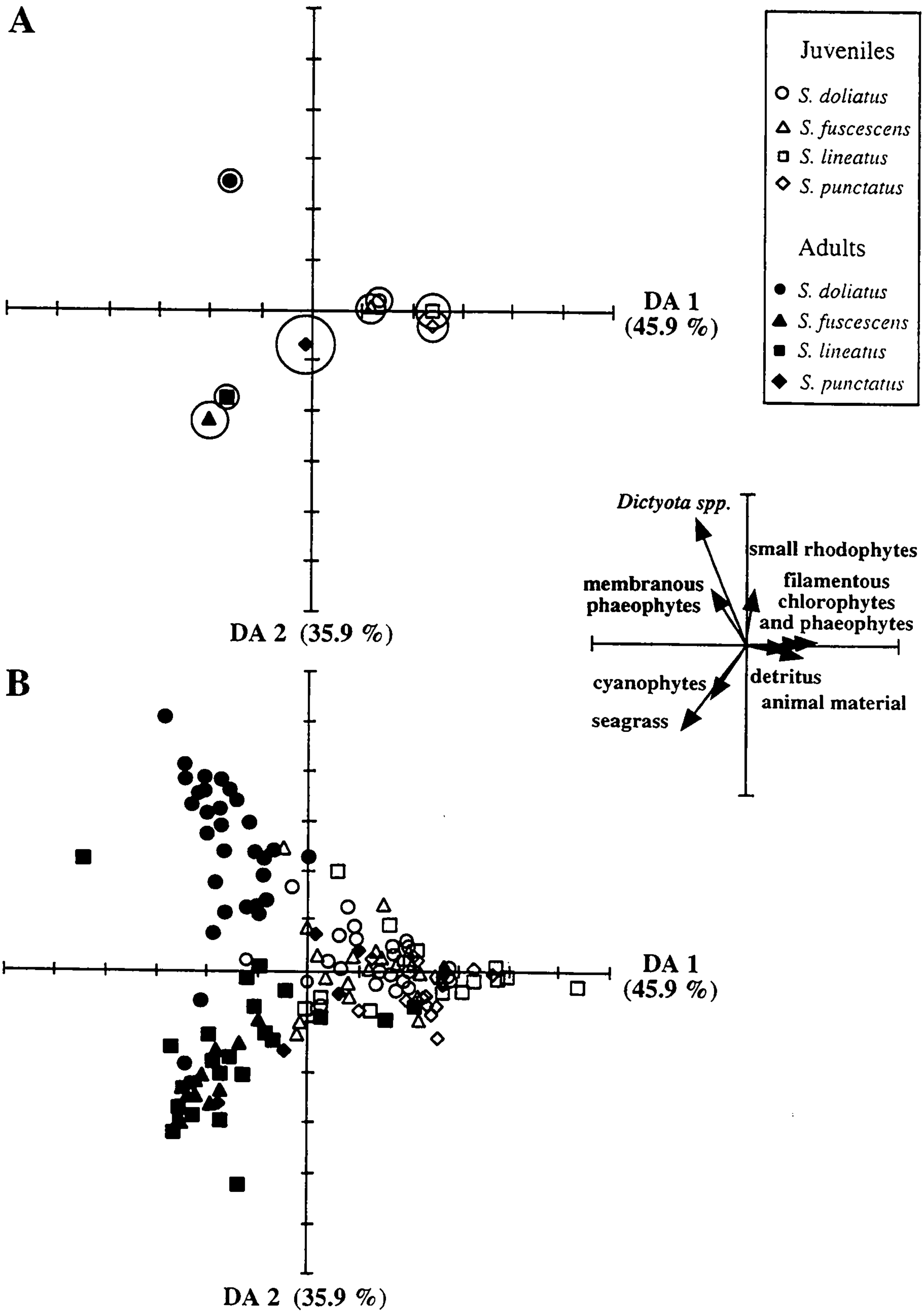


Figure 3.8 a and b. Canonical Discriminant Analysis of diet data.
Plot A shows the position of the group centroids, with 95 % confidence ellipsoids, on the first two discriminant axes. Plot B shows the spread of all species / age groups. Discriminant axes 1 and 2 account for 81.8 % of the variation in the data. The inset trend plot shows the relationship between these new axes and the original variables.

CHAPTER 4

ECOMORPHOLOGY OF SIGANIDS:

Ontogenetic and interspecific comparisons of feeding and digestive morphology

4.1 INTRODUCTION

The study of ecomorphology is based on the assumption that morphology reflects feeding ecology, and that differences in diet are correlated with morphological differences (Keast and Webb, 1966; Motta, 1988; Norton, 1995; Wainwright, 1996). There are numerous studies detailing the gross morphological differences between the feeding apparatus and alimentary tracts of fishes with different feeding habits, but many are concerned with the dramatic differences that can be seen between carnivores, omnivores, and herbivores (Suyehiro, 1942; Al-Hussaini, 1949; Zihler, 1982; Hofer, 1988). Some studies have compared morphological adaptations to the various levels of carnivory (Keast and Webb, 1966; de Groot, 1971; Turingan and Wainwright, 1993). There are examples of morphological specialisation between sympatric congeners (Murie, 1994; Wainwright, 1996) and of morphological differences between isolated populations of a species with varying food sources (Alevizon, 1976).

Herbivores are more often classified by their mode of feeding (browsing or grazing: Hiatt and Strasburg, 1960; Jones, 1968a; Ogden and Lobel, 1978; Horn, 1992), or by their digestive strategy (Horn, 1989), rather than by the size or taxon of the food items they consume. Comparisons have been made between browsers and grazers (Clements and Bellwood, 1988) and between digestive strategies (Jones, 1968a). An analysis of the Scaridae (Bellwood and Choat, 1990) has shown that, in this family, two functional groups, with distinct morphologies and behaviours, exist within the grazing mode. Thus, although siganids are all considered browsers with Type I digestive mechanisms (Horn, 1989, 1992), the dietary differences between siganids at Green Island Reef (Chapter 3) suggest that associated differences in morphology may be present.

4.1.1 Allometric growth patterns

Few structures within a growing organism retain the same relative proportions (isometric growth) because of the need to maintain their various physiological or mechanical functions (Gould, 1966). Maintaining function via differential growth rates often results in changes in shape (allometric growth), which may have ecological consequences (Moltschaniwskyj, 1995). Allometric growth often occurs in structures whose physiological functions are area-dependent, because area and volume respond differently to increased length (Gould, 1966). The digestive system falls into this category because the absorption of digested food is a function that is dependent on surface area. In addition, mechanical and size restrictions of other body structures may force juveniles and adults to lead different lifestyles (Werner and Gilliam, 1984).

4.1.2 Gut development and the importance of gut structure in digestion

With a few exceptions, herbivorous fishes have longer digestive tracts than non-herbivorous species of the same size (Barton, 1982; Horn, 1989). Greater gut volume increases the quantity of food that can be retained in the gut, allowing for a trade-off between food quantity and quality while maintaining the amount of time allowed for digestion (Sibly and Calow, 1986; Horn, 1989). Although increased storage could also be achieved by increasing the diameter of the alimentary tract, an increase in length provides a greater increase in absorptive surface area relative to volume provided the mucosal pattern (folded, smooth, etc.) remains the same. Thus, an increase in gut length is associated with an increase in the capability to digest macroalgae (Benavides *et al.*, 1994). For this reason, gut length is the most common morphometric measure in studies of herbivorous fishes. However, relative gut length is highly variable, and may be affected by the nutritional status of the fish (Montgomery and Pollak, 1988; Horn, 1989), resulting in the need for a cautious sampling protocol.

In the many species which have a carnivorous or omnivorous juvenile stage, and then become herbivorous later in life, an increase in relative gut length usually accompanies the ontogenetic change in feeding habits (Barton, 1982; Horn, 1989). Greater relative growth of the gut during the juvenile phase or rapid transitional increases in gut length are exhibited by a number of herbivorous species (Montgomery, 1977; Lassuy, 1984; Rimmer, 1986; Clements and Choat, 1993; Benevides *et al.*, 1994). However, these studies of gut development in herbivores have all centred on single species. Although there have been comparative studies of adult fish (e.g. Jones, 1968a), there was no ontogenetic component in the comparisons.

Buddington and Diamond (1986) have suggested that the pyloric caeca of fishes may provide an additional means of increasing the surface area of the gut. A number of functions have been suggested for the caeca, including the secretion of proteolytic enzymes and the absorption of the products of digestion (Overnell, 1973; Buddington and Diamond, 1986 and 1987). However, most recent studies have been conducted on carnivorous species (Overnell, 1973; Buddington and Doroshov, 1986; Pedersen and Falk-Pedersen, 1992). Little is known about the role of pyloric caeca in herbivorous fishes, although Buddington and Diamond (1987) have implied that caeca have a less significant role in herbivores than carnivores because they are generally less well developed. However, several herbivorous species have large numbers of caeca (Horn, 1989) and their potential role in digestion should not be ignored.

The varying digestive strategies in herbivorous fishes are largely centred around morphological specialisations (Horn, 1989), and it is possible that, even in closely related species, dietary differences may be associated with differences in gut morphology (Murie, 1994; Clements and Choat, 1997). Although the closely related acanthurids display a variety of intestinal coiling patterns (Mok, 1977), the pattern for siganids appears to be consistent between species, and the general layout of the gut is the same (Suyehiro, 1942; Bryan, 1975; Bryan and Madraisau, 1977). It seems unlikely that there will be any dramatic differences in gut structure between species, but small variations are possible.

4.1.3 The role of head structure in feeding

Comparative ecomorphological studies of tropical herbivores have focussed on feeding morphology, particularly differences in jaw and tooth structure, and differences in the pharyngeal apparatus (Clements and Bellwood, 1986; Bellwood and Choat, 1990; Purcell and Bellwood, 1993). The shape of the teeth has been shown to be a key factor in the differential food procurement of some acanthurids (Purcell and Bellwood, 1993), but in siganids teeth are considered identical between species (Woodland, 1990).

Siganids are unusual among teleosts in that their upper jaw is not protrusible (Woodland, 1990). Their nibbling biting action is the result of the jaw rocking up and down on the tip of the palatine, which is firmly attached to the nasal bone and thus cannot initiate protrusion (Alexander, 1967; Woodland, 1990). As jaw protrusion can influence the aperture of the mouth and is often associated with bottom feeding (Alexander, 1967), this characteristic may have important consequences for a benthic herbivore. Both the height of the gape and access to the substratum could be affected.

Protrusion and free movement of the jaws are important means of increasing gape height and thereby the amount of contact with the feeding surface in the grazing feeding behaviours exhibited by some scarids and acanthurids (Bellwood and Choat, 1990; Purcell and Bellwood, 1993). In contrast, restricted jaw movement is usually associated with smaller gapes and an increase in bite power needed to crush hard prey or excavate hard substrata (Bellwood and Choat, 1990; Turingan and Wainwright, 1993). This seems an unlikely adaptation for a browsing herbivore however, but the effects of this lack of protrusibility on the gape height of siganids have not yet been investigated.

Juvenile siganids appear morphologically similar, but during development superficial differences in morphology between pairing and shoaling species become apparent (pers. obs.). Generally, the shoaling species attain a larger terminal size than the pairing species (Woodland, 1990), although *Siganus punctatus* is an exception. More specifically, *S. doliatus* and *S. punctatus* appear deeper bodied with slightly protuberant snouts, while *S. fuscescens* appears streamlined with a rounder snout. *S. lineatus* appears to fit between these two groups, possessing the deeper body form, but with the rounder snout. The intention is to quantify these differences and examine them in the context of the dietary differences between the four species.

4.1.4 Aims and objectives

The aim of this study was to describe the structures associated with feeding and digestion in the four study species, looking specifically for ontogenetic and interspecific differences in morphology. The relative growth of the intestinal tract, both as a whole and in terms of specific structures, was compared between species. Interspecific differences in stomach structure were compared qualitatively. Development of the pyloric caeca was compared between species. Ontogenetic changes and interspecific differences in head dimensions and gape height were assessed. The objective was to examine any morphological differences in the context of ontogenetic development and known interspecific differences in diet (Chapter 3).

4.2 MATERIALS AND METHODS

Specimens of the four study species were collected as described in Chapter 3. Standard lengths were measured at the time of collection. Adult gut length measurements were taken from fresh material in the field laboratory on Green Island, while head measurements were taken from frozen specimens in the laboratory at J.C.U. All juvenile measurements were taken in the laboratory from frozen specimens. A variety of different morphometric measurements, as described in the following sections, were made on each individual. The number of specimens used per species / age group is listed in Table 4.1.

Table 4.1. Sample sizes for morphometric analyses, and the standard length range of individuals in the sample.

	S. doliatus	*S. fuscescens*	*S. lineatus*	*S. punctatus*
Juveniles	26	22	22	18
(SL range)	(24.5 - 76.8 mm)	(25.5 - 102.4 mm)	(24.5 - 76.4 mm)	(27.4 - 94.4 mm)
Adults	52	13	45	5
(SL range)	(113 - 211 mm)	(135 - 247 mm)	(191 - 335 mm)	(220 - 285 mm)

4.2.1 Alimentary tract measurements

The alimentary tract was dissected out, unravelled, and the lengths of the following sections measured: oesophagus, cardiac (anterior) stomach, pyloric (posterior) stomach, the intestine as far as the "s" bend (Suyehiro, 1942) and the intestine from the "s" bend to the anus. The total length of the alimentary tract was the sum of these component measurements. The pyloric caeca were counted, and the lengths of the smallest and largest caeca in each fish were measured. Adult material was measured to the nearest millimetre using a 50 cm ruler, while juvenile material was measured to the nearest 0.1 mm using a dissecting microscope and a micrometer eyepiece or vernier callipers.

In a subsample of the adult specimens, the thickness of the stomach wall was measured from the preserved (10 % formalin in seawater) gut material once the stomach contents had been removed for analysis. Measurements of the cardiac and the pyloric sections of the stomach wall were taken using vernier callipers. Care was taken to avoid the thickened area associated with the pyloric sphincter. Ten individuals of *Siganus doliatus*, *S. fuscescens* and *S. lineatus* were measured, along with the five individuals of *S. punctatus*. Due to the limitations associated with measuring such thin material with vernier callipers, the measurements were classified into broader categories (<1 mm and >1 mm) that would still demonstrate the differences between the species. The actual values recorded can only be viewed as approximations.

4.2.2 Head measurements

The height of the gape and the depth and length of the head were measured with vernier callipers. The depth of the head was measured in two places: behind the eye and at the base of the first dorsal spine (D1) (Figure 4.1). Adult material was measured to the nearest millimetre, while juvenile material was measured to the nearest 0.1 mm.

4.2.3 Data analysis

All raw data were examined graphically. The gut length data displayed a non-linear growth pattern and, of the line types fitted to the data, the power curve provided the best r^2 values. At this point, seasonal information (summer or winter collection dates) were superimposed on the individual data points to determine whether there were any patterns in the variation around the curve that could be related to seasonal influences.

The data were then transformed (natural logarithm) to allow an assessment of relative growth rates based on the allometric growth (power) equation (Gould, 1966):

$$y = bx^a$$

where y was the length of the alimentary tract, b was a constant, x was the standard length of the fish, and a, the power exponent, was the ratio of the specific growth rates of y and x. This ratio is also known as the coefficient of relative growth, and describes the rate of increase in y relative to the rate of increase in x. The natural logarithm transformation linearises allometric data and the power exponent, a, becomes the slope of the linear regression line, facilitating the calculation of confidence intervals and permitting comparisons between species. For each species, the lack of subadult specimens resulted in adults and juveniles appearing as two separate groups in the regression analysis. This arrangement tends to produce a slope with a high correlation value, regardless of the true relationship. To confirm that the data represented a single growth rate relationship, separate regressions were performed for each group (Appendix I). On the basis that overlapping confidence intervals showed no significant difference between the regression slopes, the data were then analysed as single samples.

The relative growth rates of each of the five gut sections were examined individually, in order to ascertain whether all sections grew at the same relative rate, or if there were certain sections of the gut that were primarily responsible for the observed relationship between total gut length and standard length. Again, separate regressions were performed on the adult and juvenile groups to determine whether the data represented a single growth rate relationship (Appendix I), and overlapping confidence intervals were the basis for proceeding with a regression of the entire sample. For each section of the gut, analysis of covariance (ANCOVA) was used to compare the regression slopes of the section against standard length between species.

The mean length of the largest caecum from the adults of the four species was compared using analysis of variance (ANOVA). On the basis of a significant difference, contrasts were analysed to determine whether the difference was related to the terminal size of the species. As this could be construed as a *post hoc* test, α for this test was set at the more conservative level of 0.01 as a precaution (Sokal and Rohlf, 1981).

Gape height and the depth of the head showed linear growth patterns with respect to head length. Separate regressions were performed on the adult and juvenile groups to determine whether the data represented a single growth trajectory (Appendix I), and overlapping confidence intervals were the basis for proceeding with a regression of the entire sample. A square root transformation was applied to the data in order to satisfy the assumptions of normality and homogeneity of variances required by further parametric statistical tests. This transformation is less extreme than the more traditional natural or base 10 logarithmic transformations which, in this instance, reduced linearity and homogeneity without improving normality. ANCOVA was used to compare the regression slopes of the transformed gape height data of the four species. The regression slopes for the two measures of head depth were compared within each species. Then, for each measure of head depth, the relative positions of the regression slopes for each species were described using difference parameterisation, a form of multiple regression which compares the relative position of several regression slopes using one slope as a reference line.

4.3 RESULTS

4.3.1 Alimentary tract

The allometric relationship between total gut length and standard length in the four study species was demonstrated by the power curves fitted to the data (Figure 4.2). Strong linear relationships were apparent in the log-transformed data for all four species, with r^2 values of 0.974 to 0.987 (all with $p < 0.0001$, Figure 4.3 and Table 4.2). The slopes of the regression lines, which describe the rate at which the gut lengthens relative to the growth rate of the fish as a whole (standard length), were between 1.16 and 1.18. The slope values and their confidence intervals were all greater than 1 (Table 4.2), indicating that the alimentary tract displayed positive allometric growth in all four species. The similarity of the relative growth coefficients and their confidence intervals (Table 4.2) indicated that there were no significant interspecific differences in the relative growth rate of the alimentary tract.

For adult fish, superimposing the sampling season (winter / summer) information on the data points in Figure 4.2 produced no discernible pattern in the variance around the curve, indicating that total gut length was not affected in any consistent way by seasonal factors. An interesting feature of the *Siganus fuscescens* data was the difference in total gut length between juveniles A and B (marked with arrows in Figure 4.3). These were the smallest *S. fuscescens* juveniles sampled, and were probably new recruits. Both individuals had a standard length of 25.5 mm, but juvenile A had a total gut length of 31.1 mm, while juvenile B had a total gut length of 60.4 mm. Juvenile A was regarded as an outlier and was not included in the regression calculations.

The five gut sections increased in length at different rates relative to the fish as whole, but the relative growth of a given gut section was fairly consistent between species (Table 4.3). The three cylindrical sections of the gut, the oesophagus and the two intestinal sections, all showed positive allometric growth (based on the slope values of the regression lines and their 95 % confidence intervals, which were all greater than 1, with the exception of the lower confidence interval of the oesophagus in *S. punctatus*). Relative growth rates were approximately 1.1 for the oesophagus, and 1.2 for the two intestinal sections. Results of the ANCOVAs showed that there were no significant interspecific differences in the relative growth rates of the oesophagus ($F = 0.47$; $df = 3$; $p = 0.702$), the anterior intestine ($F = 0.16$; $df = 3$; $p = 0.925$), or the posterior intestine ($F = 0.65$; $df = 3$; $p = 0.583$). Also, there were no significant differences between the relative growth rates of the two intestinal sections within species (based on the 95 % confidence intervals).

The two stomach sections displayed primarily isometric growth in length, with only one of the relative growth coefficients being significantly different from 1, but interspecific differences in relative growth rates were apparent. In *S. fuscescens*, the relative growth of the anterior section of the stomach was greater than in the other three species. ANCOVA detected heterogeneity of slopes when all four species were analysed ($F = 2.83$; df = 3; $p = 0.040$), but no significant differences were found when *S. fuscescens* was removed from the analysis ($F = 1.05$; df = 2; $p = 0.353$). *S. lineatus* was the only species where the posterior section of the stomach displayed positive allometric growth (based on the regression slope and the confidence intervals). ANCOVA found the regression slopes to be heterogeneous when all four species were analysed ($F = 5.44$; df = 3; $p = 0.001$), but no significant difference was found between *S. doliatus*, *S. fuscescens* and *S. punctatus* ($F = 2.97$; df = 2; $p = 0.055$).

S. doliatus and *S. punctatus* both had stomachs which are typical of Type I herbivores, with smooth, thin walls that are consistently less than 1 mm thick (Table 4.4, Plate 4.1). The stomachs of *S. fuscescens* and *S. lineatus* do not conform as closely with this description as the other species. The stomachs of these latter two species had thicker walls, particularly in the pyloric section of the stomach (Table 4.4, Plate 4.1). In these species the mucosa in the pyloric section of the stomach had a ridged surface, which appears keratinised, with folds extending in a longitudinal direction (Table 4.4, Plate 4.1).

The number of pyloric caeca per fish ranged from 4 to 7 (Figure 4.4). For all four species, an increase in the mean number of caeca through ontogeny was obvious, as the distributions shifted to the right. It also appeared that the pairing species had more caeca on average at a given age than the shoaling species, and that the maximum number of caeca was lower for the shoaling species.

The caeca within an individual fish were not of uniform length. The pattern generally consisted of a single small caecum with several (3 to 6) large ones. There was considerable variation in the size difference between the smallest caecum and the largest (Table 4.5). From the increase in maximum length ranges between the juvenile and the adult groups (Table 4.5) it appears that the caeca increase in length through ontogeny. The ANOVA found a significant difference in the mean length of the largest caecum between adults of the four species ($F = 46.45$; df = 3; $p < 0.0001$; Means are given in Table 4.5). Based on this significant difference, contrasts were used to determine whether the effect was due to differences in the terminal size of the species. This test found a significant difference in the length of the largest caecum between the small (*S. doliatus* and *S. fuscescens*) and large (*S. lineatus* and *S. punctatus*) species ($F = 60.53$; $df = 1$; $p < 0.0001$). No significant differences in maximum caecum length were found between *S. doliatus* and *S. fuscescens* (the two small species: $F = 0.79$; $df = 1$; $p = 0.375$) or between *S. lineatus* and *S. punctatus* (the two large species: $F = 0.10$; $df = 1$; $p = 0.75$).

4.3.2 Head

Gape height showed a linear relationship with head length in all four species. The square root-transformed data produced strong regressions with r^2 values between 0.939 and 0.98 (all with $p < 0.0001$, Figure 4.5). The height of the gape was small relative to the length of the head (approximately 27 %). An examination of the slope values and their confidence intervals (Figure 4.5, Table 4.6) suggested that the relationship was similar in *S. doliatus*, *S. fuscescens* and *S. lineatus* (slope values between 0.52 and 0.54), while *S. punctatus* (slope value = 0.45) appeared to show lower proportional growth. ANCOVA found a significant difference when *S. punctatus* was included in the analysis ($F = 3.99$; $df = 3$; $p = 0.009$), but there was no significant difference between the other three species ($F = 0.25$; $df = 2$; $p = 0.782$). Thus, in *S. punctatus* the gape was significantly smaller relative to the size of the head.

