

A LONG-TERM STUDY ON THE BEHAVIOR AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTER, *HOMARUS AMERICANUS*, IN THREE NATURALISTIC SUBSTRATES: EELGRASS, MUD, AND ROCKS

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ABSTRACT

An 8-month study on the behavior, growth, and survival of early juvenile American lobsters, *Homarus americanus*, was conducted in three different naturalistic habitats of mud, rocks with algae, and eelgrass. Fifteen narrow aquaria (10 cm wide) allowed visual observations of American lobster's activities in five replicates of each of the three habitats. After a 3-month acclimation period to establish "natural" benthic communities which entered through the water supply, three stage IV American lobsters were introduced into each aquarium. Observations were made on the settling, burrowing, activity, and feeding behavior of these lobsters.

American lobsters in eelgrass and rock habitats settled into the substrate more quickly, had burrows a greater percent of the time, and spent less time repairing their burrows than lobsters in mud habitats. The lobsters in eelgrass had a lower mortality rate than lobsters in either rocks or mud. None of the lobsters in any substrate were observed foraging for food outside of their burrows. However, the behavior of these American lobsters indicated that they were able to capture plankton drawn into their burrows by pleopod fanning. Six lobsters molted during the coldest part of the year when the water temperature was approximately 1° to 2°C.

Stage IV of the American lobster, *Homarus americanus*, is best described as transitional between larval and juvenile (Phillips et al. 1980). During this stage major behavioral changes take place, which coincide with the morphological changes occurring in the molt. These behavioral and morphological changes cause the stage IV lobsters to descend from the upper layers of the water column to the bottom where they build a burrow (Botero and Atema 1982; Ennis 1975).

Knowledge of the American lobster's behavior from the onset of settlement until they reach a size of approximately 20 mm in carapace length (CL) remains limited because juveniles of this size range have been found in the field only sporadically.

Several laboratory experiments sought to determine the substrate preferences of stage IV American lobsters. Howard and Bennett (1979) found that lobsters (*H. gammarus*) generally choose the largest size of gravel provided (approximately 20 mm in diameter), because larger rocks have more available

space between them for burrows. If given a choice between a gravel substrate or a silt/clay substrate, American lobsters prefer the gravel (Pottle and Elnor 1982). In choice tests, stage IV American lobsters preferred rocks with macroalgae, followed by, in order of decreasing preference, mud, rocks on sand, and sand. If not afforded a choice, the lobsters settled most quickly on the rocks with macroalgae, followed by rocks on sand, mud, and sand (Botero and Atema 1982).

MacKay (1926) recorded observations on the lobsters' ability to burrow in mud. Subsequently Cobb (1971), Berrill and Stewart (1973), and Botero and Atema (1982) have described the methods by which juvenile American lobsters make burrows in both mud and rocky substrates. No observations have been made on American lobsters burrowing into other substrates, such as eelgrass or peat.

Cobb et al. (1983) followed stage IV *H. americanus* for short periods of time following their release into the field. They observed behavior which may indicate that American lobsters test different substrates and continue moving if they are on unsatisfactory substrates such as sand or mud; however, only two lobsters were actually seen rejecting a substrate.

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Predation upon postlarval lobsters *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crabs *Neopanope sayi* on three different substrates: eelgrass, mud and rocks

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ABSTRACT: To assess the anti-predator function and efficiency of burrows formed in different substrates, late Stage IV or early Stage V lobsters were placed in seawater tables with mud, rocks (some with algae), or eelgrass. They were allowed 4 d in which to settle and build burrows, after which predators were placed into half of the seawater table sections. The remaining sections served as predator-free controls. Censuses were taken of the number of lobsters without burrows during the 4 d preceding predator introduction. Following predator introduction, behavior of both lobsters and predators was observed to note how predators located and captured lobsters and how, if at all, lobsters escaped. The census data showed that more lobsters had burrows in the rock substrates than in either the eelgrass or mud substrates. Fewer lobsters had burrows in mud substrates than in eelgrass substrates. When subject to predation by cunners *Tautogolabrus adspersus*, no predation occurred in the rock substrate. However, significant predation occurred in the mud and eelgrass substrates. When subject to predation by mud crabs *Neopanope sayi*, predation occurred in all 3 of the substrates.

