

Post-settlement Diet Shift of *Chlorurus sordidus* and *Scarus schlegeli* (Pisces: Scaridae)

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Li-Shu Chen (2002) Post-settlement diet shift of *Chlorurus sordidus* and *Scarus schlegeli* (Pisces: Scaridae). *Zoological Studies* 41(1): 47-58. Ontogenetic changes in the development of feeding structures and feeding habits of juvenile parrotfishes *Chlorurus sordidus* and *Scarus schlegeli* (Family: Scaridae) were examined at Lizard Island on the northern Great Barrier Reef, Australia. A shift from omnivorous feeding to feeding on plant materials was observed, and this occurred over the size range of 15-30 mm TL. Ontogenetic changes were observed in teeth as well as in gut coiling patterns. Individual teeth were present in newly settled scarids (10 mm TL) but were totally lost when size increased to 26 mm TL. The change in gut coiling patterns occurred mainly in the mid-intestine, from being non-constricted to having a constricted ilial wall. The tracts also changed from 1 sinistral loop to 2 loops by the end of the observation period. The difference in gut length between the 2 species was caused by the different coiling patterns. Small individuals (15 mm TL) of both species were omnivorous with diets dominated by crustaceans and foraminifera. Significant increases in the amounts of algal material and sediment taken were seen as fish grew. With respect to microhabitat utilization, both species fed mainly on dead coral and rocky substratum. Algae, with their associated high density of crustaceans, were used by both species as a feeding substratum when individuals were small (TL < 20 mm). Dietary changes of post-settled *C. sordidus* and *S. schlegeli* were directly related to morphological changes in the alimentary tract rather than the differences of habitat utilization. <http://www.sinica.edu.tw/zool/zoolstud/41.1/47.pdf>

Key words: Digestive system, Parrotfish, Feeding habitats, Functional morphology, Foraging.

Coral reefs present predominantly a hard substratum, but one which is topologically far more complex than any other for fish. Reefs offer a diversity of shapes and sizes of shelter which is used by fish. Coral reefs are also a very patchy environment (Sale 1991). Three major fish taxa are associated with coral reefs: the chaetodontids, the acanthuroids, and the labroids (Choat and Bellwood 1991). Most coral reef fishes undergo a transition from a planktonic larval stage to a settled juvenile stage closely associated with the reef (Victor 1991). Compared to other herbivores, scarids settle onto the reef at a relatively small size. For example, acanthurids settle at 18-30 mm standard length (SL) and siganids at 20-30 mm SL, with both being ready to feed on algae at the beginning of their settlement. Scarids, however, settle at a rather smaller size of

7.5-8.5 mm SL (Brothers et al. 1983, Leis and Rennis 1983, Leis and Richards 1984, Bellwood 1988, Lou 1993). The trade off of an early settlement strategy may reduce the risk of predation in the water column; however, it also increases the risk of predation on the reef itself (Victor 1991).

A key feature of scarid feeding is the scraping off of food items by the oral jaws and subsequent grinding of these materials by the upper and lower pharyngeal teeth (Choat and Randall 1986). The study of early settlement offers us a chance to investigate the development of scarid feeding structures. Bellwood (1988) indicated that juvenile scarids are carnivorous, and suggested that particular attention should be paid to changes in diet with size and age. For this reason the investigation of pharyngeal teeth and dentition change has scientific merit.

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The study of feeding habits of scarids has traditionally been concentrated on adults. To the present, these studies include resource use by sympatric species (Bruggemann et al. 1994b, McAfee and Morgan 1996), selective foraging (Lobel and Ogden 1981, Bruggemann et al. 1994a), daily feeding rhythms (Choat and Clements 1993), changes of functional morphology of feeding apparatus (Bellwood and Choat 1990), and effects of grazing on benthic community structure (Brock 1979) and on structural changes of coral reefs (Frydl and Stearn 1978, Frydl 1979). The foraging activities of post-settlement juvenile scarids, on the other hand, have received very little attention (Bellwood 1988, Overholtzer and Motta 1999 2000). In light of recent findings that scarids are a dominant and conspicuous part of herbivorous reef fish communities (Choat and Bellwood 1985, Jones 1991) and can shape the structure of coral reefs (Frydl and Stearn 1978, Frydl 1979), the study of ontogenetic changes of diets of post-settlement scarids could lead to better understanding of ecological roles of these fishes at the juvenile stage. The foraging pattern of juveniles in the field was investigated immediately after settlement in the present study. This has provided information on changes in habitat associations and feeding substrates for juveniles with increasing size and changes in diet. The pattern of foraging behavior is hypothesized to be related to their diet or habitat. More specifically, the objectives of this study were: 1) to qualitatively and quantitatively investigate diet changes during ontogeny; 2) to examine the relationship between juvenile foraging activities and habitats; and 3) to examine morphological changes in feeding apparatus and alimentary tract structure associated with dietary changes.

MATERIALS AND METHODS

Observations and specimen collections of *Chlorurus sordidus* and *Scarus schlegeli* were conducted using scuba diving at Mermaid Cove, Granite Bluffs, and Turtle Bay around Lizard Island (14°10'S, 145°28'E) on the northern Great Barrier Reef, Australia (Fig. 1). The work was conducted between January 1995 and February 1996, when water temperature was 29-30 °C. Juvenile scarids were captured using a fine-mesh hand net. Larger fish were caught using either small clear self-sealing polythene bags (200 x 120 mm), or larger clear polythene bags (940 x 615 mm), or a 7-mm-square mesh barrier net (2 m long, 1 m wide), or a 10-mm-square mesh mono-gill net (30 m long, 1.5 m wide).

Fish were killed soon after collection by placing them into an ice-filled box. They were then transferred to 70% ethanol for further otolith analysis. For diet analysis use, specimens were fixed in 10% formalin in seawater shortly after collection. Identification of juvenile scarids followed the methods described by Bellwood and Choat (1989). Because juveniles settle predominantly during the summer, only in November and December were there sufficient numbers for collection (pers. observ.).

Diet analysis

Specimens were dissected, and their alimentary tracts were removed for microscopic examination. Food items were identified and grouped into 6 major categories: benthic crustaceans, foraminifera, dinoflagellates, filamentous algae, sand, and detritus. These categories were selected on the basis of previous work on juvenile diets (Bellwood 1988).

Where possible (e.g., for crustaceans, foraminifera, and dinoflagellates) items were counted to the individual; however, relative amounts of sand, algae, and detritus were determined visually by estimating their percentage cover, according to the following method (Hyslop 1980). Five 5-cm-long and 1-cm-apart transect lines were marked on graph tracing paper with 1 x 1-mm grids. The paper was secured to a glass Petri dish (9 cm in diameter) so that the grid was visible through the base. The entire alimentary tract was emptied into the dish and examined under a dissecting microscope to ensure that all material was extracted. The contents of the gut were spread 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 out by haphazardly removing small amounts of material and spreading out the rest.

Gut contents were quantified by use of a dissecting microscope with a 1-cm cross-hair micrometer eyepiece and the intercept method of Jones (1968). The grid was positioned by aligning the center of the cross hairs with the centimeter marks on the transect lines. There were 30 marks on the transect lines, but since the original method required only 27 grids, 3 randomly selected marks were omitted.

Food items in the diet were quantified in 2 ways: (a) as a percentage of occurrence, and (b) as a mean number of individuals or mean estimated percentage to total volume of the gut contents, after Hyslop (1980).