The aim of the double regression plots (Figure 4.6) was to demonstrate the relative difference between the two measures of head depth (one taken behind the eye and the other at the first dorsal spine) with size, as an indication of head shape through ontogeny. Both of these measures increase isometrically with head length. In all species, these two measurements were initially similar, but the depth of the head at the first dorsal spine had a significantly greater proportional growth rate (based on the confidence intervals of the regression slopes, Table 4.7). This leads to greater differences between the two measurements as the size of the fish increases, and the divergence of the two regression slopes indicates a steepening of the head profile through ontogeny. Low slope values for both regression lines, such as are displayed by *S. fuscescens*, are indicative of a streamlined profile, as the head is comparatively less deep relative to its length. Large slope values are indicative of a steep head profile.

The difference parameterisation regression of head depth behind the eye (with *S. doliatus* as a reference) showed that there was no significant difference between the reference and *S. punctatus* (slope = +0.03; $t = 1.00$; $p = 0.317$). The *S. fuscescens* regression had the lowest slope (-0.15 relative to the reference), with the *S. lineatus* regression slope lying between it and the reference (-0.08). Both slopes were significantly lower than the reference (t = -5.54 and t = -3.97 respectively; $p < 0.0001$ for both). The difference parameterisation regression of head depth at the first dorsal spine (with *S. doliatus* as a reference) showed that there was no significant difference between the reference and *S. lineatus* (slope = +0.04; t = 1.80; p = 0.074). The *S. fuscescens* regression had a significantly lower slope than the reference (relative slope = -0.06; t = -2.07; p = 0.040), while *S. punctatus* had a significantly higher slope than the reference (slope = +0.10; t = 3.17; p = 0.002).

Both measures of head depth showed the lowest proportional growth in *S. fuscescens* (Table 4.7). In *S. lineatus*, the depth of the head behind the eye showed greater proportional growth than in *S. fuscescens*, but significantly lower proportional growth than that measure in the two pairing species. In contrast, the depth at the first dorsal spine showed similar proportional growth in *S. lineatus* and *S. doliatus*. *S. punctatus* consistently displayed the greatest proportional growth rates. It seems that the depth of the head immediately behind the eye, when examined relative to the length of the head, is a reasonable indication of the roundness of the snout, with lower values associated with the profiles of *S. fuscescens* and *S. lineatus*, and high values associated with the steeper profiles of *S. punctatus* and *S. doliatus*. The depth of the head at the first dorsal spine is more correlated with the terminal size and body form of the species.

4.4 DISCUSSION

In siganids, as in a number of other herbivorous species (Horn, 1989), there is continued elongation of the gut relative to the length of the fish which persists well beyond the early developmental stages. In the four study species, the relationship between total gut length and standard length is well described by the power function recommended by Gould (1966) and Peters (1983), and the gut displays significant positive allometric growth. The fit of the power function indicates that the specific growth rate of the gut (i.e. growth expressed relative to present gut length) is consistently approximately 17 % greater than the overall specific growth rate of the fish (i.e. percentage increase in standard length) (Kaufman, 1981; Shea, 1985), and the ratio of gut length to standard length increases with increasing size (Gould, 1966). A similar growth pattern may be present in the gut of the aplodactylid *Aplodactylus punctatus* (Benevides *et al.*, 1994), where the gut appears to elongate at twice the rate of standard length, but it this difficult to confirm because of the manner in which the data are presented.

This type of growth pattern indicates that the gut, like the whole organism, displays asymptotic growth in length, but that the gut must elongate at a consistently greater percentage rate than the organism in order to maintain functionality. There is no indication that relative growth of the gut levels off after maturity, as occurs in the stichaeid *Cebidichthys violaceous* (Montgomery, 1977) and the pomacentrid *Stegates lividus* (Lassuy, 1984). Such a growth pattern would indicate allometric growth up to a functional threshold followed by isometric growth in order to maintain the same relative proportions. In all species the growth trajectory appears to be smooth, without the upwards shift that would result from a rapid burst of growth associated with a sudden change in diet. This type of transitional elongation is clearly present in Rimmer's (1986) data on gut length of the kyphosid *Kyphosus cornelii.*

The expression of the herbivorous habit very early in the ontogeny of the four study species (Chapter 3) suggests that the greatest change in gut morphology occurs at settlement. Siganid larvae have an unusually well developed gut (Leis and Rennis, 1983), which may facilitate such a rapid change and allow these species to become herbivorous almost immediately upon settlement. Bryan and Madraisau (1977) recorded a distinct and rapid elongation of the gastrointestinal tract of *S. lineatus* that was associated with metamorphosis. Within this data set, there is an indication of a similar, transitional-type elongation of the gut at settlement. The two smallest individuals of *S. fuscescens* that were examined (those labelled A and B in Figure 4.3) both had standard lengths of 25.5 mm, and were newly recruited. The total gut length of one fish was 31.1 mm, while the other fish, caught two days later at the same site, had a total gut length of 60.4 mm. Although these observations do not provide conclusive evidence for a period of transitional gut elongation at settlement, they do suggest that the pattern found in *S. lineatus* by Bryan and Madraisau (1977) may be representative of siganids in general. Investigation of the morphological, physiological and histological changes during the settlement period presents an opportunity for further research.

Although relative gut length does not differ between the four study species, the greater absolute gut length of the three species with larger terminal sizes may influence their ability to consume seagrasses (Chapter 3). The increased length may represent a functional threshold associated with a minimum processing time to ensure absorption of nutrients, or the increase in volume may indicate a minimum amount of seagrass that must be consumed to fulfil energy requirements from this more refractory material.

Relative gut length is highly variable, and may be affected by time of day and food deprivation (Montgomery and Pollak, 1988; Horn, 1989), suggesting a facility for the reabsorption of gut material during times of food shortage or diversion of resources. There was no indication in this data set of seasonal differences in total gut length relative to standard length that might be associated with variable food availability or the reproductive cycle.

The examination of the relative growth patterns of the various gut sections shows that the overall elongation pattern of the gut is due to the allometric growth of the cylindrical sections (oesophagus and intestine), which grow at similar relative rates in the four study species. There is thus no indication of species-specific adaptations to digestion in these sections of the gut. The length of the stomach sections increases approximately isometrically (except in *S. lineatus*), and the stomach is the only part of the gut where interspecific differences in relative growth rates are present. These differences in stomach development may contribute to species-specific digestive strategies. However the stomach also undergoes considerable growth in other dimensions, unlike the cylindrical sections of the gut. In this regard, weight or volume might be a more appropriate measure of stomach development in future studies, and may well show an allometric growth pattern. In the present study, useful information may be obtained from the measurements of stomach wall thickness and other qualitative descriptions.

An important observation is the differing thicknesses of the stomach wall between the pairing and shoaling species. *S. doliatus* and *S. punctatus* fit the description of a thin-walled stomach which typifies an acid-based digestive mechanism (Horn, 1989). The description of *S. fuscescens* stomachs in the present study concurs with the description and photograph in Suyehiro's (1942) study, and the photographs in Plate 4.1 show the similarities between the stomachs of both *S. fuscescens* and *S. lineatus* and the details given in this earlier publication. Bryan's (1975) description of *S. spinus*, another shoaling species, is similar, although he describes a slightly thinner stomach wall. The structure of the stomach in *S. fuscescens* and *S. lineatus* is similar to that described for *Acanthurus nigrofuscus*, which has a V-shaped stomach with a thin cardiac section, a thicker pyloric section, and a central constriction (Montgomery and Pollak, 1988). These authors also recorded acidic conditions in the stomach. They refer to the pyloric section of the stomach in this fish as "moderately muscular" when comparing the 3 mm thick wall to the gizzard-like pyloris found in some other acanthurids such as *Ctenochaetus spp.*, some *Acanthurus spp.* and *Prionurus punctatus* (Jones, 1968a; Lobel, 1981), as well as girellids and mugilids (Horn, 1989, 1992). The wall of this grinding structure can be nearly 10 mm thick, and it is more spherical in shape (Montgomery and Pollak, 1988).

Rather than acting as a grinding facility, the moderately muscular stomach might act to aid acid-based digestion by mixing the stomach contents more fully with the gastric secretions. A palpating action might also serve to increase the release of the cell contents through the gaps between the cell wall components of more refractory food items. These functions could contribute to the digestion of seagrass by the shoaling species. The role of the apparently keratinised folds in the mucosa is unclear. More accurate investigations of the stomach structure will require transverse sectioning and staining techniques. This would allow more accurate measurement of wall thickness, as well as providing information about the underlying tissue structure and the keratinisation of the epithelium in the shoaling species.

The general pattern of the pyloric caeca, with a single small appendage and several larger ones, is similar to that described by Suyehiro (1942) and reinforces the implication in Figure 4.4 that the number of caeca increases, one by one, through ontogeny. This was first observed by Raitt (1962), who suggested that the total number of caeca increased with the size of the fish. The size ranges of the caeca increased through ontogeny, implying that the caeca continue growing as the fish grows. Their ultimate size appears to be dependent on the terminal size of the fish. The combination of these features suggest an underlying allometric growth response.

The pyloric caeca form from projections of the intestinal wall, usually during metamorphosis, and their epithelial structure is therefore identical to that of the intestine (Tanaka, 1971; Pedersen and Falk-Pedersen, 1992). This suggests that the caeca may perform functions similar to the intestine. Buddington and Diamond (1987) showed that small particles transit the caeca at rates which are similar to their passage through the intestine. Sabapathy and Teo (1993) found the same digestive enzymes in the pyloric caeca and the intestine of siganids, with similar activities in both locations, confirming their secretory role. Whether the caeca have an absorptive role in siganids is unclear. The data in this study imply that the caeca serve as a means of increasing the relative surface area of the gut, as suggested by Buddington and Diamond (1986). This explains their increase in number and size with the size of the fish. An estimate of the total caecal surface area per fish is required to determine whether this increase is allometric. The greater total number of caeca in adult *S. doliatus* suggests a compensatory mechanism. Given the restrictions imposed by the size of the gut cavity, the caeca in this species cannot grow as large as they do in the other species, so this is compensated for by an increase in total number. Although *S. punctatus* also appears to have more caeca, I believe that this is an artefact resulting from the bias of the small sample towards larger individuals.

The gapes of *S. doliatus*, *S. fuscescens* and *S. lineatus* follow similar growth trajectories, with head length the only factor influencing the increase of gape height. The greater absolute gapes of the larger two species may enable them to consume larger food items, such as seagrasses, more readily (Setran and Behrens, 1993). The proportionally smaller gape of *S. punctatus* may be a result of the more protuberant snout in this species. It is possible that this is linked to their continued consumption of sessile invertebrates beyond the juvenile stage, and also to their consumption of seagrass (Chapter 3). Compared to the other species, the area of substrate that they can access per bite may lead to a lower proportional intake rate when feeding on turf algae on a flat surface. In contrast, the irregular surfaces of soft corals, sponges and colonial ascidians tend to have small projections that can be bitten off, providing a greater volume of food for a given gape height. This could also apply to seagrass blades growing up from the bottom. Alternatively, the continued consumption of animal material may simply reflect a substitution of higher quality food in the face of reduced intake. Further study of interspecific differences in gape, and the resulting influences on diet, would benefit from the measurement of gape angle and the amount of substratum contact, ideally during feeding by live specimens.

S. fuscescens and *S. lineatus* develop rounder head profiles than the two pairing species. This type of head profile places the eyes nearer to the mouth than a steeper profile

(Jones, 1968a). This may enable them to feed more efficiently in seagrass beds, where the only available feeding surface is horizontal. As they feed head down in areas of dense seagrass growth, a steeper head profile would result in the mouth and the lower part of the seagrass blade (the preferred food section - see Chapter 3) being obscured from sight. It is also possible that a rounder head might reduce the angle between the body and the substrate when feeding.

The steeper head profiles in *S. doliatus* and *S. punctatus* are more suited to feeding in coral areas, where there are many vertical or near vertical surfaces to feed on. These two species have been frequently observed feeding on such surfaces (pers. obs.). In addition, when these species do feed on more horizontal surfaces, the angle between the body and the substrate appears greater than for the shoaling species feeding in the seagrass. The apparent paradox resulting from the fact that *S. punctatus* also feed on seagrass may be partly explained by a consideration of the seagrass areas they feed in. Both *S. fuscescens* and *S. lineatus* migrate to the dense reef flat seagrass beds to feed (Chapter 6), while *S. punctatus* consumes seagrass from the sparser growth that is adjacent to the coral areas (pers. obs.). In such areas, the base of the leaves would rarely be out of sight, even if the eyes were some distance from the mouth.

The relationship between head structure and diet is not as clear cut as that between gut structure and diet. Head shape is influenced by factors other than feeding, including hydrodynamic considerations and limitations to the visual field. No such additional constraints affect the relationship between gut and diet. All aspects of head structure would benefit from further measurements similar to those made by Jones (1968a) in conjunction with videotaped observations of feeding behaviour in order to clarify these relationships.

The paucity of samples from the intermediate size classes (i.e. the subadult stage) is a limitation of this data set. Unfortunately, the subadults were in a size range and behaviour window that was minimally susceptible to both of the sampling methods. By the time individuals had reached a standard length of approximately 100 mm, most of them had already moved from the seagrass beds to the coral areas. At this small size however, they were able to shelter effectively amongst the coral, and could not be targeted successfully by spear gun. It could be contended that the significance of the regressions produced using this data set is based on the presence of two discreet groups of data, rather than representing a true relationship between the variables. The separate analyses of the juveniles and adults (Appendix I) showed that, with two exceptions, there were no significant differences between regression slopes for the two groups, and that it was therefore reasonable to analyse them as single samples. In addition, it is clear that in all cases the individual data points follow the trajectory of the regression line, rather than comprising distinct and separate clusters. This is the most important consideration, as the aim of the analyses was to identify and compare these growth trajectories, rather than to establish relationships or prediction models. Jones and Marsh (1993) recommend the use of ANOVA to confirm the significance of regressions where the independent variable may not have a normal distribution. The transformations applied to the data improved normality and the homogeneity of the variances to acceptable levels. The r^2 values were all very high and p values in all cases were < 0.0001. Small sample sizes are also a limitation of this data set, particularly for *S. punctatus*, and in this sense, the data are not robust. Therefore, although some interesting features have emerged, the interpretations should be considered preliminary and they should be applied with caution.

4.5 CONCLUSIONS

In siganids, the development of the alimentary tract seems to be under the control of allometric growth functions, which persist after maturity. Relative gut length is consistent between species, and is adapted to a general, rather than specific, herbivorous diet. There is the possibility that a functional threshold associated with size exists for bulk processing and / or absorption, and this may influence the ability of the larger species to maintain a positive energy balance from more refractory dietary items such as seagrass. The caeca are the only part of the gut where interspecific differences in relative absorptive area may be present, but this requires confirmation. The differences in stomach structure between the pairing and shoaling species are the most interesting aspect of this research, and may assist in explaining how seagrasses can be utilised by Type I herbivores. However further histological studies are needed in this area.

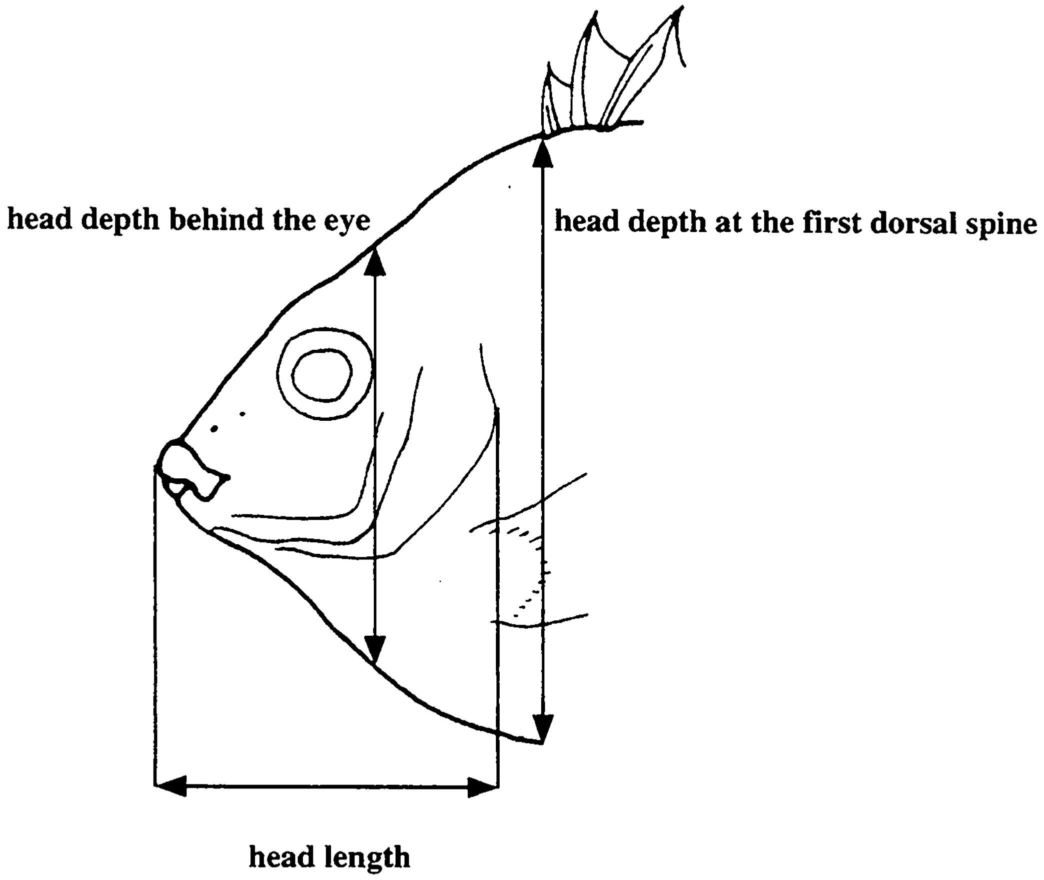


Figure 4.1. Generalised profile of a siganid, showing how head length and the two measures of head depth were determined.

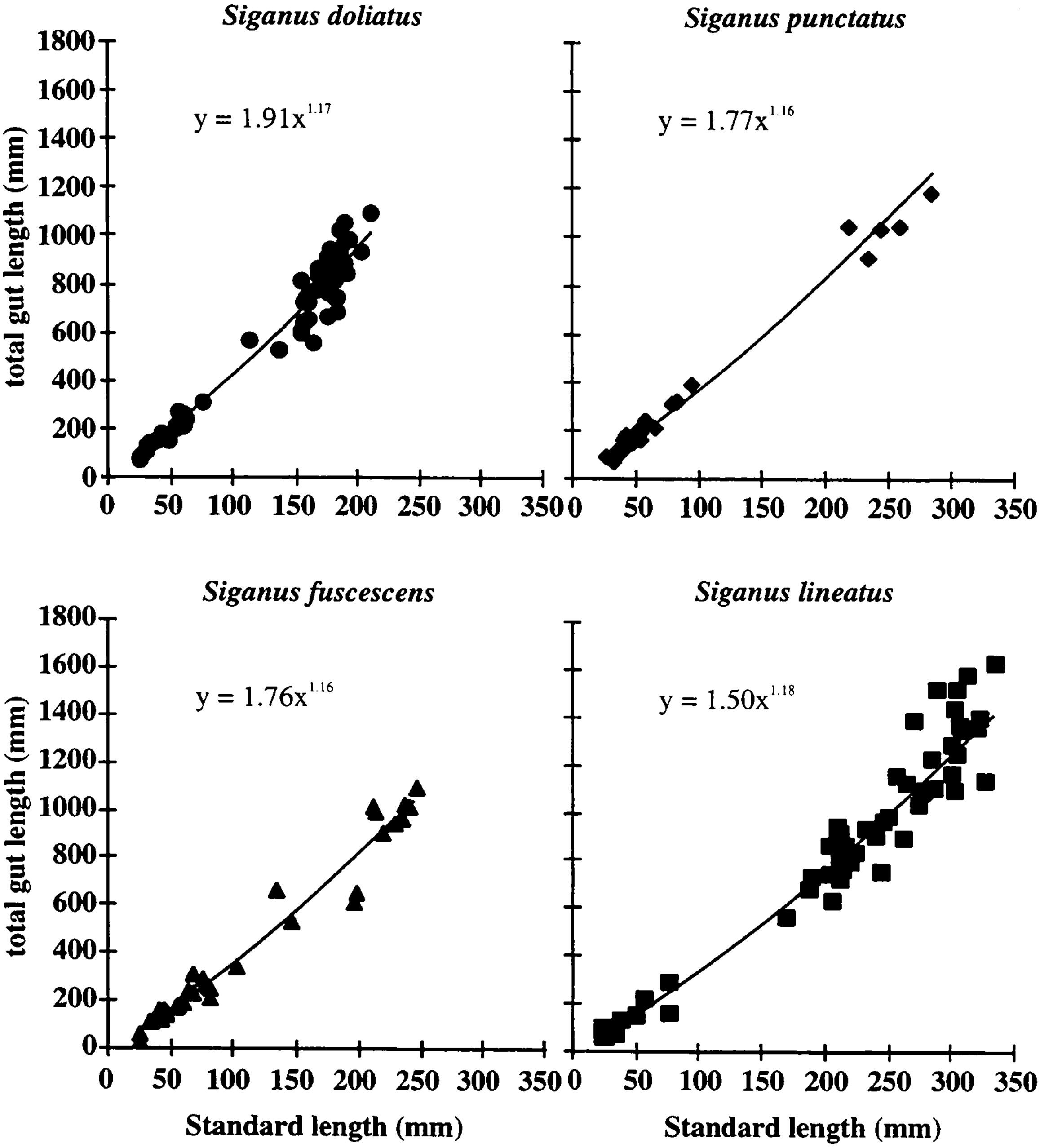


Figure 4.2. Plots of total gut length against standard length for each of the four study species. Power curves have been fitted to the data, and the equations for the curves are included in the plots.

