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Different early post-settlement strategies between American lobsters *Homarus americanus* and rock crabs *Cancer irroratus* in the Gulf of Maine

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ABSTRACT: The abundance of many invertebrates with planktonic larval stages can be determined shortly after they reach the benthos. In this study, we quantified patterns of abundance and habitat utilization of early benthic phases of the American lobster *Homarus americanus* and the rock crab *Cancer irroratus*. These 2 decapods are among the most common and abundant macroinvertebrates in coastal zones of the Gulf of Maine, with similar densities of larger individuals. Settlement and early post-settlement survival indicate that lobsters are highly substrate-specific early in life, settling predominantly in cobble beds. Crabs appear to be less selective, settling both in cobble and sand. Cumulative settlement of crabs, inferred from weekly censuses over the summer, was an order of magnitude greater than that of lobsters over the same time period. However, only crabs showed significant post-settlement losses. Although the identity of specific predators is unknown, predator exclusion experiments and placement of vacant uninhabited nursery habitat suggested that post-settlement mortality rather than emigration was responsible for these losses. The selective habitat-seeking behavior and lower post-settlement mortality of lobsters is consistent with their lower fecundity and later onset of reproductive maturity. The patterns observed for crabs, however, suggest a different strategy which is more in accordance with their higher fecundity and earlier onset of maturity. It is possible that lower fecundity but greater per-egg investment, along with strict habitat selection at settlement and lower post-settlement mortality, allows adult lobster populations to equal adult populations of crabs. This occurs despite crabs being more fecund and less habitat-selective settlers but sustaining higher post-settlement mortality.

KEY WORDS: Settlement · Early post-settlement · Predation · Mortality · Survivorship · Substrate type · *Cancer irroratus* · *Homarus americanus*

INTRODUCTION

Marine animals that release planktonic larvae generally distribute along a continuum, from those having few but larger eggs to those having more numerous but smaller eggs. These 2 end-point strategies can have further implications at the time of settlement if proportional losses occur during the pelagic transition. Larval mortality is generally assumed to be greater when adults are highly fecund and larvae are small (Rumrill 1990, Havenhand 1995). However, there is

growing evidence that the demography of many benthic species with pelagically dispersed larvae is influenced by processes operating around the time of settlement. Locally variable larval supply can dramatically impact the spatial distribution and abundance of settlers (Connell 1985, Gaines & Roughgarden 1985, Hughes 1990, Reed 1990, Sutherland 1990, Gaines & Bertness 1992). However, processes operating immediately after settlement can obliterate this initial signal. Early post-settlement mortality affects cohort abundance in groups as diverse as corals (Carlson & Olson 1993), barnacles (Minchinton & Scheibling 1991), bryozoans (McKinney & McKinney 1993), and benthic fish (Forrester 1990, 1995, Jones 1990, Doherty & Fowler

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1994, Carr & Hixon 1995, Tupper & Boutilier 1996). For sessile organisms, the space available at the time of settlement, along with competition or predation after settlement, determines their abundance. This has been shown for example for bryozoans (Young & Gotelli 1988, Osman & Whitlatch 1995a) and ascidians (Young & Gotelli 1988, Osman & Whitlatch 1995b). In contrast, post-settlement movement among mobile organisms can relieve the crowding imposed by high settlement density (Wahle & Incze 1997).

Habitat-specific settlement success results from either active habitat selection or differential mortality after non-selective settlement. Habitat selection has been shown for settling ascidians (Stoner 1990), Dungeness crabs (Eggleston & Armstrong 1995), stomatopods (Steger 1987), Nassau grouper (Eggleston 1995), and blue crabs (Morgan et al. 1996). In theory, this is the most economic means by which settling organisms populate nursery grounds, defined as habitats with highest early post-settlement survival. Organisms may also move to high survival habitats shortly after settlement. Differential mortality refers to indiscriminate settlement with survival concentrated in nursery grounds. For example, Atlantic cod settle indiscriminately but suffer high mortality in relatively featureless bottoms (Lough et al. 1989, Gotceitas & Brown 1993); reef-building polychaetes have the highest survivorship when they settle on rough surfaces (Zamorano et al. 1995); mytilid bivalves are more successful when they settle on red algae (Moreno 1995). This less economical means of settlement results in much higher early post-settlement mortality.

In coastal zones of the Gulf of Maine 2 large decapods, the rock crab *Cancer irroratus* and the American lobster *Homarus americanus*, are ecologically and economically important as large-bodied benthic invertebrates (Ojeda & Dearborn 1990, Fogarty 1995, Lawton & Lavalli 1995). Both species live in similar habitats and eat similar food (Richards et al. 1982, Moody & Steneck 1993). Their coexistence could result from differential use of resources with increasing size, and from the trophic and habitat 'flexibility' of the rock crab (Hudon & Lamarche 1989). The 2 species have pelagic planktotrophic larvae that settle from July to September. These 2 species also represent 2 end points in the decapod body morphology. Lobsters are macrurans with a large abdomen, while crabs are brachyurans with an abdomen completely folded beneath the cephalothorax. The co-occurrence of these 2 species creates the opportunity to compare the performance of phylogenetically distinct decapods in the same environmental setting. Crabs mature earlier, are more fecund and have smaller eggs (Bigford 1979). In contrast lobsters mature later, are less fecund and have larger eggs (Waddy et al. 1995). Although the 2 species coexist, are conspicuous in coastal

habitats, and are easily quantified by the same sampling methods, simultaneous and comparative studies of their post-settlement strategies are lacking.

