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## Predation and its Influence on the Condition of a Newly Settled Tropical Demersal Fish

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**Abstract.** The effects of predation by a common tropical piscivore on levels of variability in size and body composition of a demersal fish at settlement were examined in a series of laboratory experiments. Wild-caught, newly metamorphosed goatfish (*Upeneus tragula*) were placed in large tanks and subjected to predation by lizardfish (*Synodus variegatus*). Three trials failed to show an influence of predation on the size distribution of the newly settled prey. In a second experiment, mid-larval-phase goatfish were subjected to one of two feeding regimes; this resulted in two groups of metamorphs that differed markedly in biochemical composition (i.e. total lipid levels). Twenty fish from each treatment were randomly chosen, under the constraint of a similar mean size, and subjected to predation. Susceptibility of newly metamorphosed fish to predation by the lizardfish was independent of their initial biochemical composition. These results suggest that predation by this common tropical reef fish predator may be non-selective with respect to both size and body composition of *U. tragula*. Consequently, the high variability found in these body attributes at settlement may extend its influence into the juvenile population.

*Extra keywords:* settlement, metamorphosis, reef fish, size selectivity.

### Introduction

Predation has been argued to be one of the main mechanisms controlling the replenishment of temperate fisheries (Bailey and Houde 1989), and more recently, of tropical reef fish populations (Hixon 1991; Caley 1993; Hixon and Beets 1993). Despite this, there is a paucity of information in both systems showing how predation influences the recruitment of juveniles into an adult population of demersal fishes. This is surprising since predation within the first 7 days of settlement may remove 30% to 78% of the newly settled fishes to a coral reef (Doherty and Sale 1985; Victor 1986; Booth 1991), and between 73% and 85% of newly settled flounders from a temperate sediment flat (van der Veer and Bergman 1987; Tanaka *et al.* 1989).

Studies of the mechanics of fish predation have focused on early larval stages of temperate fisheries species at, or immediately following, the completion of yolk sac absorption. Results suggest that the interaction of predation with the size and nutritional status of larval fishes is an important component in the determination of cohort strength (Pepin *et al.* 1992; Rice *et al.* 1993). Predation on the early larval stages is often dependent on size or age, although it does not necessarily favour those fishes that are larger, older or in better nutritional condition (e.g. Neilson *et al.* 1986; Litvak and Leggett 1992; Pepin *et al.* 1992; Mesa *et al.* 1994). However, rapid development of the sensory system

and musculature, and the evolution of complex behavioural patterns during the larval phase, limit extension of the conclusions from these studies to later life-history stages.

Predation during the settlement transition (*sensu* Kaufman *et al.* 1992) has the potential to act as an important selective agent influencing the range of body attributes of the juvenile population that are important to survival. The importance of selective forces to subsequent population dynamics will be accentuated when the attributes targeted exhibit high levels of variability and are linked to the ability of the juvenile to survive to adulthood.

Recently, attention has turned to the levels of variability in the size, growth and nutritional condition of tropical reef fishes at metamorphosis and settlement. McCormick and Molony (1993) found that there were high levels of variability among individuals in nine commonly used measures of body condition and performance in the goatfish *Upeneus tragula* at metamorphosis. Similarly, Kerrigan (1996) showed that two damselfish species varied widely in their nutritional condition at settlement both between cohorts and year-classes. These high levels of variability in growth characteristics support the results of similar studies of cultured temperate flatfish populations (e.g. Chambers and Leggett 1987). Assessment of how selective agents, such as predation, influence these levels of individual variability is crucial to understanding the mechanisms that regulate the abundance of the older demersal life-stages.

To date, only one experimental study has assessed the selectivity of predation for characteristics important to the survival of settled stages. Bertram and Leggett (1994) examined the vulnerability of newly metamorphosed winter flounder, *Pleuronectes americanus*, to predation by the shrimp *Crangon septemspinosa*. They found that neither size of fish at a particular age nor age for a restricted size influenced the vulnerability of individual fish to predation. The present study is the first comparable attempt to assess experimentally whether variation in body attributes of a tropical reef fish at settlement affects the probability of being preyed on.

