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Influence of size and delayed settlement on the recapture rate of newly settled American lobsters *Homarus americanus*

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ABSTRACT: Postlarval American lobsters *Homarus americanus* exhibit variation in size at settlement and timing of settlement but it is not known if this variability influences future survival. The ability to track the fate of individual newly settled lobsters has become possible with the advent of micro-wire tags. In this study micro-wire tags were used to identify individual postlarval and fifth instar lobsters that were released into the field and then recaptured 1 wk later. The influence of size at settlement and timing of settlement on subsequent recapture rate were determined. The overall recapture rate for tagged postlarvae and fifth instars was approximately 15%. Larger sized postlarvae and fifth instar lobsters were recaptured significantly more frequently than their smaller counterparts. There was no difference in recapture rate for postlarvae that delayed settlement, as compared to those that settled at the normal time. Differences in recapture rates between large- and small-sized newly settled lobsters might be associated with emigration, behavioral interactions, or differential survival.

KEY WORDS: *Homarus americanus* · Postlarvae · Micro-wire tag · Settlement

INTRODUCTION

Many marine crustaceans undergo an ontogenetic habitat shift from the planktonic to the benthic environment, yet little work has been done to explore the consequences of variability in body size and timing of this habitat transition. The American lobster *Homarus americanus* is one marine crustacean that has such a transition in its life history. The first 3 larval instars of the American lobster are entirely planktonic and the fourth instar, or postlarva, undergoes the behavioral and ecological transition from the planktonic larval habitat to the adult benthic habitat. The postlarva remains in the plankton for most of the instar, settling to the benthic habitat towards the end of the postlarval instar (Cobb et al. 1983,1989). Shortly after settlement the postlarva molts to the fifth instar, becoming a truly epibenthic organism, and enters the shelter restricted phase of the life cycle (Charmantier et al. 1991, Lawton & Lavalli 1995). The period of transition, encompassing the postlarval and the fifth instar, may be a 'critical' phase during the life history of the American lobster when cohort size might be determined (Langton et al. 1996). However, factors influencing survival during and immediately after the transition to the benthos are not well understood. James-Pirri et al. (1998) have shown that planktonic postlarvae exhibit up to 30% variation in carapace length (CL), but it is unknown if this size variation influences settlement success. Relatively higher mortality rates are associated with smaller juvenile lobsters (Barshaw & Lavalli 1988, Smith & Herrnkind 1992 for spiny lobsters, Wahle & Steneck 1992) and it is likely that size-specific mortality may also occur in the younger, newly settled instars.

Additionally, the timing of settlement may also influence survival. In coastal Rhode Island (USA) waters, postlarval lobsters usually settle at molt cycle stages D_0

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to D_1 (Cobb et al. 1989). Postlarvae are capable of delaying settlement if suitable substrate is not available or if a thermocline is present, thus settling at a later molt cycle stage than normal (Botero & Atema 1982, Boudreau et al. 1992). Postlarvae that delay settlement may have a higher risk of mortality due to an increased demand on energy reserves, prolonged exposure to planktonic predators, decrease in the time remaining to find suitable shelter before molting to the fifth instar, or may settle in less suitable substrates (Boudreau et al. 1993, Lawton & Lavalli 1995). Delayed settlement in other benthic invertebrates has been shown to be detrimental to post-metamorphic and juvenile fitness (Pechenik 1990, Gebauer et al. 1999).

In this study, we examined the influence of carapace length and developmental age (molt cycle stage) on recapture rate (a proxy for settlement success) of newly settled postlarval and fifth instar American lobsters *Homarus americanus*. We hypothesized that a larger size at settlement is advantageous and that delayed settlement is disadvantageous to post-settlement success. We used micro-wire tags as a method to identify individual newly settled lobsters in a series of field-based experiments designed to address these hypotheses.