The purpose of this study was to characterize the patterns of settlement and early post-settlement survival of these 2 decapod species. While it is known that settling lobsters display high habitat selectivity and high post-settlement survivorship (Cobb & Wahle 1994), no similar studies for crabs exist. Patterns of post-larval habitat selection and post-settlement abundances were quantified in different locations and on different substrate types. We chose experimental substrates based on previous information that revealed a strong preference for cobble substrata by lobsters at the time of settlement (Wahle & Steneck 1991) and because newly settled crabs are also found there (Clancy 1995). Sand was used as a contrasting fine-grained alternative substrate in which newly settled rock crabs have also been found (Clancy 1995). Finally, manipulative field experiments were designed to differentiate between the relative importances of emigration and mortality due to predation.

MATERIALS AND METHODS

Post-settlement abundance and size distribution.

Field observations were made at 3 sites on the central coast of Maine: Lower Johns Bay, the east side of Damariscove Island, and the west side of Damariscove Island (hereafter referred as LJB, DIE, and DIW respectively; Fig. 1), all of which have rocky and sedimentary habitats. Post-settlement survival was determined at the end of the settlement season in mid-September when natural and previously placed artificial substrata were surveyed (see Incze & Wahle 1991). The 2 natural substrata considered were cobble and sand and the artificial substratum was larval decapod collectors constructed of PVC (polyvinyl chloride) (Steneck & Wahle unpubl.). Samples were taken and collectors deployed between 5 and 10 m depth which corresponded to the depths of highest settlement densities for lobsters and crabs (Steneck & Wahle unpubl.). In natural habitats at all sites, divers haphazardly tossed at least twenty 0.5 m² quadrats, overturned rocks, and all organisms and material present in that area was suction sampled to a depth of 15 cm. The content of each quadrat was collected in bags with a 1 mm mesh, thus capturing all recently settled decapods. For details on the air-lift suction sampling procedure see Wahle & Steneck (1991). All surveys of natural habitats were performed between June and October of 1994 and 1995.

The PVC collectors were used to estimate post-settlement densities of crabs and lobsters. The collectors also harbored larger crabs and lobsters [to 50 mm CW (cara-

pace width) and 21 mm CL (carapace length), respectively] moving along the bottom. Comparison of the size structure of individuals in collectors to that in natural cobble habitats served as an indication of the size-specific propensity of crabs and lobsters to migrate. Collectors were 0.36 m² square structures (60 × 60 × 9 cm) made of 3 cm diameter gray PVC pipes spaced 1 cm apart and stacked 3 rows deep in alternating tiers. The stack was placed on Astroturf™ inside a wire basket lined with 1 mm mesh nylon screen. The basket was made of 3.5 cm mesh vinyl-coated wire commonly used for lobster traps. The collectors were deployed at the beginning of the settlement season of 1995 (July 7) and retrieved at the end (September 21). Tests showed these collectors capture post-larval lobsters and crabs as effectively as cobble substrata. Divers retrieved the collectors by covering them with screening (1 mm mesh) and bringing them to the surface to be searched in the laboratory. Crabs and lobsters were counted and measured with calipers to the nearest 0.1 mm (CW for crabs and CL for lobsters).

The abundance of crabs and lobsters older than 1 yr (> 10 mm CW and CL, respectively) was determined by visual SCUBA surveys. In each site over the same depth range, 1 m² quadrats were haphazardly tossed on sand and cobble substrates. All movable rocks were overturned during sampling. All individuals were counted and measured *in situ*, then released.

Substrate selectivity and post-settlement survival. To establish whether the 2 decapods differ in the density of settlement or in post-settlement survival, we chose 2 sites with markedly different larval supplies: DIW and DIE. The 2 sites have a long history of high (DIW) and low (DIE) post-larval supply and recruitment (Incze & Wahle 1991, Wahle & Incze 1997). To monitor the magnitude and timing of substrate-specific settlement for crabs and lobsters over the summer of 1994, experimental monitoring plots were established. For this, sixteen 1 m² plots were established at a depth of 8 m on a large patch of sand at each side of the island for a total of 32 plots. A wooden frame (100 × 100 × 6 cm) embedded in the sand defined the perimeter of each plot. Eight frames were filled with cobbles and 8 remained full of sand. In order to ensure substrate with natural size and