INTRODUCTION

Numerous studies have suggested that postlarval and juvenile lobsters are subject to high predation pressure by fishes and crabs. Cunners have been found to have early juvenile lobsters in their guts (Bigelow & Schroeder 1953). Roach (1983), in cage experiments in the field, found that crabs *Cancer irroratus* and fish *Myoxocephalus* spp. were able to capture lobsters in mud substrates, but these predators were not successful in rock substrates. Lavalli & Barshaw (1986) found that, although burrows in rocks protected early juvenile lobsters from cunners *Tautogolabrus adspersus*, they did not protect the juveniles from mud crabs *Neopanope sayi*. Johns & Mann (1987) found that bricks with vegetation reduced predation upon juvenile lobsters by cunners, but mortality was still high. Many investigators have assumed that if settling lobsters are able to build a burrow in an appropriate substrate they will be free from predation (Atema et al.

1982, Botero & Atema 1982, Pottle & Elner 1982, Aiken & Waddy 1986). Clearly, the above-mentioned experiments do not support this assumption in the literature.

Barshaw & Bryant-Rich (in press) found that lobsters started burrowing more quickly in eelgrass and rocks than in mud. Both Herrick (1895) and MacKay (1926) noted that juvenile lobsters were occasionally found in eelgrass. Thus, eelgrass, which had not been previously tested in conjunction with lobsters, might be an appropriate substrate for early juvenile lobsters and should be included in experiments comparing lobster behavior in different habitats. This experiment expands on the previous experiment of Lavalli & Barshaw (1986), by comparing the protective qualities of 3 substrates in which postlarval lobsters can burrow: mud, eelgrass and rocks, against the same 2 predator species used previously, cunners and mud crabs.

MATERIALS AND METHODS

Large seawater tables were divided into thirds by plastic partitions with holes which allowed water to flow through the sections, but prevented movement of

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EFFECTS OF DRILLING MUD ON THE BEHAVIOR, GROWTH AND SURVIVAL
OF EARLY JUVENILE LOBSTERS, HOMARUS AMERICANUS

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ABSTRACT

A long term study was conducted on the effects of J-5 drilling mud (DM) on early juvenile lobsters. Lobsters in the DM treatment settled significantly later and suffered higher mortality than lobsters in the barite/bentonite (BB) or Mud treatments. BB is the major constituent of DM, without its sometimes toxic additives. It was used to separate the purely physical effects of DM from those caused by added chemicals. Lobsters in both the DM and BB treatments lacked burrows for a significantly greater amount of time than the lobsters in the Mud treatment. However, the BB lobsters spent more time trying to build new burrows than did the DM lobsters. Finally there was a significantly lower biomass of other organisms residing in the sediments in the DM treatment than in the other two treatments. These data show that long term exposure to low levels of J-5 DM have deleterious effects on the survival and behavior of early juvenile lobsters and that the physical properties of DM alone caused part of the problem.

INTRODUCTION

Large quantities of drilling muds (DM) are discharged during offshore drilling for oil and gas (Meek and Ray, 1980). Drilling muds are complex mixtures of compounds that are used to: cool rotating bits, carry rock cuttings to the surface, lubricate drilling strings, and to act as a plaster to prevent the drilled rock formation from collapsing (Land, 1974; Wright, 1975). The base of most DMs is composed of clay i.e. barite/bentonite (BB), however, many chemicals are added to the clay mixture depending on the type of sediment being drilled in and the depth of the drilling operation. These additives include heavy metals and many fractions of petroleum hydrocarbons known to be toxic to marine organisms (Decoursey and Vernberg, 1972; Laporte and Talbott, 1977; Stekall et al., 1980; Cappuzzo and Lancaster, 1981). Table 1 shows the heavy metals and hydrocarbons found in the DM used in this study.

Most of the studies done on the effects of DMs on marine organisms have either been LC₅₀ tests to establish lethal concentrations (Cabrera, 1971; Chesser and McKenzie, 1975; Sprague and Logan, 1979), or have been short term or done under artificial conditions (Atema et al., 1982). However, to truly understand the effect that a pollutant will have on a species it is crucial to administer the chemical at relevant concentrations to determine the long term effects in its natural environment.