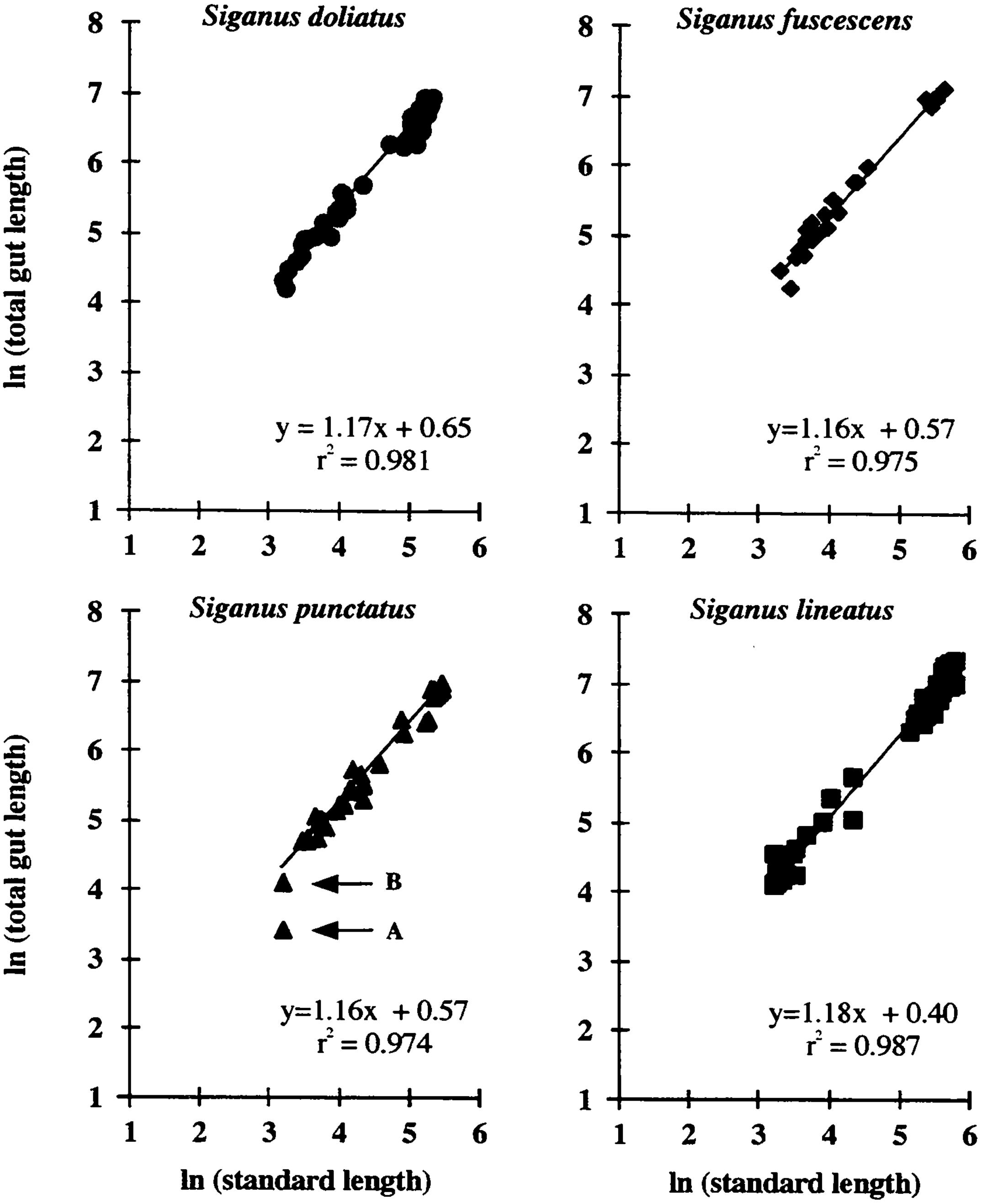


Figure 4.3. Regressions of log-transformed gut length and standard length data, including slope values and r^2 values. Arrows indicate *S. fuscescens* juveniles A and B, as discussed in the text. Juvenile A is not included in the regression calculation.

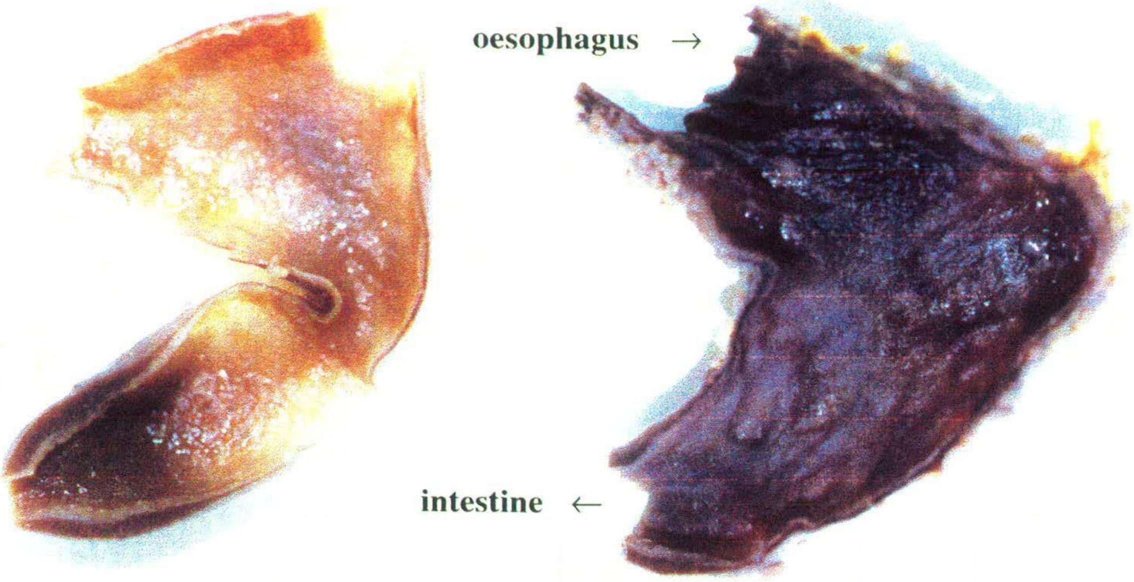
Table 4.2. Growth coefficients, and 95 % confidence intervals, describing positive allometric growth of the gut in the four study species.

Species	Slope	95 % Confidence Interval	r^2
S. doliatus	1.17	1.13 to 1.21	0.981
S. fuscescens	1.16	1.09 to 1.22	0.974
S. lineatus	1.18	1.14 to 1.21	0.987
S. punctatus	1.16	1.08 to 1.24	0.975

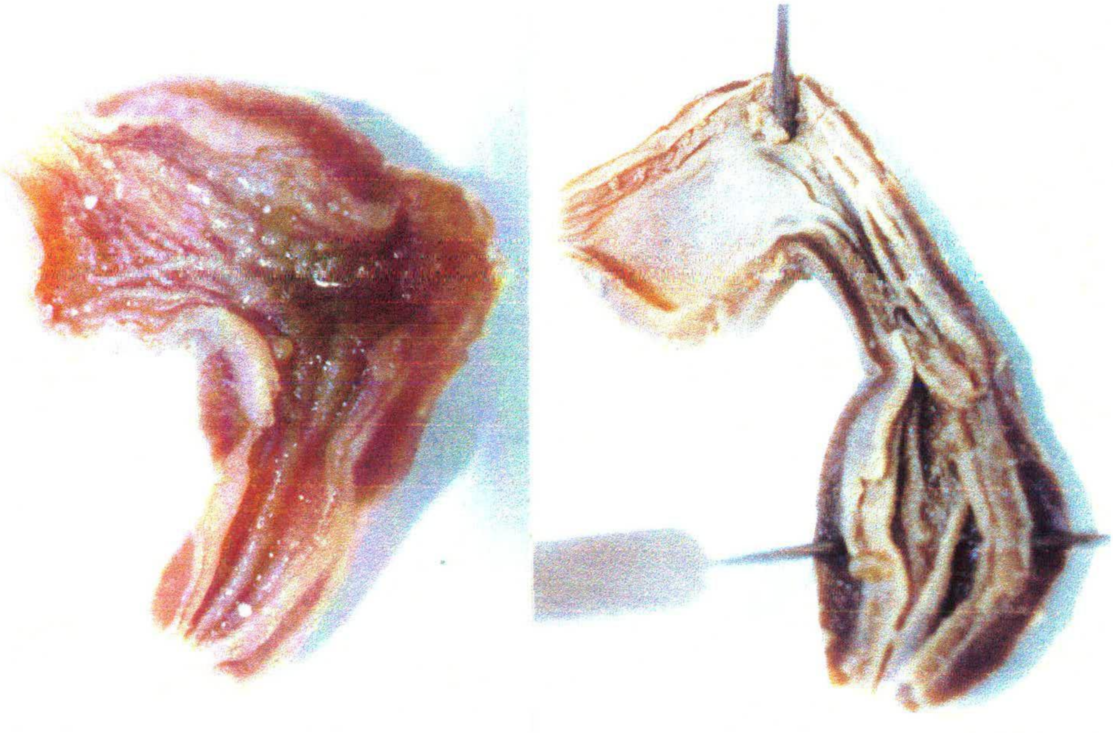
Table 4.3. Growth coefficients (± 95 % confidence limits) and regression coefficients of natural log-transformed length data of the intestinal sections against standard length for the four study species.

	S. doliatus	*S. fuscescens*	*S. lineatus*	*S. punctatus*
oesophagus	1.11	1.10	1.11	1.05
slope (95 % CL)	(1.05 - 1.17)	(1.02 - 1.18)	(1.08 - 1.14)	(0.95 - 1.14)
r^2	0.947	0.954	0.986	0.968
cardiac stomach	0.95	1.09	0.96	0.85
slope (95 % CL)	(0.86 - 1.03)	(0.96 - 1.22)	(0.91 - 1.01)	(0.70 - 1.00)
r^2	0.868	0.890	0.952	0.884
pyloric stomach	1.06	1.02	1.11	0.89
slope (95 % CL)	(0.99 - 1.13)	(0.89 - 1.15)	(1.06 - 1.16)	(0.75 - 1.04)
r^2	0.918	0.878	0.968	0.884
intestine to "s" bend	1.19	1.21	1.19	1.18
slope (95 % CL)	(1.14 - 1.24)	(1.11 - 1.31)	(1.15 - 1.22)	(1.04 - 1.29)
r^2	0.964	0.945	0.987	0.968
intestine to anus	1.17	1.26	1.24	1.11
slope (95 % CL)	(1.11 - 1.23)	(1.14 - 1.38)	(1.11 - 1.37)	(1.02 - 1.20)
r^2	0.956	0.932	0.843	0.973

Plate 4.1. Cut-away sections of the stomachs of the four study species, illustrating differences in mucosa structure and stomach wall thickness .



S. doliatus (x 1.5) *S. punctatus* (x 2)



S. fuscescens (x 2) *S. lineatus* (x 1.5)

Table 4.4. Descriptions of siganid stomachs.

	S. doliatus	*S. fuscescens*	*S. lineatus*	*S. punctatus*
Cardiac section				
wall thickness	< 1 mm	> 1 mm	> 1 mm	< 1 mm
(range)	(0.6 - 0.9 mm)	(1.1 - 1.7 mm)	(1.1 - 2.4 mm)	(0.7 - 0.9 mm)
mucosa texture	smooth	slight ridges	slight ridges	smooth
Pyloric section				
wall thickness	< 1 mm	> 1 mm	> 1.5 mm	< 1 mm
(range)	(0.6 - 0.9 mm)	(1.1 - 1.6 mm)	(1.7 - 3.6 mm)	(0.7 - 0.9 mm)
mucosa texture	smooth	ridges	deep ridges	smooth

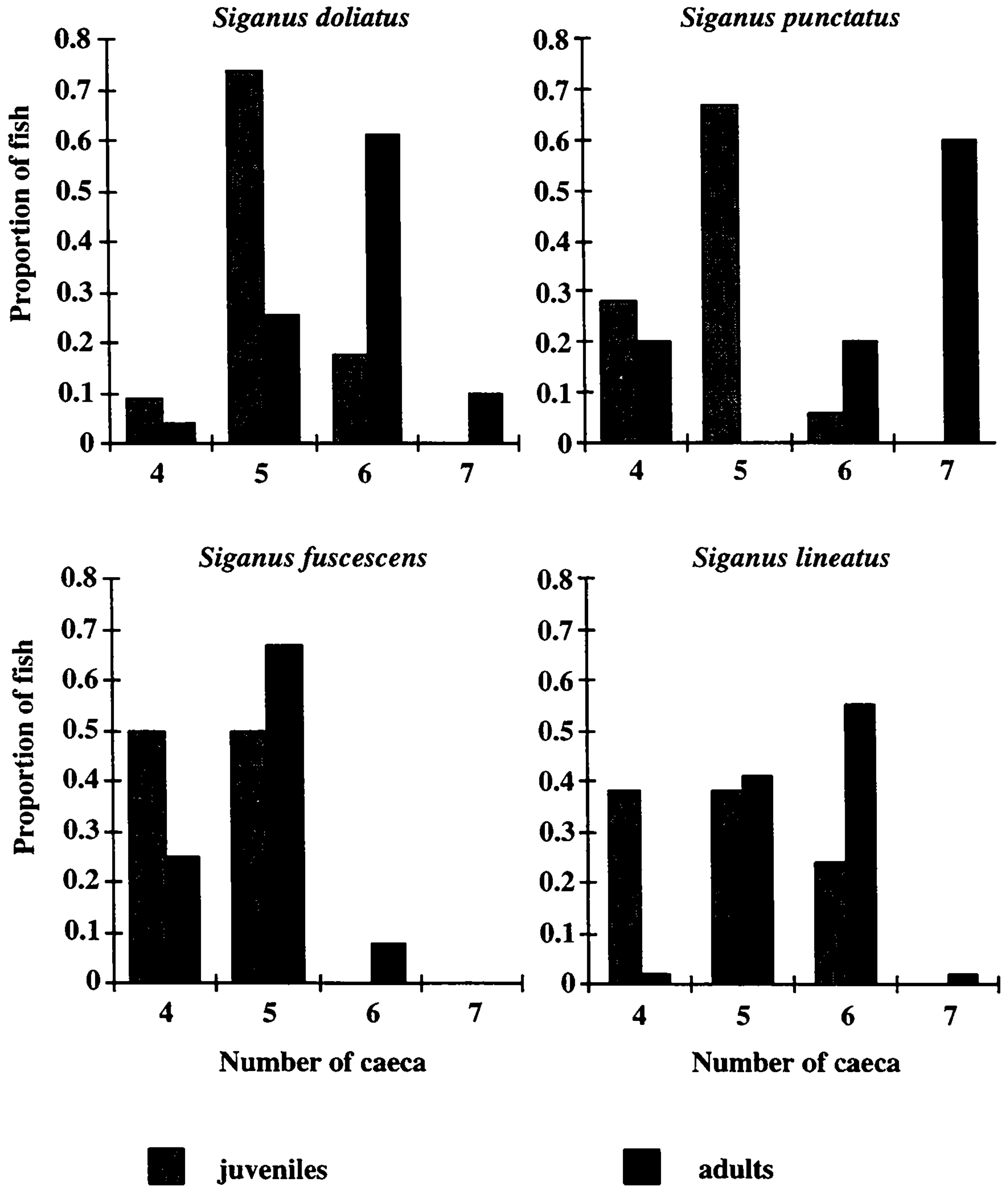
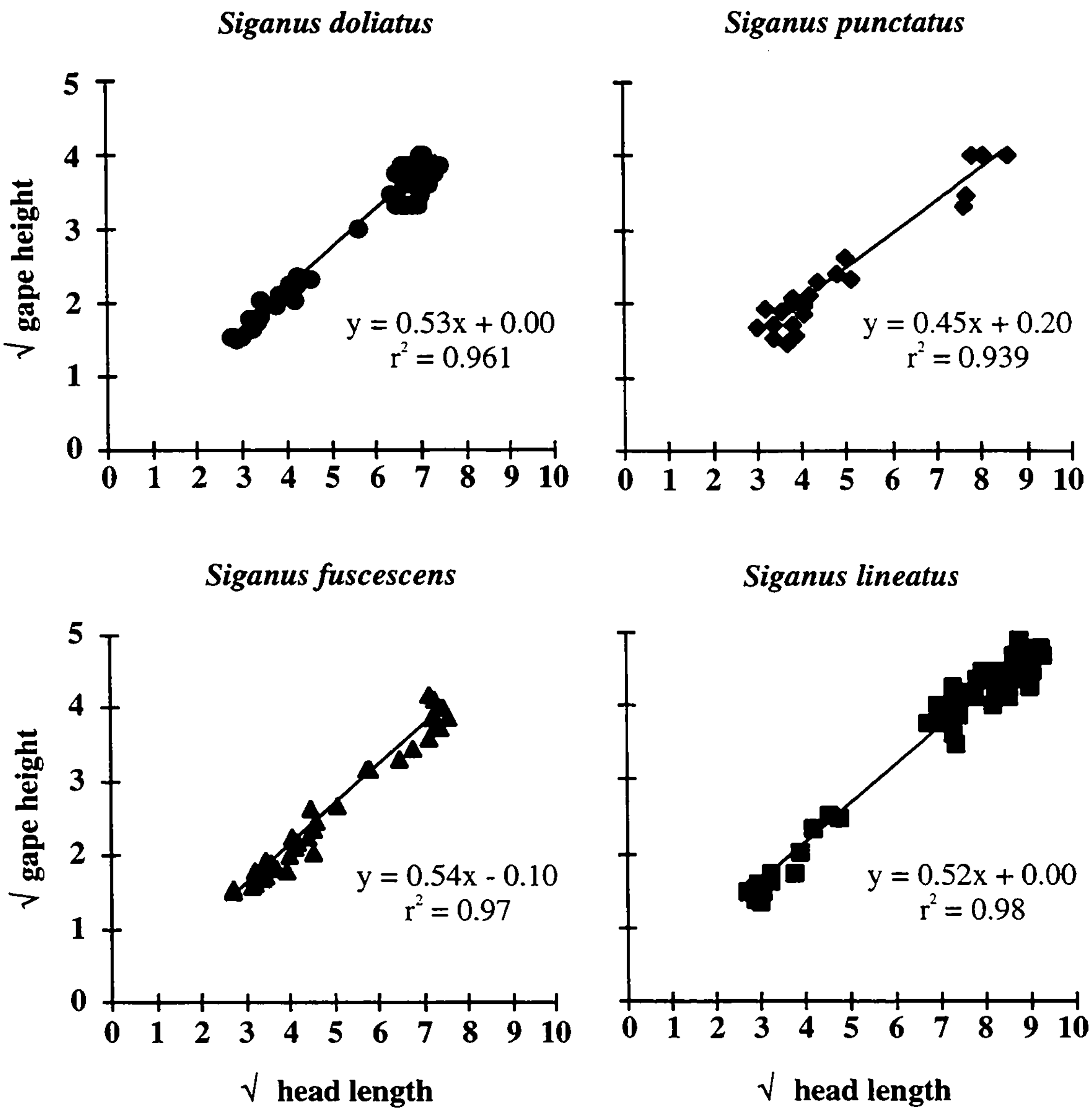


Figure 4.4. Frequency histograms showing the number of caeca in juvenile and adult fish of the four species, demonstrating the increase in the number of caeca through ontogeny.

Table 4.5 Length ranges of smallest and largest caeca, in mm.

Species	Juvenile range smallest (mm)	 largest (mm)	Adult range smallest (mm)	 largest (mm)	Mean largest adult caecum ± S.E. (mm)
S. doliatus	0.8 - 4.5	6.4 - 15.5	5 - 17	21 - 41	29.10 ± 0.75
S. fuscescens	1.0 - 7.1	2.0 - 15.5	2 - 20	22 - 50	32.46 ± 3.05
S. lineatus	0.5 - 5.0	3.0 - 17.0	6 - 45	26 - 87	55.52 ± 2.68
S. punctatus	1.1 - 10.3	3.0 - 29.0	9 - 23	45 - 76	57.80 ±5.40



Siganus doliatus

Siganus punctatus

Siganus fuscescens

Siganus lineatus

Figure 4.5. Regressions of square root - transformed data of gape height against head length for each of the four study species. Slope values are given in the equations, along with the r² values. Details of the confidence intervals are given in Table 4.6.

Table 4.6. Confidence interval information for the transformed gape height regressions illustrated in Figure 4.5.

Species	Intercept	Slope
S. doliatus	-0.13 to 0.14	0.51 to 0.56
S. fuscescens	-0.22 to 0.10	0.51 to 0.57
S. lineatus	-0.14 to 0.14	0.50 to 0.54
S. punctatus	-0.07 to 0.46	0.40 to 0.50

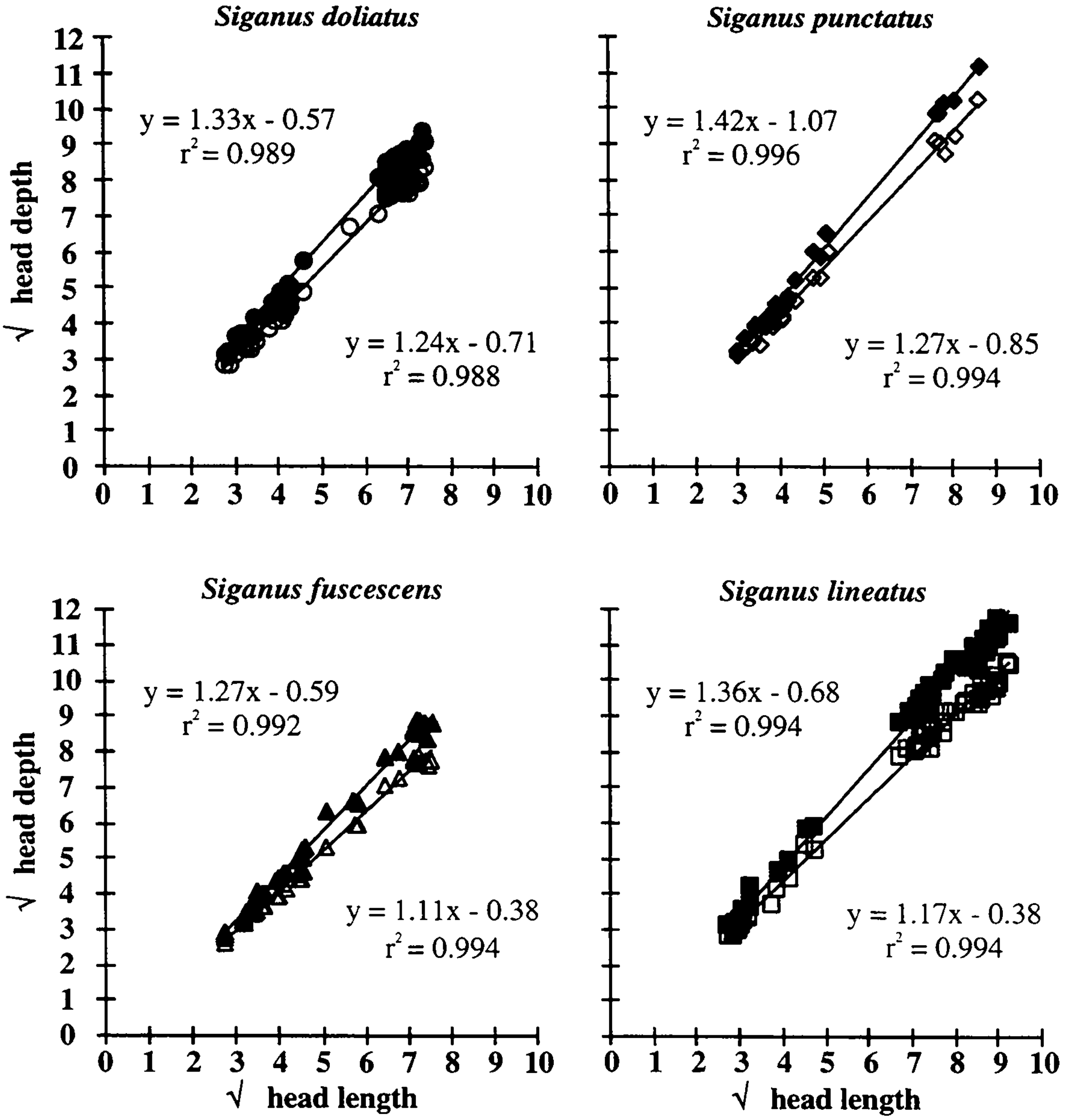


Figure 4.6. Regressions showing relative head depth through ontogeny. These regressions plot the square - root transformed data of the two head depth measurements against head length. The filled symbols are the depth at the first dorsal spine (D1), while the open symbols are the depth posterior to the eye. Confidence intervals have been excluded from these plots for clarity, and are available in Table 4.7.

Table 4.7. Confidence intervals for the four pairs of head depth regressions illustrated in Figure 4.6.