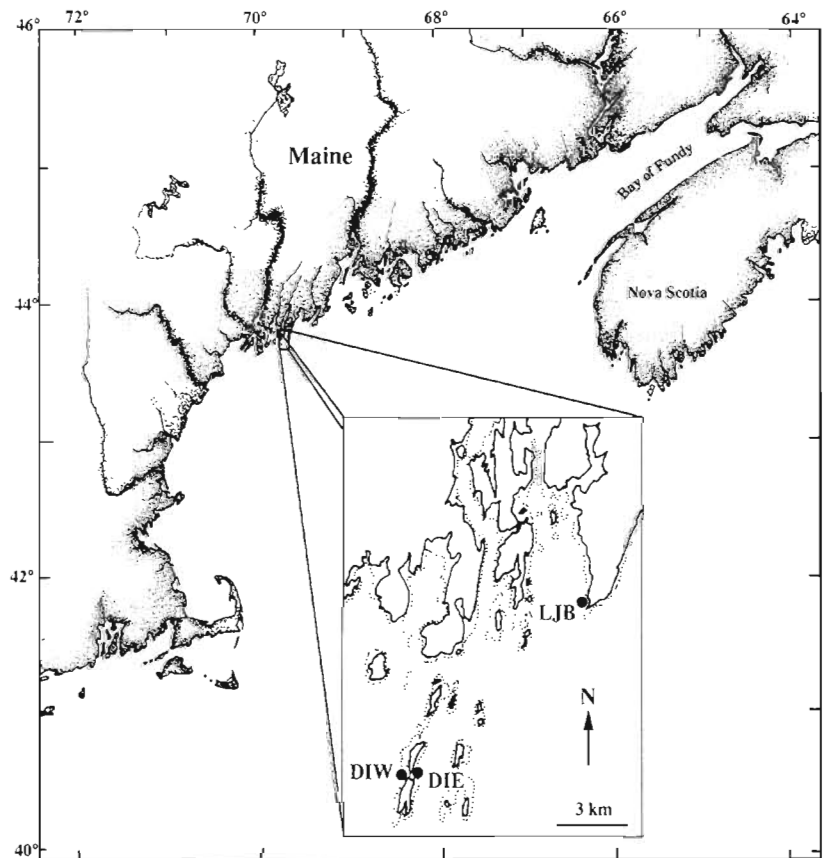


Fig. 1 The Gulf of Maine. The 3 study sites are indicated; LJB: Lower Johns Bay; DIW: Damariscove Island West; and DIE: Damariscove Island East

shapes that were free of epiphytes, or resident predators, cobbles for the plots were collected from a local quarry. Half of the cobble and half of the sand plots were suction-sampled every week for 7 wk (i.e. weekly samples). The remaining plots were sampled once at the end of the settlement season to provide a measure of final recruitment (i.e. end of settlement season samples). The experiment ran from July 26 to September 10, 1994. The weekly sample values were added to estimate inferred settlement (i.e. sum of weekly samples). This inferred settlement is conservative because it is likely that some post-settlement mortality could occur, and the settling decapods could be missed, between the weekly sampling. Counts from end-of-season plots were taken to estimate recruitment or early post-settlement survival.

To contrast the abundance of settlers and individuals older than 1 yr on different substrates (sand and cobble), we used 2-factor and 1-factor analyses of variance for crabs and lobsters respectively (SYSTAT 1992). Since these data were counts with many observations involving zeros, a square root transformation was appropriate (Zar 1974). Additional corrections were made for cases of unbalanced comparisons. For the settlement magni-

tude, substrate selectivity, and post-settlement survival experiment on the 2 sides of Damariscove Island, 3-factor and 2-factor ANOVAs were performed for crabs and lobsters, respectively. Factors were: treatment (cumulative settlement vs end of season post-settlement survivors); island side (DIW vs DIE); and substrate type (only cobble for lobsters; cobble vs sand for crabs). Despite the small sample size in each treatment ($n = 4$), no violations of the assumptions of normality or homogeneity of variance were found. The size-frequency data were subject to a Kernel smoothing method to identify modality (SYSTAT 1992). The estimator shows size classes where the data are most concentrated (i.e. modes; see Manly 1996).

Predator exclusion for crabs. To test the potential importance of benthic predation on settling crabs we used exclusion cages. Only crabs were quantified because important early post-settlement losses have not been observed for lobsters (Wahle & Incze 1997). In the summer of 1995 an exclusion experiment was placed at DIW on the same sand patch utilized in 1994. This was a 2-way, fixed-factor design with substrate and cage treatments as factors and number of recent settlers as the response variable. The cage treatments consisted of exclusion cages (completely covered), cage-control (only a frame defining the area), and partial-exclusion cage roofs (defined area and roof but no walls). The partial exclusion treatment was intended to detect possible cage artifacts due to shading or water flow restriction. Each unit consisted of a 0.5 m^2 ($71 \times 71 \text{ cm}$) wooden frame filled with either cobble or sand. The exclusion and the partial exclusion cages were 20 cm tall. The total exclusion treatment consisted of a green vinyl-coated wire cage (3.5 cm mesh) covered with plastic Vexar™ (4 mm mesh). We chose this mesh size since it was the minimum size that would allow settling crabs to enter the cage (from preliminary observations in laboratory trials with different mesh sizes), but not older conspecific or predators, such as small predatory fish. Settling crabs range in size from 2.5 to 3.0 mm CW. Settling postlarval lobsters are 4 to 5 mm CL and were not expected to enter the cages. To hinder intruders, the frames were also covered with Vexar on the bottom. The partial exclusion consisted of only a roof of the same material. There were 5 replicate plots for each of the 6 treatment combinations for a total of 30 plots. Treatments were randomly interspersed and placed 1.5 m apart over the 5×6 array, covering a surface of $10 \times 12 \text{ m}$. To prevent excessive fouling that might

