

The influence of stage-dependent dispersal on the population dynamics of three amphipod species

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Abstract In metapopulations, the maintenance of local populations can depend on source–sink dynamics, where populations with positive growth rate seed populations with negative growth rate. The pattern and probability of successful dispersal among habitats can therefore be crucial in determining whether local populations will become rare or increase in abundance. We present here data on the dispersal strategy and population dynamics of three marine amphipods living in pen shells (*Atrina rigida*) in the Gulf of Mexico. The three amphipod species in this study disperse at different life stages. *Neomegamphopus hiatus* and *Melita nitida* disperse as adults, while *Bemlos unicornis* disperses as juveniles. The two species that disperse as adults have the highest initial population sizes when a new shell becomes available, likely caused by the arriving females releasing their brood into these recently occupied shells. This dispersal pattern results in initially higher population growth, but fewer occupied shells, as noted by their clumped distribution. In contrast, the species that disperses as juveniles accumulates more slowly and more evenly

across habitats, eventually dominating the other two in terms of numerical abundance. The metapopulation dynamics of the three species seems to be highly dependent on the life history stage involved in dispersal.

Keywords Metapopulation · Benthic invertebrates · Life history stage · Abundance-distribution relationship

Introduction

In spatially structured populations, or metapopulations, source–sink dynamics can sustain local populations that are unable to maintain themselves with their own reproductive output (Pulliam 1988; Amarasekare 2004). Areas with positive population growth are regarded as sources, from which individuals emigrate; conversely, areas with negative population growth are sinks, where populations can only persist through the input of immigrants. Two major theoretical advances have been made with regards to dispersal in metapopulations. The first consists of the role of density-dependent dispersal, where the number of dispersers is dependent on the density of the source population, allowing species to either increase when rare at the local scale (negative density-dependent dispersal), or reduce a population size if dispersal increases with density (Amarasekare 2004). In the second, the cost of dispersal from sources can cause population growth rates to become negative (Gundersen et al. 2001) or even cause local populations to go extinct (Holt 1993). In this article, we present data on three marine amphipod species that suggest that the life history stage in which dispersal occurs can influence population dynamics and cause species to become rare or common.

Marine organisms can disperse at a variety of life history stages. These include the dispersal of broadcast spawned

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gametes (Scheltema 1986; Grosberg 1991; Swearer et al. 1999; Gilg and Hilbish 2003), the release of brooded larvae from maternal adults (Olson 1985; Sotka et al. 2004), and the movement of both juveniles (Martel and Chia 1991; Olivier et al. 1996) and adults (Junkins et al. 2006). The consequence of stage-specific dispersal is stage-specific colonization. Population dynamics at a local habitat will be affected by the life history stage of the founding individuals and subsequent recruits. These differences include size-dependent survivorship, the likelihood of producing offspring and the genetic structure of the founding population (e.g., Highsmith 1982; Todd et al. 1998).

Variation in the stage of dispersal may also affect the distributional pattern of recruits and adults. Recruitment can be patchy in time and space (e.g., Caffey 1985), and this patchiness is likely to be reduced or magnified by the dispersal stage. Direct developers with limited dispersal ability can clump around benthic egg capsules (Gosselin and Chia 1995) or parental females (Gerrodette 1981). The dispersal of adults could result in an over-dispersed distribution if territorial, or a highly clumped distribution if, for example, they bring a brood of juveniles into the new habitat. Unfortunately, however, most studies on dispersal tend to focus on juvenile or larval propagules as the dispersing agent (Palmer et al. 1996). The combination of qualitative differences in the stage of recruits (e.g., adults versus juveniles) and the distribution of these recruits is likely to exert an influence on the local and regional population dynamics of these organisms.