MATERIALS AND METHODS

A series of field experiments were conducted during the summer of 1993 and 1994. In these experiments, postlarval or fifth instar lobsters were released into the field and recaptured 1 wk later. In 1993, fifth instar lobsters, originating from laboratory reared stock, were released into the field. Laboratory reared fifth instars were used due to a scarcity of field collected planktonic postlarvae in this year. The laboratory reared fifth instar lobsters (4.4 ± 0.5 mm CL) were similar in size to wild-caught postlarvae (4.7 ± 0.3 mm CL).

In 1994, postlarval lobsters were collected from June through mid-August near Point Judith, Rhode Island, USA. Postlarvae were collected during the day using paired neuston nets (500 µm mesh, mouth opening 1 m · 0.5 m), equipped with flow meters, and towed from a small research vessel. All postlarvae were immediately removed from the net, placed in jars of seawater and held on ice. In the laboratory, CL for all postlarval lobsters was measured to the nearest 0.1 mm with a dissecting microscope and ocular micrometer. Molt cycle stage, an indicator of developmental stage within a specific instar (from post-ecdysial through ecdysial), was determined by examining the uropods for the degree of new integument growth (after Sasaki 1984). We will use the term 'molt cycle stage' to indicate the developmental phases (C, D_0, D_1, D_2) within a specific instar (postlarval or fifth) (see Cobb & Wahle 1994).

Binary coded micro-wire tags, 0.25 mm in diameter · 0.5 mm in length, (Northwest Marine Technology, Shaw Island, Washington, USA) were used to identify individual postlarval and fifth instar lobsters. Tags were manually injected, using a modified syringe, into the abdominal muscle on the ventral side of the second abdominal segment. Before tagging, each lobster was immobilized by chilling in a vial of seawater held on ice for a few minutes. All tagging was done with the aid of a dissecting microscope. Immediately after tagging, each lobster was placed in a bowl of seawater and allowed to recover for approximately 5 min. Once recovered (signified by normal behavior such as swimming and/or walking) tagged lobsters were transferred to individual mesh containers, 8 cm in length · 6 cm in diameter. Tagged lobsters were held in the laboratory in flow-through ambient seawater and fed frozen adult brine shrimp *ad libitum* for 2 to 4 d prior to release into the field. This time period allowed postlarvae to settle by supplying a substrate (the bottom and sides of the container). All lobsters (fifth and postlarval) used in the field experiments exhibited behaviors consistent with settlement (i.e walking and not swimming). Only vigorous lobsters were released into the field.

To determine if the tagging procedure influenced growth or intermolt duration, a portion of the field-caught postlarvae were divided into 2 treatments, tagged and untagged, and reared in the laboratory through the eighth instar. The tagging procedure and rearing conditions were the same as previously described. Molt date and size at each molt were recorded for both treatments. Size and intermolt duration for each instar (IV to VIII) were compared between the treatments using repeated measures analysis of variance (ANOVA).

In all field experiments, 3 tagged lobsters (fifth instar lobsters in 1993 and postlarval lobsters in 1994), each with a different tag code, were released into a standardized plot. Each plot consisted of a square plastic frame, 0.7 m per side, (total area 0.5 m^2) with 10 cm high sides (Fig. 1). The bottom of the square frame was lined with 1 mm mesh to prevent lobsters from burrowing out of the plot. A pile of stones (8 to 12 rounded stones, each approximately 15 to 20 cm in diameter) was placed in the center of each plot. Thirty plots, each separated by 1 m, were arranged in a rectangular grid on an expansive area of sand substrate in 5 m of water in the Harbor of Refuge, Point Judith. The nearest natural cobble was approximately 400 m from the plots. Plots were placed in the water approximately 2 wk prior to the release the lobsters. Each group of 3 lobsters was randomly assigned a plot within the grid. Lobsters were released by hand into the plots by divers using SCUBA. Upon release, the lobsters would enter the crevices between the stones and disappear from view. None of the lobsters were observed to swim away from the plots at the time of release. Plots were sampled by divers, using a benthic airlift suction sampler, 7 d (weather permitting) after the release of lobsters. During sampling to recover tagged lobsters, care was taken to suction under and around each stone, and along the inside of the plastic frame down to the mesh bottom. After sampling, the stones were replaced and another set of tagged lobsters was released. Suction samples were sorted immediately and all lobsters captured were returned to the laboratory where each lobster was measured, molt cycle stage was determined, and the individual was identified by extracting the tag and reading the code.