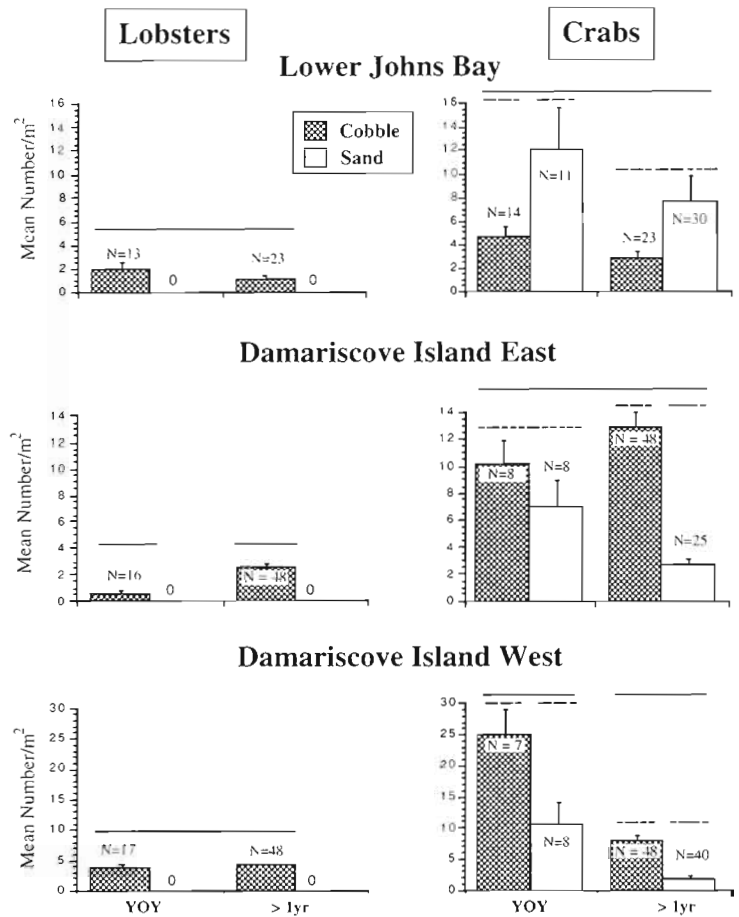


Fig. 2. *Homarus americanus* and *Cancer irroratus*. Mean young-of-year (YOY) density and older individuals (> 1 yr) (± 1 SE) of lobsters and crabs on natural (sand and cobble) substrates measured at the end of the settlement season (mid-September 1994) at the 3 study sites. Numbers represent the number of 0.5 m^2 quadrats surveyed at each site. Continuous horizontal lines represent comparison within species by age and dashed horizontal lines represent comparison within species by substrate. Interupted lines represent significant differences, see Table 1

affect passage of settlers through the mesh, all cages were scrubbed clean weekly with a brush. The experiment started on July 27 and continued throughout September 16, 1995. To minimize possible cannibalism inside the cages by individuals that outgrew the mesh size, the first trial was terminated mid-season (August 19) to remove all individuals, and then a second trial was started immediately.

The predation exclusion experiment was a 2-factor experiment with substratum (sand and cobble) and cage treatment (full cage, roof, and no cage) as independent variables. The response variable was number of settling crabs m^{-2} . They were analyzed with a 2-factor ANOVA and it was possible to pool the August and September data sets since their mean square errors were very similar (197 and 210 respectively).

Table 1. ANOVA of lobsters and crabs density in the 3 study sites: Lower Johns Bay (LJB), Damariscove Island East (DIE), and Damariscove Island West (DIW). Factors are age (YOY or >1 yr) for lobsters and also substrate type (sand or cobble) for crabs. The response variable is number of individuals m^{-2} . Lower level analyses were performed when interactions were significant. Although there are obvious differences in population densities of lobsters in different substrates (Fig. 2), analyses could not be performed because no lobsters were found in sediment

Source	df	Sum of squares	Mean square	F-value	p-value
Lobsters					
Age (LJB)	1	4.787	4.787	1.276	0.2665
Error	34	127.518	3.751		
Age (DIE)	1	45.047	45.047	11.544	0.0012
Error	62	241.938	3.902		
Age (DIW)	1	1.991	1.991	0.168	0.6835
Error	63	748.009	11.873		
Crabs					
LJB					
Substrate	1	618.745	618.745	7.780	0.0067
Age	1	159.879	159.879	2.010	0.1604
YOY	1	333.426	333.426	4.684	0.0411
Error	24	1637.214	71.183		
Substrate \times Age	2	27.188	13.594	0.342	0.5605
Error	74	5885.485	79.534		
DIE					
Substrate	1	556.460	556.460	15.994	0.0001
Age	1	10.673	10.673	0.306	0.5818
>1 yr	1	1652.614	1652.614	45.684	<0.0001
Error	71	2568.427	36.175		
Substrate \times Age	2	153.243	76.621	4.405	0.0388
Error	85	2957.302	34.792		
DIW					
Substrate	1	1306.682	1306.682	42.935	<0.0001
Age	1	2025.085	2025.085	66.540	<0.0001
>1 yr	1	720.319	720.319	38.550	<0.0001
Error	86	1606.954	18.686		
YOY	1	784.933	784.933	7.258	0.0184
Error	13	1406.000	108.154		
Substrate \times Age	2	244.303	122.151	8.027	0.0056
Error	99	3012.954	30.434		

Parametric statistics were used throughout the study. The assumptions of normality, homogeneity of variance, and independence of observations were tested and the appropriate transformations were performed when necessary (Sokal & Rohlf 1995). In all the analyses, lower level ANOVAs were performed in cases where higher level comparisons showed significant interactions. A significance level of $p \leq 0.05$ was considered throughout the study.