The linkage between dispersal stage and local population dynamics is particularly evident in marine systems where fecundity and juvenile mortality are high. Flooding the environment with large numbers of highly dispersed offspring will potentially reduce the variance in recruitment to a wide variety of local habitats. In contrast, the dispersal of adults ready to reproduce can have a large influence on the dynamics of the few local habitats that they successfully colonize. In the extreme, the dispersal of brooding females can rapidly found a new local habitat with a population of siblings. Understanding the consequences of these different dispersal strategies to population dynamics can be problematic because they often involve widely disparate taxa, potentially confounding phylogenetic considerations, or different habitats where studies focus on the effects of different environmental conditions (e.g., patch size and resource availability) on the recruiting ability of species.

In the present study we explore the population consequences of different dispersal strategies in three co-occurring amphipod species that are part of pen shell communities in the Gulf of Mexico. In particular, we asked the following questions (1) What is the life history stage in which these species arrive to shells? In spatially structured habitats such as pen shell communities, theory suggests that propagule release as well as the settlement of new recruits

can strongly influence population dynamics: species that colonize with reproductive individuals should have faster population growth rates relative to species that disperse with non-reproductive individuals. (2) Is recruitment dependent on the age of the community (i.e., the successional stage or the time since the shell became available) or is it dependent on temporal patterns (i.e., the conditions when the shell became available, or lunar cycles)? If successional stages are important for recruitment, then community age could determine species' abundance and distribution patterns. Alternatively, if temporal patterns are important, then these could explain dispersal limitation, in particular for rare species. We performed an experiment where pen shells were anchored at different times within a month but left in the water for the same amount of time. Furthermore, we tested the influence of lunar stages to determine whether an environmental cue could influence dispersal in these amphipod species and synchronize individuals in the water column. (3) How does the stage-dependent dispersal of these species affect short- and long-term local population dynamics and distribution? The mode by which species disperse may become crucial for determining growth rates and, therefore, potential sources and sinks in metapopulations. The three amphipod species, *Neomegamphopus hiatus*, *Melita nitida*, and *Bemlos unicornis* are not endemic to pen shells; however they colonize this substrate in high densities relative to the surrounding habitat, therefore behaving as metapopulations (Munguia 2007).

Methods

Our study was conducted during the springs and summers of 2001–2005 in St. Joe Bay, Florida, a shallow, well-protected bay with patches of sea grass beds. Within the sea grass beds, pen shells (*Atrina rigida*; bivalves with average length of 19 cm) live anchored to the bottom with byssus threads (Kuhlmann 1996; Munguia 2004). These shells offer settling substrate for many invertebrates when the mollusk dies. Pen shells are the most abundant source of hard substrate, in essence becoming “islands” of habitat within the grass beds and sandy substratum for many species found in St. Joe Bay (Munguia 2004, 2007).

Among the inhabitants of pen shells are a number of amphipod species, including *M. nitida*, *B. unicornis*, and *N. hiatus*. Amphipods are direct developers where females carry their brood in a marsupium and release their offspring during molting events (Borowsky 1990). Males tend to latch onto the backs of females before a female molts, guarding her from other males attempting to mate. All three amphipod species display sexually dimorphic characters; males have a large secondary gnathopod relative to females, and reproductively active females have a brood

pouch. Consequently, it is relatively easy to distinguish between the sexes in adult individuals. In St. Joe Bay, these three amphipod species are most abundant on pen shells and very rare in sea grass beds where pen shells are not present, probably because they require or prefer the combination of hard substrate and protection these bivalves provide (Munguia 2007). *M. nitida* is a relatively common amphipod that occurs subtidally along the northwestern Atlantic coast (Bousfield 1973) and *B. unicornis* has been reported in the Gulf of Mexico (Thomas 1993). *N. hiatus* is a tube-dwelling amphipod that can occur in large aggregations of individuals (Thomas 1993; P. Munguia unpublished data).