Species	**Depth at eye**		**Depth at D1**	
	Intercept	Slope	Intercept	Slope
S. doliatus	-0.89 to -0.51	1.22 to 1.28	-0.76 to -0.38	1.30 to 1.36
S. fuscescens	-0.53 to -0.22	1.08 to 1.14	-0.79 to -0.39	1.23 to 1.31
S. lineatus	-0.50 to -0.20	1.15 to 1.19	-0.87 to -0.50	1.33 to 1.39
S. punctatus	-1.07 to -0.63	1.23 to 1.32	-1.28 to -0.85	1.38 to 1.47

CHAPTER 5

MICROHABITAT CHOICE BY JUVENILE SIGANIDS:

Associations between behaviour and habitat complexity

5.1 INTRODUCTION

The role of seagrass beds as nursery areas for juvenile coral reef fishes has received considerable attention (see review in Parrish, 1989). The demonstrated ability of many coral reef fish species to select specific microhabitat types at settlement (Sale et al., 1984; Eckert, 1985) suggests that recruitment to seagrass beds is adaptive and may lead to enhanced survival rates amongst species which commonly settle in this habitat (Parrish, 1989). Potential advantages include reduced predation rates, an abundant food supply, reduced competition for resources and wider availability of the habitat to settling larvae (Ogden and Zieman, 1977; Ogden, 1980; Pollard, 1984; Bell and Pollard, 1989; Parrish, 1989). The relative importance of these factors to juveniles of a given species may affect their utilisation of the seagrass bed habitat.

Although by no means the sole determinant of community structure, predation is an important factor in the structuring of marine communities (Leber, 1985; Hixon, 1991; Hixon and Beets, 1993; Caley and St. John, 1996). A considerable body of literature has built up regarding the effects of habitat complexity (= refuge availability) on predator - prey interactions in aquatic habitats (reviews in Nelson and Bonsdorff, 1990, Hixon, 1991 and Milinski, 1993; Hixon and Beets, 1993), with the general conclusion being that increased habitat complexity results in increased survival of prey species. Refuge from predation may be described as permanent or transient: the former physically excludes predators (e.g. small holes), while the latter increases the probability that an individual will elude predators (e.g. structurally complex habitats which interfere with visual hunting) (Caley and St. John, 1996).

Small or young fish are more vulnerable to predation than larger or older fish (Hixon, 1991). As a result, habitat structure, and its effect on predation rates, has emerged as the leading factor thought to influence the survival of juvenile fishes in seagrass beds (Ogden and Zieman, 1977; Heck and Orth, 1980; Pollard, 1984; Shulman, 1985; Bell and Pollard, 1989; Parrish, 1989). Research has demonstrated that the effectiveness of structural complexity as a refuge from predation is often dependent on the size of the structure relative to the size of the individual (Ebeling and Laur, 1985; Behrents, 1987; Hixon and Beets, 1989, 1993; Connell and Jones, 1991). It has been suggested that it is this difference in scale which enables seagrass to provide shelter that is suitable for juvenile fishes (Ogden and Zieman, 1977; Ogden, 1980). In addition to the basic structure of the seagrass, macroalgae may also play a role in the provision of shelter for juveniles fishes (Ebeling and Laur, 1985; Carr, 1989; Levin, 1991; Eggleston, 1995).

Shoaling behaviour, the aggregation of fishes in social groups, also has an important role in reducing the success of predation (review by Pitcher and Parrish, 1993). Fishes utilise a wide variety of group strategies to enhance survival rates, and the presence of social companions facilitates faster detection of predators while reducing risk to the individual (Pitcher and Parrish, 1993). Shoal size has been shown to be an important factor influencing the behaviour of fishes, including their patterns of habitat utilisation (Savino and Stein, 1982; Magurran and Pitcher, 1983). In the Siganidae, where some species shoal while others do not (Woodland, 1990), this aspect of behaviour could have significant implications for the distributions of species among habitats.

There has been much debate regarding the relative roles of recruitment and post-recuitment processes in the structuring of coral reef communities (reviews by Doherty, 1991, Jones, 1991, Williams, 1991 and Hixon, 1991). Even early in the juvenile phase, the distinction is made between settlement patterns and distributions resulting from post-recruitment processes such as competition (Jones, 1988), predation (Shulman, 1985) and migration (Robertson, 1988; Lewis, 1997). The role of predation in structuring post-recruitment distributions may be direct (via consumption of prey in open areas), or indirect (as an evolutionary selection pressure for a preference of habitats where predation success is reduced) (Shulman, 1985; Bell and Westoby, 1986; Bell and Pollard, 1989; Connell and Jones, 1991; Sweatman and Robertson, 1994). In coral reef environments, the time when habitat selection occurs has been shown to vary between species, with some species settling directly to specific substrates and others migrating as post-recruits (Sale *et al.*, 1984; Eckert, 1985; Lewis, 1997). It has been suggested that, in seagrass beds, selection of microhabitats often occurs after, rather than at, settlement, and that predation is an indirect cause of the final observed distributions (Bell and Westoby, 1986; Bell and Pollard, 1989; Bell *et al.*, 1992; Sweatman and Robertson, 1994).

Most studies on the nursery function of seagrass beds have been carried out in the Caribbean (e.g. Ogden and Zieman, 1977; Weinstein and Heck, 1979; Shulman, 1985; Parrish, 1989; Baelde, 1990; Sweatman and Robertson, 1994). Studies in the Indo-Pacific (Jones and Chase, 1975; Harmelin-Vivien, 1983; Blaber *et al.*, 1992) and the Great Barrier Reef region (Coles *et al.*, 1993; Lee Long *et al.* 1993) have been less numerous. Siganids are among the species known to recruit to the seagrass beds of Indo-Pacific islands in large numbers (Tsuda and Bryan, 1973; Von Westernhagen, 1973; Lam, 1974; Jones and Chase, 1975; Kami and Ikehara, 1976; Hasse *et al.*, 1977; Blaber *et al.*, 1992; Pinto and Punchihewa, 1996). Similar recruitment has been recorded in the coastal seagrass beds of both the Red Sea and Mediterranean Sea (Popper and Gundermann, 1975). The annual appearance of large shoals of recruits on the reef flat is predictable, and usually follows a lunar cycle during the late spring / early summer months (Tsuda and Bryan, 1973; Kami and Ikehara, 1976; Hasse *et al.*, 1977). Beyond this, there is only anecdotal information on how these juveniles utilise the seagrass bed habitat (Popper and Gundermann, 1975; Hasse *et al.*, 1977).

5.1.1 Aims and objectives

The aim of this study was to determine the habitat use patterns of juvenile siganids in the seagrass beds on the reef flat of Green Island Reef, with the objective of assessing the roles of various factors in influencing their distribution. It was hypothesised that factors such as habitat complexity, activity, shoal size and fish size might influence microhabitat choice. Further points of interest were whether there were any differences in the distributions of the four study species and whether the slight differences between the three reef flat sites (Chapter 2) led to any discernible differences in microhabitat use.

5.2 MATERIALS AND METHODS

5.2.1 Field observations

The behaviour and habitat use patterns of juvenile siganids at the three seagrass sites on the reef flat (Chapter 2) were observed between November 1994 and March 1996. Observation sessions took place monthly during the summer of 1994-1995 and in alternate months in the summer of 1995-1996, giving 9 sets of observations in all. Observations were conducted at mid-tide using snorkel equipment. This strategy was adopted because the sites were often exposed at low tide, but under 3 m of water at high tide, and the time taken to search the sites made the use of SCUBA impractical. Observations were carried out between 09:00 and 15:30 to avoid the crepuscular periods of reduced activity.

During the course of an observation session, the entire site was searched thoroughly and brief, "snap-shot" observations were made of all juvenile siganids encountered during that time. In order to preserve the independence of the observations, a randomly selected fish from each social unit was used as a "focal individual" (Crook, 1997) for a single observation related to that group, and the search was structured to ensure that areas were not revisited. The site was divided up into 5 m wide belts that were marked with polystyrene floats to serve as guides. Scanning the width of the belt and the area from directly below the eyeline out to 2.5 m ahead was adequate for detecting and counting juveniles in the open seagrass, and reduced the likelihood of re-recording individuals in the path ahead. Complex microhabitats such as *Sargassum* reefs (see Chapter 2) were investigated more closely because of the difficulty in observing fish associated with them. Most *Sargassum* reefs were recognisable via certain aspects of their structure or associated sessile fauna. This, in combination with the floats, avoided the possibility of a given area, and the individual fish in it, being inspected more than once during an observation session.

Information about the activities and habitat associations of the juveniles observed were recorded on an underwater slate. The recording process was simplified by the use of codes and an observation could be completed in approximately 15 seconds. For each fish or shoal of fish observed, the following information was recorded:

Species (of focal individual): *Siganus doliatus*, *S. fuscescens*, *S. lineatus* or *S. punctatus*.

Fish size: Total length of the focal individual was estimated in terms of 4 size classes: <30mm, <50 mm, <70 mm and >80 mm. These corresponded to size at settlement (Bryan and Madraisau, 1977; Thresher, 1984) and size at approximately 1, 2, and 3 or more months post-settlement (pers. obs.). Size estimates were checked against the samples used for dietary and morphometric analyses (Chapters 3 and 4). In the analysis, size classes were combined so that fish were categorised as <50 mm or >50 mm. These two categories represented fish in the first 4 to 6 weeks after settling in the seagrass beds, and those which had been settled for 2 months or more. Hasse *et al.* (1977) noted that juveniles often shoaled together regardless of size during the first month or so after settlement, but were in more size restricted shoals thereafter. My own observations of similar behaviour in fishes <50 mm supported the decision to separate the size classes at this point.

Shoal size: The total number of individuals in a shoal was counted, or estimated when numbers were greater than 20. A shoal was defined as a cohesive group, regardless of activity, with the term "schooling" reserved for synchronised swimming behaviour (Pitcher and Parrish, 1993), and heterospecifics were included in the count when present. For the analysis, categories were defined as: 1 to 3 fish; a shoal of 4 to 10 fish; or a large shoal of more than 10 fish.

Habitat: Microhabitat type was recorded based on the categories of the Habitat Complexity Scale (Table 2.1, Chapter 2): 2 - short, sparse seagrass (Plate 5.1a); 3 - tall, dense seagrass (Plate 5.1b); 4 - small reef or *Sargassum* clump; 5 - large *Sargassum* reef (Plate 5.2a); 6 - low algae / soft coral reef. For the analysis, categories 2 and 3 were combined under "seagrass" and categories 4 to 6 were combined as "*Sargassum* reefs".

Activity: Activities were categorised as feeding: biting movements observed; roving: active, directional swimming; hiding: remaining relatively still while associated with the substratum or other structure, and moving only to maintain position.

5.2.2 Data analysis

Log-linear modelling is a frequency analysis technique for multidimensional contingency tables. It has traditionally been used in the behavioural and social sciences (Colgan and Smith, 1978; Tabachnick and Fidell, 1989), and has recently been utilised in an analysis of fish behaviour (Crook, 1997). The main advantage of this technique is that it is designed specifically for categorical data. It is also more flexible than most parametric techniques since there are no assumptions regarding the distribution of the population (Tabachnick and Fidell, 1989; Everitt, 1992). Log-linear analysis tests all hypotheses related to a multidimensional data set without resorting to multiple tests, and thus avoids inflating the significance of the results (Everitt, 1992). The modelling process searches for associations (known as interactions) among the variables influencing the data. In backwards elimination, interaction terms are sequentially removed from a saturated model (containing all possible interaction effects), and partial chi square (χ^2) values are calculated. This allows the relative importance of each interaction to be assessed using p values and standardised residuals (partial χ^2 / df). Low p values and high residual values are associated with important interactions. Once the key interactions have been identified, the underlying correlations can be expressed by means of odds ratios, which are ratios of probabilities calculated from the relevant subsection of the contingency table (Crook, 1997).

A large final data set was generated from the field observations (n = 1887), and the data were arranged into a multidimensional contingency table for log-linear analysis. A saturated backwards elimination model was applied to the data, and interaction terms with p values <0.001 were selected from the association table produced. A low p value was used to avoid the selection of too many terms. The relative importance of these interactions was determined from the standardised residual values (χ^2 / df), and they were ranked accordingly. In order to identify the correlations underlying these interactions, the appropriate subsection of the multiway contingency table was examined, and odds ratios were calculated from the relevant probabilities. For example, large juveniles were observed in seagrass (as opposed to *Sargassum* reefs) 227 times out of 774 (= 0.293), while small juveniles were only observed in seagrass 195 times out of 1113 (= 0.175). The probability of a large juvenile being observed in seagrass was therefore 0.293 / 0.175 = 1.7 times greater than that of a small juvenile.

To confirm the accuracy with which the key interactions described the observed data, predicted values from a single entry model based on those interactions were tested for overall goodness of fit using the Maximum Likelihood Ratio χ^2. Using this method, the effects of structural zeros (combinations of variables which do not, or cannot, occur), and sampling zeros (combinations of variables which were not observed), were taken into account by adjusting the degrees of freedom associated with the model (Feinberg, 1970; Everitt, 1992). Modelling calculations were performed using the SPSS (v. 6.1) statistical package.

5.3 RESULTS

The observations of habitat use patterns by juvenile siganids at the three seagrass bed sites resulted in the generation of a multiway contingency table (Appendix II). An examination of the partial chi-square values in the association table produced from the saturated backward elimination model showed that there were thirteen interaction terms with p values < 0.0001. These included most of the two-way interactions, and two three-way interactions (Table 5.1). The relative importance of these interactions was determined from the standardised residual values (χ^2 / df), and they have been ranked accordingly (Table 5.1). The odds ratios which quantify the correlations underlying the interactions are given in Table 5.2. The distribution of observations between the categories of the variables is given, followed by descriptions of the interaction terms.

Main Effects

Site

The ratio of observations made at the three sites (north : flat east : flat west) was 662 : 542 : 683, which approximates to 1 : 1 : 1.

Species

The frequency of observations of the different species (*S. doliatus* : *S. fuscescens* : *S. lineatus* : *S. punctatus*) was 1080 : 602 : 77 : 128, or ≈ 14 : 8 : 1 : 2, showing that *S. doliatus* was the most common species, while juvenile *S. lineatus* and *S. punctatus* were comparatively rare.

Size

The ratio of recent recruits (<50 mm TL) to older juveniles (>50 mm) was 1113 : 774, or 3 : 2. This illustrates the continued recruitment through the summer season, and the gradual mortality (and, possibly, emigration) of older individuals.

Shoal size

The ratio of the different shoal sizes observed (1 to 3 : 4 to 10 : >10) was 1230 : 436 : 221, ≈ 6 : 2 : 1. Small groups were the most common, and large shoals were rare.

Habitat

The ratio of fish observed in seagrass as opposed to *Sargassum* reefs was 422 : 1465, ≈ 2 : 7, showing a definite association between juvenile siganids and the *Sargassum* microhabitat.

Activity

The ratio of activity patterns (feeding : roving : hiding) was 192 : 442 : 1253, ≈ 1 : 2 : 6, This shows a tendency for juvenile siganids to remain hidden most of the time, and venture out to forage occasionally.

Interaction Effects

Activity * Habitat

The interaction between activity and habitat type was the most important, with a standardised residual value of 405.14. Hiding was very strongly associated with *Sargassum* reefs, being 122 times more likely to occur there than in seagrass (odds ratio = 121.9). In contrast, roving and feeding were 8.7 times and 4 times respectively more likely to occur in seagrass.

Fish size * Shoal size

Small juveniles were 4.4 times more likely than large juveniles to occur in shoals of more than 10, and 1.5 times more likely to occur in shoals of 4 to 10. Large juveniles were 1.4 times more likely than small juveniles to occur in groups of 1 to 3. This association was also very strong (standardised residual = 106.5).

Fish size * Habitat * Site

Although the majority of juveniles were associated with the *Sargassum* microhabitat (see Habitat main effect), small juveniles at the northern site were 2.1 and 8.1 times more likely to be observed in the seagrass than small juveniles at the flat east site and the flat west site respectively. Larger juveniles at all three sites were distributed between the two microhabitats in a similar manner to the juveniles at the northern site.

Activity * Site

Juvenile siganids at the north site were 2.1 and 3.3 times more likely to be roving than those at the flat east and flat west sites respectively. Juveniles were also more likely to be feeding at the north site than the other two sites (odds ratios of 1.6 and 1.8 respectively). At the eastern and western flat sites, juveniles were 1.5 and 1.7 times more likely to be hiding than at the north site.

Shoal size * Site

Shoals of more than 10 individuals were most common at the north site, being 1.8 and 7.2 times more likely to occur there than at the flat east and flat west sites. Groups of 1 to 3 comprised a greater proportion of observations from the flat west and flat east sites.

Fish size * Habitat

Large juveniles were 1.7 times more likely to use the seagrass habitat than the small juveniles, which were more strongly associated with the *Sargassum.*

Habitat * Species

S. fuscescens was the species observed most often in the seagrass, being 4 to 6 times more likely to use that habitat than the other three species. *S. doliatus*, *S. lineatus* and *S. punctatus* were more strongly associated with the *Sargassum.*

Activity * Fish size

Large juveniles were twice as likely to be feeding as small juveniles (odds ratio = 1.9). Large juveniles were also more likely to be roving, while small juveniles were more likely to be hiding.

Fish size * Site * Species

Large *S. lineatus* were much more likely to occur at the flat west site than the northern or flat east sites (odds ratios of ≈ 641 and 11.65 respectively). Size classes of the other three species were relatively evenly distributed.

Activity * Shoal size

Shoals of 4 to 10 and shoals of greater than 10 were more likely to be feeding than groups of 1 to 3 (odds ratios of 2.6 and 1.9 respectively). These larger shoals also roved more than groups of 1 to 3, being 2.9 and 1.8 times more likely to engage in this activity. In contrast, groups of 1 to 3 were 1.4 and 2.3 times more likely to be hiding than shoals of 4 to 10 and shoals of greater than 10 respectively.

Habitat * Shoal size

Shoals of 4 to 10 and shoals of greater than 10 were more likely to use the seagrass than groups of 1 to 3 (2.1 and 3.4 times respectively). Groups of 1 to 3 were more strongly associated with the *Sargassum.*

Shoal size * Species

S. fuscescens was the species most commonly observed in shoals of greater than 10, being 2.5, 2.6 and 6.6 times more likely to occur in such large shoals than *S. doliatus*, *S. lineatus* and *S. punctatus* respectively. This species was also more likely to occur in shoals of 4 to 10 (odds ratios of 1.6, 1.8 and 1.5 respectively).

Site * Species

The four study species did not occur evenly across the three sites. *S. doliatus* were slightly more numerous at the flat west site (≈ 2 : 2 : 3, north : flat east : flat west). *S. fuscescens* were most abundant at the north site (≈ 9 : 6 : 5). There were more *S. lineatus* at the flat west site (≈ 1 : 1 : 2), while *S. punctatus* were less abundant there (≈ 9 : 10 : 7).

The single entry hierarchical model based on these thirteen interactions (which includes lower order interactions and main effects) produced expected cell values that were not significantly different from the observed values (Likelihood Ratio χ^2 = 372.856, df (adjusted) = 345, p = 0.145).

Non-interaction effects

Conditional independence of effects can be determined from a knowledge of all significant two-way interactions. The association table of partial relationships, produced from the saturated model, showed that there was no significant interaction between fish size and site (p = 0.40). There were approximately equal numbers of observations of small juveniles and large juveniles at the three sites, but this independence is conditional upon the habitats and the species mix remaining constant and being considered as a whole. Referring to the three-way interactions in the previous section, it can be seen that when microhabitat or species distinctions are made, indirect correlations between fish size and site become apparent.

Summary

In the seagrass beds at Green Island Reef, juvenile siganids were generally observed hiding in the *Sargassum* plants. Fish of all species and sizes were observed in this microhabitat, usually in small groups. The few large shoals were comprised of small juveniles. Juveniles were also observed roving and feeding in the open seagrass, particularly at the northern site. The majority of these were from the larger size class, and occurred in small groups and shoals of 4 to 10. *S. fuscescens* was the species most commonly observed in these activities. The few observations of small juveniles utilising the seagrass showed all species (but especially *S. fuscescens*) occurring in large shoals, predominantly at the northern site. *S. lineatus* in the larger size class were observed predominantly at the flat west site.

5.4 DISCUSSION

These results clearly demonstrate that juvenile siganids utilise microhabitats within the seagrass beds at Green Island in a nonrandom fashion, and that their distributions are influenced by a number of factors. The uneven distribution of juveniles between the seagrass and the structurally complex *Sargassum* reefs, with fish strongly associated with the more complex yet less abundant microhabitat (Chapter 2, Plate 5.2 a and b), is an important main effect. It implies a preference for, or survival advantage associated with, the microhabitat with greater structural complexity which theoretically confers a lower risk of predation (Hixon, 1991; Hixon and Beets, 1993; Caley and St. John, 1996). In temperate regions, macroalgae have been shown to play a similar role in the provision of shelter for juvenile fishes in otherwise two-dimensional habitats (Ebeling and Laur, 1985; Carr, 1989; Levin, 1991), and Eggleston (1995) provides a tropical reef example. The attraction of juvenile fishes towards experimental structures in Caribbean seagrass beds (Shulman, 1985; Hixon and Beets, 1989; Sweatman and Robertson, 1994) also suggests a preference for more complex structures within seagrass beds where they are available.

In addition, the importance of the interaction between activity and microhabitat type implies the presence of strong behavioural patterns which allow the juveniles to maximise their advantage in both microhabitat types. The Activity * Habitat interaction is driven by the nearly exclusive occurrence of hiding in the *Sargassum* reef microhabitat, which makes the most efficient use of the visual concealment provided by the complexity of that habitat (Savino and Stein, 1982). The use of seagrass for hiding was rare (only 3 observations out of 422), and fish were still highly visible when trying to hide in this microhabitat. In contrast, activities such as roving and feeding were more likely to occur in seagrass than in the *Sargassum* microhabitat. Activities involving a significant degree of movement will be visible to predators regardless of the structure of the habitat, and may be more efficient in areas of lower complexity where there is less structure to impede movement (Crowder and Cooper, 1982; Bell and Westoby, 1987). Such adaptive interactions between behaviour and habitat have also been noted in other studies (Savino and Stein, 1982; Magurran and Pitcher, 1983; Main, 1987).

This interpretation is supported by the interactions of Activity * Shoal size and Habitat * Shoal size, ranked 10 and 11, which suggest shoaling behaviour as a mediator for the association between activity and habitat. Shoals of 4 to 10 fish were associated with both roving and feeding, and with the seagrass habitat. Larger shoals (>10) had similar associations, but they were less strong. In contrast, fish in small social units (1 to 3) were more likely to be hiding and utilising the *Sargassum* reef microhabitat. Shoaling behaviour in fishes has an important anti-predator function (Pitcher and Parrish, 1993), and in this situation it appears that shoaling is being used as an alternative to the protection of a complex habitat during activities which are more efficiently conducted in the seagrass. This agrees with experimental studies showing that shoal size increases in more exposed areas, while dispersal and hiding behaviour occurs when habitat complexity is greater or there are few social companions (Savino and Stein, 1982; Magurran and Pitcher, 1983). Other authors have also shown that larger shoals will accept a greater risk of predation (see Milinski, 1993). It should not be forgotten that shoaling also confers foraging advantages, as it increases the efficiency of food location and predator monitoring (Pitcher and Parrish, 1993), but for herbivorous fishes the anti-predator function is likely to be the more important.

The strong association between fish size and shoal size (the second most important interaction) is primarily a function of the very large recruitment schools formed by settling siganids when they first appear on the reef flat (Tsuda and Bryan, 1973; Popper and Gundermann, 1975; Kami and Ikehara, 1976; Hasse *et al.*, 1977). The number of individuals observed in a recruitment school on Green Island Reef varied between 50 and 300, with the greatest numbers occurring at the peak of the recruitment season in December and January. These values compare to figures in the literature which range from 200 to 5000 (Popper and Gundermann, 1975; Hasse *et al.*, 1977). Recruitment schools roamed the seagrass beds, and gradually became smaller as individuals and small shoals remained behind in *Sargassum* reef habitats that were encountered (pers. obs.). Predation also presumably had a role in the decreasing size of the shoals. By the time juveniles were larger than 50 mm (SL), the majority of them were observed in social units of 1 to 3.

