Effects of Prior Experience on Shelter-Seeking Behavior of Juvenile American Lobsters

SKYLAR R. BAYER[1,*,†], KATHERINE M. BIANCHI[1,‡],
JELLE ATEMA[1,§], AND MOLLY W. JACOBS[1,¶]

[1] *Woods Hole Oceanographic Institution, 266 Woods Hole Road, Woods Hole, Massachusetts 02543*

Abstract. Shelter-seeking behaviors are vital for survival for a range of juvenile benthic organisms. These behaviors may be innate or they may be affected by prior experience. After hatching, American lobsters *Homarus americanus* likely first come into contact with shelter during the late postlarval (decapodid) stage, known as stage IV. After the subsequent molt to the first juvenile stage (stage V), they are entirely benthic and are thought to be highly cryptic. We hypothesized that postlarval (stage IV) experience with shelter would carry over into the first juvenile stage (stage V) and reduce the time needed for juveniles to locate and enter shelters (sheltering). We found some evidence of a carryover effect, but not the one we predicted: stage V juveniles with postlarval shelter experience took significantly *longer* to initiate sheltering. We also hypothesized that stage V juveniles would demonstrate learning by relocating shelters more quickly with immediate prior experience. Our findings were mixed. In a maze, juveniles with immediate prior experience were faster to regain visual contact with shelter, suggesting that they had learned the location of the shelter. In contrast, there was no significant effect of immediate prior experience on time to initiate sheltering in an open arena, or in the maze after juveniles had regained visual contact. We conclude that very young (stage V) juvenile lobsters modify their shelter-seeking behavior based on prior experiences across several timescales. Ecologically relevant variation in habitat exposure among postlarval and early juvenile lobsters may influence successful recruitment in this culturally and commercially important fishery species.

* To whom correspondence should be addressed. E-mail: skylar.bayer @maine.edu

† Current address: Darling Marine Center, University of Maine, School of Marine Sciences, 193 Clark's Cove Road, Walpole, Maine 04573

‡ Current address: Mount Holyoke College, 50 College Street, South Hadley, Massachusetts 01075

§ Current address: Boston University Marine Program, Boston, Massachusetts 02215

¶ Current address: McDaniel College, 2 College Hill, Westminster, Maryland 21157

Introduction

Most benthic organisms are vulnerable to predators throughout their life histories, and particularly during their early development. Classes of vulnerable size often rely on shelters for protection from predators, and limited availability of habitat refugia may cause demographic bottlenecks (Werner and Gilliam, 1984). Therefore, shelter-seeking behaviors may be critical during settlement and the early juvenile stages.

Shelter-seeking behaviors have been documented for a wide range of juvenile organisms, from reef fish (Shulman, 1985) to crayfish (Figler *et al.*, 1999). Commercially important fishery species such as the Nassau grouper *Epinephelus striatus* (Dahlgren and Eggleston, 2000), Caribbean spiny lobster *Panulirus argus* (Eggleston and Lipcius, 1992), New Zealand rock lobster *Jasus edwardsii* (Butler *et al.*, 1999), stone crab *Menippe mercenaria* (Beck, 1995), and American lobster *Homarus americanus* (Wahle and Steneck, 1992) are all highly mobile as pelagic larvae and as adults, but are shelter-restricted as early juveniles. Understanding how shelter-seeking behaviors vary across a species' life history and how early juveniles find shelter may be critically important to the conservation and management of important fisheries species such as *H. americanus* (Botero and Atema, 1982; Wahle and Steneck, 1992).

The American lobster *Homarus americanus* is a commercially important crustacean with a planktotrophic larval stage that can last for several weeks. It exhibits shelter-seeking behavior in late larval stages (Botero and Atema, 1982) and throughout its benthic life history, from foraging juvenile (Lawton, 1987; Rossong *et al.*, 2011) to mating adult (Cowan

and Atema, 1990; Hovel and Wahle, 2010). Shelter limitation may have important demographic consequences for adult lobsters (Karnofsky *et al.*, 1989; Steneck, 2006), and has been suggested as a potential demographic bottleneck for juveniles in the Gulf of Maine (Wahle and Steneck, 1991). Behavioral observations suggest that initial shelter-seeking behavior during settlement is innate (Botero and Atema, 1982), while shelter-seeking behavior after settlement in the context of shelter relocation or other post-settlement movements may be influenced by prior experiences.

Homerus americanus larvae and postlarvae in the field are typically found in the upper portion of the water column, regardless of the time of day (Harding *et al.*, 1987; Annis, 2005). Young postlarvae display photopositive behavior in the laboratory, while older postlarvae appear to be photonegative (Hadley, 1905; Botero and Atema, 1982). Adult lobsters typically are also photonegative (Karnofsky *et al.*, 1989). All negative phototactic behavioral patterns of early benthic-stage juveniles are based on observations of hatchery-reared lobsters, either in the laboratory, natural aquaria, or in the wild (Ennis, 1973; Botero and Atema, 1982; Cobb *et al.*, 1989). In laboratory studies, photonegativity may be confounded with shelter seeking because shelters appear dark.

The juvenile stage of *H. americanus* is thought to be largely shelter-restricted to avoid demersal fish predators (Barshaw and Lavalli, 1988; Wahle and Steneck, 1992; reviewed in Lawton and Lavalli, 1995). Highlighting the importance of shelter in *H. americanus*, Nielsen and McGaw (2016) found that juveniles (15–27 mm carapace length [CL]) prioritized shelter over ideal temperature regimes and food availability. Wahle (1992) demonstrated that in the presence of a predatory fish, *H. americanus* juveniles display an ontogenetic shift in behavior, from hiding at ~5 mm CL to showing aggressive displays at larger sizes (CL ~40 mm). Similarly, Rossong *et al.* (2011) showed that juvenile lobsters with CL < 35 mm increased sheltering behavior in response to predatory crabs, while juveniles with CL > 35 mm were unaffected. Juvenile lobsters typically reach 5 mm CL within their first year of life (Wahle and Incze, 1997), suggesting that very young juveniles should be the most cryptic and show the strongest shelter-seeking behaviors.