To measure the stage at which individuals arrive to shells (settlement stage), we anchored shells during the months of March–August (approximate length: 19 cm) and collected them 1 day after placement. All of the shells were placed at the same water depth (approx. 1 m) and distance from the shore. Anchoring of the shells was synchronized with either the full or new moon to determine if dispersal was linked to a lunar cycle. We then decoupled temporal effects and shell age by setting up an array of shells anchored for the same amount of time but placed and collected at different times of the month. Finally, we looked at longer term population dynamics in a series of studies of manipulated and naturally occurring pen shell communities. These studies included an examination of the distribution of the three amphipods at the time of arrival and among naturally occurring pen shell communities. Different experiments were performed at different times of the year, and in some cases we used artificial pen shells made out of PVC [Electronic Supplementary Material (ESM)1], which had a similar surface area to natural shells. Preliminary studies showed that diversity in artificial shells is not different from that found in *A. rigida* communities (P. Munguia unpublished data).

Amphipod settlement to shells

To measure colonization rates, we anchored empty and unfouled shells in the field and collected them 1 day after placement. We assumed that all individuals present after 1 day had arrived without having grown significantly in size at the new habitat. We measured head size (in millimeters) of individuals and compared sizes with individuals from older established shells (head size correlates well with body size in amphipods; e.g., Edwards and Cowell 1992; unpublished data). The anchoring of these shells coincided with either the full or new moon in order to test the lunar effect on amphipod recruitment to pen shells (the strongest recruitment contrast is between new and full moons; P. Munguia unpublished data). We performed nine 1-day surveys, four at the new moon and five at the full moon phase of the lunar cycle. Each survey consisted of ten anchored shells.

Collection consisted of placing a zip lock bag over the shell, releasing the anchor, and bringing the bag and its contents back to the surface. This provided minimum disturbance to the individuals within shells and allowed us to collect all organisms living in the shells. These samples were brought back to the laboratory where the contents were flushed with fresh water and collected in a 0.5-mm mesh. Amphipods were then identified, sorted and preserved in 70% ethyl alcohol.

Shell age and short-term population patterns

A second experiment tested the effect of shell age and temporal effects on the colonization rates and population dynamics of the three amphipod species. We set out shells and collected them at 1, 4, 8, 12, and 16 days after placement. We retrieved eight shells each collection time. Shells were placed 2 m apart, a distance considered to provide spatial independence (as indicated by preliminary studies; P. Munguia unpublished data). Subsequent shell arrays were placed on the 4th, 8th, and 12th collection dates, with each array being collected in sequence at 4-day intervals after placement (e.g., shells placed on the 4th day were collected on the 8th, 12th, and 16th collection days). This allowed us to test both the effect of shell age (the amount of time the shell spent in the water) and temporal effects (when the shell was placed in the water).

Long-term population patterns

We used data from three pen shell community succession experiments carried out in St. Joe Bay (summers of 2001, 2003, and spring of 2004) to compare populations in shells that had been in the water 20 ($n = 119$ total shells), 40 ($n = 89$), 60 ($n = 133$), and 128 days ($n = 66$). We also examined populations in naturally occurring pen shells from the summer of 2005 to compare the natural distribution and abundance patterns with our experimental data ($n = 56$ shells collected during eight sampling periods from May to July). The ages of these naturally occurring pen shell communities were not known.

Abundance–distribution relationship

In order to understand the effect of dispersal stage on the regional distribution pattern, we tested for the degree of aggregation of individuals upon arrival ($t = 1$ day) and in established shell communities using a standardized Morisita's dispersion index (Krebs 1999). We chose this index because it is not affected by population size or pen shell (i.e., plot) size, as are other indices. The standardized version of the index creates an upper and lower boundary from -1 to $+1$ based on a χ^2 distribution values (ESM2). An

index value of 0 is indicative of a random distribution, while +1 indicates a clumped distribution and -1 corresponds to a uniform distribution. With this standardized index, the 95% confidence intervals have an upper and lower boundary of +0.5 and -0.5, respectively (e.g., values above 0.5 would correspond to a clumped distribution). We first calculated the dispersion index using data from natural populations and then compared the three species by bootstrapping the data (1000 iterations) and calculating 95% confidence intervals around the indices. We also calculated dispersion indices for both males and females in those shells that were anchored for 1 day ($n = 9$ events) to understand sex-specific distribution patterns at the time of colonization. A log-likelihood ratio contingency test (Zar 1999) was used to compare the nine 1-day distributions among the three species. To compare dispersion indices between sexes for each species, we used a t -test comparing the unstandardized Morisita's index of males and females (where index values of 1 indicate random distributions, >1 represent clumped distributions, and 0 represent uniform distributions). We used JMP ver. 4.0 and SAS ver. 8.01 for all statistical analyses (SAS Institute, Cary, N.C.).