In this experiment we have done a long term study on how

GROWTH AND SURVIVAL OF EARLY JUVENILE AMERICAN LOBSTERS, *HOMARUS AMERICANUS*, ON A DIET OF PLANKTON

Larval American lobsters, *Homarus americanus*, are planktonic and are known to feed raptorially on zooplankton (Herrick 1895; Williams 1907; Templeman 1936). However, the benthic, postlarval stages of the American lobster are not routinely found in the field, and their natural habitat and feeding behavior are not known. Consequently, the natural diet of these stages is unknown. Stomach content analyses of larger juveniles and adult lobsters show that they feed on a great variety of benthic animals, including polychaetes, molluscs, macroalgae, and other crustaceans (Leavitt et al. 1979; Carter and Steele 1982).

Older juvenile and adult American lobsters, however, seem to have fundamental differences in their behavior compared with the early juvenile stages used in this study. Laboratory studies and field observations indicate that early juveniles are more (perhaps exclusively) shelter bound (as Cooper unpublished data in Cooper and Uzmann 1980; Lawton 1987; Barshaw and Bryant-Rich 1988). If the early juveniles do not forage for food outside of their burrows, they must feed in a different manner and on a different diet than that of older lobsters. During behavioral observations in naturalistic substrates, early juvenile lobsters were seen to generate a current through their U-shaped burrows by pleopod fanning (Barshaw and Bryant-Rich 1988). They appeared to catch and feed on the plankton that was carried in by this current. These observations form the basis for the hypothesis that early juvenile lobsters can feed upon plankton.

Materials and Methods

Stage IV lobster siblings from the Department of Fisheries and Oceans Laboratory, St. Andrews, New Brunswick, Canada were held in plankton "kreisels" (Hughes et al. 1972) for one day after being transported to Woods Hole, MA. These lobsters had all molted into Stage IV approximately two days before they were transported and were all fed on frozen brine shrimp until the experiment started. At the start of the experiment, individual lobsters were placed into 72 trays (22 cm long \times 6.4 cm wide \times 5 cm deep; water volume = 750 mL). Each tray was provided with filtered, ambient, running seawater, kept on a natural light/dark regime, and had an artificial lobster shelter made of black tubing glued to the bottom. The lobsters were allowed four

days to acclimate to the trays before the experiment began. During this time, all of the lobsters were fed once on frozen brine shrimp (*Artemia*), and any dead lobster was replaced by another sibling. The 72 lobsters were then randomly divided into three groups of 24; one group was starved, one group was fed daily on five frozen brine shrimp per lobster, and the last group was fed daily on plankton. Dead, settled plankton was not used; only plankton which appeared living was presented to the lobsters. The trays were cleaned daily and any uneaten shrimp or plankton were removed.

The plankton was collected every other day by plankton tows in the Woods Hole area. After collection, the plankton was sieved through a 1 mm mesh. Half of the plankton was kept alive for 24 hours, while the rest was fed to the lobsters immediately. Representative subsamples from the daily portions were rinsed with distilled water, filtered, dried, and weighed; the same was done with the daily portion of frozen brine shrimp.

For one hour at the onset of feeding, the flow of seawater through all the trays was stopped so that the plankton-fed lobsters had a chance to feed before the plankton was flushed out of the trays. During this hour, informal observations were made on the behavior of the feeding lobsters. Movements of the lobsters in the trays, pleopod-fanning and mouth part activity were observed.

The experiment continued until all surviving lobsters had completed two molts; this took 65 days, from 14 October to 17 December 1984. During that time, all molts and deaths were recorded. The lobsters' weight and carapace length (CL) were taken after 40 days and at the end of the experiment. To make these measurements, each lobster was carefully removed from its tray and placed on absorbent paper to remove excess water. The lobster was then weighed to 0.01 mg on a Mettler balance; CL was measured to the nearest 0.1 mm using calipers. This procedure took less than two minutes and did not appear to adversely affect the lobsters.

Results

There was no significant difference in American lobster survival between the group fed brine shrimp (75% survival) and the group fed plankton (83% survival). All of the starved lobsters died by day 39 of the experiment (Fig. 1). This group is significantly different from the other two (χ^2 , $P < 0.001$).

