Predator-prey interactions in opisthobranch gastropods: effects of prey body size and habitat complexity

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ABSTRACT: This study examines size-specific predation by navanax *Aglaja inermis* (Gastropoda: Opisthobranchia), upon the sea hare *Aplysia californica* (hereafter *Aplysia*) (Gastropoda: Opisthobranchia). *Aplysia* reach a refuge in size from navanax predation at ca 10 cm in length, but very few individuals reach this size. Most *Aplysia* in the field were ≤ 3 cm long. Navanax diet in the field was disproportionately composed of larger *Aplysia* (> 2 cm long). Laboratory experiments with 0.5, 1.0 and 2.0 cm *Aplysia* and 2 levels of habitat complexity revealed that encounter rates, which rose with *Aplysia* size, were overwhelmingly important in determining size-selectivities. Attack probabilities (given an encounter) were always equal to 1, and capture success probabilities (given an attack) rose slightly with *Aplysia* size. Increasing habitat complexity reduced encounter rates disproportionately for 0.5 cm *Aplysia* as compared with 2.0 cm *Aplysia*. The results suggest that the effects of body size and habitat complexity on predation may interact strongly in a way which depends upon the specific foraging biology of the species involved and upon the predator-prey ratios used.

INTRODUCTION

Predation is commonly characterized by at least 3 components: encounter rate, attack probability (given an encounter) and capture success probability (given an attack). The relative body sizes of predator and prey can affect predator-prey interactions in complex ways by influencing any or all of these components (Bence & Murdoch 1986, Allan et al. 1987, Ryer 1988, Osenberg & Mittelbach 1989). A major question in the field of foraging ecology is to what extent predator diets are explained by 'passive components' of predation (encounter rates and capture success) as opposed to active choice by the predator (attack probability).

Physical structure of the habitat can strongly mediate predator-prey interactions, affecting not only total predation rates, but also modifying selectivities for different prey species or size classes (Orth 1977, Stoner 1979, Savino & Stein 1982, 1989, Anderson 1984, Ryer 1988). Hence, the effect of habitat structure can potentially interact with that of body size. However, few studies have examined this interaction.

In this paper, I examine size-specific predation by navanax *Aglaja inermis* (Cooper), upon the sea hare, *Aplysia californica* (Cooper) (hereafter *Aplysia*), in the field and in the laboratory. Based upon laboratory studies, I evaluate the relative importance of encounter rates, attack probabilities, gape limitation, capture success probabilities and habitat structure in generating the size-selectivity patterns observed in the field. The results suggest that encounter rates are far more important than attack probabilities, gape limitation or capture success probabilities in explaining field patterns of selectivity by navanax. In addition, laboratory experiments varying the amount of structure show that the effect of structure interacts with that of body size: smaller *Aplysia* gain a disproportionate amount of protection from predation from habitat structure.

SPECIES DESCRIPTION

The navanax *Aglaja inermis* is a carnivorous opisthobranch mollusc that ranges from Monterey, California, USA, to Baja California, Mexico; grows to a maximum size of ca 20 cm; and feeds primarily on other opisthobranchs which it swallows whole (Paine 1963). It forages by following slime trails; detection of slime trails and discrimination of potential prey are based on contact chemoreception (Blair & Seapy 1972, Murray &

Lewis 1974). At Santa Catalina Island, California, navanax are found in shallow subtidal sandy bays, and on rocky reefs. On rocky reefs, navanax are found primarily in the red alga *Plocamium cartilagineum* (Pennings 1989a), where they forage, mate, and lay eggs.

The sea hare *Aplysia californica* is a large herbivorous opisthobranch mollusc endemic to the west coast of North America. Its complete life cycle takes ca 1 yr (Audesirk 1979). Larvae spend 1 mo or more in the plankton before settling onto benthic algae and metamorphosing (Kriegstein et al. 1974). At Santa Catalina Island, most recruitment takes place in January–February and June–September (Pennings 1989b, unpubl. data). Small individuals < 3.0 cm long, which comprise the vast majority of the population, are found almost exclusively in the red algae *Plocamium cartilagineum* and *Laurencia pacifica* (Audesirk 1979, Pennings 1989b, own unpubl. data). Reproductive activity peaks in the summer and fall, when mature individuals aggregate to mate and lay eggs, and large adults die in the late fall (Audesirk 1979).