This study examined whether the body size or biochemical condition of newly metamorphosed and settled individuals of a goatfish, *Upeneus tragula* (Mullidae), influences the risk of predation. Variable age at metamorphosis was not factored into the design of the experiment since, in this species, age at metamorphosis is generally not correlated with fish size (McCormick 1994) or body condition (McCormick and Molony 1993). This experimental study used newly metamorphosed, wild-caught fish, to address two aspects of the conventional size-based (i.e. 'bigger is better', Miller *et al.* 1988) theories of survival. First, we hypothesized that larger prey will be more effective at escaping a natural predator. Secondly, we hypothesized that fish in better condition will be less vulnerable to predation. Condition of prey may influence selection of prey by a predator by either (a) enhancing the ability of prey in better condition to escape a predator (passive selection), or (b) predators choosing prey of lower condition (active selection).

## Materials and Methods

*Upeneus tragula* settles into shallow seagrass beds and into deeper seagrass beds containing *Halimeda* sp. on the Great Barrier Reef (GBR), Australia. Within days of settling, fish form schools with other newly settled fishes from a number of families, including lutjanids, lethrinids and nemipterids. These schools can contain tens of individuals (McCormick, personal observation).

Lizardfish (Synodontidae) are a common component of the demersal fish assemblage in sand and sand-rubble habitats of shallow tropical and subtropical seas (Thresher *et al.* 1986). Evidence from dietary and behavioural studies suggests that they are voracious piscivores (Hobson 1974; Sweatman 1984). The lizardfish *Synodus variegatus* is a common component of patchy seagrass beds around coral reefs and is thought to be one of the most numerically important predators on newly settled reef fishes on the GBR (Sweatman 1984). In a behavioural study at Lizard Island, GBR, Sweatman (1984) reported that a lizardfish attacks other fishes every 35 min on average, and consumes about 650 fishes per year. In a mixed sand-and-seagrass habitat, lizardfish bury themselves in the sand with only the top of their head exposed and await prey that stray close enough to strike (personal observation). During our observations of seagrass habitats, we have seen *S. variegatus* capture *U. tragula*.

Samples of larval *U. tragula* were collected 5 km north of Eagle Island (14°42'S, 145°23'E) on the northern GBR during January 1991. Floating plastic rafts (1 × 1 m) were used to aggregate larvae that were caught with a 14 × 2 m plankton-mesh purse-seine (see McCormick and Milicich 1993 for method details). The larvae were dip-netted from the purse-seine,

transferred to black plastic tanks of aerated sea water, transported to the Lizard Island research station aquarium system and placed in tanks receiving a constant feed of fresh sea water. Handling mortality was usually <10% and confined to the earlier larval stages that were most susceptible to capture-related stress.

### Experiment 1: Does Body Size Influence Predation Risk?

After capture, some of the *U. tragula* larvae quickly metamorphosed and settled to the bottom of the holding tanks; 50 newly settled fish of the broadest possible size range were introduced into a 102-L tank with sand and seagrass. Seagrass was organized into two square patches separated by a narrow sand corridor and occupying one-third of the area of the bottom of the tank. The standard length of each goatfish was measured with calipers as it was transferred into the experimental tank, by placing it into a small plastic bag partially filled with water; this allowed restraint of the fish without scale damage. A comparison of the standard length measurements from live fish using this method with measurements made after the fish had been killed by cold shock showed that measurements of live fish were precise (mean 0.4% underestimate, s.e. 0.27,  $n = 10$ ). After handling, fish were left 12–18 h to acclimate to the conditions of the experimental tank, and then two freshly caught predators (*S. variegatus*) were introduced (size range: 130–143 mm SL). Different lizardfish were used for each trial. Goatfish were fed 36- to 48-h-old nauplii of *Artemia* sp. (*Artemia* 90 brand) throughout the experiment. The lizardfish were removed from the tanks when approximately half of the prey had disappeared. The remaining goatfish were killed by cold shock and remeasured.

A control for growth during each trial was run concurrently by treating 30 goatfish in exactly the same way but without predators. Fish were remeasured when the associated predator trial was terminated. The mean increase in standard length of the control fish was subtracted from the lengths of the survivors in the predation trial, which enabled comparisons of the size distributions before and after the predation episode. The experiment was repeated three times.