Results

Patterns of amphipod arrival

The three amphipod species were found to have different dispersal modes. *M. nitida* tends to disperse as adults - 97% of all recruits were adults and almost 50% of the females were brooding (Table 1). *N. hiatus* also recruited as adults (95% of all arriving individuals) with nearly 40% of females brooding offspring. In contrast, *B. unicornis* arrived at shells as juveniles (60%) or juvenile-sized adults (40%). Shell occupancy varied across species, with *M. nitida* occupying all of the anchored shells, followed by *N. hiatus* (87% of shells occupied), and *B. unicornis* (38%). The size of *B. unicornis* juveniles and "adults" did not differ at day one (juvenile head size = 0.33 ± 0.07 mm, head size of adults at day 1 = 0.37 ± 0.11 mm; t -test: $df = 25$, $t = 0.726$,

$P = 0.47$). These small *B. unicornis* adults were much smaller during recruitment at day 1 than the adults found in older, established shells (head size in older shells = 0.61 ± 0.12 mm; t -test: $df = 53$, $t = 7.769$, $P < 0.0001$), suggesting that these small adults recently attained a sexually dimorphic stage, perhaps just prior to or immediately after arrival to these pen shells.

Short-term population dynamics

After 16 days of habitat establishment, *N. hiatus* and *M. nitida* had more juveniles than *B. unicornis* (ANOVA at 16 days: $df = 2$, 32, $F = 3.77$, $P = 0.03$; Fig. 1a), while *N. hiatus* had the most adults (ANOVA at 16 days: $df = 2$, 32, $F = 17.49$, $P < 0.001$; Fig. 1b). Overall, there were significant differences in total abundances among all three species with *N. hiatus* being most the abundant, followed by *M. nitida* and *B. unicornis* (ANOVA at 16 days: $df = 2$, 32, $F = 14.08$, $P < 0.001$; Fig. 1c).

The rates of total population growth were tested with an ANCOVA using shell age as the covariate to assess the main effects of species (Table 2). There was a significant interaction between shell age and species, indicating that these species have different rates of population growth. We then conducted independent regression analyses of each species and noted a significant polynomial term in *N. hiatus* and *M. nitida*, indicating that population growth decreased over this interval. In contrast, *B. unicornis* had a linear relationship (no significant polynomial term), indicating a constant increase in numbers over this 16-day interval (Table 2).

Over this 16-day time interval, all three species had local populations dominated by females (Fig. 1d). An analysis of covariance indicated that during this 16-day interval the proportion of adults that were male decreased in all three species and that there was a significant main effect of species, with *N. hiatus* having the highest proportion of males, followed by *B. unicornis* and *M. nitida* (ANCOVA: $df = 5$, 346, $F = 9.79$, $P < 0.0001$; species effect: $F = 20.46$, $P < 0.0001$; collection time: $F = 8.36$, $P = 0.004$; interaction: $F = 0.027$, $P = 0.97$).

Table 1 Species abundances and proportions of recruits after 1 day of recruitment

Species	Number of individuals		Proportions	
	Adults	Juveniles	Males: adults	Gravid (pregnant): females
<i>Neomegamphopus hiatus</i>	6.24 (1.13) a	0.30 (0.16)	0.42 (0.04)	0.37 (0.04)
<i>Melita nitida</i>	7.57 (0.59) a	0.22 (0.14)	0.24 (0.02)	0.47 (0.04)
<i>Bemlos unicornis</i>	0.27 (0.09) b	0.41 (0.1)	0.30 (0.09)	0.07 (0.08)*

Asterisk represents a significant departure from random proportions (Heterogeneity test, $P < 0.05$)