Percent recapture rate, calculated as the number of individuals recaptured relative to the total number of lobsters released per treatment, was used as an indication of settlement success. There were 2 tagging experiments: the first experiment was designed to investigate the influence of individual size on subsequent recapture rate and the second experiment was designed to determine if delayed settlement influenced recapture rate.

To determine if size at settlement influenced recapture rate, 3 size treatments of lobsters were used: small 4.0–4.5 mm CL, medium 4.6–4.9 mm CL, and large 5.0–5.5 mm CL. The medium size class represented the average size of postlarvae sampled from this area in previous years (James-Pirri et al. 1998), while the small and large size classes reflected the lower and upper ranges, respectively, of postlarval sizes observed in this area from 1994 to 1998 (J.S.C. unpubl. data). If possible, the sizes of the 3 lobsters in a plot were exactly equal (e.g. for medium treatment, all 3 individuals were 4.7 mm CL). As postlarvae in molt cycle stage D_0 and later are behaviorally competent to settle (Cobb et al. 1989), all lobsters used in the size treatments were in molt cycle stage D_0 or D_1 when released into the plots.

In the second experiment, we examined the influence of delayed settlement on subsequent recapture rate. Based on the distribution of molt cycle stages among planktonic lobster postlarvae in this region, settlement to the benthos usually occurs prior to molt cycle stage D_2 (Cobb et al. 1989, Incze & Wahle 1991, Cobb & Wahle 1994). In this experiment, lobsters were released into the plots in molt cycle stage D_2, approximately 1 wk later than the normal timing of settlement. In 1993, due to a shortage of laboratory-reared lobsters, only the small treatment of fifth instar lobsters were transplanted in molt stage D_2. In 1994, field-collected postlarvae were held in the laboratory until reaching molt cycle stage D_2 (approx. 7 d) prior to release into the plots.

G-tests were used to test the 'null hypotheses of no difference' for recapture rate among treatments for each experiment. Separate *G*-tests were performed for each year (1993 and 1994) since the lobsters originated from different stock (laboratory vs wild) and were different instars (fifth vs postlarval) at the time of release. Since the expected number of individuals recaptured for the large treatment in all experiments was less than 5, the medium and large size treatments were pooled in all experiments in order to fit the assumptions for expected values for this test. Freeman-Tukey Deviates (Sokal & Rohlf 1995) were calculated to determine the treatments that deviated from expected recapture rates.

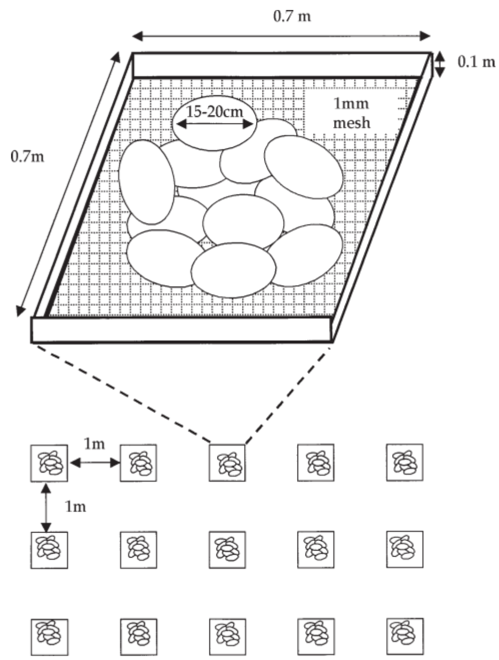

Fig. 1. Grid of plots (15 of 30 shown) and of a single plot into which 3 tagged lobsters were released during the field experiments. Plots were 0.5 m^2, were lined with a 1 mm mesh bottom, and had 8 to 12 stones (15 to 20 cm in diameter) placed in the center of the plot

RESULTS

In the laboratory, no mortality was observed for either the tagged or untagged postlarvae reared through the eighth instar. There was also no difference in growth or intermolt duration between tagged and untagged postlarvae reared through the eighth instar (Table 1, repeated measures ANOVA, growth: $F = 1.07$ df = 20, p = 0.31; molt duration: $F = 0.03$, df = 17, p = 0.86).