Spatial learning has been demonstrated in a wide range of mobile benthic crustaceans (Vannini and Cannicci, 1995), and there is some evidence of spatial learning during long-distance homing behavior in adult *H. americanus* (Pezzack and Duggan, 1986; Karnofsky *et al.*, 1989). One-year-old juvenile European lobsters *Homarus gammarus* exposed to shelter can locate and settle into shelter more quickly than inexperienced juveniles (van der Meeren, 2001). However, spatial learning and navigation have not been studied in *H. americanus* juveniles or, to our knowledge, in any decapod at very young (< 1 y) juvenile stages.

Homerus americanus postlarvae (stage IV) (Botero and Atema, 1982) and at early juvenile stages (Johns and Mann,

1987; Wahle and Steneck, 1992) are selective about habitat, preferring cobble and macroalgae to sand, consolidated mud, and gravel (Cooper and Uzmann, 1980; Wahle *et al.*, 2009); but they are remarkably efficient in making burrows in mud if it is the only available substrate (Botero and Atema, 1982). In the Gulf of Maine, settlement density is highest in shallow subtidal cobble habitats (Wahle and Steneck, 1992; Incze *et al.*, 1997; Wahle and Incze, 1997). However, these habitats are relatively rare (11% of 60.2 km of shoreline) in mid-coast Maine (Wahle and Steneck, 1991). Given the limited availability of habitat, crowding and competition for shelter are likely during early juvenile life.

Larval experiences affect juvenile performance in a broad array of organisms (reviewed by Pechenik, 2006), but studies of these "carryover effects" typically have focused on physiological and morphological effects, not on learning or behavior. American lobsters are ideal candidates in which to study behavioral carryover effects because postlarvae are morphologically very similar to juveniles and spend time in benthic juvenile habitats. Thus, habitat information learned by postlarvae has a high likelihood of being useful to early instar juveniles. Postlarval experience with juvenile habitat is also likely to vary widely across lobster populations; postlarvae that spend more development time in shallow nursery habitats may accumulate extensive shelter experience, while postlarvae that travel long distances in the plankton cannot accumulate benthic experience prior to settlement.

We examined the effect of shelter experience on shelter-seeking behaviors in newly metamorphosed (stage V, CL < 5 mm) juvenile lobsters across long-term (days) and short-term (min) time scales. We hypothesized that a) postlarval (stage IV) experiences with shelter would carry over into the first juvenile stage and thus reduce the time to locate shelters and initiate sheltering behavior, and b) newly molted, first instar (stage V) juveniles would learn the location of shelters and relocate them more quickly with immediate prior experience.

Materials and Methods

All rearing and experiments took place indoors in the Environmental Systems Laboratory at Woods Hole Oceanographic Institution (WHOI), using ambient temperature flow-through seawater (18–20 °C). Sand and cobbles were collected from the beach near WHOI and washed in flow-through seawater for at least two weeks prior to the start of the experiments. Lobster larvae were collected at hatching and were reared in large kreisels (*i.e.*, smooth-sided upwelling tanks designed for culturing planktonic organisms; Hughes *et al.*, 1974) until they metamorphosed into postlarvae (stage IV). Immediately after they metamorphosed, postlarvae were transferred to 1 of 2 large (244-cm diameter, ~60 cm depth) arenas featuring flow-through seawater entering along the side and draining from a central standpipe. "Naive" postlarvae were placed

in an arena containing only a 5-cm layer of sand on the bottom, while "conditioned" postlarvae were placed in a "conditioning arena" containing a 5-cm layer of sand and 7 ~15-cm diameter piles of cobble ("cobble shelters") spaced around the perimeter (Fig. 1A). The cobble shelters were not glued together and could be easily dismantled to retrieve test subjects. Cobbles were large enough (2–5 cm) to prevent displacement by the activities of the juvenile lobsters during the experiments. Both tanks received a continuous inflow of seawater, which exited through a standpipe. The standpipe was securely covered in mesh to prevent the loss of swimming postlarvae. The population in each arena changed daily as new postlarvae entered and older individuals were removed (when they died or molted to stage V), but postlarval densities of 10–15 individuals were maintained in each arena throughout the culture period. Our pilot experiments in the same tank indicated no effect of crowding on shelter choice at postlarval densities less than 20, and the cobble shelters readily accommodated 3–4 individuals in separate areas of the cobble (M. W. Jacobs, unpubl. data). All postlarvae were fed twice per day following the rotation diet suggested by Tlusty *et al.* (2005). When postlarvae molted into first instar (stage V) juveniles, they were removed from their respective arenas and placed individually into mesh holding pens located in a flow-through sea table. All juveniles did not vary greatly in size based on visual assessment (CL ~0.5 cm) and were tested within 24–48 h of molting to stage V.

Experiment 1: Effect of postlarval conditioning with shelter on juvenile shelter-seeking behavior

We compared the shelter-seeking behavior of sand-arena (naive) *versus* shelter-arena (conditioned) stage V juveniles in a 244-cm diameter, circular open arena with continuous seawater flow, covered by a 5-cm layer of sand but containing only a single rock pile shelter (Fig. 1B). The shelter was visible from all areas of the arena except for a small region located immediately behind the central standpipe. We divided the open arena into three uneven areas based on distance from the shelter: the shelter itself, the area within 10 body lengths of the shelter, and the rest of the tank (greater than 10 body lengths from the shelter, approximately 89% of the tank). A line of pebbles (diameter < 1 cm) pressed into the sand denoted these concentric rings around the shelter (Fig. 1B).

