

Ontogenetic variation in the diet of the cleaner fish *Labroides dimidiatus* and its ecological consequences

Alexandra S. Grutter*

Department of Marine Biology and Aquaculture, James Cook University, Townsville, Queensland 4811, Australia

ABSTRACT: Ontogenetic changes in the diet of the cleaner wrasse *Labroides dimidiatus* (Labridae) were examined at Lizard Island, Great Barrier Reef. Cleaner fish of all sizes mainly ate gnathiid isopod juveniles; the proportion of these (77 to 85%) did not differ among size classes. However, the proportion of the remaining items (scales, parasitic copepods, and non-parasitic copepods) differed significantly among size classes largely due to small juveniles which ate more non-parasitic copepods. The number of gnathiid isopods and scales in the diet of *L. dimidiatus* increased with the size of fish, with adult cleaners having 7 times as many gnathiids and 4 times more scales compared to small juveniles. The size-frequency distribution of gnathiids differed among size classes of cleaners; small juvenile cleaners had more small gnathiids in their diet than medium-sized juveniles and adult cleaners. The 'throat width' increased with the size of cleaner; on small juvenile cleaners the throat width was equal to or less than the width of the larger gnathiids sampled on a common client fish *Hemigymnus melapterus* (Labridae). Mouth size constraints may, therefore, explain the low number of large gnathiids found in the diet of these small cleaners. The lower number and smaller size of gnathiids in the diet of juvenile cleaners compared to adult cleaners suggests that any potential impact of small cleaner fish on gnathiids abundance will be less than that of larger cleaners and will be largely on small gnathiids. In addition, although clients may benefit more from cleaning by the larger cleaners, because they remove more parasites, the costs in the form of loss of scales, which are also removed in larger numbers, will also be higher.

KEY WORDS: *Labroides* · Cleaner fish · Feeding ecology · Gape limited feeding · Labridae · Gnathiidae · Parasites · Prey selection · Fish diets · Feeding constraints · Prey size

INTRODUCTION

Most fish undergo an ontogenetic shift in diet. This ontogenetic change in diet may be due to an interaction of changes in external factors (e.g. habitat, food supply, predation risk) and internal conditions (e.g. anatomical structures, behaviour, physiological demands) (Luczkovich et al. 1995). In many species, diet changes are associated with major habitat shifts (Bailey et al. 1975, Godin 1981). Changes in the size of the mouth and oral anatomy may also correspond with ontogenetic dietary shifts (Wainwright & Richard 1995).

Labrid fishes belonging to the genus *Labroides* have a feeding mode which involves removing parasites from apparently cooperating fish (clients) (Randall 1958, Feder 1966). Despite many studies, the ecological role of cleaning is still unclear (Losey 1987, Poulin & Grutter 1996). Recently, however, Grutter (1999a) showed, in a field experiment, that *L. dimidiatus* caused 4.5-fold differences in the abundance of parasites (gnathiid isopods) on caged clients (*Hemigymnus melapterus*) within 12 h (dawn to sunset). Thus, cleaners may cause the daily decline in gnathiid isopods observed on wild caught *H. melapterus* (Grutter 1999b). Most of the cleaning in the above experiment involved juvenile cleaners (Grutter 1999b). However, despite their potential importance in cleaning interactions, little is known about the diet of juveniles.

*Present address: Department of Zoology and Entomology, The University of Queensland, Brisbane, Queensland 4072, Australia. E-mail: a.grutter@mailbox.uq.edu.au

Interestingly, juvenile *Labroides dimidiatus* behave like adults when cleaning and begin cleaning immediately or very soon after settling on to the reef (Randall 1958, Potts 1973) and continue to do so throughout their lives. This raises the question of whether *L. dimidiatus* undergo an ontogenetic shift in diet like most other fish. Adult *L. dimidiatus* eat large numbers of parasites (1200 d⁻¹) and selectively feed on gnathiids (Grutter 1997a) of which they select the larger individuals (Grutter 1997b). Although some gut analyses of juvenile cleaner fish indicate they feed on parasites (Randall 1958), no detailed comparisons of the diet of juveniles and adults have been made. Information on what cleaner fish, particularly juveniles, eat is needed to understand the dramatic impact their predation has on parasites. Variation in the proportion of items obtained by removing items costly to the client, such as scales, with size of cleaner can provide information on how the relationship between cleaners and clients varies ontogenetically.