Values are given as the mean \pm the standard error (in parenthesis). Values followed by different letter indicated statistically different abundances between species as determined by a Tukey post hoc test ($P < 0.01$, $n = 90$)

Fig. 1 Abundance (mean ± SE) of juveniles (a), adults (b), and total individuals (c), and the proportion of males (d) from the total number of adults for the three amphipod species *Melita nitida* (filled circle), *Bemlos unicornis* (open circle), and *Neomegamphopus hiatus* (filled triangle) after 1–16 days of shell establishment in 2001–2005 in St. Joe Bay, Florida. Different letters represent statistically different ($P < 0.05$) values at 16 days, as determined using a Tukey HSD test. Note log-scale in panels a, b, and c

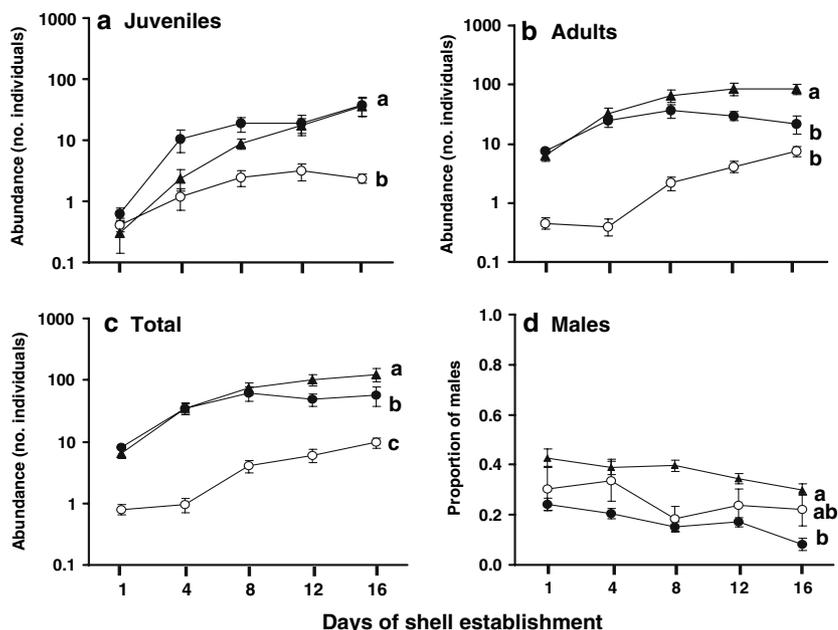


Table 2 Among-species comparison of abundance (e.g., total number of individuals per shell) levels in terms of short-term population dynamics and polynomial regression values for each species abundance over a 16-day period

ANCOVA on all three species				
ANCOVA	df	F-ratio	P	
Species	2	82.8683	<0.0001	
Time	1	35.9409	<0.0001	
Species × time	2	4.7643	0.0092	
Regressions on each species				
Term	Estimate	Standard error	t-ratio	P
<i>N. hiatus</i>				
Intercept	1.374	0.11	12.32	<0.0001
Time	0.348	0.028	12.22	<0.0001
(Time) ²	-0.02	0.004	-4.64	<0.0001
<i>M. nitida</i>				
Intercept	2.072	0.088	23.53	<0.0001
Time	0.229	0.024	9.25	<0.0001
(Time) ²	-0.02	0.0036	-5.31	<0.0001
<i>B. unicornis</i>				
Intercept	0.246	0.0717	3.44	0.0008
Time	0.116	0.01838	6.32	<0.0001
(Time) ²	0.000	0.0026	0.14	0.8856

Short-term lunar and temporal patterns of recruitment

The moon phase significantly influenced recruitment patterns in two of the three species. One of the two species that recruits as adults, *M. nitida*, mostly recruited as brooding females during the new moon (81% of females brooding;

ESM3). During the full moon phase, only 23% of females carried a brood (t -test: $df = 62$, $t = 5.851$, $P < 0.0001$). The species that recruited as juveniles, *B. unicornis*, showed a 16-fold increase in juvenile recruitment during the full moon (t -test: $df = 50$, $t = 2.771$, $P = 0.007$).

