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Burrows protect postlarval lobsters *Homarus americanus* from predation by the non-burrowing cunner *Tautogolabrus adspersus*, but not from the burrowing mud crab *Neopanope texani*

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ABSTRACT: Groups of 10 late Stage IV or early Stage V lobsters *Homarus americanus* were introduced into seawater table sections consisting of either a bare sand substrate or a rocky substrate from a subtidal area with some rocks covered by *Fucus* spp. The lobsters were given 2 d in which to build burrows or depressions. Predators were then introduced into all sections, except those which had been designated as predator-free, sand control tanks. These latter tanks served as an estimate of the natural mortality of the lobsters without predation. After 8 d, or after all of the lobsters in a section were consumed, the predators were removed and the number of surviving lobsters was counted and compared to the number surviving in the predator-free control tanks. When subject to predation by non-burrowing fish *Tautogolabrus adspersus*, more lobsters survived in the rocky substrate than in the sand substrates. However, when burrowing mud crabs *Neopanope texani* were used as the predator, no significant difference was apparent between the number of lobsters surviving in the rocky and the sand substrates, although significant differences were found between the rocks and controls and the sand and controls. Thus predation occurred in both substrates with the crab predators, indicating that lobsters burrowed under rocks are not protected from burrowing predators. Natural mortality without predation was low during the entire group of experiments.

INTRODUCTION

While many studies have examined the burrowing abilities and substrate preferences of settling Stage IV lobsters, few have determined the advantages, if any, that each substrate may confer with regard to protection against predators. Postlarval, juvenile, and adult lobsters show distinctive preferences when given a choice of substrates in which to burrow. Howard & Bennett (1979) found that *Homarus gammarus* preferred the largest sized particles provided (7 to 20 mm diameter), presumably because crevices of the correct dimensions are provided in which to build burrows. Cobb (1971) found that lobsters either choose or construct burrows where the height of the burrow is less than the width. Botero & Atema (1982) found that seaweed-covered rocks over sand were preferred to mud substrates, and mud was preferred to gravel and sand substrates. In sand, and to a small degree in mud, substrates, lobsters will delay burrow construction (Botero & Atema 1982). Similarly, Howard & Bennett (1979) and Pottle & Elner (1982) found that Stage VII to X lobsters *Homarus gammarus* and *Homarus americanus* preferred substrates of small rocks over those of mud or silt. Furthermore, Dybern (1973) noted that the typical habitat of *Homarus gammarus* (as *H. vulgaris*) consists of rocky or soft bottoms overlain with boulders and stones. However, most of these studies have been conducted in the laboratory, and, as yet, early juvenile lobsters have not been found with any regularity in the field.

Recently, Barshaw & Bryant (unpubl.) observed that Stage IV lobsters settled more quickly in eel grass substrates than in substrates of rocks over sand or mud. These and other authors have assumed that if settling lobsters are able to build burrows in an appropriate substrate, such as rocks over sand or mud, or eel grass, they will be relatively free of predation (*Homarus americanus:* Atema et al. 1982, Botero & Atema 1982, Pottle & Elner 1982; *H. gammarus* (as *H. vulgaris*): Berrill 1974; adult *Nephrops norvegicus:* Chapman & Rice 1971). Kittaka et al. (1983), however, released 1 yr

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old lobsters *Homarus americanus* in Japan waters over a sandy substrate with blocks provided for shelter and noted that small crabs of the family Portunidae *(Thalamita sima)* preyed upon lobsters under the blocks. The behavior of fishes in the area led Kittaka et al. to believe that they too were an important factor in the mortality of the lobsters. Moreover, Barshaw (pers. obs.) noted that Stage IV lobsters were preyed upon by the mud crab *Neopanope texana* during initial burrowing in substrates of eel grass, rocks over sand, and mud. Similarly, Richards & Cobb (in press) found that shelter-limited, late juvenile lobsters were subject to greater predation by fishes than those provided with sufficient numbers of shelter. Roach (1983) recently found that crabs *Cancer irroratus* and fish *Myoxocephalus* spp. were able to capture lobsters in mud substrates, where the burrows were more exposed. Predation in substrates of rocks or rocks with vegetation was not evident.

This laboratory experiment was designed to investigate the degree to which burrows in rock substrates protect settled lobsters from both burrowing and non-burrowing predators.

METHODS

Large seawater tables were divided into thirds by plastic partitions with holes which allowed water to flow through the sections (dimensions of each section: 76 cm long × 44 cm wide × 40 cm high). The sections contained either a sand substrate (10 cm deep) or a rocky substrate (12 cm deep) composed of rocks of a natural size distribution (1 to 20 cm in diameter), some of which were covered with *Fucus* spp. Both sand and rocks were obtained from subtidal areas in Woods Hole, Massachusetts, USA, and after introduction to the sections, the substrates were allowed to acclimate for 1 wk. Three treatments were set up: 5 replicate sections containing bare sand and predators, 5 replicate sections containing rocks and predators, and 3 replicate sections consisting of sand but with no predators. The latter tanks served as controls to estimate the natural mortality of the lobsters without predation during the time course of the experiment. One test using cunners *Tautogolabrus adspersus* as the predator and 2 tests using mud crabs *Neopanope texana* were conducted. In both the cunner test and one of the mud crab tests we had to delete a rock replicate because extra lobsters were inadvertently placed into the section.

We did not have predator-free, rock control tanks in these experiments due to space constraints. However, mortality without predators has been found to be either the same between rock and sand substrates (Cobb 1968), or less in rock substrates compared with other substrates (Roach 1983). Thus, we believe that our sand control tanks gave the highest estimate of natural mortality during the experiment.