RESULTS

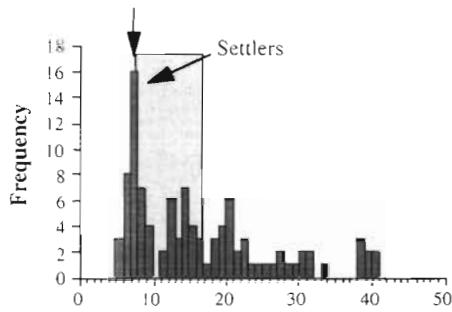
Patterns of settlement, abundance, size structure and substrate associations

Our site censuses indicated that settling lobsters have higher habitat specificity than crabs. Lobsters only settled in cobble while crabs settled in both sand and cobble substrata (Fig. 2). Densities of young-of-

year (YOY) crabs were consistently higher than those of lobsters although abundances were quite variable among sites (Fig. 2). At most of the sites for both species, there were no significant differences between number of YOY and the number of older individuals. Only at the DIE site was the density of settling lobsters significantly lower than that of older individuals. For crabs, only at the DIW site were the YOY consistently more abundant than older individuals in the 2 substrata (Fig. 2, Table 1). When the 2 different substrata were considered, overall preference for either type of substrate was detected for younger individuals (YOY) and older individuals (>1 yr). The only exceptions were for older individuals at LJB and younger individuals at DIE (Fig. 2, Table 1).

The size frequency distribution of both lobsters (Fig. 3) and crabs (Fig. 4) sampled from natural cobble substrata showed a strong mode of settlers, which skewed the distribution to the right (lobster mode: 7.0 mm; crab mode: 8.0 mm). Intermediate size lobsters

A. Natural Cobble Substrates



B. PVC Collectors

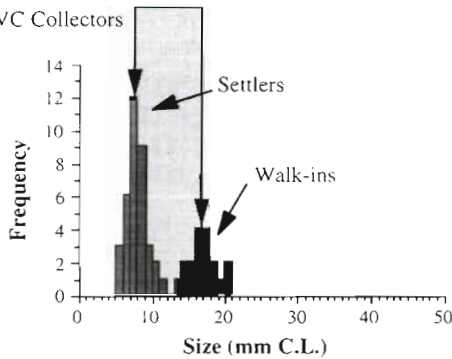
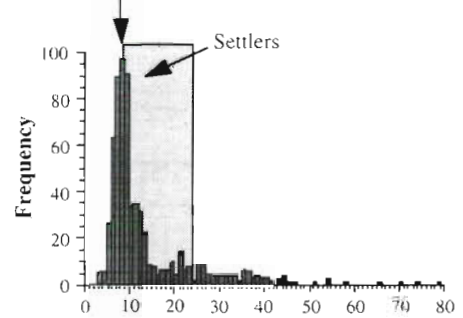


Fig. 3. *Homarus americanus*. Size distribution of lobsters on (A) natural unbound cobble substrate (39 × 0.5 m² quadrats) and (B) PVC collectors (20 × 0.36 m²) at the end of the settling season (mid-September 1994). In each case the 3 sites were pooled together. Modes indicated by the Kernel analysis are indicated by vertical arrows. Shading indicates size-range between the modes observed inside the collectors. Lobsters with sizes within the shaded region of the graph are abundant in natural habitats adjacent to the collectors. Lower densities in the collector indicates they do not migrate into the collectors

A. Natural Cobble Substrates



B. PVC Collectors

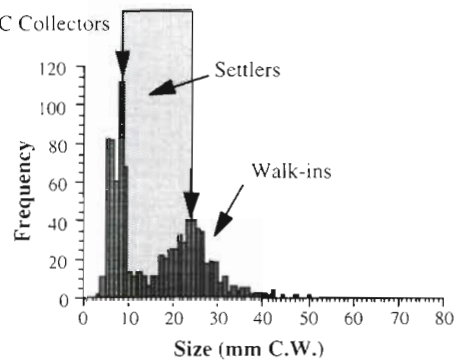
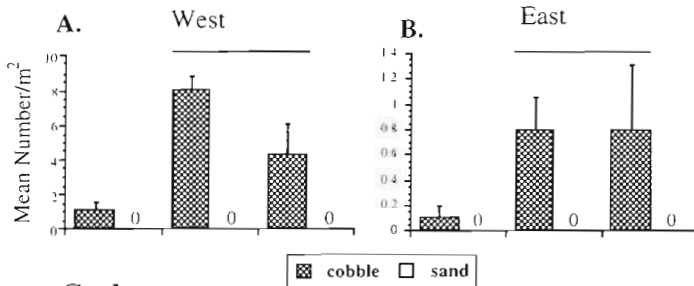
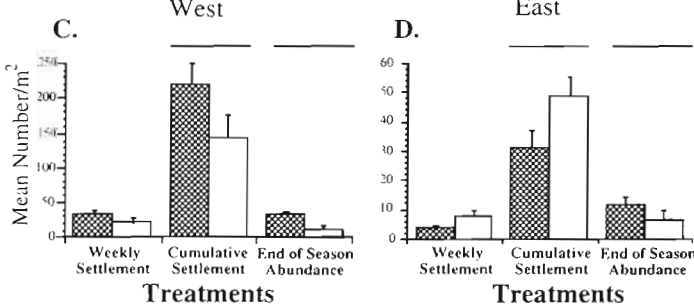