METHODS

All field and laboratory research was conducted at the Catalina Marine Science Center, Santa Catalina Island, California, USA (33° 27' N; 118° 29' W). Shallow (< 10 m) subtidal rocky reefs in the vicinity of the laboratory are typically dominated by foliose algae less than 0.5 m tall which cover > 50 % of the free space. This algal community is dominated by the erect coralline *Lithothrix aspergillum* and a variety of brown algae including *Sargassum palmerii*, *Dictyopteris undulata*, *Dictyota flabellata*, *Zonaria farlowii* and *Cystoseira osmundacea*. *Plocamium cartilagineum* usually covers less than 10 % of the substrate, and *Laurencia pacifica* is uncommon (< 1 % cover).

Size-selective predation in the field. To determine the size-specific pattern of predation in the field, I compared the size-frequency distribution of *Aplysia* that were available on the reefs with the size-frequency distribution of *Aplysia* that were eaten by navanax. Estimates of the size-frequency distribution of *Aplysia* were obtained by collecting up to 10 ca 100 g samples of *Plocamium cartilagineum*, their primary habitat, from each of 12 to 13 reefs in the vicinity of the laboratory, and carefully removing all *Aplysia* present by sorting and rinsing in fresh water. Length of all *Aplysia* was measured to the nearest 0.1 cm while they were in a standard crawling posture. This method accurately samples all but the largest (> 5 to 6 cm) individuals which comprise ≤ 1 % of the total population and no longer live in *P. cartilagineum* plants, and the newest

recruits < 0.2 cm long which are difficult to see. Algal collections were made in June, July, and August 1987. Because the size-frequency distributions of *Aplysia* were relatively similar during the three sampling periods (see 'Results'), I pooled the samples to yield a single size-frequency distribution for subsequent analysis.

To determine the size-frequency distribution of *Aplysia* eaten by navanax, I collected 33 navanax from the field during June, July and August 1987. These navanax were collected from a variety of reefs and algal substrates and allowed to defecate in the laboratory for 24 to 48 h. *Aplysia* shells were removed from the navanax feces under a dissecting microscope, and the length of all shells was measured to the nearest 0.025 cm. Length of *Aplysia* was estimated from shell length based on the equation: *Aplysia* length (cm) = −0.651 + 5.95 × shell length (cm) (r = 0.92, N = 102, p < 0.0001) (Pennings unpubl. data).

Size-selectivity was determined by calculating Manly's index

$$\alpha_i = (r_i/n_i) / \sum_{j=1}^{k} (r_j/n_j),$$

where i = 1, ..., k; r_i is the number of prey of type i in the diet; and n_i is the number in the environment (Chesson 1983). This index varies from 0 to 1 for any prey type, and takes on the value 1/k for each prey type if there are k prey types available and predation is random.

Aplysia size refuge. To determine whether *Aplysia* had a refuge in size from navanax, I presented *Aplysia* measuring 0.3 to 10.0 cm to individual navanax measuring 1.1 to 18.0 cm in laboratory arenas. Navanax were collected from the field and starved for 24 to 48 h. They were then placed in a shallow 24 × 30 cm plastic container and allowed to begin normal searching behavior. A single *Aplysia* was then presented in a standardized head-on position to the navanax, and I recorded whether or not the *Aplysia* was consumed. Trials had 1 of 3 outcomes: (1) the navanax quickly swallowed the *Aplysia*, usually within 1 min; (2) the navanax attempted to swallow the *Aplysia* and then quickly rejected it; and (3) the navanax partially swallowed the *Aplysia*, was unable to make further progress, but retained its hold on the partially swallowed prey for an extended period of time (20 min to hours). Although navanax in this situation in the laboratory may partially digest some oversize prey (Susswein & Bennett 1979), I observed that navanax which failed to swallow *Aplysia* within 20 min usually released them undigested within a few hours. Whether or not the *Aplysia* survived depended upon whether or not the flow of water across the gills had been obstructed. Release occurred much sooner if there was any disturbance to the pair. Since navanax at Santa Catalina Island are found on relatively exposed

reefs with a fair amount of wave surge, rather than in sheltered lagoons, I concluded that *Aplysia* in the field which were not readily swallowed would eventually be released with little benefit to the navanax. Hence, I classified any encounters which were unresolved after 20 min as unsuccessful attacks.