The decrease in shoal size following settlement would have been better demonstrated by the inclusion of a wider range of shoal sizes in the analysis. The observational categories were set up in order to do this, but the number of shoal sizes was restricted by the complexity of the analysis, the low numbers of observations of large recruitment schools, and the need to reduce the number of structural zeros resulting from shoal size categories that did not occur among the larger juveniles (with the exception of *S. fuscescens*). The extremely large size of these shoals may serve a variety of functions, but the most obvious role is in the reduction of predation at this critical point in the life cycle.

Two further interactions that are worth considering at this point are Fish size * Habitat (rank 6) and Activity * Fish size (rank 8). Smaller juveniles used the seagrass much less than the larger ones, and were observed feeding less frequently. The smaller juveniles, being more susceptible to predation, have a stronger dependence on structural protection than larger ones (Behrents, 1987; Carr, 1989). Given that feeding is more likely to occur in seagrass (see Activity * Habitat), it appears that smaller juveniles are prepared to accept reduced feeding returns as the price of greater safety, a trade-off which has been demonstrated in other studies (Werner *et al.*, 1983; Schlosser, 1987). Hasse *et al.* (1977) observed that new recruits of *Siganus canaliculatus* often stopped feeding for up to half an hour, and settled, motionless, near the substrate or among the seagrass blades. Referred to as "resting", this behaviour could fit the definition of "hiding" in the behavioural categories used here. Although strongly suggestive of a compromise of foraging in favour of security, new recruits may simply require less food.

The interactions ranked 3 to 5 are a result of features specific to Green Island, the distribution of the seagrass beds and subtle variations between the three study sites (see Chapter 2). Of these, the interaction between fish size, habitat and site was the most important, but it is easier to consider all three interactions together. The north site was associated with small juveniles that were uncharacteristically utilising the seagrass (refer to Fish size * Habitat above), and roving behaviour and large shoals were also disproportionately represented compared to other two sites. These interactions imply that this site is the first point of contact for the large recruitment schools mentioned previously. The north site and the flat east site are both in a good position to intercept settling larvae, whose arrival may be influenced by the prevailing southeasterly currents and winds. The northern site tends to receive more recruits because the rocky rim of the reef extends around the southern side of the flat and cuts off water flow to the other two sites during low tides, but stops short of the north seagrass site. The occurrence of extreme low tides at night during summer new moon periods, the time of recruitment for siganids (at Green Island Reef at least - pers. obs.), would effectively prevent larvae from settling directly to the southern sites. The occurrence of some large shoals of small juveniles at flat east and hardly any at flat west suggests that recruits move clockwise round the island in progressively smaller groups in the period following settlement.

There were four interactions which highlighted differences between the study species. *S. fuscescens* was more likely to use the seagrass habitat than the other species, and was also most commonly observed in larger shoals. *S. fuscescens* remains in shoals as an adult, and this is undoubtably the reason behind the persistance of the larger shoal sizes which were associated only with recruitment in the other species. This can be viewed as correlative support for the hypothesis that shoaling behaviour is the mediator for microhabitat use patterns. *S. fuscescens* was more abundant at the north site and, along with the recruitment schools, almost certainly influenced the Site * Activity and Site * Shoal size interactions. The taller, denser seagrass at the north site (Chapter 2, Plate 5.1) suggests that it is the greater protection available in the seagrass at this site, relative to the other two sites, that may be the driving force behind these interactions (Stoner, 1983; Stoner and Lewis, 1985; Blaber *et al.*, 1992).

S. lineatus were most likely to occur at the flat west site, and larger individuals were particularly associated with this site rather than the northern or flat east sites (odds ratios of ≈ 641 and 11.65 respectively). *S. lineatus* appears to recruit to the northern site, and move around the reef flat, through flat east to flat west, resulting in the greater numbers of larger juveniles at the third site. Although adult *S. lineatus* form shoals, the post-recruitment juveniles did not occur in large shoals as *S. fuscescens* juveniles did. This is largely due to the low recruitment levels evident for this species (although sporadic recruitment of very strong cohorts seems to drive the population, pers. obs., 1994). Adult *S. lineatus* were regularly observed foraging at the flat west site (Chapter 6), suggesting an hypothesis to explain the preference of larger juveniles for that site. It is possible that, during years of poor recruitment when there are not enough juveniles to form a shoal on their own, older juveniles at the flat west site are assimilated into the large foraging shoals (which usually contain adults of a variety of year classes) as a means of making the transition to the coral habitat and the adult lifestyle.

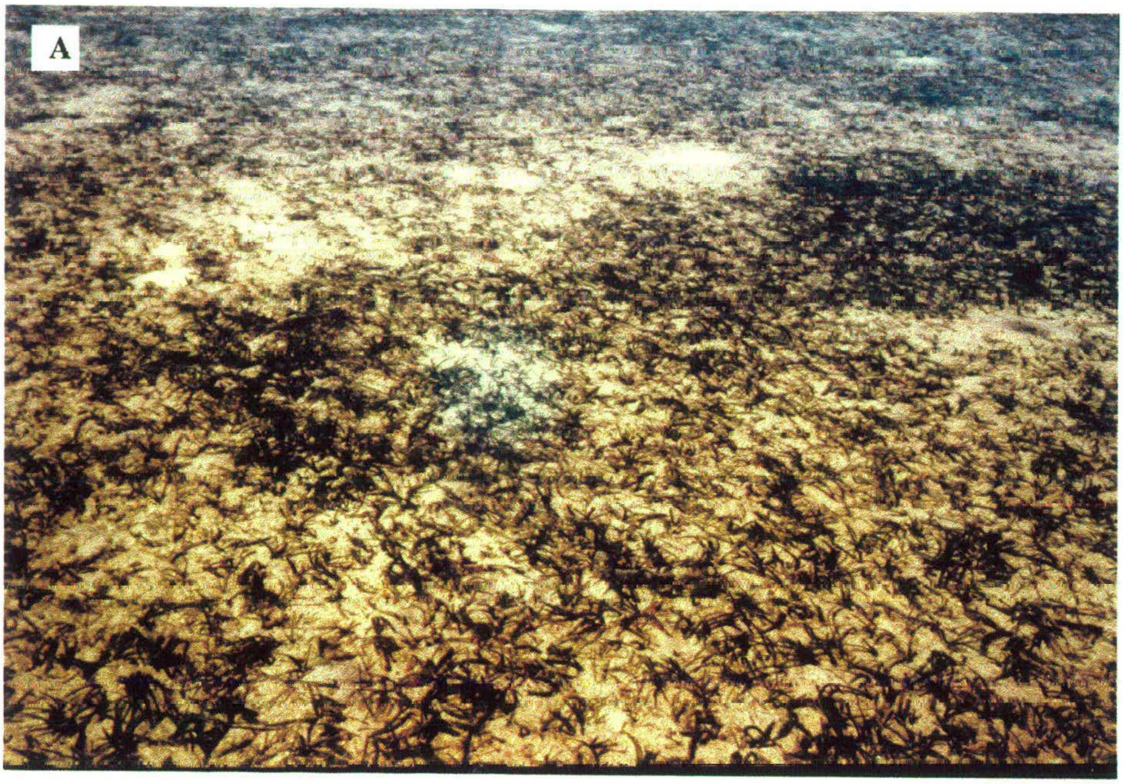
The possibility of alternate juvenile strategies in the two shoaling species is interesting, but a long-term study of recruitment patterns (in order to capture sporadic events) would be required to clarify this hypothesis. Aside from the preference for the flat west site, *S. lineatus* appears to have similar habitat use patterns to the juveniles of the two pairing species, being primarily associated with the *Sargassum* reef microhabitat. The continued shoaling of *S. fuscescens* after the initial recruitment period allows this species to make greater use of the seagrass habitat, particularly where the seagrass is taller and denser. These differences appear to be relatively minor factors in the overall picture of juvenile distributions however.

5.5 CONCLUSIONS

It is seems likely that predation and / or predation-motivated behaviour patterns are responsible for the major distribution patterns observed among juvenile siganids. There has been no attempt to specifically determine whether predation is the direct cause of distributions (where individuals in predation-prone habitats are preyed upon with disproportionate success), or the indirect cause (having been the selective pressure over evolutionary time which has resulted in currently observed habitat preferences). Given the strong behavioural patterns that appear to have developed in association with these distributions, the role of predation here seems to be as the indirect cause of preferences for structurally complex microhabitats. Such adaptations imply that fish are aware of the greater protection that is afforded by more complex microhabitats, and thus should seek to alter their distributions in such a manner as to favour their survival.

The overall distribution patterns, particularly the differences between new and older recruits and the suggestion of a preference for more complex microhabitats, support Bell and Westoby's (1986) theory that settlement to seagrass beds operates in a non-selective manner, and that the observed habitat distributions occur because of microhabitat selection in the first month or so post-settlement (see also Bell and Pollard, 1989 and Bell *et al.*, 1992). In siganids, this strategy appears to be mediated by the large size of recruitment shoals, which provides some protection from predators during this intermediate period.

Plate 5.1 a and b. Short, sparse seagrass on the exposed, southern side of the island (A) and tall, dense seagrass on the sheltered, northern side of the island (B).



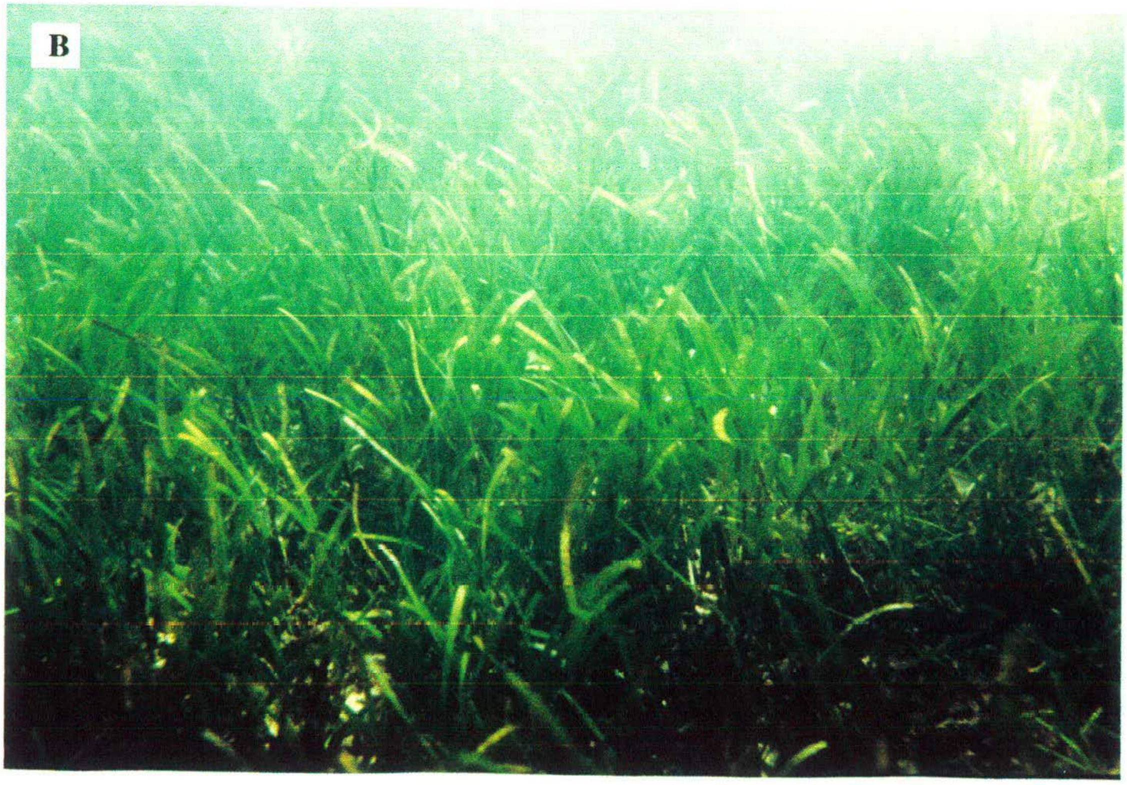


Plate 5.2 a and b. *Sargassum spp*. "reef" (A) and the distribution of *Sargassum spp*. "reefs" on the northern side of the island (B).

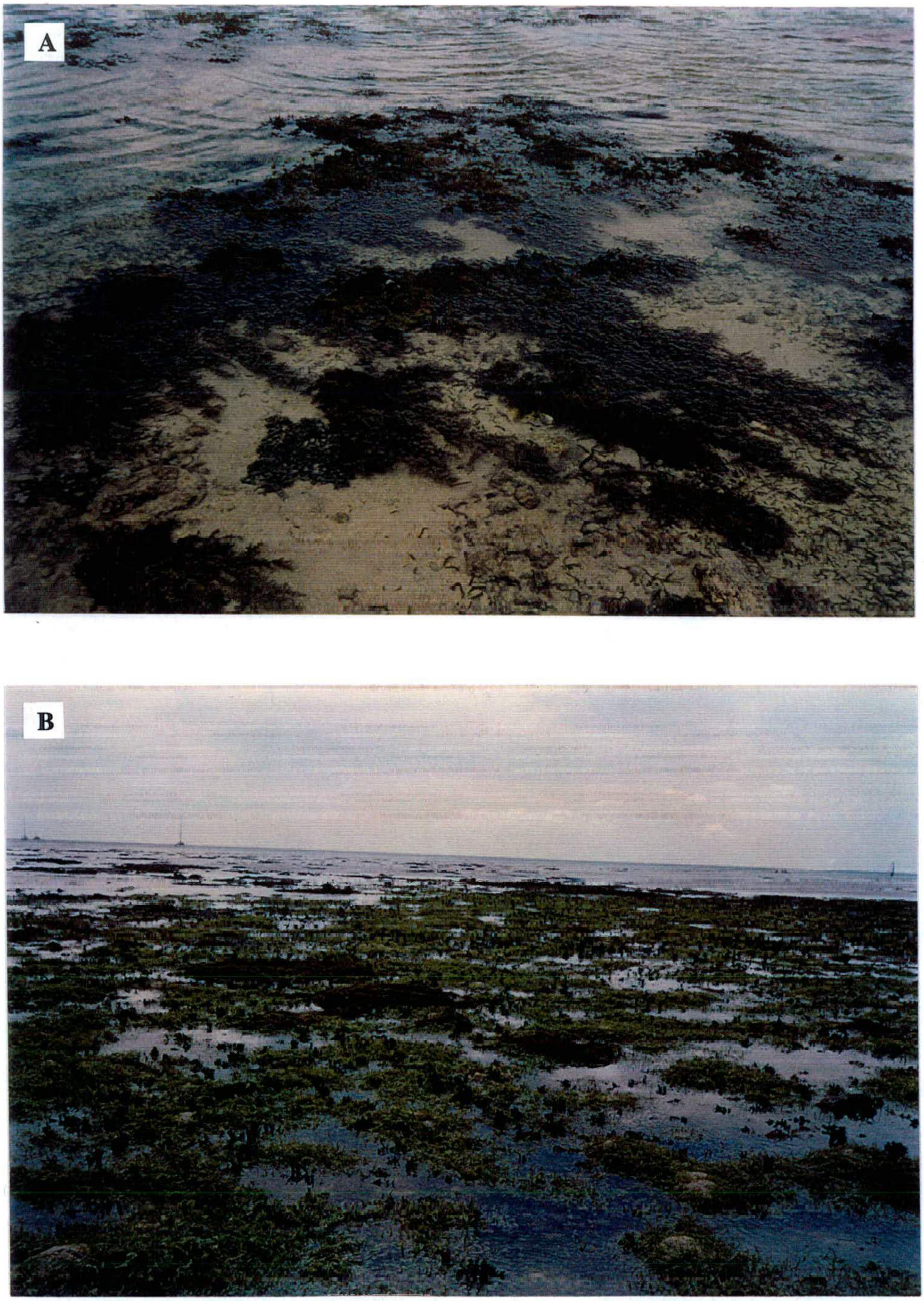


Table 5.1. Interactions where $p < 0.0001$ in the saturated model produced using data in Appendix II. Large standardised residual values correspond to the most important interactions and are ranked accordingly.

Interaction	Partial chi square (χ^2)	Degrees of freedom (df)	Standardised residual (χ^2/df) rank
Activity * Habitat	810.270	2	1
Fish size * Shoal size	213.170	2	2
Fish size * Habitat * Site	46.568	2	3
Activity * Site	92.049	4	4
Shoal size *Site	74.435	4	5
Fish size * Habitat	17.207	1	6
Habitat * Species	40.563	3	7
Activity * Fish size	26.746	2	8
Fish size * Site * Species	63.015	6	9
Activity * Shoal size	36.106	4	10
Habitat * Shoal size	15.388	2	11
Shoal size * Species	41.581	6	12
Site * Species	28.146	6	13

Table 5.2. Odds ratios associated with the correlations underlying the significant interactions in Table 5.1. For the comparison involving a sampling zero, 0.001 was added to the probability to produce an approximate ratio, denoted ≈.

Interaction	Underlying correlation(s)	Associated odds ratio(s)
Activity * Habitat	feeding in seagrass.	3.9
	roving in seagrass.	8.7
	hiding in *Sargassum* reefs.	121.9
Fish size * Shoal size	large fish in groups of 1 - 3.	1.4
	small fish in shoals of 4 - 10.	1.5
	small fish in shoals >10.	4.4
Fish size * Habitat * Site	small fish at the north site in seagrass.	2.1; 8.1
Activity * Site	feeding at the north site	1.6; 1.8
	roving at the north site.	2.1; 3.3
	hiding at the east and west sites.	1.5; 1.7
Shoal size * Site	shoals >10 at the north site.	1.8; 7.2
	groups of 1 to 3 at the west site.	1.2; 1.5
Fish size * Habitat	large fish in seagrass.	1.7
Habitat * Species	*S. fuscescens* in seagrass.	3.9; 5.9; 4.2
Activity * Fish size	large fish fed more.	1.9
	large fish roved more.	1.3
Fish size * Site * Species	large *S. lineatus* at the west site.	≈ 641; 11.65
	small *S. lineatus* at the north and east sites.	2.8; 2.6
Activity * Shoal size	shoals of 4 - 10 and >10 feeding.	2.6; 1.9
	shoals of 4 - 10 and >10 roving.	2.9; 1.8
	groups of 1 - 3 hiding.	1.4; 2.3
Habitat * Shoal size	shoals of 4 - 10 and >10 in seagrass.	2.1; 3.4
	groups of 1 - 3 in *Sargassum* reefs.	1.2; 1.7
Shoal size * Species	*S. fuscescens* in shoals of 4 - 10.	1.6; 1.8; 1.5
	S. fuscescens in shoals >10.	2.5; 2.6; 6.6
Site * Species	*S. doliatus*	332 : 289 : 459
	S. fuscescens	265 : 185 : 152
	S. lineatus	20 : 18 : 39
	S. punctatus	45 : 50 : 33

CHAPTER 6

HABITAT UTILISATION BY ADULT SIGANIDS:

Differences between species and between habitat types

6.1 INTRODUCTION

An important element in the interpretation of an organism's distribution is the concept of scale. Broad scale distributions result from the summation of all biotic and abiotic processes acting on a species; at a fine scale, the distribution of a species is presumed to reflect the utilisation of the resources available in a given area by the individuals resident there (Williams, 1991; Caley, 1995; Syms, 1995; Gutt and Ekau, 1996). Regardless of scale, pattern is often used to infer the underlying processes. Some functions of habitat can be examined through experiments which alter the existing features and then measure the responses of organisms (e.g. Choat and Ayling, 1987; Connell and Jones, 1991). In coral reef fish communities, studies have concentrated on identifying assemblages and correlating species with features of their habitat, but direct observations of processes are not often included (Williams, 1991). Direct observations of broad-scale processes such as recruitment are often difficult to facilitate but, at a local level, basic processes related to resource use are more readily quantified. A more accurate picture of interactions between organism and habitat may then be used to infer the roles of community-level processes such as competition and predation.

Many species of fish, including siganids, exhibit ontogenetic changes in habitat use (Bryan 1975; Popper and Gundermann, 1975; Helfman, 1978; Gundermann *et al.*, 1983; Werner and Gilliam, 1984; Jones, 1991). In tropical marine habitats, these changes may involve utilising the same type of substratum at a different depth (Green, 1996), changing microhabitat within the same broad habitat type (Lirman, 1994; Eggleston, 1995), or even changing habitat types altogether (Shulman and Ogden, 1987). Such changes are indicative of differences in the food and shelter resources required by juvenile and adult fish, and may be related to changes in their social behaviour or vulnerability to predation (Helfman, 1978; Werner, 1984). Physical aspects of the habitats may play a role, as the size of structures relative to the size of the individual affects the shelter potential of a given habitat (Luckhurst and Luckhurst, 1978; Roberts and Ormond, 1987; Hixon and Beets, 1989 and 1993). Other factors which may influence fish - habitat associations include reef size and height, depth, live coral cover, substrate heterogeneity and water movement (reviewed in Jones, 1991 and Williams, 1991).

The distributions of fishes in the vicinity of shallow flats and banks may be affected by the tidal cycle, which is an important influence in marine environments (Bakus, 1967 and 1969; Ralston and Horn, 1986; Sogard *et al.*, 1989). Shallow habitats become available when covered with water at high tide but must be vacated again as the water recedes, resulting in migrations that follow the tidal cycle (Bakus, 1967 and 1969; Robertson, 1980; Sogard *et al.*, 1989). There is considerable documentation of fishes moving between tropical marine habitats in the Caribbean, particularly during foraging (Ogden and Zieman, 1977; reviewed in Bell and Pollard, 1989 and Parrish, 1989; Sogard *et al.*, 1989). Similar associations have been noted around islands in the Indo-Pacific (Harmelin-Vivien, 1981; Ogden and Ogden, 1982; Gates, 1986). However, most seagrass beds in the Great Barrier Reef region are coastal, while the coral reefs are further offshore (Coles *et al.*, 1987). Green Island is therefore one of only a few locations in the region where seagrass beds and coral reefs are in close enough proximity to provide interacting habitats (Coles *et al.*, 1989; Lee Long *et al.*, 1993). Adult siganids are known to utilise a variety of habitat types, including coral reefs, seagrass beds and rocky shores, and often move between different habitats (Bryan, 1975; Gundermann *et al.*, 1983; Pinto and Punchihewa, 1996), and Woodland (1990) specifically describes *Siganus lineatus* moving between the lagoon and the reef flat at Heron Island, a coral cay with a similar structure to that of Green Island Reef.

In adult siganids, where the dichotomy between the pairing and shoaling species is most apparent (Woodland, 1990), this aspect of behaviour could have significant implications for the distributions of species among and within habitats. Shoaling behaviour, the aggregation of fishes in social groups, serves a variety of functions and may confer anti-predator, foraging and migration advantages, as well as reproductive advantages for adult fish (Pitcher and Parrish, 1993). Shoal size has been shown to be an important factor influencing the behaviour of fishes, including their patterns of habitat utilisation (Savino and Stein, 1982; Magurran and Pitcher, 1983; Chapter 5). The anti-predator functions of shoaling appear to allow large shoals to access habitats with low structural complexity, where there is no other protection from predators.