American lobsters are thought to be more active at night and more shelter-restricted during the day (Karnofsky *et al.*, 1989). All trials were conducted during daylight hours (between 09:00 and 17:00) by a single observer (S. Bayer) who was blind to the treatment group (naive or conditioned) of the juveniles being tested. At the start of each trial, the observer transferred a single stage V juvenile from its mesh holding pen to a mesh acclimation pen in the open arena, using gentle suction from a wide mouth turkey baster. After the stage V juvenile's 2-min acclimation period, the pen was removed and the observer recorded the location of the juvenile every 5 s for 5 min (Gerlach *et al.*, 2007). Juvenile location was a categorical variable with three possible values: "shelter" if any part of the juvenile was in contact with the shelter, "within 10 body lengths" if any part of the juvenile was touching the line or within the 10 body lengths of the line but not in contact with the shelter, or "rest of the tank" (all other locations).

The 5-min time period was chosen based on prior behavioral work (Gerlach *et al.*, 2007) on behavioral observations of more than 250 postlarvae in a similar arena, in which about 75 percent initiated settlement within 5 min of exposure to shelter (M. W. Jacobs and N. Shutari, unpubl. data), and on a pilot experiment in which 5 of 5 newly metamorphosed juve-
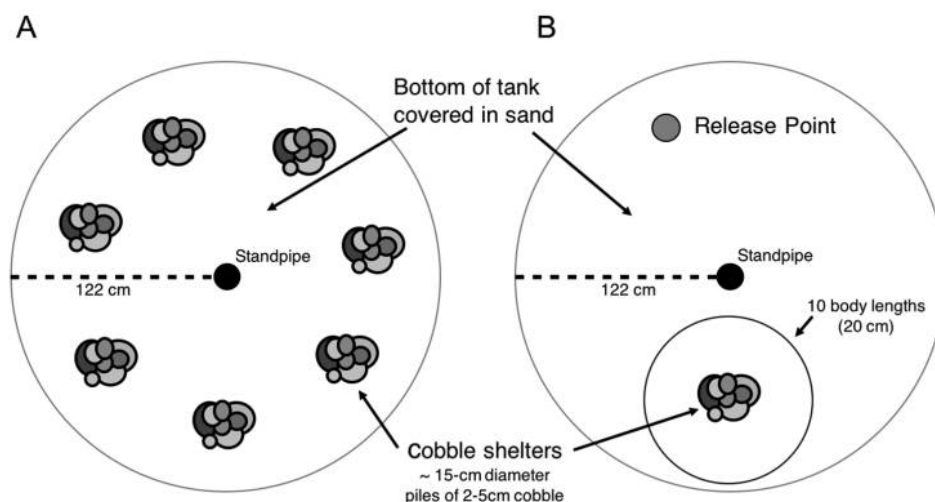

Figure 1. (A) Tank used for conditioning postlarvae for the open arena experiment. (B) Open arena, used to measure settlement behavior as a function of conditioning treatment and immediate prior experience.

niles initiated settlement within 5 min (S.R. Bayer and M.W. Jacobs, unpubl. data). The juvenile was considered to have initiated sheltering if it came in contact with the shelter and remained there for at least 2 min after initial shelter contact. Six of 18 naive and 5 of 19 conditioned juveniles (30% overall) did not initiate sheltering within the 5-min trial period. These individuals were monitored for an additional 15 min to see if sheltering occurred, although the location of the juvenile was no longer recorded every 5 s. The shelter was dismantled between trials and allowed to flush with flow-through seawater for at least 5 min before reconstruction.

We tested our data for normality using Shapiro-Wilk tests and for homogeneity of variance using Levene's test, and then the data were transformed by log $(x+1)$ to homogenize variances and normalize distributions. We used *t*-tests to compare sheltering times between naive and conditioned stage V juveniles. For all juveniles that initiated sheltering during the 5-min trial, we compared total time to initiate sheltering, and time to initiate sheltering after coming within 10 body lengths of the shelter. We also compared total time to initiate sheltering for the longer dataset (all individuals that initiated sheltering within 20 min).

Experiment 2: Effect of immediate prior experience with shelter on stage V shelter-seeking behavior

We tested the hypothesis that stage V juveniles would learn the location of shelter and find shelter faster with immediate prior experience in two environments: the open arena described above for Experiment 1 (Fig. 1B) and a maze (Fig. 2). First, all sheltered juveniles from Experiment 1 were gently removed from their shelters after 2 min. Cobbles were removed one at a time until the juvenile was visible, and then gentle suction from a wide mouth turkey baster was used to collect the juveniles and place them back into the mesh holding pen at the release point. After 2 min of reacclimation, ju-
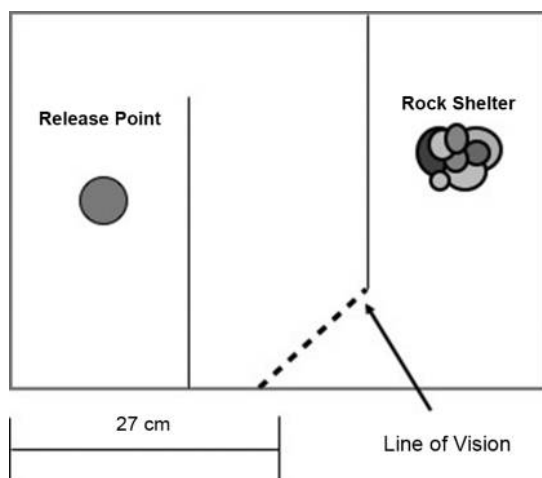

Figure 2. Maze used to measure settlement behaviors as a function of immediate prior experience.

veniles were re-released and monitored, as described in Experiment 1. We used repeated measures ANOVA to compare time to initiate sheltering between the two trials, with treatment group (naive juveniles *vs.* conditioned juveniles) as a fixed factor.

Second, we designed a simple flow-through maze within a 54×38 cm tank with a sand-covered floor and a rock shelter at one end of the tank (Fig. 2). We marked the line of sight, defined as the location where juveniles could come into visual contact with the shelter, about 5–10 body lengths away from the shelter (Fig. 2). Rhodamine dye-tracing experiments revealed that the bulk of the seawater flow (4–6 cm s^{-1}) moved steadily from the lobster release point toward the shelter, although a small countercurrent also moved along the bottom of the tank in the opposite direction.