This study examined whether the diet composition and number of common items in the diet varied with the size of cleaners. To determine if the size of prey also varied with cleaner size, the most common parasite (gnathiids) in the diet was measured. The cross-sectional diameter of prey is likely the dimension that limits the fish's ability to fit the prey in its mouth (Wainwright & Richard 1995). Similarly, Hambright (1991) suggested that prey body depth is more useful than the traditional measure of prey length as a common measure for prey size selection. Hence, in addition to prey length, the width was also measured. To determine whether ontogenetic changes in the diet were due to constraints in mouth size, the 'throat width' of cleaners was measured.

MATERIALS AND METHODS

Labroides dimidiatus were collected for diet analysis (n = 40) in December 1991 from 5 sites and for 'throat width' measurements (n = 37) from 4 sites at Lizard Island (14° 38' S, 145° 24' E). Large cleaner fish (≥4.5 cm total length, TL) were collected with a 10 mm mesh barrier net and handnet; smaller individuals were collected with a handnet only. For diet analyses, *L. dimidiatus* were killed with a blow to the head and their guts fixed immediately underwater by injecting 20% formalin into the gut cavity. Whole fish were fixed 1 to 2 h later in 10% formalin in seawater. Fish for 'throat width' measurements were fixed in 70% ethanol.

Gut contents were quantified using a dissecting microscope at ×35 magnification. Food items were counted and categorized as gnathiid isopods, scales, parasitic copepods, and non-parasitic (most likely benthic) copepods following Grutter (1997a).

Apart from its length, the widest part of a gnathiid is its gut; when it is empty it is approximately as wide as its head but can expand up to almost 3 fold when engorged (see diagrams in Wägele 1987). The head and gut widths of 99 gnathiids were determined using a dissecting microscope at ×35; the length of gnathiids included mouth parts but no uropods. Gnathiids measured were fixed in 10% formalin and were from 23 specimens of the wrasse *Hemigymnus melapterus* collected from dawn to sunset at Lizard Island (Grutter 1999b). DNA studies indicate there are at least 2 species of gnathiids found on this fish species at Lizard Island (Grutter et al. in press). To determine if the size of gnathiids in the diet was restricted by the 'throat width' of cleaners, the internal distance between the dentary coronoid processes was measured, as this is likely to be one of the narrowest parts of the jaws (D. Bellwood pers. comm.).

Whether the proportion of gnathiids eaten by cleaners varied with size class of cleaners was tested with a 1-way analysis of variance (ANOVA); to satisfy the assumption of homogeneity of variance of the analysis, 1 outlier with 605 gnathiids was omitted and data were transformed by taking the square root of the percent of gnathiids of total diet-count (abundance + 50). The size classes tested were defined as small juveniles (<25 mm), medium juveniles (30 to 50 mm), and adults (>60 mm) (TL). As gnathiids dominated the data, whether the proportion of the remaining 3 categories (scales, parasitic copepods, and non-parasitic copepods) varied among size classes was tested separately using logistic regression; to avoid large numbers of zero values and to reduce the inter-fish variation, only fish with 2 or 3 categories were included. Post-hoc logistic regression analyses were then done to compare the diets 2 at a time; only fish which had the 2 categories being tested were used. Separate ANOVAs were used to test for differences in the log₁₀(number of gnathiids + 1) and the log₁₀(number of scales + 1) per size class of *Labroides dimidiatus*. χ^2 analysis was used to determine whether the size-frequency distribution of gnathiids among gnathiid size classes varied with the size class of cleaner fish. Relationships between log₁₀('throat width') and log₁₀(length of cleaner), log₁₀(gnathiid gut width) and gnathiid length, and log₁₀(gnathiid head width) and log₁₀(gnathiid length) were examined using separate simple linear regressions; the log₁₀ transformations were done to satisfy the assumption of linearity in the regressions.