Given the contrasting pairing and shoaling behaviours of the four study species (Woodland, 1990), and the differences in dietary composition observed between the pairing and shoaling species (Chapter 3), it seems likely that there will be corresponding differences in the resource use patterns of these species. Green Island Reef comprises a variety of habitat types, which are patchily distributed and differ widely in their extent and structure. The selected study sites (Chapter 2), which represent these habitat types, provide an intermediate scale at which to examine the distributions of the study species. Even within these study sites, different areas have slightly different characteristics (Chapter 2). The recognition of subsections at these sites provides a finer scale at which to examine habitat utilisation.

6.1.1 Aims and objectives

The aim of this study was to describe the habitat use patterns of adult siganids at Green Island Reef, particularly their utilisation of the seagrass and coral habitats. The objective was to assess the roles of the various habitats in the provision of food and shelter for adults of the four study species, and to examine potential factors affecting any interspecific differences. It was hypothesised that activity, the structural features of the selected study sites (defined in Chapter 2) and the pairing versus shoaling habits of the species would be the main factors influencing habitat utilisation patterns, along with the effect of tidal height on site accessibility. It was hoped that simultaneous observations of behavioural activities and habitat associations would facilitate a meaningful interpretation of the observed patterns.

6.2 MATERIALS AND METHODS

6.2.1 Field observations

The highly mobile nature and relatively low densities of adult siganids (Bouchon-Navaro and Harmelin-Viven, 1981; Russ, 1984a and b) make transect-based surveys of relative abundances an inefficient means of assessing habitat use by these species. Encountering enough fish to establish a picture of habitat utilisation required a survey technique which could rapidly cover large areas of reef and seagrass beds, and would be readily transferable between habitat types. The categorical nature of the behaviours to be quantified and the large number of variables thought to influence them presented an additional challenge. Log-linear modelling, a technique for analysing multidimensional contingency tables, is suitable for this type of information, and observations were conducted according to the requirements of this analysis.

The behaviour and habitat use patterns of adult siganids were systematically observed at the four coral sites and at two of the reef flat seagrass sites at Green Island Reef (Chapter 2) between November 1994 and August 1996. Observations were made on 14 occasions at both high and low tide at each of the coral sites, giving 28 sets of observations for each site. To encompass diel variation, sampling sessions took place throughout the day, including early morning (8 sets), mid-day (12 sets) and late afternoon (8 sets). As the reef flat was exposed at low tide, observations at the northern and southwest reef flat seagrass sites were only made at high tide, giving 14 sets of observations for each of these sites. In addition, to remove seasonal biases, half of the sampling took place during the summer, and the other half during winter months. Observations were conducted using snorkel equipment.

During an observation session, an entire site was searched thoroughly and brief, "snap-shot" observations were made of all adult and subadult siganids encountered during that time. To preserve the independence of the observations, a randomly selected fish from each social unit was used as a "focal individual" (Crook, 1997) for a single observation related to that group, and the search was structured to ensure that areas were not revisited. The seagrass sites were searched in 5 m wide belts, as detailed in Chapter 5.

The coral sites were searched using a "U" pattern search (Graver and Wohlers, 1984), swimming back and forth perpendicular to the long axis of the site. The width of the search pattern (5 m to 20 m) was determined by the prevailing visibility. Scanning the width of the section and the area from below the eye line out to 5 m ahead was adequate for detecting and counting fish, and reduced the likelihood of re-recording individuals in the path ahead. The sloping nature of the front ledge and channel sites meant that direction could be easily maintained by orientating up or down the slope. At the near-shore and lagoonal patch reef sites, the size and shape of individual reefs was used to determine and maintain the direction of the search. At all the sites, natural features such as distinctively shaped coral heads aided navigation, and frequent checks were made against shipping markers and landmarks on the island. This prevented an area, and the fish there, being examined more than once during a given observation session.

Information about the activities and habitat associations of the fish observed were recorded on an underwater slate. The recording process was simplified by the use of codes and an observation could be completed in approximately 15 seconds. For each fish or shoal of fish observed, the following information was recorded:

Site: North seagrass, Southwest reef flat seagrass, Nearshore patch reefs, Lagoonal patch reefs, Channel edge and Front ledge.

Species (of focal individual): *Siganus doliatus*, *S. fuscescens*, *S. lineatus* or *S. punctatus*.

Site section: Fish were classified as being in the "centre" or on the "edge" of the site. At the shallow coral reef sites, the edge of the consolidated reef matrix was considered the edge of the reef, and fish utilising the vertical sides, in midwater or associated with isolated coral colonies in the adjacent sandy area were classified as being on the edge of the site. The boulder zone (see Chapter 2) was defined as the edge of the front ledge site. At the two seagrass sites, the edge of the site was defined as the sandy or rocky area on the shoreward side of the site, where seagrass growth ceased.

Activity: Activities were categorised as feeding: biting movements observed; roving: active, directional swimming; hiding: remaining relatively still while associated with the substratum or other structure, and moving only to maintain position. A type of hiding behaviour referred to as "hanging" was observed only in shoals of *S. lineatus* (Plate 6.1).

The state of the tide (high or low) at the time of the observation session was also recorded.

The number of fish in each social group was noted at the time of the observation.

6.2.2 Data analysis

Log-linear modelling is a technique for analysing multidimensional contingency tables. It has traditionally been used in the behavioural sciences (Colgan and Smith, 1978; Tabachnick and Fidell, 1989), and most recently in an analysis of fish behaviour (Crook, 1997). The technique is designed specifically for categorical data, and is more flexible than most parametric techniques since there are no assumptions regarding the distribution of the population (Tabachnick and Fidell, 1989; Everitt, 1992). Log-linear analysis tests all hypotheses related to a multidimensional data set without resorting to multiple tests, and thus avoids inflating the significance of the results (Everitt, 1992). The modelling process searches for associations (known as interactions) among the variables influencing the data. Interaction terms are sequentially removed from a saturated model (containing all possible interaction effects), and partial chi square (χ^2) values are calculated. This allows the relative importance of each interaction to be assessed using p values and standardised residuals (partial χ^2 / df). Once the key interactions have been identified, the underlying correlations can be expressed by means of odds ratios (Crook, 1997).

A large final data set was generated from the field observations (n = 2945), and arranged into a multidimensional contingency table for log-linear analysis. A saturated backwards elimination model was applied to the data, and interaction terms with p values <0.001 were selected from the association table produced. A low p value was used to avoid the selection of too many terms. The relative importance of these interactions was determined from the standardised residual values (χ^2 / df), and they were ranked accordingly. To identify the correlations underlying these interactions, the appropriate subsection of the multiway contingency table was examined, and odds ratios were calculated from the relevant probabilities. For example, *S. lineatus* were observed engaged in hanging behaviour (as opposed to feeding or roving) 238 times out of 299 (= 0.796), while *S. doliatus* were only observed hanging or hiding 24 times out of 2218 (= 0.011). The probability of *S. lineatus* being observed hanging was therefore 0.796 / 0.011 = 72.6 times greater than that of *S. doliatus*.

To confirm the accuracy with which the key interactions described the observed data, predicted values from a single entry model based on those interactions were tested for goodness of fit using the Maximum Likelihood Ratio χ^2. Using this method, structural zeros (combinations of variables which do not, or cannot, occur) and sampling zeros (combinations which were not observed) were taken into account by adjusting the degrees of freedom associated with the model (Feinberg, 1970; Everitt, 1992). Modelling calculations were performed using the SPSS (v. 6.1) statistical package.

6.3 RESULTS

6.3.1 Results of the log-linear model

The observations of habitat use patterns by adult siganids at the six sites resulted in the generation of a multiway contingency table (Appendix III). Examination of the partial chi-square values in the association table produced by the model showed that there were ten significant interaction terms (p values < 0.001), involving both behavioural and habitat variables. These included most of the possible two-way interactions, and two of the three-way interactions (Table 6.1). The relative importance of these interactions was determined from the standardised residual values (χ^2 / df), and they have been ranked accordingly (Table 6.1). The odds ratios which quantify the correlations underlying the interactions are given in Table 6.2. The distribution of observations between the categories of the main variables is given here, followed by a description of each of the significant interactions.

Main Effects

Tide height

The ratio of observations made during low tide and high tide sampling sessions was 1486 : 1459, ~ 1 : 1.

Site

The ratio of observations made at the six sites (north seagrass : southwest seagrass : Near patch reefs : Lagoonal patch reefs : Channel edge and South ledge) was 26 : 27 : 235 : 388 : 1377 : 892, approximately 1 : 1 : 9 : 15 : 53 : 34. This reflects the tidal effects on the availability of the seagrass sites and the limited utilisation of these sites by adult fish, as well as the differences in area of the four coral sites.

Species

The most frequently observed species was *Siganus doliatus*. The distribution of observations between the four species (*S. doliatus*: *S. fuscescens* : *S. lineatus* : *S. punctatus*) was 2218 : 216 : 299 : 212, approximately 21 : 2 : 3 : 2.

Site section

The ratio of observations made in the centre of the sites as opposed to at the edge was 2253 : 692, approximately 3 : 1, showing a general association between adult siganids and the centre of the sites.

Activity

The ratio of the various activity categories (feeding : roving : hiding) was 346 : 2329 : 270, approximately 4 : 26 : 3, showing that adult siganids spent most of their time roving. Feeding and hiding behaviours were observed occasionally.

Interaction Effects

Activity * Species

The interaction between species and activity was the most important, with a standardised residual value of 159.417. The driving force behind this interaction was the hanging behaviour of *S. lineatus*: This species was 28.4 to 88.4 times more likely to be observed hanging / hiding than the other three species. In contrast, *S. doliatus*, *S. fuscescens* and *S. punctatus* were all approximately 6 times more likely to be observed roving than *S. lineatus*. Feeding was the least frequently observed activity for all four species, but *S. doliatus* was up to twice as likely to be observed feeding as the other three species.

Site section * Species

S. lineatus was more likely to utilise the edge of the sites than the other three species. The greatest differences were in comparison to *S. doliatus* (3.2 times more likely) and *S. punctatus* (2.7 times more likely). *S. fuscescens* was frequently observed using the edge areas, resulting in a lower likelihood ratio (1.3).

Site section * Site

Despite the general association between siganids and the central areas of the defined sites (see site section main effect), extensive use of the site edge was observed at the southwest reef flat seagrass site. Adult siganids were 2.1 to 5.8 times more likely to use the edge at this site than at any of the coral sites; there were no observations of siganids utilising the edge of the northern seagrass site.

Site * Species

S. fuscescens was the only species of siganid observed at the northern seagrass site as an adult, and shows up in the analysis as the species most likely to occur there, but the greatest number of observations of this species were made at the channel edge site. *S. lineatus* was the species most likely to be observed at both the southwest seagrass site and the lagoonal patch reefs site, but the latter was the site at which the greatest number of observations were made. *S. doliatus* and *S. punctatus* were both 1.5 and 2.5 times more likely to be observed at the channel edge site than *S. fuscescens* and *S. lineatus* respectively. The channel edge was also the site where the greatest number of observations were made of both *S. doliatus* and *S. punctatus*. The species mix at the front ledge was similar to that at the channel site, but absolute numbers were lower.

Activity * Site

Adult siganids at the southwest reef flat site were 2.1 to 16.2 times more likely to be observed feeding than those at any other site. The northern seagrass site was the only other site where a notable proportion of fish were observed feeding. Adult siganids at the lagoonal patch reef site were 1.9 to 8.1 times more likely to be observed hanging / hiding than those at any of the other coral sites or at the northern seagrass site; no hiding was observed at the southwest reef flat site. At the lagoonal patch reef site, roving was still the most frequently observed activity, as it was at all sites except the southwest reef flat.

Site section * Tide height

The edge of the sites received greater use at low tide, with observations being 1.3 times more likely to occur there at low rather than high tides. There was a corresponding decrease in the use of the centre of the sites at low tide.

Site * Tide height

The inaccessibility of the two reef flat sites at low tide is the driving force behind this interaction, with fish being nearly 20 times more likely to occur at these sites during high tide.

Activity * Site section

Siganids observed at the edge of sites were 1.8 and 2.5 times more likely to be hiding / hanging than feeding or roving respectively. In contrast, fish in the centre of the sites were 1.1 and 1.6 times more likely to be roving than feeding or hiding / hanging respectively.

Site section * Site * Species

S. doliatus and *S. punctatus* were generally observed in the centre of the coral sites, but these species were more likely to utilise the edge of the reef at the front ledge and near patch reefs sites. In contrast, *S. fuscescens* and *S. lineatus* were generally more associated with the edges of the study sites, but *S. fuscescens* was more likely to utilise the centre of the north seagrass site (and also of the front ledge site to a lesser degree), while *S. lineatus* was more likely to utilise the centre of the lagoonal patch reefs site (and also of the near patch reefs site to a lesser degree).

Activity * Site section * Site
Feeding activity was generally observed in the centre of the sites, but was more likely to occur at the edge of the southwest reef flat site. Roving showed a similar pattern, being more likely to occur at the site edge at the southwest reef flat. Hanging was associated with the edge (rather than the centre) at the front ledge and the channel edge sites.

The single entry hierarchical model based on these ten interactions (which includes lower order interactions and main effects) produced expected cell values that were not significantly different from the observed values (Maximum Likelihood Ratio χ^2 = 131.818, df (adjusted) = 116, p = 0.150).

Non-interaction Effects

The independence of effects can be determined using information on two- and three-way interactions in the association table generated by the saturated model. Overall activity patterns have been shown to be independent of the height of the tide (standardised residual = 2.036, p = 0.361).

Summary

S. doliatus and *S. punctatus* only occurred at the coral sites. They made greater use of the site edges at the near patch reefs and front ledge sites, and greater overall use of the edge was associated with low tide. The highest incidence of feeding was observed for *S. doliatus*. *S. lineatus* and *S. fuscescens* were the only two species observed in the seagrass beds sites at high tide (southwest reef flat and northern sites respectively), and their presence at these sites was associated with a high likelihood of feeding. *S. lineatus* was also consistently observed engaged in hanging behaviour at the lagoonal patch reefs site. *S. fuscescens* was the only species that was observed at all six of the sites. *S. lineatus* was the species most likely to be observed at the edges of sites, feeding or roving (at the southwest reef flat site), or hanging (at the front ledge and channel edge sites). *S. fuscescens* also utilised the site edges to a lesser degree.

6.3.2 Associations between shoal size, activity and site for *Siganus lineatus*

The number of individuals in a social group (shoal size) could not be utilised as factor in the log-linear model because it resulted in too many zero observations (i.e. the pairing species were not observed in large shoals), but it is implicit, at a basic level, in the overall pairing or shoaling tendencies of the study species. The number of fish in the observed social groups was fairly consistent for a given species, with *S. doliatus* and *S. punctatus* generally being observed in pairs, with occasional single fish, and the shoaling species usually occurring in groups of 3 to 30.

However it became clear during the course of the observations that the number of fish in shoals of *S. lineatus* varied considerably during different activities at the various sites (Figure 6.1). Most *S. lineatus* shoals at the coral sites were comprised of 3 to 20 fish, with pairs / individuals being the second most commonly observed units (except at the lagoonal patch reefs). At the near shore patch reefs, no shoals of greater than 20 fish were observed, and most shoals were comprised of 10 or fewer individuals. Shoals of greater than 20 fish were frequently observed at both the lagoonal patch reefs and the southwest reef flat, but comprised a greater proportion of the observations, relative to medium-sized shoals (3 to 20), at the seagrass site. In addition, very large *S. lineatus* shoals at the southwest reef flat site were frequently comprised of 50 to 100 individuals. As feeding was the most commonly observed activity at the southwest reef flat site, there is also an association between feeding and large shoal sizes.

6.4 DISCUSSION

These results clearly demonstrate that adult siganids utilise the habitats and subhabitats at Green Island Reef in a non-random fashion. Their distributions are largely influenced by species-specific and site-specific factors, and activity patterns differ between species. The importance of both behavioural and habitat variables in the significant interactions indicates a multicausational basis for the observed patterns and the important role of habitat in structuring resource use at the scales used.

The importance of the species * activity interaction is the first indication of interspecific differences in habitat utilisation patterns. The distribution of observations among the activity categories shows that, across species, adult siganids were most frequently observed roving. This is a notable change from the activity patterns of the juvenile phase, when hiding was the dominant activity (Chapter 5). *Siganus lineatus* was the only species that was regularly observed hiding as an adult, and most observations were of the subcategory referred to as "hanging" (Plate 6.1). These inactive shoals were consistently observed at the lagoonal patch reefs site, as well as at the other coral sites. However, *S. lineatus* also utilised the southwest reef flat seagrass site, where feeding was likely and no hiding was observed. As seagrass comprised 53.1 % of the diet of *S. lineatus* (Chapter 3), this concurs with dietary data for this species. Consideration of all the two-way interactions of species, activity and site shows that *S. lineatus* makes distinct forays to the southwest reef flat seagrass site, and has resting periods which are spent hanging in the coral habitats (particularly the lagoonal patch reefs).

S. fuscescens was frequently observed feeding at the northern seagrass site, but this species does not exhibit resting periods and was also observed feeding in the coral areas (particularly at the channel edge site). Seagrass comprised 44.5 % of the diet of *S. fuscescens* however (Chapter 3), and the seagrass beds appear to be their main feeding habitat. In this respect *S. fuscescens* is similar to *S. lineatus* but the two species utilise different seagrass sites. In contrast, *S. doliatus* and *S. punctatus* were only observed in the coral areas, particularly the two areas of contiguous coral habitat (the channel edge and the front ledge), and were observed feeding at these sites. Based on the interactions of species, activity and site, it appears that adult siganids at Green Island Reef partition their feeding activities on a spatial basis, with *S. lineatus* and *S. fuscescens* utilising different areas of the seagrass beds and *S. doliatus* and *S. punctatus* utilising the coral sites.

The contrast between the shoaling and pairing species suggests that this aspect of their behaviour may mediate the interspecific differences in habitat utilisation. Foraging in shoals may increase the efficiency of food location and consumption (Pitcher and Parrish, 1993), but as the shoaling siganids at Green Island Reef eat mostly seagrass (Chapter 3), locating food is likely to be of little importance. A foraging advantage specific to shoaling herbivores is the use of large numbers to overcome the territoriality of competitors (Jones, 1968a; Robertson *et al.*, 1976). However, the few small territorial herbivores in the seagrass beds at Green Island Reef (mostly *Dischistodus spp.*, pers. obs.) defended areas of turf growing on hard substrata, and did not utilise the seagrass that forms the major part of the diet of the shoaling siganids. Therefore the anti-predator functions of shoaling (see Pitcher and Parrish, 1993) are likely to be more important in this situation. It appears that the added protection of the shoal allows *S. fuscescens* and *S. lineatus* to utilise the seagrass habitat, which provides little structural protection for fish of this size, and where there is thus a greater risk of predation. In contrast, the two pairing species are restricted to the coral areas. This agrees with experimental studies showing that larger shoal sizes occur in more exposed areas, and will accept a greater risk of predation (Savino and Stein, 1982; Magurran and Pitcher, 1983; Milinski, 1993).

The additional data showing the observed shoal size of *S lineatus* during different activities at the various sites (Figure 6.1) supports this hypothesis. Most shoals at the coral sites were comprised of 3 to 20 fish, while the majority of shoals at the southwest reef flat site were comprised of between 21 and 100 individuals. In addition to supporting the anti-predator hypothesis, this observation suggests that small shoals from the coral areas amalgamate to form the large foraging schools in the seagrass beds. Amalgamation of shoals during the nocturnal foraging migrations of carnivorous species is well known (Helfman *et al.*, 1982; Helfman, 1993). Other herbivorous fishes (acanthurids and scarids) undertake diurnal foraging migrations (Fishelson *et al.*, 1987; Helfman, 1993) and the amalgamation of resting shoals of *Scarus croicencis* (now *S. iserti*) into large, migratory foraging groups has been documented (Ogden and Buckman, 1973). For the shoaling siganids at Green Island Reef, feeding sites are distinct and distant from the coral sites (refer Plate 2.1), and the migration advantages of shoaling - route learning and accuracy of homing (Helfman *et al.*, 1982; Pitcher and Parrish, 1993) - may also apply to these foraging schools of *Siganus lineatus*.

The effects of tidal height on the use of different sites and site sections are logical results of falling water levels. As the seagrass sites become exposed and there is less water over the centre of the coral areas, fish must move to deeper areas. However, there is no significant interaction between tide * species * site, which would result if

S. lineatus were absent from the coral sites at high tide as a result of forays to the seagrass bed. In fact, there is a consistent presence of fish at the lagoonal patch reefs, even at high tide. While there may have been a decrease in absolute numbers of *S. lineatus* at the lagoonal patch reefs at high tide, the data suggest that the individuals in the reef flat feeding shoals are primarily from the other three coral sites. Another possibility is that only part of a resting shoal will participate in any given foray, while the remainder of the shoal stays behind to maintain a presence at the resting site.

It is possible that fish from the two patch reef sites feed in the deeper seagrass nearer their home reefs. From the aerial photograph of the area (Plate 2.2), the formation of grazing "halos" (*sensu* Randall, 1963; Ogden and Zieman, 1977) around the near shore and lagoonal patch reef sites cannot be ruled out. However an examination of similar aerial photographs from 1983 shows that, while the open, sandy areas surrounding the patch reefs may be the result of herbivore grazing, they may also be an artefact of the manner in which the seagrass bed is advancing towards these reefs. These photographs imply that if halo-type feeding is occurring, it must be a recent development because the distance of the seagrass from these reefs in years past would have made it impractical. As there have been no observations of halo-type feeding, these suggestions are purely speculative. Confirming the exact foraging strategies of *S. lineatus* at Green Island Reef would require simultaneous monitoring of all six of the study sites through replicate 24-hour periods, an operation beyond the scope of this study.

The interactions discussed so far indicate the partitioning of feeding activities between the coral and seagrass sites by the four study species. However, the various two- and three-way interactions of site section, site, species and activity indicate differences in distributions within sites. These differences are both species-specific and site-specific, indicating that while it is possible to make generalisations regarding the distributions of species in a given habitat type, species may respond to the features of a particular site in ways that reflect small scale differences in their resource base. Local-scale habitat heterogeneity has also been shown to influence resource use by other herbivorous families (Choat and Bellwood, 1985). An understanding of the resource in question (i.e. what exactly the organism uses that particular habitat for - feeding, shelter etc.) is essential for interpreting these finer scale differences.

The overall distribution pattern showed that the two pairing species and roving behaviour were associated with the centre of the sites, while the shoaling species and hanging behaviour were associated with the site edges. The southwest reef flat seagrass site was where the site edge was most utilised. Feeding behaviour, across sites and species, was distributed fairly equally between the centre and the edge of sites, but the three way interaction site showed most observations of feeding at site edges involved *S. lineatus* at the southwest reef flat seagrass site. Roving was also uncharacteristically associated with the edge at this site. In contrast, *S. fuscescens*, using the northern seagrass site for the same activities, only used the centre of the site. The difference between the two sites is the presence of the beachrock at the shoreward edge of the southwestern site (refer to Plate 2.2). This consolidated rocky ledge and the associated freestanding rocks provide an added degree of structural complexity compared to the open seagrass bed. At the northern site, the shoreward edge is bare sand, which offers no protection, while the slightly longer seagrass at this site (Chapter 2) increases the complexity of the vegetated areas (Stoner, 1983; Stoner and Lewis, 1985; Blaber *et al.*, 1992). It thus appears that these species are utilising the sections of their respective feeding sites which offer the greatest chances of escaping predation (Hixon, 1991; Milinski, 1993; Caley and St. John, 1995).