For the maze experiment, we used a separate set ($n = 39$) of newly molted stage V juveniles from naive postlarvae. Juveniles were gently transferred to a mesh cage at the release point, using a wide mouth turkey baster, allowed to acclimate there for 2 min, and then released (trial 1). A single observer (K. Bianchi) recorded the time when the juvenile first crossed the line of sight, and the total time to initiate sheltering, defined as for the arena experiments above (juveniles were considered sheltered when they remained in the shelter for 2 min after initial contact with the shelter). Sheltered juveniles were removed as described above for the arena experiments, reacclimated for 2 min, and then immediately re-released and monitored as before (trial 2).

We tested the data for normality using Shapiro-Wilk tests and for homogeneity of variance using Levene's test, and then the data were transformed by log $(x+1)$. This transformation homogenized variances in all cases and also normalized distributions in all cases except for the time from crossing the line of sight until sheltering. We used a paired *t*-test to compare time from release until crossing the line of sight between trials 1 and trial 2, and a Wilcoxon signed rank test to compare time from crossing the line of sight until initiation of sheltering between trials 1 and 2. We also used a chi-square test to compare the number of juveniles that sheltered in trial 1 with those in trial 2, based on the results of the experiment (expected values for both trials were as follows: sheltered = 32.5 juveniles, non-sheltered = 6.5 juveniles; df = 1).

Results

Effect of postlarval conditioning on time to initiate sheltering

During the 5-min trial period in the open arena, conditioned stage V juveniles (exposed to shelter as postlarvae) took significantly longer than naive juveniles to initiate sheltering during trial 1 (Fig. 3A, $t_{24} = 2.35$, $P = 0.03$). These juveniles also took significantly longer to initiate sheltering after coming within 10 body lengths of the shelter (Fig. 3C, $t_{24} = 2.37$, $P = 0.03$). When individuals that failed to initiate sheltering
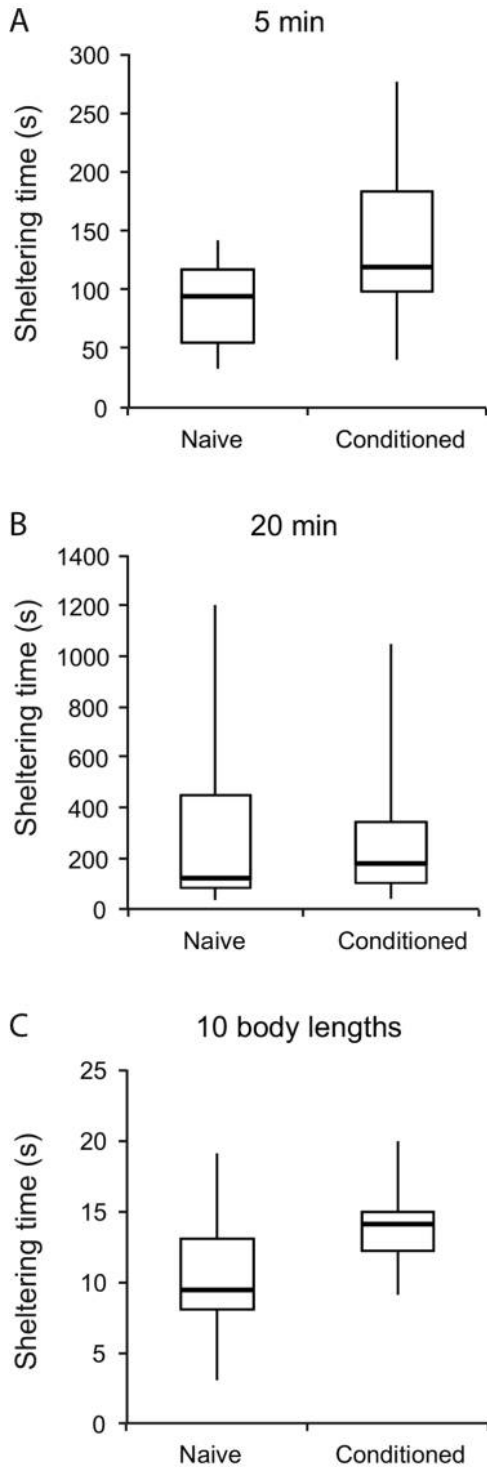
Figure 3. Box and whisker plots displaying maximum, minimum, upper and lower quartiles, and median times to initiate sheltering for naive *versus* conditioned stage V juveniles for the (A) 5-min trial period, (B) 20-min trial period, and (C) from 10 body lengths from the shelter.

within 5 min were included (the 20-min data set), there was no significant effect of postlarval shelter conditioning on time to initiate sheltering (Fig. 3B, $t_{35} = 1.29$, $P = 0.20$).

Effect of immediate prior experience on time to initiate sheltering

In the open arena, where juveniles had a clear line of sight to the shelter at all times, there was no significant difference in time from release to initiation of sheltering between trials 1 and 2 ($t_{36} = 1.48$, $P = 0.148$), regardless of conditioning treatment (Fig. 4, $F_{1,35} = 1.27$, $P = 0.27$). Thirty-six of 37 juveniles sheltered within the 20-min time limit during trial 1, and all 37 juveniles sheltered within 20 min in trial 2.

In the maze, juveniles took significantly less time to reach the line of sight during trial 1 (Fig. 5, $t_{38} = -2.23$, $P = 0.03$). Once juveniles crossed the line of sight, there was no significant difference between trials in the time it took for juveniles to initiate sheltering (Fig. 5, $W = -24.5$, $P = 0.54$). Interestingly, the percentage of juveniles that sheltered within 20 min decreased from 100 percent in trial 1 to 67 percent in trial 2 ($\chi^2 = 15.6$; $P < 0.0001$). Of the 13 juveniles that failed to settle, 7 made contact with the shelter but never initiated sheltering behavior, and 6 failed to make contact with the shelter at all.