Successful and unsuccessful attacks were analyzed using logistic regression, with the ratio of prey length to predator length as the independent variable. This ratio is often used to scale predator-prey interactions, and is biologically reasonable since gape increases linearly with length for many predators (Bence & Murdoch 1986, Osenberg & Mittelbach 1989).

Effect of habitat complexity on size-selectivity. To determine the mechanism(s) behind the size selectivity of navanax in the field, I offered groups of *Aplysia* of 3 sizes to navanax in laboratory arenas. *Aplysia* measuring ca 0.5, 1.0, and 2.0 cm were placed in 24 × 30 cm plastic containers filled with seawater, and navanax were then introduced. All navanax were large enough (6 to 13 cm) to easily swallow 2.0 cm *Aplysia* in < 30 s. Consequently, they were not gape limited, and handling time was a minor part of each trial's total time. Trials were run in bare containers, simulating a rocky environment with no algal structure, or with *Plocamium cartilagineum* loosely covering the bottom of the containers, simulating algal patches. Two *Aplysia* of each size class, for a total of 6, were placed in each bare container, and 4 *Aplysia* of each size class, for a total of 12, in each *P. cartilagineum*-filled container. More *Aplysia* were used in *P. cartilagineum*-filled containers so that the total number of encounters by each predator would be similar between habitat types. *Aplysia* were replaced as they were consumed, so that densities remained constant.
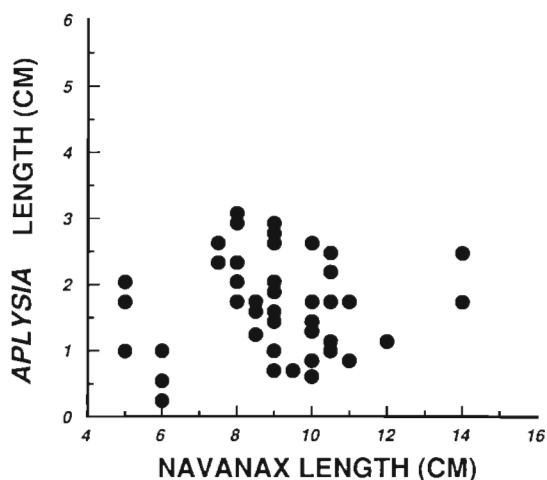
Navanax were collected from the field and starved at least 48 h before each experiment, and each navanax was used only once on each substrate. Navanax were scored as encountering *Aplysia* when they contacted an *Aplysia* with their oral region and flinched in a stereotyped manner. Once navanax encountered *Aplysia*, I recorded if they attacked, and if so, if the attack was successful. Trials were terminated after ca 1 h or when navanax were satiated and stopped searching for prey. The number of encounters with each size class was converted to a per capita encounter rate/h (number of encounters/number of *Aplysia*/length of trial in hours), and log-transformed to reduce mean-variance correlations.

RESULTS

Size-selective predation in the field

Fecal samples from navanax ranging in length from 5 to 14 cm contained shells from *Aplysia* which were estimated to range from 0.2 to 3.1 cm in length (Fig. 1). Individual navanax had from 0 to 6 *Aplysia* shells in their feces (mean = 1.4, N = 33). Maximum size of prey did not increase with size of predator (N = 18, r = 0.01, p = 0.97).

The *Aplysia* available in the field were concentrated in the smaller size-classes (Fig. 2 upper). Individuals > 2.0 cm comprised only 1.2 % of the population. In contrast, the *Aplysia* which navanax ate were relatively large (Fig. 2 middle). Consequently, selectivity increased with *Aplysia* size (Fig. 2 lower), indicating that larger *Aplysia* were eaten disproportionately often compared with their abundance in the population.