RESULTS

The proportion of gnathiids in the diet did not vary among size classes of cleaner fish ($F = 0.185$, $df = 2, 35$,

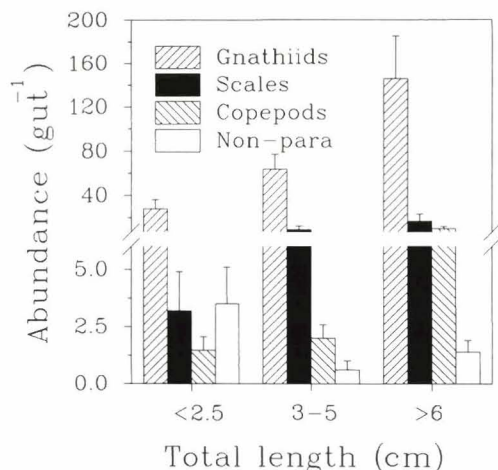


Fig. 1. Mean abundance of items per fish gut among 3 size classes of *Labroides dimidiatus*. Non-para: non-parasitic copepods

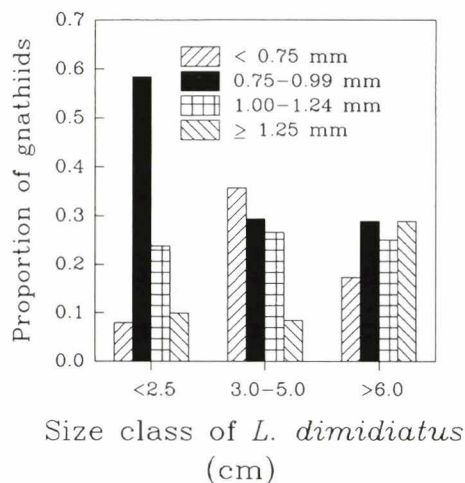


Fig. 2. Proportion of gnathiids per gnathiid size class among 3 size classes of *Labroides dimidiatus*

$p = 0.8322$) and was 71 to 77% of the total number of items in the diet (Fig. 1). In contrast, the relative abundance of the remaining categories in the diet (scales, copepods, and non-parasitic copepods) varied significantly among size classes of cleaners (Table 1). Post-hoc comparisons of 2 categories at a time were all significant (Diet and Diet \times Size, both $p < 0.05$); an examination of the analysis of maximum-likelihood estimates showed that small cleaners, <25 mm TL, were only 1.1 and 1.3 times more likely to eat scales and parasitic copepods respectively than non-parasitic copepods. In contrast, 30 to 50 mm TL cleaners were 11.7 times more likely to eat scales than non-parasitic copepods, but had similar likelihoods of eating parasitic copepods and non-parasitic copepods. The largest cleaners, >60 mm TL, were 12.3 times more likely to eat scales than non-parasitic copepods and 17.9 times more likely to eat parasitic copepods than non-parasitic copepods (Fig. 1).

The abundance of gnathiids in the gut of *Labroides dimidiatus* differed significantly among size classes of cleaners ($F = 11.71$, $df = 2, 37$, $p < 0.0001$); small cleaner fish had, on average, one-seventh the number of gnathiids that large cleaner fish had (Fig. 1). Similarly, the abundance of scales in the gut also differed

Table 1. Maximum-likelihood analysis of variance in the logistic regression analysis testing whether the relative abundance of scales, copepods, and non-parasitic copepods in the diet of cleaner fish varied among size classes of cleaner fish

Source	df	χ^2	p
Diet	2	129.27	<0.0001
Diet \times Size	4	83.16	<0.0001

significantly among size classes of cleaners ($F = 6.18$, $df = 2, 37$, $p = 0.0048$) with one-fourth the number of scales in the guts of small cleaners compared to large cleaner fish (Fig. 1).

The number of gnathiids per size class of gnathiid also differed significantly among size classes of *Labroides dimidiatus* ($\chi^2 = 74.5$, $df = 6$, $p < 0.0001$), with small cleaners having more small gnathiids compared to adult cleaners (Fig. 2).