Discussion

Behavioral carryover effect

We observed a potential behavioral carryover effect between postlarvae (stage IV) and first instar juveniles (stage V); however, contrary to our hypothesis, juveniles that had been exposed to shelter as postlarvae took *longer* to initiate sheltering over short time scales. This result was surprising because early instar juveniles are broadly characterized as being extremely cryptic and shelter-restricted (reviewed in Lawton and Lavalli, 1995), and we predicted that prior experience would facilitate faster sheltering.
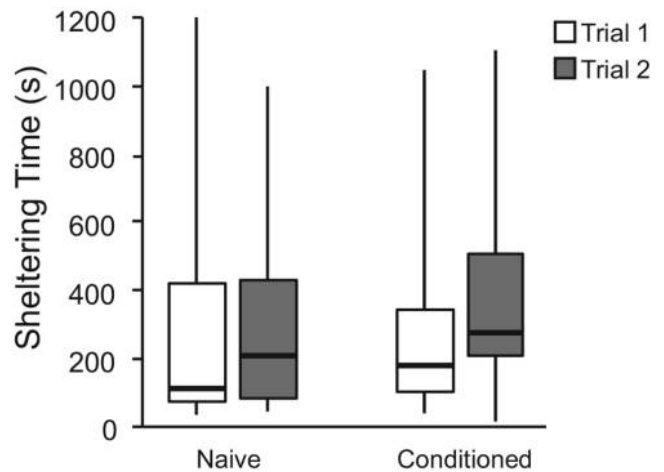

Figure 4. Box and whisker plots displaying maximum, minimum, upper and lower quartiles, and median times to initiate sheltering in the open arena as a function of immediate prior experience (trial 1 *vs.* trial 2) and conditioning treatment (naive *vs.* conditioned).
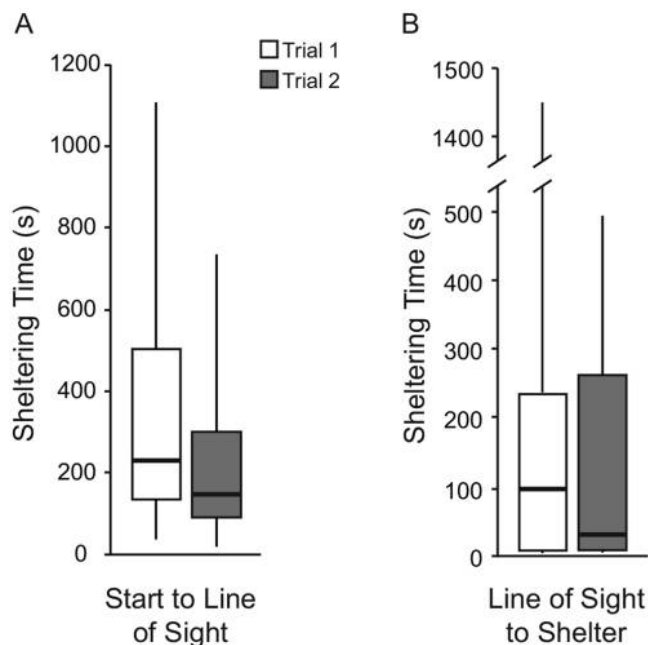
Figure 5. Box and whisker plots displaying maximum, minimum, upper and lower quartiles, and median times from release to the line of sight (LOS) and from LOS to shelter as a function of immediate prior experience (trial 1 *vs.* trial 2).

Juveniles with postlarval experience may be slower to initiate sheltering because they spend more time sampling their environments or engaging in other benthic-specific behaviors. Our experiments were not designed to test for this, although qualitatively we did not observe any obvious behavioral differences between juveniles in the two treatment groups. Alternatively, juveniles with postlarval shelter experience may be more selective about shelter location. Data from hatchery-reared *versus* wild-caught juvenile fish (reviewed in Huntingford, 2004) are consistent with this premise: wild-caught red drum *Sciaenops ocellatus* juveniles strongly prefer structured habitat, but hatchery-reared juveniles are far less selective (Stunz *et al.*, 2001).

There are several potential causes of increased selectivity. Juveniles may alter their sheltering behavior based on their postlarval experiences: juveniles from postlarvae reared in the presence of shelters may be more selective because they have learned that shelters are abundant, while juveniles from naive postlarvae may base their initial behavior on the premise that shelters are rare. It is also possible that juveniles from experienced postlarvae were more selective because they were more cautious. Shelters in the postlarval conditioning arena were sometimes disturbed in order to remove newly molted juveniles or to census remaining postlarvae, and so juveniles with these experiences may have been more cautious about reentering a similar-appearing rock pile shelter during the behavioral trial. Crustaceans are known to learn shelter aversion very quickly in some circumstances. For example, Magee and Elwood (2013) found that the shore crab *Carcinus*

maenas learns to avoid specific shelters in response to very strong negative stimuli (electric shocks) after only two experiences. However, their control crabs were handled in a manner that was very similar to our protocol (removed from their shelters after 2 min and then re-released), and they did not display any decrease in shelter-seeking behavior across ten trials. We also did not observe any evidence of learned shelter aversion in the maze trials. These results suggest that a single, gentle removal from a shelter is unlikely to trigger shelter aversion in benthic crabs and lobsters.

Finally, it may be important to differentiate between innate shelter-seeking behavior during initial settlement and other subsequent shelter-seeking behaviors that may be influenced by prior experience. Initial settlement would have occurred during the postlarval stage (stage IV) in our conditioned treatment but during trial 1 of our experiments in the naive treatment. It is possible that naive and conditioned juveniles behaved differently because naive juveniles were engaging in settlement, an innate behavior, while conditioned juveniles were engaged in post-settlement exploration and shelter seeking.