Aplysia size refuge

The probability that a navanax would successfully swallow an *Aplysia* fell sharply for *Aplysia* which were greater than about half the navanax's length (Fig. 3; logistic regression, $X_1^2 = 63.4$, p < 0.001). Observations indicated that success was lower for navanax which struck at *Aplysia* from the side, rather than from the end. Depending on how most encounters occur, these data may slightly overestimate success probabilities for navanax in the field. The largest navanax I ever found at Santa Catalina Island was 18 cm in length; Paine (1963) gives the maximum size of navanax as about 20 cm. This would suggest that *Aplysia* ≥ 10 cm in length at Santa Catalina Island are relatively free from navanax predation. However, most of the *Aplysia* population is < 2 cm in length (Fig. 2 upper): few individuals ever reach the size refuge.

Fig. 1 *Aplysia*. Sizes eaten by field-collected navanax. Estimates based on shell length-body length regression. N = 47 *Aplysia*, N = 18 navanax
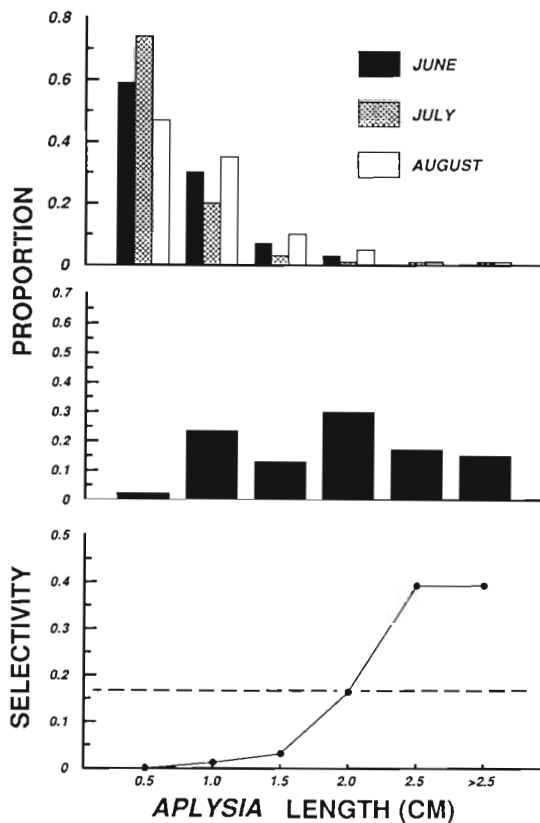
Fig. 2. *Aplysia*. Comparison of size-frequency distribution in the field and the estimated size-frequency distribution of *Aplysia* consumed by navanax in the field. Upper: proportion of *Aplysia* in six 0.5 cm size classes in the field during 3 summer months. Numbers on the x-axis indicate the upper limit of each 0.5 cm size class. June: N = 706; July: N = 1164; August: N = 620. All size classes represented by a total of ≥ 14 individuals. Middle: proportion of *Aplysia* in 6 size classes eaten by navanax in the field. N = 47. Lower: Selectivity (Manly's index) by navanax for *Aplysia* in 6 size classes. Dashed line indicates random consumption with respect to *Aplysia* size
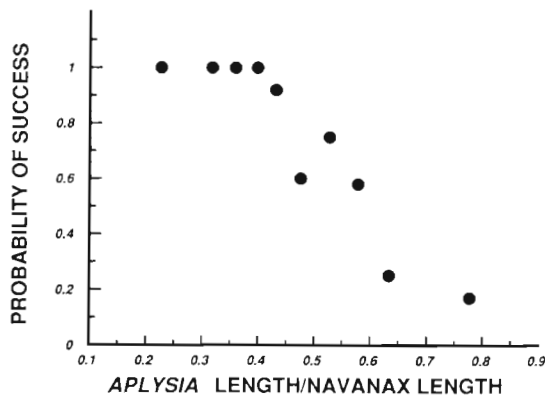
Mechanisms of size-selectivity

Navanax ate 5 to 18 *Aplysia* per trial. Per-capita encounter rates were higher in bare containers than on *Plocamium cartilagineum*, and were higher for larger size classes of *Aplysia* on both substrates (Fig. 4, Table 1). The significant interaction term in the ANOVA model (Table 1) indicates that *P. cartilagineum* reduced the encounter rate of navanax with the smaller *Aplysia* disproportionately more than it reduced their encounter rate with the larger *Aplysia*.