Recruitment was dependent on the date of initiating the experiment for two of the three species (Fig. 2). *N. hiatus* did not show any differences in abundance at day 4 for any of the collection times, suggesting no effect of date on colonization ability (ANOVA: $df = 3, 35$, $F = 1.07$, $P = 0.37$). *M. nitida* had a significantly higher abundance at the 4-day census for shells placed during the new moon (ANOVA: $df = 3, 35$, $F = 4.63$, $P = 0.008$), despite a non-significant lower rate of adult arrival at day 1 for this census (t -test: $df = 49$, $t = 1.587$, $P = 0.11$; ES3). This indicates that this high abundance was driven by the release of juveniles from the high proportion of arriving females that were brooding. In contrast to the other two species, *B. unicornis* showed a gradual increase in recruitment over a 4-day period at these four dates of shell establishment (Fig. 2; ANOVA: $df = 3, 35$, $F = 5.95$, $P = 0.002$).

Long-term population dynamics

Results from longer term experimental studies of colonization and natural surveys of established pen shell communities exhibited patterns consistent with the short-term dynamics. Experimental studies showed that – consistent with the short-term dynamics – *N. hiatus* and *M. nitida*, which showed a decreasing population growth over 16 days, had a slightly negative population growth on individual shells over several months (Table 3). In contrast, *B. unicornis*, which had linear positive population growth

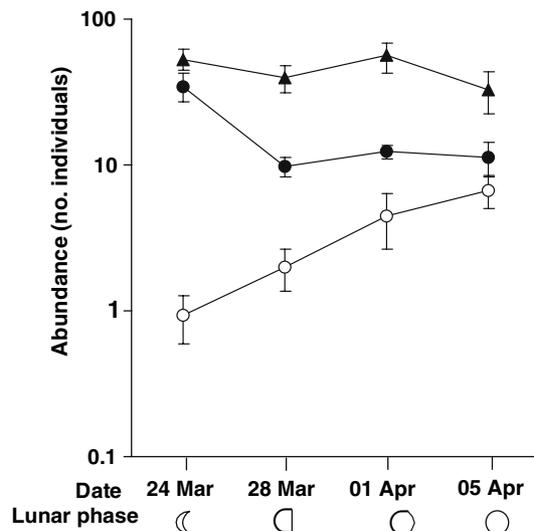


Fig. 2 Abundance (mean \pm SE) of *M. nitida* (filled circle), *B. unicornis* (open circle), and *N. hiatus* (filled triangle) collected from pen shells set in the water at four different lunar phases in March and April, 2001–2005. All shells were in the water for 4 days. The new moon occurred on 20 March. Note log-transformed data

Table 3 Among-species comparison of amphipod abundance levels from long-term population dynamics in experimental pen shells

ANCOVA on all three species from long-term experiments				
ANCOVA	df	F-ratio	P	Slope
Species	2	0.46	0.4969	
Time	1	28.98	<0.0001	
Species \times time	2	19.52	<0.0001	
Regression on <i>B. unicornis</i>				
Time	1	39.24	<0.001	0.28
ANCOVA on <i>N. hiatus</i> and <i>M. nitida</i>				
Species	1	48.1	<0.001	
Time	1	8.25	0.0042	-0.06
Species \times time	1	0.29	0.586	

Because the interaction term in the ANCOVA was significant, *B. unicornis* data were taken out and regressed independently, and the ANCOVA was performed again for *N. hiatus* and *M. nitida*

over 16 days, continued to increase in abundance on each shell over several months (Table 3). These differences in population growth resulted in *B. unicornis* being the most abundant amphipod species after 128 days, with an average of 18.3 individuals per shell compared to 14.8 and 2.27 for *N. hiatus* and *M. nitida*, respectively (ANOVA: $df = 2, 63, F = 13.61, P < 0.0001$, see Fig. 3).