Nine of the starved lobsters molted to Stage V before dying. All of the surviving lobsters in the two

Deep burial as a refuge for lady crabs *Ovalipes ocellatus*: comparisons with blue crabs *Callinectes sapidus*

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ABSTRACT: Lady crabs *Ovalipes ocellatus* use a reversed gill current for respiration. Our evidence suggests that this adaptation allows small lady crabs to use deep burial in high energy sand habitats as a refuge from predation unavailable to other species of crabs. In laboratory experiments lady crabs buried deeper into sand than blue crabs *Callinectes sapidus*, and such burial was shown to protect lady crabs from predation by larger blue crabs. In field experiments lady crabs and blue crabs were tethered and placed in sand and macroalgae (*Ulva lactuca*)/mud habitats. In the sand habitat more of the small lady crabs survived than the small blue crabs. There was no difference in survival between large crabs of the 2 species. In a macroalgae/mud habitat there were no differences in survival between size classes of crabs or between the 2 species of crabs. These data help to explain the distribution of these crabs.

INTRODUCTION

Lady crabs *Ovalipes ocellatus* (Portunidae), one of the dominant decapods along the eastern coast of the United States (Epifanio 1988, Dittel & Epifanio 1982, Stehlik et al. unpubl.), range from Canada to Georgia (Williams 1984). The common habitats of these crabs are sandy beaches (Pearse et al. 1942, Leber 1982). They are also found in the high salinity portions of estuaries and over the continental shelf to depths of 100 m (Stehlik et al. unpubl.). Members of the genus *Ovalipes* are major predators of bivalves (*O. stephensoni*: Haefner 1985; *O. catharus*: Davidson 1986, Haddon et al. 1987). On the other hand the genus is an important prey item for other crabs and many species of fish including summer flounder, black seabass, striped bass, and Atlantic croaker (Stehlik et al. unpubl.). Despite the abundance of lady crabs and the important role they play in coastal ecosystems, there have been few ecological studies on this genus. In the following 3 experiments we investigated the burial depth and susceptibility of lady crabs to predation in the laboratory

and the field relative to the sympatric portunid *Callinectes sapidus* (blue crab).

METHODS AND MATERIALS

The crabs used in all 3 experiments were collected by trawling and seining in Great Bay, New Jersey, USA. Blue crabs and lady crabs were held separately in tanks with ambient running seawater and fed fish daily. Prior to each experiment all crabs were examined to ensure that they had all their appendages and were intermolt.

Burial depth. Sand collected from a high energy sand bar in Great Bay was placed to a depth of 15 cm in a plastic tray (60 cm long, 40 cm wide, 25 cm deep) and submerged in a seawater table with flowing, ambient (14 to 25 °C) seawater for 24 h. Individual crabs of both species were randomly selected, measured with calipers to determine carapace width (CW; 15 to 35 mm), and placed into the tray. If a crab buried before 5 min had elapsed, the time until burial was recorded and the depth of the crab in the substrate was determined at the anterior (minimum depth) and posterior (maximum depth) portion of the carapace using a stiff piece of wire calibrated in millimeters. The minimum and maximum depth to which each crab was buried was averaged for

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Tethering as a Technique for Assessing Predation Rates in Different Habitats: An Evaluation using Juvenile Lobsters *Homarus americanus*

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Tethering has been used successfully to assess predation rates of a variety of predator-prey systems in several different habitats. The majority of these experiments have used tethered crabs as prey (Heck and Thoman 1981, Wilson 1985, Wilson et al. 1987, Heck and Wilson 1988, Wilson et al. 1990, Barshaw and Able In press). Fish have also been tethered in different habitats; however, in these experiments the tethered fish could not act naturally, and therefore the technique only showed the differences in predator encounter rate in different habitats (Shulman 1985, McIvor and Odum 1988). Other organisms are presently being used in tethering experiments including molluscs (R.N. Lipcius and L.S. Marshall, Jr., Coll. William and Mary, Va. Inst. Mar. Sci., Gloucester Pt., VA 23062, unpubl. data) and spiny lobsters (Herrnkind and Butler 1986).