In 1993, a total of 34 plots (102 laboratory-reared fifth instar lobsters) were used in the field tagging experiment. In 1994, a total of 73 plots (219 field-collected postlarvae) were used in the tagging experiment. The

Table 1. Mean CLs (mm), intermolt duration (d) and sample size (n) of tagged and untagged individual lobsters followed from postlarval to the eighth instar

Instar	Tagged CL (mm ± SD)	Untagged CL (mm ± SD)	Tagged intermolt duration (d ± SD)	Untagged intermolt duration (d ± SD)
Postlarval	4.5 ± 0.1 (8)	4.5 ± 0.2 (17)	–	–
V	5.1 ± 0.1 (8)	5.1 ± 0.1 (17)	17 ± 3.4 (8)	16 ± 1.5 (17)
VI	6.2 ± 0.2 (8)	6.3 ± 0.2 (17)	14 ± 0.9 (7)	15 ± 2.1 (15)
VII	7.1 ± 0.4 (8)	7.3 ± 0.3 (17)	16 ± 2.8 (7)	16 ± 3.5 (12)
VIII	8.1 ± 0.5 (8)	8.5 ± 0.3 (14)	–	–

number of plots per treatment for both years is shown in Table 2.

Tagged lobsters in all treatments were at liberty, on average, for 1 wk (7 ± 1 d). In 1993, the overall recapture rate of laboratory-reared fifth instars (all treatments combined) was 21%. In 1994, the overall recapture rate (all treatments combined) for tagged postlarvae was 13%. Eleven untagged wild lobsters, ranging in size from 4.75 to 7.3 mm CL (representing instars IV to VII, see James-Pirri et al. 1998) were also sampled from the plots in 1994. These lobsters either settled naturally or emigrated into the plots. Other animals sampled from the plots included newly settled and juvenile *Cancer* spp. crabs, hermit crabs, small fish (cunner and sculpin), and amphipods. Over the course of the experiment, some epifaunal growth occurred on the stones in the plot; however, the weekly suctioning and movement of the stones prevented extensive growth. Epifaunal growth did not appear to influence recapture rate, as similar numbers of lobsters were recovered during each sampling period throughout the duration of the experiments.

In 1993, there was a significant difference in the recapture rate between the small and the pooled medium/large size class of fifth instar lobsters released at the normal time of settlement (*G*-value 5.81, df = 1, p = 0.02). Freeman-Tukey Deviates indicated that the smaller size class was recaptured less frequently than expected, while the pooled medium/large size class was recaptured at a higher frequency than expected (Table 3). In 1993, the delayed settlement treatment consisted of only the small size class and the recapture rate for this treatment was 14% (Table 2). There was no significant effect of settlement time (normal vs delayed) on the recapture rate for the small size class of fifth instars (*G*-value 0.02, df = 1, p = 0.89).

In 1994, there was a significant difference in the recapture rate between the small and the pooled medium/large size class for postlarvae released at the normal time of settlement (*G*-value = 8.41, df = 1, p = 0.00). The

Table 2. No. of plots, no. of lobsters released per treatment, no. of individual lobsters recaptured and percent recapture rate per treatment for the 1993 and 1994 tag-recapture experiments. Percent recapture rate was calculated as no. of lobsters recaptured relative to the total no. of lobsters per treatment. Each plot contained 3 tagged lobsters. In 1993 the tag-recapture experiments transplanted laboratory reared fifth instar lobsters. In 1994 wild caught postlarvae were used in the tag-recapture experiments