Consistent with these experimental data, these patterns of abundance at 128 days were similar with a survey of naturally occurring shells (Fig. 3). In natural shell communities, *B. unicornis* had the largest populations (mean = 6.38 ± 1.12), followed by *N. hiatus* (1.91 ± 6.66) and *M. nitida*

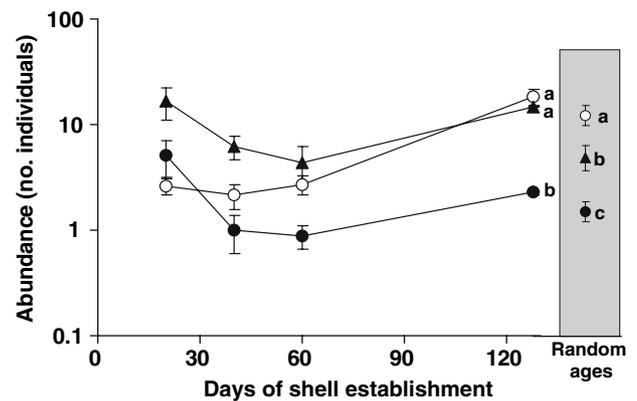


Fig. 3 Abundance (mean \pm SE) of *M. nitida* (filled circle), *B. unicornis* (open circle), and *N. hiatus* (filled triangle) on shells in water for 16–128 days and on naturally occurring shells of random ages (shaded box). Different letters represent statistically different ($P < 0.05$) abundances at 128 days and random ages using a Tukey HSD test. Note log-transformed data

(0.437 ± 0.88). In addition, there was a significant seasonal pattern in these surveys. Over the period from late spring to summer, *B. unicornis* had a positive increase in abundance (slope = 0.17, $F = 13.35, P < 0.001$), while *N. hiatus* showed no change in abundance (slope = 0.03, $F = 0.34, P = 0.54$) and *M. nitida* had a significant decrease in abundance (slope = $-0.14, F = 9.69, P = 0.003$). *M. nitida* occupied the lowest proportion of shells (56% of shells occupied), followed by *N. hiatus* (65%) and *B. unicornis* (69%).

Abundance-distribution relationship

These three amphipod species have different patterns of distribution. In naturally occurring pen shells, both *M. nitida* and *N. hiatus* (the adult dispersers) have significantly clumped distributions (mean \pm confidence interval; $Id = 0.53 \pm 0.008$ and $Id = 0.52 \pm 0.009$, respectively). In contrast, *B. unicornis* (the juvenile disperser) is distributed randomly ($Id = 0.45 \pm 0.003$). A similar distribution pattern emerges during colonization; *M. nitida* and *N. hiatus* have clumped distributions, while *B. unicornis* has a random distribution of individuals ($\chi^2 = 68.95, df = 4, P < 0.001$). It is interesting to note that males of the tube-building species, *N. hiatus*, clump more than females (t -test, $df = 9, t = 2.28, P = 0.04$), while the males of the other two species do not ($P > 0.1$).

Discussion

Consequences of variation in dispersal stage among amphipod species

This study presents three examples of population consequences of dispersal in marine invertebrates. The three

amphipod species disperse at different life stages (Table 1). *N. hiatus* and *M. nitida* disperse as adults, while *B. unicornis* disperses as juveniles. The two species that disperse as adults have the highest initial population sizes, likely caused by the arriving females releasing their brood into these recently occupied shells. This dispersal pattern results in initially higher population growth but fewer occupied shells, as noted by their clumped distribution. In contrast, the species that disperses as juveniles accumulates more slowly and more evenly across habitats, eventually dominating the other two species in terms of numerical abundance (Fig. 3). Overall, the two species that recruit as adults and brooding females have a more clumped distribution than the juvenile dispersing species that has a random distribution. The clumped distribution in the species that disperse as adults may reflect the release of juveniles from brooding females. The persistence of these patterns of clumping in naturally occurring shells indicates the important link between the stage of dispersal and patterns of distribution.