We determined if tethering was an appropriate technique to assess predation on species that burrow (i.e., juvenile lobsters *Homarus americanus*). Lobsters were chosen for this study, in part, because their behavior has been well studied and, therefore, a baseline of "normal" behaviors is available (Botero and

Atema 1982, Barshaw and Bryant-Rich 1988).

Lobsters use different methods of constructing burrows in different habitats; therefore we tested three habitats known to be important for early juvenile lobsters: mud, cobble, and *Spartina* peat (Able et al. 1988, Barshaw and Lavalli 1988).

Methods and materials

Six "ant farm" aquaria (10 cm wide, 30 cm long, 45 cm deep) were $2/3$ filled with either cohesive mud, cobble of a natural size distribution, or *Spartina* peat substrates (two replicates per substrate type) and provided with running, unfiltered seawater. Early juvenile lobsters (8–14 mm carapace length) were individually tethered to monofilament line using "super glue" to attach it to their carapace. Individual tethered lobsters were placed into half the tanks while similar-sized untethered control lobsters were placed into the remaining tanks.

A discrete reading of each lobster's behavior was recorded every

minute for the first 20 minutes, every 5 minutes for the next 35 minutes, and then every hour for 6 hours. A final assessment of each lobster's burrow was made after 24 hours. Therefore, each lobster was observed 33 times over 24 hours in each test. Seven tests were run using all the substrates, with two extra tests run only with mud; thus observations were made on a total of 14 lobsters in cobble, 14 in peat, and 26 in mud. The behaviors observed are described in Table 1.

The behaviors of the tethered and untethered lobsters were compared by calculating the percent of the 33 observations in which the lobsters were engaged in each of the behaviors for each test. Since this experiment was designed only to compare tethered and untethered lobsters, no comparisons were made between different behaviors or between different substrates (comparisons of that nature were studied in Barshaw and Bryant-Rich 1988). The percent of observations was transformed using the arc-sign transformation, and analyzed with a Student's *t* test. The numbers of the tethered and untethered lobsters that had burrows at the end of the experiment were analyzed for each substrate using 2×2 contingency tables and chi-square tests.

Results

The tethering of juvenile lobsters resulted in substrate-specific differences in behavior and the ability to construct burrows. There were no significant differences between the behavior of tethered and untethered lobsters in the peat or cobble substrates (Fig. 1); in both peat and cobble, all the tethered (7/7) and all the untethered (7/7) lobsters had burrows that they constructed and maintained throughout the experiment.

Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

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ANTI-PREDATOR BEHAVIORS OF THE MEDITERRANEAN SLIPPER LOBSTER, *SCYLLARIDES LATUS*

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ABSTRACT

Mediterranean slipper lobsters were tethered inside and outside an artificial reef to test shelter-based protection against predation. Mortality was significantly lower among the lobsters in the reef (7%) compared to those in the open area (77%), indicating that sheltering is an effective protective strategy. All predation was found to occur during the daylight. Lobsters tethered in the open were observed to camouflage by placing themselves alongside rocks, thus enhancing the effectiveness of their cryptic coloration. When detected, lobsters tended to initially cling to the substrate. Gray triggerfish were observed to prey upon lobsters in the open, but were only able to kill a lobster after breaking its hold on the substrate, catching it as it tried to swim away, and biting through its ventral exoskeleton.