Patterns of daily food consumption

Gut contents of different times of day were analyzed to investigate whether temporal feeding activities differed with time. The sampling method used by Horn et al. (1990) in the study of diurnal feeding periodicity of a herbivorous blenniid fish was used. Juvenile scarids of both species were collected during 3 time periods: 0800-1000 h, 1100-1300 h, and 1400-1600 h. The choice of sampling times was also dictated by the availability of manpower as well as the diurnal feeding habits of scarids. Specimens were dissected in the laboratory, where the viscera were removed, and the gut and liver separated. Gutted body weight and full gut weight were measured separately. The gut was opened using scissors, and the contents were

washed out with water. The empty gut was dabbed dry with tissue paper and re-weighed. Thus, the net gut content weight and relative gut content weight were calculated as: Net wet gut content weight (g) = Full wet gut weight (g) - Empty wet gut weight (g); and Relative wet gut content weight = Net wet gut content (g)/Gutted body weight (g).

The relationship between net gut content and total length was calculated and plotted for each species and for the 3 sampling periods.

Microhabitat utilization and substratum availability

To quantify substratum availability, 10 tran-

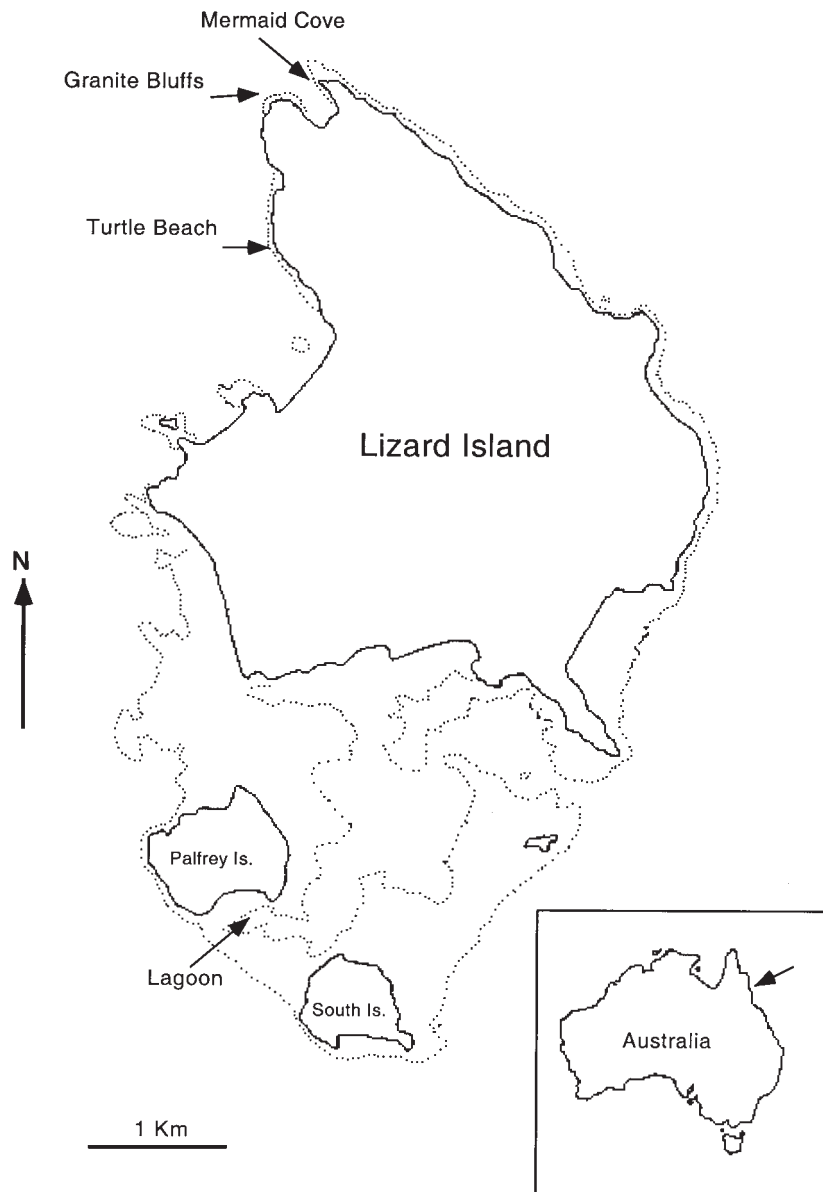


Fig. 1. Sampling sites (arrows) at Lizard Island, Great Barrier Reef, Australia.

sects were sampled at each of 2 locations, Mermaid Cove and Granite Bluffs (Fig. 1). Each transect (10 m) had 20 randomly generated intersection points, and the substratum type under each point was recorded. The microhabitats were categorized as: sand (grain diameter < 1 cm), rubble (dead coral eroded to small pieces, 1-7 cm long), rock (diameter > 7 cm), dead coral (diameter > 7 cm and still maintaining a characteristic coral shape), algae, soft coral, and live coral.

To examine microhabitat utilization, juvenile fish were chosen randomly and observed for 5 min. During this time, the number of bites and the types of substrata bitten were recorded. By sampling during the course of a linear swim (aided by a compass) across a study area of 500 m x 200 m, the possibility of recording information from the same individual was minimized. Substratum availability and microhabitat utilization by juvenile scarids were compared for different sizes and species of fish.

Anatomy and scanning electron microscopy

Structures of the oral jaw and dentition, pharynx, and alimentary tract of juvenile scarids were examined. The body cavity was opened by making an incision, beginning at the vent and continuing dorsally and cranially to the lateral line, until a flap of tissue could be folded away exposing the viscera. The esophagus was identified by its anatomical position. Designation of sections of the alimentary tract follow the nomenclature of Gohar and Latif (1959). The anterior intestine extends from the

junction of the gall bladder to the beginning of the constriction in the gut; the mid-intestine starts where the gut is constricted; and the posterior intestine extends from the ileorectal valve to the anus.

Whole fresh fish samples were fixed in 70% ethanol. The heads of the specimens were horizontally dissected into 2 halves for examination of the taste buds inside the mouth. After dehydration in an ethanol series, specimens were dried at critical point (31.1 °C, 1200 psi), and then coated with gold. Specimens were observed and photographed under a scanning electron microscope in the Analytical Center, James Cook Univ.

RESULTS

Diet analysis

Both species showed ontogenetic changes from a carnivorous to an herbivorous diet (Table 1). A carnivorous diet was observed in individuals smaller than 30 mm TL for *C. sordidus* and 50 mm TL for *S. schlegeli*. However, a decrease in the number of crustaceans ingested was evident by the time fishes were larger than 15 mm TL for *C. sordidus* and 30 mm TL for *S. schlegeli*. Concurrent with this decrease, there was an increase in the percentage of algal consumption. The percentage of sand in the gut content also increased with body size. Foraminifera were present in the gut of small juvenile scarids, but the amount of foraminifera was greater than that of sand in small juveniles (TL < 15

Table 1. Diet composition of *Chlorurus sordidus* and *Scarus schlegeli* classified into 5 size classes. Data are presented as the percentage occurrence and mean number (Crustacea, Foraminifera) or mean percentage cover (algae, sand)

