Role of habitat complexity in mediating predation by the gray damselfish *Abudefduf sordidus* on epiphytal amphipods

Anthony R. Russo*

Florida Institute of Technology, Department of Oceanography and Ocean Engineering, Melbourne, Florida 32901, USA

ABSTRACT: In laboratory experiments with artificial substrata, Hawaiian epiphytal amphipods did not select substrata for their complexity. Increased substrata complexity did mediate predation by the Hawaiian damselfish *Abudefduf sordidus*. The data also suggest that prey amphipod motion elicits predator fish strikes. These results corroborate recent studies which directly relate habitat complexity with increased prey survival from predation and contributes additional information on the mechanism of prey selection by predators.

INTRODUCTION

Predation is considered a structuring force in animal communities (Menge & Sutherland 1976, Glasser 1979, Nelson 1981). Local animal species diversity is related to the number of predators in a community and to their efficiency in preventing single species from monopolizing an important limiting resource (Paine 1966, Ware 1972). The abundance and diversity of epifauna living on marine macrophytes is affected by predator efficiency (Nelson 1979, 1981, Russ 1980) which is a function of the complexity of macrophyte substrata (Crowder and Cooper 1982, Stoner 1982). Heck & Wetstone (1977) suggested that decapods are afforded refuge from predators by increasing plant biomass.

That fish capture prey less efficiently in more complex environments has been observed by many workers (Nelson 1979, Virnstein 1979, Coen et al. 1981, Stoner 1982). For example, the complexity of artificial macrophytes enhanced the species richness and abundance of pond macrofauna and these survived predation by bluegill sunfish better than invertebrates in uncovered areas (Gillinsky 1984). However, for such invertebrates as amphipod crustaceans, different macrophyte species vary in their value as refugia depending on their structural complexities (Edgar 1983). This

may be a function of predator behavior since the foraging behavior of pinfish *Lagodon rhomboides* has been shown to be a complex function of predator-prey interactions and macrophyte complexity (Stoner 1982, Main 1983). Additionally, Kulczycki et al. (1981) speculated that drift algae biomass increased macrofaunal survival from predators while Nelson (1979) concluded that habitat complexity played an important role in the predatory effectiveness of both pinfish *L. rhomboides* and shrimp *Paleomonetes* sp. Increased microhabitat complexity also reduced the predatory effectiveness of the shrimp *Penaeus* sp. on seagrass fauna (Leber 1983).

Mechanisms involved in prey selection by predatory fish have been the focus of several studies in the marine environment (Nelson 1979, 1981, Main 1983, Clements & Livingston 1984). Main (1985) concluded that predator choice was primarily determined by prey size and suggested that the choice was also determined by prey motion, while Clements & Livingston (1984) suggested that prey pigmentation directly affected the choice of prey by the fringed filefish *Monacanthus ciliatus*.

In this study artificial substrata were used in laboratory experiments to test the following hypotheses: (1) that, in the absence of predators, amphipods select artificial substrata based on their complexity; (2) that amphipod survivorship from predation is greater on more complex substrata; and (3) that prey choice, by a specific predatory fish, is related to prey motion.

* Present address: Science Division, Leeward Community College, University of Hawaii, Pearl City, Hawaii 96782, USA

MATERIALS AND METHODS

Experimental organisms. Clumps of algae, with associated fauna, were removed from the field (Maile Point, Oahu, Hawaii, USA) and transported in portable aerated plastic containers filled with seawater back to the laboratory. The algae were shaken vigorously into 8 l aquaria with seawater to dislodge epifauna. Two h before use in an experiment, amphipods were transferred to 1 l aerated glass bowls with a wide-mouth pipette for better sorting and selection. Juvenile gray damselfish *Abudefduf sordidus,* a readily obtainable omnivore (Hobson 1974), whose diet consists partly of amphipods, were removed with dip nets from tide pools at Diamond Head State Park, Oahu. The adults, which are the largest Hawaiian pomacentrids (150 to 200 mm), are numerous among rocky crevices and boulders at the base of Hawaiian reefs (Hobson 1974). Fish were transported to the laboratory in portable aerated plastic containers and place into 12 l aquaria filled with seawater.