Slipper lobsters, family Scyllaridae, lack obvious protective morphological features, e.g., powerful claws like Nephropidae (clawed lobsters) or sharp spines like Palinuridae (spiny lobsters) (Cobb, 1981; Zimmer-Faust et al., 1985). Experiments on the effect of predation on clawed and spiny lobsters have been done almost exclusively on the juvenile stages of these organisms because the adults are less vulnerable (Marx and Herrnkind, 1985; Lavalli and Barshaw, 1986; Herrnkind and Butler, 1986; Ford et al., 1988; Barshaw and Lavalli, 1988; Eggleston et al., 1990; Wahle and Steneck, 1991). Indeed, there is evidence that as the protective morphology of clawed and spiny lobsters develop their behavior changes from being escape-oriented to being defensive and able to stand their ground (Lang et al., 1977; Kanciruk, 1980; Zimmer-Faust et al., 1985; Zimmer-Faust and Spanier, 1987; Barshaw and Bryant-Rich, 1988; Spanier and Zimmer-Faust, 1988). For example, adult spiny lobsters, during migration, form protective pods with their spines pointing outward in a defensive circle (Kanciruk, 1980) and clawed lobsters change from quickly fleeing to standing their ground when their crusher claws start to develop (Lang et al., 1977; Barshaw and Bryant-Rich, 1988). Slipper lobsters, however, do not possess morphological weaponry and it has been suggested that even as adults they continue to rely on sheltering (Spanier et al., 1988), camouflage (Ogren, 1977), and escape (Spanier et al., 1991) to avoid being preyed upon. Slipper lobsters can swim more efficiently than palinurid lobsters (Jacklyn and Ritz, 1986) or than the cumbersome clawed lobsters (Newland et al., 1988, 1992). Laboratory experiments demonstrate that the escape swimming of the Mediterranean slipper lobster can be fast (up to $3.6 \text{ body lengths} \cdot \text{s}^{-1}$), although it is of short duration and consumes much energy compared to open water fish (Spanier et al., 1991).

In the past, experiments on the behavior and ecology of slipper lobsters were thwarted by the wide spread and deep water distribution of these lobsters and the difficulty of finding a stable population. To overcome these problems artificial reefs were built and placed at a depth of 18.5 m off the coast of Haifa, Israel. There, continuous studies could be conducted because the diving was relatively easy. The reefs were constructed of used car tires connected with 18 mm steel bars and weighed with concrete (see Spanier et al., 1988, 1990). Suitable natural shelters for the Mediterranean slipper lobster are rare and probably limiting off the coast of Israel. Lobsters were, therefore, quickly attracted to the artificial reefs

NOTE

Salt marsh peat reefs as protection for postlarval lobsters *Homarus americanus* from fish and crab predators: comparisons with other substrates

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ABSTRACT: This evaluation of habitat quality for early juvenile lobsters *Homarus americanus* was based on 2 measures: time to settle and degree of survival. Predation upon settling postlarval lobsters by fish (cunners *Tautogolabrus adspersus*) and crabs (green crabs *Carcinus maenas*) was compared in 3 different substrates (cobble, peat and sand). Cobble provided lobsters with significantly more protection from fish than either peat or sand, and peat provided significantly more protection than sand. Cobble also provided lobsters with significantly more protection from crabs than peat or sand. However, rates of predation between peat and sand were not consistent with crabs as the predator. The postlarvae quickly settled into cobble and peat, but delayed settling into sand, suggesting that cobble and peat were preferred habitats, which is generally consistent with the predation levels observed.

KEY WORDS: Lobster · *Homarus americanus* · Salt marsh · Predation · Habitat

The role of various substrates as refuges has been examined for early juvenile lobsters. Of the substrates tested, rock consistently provided the most protection, with eelgrass and mud providing better protection than sand (Roach 1983, Barshaw & Lavalli 1988, Wahle & Steneck 1992).

However, Able et al. (1988) found high densities (range 0 to 5.7 ind. m⁻², mean 2.5) of early juvenile lobsters *Homarus americanus* (<40 mm carapace length, CL) in a previously untested and undescribed habitat, salt marsh 'peat reefs' on Cape Cod, Massachusetts, USA. These consist of large (between 5 and 7 m long), irregular blocks of salt marsh peat and living marsh plants that break off from the marsh surface and fall into adjacent marsh creek channels. Green crabs

Carcinus maenas and the fish, cunners *Tautogolabrus adspersus* are some of the most abundant potential lobster predators found in this habitat (Able et al. 1988).

The purpose of this study was to evaluate the quality of peat reef as juvenile lobster habitat in comparison with 2 other substrates: cobble and sand, previously determined to be good and poor habitats, respectively (Botero & Atema 1982, Lavalli & Barshaw 1986, Barshaw & Lavalli 1988). Comparisons were based on 2 measures of habitat quality: time to settling and survival against 2 different types of predators, green crabs and cunners.