Of the 410 encounters observed, 409 led to attacks. Satiated navanax do not always strike at prey they encounter (Susswein & Bennett 1979, own obs.); however, hungry navanax invariably do. It is not known how often navanax are satiated under field conditions.

The proportion of attacks which were successful did not differ between substrate types, but did differ between size classes of *Aplysia* (Fig. 5; logistic regression, Size: $X_1^2 = 16.8$, $p < 0.001$, Substrate: $X_1^2 = 0.7$, NS). Smaller *Aplysia* did not escape predation because
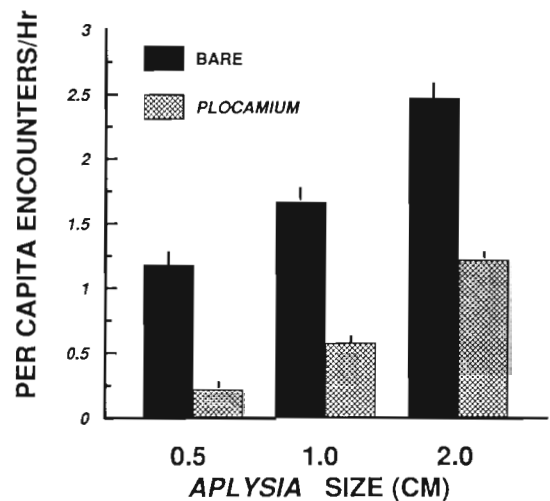
Fig. 4. Per capita encounter rates (number of encounters/number of *Aplysia*/length of trial in hours) of navanax with 3 sizes of *Aplysia* in containers lacking structure (N = 23) and in containers with structure (*Plocamium cartilagineum*) (N = 16). Vertical bars indicate 1 SE

Table 1. ANOVA for log-transformed per capita encounter rates of navanax with 3 size classes of *Aplysia californica* in bare containers and in containers with a layer of *Plocamium cartilagineum* on the bottom

| Source	df	SS	F	Significance
Substrate	1	16.16	12.29	p < 0.0007
Size	2	76.08	28.94	p < 0.0001
Habitat × size	2	14.88	5.66	p < 0.0046
Error	111	145.92		

Fig. 3. Probability of navanax successfully swallowing *Aplysia* as a function of the 2 species' relative lengths. Binary data are grouped for clarity of presentation. N = 118 (each point represents 11 or 12 independent trials)
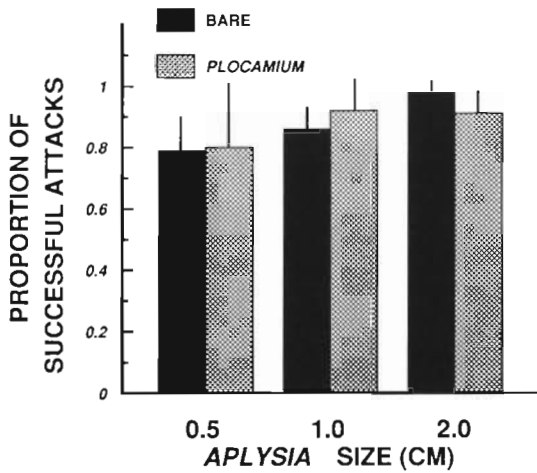
Fig. 5. *Aplysia*. Proportion of successful attacks by navanax on 3 sizes of *Aplysia* in containers lacking structure (N = 285 attacks) and in containers with structure (*Plocamium cartilagineum*) (N = 138 attacks). Vertical bars indicate binomial 95 % confidence intervals. Data were analyzed using logistic regression. See text for details
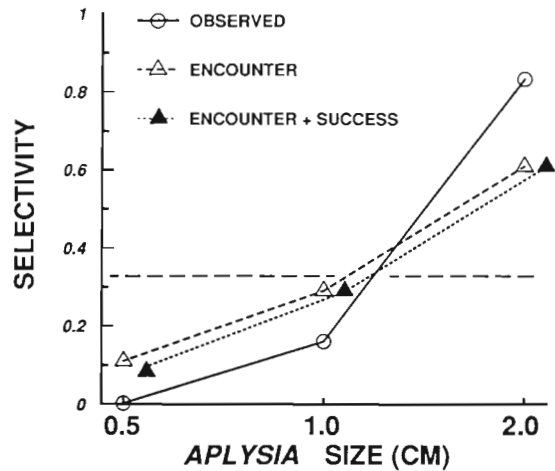