After the 1 wk acclimation period, 10 late Stage IV or early Stage V lobsters *Homarus americanus* were placed into each section. Upon release into each tank, the lobsters were allowed 2 d in which to settle and build burrows (in the rocks) or depressions (in the sand), as seen in other studies (Atema et al. 1982). During this time, the lobsters were fed once daily with frozen brine shrimp. On the third day, we stopped feeding the lobsters and introduced the predators. For each test we introduced either 3 cunners or 5 mud crabs into each section, except those of the controls. The cunners ranged in size from 6 to 10 cm (total length) while the mud crabs ranged from 8 to 25 mm in carapace width. Prior to introduction into the sections, the cunners were held communally for approximately 1 mo and were fed Stage IV lobsters; however, they were not fed daily due to a lack of sufficient lobsters. For the 2 d immediately preceding the test, the fish were starved. The crabs were likewise held communally prior to testing and also fed Stage IV lobsters. They were starved for 3 d before being used in the tests. Following introduction, the sections were checked daily and dead predators were replaced: 5 fish died (4 in the rock sections) and 4 crabs died during the 2 tests. There was a large difference between the 33 % mortality of the cunners in the rocky substrate sections and the 6.6 % mortality in the sand sections. While no post-mortems were performed on the dead fish, we do not believe they could have died from a disease specific to the rocky sections. Had a disease been present in those sections, it should have spread to the sand sections, since water flowed through the partitions of the different substrates.

Each test lasted either 8 d or until all of the lobsters in a section were consumed, whichever came first. At the end of the test, the predators were removed and the substrate was sorted to determine the number of surviving lobsters. The number of surviving lobsters in each of the predator sections was then compared to the number surviving in the predator-free control sections to determine if predation had occurred. The results were organized into a 3 × 2 contingency table and 3 (1 for each treatment) 2 × 2 contingency tables. They were then subjected to a Chi-square analysis for differences in mortality between the treatments. The 2 crab tests were combined after testing to ensure that there were no significant differences between the tests.

These experiments were conducted from July to September 1985 at the Marine Biological Laboratory in Woods Hole, Massachusetts, USA. Water temperatures ranged from 21.5 to 23.5 °C during the entire group of experiments.

Table 1. *Homarus americanus*. Total number of lobsters both living and dead at the end of the tests in the treatments with cunners *Tautogolabrus adspersus* and mud crabs *Neopanope texana* as predators

Predators	Rocks with *Fucus*		Bare sand		Sand controls (no predators)		Chi-square test
	Alive	Dead	Alive	Dead	Alive	Dead	
Cunners	33	7	0	50	28	2	Rocks *vs.* Sand, $p < 0.001$ Rocks *vs.* Control, NS Sand *vs.* Control, $p < 0.001$
Mud crab (2 tests combined)	54	36	46	54	54	6	Rocks *vs.* Sand, NS Rocks *vs.* Control, $p < 0.001$ Sand *vs.* Control, $p < 0.001$

RESULTS

Cunners were unable to prey upon the settled lobsters in the rocky substrate, as there were no significant differences in lobster survival between the predator-free control sand sections and the rocky sections. Significant predation upon the lobsters, however, did occur in the sand tanks where the cunners consumed all of the lobsters by the 4th day of the experiment (Chi-square, $P<0.001$, Table 1).

In contrast, the crabs were able to consume settled lobsters in both rocky and sand sections. Survival of the lobsters in both of these substrates was significantly lower than lobster survival in the predator-free control sections (Chi-square, $P<0.001$, Table 1). There was no significant difference, however, between the amount of predation occurring in rocky substrates and sand substrates.

DISCUSSION

Our results indicate that lobster burrows in a rocky subtidal substrate do not offer as much protection against predation as has often been assumed in the literature (*Homarus americanus:* Atema et al. 1982, Botero & Atema 1982, Pottle & Elner 1982; *H. gammarus* (as *H. vulgaris*): Berrill 1974; adult *Nephrops norvegicus:* Chapman & Rice 1971). Against small, burrowing mud crabs, burrows in rocks provide as little protection as depressions made by lobsters in sand substrates (Table 1). This result is supported by observations of Kittaka et al. (1983) where crabs *Thalamita sima* successfully captured lobsters which had burrowed under blocks. However, *Thalamita sima* does not overlap the natural range of *Homarus americanus,* whereas the mud crab *Neopanope texana* is found from the arctic to south of Virginia (Gosner 1971) and thus completely overlaps the American lobster's geographic range (Cooper & Uzmann 1980).

Roach (1983) concluded that the faster a larval lobster takes cover upon reaching the bottom, the greater its chance for survival. He found that crab predators *Cancer irroratus* (50 to 80 mm carapace width) were unable to capture lobsters burrowed in substrates of bare rock or rocks covered with vegetation. They were, however, able to capture lobsters burrowed in mud substrates. As opposed to *Neopanope texana, C. irroratus* is a large crab and should not, therefore, be expected to burrow under the same sized rocks that a postlarval lobster could (1 to 20 cm in diameter). His data on fish predation agree with ours in that non-burrowing fish (sculpins or cunners) are unable to capture lobsters in a rocky substrate (with or without vegetation).

While our results indicate that burrows in rock substrates do not protect early juvenile lobsters from a burrowing predator (the mud crab), further tests should be conducted to determine whether different substrates offer better protection against burrowing predators in general. Both mud crabs *Neopanope texana* and cunners *Tautogolabrus adspersus* are ideal predator choices for further comparative tests in that they are found in substrates of mud, bare sand, rocks, and eel grass (Bigelow & Schroeder 1953, Barshaw pers. obs.) and they overlap the natural geographic range of *Homarus americanus.* Although these 2 predators are ubiquitous over the range of the American lobster, we cannot state that they live in precisely the same habitat as the lobsters because the habitat(s) of the early juveniles is unknown at this time.

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