Fig. 4. *Cancer irroratus*. Size distribution of crabs on (A) natural cobble substrate (39 × 0.5 m² quadrats) and (B) PVC collectors (20 × 0.36 m²) at the end of the settling season (mid-September 1994). In each case the 3 sites were pooled together. Modes indicated by the Kernel analysis are indicated by vertical arrows. Shading indicates size-range between the modes observed inside the collectors. Crabs with sizes within the shaded region of the graph are abundant in natural habitats adjacent to the collectors. Lower densities in the collector indicates they do not migrate into the collectors

Lobsters



Crabs



and crabs were proportionally less common in the collectors, resulting in bimodal size distributions. Both species had a distinct gap between the YOY settlers and larger individuals that immigrated into the collectors from the surrounding environment (see shaded sizes in Figs. 3 & 4).

Although lobster recruitment was significantly higher at DIW, we detected no difference between cumulative settlement and early post-settlement survival (end of season abundance) on either side (Fig. 5). Thus, the abundance of surviving settlers at the end of the settlement season equaled the sum of those counted in

Fig. 5. *Homarus americanus* and *Cancer irroratus*. Density of (A, B) lobsters and (C, D) crabs in 1 m² plots on 2 substrate types at the west and east side of Damariscove island during the settling season of 1994. The 2 treatments were cumulative settlement and end of season abundance. Bars represent 1 SE. Interrupted horizontal lines represent significant differences, see Table 2

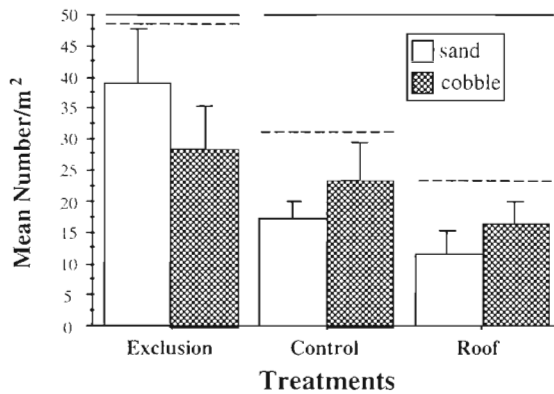


Fig. 6. *Cancer irroratus*. Settlers in a predator exclusion experiment during the settling season of 1995. 'Exclusion': fully caged; 'Control': uncaged; 'Roof': open sides with a caged top. Continuous horizontal lines represent comparison by treatment and dashed horizontal lines represent comparison by substrate. Interrupted lines represent significant differences, see Table 3. Bars represent mean number of settlers m^{-2} and 1 SE

weekly samplings. No recently settled lobsters were found on sand and the highest settler densities found in weekly samplings were in cobble substrata at DIW (Fig. 5). A similar pattern was observed at DIE, although the overall densities were an order of magnitude lower (Fig. 5, Table 2).

Crab early post-settlement survival was also higher at DIW than DIE. Cumulative settlement of crabs at the west side of the island was as much as 2 orders of mag-

nitude greater than that of lobsters on that side (Fig. 5). We detected no difference in settlement densities in cobble or in sand (Table 2). For both substrates, the cumulative settlement was significantly higher than abundance of post-settlers found at the end of the season. That is, the abundance of surviving settlers in the sample plots was much lower than the sum of weekly samples. A similar difference was observed at DIE and although the overall magnitude was lower, again we detected no difference in settlement densities in cobble or in sand (Fig. 5D, Table 2).

Despite differences in settling densities of lobsters on opposite sides of the island, the abundance of individuals older than 1 yr was the same (Fig. 2) ($F = 0.049$, $p = 0.829$; DIW: 4.1 ± 0.51 , DIE: 2.5 ± 0.32 ind. m^{-2}). In contrast, the density of larger crabs was significantly higher at the east side (Fig. 2) ($F = 12.51$, $p = 0.004$; DIW: 8.02 ± 0.66 , DIE: 12.67 ± 1.05 ind. m^{-2}).