Spatial learning and navigation behavior

Some of our results suggest that very young (stage V) juvenile lobsters can learn the locations of shelters, but our findings are mixed. In the maze, lobsters reached the line of sight more quickly in trial 2. A compelling explanation—and one that is consistent with our hypothesis and with evidence from adult crustaceans (*e.g.*, Cannicci *et al.*, 2000; Boles and Lohmann, 2003; Layne *et al.*, 2003a, b; Kamran and Moore, 2015)—is that juveniles learned the location of the shelter during trial 1 and were thus able to navigate back to it more quickly in trial 2.

In the open arena, in contrast, we observed no difference in sheltering time between trials 1 and 2. We also observed no difference in sheltering time in the maze after the lobsters had crossed the line of sight. If the juveniles did not learn the location of shelters, then an alternative explanation is required for why they reached the line of sight faster in trial 2 in the maze. Conversely, if the juveniles did learn the location of shelters, then an alternative explanation is required for why they failed to return to the shelters faster in trial 2 in the open arena (and after the line of sight in the maze).

It is possible that juveniles during trial 2 in the maze randomly encountered the shelter faster because they increased their overall activity levels (Gilliam and Fraser, 2001; but see also Lima and Dill, 1990). We did not quantify total activity level and thus cannot reject this explanation, but it is unclear why the increased activity would apply only to the maze, and only before the juveniles crossed the line of sight.

An intriguing alternate explanation is that we underestimated the importance of exploratory behaviors in early juveniles. Juvenile lobsters are known to avoid open spaces in

both the laboratory (Johns and Mann, 1987) and the field (Wahle, 1992; Wahle and Steneck, 1992), and our experiments were based on the premise that newly molted (stage V) juvenile lobsters are extremely cryptic (Lawton and Lavalli, 1995) and should be strongly motivated to find shelter as quickly as possible. Periodic benthic explorations by juvenile lobsters to find shelter are highly risky (Wahle and Steneck, 1991), but may be critical for survival because shelter limitation is thought to contribute to a population bottleneck amongst newly settled juvenile lobsters (Wahle and Steneck, 1992; Wahle and Incze, 1997).

Consistent with this idea, Pottle and Elner (1982) demonstrated that some juvenile American lobsters move between multiple shelters, and Castro and Cobb (2005) found that wild-caught, stage V juvenile lobsters kept in dark conditions spend significant periods of time foraging instead of sheltering. Our results suggest that even during daylight hours, juvenile lobsters sometimes prioritize exploration over shelter fidelity. Experience with shelter in the postlarval (stage IV) and early juvenile (stage V) stages may facilitate this exploration.

Importance of vision

Our findings suggest an interesting potential role for vision in sheltering behavior. Immediate prior experience did *not* decrease sheltering time in the open arena, where lobsters had a clear line of sight to the shelter at all times, or in the maze after the lobster had crossed the line of sight. In the maze, the proportion sheltering also decreased after trial 2. Our experiments were not designed to specifically examine the role of vision in sheltering behavior, but, based on our results, we hypothesize that visual contact with shelter (having a clear line of sight) may facilitate small-scale exploration by early juvenile (stage V) lobsters.

Vison plays a critical role in sheltering, navigation, and other behaviors in a range of benthic decapods. The fiddler crab *Uca rapax* angles its body so that the burrow is always within visual range, allowing it a quick and direct escape route (Layne *et al.*, 2003a, b). Stomatopods famously rely on vision during foraging to recognize prey (Caldwell and Childress, 1990) and conspecifics (Vetter and Caldwell, 2015). Male and female adult rusty crawfish resolve competitive bouts more quickly under better visual conditions (Bruski and Dunham, 1987). Finally, Bologna and Steneck (1993) found that adult American lobsters in kelp beds remain on the outer edges of the kelp to keep shelter within visual range while they forage.

If our hypothesis is correct, juvenile lobsters in our maze experiment learned the location of shelter in trial 1 and then, during trial 2, navigated quickly back until they regained visual contact. In the open arena, the shelter was almost always in sight and so juveniles may have prioritized exploration. It is also possible that juvenile lobsters with at least one shelter in view are more exploratory because they are more selective (see *Behavioral carryover effect* above).

The importance of vision during shelter-seeking behavior may change with ontogeny. The larval eye forms the basis of the adult eye in crustaceans, but it undergoes extensive modification as its hexagonal facets gradually square off into the square ommatidia of the adult eye (Cronin and Jinks, 2001). It is likely that these ontogenetic changes in the eye of lobsters are associated with a decrease in spatial resolution and an increase in dark adaptation (Atema and Voigt, 1995). Yet, recent experiments have shown a role of vision in recognizing individuals and estimating size in dominance fights between adult lobsters (M. Bruce, J. Kaplan, T. Doherty, and J. Atema, unpubl. data). It would be interesting to examine the relationship between visual acuity, dark adaptation, and shelter-seeking behaviors in juveniles.

Summary and conclusions

Shelter-seeking behavior of very young juvenile lobsters is influenced by their prior experiences at several different timescales. Postlarval shelter experience resulted in an apparent behavioral carryover effect: juveniles took longer to enter into and remain in shelters. Postlarval experience may alter bethedging by juveniles, or it may affect juvenile habitat selectivity. Alternatively, shelter seeking during the initial shelter experience (settlement) may be behaviorally distinct from subsequent shelter-seeking behaviors. Immediate prior shelter experience for juvenile stage lobsters decreased the time to return to the vicinity of the shelter in a maze, suggesting that juveniles learned the location of shelters. In contrast, in an open arena and in the maze when juveniles were in visual contact with the shelter, there was no effect of immediate prior experience. Juvenile lobsters face trade-offs between sheltering and exploratory behaviors, and vision may play a role in facilitating exploration by allowing juveniles to maintain a clear escape route.