Species	TL (mm)	N	Crustacea		Foraminifera		Algae(%)		Sand(%)	
			Occurrence	Mean ± SE	Occurrence	Mean ± SE	Occurrence	Mean ± SE	Occurrence	Mean ± SE
<i>C. sordidus</i>										
	<15	9	100.0%	12.9+3.6	77.8%	1.33	11.1%	0.6+0.4%	11.1%	1.0+0.7%
	15-20	8	62.5%	10.8+5.8	50.5%	2.5	88.9%	11.9+0.3%	62.5%	7.5+1.9%
	20-30	10	60.0%	1.25+0.5	40.0%	0.9	100.0%	6.8+1.9%	90.0%	4.5+1.6%
	30-50	10	0.0%	0	0.0%	0	100.0%	10.0+2.0%	100.0%	7.0+2.0%
	50-70	10	0.0%	0	0.0%	0	100.0%	8.2+3.0%	100.0%	5.6+2.1%
<i>S. schlegeli</i>										
	<15	14	100.0%	12.3+2.0	81.8%	4.09	0.0%	2.5+1.4%	76.9%	2.3+0.7%
	15-20	6	100.0%	12.8+5.1	66.7%	1.5	100.0%	3.8+1.0%	100.0%	2.5+0.5%
	20-30	10	75.0%	4.4+1.7	50.0%	1.6	100.0%	8.4+1.9%	100.0%	1.1+0.9%
	30-50	8	50.0%	1.7+0.7	57.1%	0.7	100.0%	10.3+6.0%	100.0%	5.5+2.1%
	50-70	13	7.0%	0.1+0.0	0.0%	0	00.0%	8.0+2.6%	100.0%	4.8+1.9%

mm) of both species. The ingestion of foraminifera and dinoflagellates exhibited a similar trend in both species with smaller individuals consuming greater relative amounts than larger individuals. Neither of these 2 food items were found in the gut of fish exceeding 30 mm TL for *C. sordidus*, or 50 mm TL for *S. schlegeli* (Table 1). The maximum size of sand granules ingested varied with fish size from 250 μm for individuals at 12-13 mm, 125 μm for individuals at 15-20 mm, and 350 μm for individuals at 50-60 mm TL.

Patterns of daily food consumption

Relative gut content weights differed during the 3 times of day examined and also between the 2 species (Fig. 2). For *C. sordidus*, gut content weight in the afternoon (1400-1600 h) was the highest, followed by that in the middle of the day (1100-1300 h). However, for *S. schlegeli*, net gut content weight in the middle of the day (1100-1300 h) was the highest, followed by the afternoon (1400-1600 h). For both species, the net gut content weight in the early morning (0800-1000 h) was the lowest.

When comparing relative gut contents in *C. sordidus*, differences were found between times of day but not between fish sizes, although the trend was for an increase in relative gut content weight from 4% to

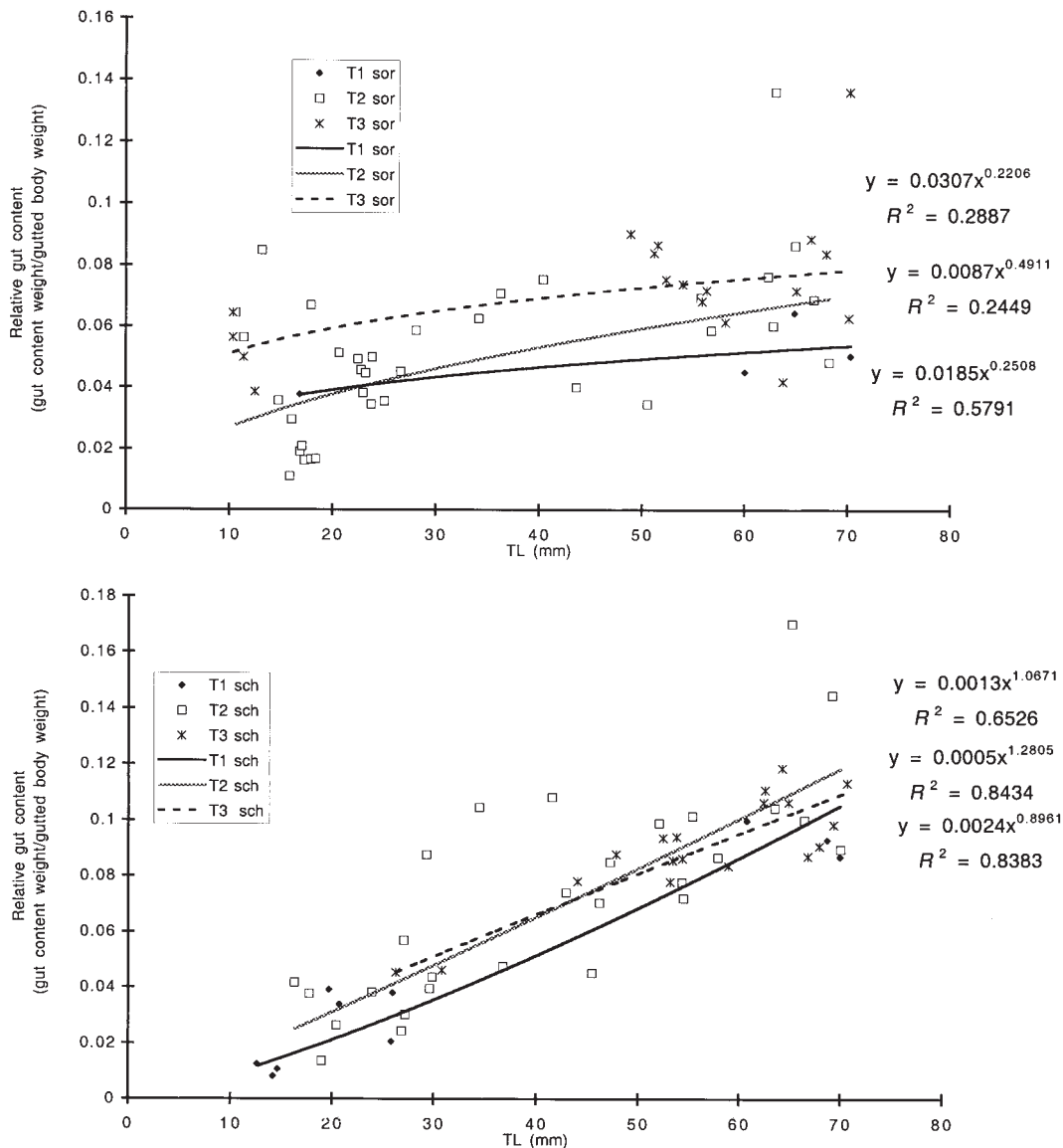


Fig. 2. Ontogenetic changes in the relationship between relative gut content (= gut content weight/gutted body weight) and fish size of *Chlorurus sordidus* (sor) and *Scarus schlegeli* (sch) for different times of day (T1: 0800-1000 h; T2: 1100-1300 h; T3: 1400-1600 h).

7% with increased size (Fig. 2). For *S. schlegeli*, relative gut contents differed between times of day and were also significantly different between fish sizes. Relative gut contents increased from 2% to 10% of gutted body weight as body size increased.

Microhabitat utilization and substratum availability

In Mermaid Cove, rubble was the dominant substratum, followed by rocks and dead coral, whereas at the Granite Bluffs site, dead coral was the dominant substrate, followed by rubble and rocks (Fig. 3). There was a distinct difference in habitats selected by different sizes of juvenile scarids. At both sites, algae represented less than 8% of substratum cover but juveniles of *C. sordidus* and *S. schlegeli* smaller than 20 mm TL showed a higher degree of utilization of algae than would be expected by availability alone. However, the frequency of feeding on algal substratum decreased with the increase of fish size, and this coincided with an increase in the percentage of feeding time

spent on rocky substratum (Fig. 4). All sizes of juvenile *C. sordidus* were observed feeding on dead coral, and the same was true for *S. schlegeli*, but only for those individuals larger than 15 mm TL. There was an exception in that juvenile scarids of both species smaller than 20 mm TL were observed feeding in the water column for zooplankton, which is not designated as a substratum category.