Of the four coral areas, *S. lineatus* was more closely associated with the two patch reef sites, and used the centre of these sites as well as the edge. Although it may seem contradictory for large shoals of fish to prefer small areas of reef, the knowledge that they use these areas for sheltering rather than foraging permits speculation on the motivation behind this. On small reefs, prey species retain the advantage of structural protection, but wider ranging predators must approach through open areas and will thus be more readily detectable. When *S. lineatus* occur at the larger sites, they utilise sections of the site that provide protection amidst similar levels of isolation - the boulder zone at the ledge site and large coral head outcrops at the edge of the channel.

In contrast, *S. doliatus* and *S. punctatus* were associated with the channel and front ledge sites, the two areas of contiguous coral habitat. These species feed at the coral sites, and their association with the larger sites concurs with the suggestion that roving herbivores require large areas over which to forage in order to meet their nutritional requirements (Bardach, 1959). Feeding in these species is associated with areas of low live coral cover (and thus high turf algal cover), such as the central area of the channel site and the boulder zone at the ledge site (see Chapter 2). The edge of the near patch reefs site is also utilised, but this may be a result of the shallow nature of the site and the fragmented nature of the reef.

S. fuscescens usually utilised the edges of the coral sites, but utilised the central area at the front ledge, the deepest site (Chapter 2), suggesting that their distribution may be related to water depth. Their distribution effectively reduced contact with *S. lineatus* at the front ledge and the patch reef sites, and with the pairing species at the channel site. The highly mobile nature of the *S. fuscescens* shoals meant that they rarely coincided with *S. lineatus* at the channel site, and low abundances resulted in a low encounter rate with the pairing species at the front ledge site.

The height of the structures with which the different species associate is also of interest. The coral areas where large and medium shoals of *S. lineatus* were observed (reefs A and F at the lagoonal patch reefs site, the boulder zone at the ledge site and the coral heads at the edge of the channel site) had relatively high vertical complexity (Chapter 2). The nearshore patch reefs site, which is in shallow water and less complex (Chapter 2), had fewer, smaller shoals of *S. lineatus*, usually comprising less than 10 fish. The central areas of the contiguous reef sites, where *S. doliatus* and *S. punctatus* were usually observed, provide small scale vertical complexity. This is adequate for concealing a pair of fish but would be much less effective for a large shoal. The distribution of *S. fuscescens*, which occurred in medium sized shoals, seems to be intermediate between these two main groups. A correlation between fish size and the size of available structural protection has already been established (Hixon and Beets, 1989 and 1993). It appears that this principle may be extended beyond the individual fish to encompass increases in the size of fish shoals.

Most documented examples of spatial partitioning in reef fishes involve territorial species, which exhibit a certain level of aggression towards competitors, especially heterospecifics from the same family (e.g. acanthurids - Robertson *et al.*, 1979; pomacentrids - Robertson and Lassig, 1980; but see Hallacher and Roberts, 1985, on scorpaenids). This study found no evidence of territoriality in siganids. The presence of the resting shoals of *S. lineatus* at reefs A and F of the lagoonal patch reefs was the only indication of site-attachment. No aggressive encounters, towards either congenerics or other herbivores, were observed in any of the study species. This directs the search for the cause of partitioning away from competition. Instead, it seems that the four study species utilise the sections of the reef which are most suited to their social and activity patterns, while providing the resource they require in a way which minimises their susceptibility to predation.

6.5 CONCLUSIONS

Adult siganids at Green Island Reef exhibit spatial partitioning of resources. The greatest differences in resource use occur between the pairing and shoaling species, but differences are also evident between the two shoaling species. Feeding is partitioned on two scales: by habitat (coral versus seagrass) between pairing and shoaling species, and by site within the shoaling species. However, no partitioning is apparent between the two pairing species. Space utilisation in the coral areas appears to be determined at a finer scale, and is influenced by species-specific activity patterns and the characteristics of the individual sites. The combination of behavioural and habitat association information was critical to the interpretation of these patterns. Although previously demonstrated in a temperate-zone species (Ralston and Horn, 1986), the occurrence of distinct forays and apparently extensive resting periods in *S. lineatus* is an unusual feature in a tropical herbivorous fish, and bears further investigation. Although it is possible to make generalisations regarding the distributions of the four study species, the structural features of the different study sites mean that each site is utilised in a slightly different way in order to fulfil the requirements of the each species. There was no evidence of competitive interactions between species. Rather, it appears that predation-motivated behaviour, in the context of the different social habits of the four study species, has led to activity patterns which maximise access to food resources while minimising the risk of predation.

Plate 6.1. A school of *S. lineatus* exhibiting "hanging" behaviour.

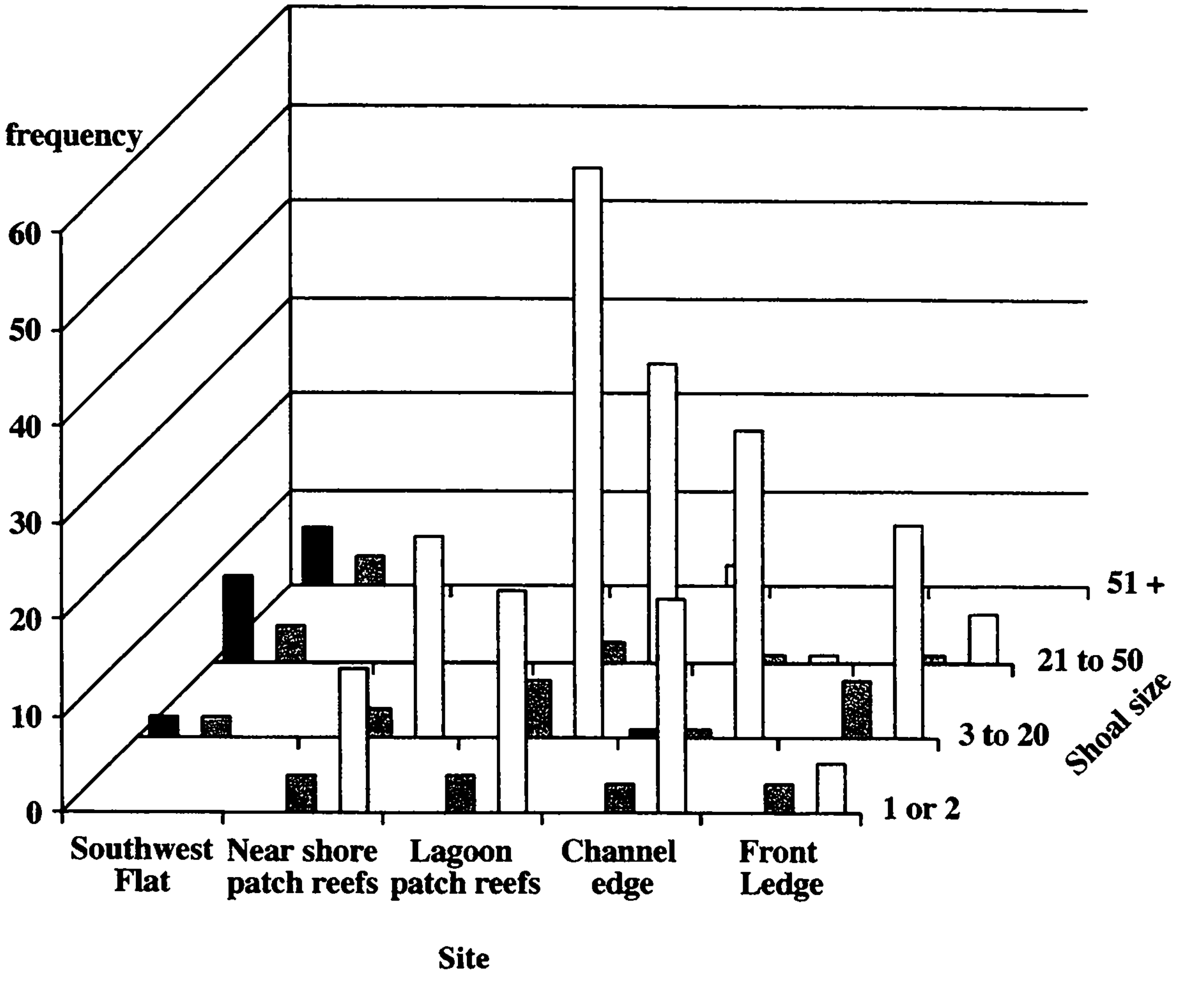
Table 6.1. Interactions where $p < 0.001$ in the saturated model produced using data in Appendix III. Large standardised residual values correspond to the most important interactions and are ranked accordingly.

Interaction	Partial chi square (χ^2)	Degrees of freedom (df)	Standardised residual (χ^2/df) rank
Activity * Species	956.499	6	1
Site section * Species	113.817	3	2
Site * Site section	164.097	5	3
Site * Species	407.249	15	4
Activity * Site	240.389	15	5
Site section * Tide height	16.856	1	6
Site * Tide height	80.007	5	7
Activity * Site section	14.139	2	8
Site * Site section * Species	69.436	15	9
Activity * Site section * Site	8.202	10	10

Table 6.2. Odds ratios* associated with the correlations underlying the significant interactions in Table 6.1.

Interaction	Underlying correlation(s)	Associated odds ratio(s)
Activity * Species	*S. lineatus* and hiding / hanging	72.6; 88.4; 28.4
Site section * Species	*S. lineatus* and the edge	3.2; 1.3; 2.7
Site * Site section	the edge of the SW reef flat	≈815; 2.1; 3.0; 5.8; 2.6
Site * Species	*S. fuscescens* at the north flat.	∞; ∞; ∞
	S. lineatus at the SW flat.	∞; 17.4; ∞
	S. lineatus at the lagoon patch reefs.	4.6; 2.5; 4.7
Activity * Site	feeding on the SW reef flat.	2.1; 14.7; 16.2; 4.2; 6.3
	hanging at the lagoon patch reefs.	8.1; ≈309; 1.9; 5.9; 7.0
Site section * Tide height	the edge of the sites at low tide	1.3
Site * Tide height	the reef flat sites at high tide.	∞; ∞
Activity * Site section	the edge and hanging / hiding	1.8; 2.5
Site * Site section * Species	*S. doliatus* at the edge of the front ledge.	∞; ∞; 1.2; 2.2; 3.4
	S. fuscescens in the centre of the north seagrass site.	≈1000; 5.6; 2.6; 1.9; 1.2
	S. lineatus in the centre of the lagoon patch reefs.	∞; 3.1; 1.2; 1.8; 2.3
	S. punctatus at the edge of the near patch reefs.	∞; ∞; 2.2; 2.3; 1.3
Activity * Site * Site section	feeding at the edge of the SW reef flat.	≈882; 2.9; 4.4; 10.8; 1.4
	roving at the edge of the SW reef flat.	≈600; 1.6; 2.7; 4.9; 2.3
	hanging at the edge of the front ledge site	≈667; ≈667; 1.4; 1.7; 1.1

* Where multiple ratios are listed, comparisons between species follow the order: *S. doliatus*, *S. fuscescens*, *S. lineatus*, *S. punctatus*; comparisons between sites follow the order: north reef flat, southwest reef flat, near patch reefs, lagoonal patch reefs, channel edge, front ledge; comparisons between activities follow the order: feeding, roving, hanging. ∞ indicates comparison to a structural zero. ≈ indicates comparison to a sampling zero, where 0.001 was added to the probability to produce an approximate ratio.



black = feeding grey = roving white = hanging

Figure 6.1. The interaction between shoal size, activity and site for *Siganus lineatus*, showing the frequency with which different sized shoals were observed feeding, roving or hanging, at the various study sites.

CHAPTER 7

GENERAL DISCUSSION

Partitioning of resources by siganids at Green Island Reef

7.1 SIGANIDS AND HERBIVORY

The Siganidae have generally been treated as a biologically and ecologically uniform family on the basis of their morphological similarity, close taxonomic relationships (Woodland, 1990) and association with coral reefs. However a detailed examination of the feeding and habitat relationships of four common species suggests that this is a simplification. There are clear differences in social behaviour between species, resulting in the designation of species as 'pairing' or 'shoaling' (Woodland, 1990). These different social behaviours are associated with differences in feeding biology and ecology. Within species, there are ontogenetic differences in diet, which appear to be related to variable metabolic needs, increased size and mechanical strength, increased digestive potential and different feeding locations. There are also distinct interspecific differences in diet between adults of the pairing and shoaling species. Fundamentally different food items are involved and this may be linked to interspecific differences in feeding and digestive morphology, as well as predation-motivated differences in habitat use patterns that result from the disparate pairing and shoaling behaviours.

Although subtle, the interspecific morphological differences have implications for feeding biology. The diets and stomach structure of the pairing species agree with the expectations for Type I herbivores (Horn, 1989, 1992). However an acid-based digestive system alone may be inadequate for processing the more refractory seagrass present in the diet of the shoaling species, and the moderately muscular stomach of these species may play a role in the mechanical processing of such material. Although the digestive tract grows at the same relative rate in all species, the absolute length is therefore longer in the species with larger terminal sizes (including the shoaling species), and this may be an important factor in the assimilation of refractory food items. Differences in gape size and head shape have the potential to affect the accessibility of different food items, and these differences may provide different advantages in different habitats. The morphological adaptations which may promote the access to, and digestion of, items such as seagrass are found in the shoaling species, which can utilise the seagrass bed habitat with a greater degree of protection from predation than the pairing species.

An important aspect of the behavioural data is the very low rates of feeding that were observed. This is in contradiction to the "rapid and continuous" feeding that is generally characteristic of herbivorous fishes, and presumably reflects a need to process large volumes of plant material in order to maintain a positive energy balance (Choat, 1991). Although low feeding rates seem to be a general feature of all four of the study species, through ontogeny, the observation of distinct forays and prolonged resting periods in adult *Siganus lineatus* is particularly interesting. Although some scarids and acanthurids exhibit segregated feeding behaviour (Ogden and Buckman, 1973; Fishelson *et al.*, 1987; Helfman, 1993; Bellwood, 1995), forays tend to last all day and resting is associated only with night time in these species.

The resting periods exhibited by *S. lineatus* could indicate that, once satiated, their activity is limited by the high energetic costs involved in digesting refractory food items (Ralston and Horn, 1986 and references therein). However if this is the case, *S. fuscescens* should exhibit similar behavioural patterns, and such patterns are not apparent in this dataset. When considered in combination with their defined stomach, the behaviour pattern of *S. lineatus* is suggestive of a fermentative digestive process (Type IV digestion, according to Horn, 1989). However Clements (1991) and Clements and Choat (1995) have examined the endosymbiotic gut biota and the levels of short chain fatty acids (by-products indicative of fermentation) in siganids, and found little evidence of fermentation in this family. Yet it seems unlikely that the shoaling siganids are strict Type I herbivores. Other species appear to possess a combination of digestive mechanisms, utilising different strategies depending on the type and availability of food (see Anderson, 1987, 1988, 1991, on *Girella tricuspidata* and Choat, 1991, on *Acanthurus nigrofuscus*). It is possible that the shoaling siganids also employ a combination of digestive strategies.

What are the implications of this research for our current views on herbivory in fishes? In the last decade, the diversity among herbivorous fishes has become apparent (Horn, 1989, 1992; Choat, 1991). Recent examinations of other herbivorous fish taxa have also shown strong interspecifc differences in feeding biology within families which were previously assumed to be uniform. Differences in mouth morphology among the

Scaridae (Bellwood and Choat, 1990) have been shown to have a profound effect on their mode of feeding, with important ecological consequences. Clements and Choat (1997) have found differences in the alimentary tract morphology of the Kyphosidae, which result in slightly different approaches to fermentation, and there are considerable differences in morphology and digestive strategies between the kyphosids and the very closely related Girellidae. This study implies that similar, though less extreme, differences in feeding ecology, and perhaps digestion, exist between the pairing and shoaling Siganidae. Different strategies for herbivory may be observed at the species level, although often the subtlety of the differences belies their potential impact. There is a temptation to place species into general functional groups, however the emerging picture of fish herbivory implies that this is an unwise practice, as the processes and mechanisms involved are often far more complicated than they appear.

7.2 RESOURCE PARTITIONING

Arthur (1987) defined resource partitioning as a small overlap in resource use, being neither identical use nor complete segregation. On a multidimensional level, partitioning is defined as allowing overlap in some dimensions, but not all, and requiring a significant disparity in at least one. Ross (1986) reviewed the literature on resource partitioning in fish communities. He concluded that trophic separation is more important in fish communities than it is in most terrestrial examples of resource partitioning. Habitat separation, at both large and small scales, is still an important factor on tropical reefs however. Ross also found that differences in resource use were lower when the study species were closely related, and that the number of resource axes involved in partitioning increased with the overall diversity of the assemblage.

7.2.1 Are siganids at Green Island Reef partitioning resources?

When interspecific differences in diet, morphology and behaviour are considered together, there is a strong case for suggesting that siganids at Green Island Reef are partitioning resources, between ontogenetic stages and between species in the adult phase. Although the four species share common dietary items, the importance of these items differs greatly between species; thus it appears that there are differences in the selection of food items. There is also a spatial aspect to these differences. First, dietary components are available in different quantities in different habitat types, which are used differently by the various species / age groups. Second, those species / age groups which have similar diets often utilise different habitats. The fine scale differences in the use of the coral sites also suggests a more general partitioning of space resources. The distinction between spatial aggregation and partitioning of space is whether there is "a consistent reason for a repeatable behavioural separation of the species". The different social habits of the pairing and shoaling species qualify in this context.

7.2.2 The resource overlap equation

Resource overlap calculations were performed using the symmetrical equation devised by Pianka (1973):

$$O_{ij} = \Sigma\, p_{ia}\, p_{ja} / {}^{\circ}\ (\Sigma\, p_{ia}^{2})\,(p_{ja}^{2})$$

where p is the partition of the *a*th resource which is used by the *i*th or *j*th species, or alternatively the number of individuals of species *i* or species *j* using the *a*th partition of the resource. Resource use overlap was calculated for four individual dimensions: diet, feeding habitat, roving habitat and sheltering habitat. Dietary overlap was calculated based on the mean proportional composition values calculated in Chapter 3. The use of habitat resources for different activities was assessed based on the observations carried out for Chapters 5 and 6. However, actual numbers of fishes observed (i.e. numbers in the entire social group rather than just the focal individual on which the observation was based) were utilised in order to calculate the proportion of fishes using different parts of the habitat at the different sites. Overlap calculations involving adults only, or comparing adults and juveniles, were based on the site section definitions (centre and edge) in Chapter 6, while resource overlap between juvenile groups was based on the microhabitats (seagrass and *Sargassum*) defined in Chapter 5.

This type of calculation measures overlap along one resource dimension only. Multidimensional overlap may be derived as the mean of individual overlaps if resource dimensions are interdependent, or as the product if resource dimensions are independent (Putman and Wratten, 1984). In this situation, the three measures of habitat use overlap are interdependent, as it is the same resource being utilised in different ways. However, food resources can be considered independent. As diet can be viewed as a specialisation within the feeding habitat (or vice versa), the product overlap was calculated for diet and feeding habitat to give an overall food utilisation overlap. The total overlap in resource use was then calculated as the mean of food utilisation overlap, roving habitat overlap and hiding habitat overlap. This procedure is summarised in the following equation:

$$\text{Total } O_{ij} = [(\text{diet } O_{ij} * \text{feeding habitat } O_{ij}) + \text{roving habitat } O_{ij} + \text{hiding habitat } O_{ij}]/3$$

There are no set criteria for evaluating the degree of overlap calculated using Pianka's (1973) equation. The method of calculation is similar to that used by Levins (1968) however, for which values of greater than 0.7 represent a high degree of overlap, and overlaps of less than 0.3 are considered insignificant (Keast, 1978). These values will be used as guidelines for evaluating the results of the overlap calculations in this study.

7.2.3 Evidence of resource partitioning

The dietary overlap calculations reflect the differences illustrated in the CDA (Figure 3.8). There is a high degree of dietary overlap among juveniles of all species (Table 7.1a), and also between the adults of the two shoaling species, *Siganus fuscescens* and *S. lineatus* (Table 7.1c). Adult *S. doliatus* showed low dietary overlap with adults of all other species (values less than 0.34, Table 7.1c), while adult *S. punctatus* showed moderate overlap with the two shoaling species (Table 7.1c). The greatest degree of dietary separation is between the juveniles and adults. Dietary overlap between juveniles and the adults of the shoaling species was generally less than 0.3 (Table 7.1b). Overlap between juveniles and the adults of the pairing species ranged from 0.27 to 0.67 (Table 7.1b), with the higher overlaps occurring between these adults and juvenile *S. fuscescens*, and moderate overlaps recorded between conspecifics (Table 7.1b).

Overlap of feeding habitats was greatest between adults of the pairing species, moderate between these adults and *S. fuscescens*, and negligible between *S. lineatus* and adults of all other species (Table 7.2c). There was no overlap in feeding habitat between adults of the pairing species and any of the juveniles (Table 7.2b), as these adults were restricted to the coral areas while the juveniles only occurred in the seagrass beds. Although the adults of the shoaling species fed in the seagrass beds, they only utilised two of the three sites occupied by the juveniles. In addition to this, adult *S. lineatus* primarily used the edge section of the southwest reef flat site, which was of little importance to the juveniles, keeping feeding area overlap between these adults and juveniles of all species at less than 0.3. In contrast, adult *S. fuscescens* primarily used the centre of the northern seagrass site, which was also heavily utilised by juveniles, and this resulted in moderate to high overlap values (0.30 to 0.64, Table 7.2b). Overlap of feeding habitats between juveniles was moderate to high (0.37 to 0.80, Table 7.1a).

Among the juveniles, overlap of both roving and hiding habitats was very high (Tables 7.3a and 7.4a). Again, there was no overlap in habitat use between juveniles and the adults of the pairing species (Tables 7.3b and 7.4b). Overlap of roving habitat between juveniles and the adults of the shoaling species was very low (less than 0.2, Table 7.3b). Overlap of hiding habitat between juveniles and adult *S. fuscescens* was 0.10 or lower, and overlap with adult *S. lineatus* was negligible (Table 7.4b). Overlap of roving habitats was greatest between adults of the pairing species and *S. fuscescens*, and moderate between *S. lineatus* and adults of all other species (Table 7.3c). Overlap of hiding habitat was high between adults of the two pairing species, and moderate to low between the other species combinations (Table 7.4c).

When all three aspects of resource use are taken into consideration, an interesting pattern emerges. In the juvenile phase, which is associated with the seagrass beds, resource utilisation patterns are very similar between species, and values for total resource overlap are high (0.69 to 0.77, Table 7.5a). As a result of the total habitat separation, there is no overlap in resource use between juveniles and the adults of the pairing species (Table 7.5b). Even between juveniles and the adults of the shoaling species, total resource overlap is very low (less than 0.12, Table 7.5b). Among the adults, the only large overlap is between the two pairing species; these species also have moderate overlaps with *S. fuscescens* (Table 7.5c). Adult *S. lineatus* have low overlap (less than 0.3) with all other adults (Table 7.5c).

7.2.4 Resource partitioning, evolution and the ontogenetic niche

Many resource partitioning studies, particularly those on coral reefs, have been ultimately concerned with species packing theory (see review by Ross, 1986), and thereby with competition as the force driving the partitioning. Herbivore populations seldom appear food limited, and have traditionally been considered as predator-limited (Hairston *et al.*, 1960). It was therefore assumed that they were not likely to compete for common resources. These conclusions were based on the obvious abundance of terrestrial vegetation, and the lack of any real visible impact of herbivores on it (Hairston *et al.*, 1960). Herbivory is known to have profound effects in coral reef habitats however, and is considered to have a far greater impact than in terrestrial habitats (Hay, 1991 a and b). Indeed, an instance of food limitation of an herbivorous fish population has been documented by Robertson (1991). In any case, food is not the only resource for which organisms compete (Hairston, 1981; Ross, 1986) - space may be equally, or more, important, particularly for herbivores (McGeoch and Chown, 1997).