To check the assumption that variable age of the metamorphs did not confound this experiment, the relationship between fish size and age was examined for a random sample of 10 metamorphs of a size range similar to that used in the experiment. Age was determined by daily increment counts on the sagittal otoliths (McCormick 1994). No relationship between age and fish size was found ( $r = -0.042$ ), supporting the results of the detailed study of McCormick (1994) for the same species.

### Experiment 2: Does Prey Condition Influence Predation Risk?

Pelagic *U. tragula* specimens were collected (as above) and fish of 20–23 mm SL were placed randomly into six 60-L tanks at densities of about 50 per tank. Tanks were stocked with *Artemia* sp. nauplii at two densities: fed *ad libitum* (1600 nauplii L<sup>-1</sup>); and fed 2/5 *ad libitum* (640 nauplii L<sup>-1</sup>). These densities were restored four times daily. To quantify the initial condition of the newly settled fish at the start of the experiments, 10 randomly chosen newly settled fish were removed from each feeding treatment for biochemical analysis. Total lipid content was used as a measure of body condition and was determined using chloroform/methanol extraction (Mann and Gallagher 1985).

To determine whether the results of the experiment were confounded by the influence of feeding history on muscle development (as shown to occur by McCormick and Molony 1992), burst speeds were obtained for a random sample of 15 newly settled fish from each of the two feeding treatments (according to the protocol of McCormick and Molony 1993). In brief, this involved placing a newly metamorphosed fish in a long narrow tank and after an acclimation period, tapping the base of the tail with a perspex probe, while video-taping the proceedings. The progression of the head was traced between frames and the maximum burst speed determined as a function of the frame speed and distance travelled between frames.

When 20 fish had settled over all three rearing tanks within a feeding treatment, they were pooled into a single trial. Three trials of the experiment were run. In two of the predation trials, newly settled goatfish fed *ad libitum* were marked by immersion for 12 h in aerated tetracycline hydrochloride (250 mg L<sup>-1</sup>). In the remaining trial, fish fed 2/5 *ad libitum* were marked with tetracycline. This prevented confounding of the experiment by the potential influence of tetracycline on the susceptibility of the fish to predation. Twenty fish from each treatment were placed into a tank with sand and seagrass patches. Fish were of a similar average size from each treatment (mean over three trials, *ad lib.*: 27.6 mm SL; 2/5 *ad lib.*: 27.03 mm SL). Fish were given 12–18 h to acclimate before the introduction of two freshly caught lizardfish. The experiment was concluded when half of the fish had been eaten. Remaining fish were killed by cold shock, weighed and measured. Their otoliths were removed and examined under u.v. light to detect the fluorescence characteristic of a fish treated with tetracycline. In this way fish could be assigned to either of the two initial feeding treatments. Variable age and size of metamorphs were not accounted for, apart from the random selection of individual fish for the two treatments, since McCormick and Molony (1993) had found no relationship between size, age and body composition of newly metamorphosed *U. tragula*.

#### Statistical Analyses

The influence of predation on fish size was examined using a  $\chi^2$  goodness-of-fit test. Results of the three trials were pooled to improve sensitivity of the test, which evaluated the null hypothesis that the size distribution of *Upeneus tragula* after predation was the same as that prior to the introduction of predators. Some size classes were pooled to meet test assumptions. The sensitivity of the test is summarized with a power analysis and the probability of failing to detect a difference in the distributions given that a difference exists (i.e. Type II error) is given.