To our knowledge, this is the first description of spatial learning and navigation behavior in very young (<1 y) juvenile decapods. American lobsters at this young age are thought to be shelter-restricted (Wahle and Steneck, 1992) in relatively sparse and patchy cobble habitats (Wahle and Steneck, 1991; Palma *et al.*, 1999). Exploratory behavior at small spatial scales after settlement could allow juveniles to upgrade their initial shelter choice and escape crowding. Our study suggests that early experience with shelter influences sheltering behavior in the American lobster, and may influence recruitment success during a bottleneck demographic stage for this important fishery species.

Acknowledgments

Literature Cited

Annis, E. R. 2005. Temperature effects on the vertical distribution of lobster postlarvae (*Homarus americanus*). *Limnol. Oceanogr.* **50:** 1972–1982.

Atema, J., and R. Voigt. 1995. Behavior and sensory biology. Pp. 313–348 in *Biology of the Lobster* Homarus americanus, J. R. Factor, ed. Academic Press, San Diego.

Barshaw, D. E., and K. L. Lavalli. 1988. Predation upon postlarval lobsters *Homarus americanus* by cunners *Tautogolabrus adspersus* and mud crabs *Neopanope sayi* on three different substrates: eelgrass, mud and rocks. *Mar. Ecol. Prog. Ser.* **48:** 119–123.

Beck, M. W. 1995. Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology* **76:** 968–980.

Boles, L. C., and K. J. Lohmann. 2003. True navigation and magnetic maps in spiny lobsters. *Nature* **421:** 60–63.

Bologna, P. A. X., and R. S. Steneck. 1993. Kelp beds as habitat for American lobster *Homarus americanus*. *Mar. Ecol. Prog. Ser.* **100:** 127–134.

Botero, L., and J. Atema. 1982. Behavior and substrate selection during larval settling in the lobster *Homarus americanus*. *J. Crustac. Biol.* **2:** 59–69.

Bruski, C. A., and D. W. Dunham. 1987. The importance of vision in agonistic communication of the crayfish *Orconectes rusticus*. I: an analysis of bout dynamics. *Behaviour* **103:** 83–107.

Butler, M. J., IV, A. B. MacDiarmid, and J. D. Booth. 1999. The cause and consequence of ontogenetic changes in social aggregation in New Zealand spiny lobsters. *Mar. Ecol. Prog. Ser.* **188:** 179–191.

Caldwell, R. L., and M. J. Childress. 1990. Prey selection and processing in a stomatopod crustacean. Pp. 143–164 in *Behavioural Mechanisms of Food Selection*, Vol. 20, NATO ASI Series, R. N. Hughes, ed. Springer, Berlin.

Cannicci, S., C. Barelli, and M. Vannini. 2000. Homing in the swimming crab *Thalamita crenata*: a mechanism based on underwater landmark memory. *Anim. Behav.* **60:** 203–210.

Castro, K. M., and J. S. Cobb. 2005. Behaviour of hatchery-reared and wild-caught 4th and 5th stage American lobsters, *Homarus americanus*. *N. Z. J. Mar. Freshw. Res.* **39:** 963–972.

Cobb, J. S., D. Wang, and D. B. Campbell. 1989. Timing of settlement by postlarval lobsters (*Homarus americanus*): field and laboratory evidence. *J. Crustac. Biol.* **9:** 60-66.

Cooper, R. A., and J. R. Uzmann. 1980. Ecology of juvenile and adult *Homarus*. Pp. 97–142 in *The Biology and Management of Lobsters*, Vol. 2, *Ecology and Management*, J. S. Cobb and B. F. Phillips, eds. Academic Press, New York.

Cowan, D. F., and J. Atema. 1990. Moult staggering and serial monogamy in American lobsters, *Homarus americanus*. *Anim. Behav.* **39:** 1199–1206.

Cronin, T. W., and R. N. Jinks. 2001. Ontogeny of vision in marine crustaceans. *Am. Zool.* **41:** 1098–1107.

Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* **81:** 2227–2240.

Eggleston, D. B., and R. N. Lipcius. 1992. Shelter selection by spiny lobster under variable predation risk, social conditions, and shelter size. *Ecology* **73:** 992–1011.

Ennis, G. P. 1973. Endogenous rhythmicity associated with larval hatching in the lobster *Homarus gammarus*. *J. Mar. Biol. Assoc. UK* **53:** 531–538.

Figler, M. H., H. M. Cheverton, and G. S. Blank. 1999. Shelter competition in juvenile red swamp crayfish (*Procambarus clarkii*): the influences of sex differences, relative size, and prior residence. *Aquaculture* **178:** 63–75.

Gerlach, G., J. Atema, M. J. Kingsford, K. P. Black, and V. Miller-Sims. 2007. Smelling home can prevent dispersal of reef fish larvae. *Proc. Natl. Acad. Sci. USA* **104:** 858–863.

Gilliam, J. F., and D. F. Fraser. 2001. Movement in corridors: enhancement by predation threat, disturbance, and habitat structure. *Ecology* **82:** 258–273.

Hadley, P. B. 1905. Phototropism in the larval and early adolescent stages of *Homarus americanus*. *Science* **22:** 675–678.

Harding, G. C., J. D. Pringle, P. W. Vass, S. Pearre, and S. J. Smith. 1987. Vertical distribution and daily movements of larval lobsters *Homarus americanus* over Browns Bank, Nova Scotia. *Mar. Ecol. Prog. Ser.* **41:** 29–41.

Hovel, K. A., and R. A. Wahle. 2010. Effects of habitat patchiness on American lobster movement across a gradient of predation risk and shelter competition. *Ecology* **91:** 1993–2002.

Hughes, J. T., R. A. Shleser, and G. Tchobanoglous. 1974. A rearing tank for lobster larvae and other aquatic species. *Prog. Fish.-Cult.* **36:** 129–132.

Huntingford, F. A. 2004. Implications of domestication and rearing conditions for the behaviour of cultivated fishes. *J. Fish Biol.* **65:** 122–142.