Predation exclusion experiment

Newly settled lobsters were found in the uncaged control treatment but were absent in both the exclusion cage and roof treatments. Recently settled crabs, in contrast, were found at significantly higher densities inside the total exclusion cages as compared to the uncaged and roof, control treatments (Fig. 6). The 2-factor ANOVA comparing the joint effect of substrate and cage treatment showed significantly higher density of

Table 2. ANOVA to compare between cumulative samples (settlement) and end of season samples (post-settlement survivors) on cobble substrate for lobsters and on cobble and sandy substrate for crabs. The east and west side of Damariscove Island was also considered. The response variable is number of individuals m^{-2} . Lower level analyses were performed when interactions were significant

Source	df	Sum of squares	Mean square	F-value	p-value
Lobsters					
Treatment	1	14.062	14.062	3.0	0.1089
Island side	1	115.562	115.562	24.653	0.0003
Treatment \times Is. side	1	14.062	14.062	3.0	0.1089
Error	12	56.250	4.688		
Crabs					
Treatment	1	72866.531	72866.531	51.995	<0.0001
Island side	1	47355.031	47355.031	33.791	<0.0001
Treatment \times Is. side	1	33217.531	33217.531	23.703	<0.0001
Substrate	1	3341.531	3341.531	2.384	0.1356
Treatment \times Substrate	1	603.781	603.781	0.431	0.5178
Is. side \times Substrate	1	5697.781	5697.781	4.066	0.0551
Treatment \times Is. side \times Substrate	1	3180.031	3180.031	2.269	0.1450
Error	24	33634.250	1401.427		
Treatment					
West side	1	102240.062	102240.062	32.168	<0.001
Error	14	44496.375	3178.312		
East side	1	3844.000	3844.000	27.443	0.0001
Error	14	1961.000	140.071		

Table 3. Results of the 2-factor ANOVA for the exclusion of predators (Treatment) on sand or cobble plots (Substrate). The response variable is number of settling crabs m^{-2}

Source	df	Sum of squares	Mean square	F-value	p-value
Substrate	1	0.121	0.121	0.000562	0.9812
Treatment	2	2681.134	1340.567	6.246	0.004
Substrate × Treatment	2	742.239	371.119	1.729	0.189
Error	45	9658.297	214.628		

settlers inside the exclusion cages irrespective of substrate, and no significant interaction (Table 3). Pairwise comparisons for the different treatment and substratum combinations were performed using Fisher's LSD test. Significant differences were only found between the total exclusions versus the open treatment ($p = 0.0159$), and the total exclusions versus the roof treatment ($p = 0.0005$) (Fig. 6).

DISCUSSION

At all study sites, early post-settlement lobsters were confined to cobble. In contrast, newly settled rock crabs were found at comparable densities in cobble and sand substrates and overall their densities were higher than those of lobsters. Since inferred settlement was significantly greater than end-year recruitment in crabs but not in lobsters, we suspect that early post-settlement mortality and possibly migration affect the abundance of crabs. Conversely, lobsters did not show evidence of early post-settlement mortality since the cumulative density of settlers was comparable to the total young-of-year determined at the end of the settlement season (Fig. 5). Further, the use of artificial collectors enabled us to rule out the possibility of emigration as the source of early post-settlement losses in both species (Figs. 3 & 4). Crabs, however, suffered significant early post-settlement mortality, and this pattern was consistent even when 2 sites with very different settlement rates were compared (Fig. 5). Because post-settlement losses appeared to be so important for crabs, the predation exclusion experiment served to evaluate the effects of predation on those losses. The experiment showed higher densities of post-settling crabs when potential predators were excluded (Fig. 6). This suggests predators are important even though the specific identity of the predator(s) is unknown.

Several ecological studies on *Homarus americanus* have recognized the importance of factors operating before and immediately after settlement. Larval supply could explain local differences in settlement (Katz et al. 1994, Wahle & Incze 1997). The well-known shelter-seeking behavior of lobsters during settlement can

dramatically improve survival during the early benthic phase (Boudreau et al. 1990, Incze & Wahle 1991, Wahle & Steneck 1991, 1992, Wahle 1992, Barshaw et al. 1994, Cobb & Wahle 1994). Previous experiments by Wahle & Incze (1997), comparing inferred settlement to recruitment in *H. americanus*, also showed high post-settlement survival in initially vacant plots. Comparatively little is known about the relative importance of pre- and post-settlement processes affecting *Cancer irroratus* (Beninger et al. 1986, Clancy & Cobb 1991, Clancy 1995). Geographical patterns in settlement (i.e. among-site differences) are similar in *C. irroratus* and *H. americanus*, suggesting they are subject to the same larval transport processes (Wahle & Incze 1997). Crabs, however, are less selective than lobsters with respect to habitat (Fig. 2). Association of individuals with protective habitats has been shown for other large invertebrates, e.g. where it is also linked to predator avoidance in several species of spiny lobsters (Jernakoff 1990, Booth & Phillips 1994, Norman et al. 1994, Yoshimura et al. 1994), gem clam (Ahn et al. 1993), and queen conch (Ray & Stoner 1995).

Local supply of post-larvae can explain the local differences in abundance of early juvenile stages of crabs and lobsters, as shown by the striking difference in the abundance of new settlers at DIW and DIE (Fig. 5). Incze & Wahle (1991) and Wahle & Incze (1997) showed a similar pattern of difference in settlement, suggesting difference in supply for lobsters at the same DIE and DIW sites in 1989 and 1990. For neither species is there a clear correspondence between the density of new recruits and older individuals. At least for lobsters, this decoupling of local densities from initial settlement patterns is due to movements that begin a year or so after settlement (Wahle & Incze 1997).