Fig. 6. *Aplysia*. Comparison of selectivities (Manly's index) observed in the field for 3 sizes with predicted selectivities based on (1) laboratory encounter rates, and (2) laboratory encounter rates and laboratory attack success. Points for the second model are offset to the right for clarity. Dashed line indicates random consumption with respect to *Aplysia* size

of any anti-predator behavior; rather, they probably escaped because they were so small a bulk stimulus that the navanax did not realize that they had successfully captured an *Aplysia*. Consequently, they would continue to strike, and in the process would inadvertently spit the small *Aplysia* out.

How well do the patterns of predation observed in the laboratory mirror the patterns observed in the field? I recalculated Manly's selectivity index for the field data using only the 3 size classes of *Aplysia* which I used in the laboratory predation experiment. I compared these values with those predicted by 2 simple models based on the data from the *Plocamium* laboratory trials: (1) selectivity estimated from encounter rates:

$$\alpha_1 = E_1 / \sum_{j=1}^{k} E_j,$$

where i = 1, ..., k; E_j = per capita encounter rate for size j; and (2) selectivity estimated from encounter rates and success probabilities:

$$\alpha_1 = E_i P_1(s) / \sum_{j=1}^{k} E_j P_j(s),$$

where i = 1, ..., k; $P_j(s)$ = probability that an attack results in successful consumption of a prey of size j. Since attack probabilities were always 1 in the laboratory, their inclusion did not affect these models. This comparison assumes that attack probabilities in the field were also always 1. Both models based on laboratory data were in qualitative agreement with the observed field selectivities (Fig. 6). However, both models somewhat overestimated the fraction of the diet which would be composed of small *Aplysia*, and underestimated the fraction of the diet which would be composed of large *Aplysia*.

DISCUSSION

Encounter rates clearly drive the size-selective predation of navanax on *Aplysia*. When navanax are hungry, attack probabilities are always 1, and addition of success probabilities improved the fit of the predictive model very little (Fig. 6). These results are similar to those of Osenberg & Mittelbach (1989) who found that encounter rates explained most of the size-selective pattern of predation by pumpkinseed fish upon snails. However, in other studies attack probabilities were also very important (Bence & Murdoch 1986, Allan et al. 1987, Ryer 1988, Savino & Stein 1989).

Encounter rates of navanax with *Aplysia*, and consequently preference, as measured by Manly's index, rose with prey size (Fig. 4). In this case, therefore, there is no need to invoke behavioral selection towards valuable prey (optimal foraging) to explain the preference for larger prey. That encounter rates rise with prey size is a general result (Richards 1982, Allan et al. 1987, Hewett 1988, Ryer 1988, Osenberg & Mittelbach 1989) which has led to a realization that the appropriate null hypothesis for optimal foraging studies is not that predators take prey at random from the population, but rather that that predators attack prey at random based on encounter rates (Greene & Landry 1985, Bence & Murdoch 1986, Greene et al. 1986, Osenberg & Mittelbach 1989).