Incze, L. S., R. A. Wahle, and J. S. Cobb. 1997. Quantitative relationships between postlarval production and benthic recruitment in lobsters, *Homarus americanus*. *Mar. Freshw. Res.* **48:** 729–743.

Johns, P. M., and K. H. Mann. 1987. An experimental investigation of juvenile lobster habitat preference and mortality among habitats of varying structural complexity. *J. Exp. Mar. Biol. Ecol.* **109:** 275–285.

Kamram, M., and P. A. Moore. 2015. Comparative homing behaviors in two species of crayfish, *Fallicambarus fodiens* and *Orconectes rusticus*. *Ethology* **121:** 775-784.

Karnofsky, E. B., J. Atema, and R. H. Elgin 1989. Field observations of social behavior, shelter use, and foraging in the lobster, *Homarus americanus*. *Biol. Bull.* **176:** 239–246.

Lawton, P. 1987. Diel activity and foraging behavior of juvenile American lobsters, *Homarus americanus*. *Can. J. Fish. Aquat. Sci.* **44:** 1195–1205.

Lawton, P., and K. L. Lavalli. 1995. Postlarval, juvenile, adolescent, and adult ecology. Pp. 47–88 in *Biology of the Lobster* Homarus americanus, J. R. Factor, ed. Academic Press, San Diego.

Layne, J. E., W. J. P. Barnes, and L. M. J. Duncan. 2003a. Mechanisms of homing in the fiddler crab *Uca rapax* 1. Spatial and temporal characteristics of a system of small-scale navigation. *J. Exp. Biol.* **206:** 4413–4423.

Layne, J. E., W. J. P. Barnes, and L. M. J. Duncan. 2003b. Mechanisms of homing in the fiddler crab *Uca rapax* 2. Information sources and frame of reference for a path integration system. *J. Exp. Biol.* **206:** 4425–4442.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Can. J. Zool.* **68:** 619–640.

Magee, B., and R. W. Elwood. 2013. Shock avoidance by discrimination learning in the shore crab (*Carcinus maenas*) is consistent with a key criterion for pain. *J. Exp. Biol.* **216:** 353–358.

Nielsen, T. V., and I. J. McGaw. 2016. Behavioral thermoregulation and trade-offs in juvenile lobster *Homarus americanus*. *Biol. Bull.* **230:** 35–50.

Palma, A. T., R. S. Steneck, and C. J. Wilson. 1999. Settlement-driven, multiscale demographic patterns of large benthic decapods in the Gulf of Maine. *J. Exp. Mar. Biol. Ecol.* **241:** 107–136.

Pechenik, J. A. 2006. Larval experience and latent effects—metamorphosis is not a new beginning. *Integr. Comp. Biol.* **46:** 323–333.

Pezzack, D. S., and D. R. Duggan. 1986. Evidence of migration and homing of lobsters (*Homarus americanus*) on the Scotian shelf. *Can. J. Fish. Aquat. Sci.* **43:** 2206–2211.

Pottle, R. A., and R. W. Elner. 1982. Substrate preference behavior of juvenile American lobsters, *Homarus americanus*, in gravel and silt-clay sediments. *Can. J. Fish. Aquat. Sci.* **39:** 928–932.

Rossong, M. A., P. A. Quijon, P. J. Williams, and P. V. R. Snelgrove. 2011. Foraging and shelter behavior of juvenile American lobster (*Homarus americanus*): the influence of a non-indigenous crab. *J. Exp. Mar Biol. Ecol.* **403:** 75–80.

Shulman, M. J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66:** 1056–1066.

Steneck, R. S. 2006. Possible demographic consequences of intraspecific shelter competition among American lobsters. *J. Crustac. Biol.* **26:** 628–638.

Stunz, G. W., P. S. Levin, and T. J. Minello. 2001. Selection of estuarine nursery habitats by wild-caught and hatchery-reared juvenile red drum in laboratory mesocosms. *Environ. Biol. Fishes* **61:** 305–313.

Tlusty, M. F., D. R. Fiore, and J. S. Goldstein. 2005. Use of formulated diets as replacements for *Artemia* in the rearing of juvenile American lobsters (*Homarus americanus*). *Aquaculture* **250:** 781–795.

Van der Meeren, G. I. 2001. Effects of experience with shelter in hatchery-reared juvenile European lobsters *Homarusgammarus. Mar. Freshw. Res.* **52:** 1487–1493.

Vannini, M., and S. Cannicci. 1995. Homing behaviour and possible cognitive maps in crustacean decapods. *J. Exp. Mar. Biol. Ecol.* **193:** 67–91.

Vetter, K. M., and R. L. Caldwell. 2015. Individual recognition in stomatopods. Pp. 17–36 in *Social Recognition in Invertebrates*, L. Aquiloni and E. Tricarico, eds. Springer International, Cham, Switzerland.

Wahle, R. A. 1992. Body-size dependent anti-predator mechanisms of the American lobster. *Oikos* **65:** 52–60.

Wahle, R. A., and L. S. Incze. 1997. Pre- and post-settlement processes in recruitment of the American lobster. *J. Exp. Mar. Biol. Ecol.* **217:** 179–207.

Wahle, R. A., and R. S. Steneck. 1991. Recruitment habitats and nursery grounds of the American lobster *Homarus americanus*: a demographic bottleneck? *Mar. Ecol. Prog. Ser.* **69:** 231–243.

Wahle, R. A., and R. S. Steneck. 1992. Habitat restrictions in early benthic life: experiments on habitat selection and *in situ* predation with the American lobster. *J. Exp. Mar. Biol. Ecol.* **157:** 91–114.

Wahle, R. A., C. Bergeron, C. Wilson, and M. Parkhurst. 2009. A vessel-deployed passive post-larval collector for the American lobster. *N. Z. J. Mar. Freshw. Res.* **43:** 465–474.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annu. Rev. Ecol. Syst.* **15:** 393–425.