Lobsters tend to stay near where they settled for approximately 1 yr. The existence of a bimodal size distribution inside collectors indirectly shows that individuals in the size range between the 2 modes (shading in Figs. 3 & 4) do not tend to walk into the collectors, although this size range is represented in collections from adjacent natural substrate. Incze & Wahle (1991) showed that local differences in density set at the time of settlement persisted through the first year, further supporting our conclusion that newly

recruited lobsters are relatively sedentary and suffer little post-settlement mortality. Evidence also suggests that early post-settlement crabs are relatively sedentary. Crabs show a similar pattern to lobsters, and the gap between modes seems to span a larger size range (from approximately 10 to 25 mm CW). Since we lack information on growth rate of *Cancer irroratus* under natural conditions, we cannot determine if this larger size range means that crabs are sedentary longer than lobsters after settling. However, individuals larger than 25 mm are clearly older than 1 yr (Reilly & Saila 1978). As for lobsters, the size distribution in natural substrata appears to be heavily shifted to the left due to the influx of new settlers (Fig. 3).

The results of the exclusion experiment demonstrate that the population density of recently settled crabs is higher when potential predators are excluded (Fig. 6). This pattern was more pronounced when sand was used as substrate, as only in this case did we observe a pairwise significant difference between exclusion and control treatments. For the cobble treatment alone, no difference existed between exclusion and control (Fig. 6, Table 3) which could indicate the effectiveness of cobble in naturally excluding predators. On the other hand, the high densities of crabs observed on sand may represent a case of habitat selection, unknown until now, and apparently reinforced when predators are excluded. Equivalent results for lobsters were not considered because the mesh size used (4 mm) prevented post-larvae from entering the caged as well as the roofed treatments. This could mean that lobsters settle vertically and move minimally in a lateral direction (a few centimeters from the bottom) after settlement (see also Aiken & Waddy 1986).

Both species undergo an ontogenetic niche shift (sensu Werner & Gilliam 1984) such that newly settled individuals are segregated from older ones (e.g. Wahle 1992, Wahle & Steneck 1992, Cobb & Wahle 1994, Eggleston 1995, Lawton & Lavalli 1995). This is even more evident for lobsters where cobble beds in shallow zones represent an almost exclusive nursery ground. It has been suggested that the requirement for cobble as shelter-providing substrata and the high risk of mortality to small lobsters without shelter could create a natural demographic bottleneck to benthic recruitment for this species (Wahle & Steneck 1991, 1992, Wahle 1992, see also Beck 1995). Although crabs were less substrate-specific and settled at much higher densities than lobsters, later in life population densities of lobsters and crabs are more similar (Fig. 2). The results obtained in 1994 at both DIW and DIE are consistent with prior observations that lobsters do not suffer significant post-settlement losses after they settle in cobble beds (Fig. 5A, B) (Incze & Wahle 1991, Wahle & Incze 1997). Crabs on the other hand experienced dra-

matic losses in the 2 substrates examined (Fig. 5C, D). Although in the exclusion experiment no significant differences were detected in the number of crab settlers between substrates, slightly larger crabs tend to be more abundant in cobble than on sand (Figs. 2 & 5). Since our collectors indicate that recently settled crabs tend not to move, we deduce that most of the losses are due to mortality. Compared to other similar experimental approaches (Beninger et al. 1986), our PVC collectors were an efficient way to assess settlement strength and the propensity of larger lobsters to immigrate to uninhabited areas. Artificial settlement substrata have also been successfully used to quantify settlement rates of other crab species (Donaldson et al. 1991, Fernandez et al. 1993, Eggleston 1995, Morgan et al. 1996). Settling densities for lobsters inside collectors were comparable to that of natural substrata, however, we noticed an over-sampling effect for crabs. This could be due to the collector's 3-dimensional lattice structure which may prevent large organisms, including predators from entering, thus acting to some degree as a predator-free environment for smaller individuals.

Although the effect of predation on early post-settling crabs was important, we lack information about the identity of the predator(s). Several species of benthic fish have been shown to prey upon *Cancer irroratus* (Reilly & Saila 1978, Malpass 1992). Field studies in this region have shown the importance of several fish species as consumers of small crabs and lobsters (Wahle & Steneck 1992). Small crabs predominate in the guts of several species of benthic fish (Palma pers. obs.) and laboratory experiments confirmed their vulnerability to demersal fish such as cunner *Tautoglabrus adspersus* and sculpins (*Myoxocephalus octodecemspinosus* and *M. scorpius*) common in coastal zones of the Gulf of Maine (Ojeda & Dearborn 1991). A similar pattern has been shown for Dungeness crabs *C. magister* (Armstrong et al. 1995). As most organisms grow, they become more predator-resistant (Connell 1975, Jones 1991, Moreno 1995). Our observations show that large crabs and lobsters in all types of habitats are less cryptic and less vulnerable to predation. A general low abundance of large predatory fish is characteristic of coastal waters of the Gulf of Maine, probably the result of a long history of intensive fishing in New England which has severely depleted stocks of important benthic predatory fish (Witman & Sebens 1992).

Large scale community changes, such as the reduction in abundance of large predatory fish in coastal waters of Maine (Witman & Sebens 1992), are likely to affect the population dynamics of these 2 large decapods. In both cases, it is the early-post-larval stages that appear to be most susceptible. Whereas crab population densities appear to be set by predators acting

some time relatively soon after settlement, lobster densities are set by their larval supply and their behavior at the time of settlement. Thus the settlement and early post-settlement ecology of these 2 species may be demographic bottlenecks that mask the effects of subsequent ecological processes.

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