The 'throat width' of cleaners increased linearly with the size of fish (Fig. 3). The gut and head width of gnathiids also increased linearly with the length of gnathiids (Fig. 4). Using simple linear regression the estimated 'throat width' of small juvenile cleaners, medium-sized juveniles, and adult cleaners was <0.80 ,

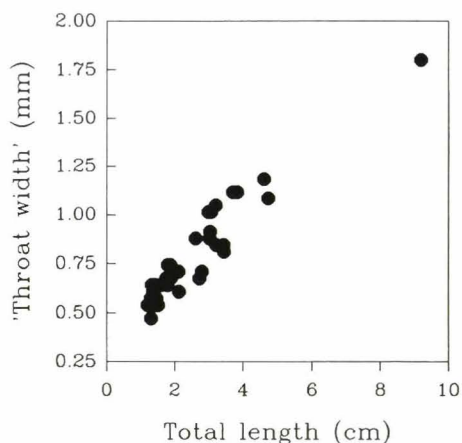


Fig. 3. 'Throat width' (internal distance between the dentary coronoid processes) compared to the total length of *Labroides dimidiatus*. $\text{Log}_{10}(\text{'throat width'}) \text{ (mm)} = -0.8980 + 0.5742 (\text{log}_{10}\text{TL})$, $r = 0.939$, $n = 37$ where TL is the total length of *L. dimidiatus* in mm

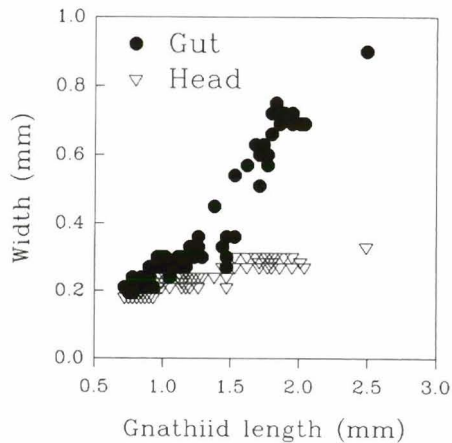


Fig. 4. Width of the head and guts of gnathiids from the wrasse *Hemigymnus melapterus* compared to the length of gnathiids. $\log_{10}(\text{gut width}) (\text{mm}) = -1.0292 + 0.4459(a)$, $r = 0.962$, $n = 99$; $\log_{10}(\text{head width}) (\text{mm}) = -0.6699 + 0.4927(\log_{10}a)$, $r = 0.902$, where a is the length of gnathiids in mm

0.90 to 1.20, and ≥ 1.33 mm respectively (Fig. 3). For gnathiids < 0.75 , 0.75 to 0.99, 1 to 1.24, and ≥ 1.25 mm in length, the estimated head widths were < 0.19 , 0.19 to 0.21, 0.21 to 0.24, and ≥ 0.24 mm respectively (Fig. 4). Thus small juvenile cleaners, which had a maximum 'throat width' of 0.80 mm, mostly ate gnathiids < 0.99 mm in length and 0.26 mm wide; medium-sized cleaners, which had a maximum 'throat width' of 1.20, mainly ate gnathiids < 1.24 mm in length and 0.33 mm wide; and adult cleaners, which had a 'throat width' ≥ 1.33 mm, ate the largest proportion of large gnathiids > 1.25 mm in length and ≥ 0.34 mm wide (Figs. 3 & 4). The width of 99% of the gnathiids sampled on *Hemigymnus melapterus* was < 0.80 mm, which is the same as the estimated throat width of 25 mm TL cleaners; the estimated throat width of smaller cleaners would thus be < 0.80 mm.

DISCUSSION

Labroides dimidiatus in all size classes mainly ate gnathiid isopod juveniles. Adult cleaners, however, ate twice as many gnathiids as medium-sized juveniles and 7 times more gnathiids than small juveniles. Hence, the impact of adult cleaners on gnathiids is likely to be much higher than that of juveniles. The rapid reduction of gnathiids by cleaner fish that Grutter (1999a) found on caged fish exposed to cleaners mainly involved juvenile *L. dimidiatus* (Grutter unpubl. data). This effect, therefore, would likely have been larger had only adult cleaners been involved.

Whether fewer parasites in the diet of juveniles is due to lower cleaning rates is unclear. Although the

cleaning intensity of a juvenile cleaner in Aldabra (Indian Ocean) was lower than that of adults, this observation was based on only 1 individual (Potts 1973). More likely, the number of gnathiids per gut is limited by the size of the gut.