The occurrence of resource partitioning in the absence of any apparent current competition, as is the case in this situation, has often been explained as "the ghost of competition past" (Connell, 1980). Divergence of competitors through coevolution is an unlikely proposition (Connell, 1980), and present ecological differences between similar species do not necessarily imply the past operation of competition in the community (Sale, 1974; Abrams, 1980; Connell, 1980; Strong, 1984). Competition is not the only basis for the partitioning of resources however, and multicausation of differential resource use is considered the rule rather than the exception (Ross, 1986). The fact that deep-bodied, pairing siganids are associated with coral reefs over a large scale, while the more streamlined shoaling species are more closely associated with coastal areas (Woodland, 1990), has received little attention. This distinction has important ecological consequences however, as the differences in diet, morphology and habitat utilisation patterns found in this study are most obvious between pairing and shoaling species.

Non-interactive partitioning of space may result from the interplay between features of the habitat and the physiological and behavioural traits of the species involved (Barton, 1982; Streams, 1987). The absence of any apparent competitive interactions in the four study species, in combination with information on their distributions, implies separate evolution of the pairing and shoaling siganid species, on reefs and in coastal habitats respectively (Woodland, 1990). Pairing and shoaling species coexist at Green Island Reef, where a suitable variety of habitats occur in close proximity, and it appears that adaptations to diet and habitat which evolved in parapatry / allopatry result in the maintenance of dietary differences to a large degree when the species are in sympatry. The interaction of habitat types (which have different food and structural complexity) with shoaling and predation-motivated behaviour results in the spatial partitioning of food and shelter between the pairing and shoaling species. The high overlap in resource use between the two pairing species may or may not be important, as the population size of *S. punctatus* is approximately 10 % of the size of the *S. doliatus* population (based on total sightings during more than 100 hours in suitable habitats).

The separation in resource use between juveniles and adults is the result of ontogenetic niche diversification (Barton, 1982; Werner, 1984; Werner and Gilliam, 1984; Schlosser, 1987). Body size has important effects on predator-prey interactions. The distributions of juvenile fishes, which in this study are strongly indicative of predation-motivated behaviour at the scale of both habitat type and microhabitat, reflect their greater vulnerability. In taxa where distinct size classes co-occur, restrictions on habitat use may mean that juveniles of different species overlap extensively in habitat or food utilisation patterns, and diverge in niche characteristics as they increase in size and become adults (Wilbur, 1980; Mittelbach, 1981; Mushinsky *et al.*, 1982; Werner *et al.*, 1983). This often leads to *de facto* resource partitioning between ontogenetic stages, but may increase interspecific competition among juveniles (and between juveniles and other small species). It is possible that interspecific competition is occurring between juvenile siganids at Green Island Reef. However, the juvenile phase is short relative to the rest of the life span, and also highly vulnerable to predation. With progressive development and the reduction of numbers due to predation, it is hard to separate the effects of competition when examining adult abundances.

7.2.5 Future research

A change in resource utilisation in response to perturbations would be consistent with resource limitation (Jones, 1991), a necessary condition if the partitioning of resources is based on competition. An interesting direction for further research on this topic would be to re-examine the resource utilisation by siganids at Green Island Reef in light of the current Crown-of-Thorns Starfish (*Acanthaster planci*) outbreak. Since November 1996, plague proportions of this coral predator have dramatically reduced live coral cover on Green Island Reef (M. Rodrigo, pers. comm.), affecting coral-algal dynamics. The potential impacts of this recurring phenomenon on herbivore populations have been addressed in three studies comparing infested and control reefs, and one before / after comparison (Hart *et al.*, 1996, and references therein). The only study that found an effect was the before / after comparison, where an increase in the abundance of herbivorous fishes was correlated with high recruitment. However this adds to the evidence for site-specific resource utilisation.

A study to investigate competition as the basis of resource partitioning by siganids at Green Island Reef should look for an increase in algal abundance at the coral study sites, possible convergence in the diets of the four study species and alterations in their behaviour, particularly regarding the use of the seagrass beds by adults of the shoaling species. If no dietary or behavioural changes occur, then competition, at least for food, could be ruled out as a factor contributing to this instance of resource partitioning. This study would also have implications for the role of herbivorous fishes in the recovery of coral reefs following *A. planci* outbreaks. Feeding by herbivores is thought to play an important role in preventing excessive algal growth, thus facilitating coral regeneration (Hughes *et al.*, 1987; Hughes, 1989; Coyer *et al.*, 1993). However, if the resource use patterns observed in siganids at Green Island Reef during this study were to remain unaltered during *A. planci* outbreak conditions, the contribution of the shoaling species to the control of turf algae would be minimal. In the absence of behavioural and dietary changes, an increase in algal abundance might lead to the increased survival of subadults of the species which currently feed in the coral areas, indicating food limitation but not competition. It would therefore also be worthwhile to monitor the survival of the subadult segment of the population.

7.3 CONCLUSIONS

The many feeding modes and digestive mechanisms apparent in marine herbivorous fishes and the effects of present and historical ecological influences, in conjunction with the many and varied aspects of the biology of marine plants, make it plain that herbivory in marine vertebrates is a highly complex issue. Added to this are the variable effects of behavioural differences between species and between ontogenetic stages, both of which have profound influences on resource utilisation patterns. This research shows the value of taking a case-specific approach in order to enable a fuller understanding of some of the more fundamental questions in this field.

Table 7.1. Dietary resource overlap between species - age groups.

Part a. Comparisons between juveniles of the four species.

	juvenile *S. doliatus*	juvenile *S. fuscescens*	juvenile *S. lineatus*	juvenile *S. punctatus*
juvenile *S. doliatus*		0.811	0.699	0.765
juvenile *S. fuscescens*			0.612	0.649
juvenile *S. lineatus*				0.665

Part b. Comparisons between juveniles and adults of the four species.

	juvenile *S. doliatus*	juvenile *S. fuscescens*	juvenile *S. lineatus*	juvenile *S. punctatus*
adult *S. doliatus*	0.545	0.604	0.340	0.267
adult *S. fuscescens*	0.152	0.227	0.158	0.168
adult *S. lineatus*	0.291	0.358	0.233	0.276
adult *S. punctatus*	0.314	0.674	0.270	0.452

Part c. Comparisons between adults of the four species.

	adult *S. doliatus*	adult *S. fuscescens*	adult *S. lineatus*	adult *S. punctatus*
adult *S. doliatus*		0.247	0.339	0.337
adult *S. fuscescens*			0.968	0.503
adult *S. lineatus*				0.504

Table 7.2. Overlap in feeding habitat utilised by species - age groups.

Part a. Comparisons between juveniles of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
juvenile *S. doliatus*		0.512	0.365	0.598
juvenile *S. fuscescens*			0.800	0.466
juvenile *S. lineatus*				0.747

Part b. Comparisons between juveniles and adults of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
adult *S. doliatus*	0.000	0.000	0.000	0.000
adult *S. fuscescens*	0.562	0.641	0.540	0.297
adult *S. lineatus*	0.026	0.009	0.000	0.267
adult *S. punctatus*	0.000	0.000	0.000	0.000

Part c. Comparisons between adults of the four species.

	adult *S. doliatus*	**adult** *S. fuscescens*	**adult** *S. lineatus*	**adult** *S. punctatus*
adult *S. doliatus*		0.661	0.003	0.942
adult *S. fuscescens*			0.003	0.730
adult *S. lineatus*				0.003

Table 7.3. Overlap in roving habitat utilised by species - age groups.

Part a. Comparisons between juveniles of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
juvenile *S. doliatus*		0.905	0.917	0.882
juvenile *S. fuscescens*			0.940	0.979
juvenile *S. lineatus*				0.965

Part b. Comparisons between juveniles and adults of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
adult *S. doliatus*	0.000	0.000	0.000	0.000
adult *S. fuscescens*	0.093	0.108	0.119	0.117
adult *S. lineatus*	0.180	0.138	0.098	0.019
adult *S. punctatus*	0.000	0.000	0.000	0.000

Part c. Comparisons between adults of the four species.

	adult *S. doliatus*	**adult** *S. fuscescens*	**adult** *S. lineatus*	**adult** *S. punctatus*
adult *S. doliatus*		0.889	0.499	0.993
adult *S. fuscescens*			0.453	0.914
adult *S. lineatus*				0.500

Table 7.4. Overlap in hiding habitat utilised by species - age groups.

Part a. Comparisons between juveniles of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
juvenile *S. doliatus*		0.917	0.907	0.969
juvenile *S. fuscescens*			0.664	0.950
juvenile *S. lineatus*				0.808

Part b. Comparisons between juveniles and adults of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
adult *S. doliatus*	0.000	0.000	0.000	0.000
adult *S. fuscescens*	0.083	0.102	0.051	0.073
adult *S. lineatus*	0.001	0.001	0.000	0.001
adult *S. punctatus*	0.000	0.000	0.000	0.000

Part c. Comparisons between adults of the four species.

	adult *S. doliatus*	**adult** *S. fuscescens*	**adult** *S. lineatus*	**adult** *S. punctatus*
adult *S. doliatus*		0.049	0.347	0.862
adult *S. fuscescens*			0.400	0.154
adult *S. lineatus*				0.114

Table 7.5. Total resource use overlap between species - age groups.

Part a. Comparisons between juveniles of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
juvenile *S. doliatus*		0.746	0.693	0.769
juvenile *S. fuscescens*			0.698	0.744
juvenile *S. lineatus*				0.757

Part b. Comparisons between juveniles and adults of the four species.

	juvenile *S. doliatus*	**juvenile** *S. fuscescens*	**juvenile** *S. lineatus*	**juvenile** *S. punctatus*
adult *S. doliatus*	0.000	0.000	0.000	0.000
adult *S. fuscescens*	0.087	0.118	0.085	0.080
adult *S. lineatus*	0.063	0.047	0.033	0.031
adult *S. punctatus*	0.000	0.000	0.000	0.000

Part c. Comparisons between adults of the four species.

	adult *S. doliatus*	**adult** *S. fuscescens*	**adult** *S. lineatus*	**adult** *S. punctatus*
adult *S. doliatus*		0.367	0.282	0.724
adult *S. fuscescens*			0.285	0.478
adult *S. lineatus*				0.205

APPENDIX I

Table comparing the slopes (with 95 % confidence intervals) of juvenile and adult subgroups in for the various regressions in Chapter 4.

Ln/ ln regression of total gut length against standard length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	1.157 (1.013 – 1.230), $r^2 = 0.924$	1.300 (0.996 – 1.609), $r^2 = 0.595$	overlapping
S. fuscescens	1.114 (0.937 – 1.295), $r^2 = 0.832$	1.047 (0.544 – 1.550), $r^2 = 0.651$	overlapping
S. lineatus	1.134 (0.912 – 1.355), $r^2 = 0.844$	1.340 (1.161 – 1.535), $r^2 = 0.823$	overlapping
S. punctatus	1.306 (1.083 – (1.528), $r^2 = 0.900$	0.644 (-0.573 – 1.860), $r^2 = 0.315$	overlapping

Ln/ ln regression of oesophagus length against standard length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	1.016 (0.722 – 1.310), $r^2 = 0.698$	1.144 (0.762 – 1.526), $r^2 = 0.424$	overlapping
S. fuscescens	0.988 (0.744 – 1.232), $r^2 = 0.761$	0.978 (0.578 – 1.378), $r^2 = 0.670$	overlapping
S. lineatus	1.200 (1.008 – 1.392), $r^2 = 0.895$	1.275 (1.081 – 1.469), $r^2 = 0.796$	overlapping
S. punctatus	1.017 (0.707 – 1.327), $r^2 = 0.778$	1.253 (0.547 – 1.960), $r^2 = 0.885$	overlapping

Ln/ln regression of cardiac stomach length against standard length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	1.293 (1.002 – 1.584), $r^2 =0.793$	1.269 (0.590 – 1.948), $r^2 = 0.211$	overlapping
S. fuscescens	1.422 (1.036 – 1.807), $r^2 = 0.735$	0.990 (0.382 – 1.598), $r^2 = 0.496$	overlapping
S. lineatus	1.426 (1.143 – 1.708), $r^2 = 0.847$	0.897 (0.606 – 1.187), $r^2 = 0.463$	overlapping
S. punctatus	0.933 (0.475 – 1.392), $r^2 = 0.567$	1.830 (-1.355 – 5.013), $r^2 = 0.369$	overlapping

Ln/ ln regression of pyloric stomach length against standard length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	1.139 (0.871 – 1.406), $r^2 = 0.779$	0.434 (-0.141 – 1.010), $r^2 = 0.026$	overlapping
S. fuscescens	1.119 (0.708 – 1.529), $r^2 = 0.586$	0.835 (0.391 – 1.280), $r^2 = 0.573$	overlapping
S. lineatus	1.509 (1.212 – 1.805), $r^2 = 0.849$	0.966 (0.694 – 1.234), $r^2 = 0.528$	overlapping
S. punctatus	1.138 (0.688 – 1.588), $r^2 = 0.674$	1.757 (-1.827 – 5.342), $r^2 = 0.264$	overlapping

Ln/ln regression of intestinal length to the 'S' bend against standard length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope and 95 % confidence interval for adult subgroup	Interval comparison
S. doliatus	1.125 (0.920 – 1.330), r^2 = 0.854	1.610 (1.120 - 2.021), r^2 = 0.555	overlapping
S. fuscescens	1.407 (1.120 – 1.694), r^2 = 0.824	1.136 (0.692 – 1.580), r^2 = 0.741	overlapping
S. lineatus	1.180 (1.018 – 1.342), r^2 = 0.920	1.367 (1.136 – 1.598), r^2 = 0.759	overlapping
S. punctatus	1.343 (1.022 – 1.664), r^2 = 0.852	0.666 (-0.884 – 2.216), r^2 = 0.179	overlapping

Ln/ln regression of intestinal length from the bend to the anus against standard length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	1.085 (0.895 – 1.276), r^2 = 0.863	1.101 (0.665 – 1.538), r^2 = 0.345	overlapping
S. fuscescens	1.318 (0.995 – 1.641), r^2 = 0.764	1.007 (0.217 – 1.797), r^2 = 0.391	overlapping
S. lineatus	1.402 (1.058 – 1.745), r^2 = 0.782	1.423 (1.174 – 1.672), r^2 = 0.745	overlapping
S. punctatus	1.068 (0.797 – 1.339), r^2 = 0.836	0.365 (-1.645 – 2.376), r^2 = -0.200	overlapping

Square root/square root regression of gape height against head length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	0.491 (0.423 – 0.559), r^2 = 0.907	0.470 (0.316 – 0.623), r^2 = 0.426	overlapping
S. fuscescens	0.500 (0.407 – 0.593), r^2 = 0.844	0.487 (0.291 – 0.682), r^2 = 0.707	overlapping
S. lineatus	0.581 (0.509 – 0.653), r^2 = 0.931	0.429 (0.338 – 0.520), r^2 = 0.715	overlapping
S. punctatus	0.439 (0.259 – 0.620), r^2 = 0.602	0.589 (-0.522 – 1.680), r^2 = 0.316	overlapping

Square root/square root regression of head depth at the eye against head length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	1.111 (0.920 – 1.302), r^2 = 0.857	0.859 (0.693 – 1.024), r^2 = 0.703	overlapping
S. fuscescens	1.032 (0.957 – 1.107), r^2 = 0.973	1.093 (0.882 – 1.305), r^2 = 0.915	overlapping
S. lineatus	1.182 (1.104 – 1.259), r^2 = 0.981	0.980 (0.904 – 1.057), r^2 = 0.944	discreet
S. punctatus	1.278 (1.142 – 1.414), r^2 = 0.959	1.287 (0.100 – 2.474), r^2 = 0.732	overlapping

Square root/square root regression of head depth at D1 against head length

Species	Slope, confidence interval and r^2 for juvenile subgroup	Slope, confidence interval and r^2 for adult subgroup	Interval comparison
S. doliatus	1.308 (1.132 – 1.484), r^2 = 0.919	0.943 (0.793 – 1.149), r^2 = 0.647	overlapping
S. fuscescens	1.274 (1.162 – 1.385), r^2 = 0.960	1.286 (1.016 – 1.555), r^2 = 0.901	overlapping
S. lineatus	1.421 (1.231 – 1.610), r^2 = 0.924	1.122 (1.034 – 1.211), r^2 = 0.941	discreet
S. punctatus	1.443 (1.280 – 1.606), r^2 = 0.953	1.363 (0.848 – 1.877), r^2 = 0.946	overlapping

APPENDIX II

Multiway contingency table showing the numbers of juvenile siganids using different microhabitats for various activities - A: Northern reef flat site

Site:	**North**							
Species	Fish size	Shoal size	Seagrass			Reefs		
			Feeding	Roving	Hiding	Feeding	Roving	Hiding
Siganus doliatus	small	1 to 3	4	11	0	7	4	80
		4 to 10	2	12	0	1	6	38
		>10	4	6	0	5	8	24
	large	1 to 3	1	8	0	16	10	68
		4 to 10	0	3	0	7	0	7
		>10	0	0	0	0	0	0
Siganus fuscescens	small	1 to 3	0	16	0	0	2	17
		4 to 10	2	18	0	0	10	8
		>10	8	37	0	2	10	7
	large	1 to 3	4	24	0	6	11	15
		4 to 10	9	22	0	2	10	6
		>10	7	9	0	1	2	0
Siganus lineatus	small	1 to 3	1	1	0	0	1	8
		4 to 10	0	0	0	0	1	4
		>10	0	2	0	0	2	0
	large	1 to 3	0	0	0	0	0	0
		4 to 10	0	0	0	0	0	0
		>10	0	0	0	0	0	0
Siganus punctatus	small	1 to 3	1	0	0	0	1	8
		4 to 10	0	1	0	0	0	3
		>10	0	3	0	0	0	1
	large	1 to 3	1	4	0	1	3	14
		4 to 10	0	0	0	0	1	3
		>10	0	0	0	0	0	0

B: Southeastern reef flat site

Site:	**Flat east**							
Species	Fish size	Shoal size		Seagrass			Reefs	
			Feeding	Roving	Hiding	Feeding	Roving	Hiding
Siganus doliatus	small	1 to 3	3	4	0	2	3	74
		4 to 10	2	3	0	1	2	38
		>10	2	4	0	3	0	18
	large	1 to 3	3	7	0	6	5	98
		4 to 10	0	4	0	0	0	6
		>10	0	1	0	0	0	0
Siganus fuscescens	small	1 to 3	1	4	0	1	5	46
		4 to 10	2	6	0	1	1	21
		>10	1	15	0	0	0	11
	large	1 to 3	4	15	0	0	2	19
		4 to 10	7	13	0	0	0	2
		>10	4	4	0	0	0	0
Siganus lineatus	small	1 to 3	0	1	0	0	0	14
		4 to 10	0	0	0	0	0	2
		>10	0	0	0	0	0	0
	large	1 to 3	0	0	0	0	0	1
		4 to 10	0	0	0	0	0	0
		>10	0	0	0	0	0	0
Siganus punctatus	small	1 to 3	1	0	0	1	1	15
		4 to 10	0	0	0	0	0	7
		>10	0	0	0	0	0	0
	large	1 to 3	0	2	0	1	0	21
		4 to 10	0	0	0	0	0	1
		>10	0	0	0	0	0	0

C: Southwestern reef flat site

Site: Flat west

Species	Fish size	Shoal size	Seagrass			Reefs		
			Feeding	Roving	Hiding	Feeding	Roving	Hiding
Siganus doliatus	small	1 to 3	3	6	0	1	10	194
		4 to 10	2	1	0	7	7	50
		>10	0	0	0	3	0	9
	large	1 to 3	3	21	1	3	4	121
		4 to 10	2	4	0	0	0	7
		>10	0	0	0	0	0	0
Siganus fuscescens	small	1 to 3	0	1	0	1	2	51
		4 to 10	1	1	0	0	0	22
		>10	0	2	0	0	0	2
	large	1 to 3	10	12	0	2	1	21
		4 to 10	5	7	2	2	0	5
		>10	2	0	0	0	0	0
Siganus lineatus	small	1 to 3	0	0	0	0	0	7
		4 to 10	0	0	0	2	0	3
		>10	0	0	0	0	0	2
	large	1 to 3	0	1	0	0	0	23
		4 to 10	0	0	0	0	0	1
		>10	0	0	0	0	0	0
Siganus punctatus	small	1 to 3	0	0	0	1	0	11
		4 to 10	0	0	0	3	0	5
		>10	0	0	0	0	0	0
	large	1 to 3	0	0	0	0	1	10
		4 to 10	1	0	0	0	0	1
		>10	0	0	0	0	0	0

APPENDIX III

Multiway contingency table showing the numbers of adult siganids using different sites for various activities:

A: *S. doliatus*

Site	Tide height	Centre			Edge		
		Feeding	Roving	Hiding	Feeding	Roving	Hiding
North reef flat	low	0	0	0	0	0	0
	high	0	0	0	0	0	0
S'west reef flat	low	0	0	0	0	0	0
	high	0	0	0	0	0	0
Near patch reefs	low	2	45	1	1	18	0
	high	5	51	0	0	15	0
Far patch reefs	low	6	91	3	3	14	0
	high	6	72	1	0	10	1
Channel edge	low	78	390	5	7	60	0
	high	89	460	5	7	25	1
South ledge	low	22	249	2	41	103	2
	high	6	237	2	13	69	1

B: *S. fuscescens*

Site	Tide height	Centre			Edge		
		Feeding	Roving	Hiding	Feeding	Roving	Hiding
North reef flat	low	0	0	0	0	0	0
	high	7	13	1	0	0	0
S'west reef flat	low	0	0	0	0	0	0
	high	0	0	0	0	0	0
Near patch reefs	low	0	2	0	1	10	0
	high	0	4	0	1	16	0
Far patch reefs	low	0	8	0	0	11	0
	high	0	6	0	0	11	0
Channel edge	low	3	14	1	2	20	0
	high	3	19	0	1	12	0
South ledge	low	0	19	0	1	3	0
	high	2	17	0	0	2	0

C: *S. lineatus*

Site	Tide height	Centre			Edge		
		Feeding	Roving	Hanging	Feeding	Roving	Hanging
North reef flat	low	0	0	0	0	0	0
	high	0	0	0	0	0	0
S'west reef flat	low	0	0	0	0	0	0
	high	2	4	0	15	5	0
Near patch reefs	low	0	5	12	0	2	9
	high	0	0	5	0	0	10
Far patch reefs	low	0	2	38	0	6	22
	high	0	3	32	0	1	23
Channel edge	low	0	2	8	0	1	28
	high	1	2	7	0	0	13
South ledge	low	0	2	6	0	4	13
	high	0	0	3	0	4	10

D: *S. punctatus*

Site	Tide height	Centre			Edge		
		Feeding	Roving	Hiding	Feeding	Roving	Hiding
North reef flat	low	0	0	0	0	0	0
	high	0	0	0	0	0	0
S'west reef flat	low	0	0	0	0	0	0
	high	0	0	0	0	0	0
Near patch reefs	low	0	5	1	0	2	0
	high	0	6	1	0	5	0
Far patch reefs	low	1	6	0	0	2	0
	high	0	9	0	0	1	0
Channel edge	low	4	36	1	0	8	0
	high	12	42	2	0	8	1
South ledge	low	1	16	0	1	5	0
	high	1	25	0	1	9	0

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