Anatomy and scanning electron microscopy

Oral jaw and dentition

In juvenile scarids examined, the mouth is small with limited protrusibility of the jaws. Both species showed similar developmental patterns in the jaw and dentition. Adult parrotfishes in general have distinctly fused teeth and short, crescent-shaped breathing valves (maxillary and mandibular valves) projected to the rear. However, the margins of the teeth plates in very small scarids (e.g., 12 mm TL; Fig. 5a, *C. sordidus*) appeared to have separate teeth. These individual teeth were

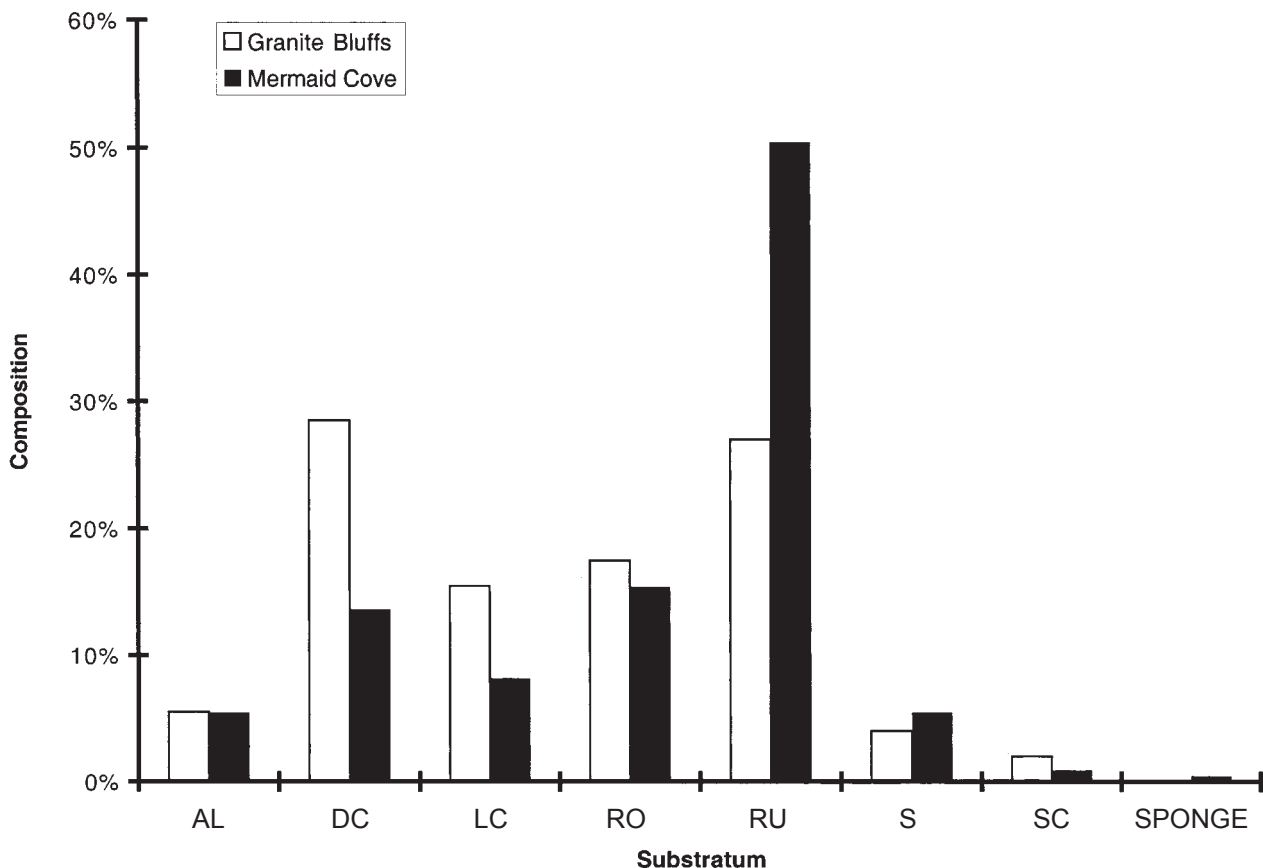


Fig. 3. Composition of the substrata at the 2 study sites, Granite bluffs and Mermaid cove, at Lizard Island, Great Barrier Reef. AL, Algae; DC, dead coral; LC, live coral; RO, rock; RU, rubble; S, sand; SC, soft coral; and sponge.

lost from the middle part to the edge of the plate in larger fish (Fig. 5b) and from the dentary (lower jaw) to the premaxilla (upper jaw) (Fig. 5b). In 12 mm TL individuals examined (Fig. 5a), it was apparent that individual teeth had worn out only on the dentary plate, and then subsequently worn out from the middle of the premaxilla when a size of 14–mm TL was reached. All middle teeth on both jaws had disappeared by the time fish were larger than 19 mm TL, but there were still some individual teeth toward the lateral edge of the jaw. For a fully developed juvenile (25 mm TL), numerous small teeth were apparent, which become packed together and attached at their proximal ends to the

jaw bones, while their distal ends formed a mosaic. The 2 dental plates, the premaxilla and dentary, were each divided vertically into 2 halves. Their surfaces were granular, and their free edges were serrated. When fish reached a size of 26 mm TL, individual teeth were absent from the functional margin of the jaw. The palate was

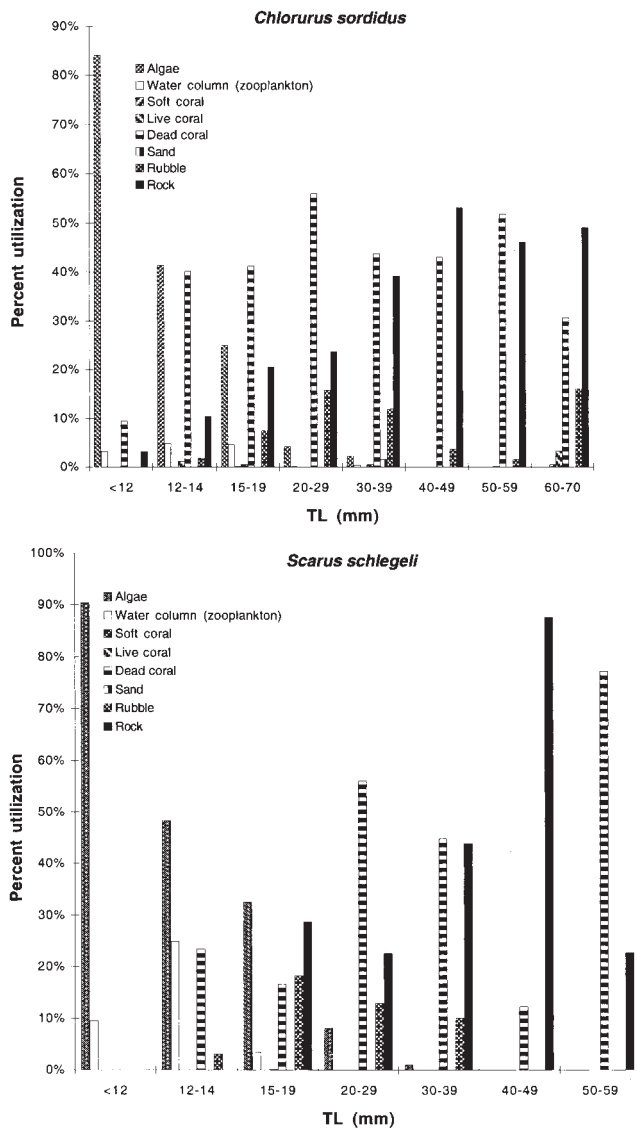


Fig. 4. Relative use of different substrata (expressed as percent of time during a 5 min observation period) by different size classes of juvenile scarids of *Chlorurus sordidus* and *Scarus schlegeli*.