## Results

### Does Body Size Influence Predation Risk?

The consumption rate of *Upeneus tragula* by *Synodus variegatus* was approximately 1.9 prey predator<sup>-1</sup> (trial 1, 1.7; trial 2, 2.25; trial 3, 1.8), similar to the natural average consumption rate observed by Sweatman (1984) of 1.8 prey day<sup>-1</sup>. In three trials, the size distribution of the prey was not altered by predation (Fig. 1, pooled trials:  $\chi^2_{11} = 3.962$ ,  $P > 0.95$ ). The sensitivity of this test, or power, was relatively low (power 0.36 at  $\alpha = 0.05$ ), with a 64% chance of failing to detect a difference in the distributions had a real difference existed. However, the difference between sample distributions before and after predation was small (effect size 0.32, Cohen 1988). Given the magnitude of this difference, 300 fish would be required in the distribution at the end of the predation trials for a real difference to be detected with a 95% certainty. In only one of the three trials were the largest or smallest individuals removed by predation. This suggests that predation by lizardfish does not reduce the size range of the prey species and that predation was random with respect to prey size.

### Does Prey Condition Influence Predation Risk?

Newly metamorphosed fish from the two feeding treatments were significantly different in total lipid content

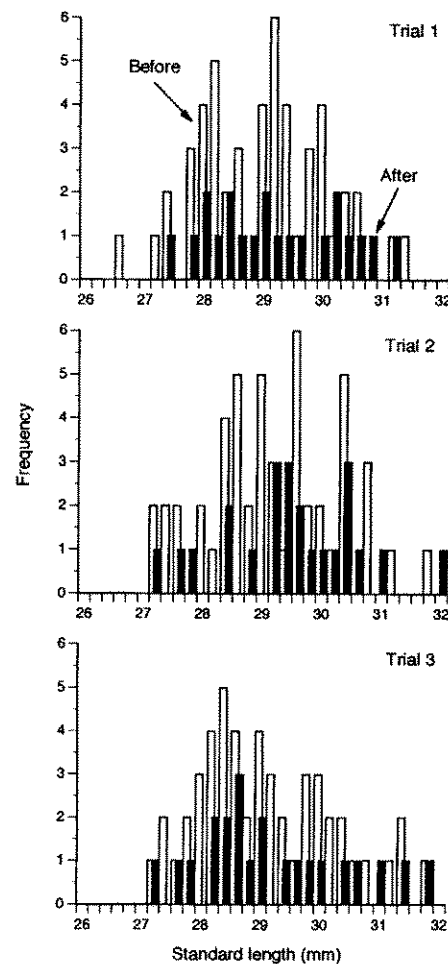


Fig. 1. Results of three independent trials of the effects of predation by two lizardfish (*Synodus variegatus*) per trial on the size distribution of newly settled goatfish (*Upeneus tragula*). Size distributions of *U. tragula* prior to predation (plain bars, corrected for growth) are compared with the distributions after approximately half the fish had been eaten (solid bars).

(means: fed *ad libitum*, 37.2 mg g<sup>-1</sup> wet wt; fed 2/5 *ad libitum*, 18.7 mg g<sup>-1</sup> wet wt;  $F_{1,18} = 42.12$ ,  $P < 0.0001$ ). Burst speed of a random sample of newly metamorphosed fish did not differ between treatments, averaging 60.5 cm s<sup>-1</sup> for the fed *ad lib.* treatment and 62.9 cm s<sup>-1</sup> for the fed 2/5 *ad lib.* treatment ( $F_{1,28} = 0.30$ ,  $P = 0.59$ ).

In three trials, the proportion of the surviving fish that had started their settled life with high lipid levels (i.e. fed *ad libitum* treatment) was 50% (9 from 18 survivors), 47.4% (11 from 23 survivors) and 52.2% (12 from 23 survivors). This suggests that susceptibility of the prey to predation is not influenced by their biochemical condition as measured by total lipid content.

### Discussion

Predation by lizardfish had no detectable effect on the range of size or condition of *U. tragula*. This contrasts with the results of a field study of the small Hawaiian damselfish *Dascyllus albisella*, in which juvenile size did influence mortality during one year of a 2-year study (Booth 1995). These results are likely to be a function of predator and prey behaviour. Lizardfish in a seagrass habitat are ambush predators that either bury themselves in the sand or wait motionless on a piece of rubble, camouflaged by their disruptive colouration. Given the loose schooling habit of *U. tragula*, it is not surprising that predation by lizardfish had no effect on its range of size or condition, since prey taken are those that by chance stray too close. This contrasts with small damselfishes, such as *Dascyllus*, that have tight social groups where strong size-related dominance hierarchies may allow subordinates less favourable access to refugia from predation.