A growing body of work suggests that selectivity curves are intrinsically hump-shaped, but that these curves in practice are often truncated because a full range of prey is not available (Scott & Murdoch 1983,

Schmitt & Holbrook 1984, Bence & Murdoch 1986, Allan et al. 1987, Osenberg & Mittelbach 1989). In this case, selectivity rose with *Aplysia* size through the largest size of *Aplysia* which was commonly available in the field (Fig. 2 lower). However, navanax were limited in the maximum size of *Aplysia* they could consume (Fig. 3) and so selectivity values for the rarer, larger *Aplysia* must, by definition, fall. However, because large *Aplysia* were so rare, this declining portion of the selectivity curve was not detected by my field sampling.

Patterns of selectivity based on the laboratory experiments generally mirrored those found in the field, suggesting that the laboratory experiments captured the important features of this predator-prey interaction. However, both laboratory-based models overestimated the proportion of the field diet of navanax that consisted of small prey, and underestimated the contribution of large prey. I believe that the most likely explanation for this variance is that I did not adequately mimic the *Plocamium cartilagineum* patches in my laboratory study. Recall that a layer of *P. cartilagineum* on the bottom of the containers reduced encounter rates with small *Aplysia* disproportionately more than it reduced encounter rates with large *Aplysia*, compared with encounter rates in bare containers. I used only a thin layer of *P. cartilagineum* so that I would be able to clearly observe the *Aplysia* and navanax. However, in the field, *P. cartilagineum* can grow to more than 20 cm tall (own obs.), and always forms three-dimensional patches, rather than the essentially two-dimensional layers used in the laboratory experiments. This three-dimensional structure in the field may confer even more protection upon the smaller size-classes, explaining the differences between laboratory and field results. The suggestion that the effect of structure may vary between prey size classes has been made before (Ryer 1988), indicating that studies of the effect of habitat complexity upon predator-prey interactions need to also consider the possibly interacting effects of body size.

A number of other hypotheses might also explain the differences between the laboratory and field results. First, I ignored spatial and temporal variation in the size-frequency distribution of *Aplysia* at Santa Catalina Island, and simply lumped all the samples. Hence, it is possible that the navanax I collected were foraging on *Aplysia* populations which, in those particular places and times, differed from the distribution used to calculate field selectivities. Second, navanax in the field forage for some prey by following slime trails (Paine 1963). This did not occur as often in the laboratory experiment because of its short duration and the frequent replacement of *Aplysia*. There simply was not time for extensive slime trails to be formed. In the field,

however, large *Aplysia* may form larger slime trails than small *Aplysia*, and be eaten disproportionately often as a result. Third, laboratory experiments were terminated when navanax became satiated. If navanax are commonly satiated in the field, this might alter their attack or success probabilities between size classes of *Aplysia* (Bence & Murdoch 1986). Any of these factors could also have contributed to the difference between laboratory and field results.

Structure has generally been shown to reduce predation rates (Orth 1977, Savino & Stein 1982, Anderson 1984, Dean & Connell 1987, Ryer 1988, but see Savino & Stein 1989). I found that structure reduced encounter rates of predators with prey, but had no effect on attack or success probabilities. I previously reported that navanax predation rates on small *Aplysia* did not differ on 5 different species of algae (Pennings 1989a). This suggests that the reduction of encounter rates found in this study on *Plocamium cartilagineum* was simply due to the presence of physical structure, and not to any special characteristics of this algal species itself.

Ryer (1988) studied the effect of structure on the predator-prey interaction between pipefish and amphipods. He also found that encounter rates increased with prey size, that structure did not affect success rates, and that structure reduced overall predation rates for some predators. However, attack rates of pipefish varied between amphipod size classes, and were affected by structure, whereas navanax attack probabilities were always 1, regardless of prey size or structure. Also, the capture success of pipefish declined with prey size, whereas the capture success of navanax increased slightly with prey size. The contrasting results of these 2 studies demonstrate that the effect of structure on predator-prey interactions will depend upon the specific biology of the species involved and the predator-prey size ratios used. For example, differences between this study and that of Ryer (1988) might be explained by the fact that pipefish are visual foragers but navanax forage using contact chemoreception. Further understanding of the effect of structure upon predator-prey interactions will require studies which carefully examine the different stages of predation under a range of predator-prey size ratios, with a variety of predator types.

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