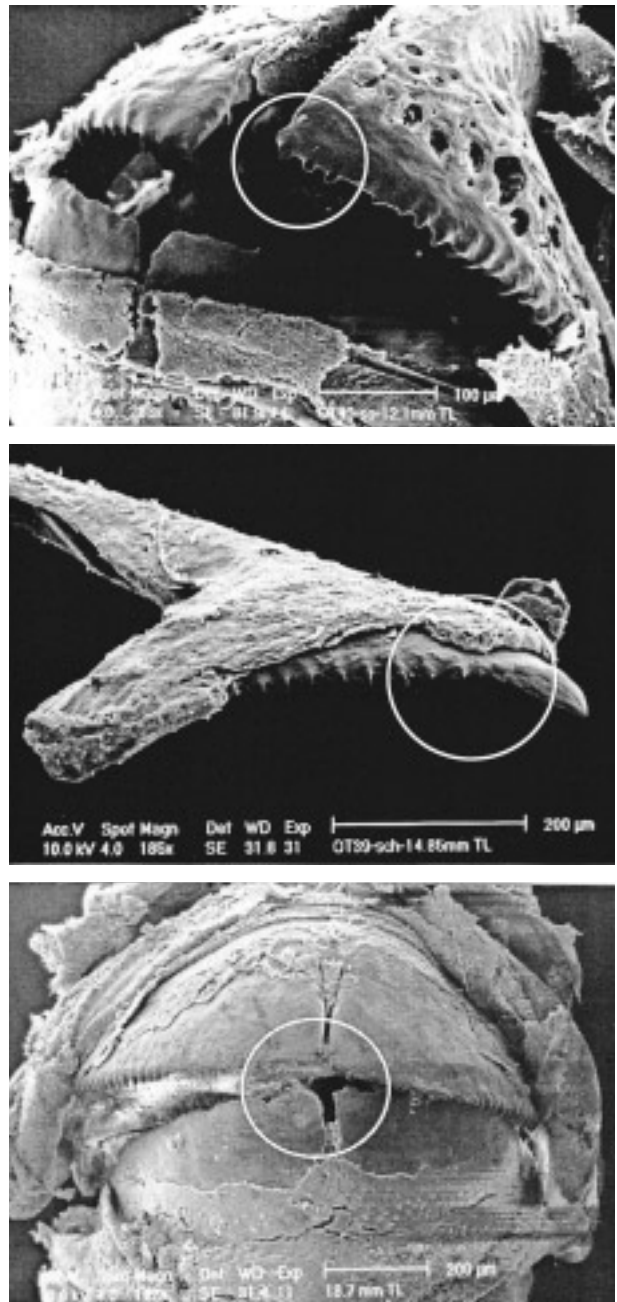


Fig. 5. Ontogenetic changes in the dental structure of juvenile scarids. (a) *Chlorurus sordidus* 12.1 mm TL; (b) *Scarus schlegeli* 14.85 mm TL; (c) *Chlorurus sordidus* 18.7 mm TL. The area enclosed in the circle represents the area that has changed.

toothless. The tongue was short and thick, and no part of it was free from the floor of the mouth.

Pharynx

The pharyngeal food processing apparatus consisted of 3 elements: 2 upper bones and 1 lower one. The upper pharyngeal bones apparently work against the lower pharyngeal bone in a process by which any hard particles ingested can be ground. In addition, the 2 upper pharyngeal bones can work against each other and shear any food attached to them to grind it into small fragments. In front of the upper pharyngeal teeth in the roof of the pharynx is a pharyngeal valve which includes a thickened pad that bulges down after a curved bar. The part of the pad adjacent to the upper tooth plates is soft.

The upper pharyngeal teeth form 1 row of large molariform teeth with a rudimentary lateral row. The number of the teeth on the pharyngeal tooth plate increased with an increase in fish size.

Alimentary tract

The patterns and forms of the alimentary tract varied both within and between species and were size dependant. Ontogenetic changes were the main form of variation within a species. A comparison of developmental changes, which occurred in gut coiling patterns between the 2 species, is shown in figure. 6. The coiling patterns of the alimentary tract changed from single to complex when size increased, with the greatest change occurring in the mid-intestine. In newly settled juveniles (11 mm TL, see Fig. 6-1b, *S. schlegeli*; Fig. 6-4b, *C. sordidus*) there is an invagination of the dextral part of the loop. This invagination enlarges and creates an elongated loop (see Fig. 6-2b, *S. schlegeli*; Fig. 6-5b, *C. sordidus*). Interspecific differences were significant after individuals reached 26 mm TL when a sinistral folding of the anterior part of the mid-intestine produces 2 sinistral loops in *C. sordidus* (Fig. 6). At about 60 mm TL, sinistral loops were seen in the mid-intestine of *S. schlegeli*; however, they were not as distinctive as those in *C. sordidus*.

The anterior intestine extended from the end of the esophagus to the beginning of the 1st curve of the gut and exhibited the same pattern in both species. *C. sordidus* possessed only 1 large right intestinal bulb (InBr) on the anterior part of the anterior intestine, while in *S. schlegeli* there were 2 bulbs, the larger one extending to the right of the anterior intestine (right intestinal bulb, IBr) and a smaller one extending to the left of the anterior

intestine (left intestinal bulb, InBl) (Fig. 6).

The mid-intestine was initially simple and increased in complexity with increasing fish size. In scarids, some sac-like structures (i.e., sacculatation) can be found in adult intestines. There was no sacculatation in the mid-intestine of newly recruited individuals. The 1st signs of sacculatation were observed when fish length was approximately 17 mm TL, and the 1st completion of the 1st sacs occurred at approximately 22 mm TL.

There was a distinct posterior intestine marked by a constriction at the iliorectal valve. The length of the posterior intestine was 30% to 40% of the visceral length, and this remained consistent throughout development. No sacculatation was observed in the posterior intestine.

DISCUSSION

Ontogenetic changes in the diet of 8 early post-settlement *Scarus* were first investigated by Bellwood (1988). Due to the limitation of fish sizes, the results of the study consisted of pooled observations, and thus detailed developmental study at the species level was not possible. In addition, the sizes of fish investigated by Bellwood were relatively small (e.g., for *C. sordidus*: 8.2 to 22 mm; for *S. schlegeli*: 10.6 to 20.0 mm). The present study covers a wider body length range, 15-70 mm for both species, and diets of each species are categorized item-by-item. Bellwood (1988) categorized food items into crustacea, algae, and sand, while the present study found that foraminifera, an item not reported by Bellwood, is a major food item for *C. sordidus* of less than 30 mm and for *S. schlegeli* of less than 50 mm (Table 1). Bellwood (1988) did observe a gradual reduction of crustaceans in the diet as juveniles grew from 7 to 35 mm. However, the present study demonstrates that crustacea can still be found in the diet of *S. schlegeli* even for those as large as 70 mm (Table 1), and neither crustacea nor foraminifera can be found in *C. sordidus* larger than 30 mm. The same trend of diet shifting from carnivory to herbivory reported by Bellwood (1988) was also observed in both species. However, it should be pointed out that even in fish as small as 15 mm, algae and sand were found in the diets of both species. A similar observation was also reported by Bellwood (1988). Taking into account the findings from these 2 studies, it is perhaps more appropriate to state that juvenile *C. sordidus* of less than 30 mm should be

considered omnivorous, while this is true for *S. schlegeli* of less than 50 mm in length.