Predation on *U. tragula* would also be independent of size if the probability of prey survival had been directly related to prey burst speed. This study found that burst speed was not influenced by the same factors as body composition (e.g. feeding history). Likewise, McCormick and Molony (1993) showed that burst speed of newly settled *U. tragula* was not related to fish size or any of eight other commonly used indicators of body condition (age, body depth, lipid content, carbohydrate content, protein content, water content, growth, or Fulton's K). This lack of correlation among measures of performance and condition, and the high levels of variability found in all these measures, suggest that general statements regarding the selectivity of predation must be made cautiously.

Researchers generally assume that indices of condition, such as size and nutritional state, affect the ability of a fish to survive in its environment. However, it is likely that the relationship between an index of condition and survival potential will vary among habitats and times. For instance, Shulman (1985), in an experimental study, found that the risk of predation for juvenile reef fishes decreased with distance away from the reef front. Under these circumstances, a particular level of stamina and burst speed for a prey species that may be adequate in the inshore seagrass beds may be insufficient to avoid the higher predation pressure at the reef front.

The only other experimental study to examine the selectivity of a predator for newly metamorphosed fishes, where a choice of prey was given (i.e. Bertram and Leggett 1994), also concluded that predation risk was independent of prey size. If the experiments are indicative of the true nature of predation during this early post-settlement life-stage, then this has important ramifications for the dynamics of recruitment. If predation operates randomly, then the levels of variability in growth and behavioural attributes of

newly settled fish can potentially be accentuated by post-settlement processes such as competition. This variability is likely to be most rapidly accentuated where recruits form small social groups, as is the case for many of the pomacentrids (e.g. *Dascyllus aruanus*; Forrester 1990); in these conditions it is of interest to know whether it is the individuals that are in 'best' condition (measured by whichever index is most appropriate) when they settle that subsequently dominate others. If this is the case then the pelagic life history has a strong influence on events in the settled population.

An alternative hypothesis is that predation on newly settled reef fish acts as a bottleneck on the variability in an aspect of body condition other than size or body lipid content. Convention suggests that those individuals that are small and in lowest body condition may be consumed in preference to larger more able settlers (e.g. Anderson 1988; Margulies 1990). However, given the poor correlations among a range of different estimates of body condition (McCormick and Molony 1993), if predation is targeted on one particular trait (e.g. body length), then it will not reduce the variability in other aspects of body condition (e.g. growth rates or biochemical composition). Under this scenario, the influence of predation on the structure of a recruit cohort, mediated through a particular aspect of quality, will depend on the combination of features of quality that are most important for success in a particular situation. For example, predation with respect to fish size will have a major effect on a population of clown fish, *Amphiprion clarkii*, in which a size-structured hierarchy governs growth and reproductive status (Moyer 1980; Hattori 1991). Predation with respect to condition factor may, however, have little influence on the status of individuals in the social group.

In addressing hypotheses concerning the effects of predation on newly settled individuals, it is desirable, although seldom possible, to use wild-caught metamorphosed fishes, or those caught close to metamorphosis. Most studies have used laboratory-reared fishes, which are naive to predators and consequently may be more vulnerable than wild-caught fish that have survived the rigours of the pelagic phase. Reared fishes are likely to have less well developed musculature and lower burst speeds than wild fish at a similar developmental stage (McCormick and Molony 1992, 1993; Gibson and Johnston 1995). The use of wild-caught fish, as in the present study, maximizes the applicability of the results to the field situation, within the confines of the artificiality of the experimental regime.

It is of interest to know whether events that occur during the pelagic life history of a demersal fish, which influence the size and body condition at settlement, influence survival probabilities of juvenile and adult life stages. Laboratory studies, such as those described here, will benefit from

comparable field experiments that track the fate of individuals of known growth history from settlement. The recent advances in microtag technology (e.g. Buckley *et al.* 1994; Beukers *et al.* 1995) make large-scale tagging of newly settled fish possible. This will enable the characteristics of individual fish (e.g. size and condition factors) to be linked to the probability of loss (e.g. through predation or emigration) from the local population. For reef fishes, there is a long way to go before we can understand how predation influences the patterns of variability in juvenile quality, and how these may interact with growth-compensatory mechanisms to influence patterns of abundance in reef fish populations.