Experiment	Size class	No. of plots (no. of lobsters per treatment)	No. of individual lobsters recaptured)	Recapture rate (%)
1993				
Lab-reared fifth instars normal settlement	Small (″ 4.5 mm CL)	18 (54)	7	13
	Medium (4.6–4.9 mm CL)	5 (15)	6	40
	Large (≥ 5.0 mm CL)	4 (12)	5	42
Lab-reared fifth instars delayed settlement	Small (″ 4.5 mm CL)	7 (21)	3	14
	Medium (4.6–4.9 mm CL)	–	–	–
	Large (≥ 5.0 mm CL)	–	–	–
1994				
Wild-caught postlarvae normal settlement	Small (″ 4.5 mm CL)	18 (54)	3	6
	Medium (4.6–4.9 mm CL)	22 (66)	8	12
	Large (≥ 5.0 mm CL)	9 (27)	6	22
Wild-caught postlarvae delayed settlement	Small (″ 4.5 mm CL)	6 (18)	2	11
	Medium (4.6–4.9 mm CL)	14 (42)	9	21
	Large (≥ 5.0 mm CL)	4 (12)	0	0

Table 3. Freeman-Tukey Deviates for field transplant experiments (Sokal & Rohlf 1995). Freeman-Tukey Deviates larger than +1.385 indicated that treatments had a higher frequency of recaptures than expected by chance. Deviates less than –1.385 indicated treatments that had a lower frequency of recaptures than expected by chance

Treatment	Significance	Small size class	Medium/large pooled size class
1993 Fifth instars normal settlement	*G*-value: 5.811 p = 0.0159	–1.526	+1.783
1994 Postlarvae normal settlement	*G*-value: 8.406 p = 0.0037	–1.364	+1.577
Postlarvae delayed settlement	*G*-value: 0.2923 p = 0.5886	–0.3180	+ 0.3312

Freeman-Tukey Deviates indicated that the pooled medium/large size class was recaptured more frequently than expected (Table 3). In the delayed settlement treatment, no significant difference in recapture rate was found between the small and pooled medium/large size class (*G*-value = 0.2923, df = 1, p = 0.5886). No significant difference was observed in the overall recapture rate between normal and delayed settlement (12 and 15% recaptured, respectively) when all sizes classes were combined (*G*-value 0.51, df = 1, p = 0.48).

Fifteen of the laboratory-reared, tagged fifth instars transplanted into plots in 1993 molted to the sixth instar in the field. The mean growth factor, the percentage increase in CL, was 16.5%. In 1994, 25 of the tagged postlarvae were recaptured as fifth instars. The growth factor for the postlarval to fifth instar transition was 17.3%. These growth factors were similar to those reported for postlarvae reared in a field growth experiment (James-Pirri 1996, James-Pirri et al. 1998). There was no difference in the mean growth increment (postlarval to fifth instar) between normal and delayed settlement treatments of postlarvae (Student's *t*-test 0.49, df = 23, p = 0.62).

DISCUSSION

Micro-wire tags have been previously used on larger juvenile American and European lobsters (Wickins et al. 1986, Krouse & Nutting 1990, Bannister et al. 1994, Uglem & Grimsen 1995), spiny lobster puerulii (W. F. Herrnkind, Florida State University, Tallahassee, and M. J. Butler, Old Dominion University, Norfolk, VA, pers. comm.), and juvenile crabs and crayfish (van Montfrans et al. 1986, Fitz & Wiegert 1991, Isely & Eversole 1998, Okamota 1999). More recently, the practice of using micro-wire tags in postlarval American lobsters has increased in popularity (Incze et al. 1997, K. Castro, University of Rhode Island, Kingston, pers. comm.). This study shows that these tags can be successfully used to identify newly settled individual lobsters in field experiments. Micro-wire tags were retained through the molt and did not influence growth or molt duration through the eighth instar. Additionally, observations from laboratory studies have shown that these tags do not influence behavior of newly settled postlarvae (James-Pirri & Cobb 1999a).