Many coral fish species of acanthurids, siganids, and pomacanthids appear to feed as herbivores immediately after settlement (Ciardelli 1967, Emery 1973, Bryan and Madraisus 1977, Lassuy 1984,

Bellwood 1988). The discovery by Bellwood (1988) and the present study indicate that there is a gradual shift from omnivory to herbivory by scarids. This is unique among coral reef fishes. Inclusion of animal protein in the diet immediately after settlement may provide needed energy as animal proteins tend to

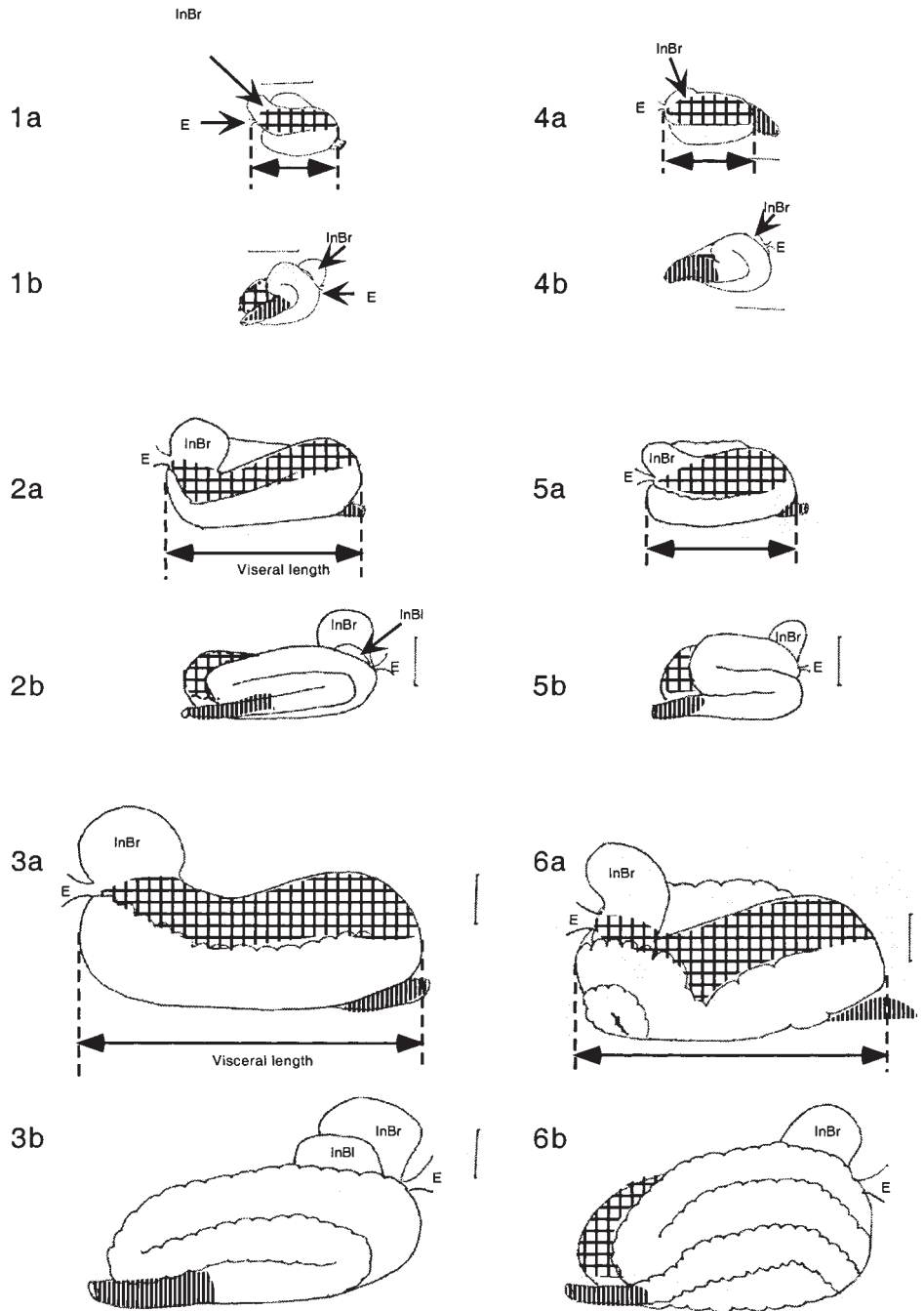


Fig. 6. Ontogenetic changes in the coiling pattern of juvenile *Scars schlegeli* (1: 10.54 mm TL; 2: 20.45 mm TL; 3: 29.62 mm TL) and *Chlorurus sordidus* (4: 10.65 mm TL; 5: 17.09 mm TL; 6: 26.7 mm TL) after removal of the liver. (a) Views when fish head is to the left, (b) Views when fish head is to the right. E: esophagus; InBr: right intestinal bulb. Scale bar = 1 mm.

anterior intestine
 mid-intestine
 posterior intestine

have higher energy content than do algae (Helfman et al. 1977, Benavides et al. 1994, Overholtzer and Motta 1999). The gradual shift of diets in scarids may also indicate that ontogenetic changes of digestive enzymes are needed to change from carnivory to herbivory. Other studies have pointed out that developmental changes of the digestive enzymes of larval fish are diet dependent (Il'ina and Turetskiy 1988, Segner et al. 1989, Oozeki and Bailey 1995, Baglote et al. 1998). Further investigation of enzyme histochemistry accompanying ontogenetic changes of scarids should help shed light on this issue.

This study shows that dietary changes occur in small scarids, which as newly settled individuals feed as carnivores and gradually shift to being herbivores. This gradual change in diet correlates well with changes in dentition and alimentary tract characteristics over the size range of 10-20 mm TL (Figs. 5, 6). A study of dental development and ontogenetic dietary shifts in a characin (*Roeboides paranensis*) (Hahn et al. 2000) demonstrated that the development of teeth in both maxillas is closely correlated with shifts of diet from microcrustaceans to fish scales (lepidophagy). The formation of teeth in the black rockfish (*Sebastes schlegeli*) was also found to coincide with the shift from passive filter feeding to active prey capture (Omori et al. 1996). There are strong relationships between dietary guild and the size and arrangement of palatine teeth in tropical ariid catfishes (Blaber et al. 1994) in which the size and number of teeth are correlated with sizes of prey. The presence of individual teeth in 12.1 mm TL *C. sordidus* (Fig. 5a) is suited for the pursuit of active prey like crustaceans (Table 1), while the gradual loss of these teeth (Fig. 5c) and the formation of toothless plates occurred in 26 mm TL individuals. Such a morphological change in dentition patterns correlates well with the need for the scraping of algae from coral reefs and the suction of sand (Table 1). Furthermore, Wainwright et al. (1991) demonstrated that pharyngeal jaws of pumpkinseed sunfish (*Lepomis gibbosus*) are more robust, and mollusc-crushing performance improved in a lake with higher mollusc densities. In a related study, Mittelbach et al. (1992) further showed that there is a positive correlation between the mass of the pumpkinseed's main crushing muscle, the levator posterior, and the percentage of molluscs in the diet. In light of the fact that coral reefs can vary by great degrees of availability of food resources to resident scarids (Victor 1991), it is likely that ontogeny of feeding morphology, i.e., trophic polymorphism, can be expected, and this hypothesis should be tested in future work. There is evidence of an early divergence between

scraping and excavating morphologies and properties in pharyngeal apparatus (L. Chen unpubl. data). Although scarids appear to be a uniform group, there is a complex pattern of species-specific differences associated with developing feeding patterns. In addition, observed size-specific foraging behaviors appear to reflect gut contents in these species.