Small juvenile cleaner fish had smaller gnathiids in their gut than medium-sized juveniles and adult cleaner fish. Thus any potential impact of small cleaner fish on gnathiid abundance will likely be mainly on small gnathiids. This was the case in the field experiment testing for an effect of cleaners on parasites (gnathiids) (Grutter 1999a) that mainly involved juvenile cleaners (Grutter in press); contrary to the prediction, based on the adult's size-selective predation of larger gnathiids, that cleaners would affect the size distribution of gnathiids the cleaners in the experiment had no effect on the size-frequency distribution of gnathiids (Grutter in press).

Diet changes are often associated with major habitat shifts (Bailey et al. 1975, Godin 1981). Juvenile cleaner fish are more frequently found on the reef slope (Potts 1973, Green 1996), while adults are abundant on the outer reef flat, reef crest, reef slope, and reef base (Green 1996). The microhabitat of juveniles also varies from that of adults with more juveniles found in sheltered crevices (Potts 1973) and under plate corals (A. L. Green unpubl. data). The variation raises the possibility that differences in gnathiid sizes among size classes of cleaners are due to differences in the client fish they service, as coral reef fish communities also vary greatly with habitat (Williams 1982, Russ 1984, Sale et al. 1984). Little is known, however, of the cleaning patterns of juvenile cleaners. At Aldabra, juvenile *Labroides dimidiatus* mainly clean the small resident populations of fish that live in the same habitat and rarely clean migrant species (Potts 1973). Randall (1958) noted that *Labroides* generally clean fish larger than themselves but that juveniles 'take care' of smaller fish. Most importantly, however, the size of gnathiids within a fish species varies greatly (Grutter unpubl. data; for sizes of fish and collection information see Grutter 1994). The size ranges of gnathiids on several fish species commonly cleaned by *L. dimidiatus* at Lizard Island are (Family names in parentheses): *Ctenochaetus striatus* (Acanthuridae), 0.66 to 2.20 mm; *Hemigymnus melapterus* (Labridae), 0.28 to 2.7 mm; *Thalassoma lunare* (Labridae), 0.54 to 2.34 mm; *Scolopsis bilineatus* (Nemipteridae), 0.60 to 1.63 mm; *Acanthochromis polyacanthus* (Pomacentridae), 0.66 to 1.20 mm; *Chlorurus sordidus* (Scaridae), 0.57 to 2.09 mm; and *Siganus doliatus* (Siganidae), 0.60 to 2.51 mm. Given such large variation within these species, it is unlikely that differences in the cleaner's diet are due to variation in gnathiid sizes among client species (and thus habitats). Finally, the size-frequency dis-

tribution of gnathiids on *H. melapterus* does not differ between the reef flat and reef slope at Heron Island (Grutter 1998).

The lack of many large gnathiids in the diet of small juvenile cleaners may be due to the small mouths of cleaners. The 'throat width' of very small juvenile cleaners was equal to or less than the width of the larger gnathiids; this may impose a constraint on the size of gnathiids they can swallow. It may also explain the lower number of scales in the diet of small cleaners, as scales were often larger than the 'throat width' of small cleaners. This is supported by other studies that have found that mouth size limits the maximum prey size that fish can eat (e.g. Schmitt & Holbrook 1984, Hambright 1991, Bremigan & Stein 1994).

In large cleaners, gnathiids in the diet were generally smaller than the 'throat size'. This is known in gape-limited predators which tend to consume prey sizes that are smaller than the maximum possible (Gillen et al. 1981, Luczkovich et al. 1995). This limitation may be due to factors such as handling time, which can increase with size of prey (Kislalioglu & Gibson 1976, Wainwright & Richard 1995). Optimal sizes, therefore, are intermediate prey sizes and always much less than the mouth diameter (Wainwright & Richard 1995). Alternatively, very large gnathiids may not be very abundant on the clients they feed on.

Usually, microcarnivorous fish preferentially eat large invertebrate prey (e.g. Brooks 1968, Werner & Hall 1974, Bartell 1982). Adult cleaner fish fall into this category and selectively feed on large gnathiids compared to the size of gnathiids found on hosts (Grutter 1997b). However, because small juvenile cleaners mainly fed on small gnathiids, which are common on client fish (Grutter 1997b), most likely the small juveniles are not as selective in their diet compared to adults.

Ontogenetic diet shifts are often explained as a reflection of the changing abilities of fish; essentially, as fish grow they become more proficient at handling larger prey which are more profitable (Werner 1974). Increasing prey size usually leads to taxonomic changes in the diet; however, for a single prey type the size often increases with predator size (Gladfelter & Johnson 1983, Wainwright 1991). This appears to be the case with cleaners, as they all ate gnathiids regardless of cleaner size while the size of gnathiids eaten increased with the size of cleaner.