We observed that larger postlarval and fifth instar lobsters were recaptured more often than smaller individuals of the same year-class, suggesting that larger individuals may have an increased probability of post-settlement success. The differences in recapture rate between the size classes in normal settlement treatment may have been attributable either to mortality, emigration, or agonistic interactions among the lobsters. The low recapture rate of the smaller lobsters may have been attributable to differential sized-based mortality. Emigration from the plots may also have been responsible for the difference in the recapture rates. There was some evidence of movement among the plots, as occasionally (5 times) a tagged lobster was sampled from a plot other than the one into which it had been released. However, this movement was not restricted to one size class, as these few individuals, identified by the tag code, were from all size classes (1 small, 2 medium, and 1 large). Based on observations during the release of lobsters, it is unlikely that swimming by postlarvae or fifth instars influenced recapture rates.

Competition for space may have resulted in agonistic interactions. Agonistic interactions such as fighting, burrow displacement, and dominance hierarchies have been observed in newly settled postlarval and fifth instar lobsters (James-Pirri & Cobb 1999b). If the lobsters in the field plots displayed this same type of behavior, it is possible that displaced individuals emigrated from the plot. There was some evidence that displacement may have occurred in the field plots. In both years, the majority of the plots that had recaptures had only 1 lobster recaptured in that plot (1993: 66%; 1994: 92%). The proportion of plots that had 1 lobster recaptured was less than the proportion of plots with no recaptures (1993: 56 and 29%, 1994: 64 and 33%, for 0 and 1 recaptures respectively), but was higher than the proportion of plots that had 2 or all 3 lobsters in the plot recaptured (1993: 12 and 3%, 1994: 3 and 0%, 2 and 3 recaptures respectively). It is possible that the single recaptured lobster was the dominant individual and that the other 2 lobsters may have emigrated from the plot due to agonistic interactions. Since dominance is also related to size (Cobb & Tamm 1975, O'Neil & Cobb 1979), one might expect larger lobsters to displace the smaller lobsters from the plots. There was some evidence of this from the untagged lobsters that recruited to the plots in this study. Eleven untagged recruited lobsters were sampled from the plots in 1994. Only 1 recruited lobster was found in association with a tagged lobster in the same plot. The other 10 recruited lobsters were sampled from plots where no tagged lobsters were recaptured, and all of the recruited lobsters were larger than the tagged lobsters that had been released into the plots.

Evidence from this study suggests that delayed settlement may not have any adverse effects, as illustrated by the similar recapture rates between the normal and delayed settlement treatments when all size classes were combined. Unlike the normal settlement treatment, there was no difference in the recapture rates between the size classes in the delayed settlement treatment. The similar recapture rates within the delayed settlement treatment may be attributed to behavioral differences among developmental stages within the same instar. Postlarvae in the delayed settlement treatment may have been more sedentary in their movements due to the short amount of time left before ecdysis, whereas postlarvae settling at the normal time may have been more active, engaging in agonistic interactions or other activities. There is some evidence of this behavior from laboratory experiments, as newly settled postlarvae spend more time in locomotory and agonistic behaviors immediately after settlement and then switch to shelter related behaviors after settlement (James-Pirri & Cobb 1999b).

Planktonic postlarvae can exhibit as much as a 30% variation in CL, and in some years postlarvae present early in the season are larger than postlarvae arriving later in the season. Additionally, these early-arriving lobsters may be 30 to 50% larger in size by the end of the first growing season (James-Pirri et al. 1998). Thus, members of a settling cohort may have differential probabilities of post-settlement success based on individual size at settlement. We have shown that larger sized, newly settled lobsters were recaptured more often, providing the first evidence that size at settlement may be important to post-settlement success. The ability to tag and follow individuals during the first season of growth will greatly aid in the effort to understand factors that influence survival during the early life history phase, and further studies focusing on the newly recruited benthic year-class should be pursued vigorously.

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