The optimal digestion hypothesis predicts that herbivorous fish should have longer digestive tracts than do carnivorous fish (Helfman et al. 1997). A study of the diet of 21 species of fish from a forest stream in Panama found that at a given size, intestine lengths of herbivores are longer than those of omnivores, which in turn are longer than those of carnivores (Kramer and Bryant 1995). Benavides et al. (1994) demonstrated that an increase in relative gut length is associated with an increase in the capacity to digest macroalgae. This allows larger fish to meet their energetic demands by consuming algae owing to their capability to digest energetically low-quality food (Benavides et al. 1994). The complexity and coiling patterns of digestive tracts of both *C. sordidus* and *S. schlegeli* increase as the fish grow (Fig. 6). Certain degrees of similarity exist in the overall coiling pattern of both species. This may reflect the fact that the diets of the 2 species are in fact quite similar (Table 1). The shifting of diet from carnivory to omnivory and finally to herbivory may explain the increased degree of complexity and length of the gut. Future efforts should be directed at correlating such a relationship as seen in other fish species.

Net gut content weights of both species were observed to vary depending on the time of day (Fig. 2), and an empty gut was not found during this study. This indicates that juvenile scarids feed continuously throughout the day. Similar results were obtained for later juveniles and adults of *C. sordidus* and *S. schlegeli* (Choat and Clements 1993). However, Smith and Paulson (1974) reported intermittent feeding for adult *S. jonesi* and *C. gibbus*. A plausible explanation for continuous feeding may lie in the fact that algal diets tend to have lower energy value and require longer times to extract the contents (Benavides et al. 1994). The positive correlation between body size and gut content of both species (Fig. 2) also indicates that larger fish need higher energy intakes to sustain growth.

Foraging patterns varying with size observed for both *C. sordidus* and *S. schlegeli* (Fig. 4) may reflect food availability among different types of habitats. This is even more evident when the habitat types of Granite Bluffs and Mermaid Cove (Fig. 3) and the percentage using each type of habitat by these 2 species (Fig. 4) are taken into account. In a study of

resource use by 5 sympatric species of parrotfish (McAfee and Morgan 1996), it was demonstrated that they partition resources with respect to habitat, food, and size but not time. Although the fishes in the current study share resources, the proportions of each resource used by the fish differ significantly among species. In the present study, some degrees of differences in the usage of resources (Table 1) as well as habitat use (Fig. 4) seen between the 2 species are similar to findings reported by McAfee and Morgan (1996). Furthermore, Green (1994) reported that microinvertebrates are more abundant in the *Dischistodus prosopotaenia* territory, which supports more algae than does rubble/sand or reef matrix. Consequently food availability may be one of the reasons that small juveniles of both *C. sordidus* and *S. schlegeli* choose to feed among algae as shown in figure. 4 even though at a length of less than 12 mm, the main diet is crustaceans (Table 1). Shelter from predators can be another reason for small juveniles to feed among algae. A comparative analysis of foraging and habitat use by the sympatric Caribbean adult parrotfish (*Scarus vetula* and *Sparisoma viride*) (Bruggemann et al. 1994a) showed that both species exhibit similar foraging activities, but they exploit algal resources differently. In future studies, attention should be devoted to the study of whether such segregation of use of both crustacean and algal resources is present in *C. sordidus* and *S. schlegeli*.

In summary, a study of dietary contents of juvenile *C. sordidus* and *S. schlegeli* shows that the feeding habit shifts from omnivory to herbivory as they grow. The shift of diets correlates with morphological changes in the feeding apparatus (e.g., teeth) as well as in the alimentary tract. Spatial differences in the use of various foraging habitats during the ontogenetic process were also observed. This study contributes to the understanding of how newly settled *C. sordidus* and *S. schlegeli* use food resources and habitats.

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REFERENCES

- Baglole CJ, GP Goff, GM Wright. 1998. Distribution and ontogeny of digestive enzymes in larval yellowtail and winter flounder. *J. Fish Biol.* **53**: 767-784.
- Bellwood DR. 1988. Ontogenetic changes in the diet of early post-settlement *Scarus* species (Pisces: Scaridae). *J. Fish Biol.* **33**: 213-219.
- Bellwood DR. 1994. A phylogenetic study of the parrotfishes family Scaridae (Pisces: Labroidae), with a revision of genera. *Rec. Austral. Mus. Suppl.* **20**: 1-86.
- Bellwood DR, JH Choat. 1989. A description of the juvenile phase colour patterns of 24 parrotfish species (family Scaridae) from the Great Barrier Reef, Australia. *Rec. Austral. Mus.* **41**: 1-41.
- Bellwood DR, JH Choat. 1990. A functional analysis of grazing in parrotfishes (family Scaridae): the ecological implications. *Environ. Biol. Fish.* **28**: 189-214.
- Benavides AG, JM Cancino, FP Ojeda. 1994. Ontogenetic changes in gut dimension and macroalgae digestibility in the marine herbivorous fish, *Aplodactylus punctatus*. *Funct. Ecol.* **8**: 46-51.
- Blaber SJM, DT Brewer, JP Salini. 1994. Diet and dentition in tropical ariid catfishes from Australia. *Environ. Biol. Fish.* **40**: 159-174.
- Broack RE. 1979. An experimental study on the effects of grazing by parrotfishes and role of refuges on benthic community structure. *Mar. Biol.* **51**: 381-388.
- Brothers EB, DM Williams, PF Sale. 1983. Length of larval life in twelve families of fishes at "One Tree Lagoon". *Mar. Biol.* **76**: 319-324.
- Bruggemann JH, MVM Kuyper, AM Breeman. 1994a. Comparative analysis of foraging and habitat use by the sympatric Caribbean parrotfish *Scarus vetula* and *Sparisoma viride* (Scaridae). *Mar. Ecol. Prog. Ser.* **112**: 51-66.
- Bruggemann JH, MJH van Oppen, AM Breeman. 1994b. Foraging by the spotlight parrotfish *Sparisoma viride*. 1. Food selection in different, socially determined habitats. *Mar. Ecol. Prog. Ser.* **106**: 41-55.
- Bryan PG, BB Madraisau. 1977. Larval rearing and development of *Siganus lineatus* (Pisces: Signaidae) from hatching throughout metamorphosis. *Aquaculture* **10**: 243-252.
- Choat JH, DR Bellwood. 1991. Reef fishes: their history and evolution. In PF Sale, ed. *The ecology of fishes on coral reefs*. San Diego: Academic Press, pp. 39-66.
- Choat JH, KD Clements. 1993. Daily feeding rates in herbivorous labroid fishes. *Mar. Biol.* **117**: 205-211.
- Choat JH, JE Randall. 1986. A review of the parrotfishes (Family Scaridae) of the Great Barrier Reef of Australia with description of a new species. *Rec. Austral. Mus.* **38**: 175-228.
- Ciardelli A. 1967. The anatomy of the feeding mechanisms and the food habits of *Microspathodon chrysurus* (Pisces: Pomacentridae). *Bull. Mar. Sci.* **17**: 845-883.
- Emery AR. 1973. Comparative ecology and functional osteology of fourteen species of damselfish (Pisces: Pomacentriade) at Alligator Reef, Florida Keys. *Bull. Mar. Sci.* **23**: 649-670.
- Frydl P. 1979. The effect of parrotfish (Scaridae) on coral in Barbados, W.I. *Int. Rev. Gesamt. Hydrobiologia* **64**: 737-748.
- Frydl P, CW Stearn. 1978. Rate of bioerosion by parrotfish in Barbados reef environments. *J. Sediment. Petrol.* **48**:

- 1149-1158.
- Gohar HAF, AFA Latif. 1963. Digestive proteolytic enzymes of some scarid and labrid fishes (from the Red Sea). *Publ. Mar. Biol. Sta. (Al-Ghardaqa, Egypt)* **12**: 4-42.
- Green AL. 1994. The early life history of labroid fishes at Lizard Island, Northern Great Barrier Reef. North Queensland, Australia: James Cook University.
- Hahn NS, CS Pavanelli, EK Okada. 2000. Dental development and ontogenetic diet shifts of *Roeboides paranesis* Pignalberi (Osteichthyes, Characinae) in pools of the upper Rio Paran floodplain (State of Paran, Brazil). *Rev. Bras. Biol.* **60**: 93-99.
- Helfman GS, BS Collette, DE Facey. 1997. The diversity of fishes. Malden, MA: Blackwell Science.
- Hyslop EJ. 1980. Stomach contents analysis--a review of methods and their application. *J. Fish Biol.* **17**: 411-429.
- Il'ina ID, VI Turetskiy. 1988. Development of the digestive function in fishes. *J. Ichthyol.* **28**: 74-82.
- Jones GP. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. *In* PF Sale, ed. The ecology of fishes on coral reefs. San Diego: Academic Press, pp. 294-328.
- Jones RS. 1968. A suggested method for quantifying gut contents in herbivorous fishes. *Micronesica* **4**: 369-371.
- Kaufman LS, KF Leim. 1982. Fishes of the suborder Labroidea (Pisces: Perciformes): phylogeny, ecology, and evolutionary significance. *Breviora* **472**: 1-19.
- Kramer DL, MJ Bryant. 1995. Intestine length in the fishes of a tropical stream: 2. Relationship to diet—the long and short of a convoluted issue. *Environ. Biol. Fish.* **42**: 129-141.
- Lassuy DR. 1984. Diet, intestinal morphology, and nitrogen assimilation efficiency in the damselfish, *Stegastes lividus*, in Guam. *Environ. Biol. Fish.* **10**: 183-193.
- Leis JM, DS Rennis. 1983. The larvae of Indo-Pacific coral reef fishes. Sydney: New South Wales Univ. Press.
- Leis JM, WJ Richards. 1984. Acanthuroidei: development and relationships. *In* HG Moser, WJ Richards, DM Cohen, MP Fahay, AW Kendall Jr, SL Richardson, eds. Ontogeny and systematics of fishes. *Am. Soc. Ichthyol. Herpetol., Spec. Publ.* 1, pp. 547-551.
- Label PS, JC Ogden. 1981. Foraging by the herbivorous parrotfish *Sparisoma radians*. *Mar. Biol.* **64**: 173-183.
- Lou DC. 1993. Growth in juvenile *Scarus rivulatus* and *Ctenochaetus binotatus*: a comparison of families Scaridae and Acanthuridae. *J. Fish Biol.* **42**: 15-23.
- McAfee ST, SG Morgan. 1996. Resource use by five sympatric parrotfishes in the San Blas Archipelago, Panama. *Mar. Biol.* **125**: 427-437.
- Mittelbach GG, CW Osenberg, PC Wainwright. 1992. Variation in resource abundance affects diet feeding morphology in the pumpkinseed sunfish (*Lepomis gibbosus*). *Oecologia* **90**: 8-13.
- Omori M, Y Sugawara, H Honda. 1996. Morphogenesis in hatchery-reared larvae of the black rockfish, *Sebastes schlegeli*, and its relationship to the development of swimming and feeding functions. *Ichthyol. Res.* **43**: 267-282.
- Oozeki Y, KM Bailey. 1995. Ontogenetic development of digestive enzyme activities in larval walleye pollock, *Theragra chalcogramma*. *Mar. Biol.* **122**: 177-186.
- Overholtzer KL, PJ Motta. 1999. Comparative resource use by juvenile parrotfishes in the Florida Keys. *Mar. Ecol. Prog. Ser.* **177**: 177-187.
- Overholtzer KL, PJ Motta. 2000. Effects of mixed-species foraging groups on the feeding and aggression of juvenile parrotfishes. *Environ. Biol. Fish.* **58**: 345-354.
- Sale PF. 1991. Introduction. *In* PF Sale, ed. The ecology of fishes on coral reefs. San Diego: Academic Press, pp. 3-15.
- Segner H, R Roesch, RH Schmidt, KJ von Poeppinghausen. 1989. Digestive enzymes in larval *Coregonus lavaretus* L. *J. Fish Biol.* **35**: 249-263.
- Smith RL, AC Paulson. 1974. Food transit time and gut pH in two Pacific parrotfishes. *Copeia* **1974**: 796-799.
- Victor BC. 1991. Settlement strategies and biogeography of reef fishes. *In* PF Sale, ed. The ecology of fishes on coral reefs. San Diego: Academic Press, pp. 231-260.
- Wainwright PC, CW Osenberg, GG Mittelbach. 1991. Trophic polymorphism in the pumpkinseed sunfish (*Lepomis gibbosus* Linnaeus): effects of environment on ontogeny. *Funct. Ecol.* **5**: 40-55.

白斑鸚哥魚 (*Chlorurus sordidus*) 和史氏鸚哥魚 (*Scarus schlegeli*) (Pisces: Scaridae 鸚哥魚科) 定棲後食性之轉變

陳麗淑*

本研究探討澳洲大堡礁北部蜥蜴島 (Lizard Island) 體長從 15-30 mm 之白斑鸚哥魚 (*Chlorurus sordidus*) 和史氏鸚哥魚 (*Scarus schlegeli*) 仔魚由雜食性轉變為草食性其消化系的發育，包括牙齒以及腸子盤旋的形式的改變。這兩種魚最初有獨立的犬齒，但成長後就消失了；腸子從簡單的一個轉折，改變為複雜的兩次轉折。體長在 15 mm 以下的仔魚，胃內含物主要為小型底棲甲殼類和有孔蟲；但隨著成長，藻類及沙子的比率都跟著增加。在棲所利用方面，這兩種仔魚都在死珊瑚和碎石上取食，但體長小於 20 mm 時，他們則以取食藻叢中的甲殼類為主。比較結果，他們食性變化的時機隨著消化器官形狀的改變決定，而非所利用棲所不同所造成。

關鍵詞：消化系統，鸚哥魚，攝食場所，功能形態學，覓食。