When disregarding gnathiids, the diet of cleaners varied ontogenetically. Small juveniles ate similar amounts of fish scales, parasitic copepods, and non-parasitic copepods. However, compared to medium-sized juveniles and adult cleaners, they ate proportionally more non-parasitic copepods. This agrees with Pott's (1973, p 255) observation that juvenile cleaners

'spend a certain amount of time picking at the encrusting organisms found on the roofs of the crevices in which they live'. Clients prefer adult cleaners over juveniles (Mahon 1994); thus small juveniles may need to supplement their diet with non-client food items such as non-parasitic copepods. Ontogenetic variation in the diet has also been found in some other labrids (Jones 1984, Wainwright 1988, Green 1994, McIlwain & Jones 1997).

The removal of scales by cleaners is likely a cost to clients. Since both medium-sized and adult cleaners ate numerically more scales than small juveniles, clients likely incur more of a cost from large cleaners than small juveniles. However, this cost is possibly outweighed by the benefits of higher parasite removal by larger cleaners. Whether scales are intentionally eaten or accidentally removed when eating firmly attached parasites is unclear. To understand how cleaning interactions are maintained as a mutualism, more information is needed on how clients balance the benefits and costs of cleaning.

Acknowledgements. Many thanks to M. Johnson for his assistance in the field, the Lizard Island Research Station staff for field support, H. J. Choat for logistical support, and A. L. Green for providing the specimens for 'throat width' measurements. The study benefitted from discussions with D. Bellwood, H. J. Choat, and A. L. Green and was supported by internal funds from the Department of Marine Biology and Aquaculture, James Cook University. This is a contribution from Lizard Island Research Station, a facility of the Australian Museum.

LITERATURE CITED

- Bailey JE, Wing BL, Matson CR (1975) Zooplankton abundance and feeding habits of fry of pink salmon, *Onchorhynchus gorbuscha*, and chum salmon, *Onchorhynchus keta*, in Traitors Cove, Alaska, with speculations on the carrying capacity of the area. *Fish Bull (US)* 73: 846–861
- Bartell SM (1982) Influence of prey abundance on size-selective predation by bluegills. *Trans Am Fish Soc* 111:453–461
- Bremigan MT, Stein RA (1994) Gape-limited larval foraging and zooplankton size: implications for fish recruitment across systems. *Can J Fish Aquat Sci* 51:913–922
- Brooks JL (1968) The effects of prey size selection by lake planktivores. *Syst Zool* 17:272–291
- Feder HM (1966) Cleaning symbiosis in the marine environment. In: Henry SM (ed) *Symbiosis*, Vol 1. Academic Press, New York, p 327–380
- Gillen AL, Stein RA, Carline RF (1981) Predation by pellet-reared tiger muskellunge on minnows and bluegills in experimental systems. *Trans Am Fish Soc* 110:197–209
- Gladfelter WB, Johnson WS (1983) Feeding niche separation in a guild of tropical reef fishes (Holocentridae). *Ecology* 64:552–563
- Godin JGJ (1981) Daily patterns of feeding behavior, daily rations, and diets of juvenile pink salmon (*Onchorhynchus gorbuscha*) in two marine bays of British Columbia. *Can J Fish Aquat Sci* 38:10–15