Artificial substrata. Black nylon bottle brushes were used as artificial substrates to eliminate any possible interaction of amphipods with allelochemicals or epibiotic food normally found on natural live plants. Bottle brush surface area:volume ratio (SA:V) was used as a complexity measure (Coull & Wells 1983). Surface area was measured by the detergent method of Harrod & Hall (1962) and Hicks (1977). Brush volume was measured by calculating the cylindrical volume of space taken up by the brush bristles. The complexity of each brush is shown in Table 1.

Table 1. Description of complexity characteristics of artificial substrata. SA: surface area; V: volume

Brush type	SA (cm^2)	V (cm^3)	SA/V (cm^{-1})
B1	326	176	1.85
B2	763	296	2.57
B3	1780	403	4.42

Laboratory experiments. *Controls.* To detect any natural mortality of amphipods in unnatural aquaria environments, a known number of amphipods was placed in each of two 8 l tanks filled with seawater and after 48 h the number of amphipods surviving in each were counted. In 2 other seawater tanks (12 l) the mortality of a known number of fish over 48 h was recorded. All the tanks contained bottle brushes. Any differences in the mean number of animals before and after 48 h were tested using t-tests. Fifteen amphipods were placed in an aquarium (12 l) without bottle brushes with 4 predatory fish in order to observe the feeding behavior of the fish for a 1 h period.

Habitat selection. To test the hypothesis that amphipods select a habitat based on its complexity, 2 brushes of each of 3 types (B1, B2, B3; Table 1) were randomly placed around the periphery of 3 seawater-filled tanks. Brushes were placed at least 10 cm from the sides of the tank to allow free movement of amphipods around the brushes. The corners of all aquaria were rounded to decrease corner effects. When the brushes had been in place for 48 h (for seasoning), 20 amphipods were placed in the centre of each tank and left to settle. After 24 h the bottle brushes and resident amphipods were quickly covered with plastic bags to prevent escape. The brushes were then removed from the tanks, and the amphipods were washed from the brushes with alcohol into sorting trays for counting and identification. Each tank was drained through fine mesh gauze to collect any amphipods which may have settled to the bottom. Experiments were performed twice; the first using 20 amphipods of the species *Maera pacifica* (Experiment 1A) and the second using 20 *M. insignis* (Experiment 1B). These amphipod species were chosen since they were very abundant on live plants during the time of sampling. Total numbers of amphipods counted on each brush were pooled for the 3 replicate tanks and a replicated goodness-of-fit test (G-statistic) was used to test for the total observed number of amphipods residing on different brush types versus the number expected. The null hypothesis is that there are no differences in the number of amphipods residing on brushes of different complexities (expected proportion of amphipods on brushes B1, B2, B3 = 1.0).

Predator inclusion. To test the hypothesis that the complexity of artificial substrata does not significantly reduce predation by fish on amphipod prey, a 12 l aquarium was divided into four 3 l compartments. Perforated dividers ensured free circulation of seawater between compartments. A bottle brush of different complexity (B1, B2, or B3) was placed in each of 3 compartments and the fourth compartment was left empty. The tank was filled with seawater to depth of 32 cm and 10 amphipods placed in each compartment. After 5 h (to allow amphipods to settle) one predatory fish (3 to 5 cm) was placed in each compartment. The fish were removed from the field 2 d before an experiment and starved for 24 h. The predatory fish was left in each compartment for 40 min and then removed. In preliminary observations fish devoured all prey in 60 to 90 min. Each bottle brush was quickly covered with a plastic bag and the bottom of the bag was secured. The brush was washed and picked clean of amphipods in a sorting tray containing alcohol for counting and identification. Each compartment was drained through fine mesh gauze to collect any amphipods on the bottom. The above procedure was repeated 7 times

(different dates) in fall 1984 using 5 amphipods *Lembos macromanus* and 5 *Maera insignis* in each compartment for each experimental trial (Experiment 2A). In spring 1985 the entire experiment (1 tank, 6 different dates) was repeated using 10 *M. pacifica* in each compartment each time (Experiment 2B). In both experiments the assignment of treatments followed a randomized blocks design. A mixture of amphipod species was used in Experiment 2A to observe whether there might be preferential selection of *L. macromanus*, which is white and conspicuously marked (spotted), versus the drab, olive-colored amphipod *M. insignis*. The amphipod *M. pacifica* was used in Experiment 2B because it was very abundant on seaweed during the time of sampling.