Materials and methods. Thirty-two replicate tanks (0.6 m wide, 0.8 m long, 0.6 m deep) were supplied with flowing, ambient, unfiltered seawater. Tanks contained either sand (10 cm deep), cobble (0.1 to 20 cm diameter, 12 cm deep) over a sand base, or peat reef (5 to 30 cm deep) also over a sand base. The cobble was collected from subtidal areas in Woods Hole, Massachusetts, while the peat reef was collected near the study area at Rutgers University Marine Field Station, Tuckerton, New Jersey, USA. For the first series of experiments (Run 1) 14 tanks were designated as predator-free controls. The remaining 18 were divided evenly between the 3 substrates and 2 predator species (Table 1).

After a 1 wk acclimation period for the substrates, 10 (= 20.8 m⁻²) late (reared) Stage IV lobsters were placed into each of the tanks in Run 1. Lobsters were allowed 2 d to settle and build burrows, and were fed daily with frozen brine shrimp. After 2 d feeding was terminated and predators introduced. Either 3 cunners (= 6.2 m⁻², 55 to 120 mm total length, TL) or 5 green crabs (= 10.4 m⁻², 35 to 65 mm carapace width, CW) were placed in each experimental tank. Predators were left for 4 d

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THE UNDISCOVERED LOBSTER: A FIRST LOOK
AT THE SOCIAL BEHAVIOUR OF THE
MEDITERRANEAN SLIPPER LOBSTER, *SCYLLARIDES LATUS*
(DECAPODA, SCYLLARIDAE)

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ABSTRACT

To investigate the behaviour of *Scyllarides latus* we built a 3000 l tank with one glass side for observations, setup with ambient, unfiltered, running seawater and a natural assemblage of organisms. Half of the bottom was covered with a substrate made up of large biogenic rocks resembling the rocky reefs where the lobsters are abundant, the other half was covered with bare sand. Eight lobsters, 3 males and 5 females, were tagged and placed in the tanks. Lobsters initially spent significantly more time on the rock substrate, however, after two months they ceased to show a preference. After five months we added two large and two small concrete shelters, placed against the glass for observation. Lobsters preferred to reside together in the large rock shelter. In aggressive displays, usually in competition for food, the slipper lobsters displayed some distinctive behaviour patterns all centered around dislodging the opponent from its grip on the substrate. A dominance matrix made from tallying these aggressive encounters revealed a fairly linear dominance hierarchy amongst lobsters in the tank with the largest female in the dominant position.

RÉSUMÉ

Afin d'étudier le comportement de *Scyllarides latus*, nous avons construit un bac de 3000 l comportant une face en verre pour les observations, alimenté en eau de mer courante, à température ambiante, non filtrée et contenant une association naturelle de divers organismes. La moitié du fond a été recouverte d'un substrat constitué de gros rochers en matière biogénique ressemblant aux rochers de récifs naturels où l'on trouve les langoustes en abondance, l'autre moitié a été recouverte de sable nu. Huit scyllares, 3 mâles et 5 femelles, ont été marqués et placés dans les bacs. Au début, les animaux ont passé significativement plus de temps sur le substrat rocheux; cependant après deux mois, ils ont cessé de montrer une préférence. Après cinq mois, nous avons ajouté deux grands et deux petits abris en ciment, placés contre la vitre pour l'observation. Les scyllares ont préféré demeurer ensemble dans le grand abri. Lors de manifestations agressives, habituellement en compétition pour la nourriture, les scyllares ont présenté des modèles de comportement différents, mais tous dans le but de déloger l'adversaire de sa prise sur le substrat.

An analysis of substrate selection by postlarval American lobsters, *Homarus americanus*, using a dynamic optimization model

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During the fourth stage of larval development the American lobster (*Homarus americanus*) leaves the plankton and becomes benthic. Before final settlement lobsters sample different substrates which may be accepted or rejected. Upon rejection the lobster returns to the plankton before sampling another substrate. In this paper we present a model of the substrate selection behavior of settling lobsters using dynamic optimization techniques. The model examines the role of substrate quality and availability, postlarval testing of substrates, and mortality associated with testing substrates, upon the decision to accept or reject the substrates sampled and predicts the eventual importance of each substrate in the recruitment of lobsters to reproductive age. Finally we apply the model using recent data on long-term survival of lobsters in the field. The model predicts that the high quality substrate (cobble) accounts for most of the adult lobster population, in spite of the much greater abundance of other, more marginal, substrates.