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### References

- Anderson, J. T. (1988). A review of size dependent survival during pre-recruit stages of fishes in relation to recruitment. *Journal of Northwest Atlantic Fisheries Science* **8**, 55–66.
- Bailey, K. M., and Houde, E. D. (1989). Predation on eggs and larvae of marine fishes and the recruitment problem. *Advances in Marine Biology* **26**, 1–83.
- Bertram, D. F., and Leggett, W. C. (1994). Predation risk during the early life history periods of fishes: separating the effects of size and age. *Marine Ecology Progress Series* **109**, 105–14.
- Beukers, J. S., Jones, G. P., and Buckley, R. M. (1995). Use of implant micro-tags for studies of populations of small reef fish. *Marine Ecology Progress Series* **125**, 61–6.
- Booth, D. J. (1991). The effects of sampling frequency on estimates of recruitment of the domino damselfish *Dascyllus albisella* Gill. *Journal of Experimental Marine Biology and Ecology* **145**, 149–59.
- Booth, D. J. (1995). Juvenile groups in a coral-reef damselfish: density-dependent effects on individual fitness and population demography. *Ecology* **76**, 91–106.
- Buckley, R. M., West, J. E., and Doty, D. C. (1994). Internal micro-tag systems for marking juvenile reef fishes. *Bulletin of Marine Science* **55**, 848–57.
- Caley, M. J. (1993). Predation, recruitment and the dynamics of communities of coral-reef fishes. *Marine Biology* **117**, 33–43.
- Chambers, R. C., and Leggett, W. C. (1987). Size and age at metamorphosis in marine fishes: an analysis of laboratory-reared winter flounder (*Pseudopleuronectes americanus*) with a review of variation in other species. *Canadian Journal of Fisheries and Aquatic Sciences* **44**, 1936–47.
- Cohen, J. (1988). 'Statistical Power Analysis for the Behavioral Sciences.' 2nd Edn. (Lawrence Erlbaum Publishers: New Jersey.) 567 pp.
- Doherty, P. J., and Sale, P. F. (1985). Predation on juvenile coral reef fishes: an exclusion experiment. *Coral Reefs* **4**, 225–34.
- Forrester, G. E. (1990). Factors influencing the juvenile demography of a coral reef fish. *Ecology* **71**, 1666–81.
- Gibson, S., and Johnston, I. A. (1995). Scaling relationships, individual variation and the influence of temperature on maximum swimming speed in early settled stages of the turbot *Scophthalmus maximus*. *Marine Biology* **121**, 401–8.
- Hattori, A. (1991). Socially controlled growth and size dependent sex change in the anemonefish, *Amphiprion clarkii*, in temperate waters of Japan. *Environmental Biology of Fishes* **31**, 139–55.
- Hixon, M. A. (1991). Predation as a process structuring coral reef fish communities. In 'The Ecology of Fishes on Coral Reefs'. (Ed. P. F. Sale.) pp. 475–500. (Academic Press: San Diego.)
- Hixon, M. A., and Beets, J. P. (1993). Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* **63**, 77–101.
- Hobson, E. S. (1974). Feeding relationships of teleostean fishes on coral reefs in Kona, Hawaii. *Fisheries Bulletin* **72**, 915–1031.
- Kaufman, L., Ebersole, J., Beets, J., and McIvor, C. C. (1992). A key phase in the recruitment dynamics of coral reef fishes: post-settlement transition. *Environmental Biology of Fishes* **34**, 109–18.
- Kerrigan, B. A. (1996). Temporal patterns in size and condition at settlement in two tropical reef fishes (Pomacentridae: *Pomacentrus amboinensis* and *P. nagasakiensis*). *Marine Ecology Progress Series* (in press).
- Litvak, M. K., and Leggett, W. C. (1992). Age and size-selective predation on larval fishes—the bigger-is-better hypothesis revisited. *Marine Ecology Progress Series* **81**, 13–24.
- Mann, K., and Gallagher, B. M. (1985). Physiological and biochemical energetics of larvae of *Teredo navalis* L. and *Bankia gouldi* (Bartsch) (Bivalvia: Teredinidae). *Journal of Experimental Marine Biology and Ecology* **85**, 211–28.
- Margulies, D. (1990). Vulnerability of larval white perch, *Morone americana*, to fish predation. *Environmental Biology of Fishes* **27**, 187–200.
- McCormick, M. I. (1994). Variability in age and size at settlement of the tropical goatfish *Upeneus tragula* (Mullidae) in the Great Barrier Reef lagoon. *Marine Ecology Progress Series* **103**, 1–15.
- McCormick, M. I., and Milicich, M. J. (1993). Late pelagic-stage goatfishes: distribution patterns and inferences on schooling behaviour. *Journal of Experimental Marine Biology and Ecology* **174**, 15–42.
- McCormick, M. I., and Molony, B. W. (1992). Effects of feeding history on the growth characteristics of a reef fish at settlement. *Marine Biology* **114**, 165–73.
- McCormick, M. I., and Molony, B. W. (1993). Quality of the reef fish *Upeneus tragula* (Mullidae) at settlement: is size a good indicator of condition? *Marine Ecology Progress Series* **98**, 45–54.
- Mesa, M. G., Poe, T. P., Gadomski, D. M., and Petersen, J. H. (1994). Are all prey created equal? A review and synthesis of differential predation on prey in substandard condition. *Journal of Fish Biology* **45**, 81–96.
- Miller, T. J., Crowder, L. B., Rice, J. A., and Marschall, E. A. (1988). Larval size and recruitment mechanisms in fishes: toward a conceptual framework. *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 1657–70.
- Moyer, J. T. (1980). Influence of temperate waters on the behaviour of the tropical anemonefish *Amphiprion clarkii* at Miyake-Jima, Japan. *Bulletin of Marine Science* **30**, 261–72.
- Neilson, J. D., Perry, R. I., Valerio, P., and Waiwood, K. G. (1986). Condition of Atlantic cod *Gadus morhua* larvae after the transition to exogenous feeding: morphometrics, buoyancy and predator avoidance. *Marine Ecology Progress Series* **32**, 229–35.
- Pepin, P., Shears, T. H., and De Lafontaine, Y. (1992). Significance of body size to the interaction between a larval fish (*Mallotus villosus*) and a vertebrate predator (*Gasterosteus aculeatus*). *Marine Ecology Progress Series* **81**, 1–12.