To analyze the data a 2-way ANOVA without replication for a randomized blocks design (treatments = brush type[+ no brush] vs blocks = dates) was used to test for significant differences in the mean numbers of amphipods surviving between compartments (complexities). Before using a randomized blocks, 2-way ANOVA without replication, independence among dates is assumed (no interaction between brush complexity and dates) (Sokal & Rohlf 1981).

Mechanism of predator choice. During Experiment 2A predator strikes on amphipods were observed in one compartment (B2) for 4 trials (40 min each) and during Experiment 2B predator strikes on amphipods were observed in the compartment containing brush type B3 for 4 trials (40 min each). During each 40 min observation period all strikes on moving or stationary prey were recorded. The null hypothesis was that all predator strikes are cued by prey motion. A goodness-of-fit (G-test) was used to compare the observed proportion of total strikes on moving prey to the expected proportion which was assumed to be 1.0.

RESULTS

No significant mortality of either amphipods (t = 0.19, df = 11) or fish (t = 0.20, df = 7) left in control tanks for 48 h was observed. Fish fed readily on amphipods of mixed species composition, devouring 11 out of 15 in 1 h.

In the habitat selection experiment no significant differences were observed between expected and observed numbers of amphipods residing on artificial substrata (B1, B2, B3) of differing complexities in either of the 2 experiments 1A (G = 0.86) or 1B (G = 0.17, df = 4, ns).

For both predation experiments (2A and 2B) there were highly significant differences (p<0.001) in the mean numbers of amphipods surviving predation among treatments (no structure, brush types B1, B2,

B3), except between brushes B2 and B3 in experiment 2B (Table 2; Fig. 1). Generally, more complex substrata resulted in increased survivorship of prey in the presence of predators. Brush B3, which had the highest surface area:volume ratio, had the highest number of amphipods surviving after 40 min, while the compartment with no structure had the least survivors (Fig. 1).

Table 2. Results of ANOVA: predator inclusion experiments

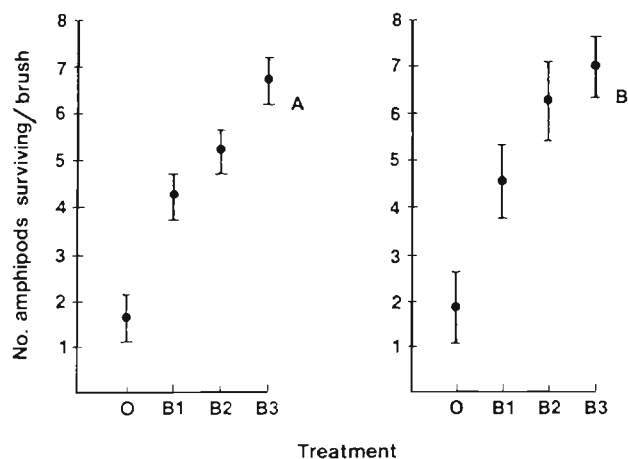| Source	df	SS	MS	F
Experiment 2A				
Dates (blocks)	6	0.543	0.091	0.38
Brush types (treatments)	3	93.3	31.1	129.7•••
Error	18	4.3	0.24	
	27			
Experiment 2B				
Dates (blocks)	5	0.88	0.18	0.17
Brush types (treatments)	3	92.1	30.7	29.5•••
Error	15	15.6	1.04	
	23			

••• p<0.001

Fig. 1. Multiple comparisons of mean amphipod survival per brush for 2 predator *(Abudefduf sordidus)* inclusion experiments. (A) Experiment 2A (*Lembos macromanus* and *Maera insignis*); (B) Experiment 2B *(Maera pacifica)*. Treatments represent artificial substrata (brush) surface area:volume ratios: 0, no structure; B1, 1.85; B2, 2.57; B3, 4.36. Error bars: minimum significant difference, 95 % confidence interval, T method and Gabriel's approximation (Sokal & Rohlf 1981). Intervals which do not overlap are significantly different

No significant difference occurred between the observed and expected proportions of *Lembos macromanus* and *Maera insignis* surviving (G = 0.22, df = 1, ns, 22 *L. macromanus* vs 19 *M. insignis*). The predatory fish did not seem to discriminate between *L. macromanus* and *M. insignis* before striking.