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Recent data on the probability of a lobster surviving from settlement until reproductive age (Bannister et al. 1994) allow us, for the first time, to actually model the optimal settlement strategy of postlarval lobsters using a dynamic optimization type of model, though we presented a hypothetical version of this model previously (Bryant-Rich and Barshaw 1988). This method allows the factors that influence an animal when making a certain choice to change. For example, if the danger of predation decreases with the size of the organism, a dynamic model would allow the organism to change its decisions depending upon its size. The added complexity of these models is made possible by using discrete-time, stochastic programming and the use of computers, rather than attempting to solve the model analytically (Mangel and Clark 1988). Dynamic

optimization models often focus on tradeoffs, particularly those tradeoffs in which the time course of a choice is important. In this paper we will use this type of model on the process of settlement in postlarval American lobsters.

The tradeoffs in testing substrates

Postlarvae (Stage IV) of the American lobster test substrates by making vertical dives through the water column before settling permanently (Cobb et al. 1983, 1989, Bertran et al. 1985). There are also data that show that Stage IV lobsters choose between substrates, at least over small areas (*H. gammarus* – Howard and Bennett 1979; *H. americanus* – Botero and Atema 1982, Pottle and Elner 1982). Furthermore, if

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Offense versus defense: responses of three morphological types of lobsters to predation

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ABSTRACT: We compared the antipredator mechanisms of 3 morphological 'types' of lobsters: slipper lobsters *Scyllarides latus*, spiny lobsters *Palinurus elephas* and clawed lobsters *Homarus gammarus*. These lobsters differ in the extent and effectiveness of their weaponry and armor, which we assessed by: (1) field tethering experiments that compared relative survival of intact and manipulated (clinging ability, antennae, or claws removed) lobsters in the face of predation, and (2) measurements of the breaking strength and thickness of the carapace of each species. Intact clawed lobsters suffered higher mortality than either intact slipper or spiny lobsters after both 4 and 24 h. At 24 h, intact spiny lobsters also had higher mortality than intact and manipulated slipper lobsters. The intact spiny and clawed lobsters suffered less predation after 4 h than the manipulated lobsters (lacking weapons); however, this advantage diminished or vanished by 24 h. This indicates that weapons provided some measure of protection in the short-term, which might be sufficient to allow the lobsters to escape from a predator using a strong abdominal tail flip. Triggerfish *Balistes carolinensis* were the primary predators on the lobsters. We also saw octopuses *Octopus vulgaris* feeding on lobsters, but these were never observed subduing a live lobster. 'Punch'-tests (i.e. puncture tests) on the carapaces of each of the 3 species showed that slipper lobsters had stronger armor than either spiny or clawed lobsters, while the spiny lobster armor was intermediate in strength. These results suggest that the defensive strong armor of slipper lobsters is a more effective antipredatory mechanism than the offensive morphological weapons of the spiny and clawed lobsters.

KEY WORDS: Predator-prey interactions · Predator-avoidance · Antipredator mechanisms · Weapons · Armor · Lobsters · *Scyllarides latus* · *Palinurus elephas* · *Homarus gammarus*

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INTRODUCTION

Related groups of animals can vary greatly in the morphology of certain characters. A possible cause of these variations is the interaction between predators and prey, since predation is an important selective force affecting the fitness of all individuals in prey populations (Edmunds 1974, Harvey & Greenwood 1978, Sih 1987, Vermeij 1987). Predators affect aspects of their prey beyond that of morphology: they also affect their prey's chemistry, physiology, ecology, and behavior (e.g. Sih 1987), and cause the evolution of a variety of defense traits which Janzen (1981)

argues are more diverse than any other array of traits.

Defense traits were traditionally lumped together under the heading of 'antipredator characteristics' (Edmunds 1974, Vermeij 1982), and it was debated whether their evolution required that some prey survived attacks (i.e. 'unsuccessful' or 'incomplete' predation) (Vermeij 1982, 1985, Sih 1985). Subsequently, Sih (1987) and Brodie et al. (1991) divided antipredator characteristics into 2 categories based on whether they functioned before or after a predator detected its prey, i.e. predator-avoidance mechanisms and antipredator mechanisms. Predator-avoidance mechanisms enable