- Green AL (1994) The early life history of labroid fishes at Lizard Island, Northern Great Barrier Reef. PhD Dissertation, James Cook University, Townsville
- Green AL (1996) Spatial, temporal and ontogenetic patterns of habitat use by coral reef fishes (Family Labridae). *Mar Ecol Prog Ser* 133:1–11
- Grutter AS (1994) Spatial and temporal variations of the ectoparasites of seven coral reef fish from Lizard Island and Heron Island, Australia. *Mar Ecol Prog Ser* 115:21–30
- Grutter AS (1997a) Spatio-temporal variation and feeding selectivity in the diet of the cleaner fish *Labroides dimidiatus*. *Copeia* 1997:346–355
- Grutter AS (1997b) Size-selective predation by the cleaner fish *Labroides dimidiatus*. *J Fish Biol* 50:1303–1308
- Grutter AS (1998) Habitat-related differences in the abundance of parasites from the coral reef fish: an indication of the movement patterns of *Hemigymnus melapterus*. *J Fish Biol* 53:49–57
- Grutter AS (1999a) Cleaner fish really do clean. *Nature* 398: 672–673
- Grutter AS (1999b) Infestation dynamics of parasitic gnathiid isopod juveniles on the coral reef fish *Hemigymnus melapterus* (Labridae). *Mar Biol* 135(3):545–552
- Grutter AS, Morgan JAT, Adlard RD (in press) Characterising parasitic gnathiid isopod species and matching life stages with ribosomal DNA ITS2 sequences. *Mar Biol*
- Hambright KD (1991) Experimental analysis of prey selection by largemouth bass: role of predator mouth width and prey body depth. *Trans Am Fish Soc* 120:500–508
- Jones GP (1984) The influence of habitat and behavioural interactions on the local distribution of the wrasse, *Pseudolabrus celidotus*. *Environ Biol Fishes* 10:43–58
- Kislalioglu M, Gibson RN (1976) Some factors governing prey selection by the 15-spined stickleback, *Spinachia spinachia* (L.). *J Exp Mar Biol Ecol* 25:159–169
- Losey GS (1987) Cleaning symbiosis. *Symbiosis* 4:229–258
- Luczkovich JJ, Norton SF, Grant Gilmore R Jr (1995) The influence of oral anatomy on prey selection during the ontogeny of two percoid fishes, *Lagodon rhomboides* and *Centropomus undecimalis*. *Environ Biol Fishes* 44: 79–95
- Mahon JL (1994) Advantage of flexible juvenile coloration in two species of *Labroides* (Pisces: Labridae). *Copeia* 1991:520–524
- McIlwain JL, Jones GP (1997) Prey selection by an obligate coral-feeding wrasse and its response to small-scale disturbance. *Mar Ecol Prog Ser* 155:189–198
- Potts GW (1973) The ethology of *Labroides dimidiatus* (Cuv. & Val.) (Labridae, Pisces) on Aldabra. *Anim Behav* 21: 250–291
- Poulin R, Grutter AS (1996) Cleaning symbiosis: proximate and adaptive explanations. *Bioscience* 46(7):512–517
- Randall JE (1958) A review of the labrid fish genus, *Labroides*, with descriptions of two new species and notes on ecology. *Pac Sci* 12:327–347
- Russ G (1984) Distribution and abundance of herbivorous grazing fishes in the central Great Barrier Reef. I. Levels of variability across the entire continental shelf. *Mar Ecol Prog Ser* 20:23–34
- Sale PF, Doherty PJ, Eckert GJ, Douglas WA, Ferrell DJ (1984) Large scale spatial and temporal variation in recruitment to fish populations on coral reefs. *Oecologia* 64: 191–198
- Schmitt RJ, Holbrook SJ (1984) Gape-limitation, foraging tactics and prey size selectivity of two microcarnivorous species of fish. *Oecologia* 63:6–12
- Wägele JW (1987) Description of the postembryonal stages of the antarctic fish parasite *Gnathia calva* Vanöffen (Crustacea: Isopoda) and synonymy with *Heterognathia* Amar & Roman. *Polar Biol* 7:77–92
- Wainwright PC (1988) Morphology and ecology: functional basis of feeding constraints in caribbean labrid fishes. *Ecology* 69:635–645
- Wainwright PC (1991) Ecomorphology: experimental functional anatomy for ecological problems. *Am Zool* 31: 680–683
- Wainwright PC, Richard BA (1995) Predicting patterns of prey use from morphology of fishes. *Environ Biol Fishes* 44: 97–113
- Werner EE (1974) The fish size, prey size, handling time relation in several sunfishes and some implications. *J Fish Res Board Can* 31:1531–1536
- Werner EE, Hall DJ (1974) Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55:1042–1052
- Williams DMcB (1982) Patterns in the distribution of fish communities across the central Great Barrier Reef. *Coral Reefs* 1:35–43

Editorial responsibility: Charles Birkeland (Contributing Editor), Mangilao, Guam

Submitted: May 5, 1999; Accepted: November 2, 1999
Proofs received from author(s): April 13, 2000