The null hypothesis that predator strikes are cued by prey motion is accepted; of the 32 predator strikes by *Abudefduf sordidus* on amphipod prey only 2 were on stationary amphipods ($G = 1.017$, df = 1, ns). Of the strikes on moving amphipods, 8 were on swimming amphipods and 22 were on amphipods moving on brushes.

DISCUSSION

The results reveal that Hawaiian amphipods do not selectively settle on artificial substrata of differing complexities within the range of complexities tested; amphipods seemed to settle on any substratum available without any pre-determination of substratum area, or volume. Results of the predator inclusion experiments do show, however, that amphipods escape predation pressure better on more complex habitats. This confirms the idea that the structural complexity of a habitat can reduce predation (Stein 1977, Russ 1980) by reducing predator foraging efficiency (Nelson 1979, Stoner 1982). Specifically, Crowder & Cooper (1982) found that structural complexity of the habitat reduces predator efficiency by reducing prey capture rates. Increased predation by fish on benthic invertebrates may not be linearly related, however, to decreasing substratum complexity. The relation may be more closely related to a step function with a threshold complexity above which predator foraging efficiency decreases (Nelson 1981, Coull & Wells 1983). This relation was not observed in my study.

Habitat complexity-predator interactions play an important role in structuring amphipod communities (Nelson 1979, Leber 1983), and selection by predators is a function of both the mechanism of choice and the accessibility of the prey (Main 1985). These mechanisms may change within the same predator species due to progressive ontogenetic changes in food habits which may cross major trophic levels (Grossman et al. 1980). Pinfish *Lagodon rhomboides*, for example, change their selection of prey as they grow, consuming copepods as juveniles and shrimp as adults. Visual acuity of predatory fish may also determine their selectivity of prey. Adult fish become more selective because of better visual perception with age (Kao et al. 1985).

Some other factors which may affect predator choice are prey size (Main 1983, 1985, Edgar 1983, Booth et al. 1985), shape (Kislalioglu & Gibson 1976), color (Clements & Livingston 1984), and motion (Pastorak 1980, Zaret 1980, Coull & Wells 1983, Main 1985). The present results suggest that juvenile damselfish *Abudefduf sordidus* selects its prey based on motion and may not distinguish between pigmented amphipods *(Lembos macromanus)* and non-pigmented ones *(Maera*

insignis). Clements & Livingston (1984) suggested that pigmentation of amphipods was the cue for predator choice, whereas Main (1985) suggested that prey motion appeared to elicit predator strikes. The full range of mechanisms may operate depending on the feeding behavior of different predator species (Eggers 1977) and on different life stages of the same species. The feeding behavior of most marine fish predators is still unknown and therefore generalizations explaining fish predator-prey interactions in the marine environment cannot be made.

That predation is a major force in structuring epifaunal communities is clear from many studies, but more information on the mechanisms of predator choice is needed to make any substantive statements about the precise role of substratum complexity in predator-prey interactions. Results of this study indicate, at least for the predator and prey chosen for observation, that amphipods may not actively select artificial substrata for their complexity but that complexity may mediate predator efficiency. However, only a portion of the diet of *Abudefduf sordidus* is amphipod prey (Hobson 1974). Amphipods rank fifth out of 12 diet items selected by this fish species (Hobson 1974). In Hawaiian algal reef environments amphipods found in the diet of *A. sordidus* may be opportunistically preyed upon by specialized foraging tactics. Other species of fish, whose diet is mainly amphipod prey, may be more adapted to feeding in their habitat where substratum complexity is not an important factor in mediating predation.

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