- Rice, J. A., Miller, T. J., Rose, K. A., Crowder, L. B., Marschall, E. A., Trebitz, A. S., and DeAngelis, D. L. (1993). Growth rate variation and larval survival: inferences from an individual-based size-dependent predation model. *Canadian Journal of Fisheries and Aquatic Sciences* **50**, 133–42.
- Shulman, M. J. (1985). Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66**, 1056–66.
- Sweatman, H. P. A. (1984). A field study of the predatory behaviour and feeding rate of a piscivorous coral reef fish, the lizardfish *Synodus englemani*. *Copeia* **1984**, 187–94.
- Tanaka, M., Goto, T., Tomiyama, M., and Sudo, H. (1989). Immigration, settlement and mortality of flounder (*Paralichthys olivaceus*) larvae and juveniles in a nursery ground, Shijiki Bay, Japan. *Netherlands Journal of Sea Research* **24**, 57–67.
- Thresher, R. E., Sainsbury, K. J., Gunn, J. S., and Whitelaw, A. W. (1986). Life history strategies and recent changes in population structure in the lizardfish genus, *Saurida*, on the Australian Northwest Shelf. *Copeia* **1986**, 876–85.
- van der Veer, H. W., and Bergman, M. J. N. (1987). Predation by crustaceans on a newly settled 0-group plaice *Pleuronectes platessa* population in the western Wadden Sea. *Marine Ecology Progress Series* **35**, 203–15.
- Victor, B. C. (1986). Larval settlement and juvenile mortality in a recruitment-limited coral reef fish population. *Ecological Monographs* **56**, 145–60.

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