Neomegamphopus hiatus arrives to shells as adults (Table 1). It shows a rapid population growth that asymptotes around 16 days (Fig. 1, Table 2) and thereafter abundance remains constant in shells that are several months old (Fig. 3). *N. hiatus* colonizes shells irrespective of the lunar phase, community successional stage, or date during the seasons of study. This species presents a clumped distribution in natural pen shell communities because adults are dispersing and because 40% of the arriving females carry broods. While this species is a tube-dweller, they are not constrained to these tubes, as they disperse as adults. Males have clumped distribution, while females are randomly distributed, possibly indicating that males are the tube-building sex, while females choose the nests. In some amphipod species, males pair with females in a single tube prior to and during copulation (Borowsky 1983). Following copulation, these males depart the tube in search of other receptive females. It may be that in this species, both sexes disperse to new habitats after mating.

Melita nitida also disperses as adults and arrives in relatively large numbers to shells (Table 1). As with the other adult disperser, *M. nitida* has a clumped distribution, both during colonization events and in natural populations of St. Joe Bay. There is no lunar pattern in the numbers of adults recruiting to new shells. However, the status of the arriving females to shells is dependent on a lunar cue: during the new moon phase the vast majority of the females arrive with brood (ESM3). This species may use the lunar cue to mate or to avoid the predation of brooding females during dispersal. This strategy allows for a periodic rapid population growth when these brooding females arrive and release their offspring, increasing local abundance (Fig. 1c). Population growth rate tends to slow within the first

16 days of colonizing new habitats (Table 2) and becomes negative in shells that are several months old (Fig. 3). Adult abundance starts declining after 12 days (Fig. 1b), but in the short term is replaced by the growth of the juvenile cohort in these localized populations (Fig. 1a). These results suggest that *M. nitida* is limited by the availability of the new habitat. Adults colonize new habitats, and the populations they establish slowly diminish, suggesting that successional stage does influence recruitment, probably by the exclusion of new recruits. However, it is not clear if this species is out-competed by other species or if they are obligate nomads and disperse as adults to new habitats. Irrespective of the answer to this question, these populations are the most ephemeral and, consequently, the least common of the three amphipods in the study.

Bemlos unicornis arrives as juveniles to pen shells (Table 1) and slowly but constantly increases in abundance over both the successional stage and season from spring through summer (Figs. 1, 3). The linear increase of abundance over time (Table 2) results in a continuous accumulation of individuals, making this species the most common in natural populations (Fig. 3). The arrival of individuals to shells is also highly linked to the full moon phase (ESM3), and the synchronized dispersal could be due to a mating behavior cue prior to this lunar phase. This species presents a random distribution both during initial colonization as well as in naturally occurring shells. The widespread dispersal of juveniles could explain the more random distribution of this species.

The two adult dispersers may be nomadic, quickly colonizing new shells and reproducing, but then dispersing to new shells as their offspring mature. Because recruitment occurs as adults, we were unable to distinguish between stable or slowly declining turnover of individuals and more stable and gradual mortality of initial colonizers. It could be that *M. nitida* adults move on after releasing their brood, which could explain why their populations decline in older shells. In contrast, *N. hiatus* adults may be less prone to moving on to new habitats because of the investment in tube building. It is possible that the dispersal of *N. hiatus* adults is density dependent (e.g., Amarasekare 2004): as tubes accumulate, excess adults move to new habitats. This is one possible explanation for the relatively stable population size after the initial burst in abundance. Unlike the other two species, *B. unicornis*' population growth may be less dependent on the local adult population, and the dynamics would be more open, with abundances reflecting overall contributions from the metapopulation rather than local production of offspring. Shell occupancy data are consistent with these views, as *M. nitida* and *N. hiatus* tend to colonize large proportions of newly available habitat, while *B. unicornis* colonizes only a small fraction of shells at a time. However, natural populations show that *M. nitida* is

the species that occupies fewer shells, suggesting that successional stage may affect this species distribution pattern. The three species show a range of metapopulation dynamics: *N. hiatus* is driven by local processes explaining population stability; *M. nitida* is under a combination of local processes where individuals are born and regional processes where environmental cues play a role across populations; *B. unicornis* is driven by long-term seasonal processes with little or no local retention and a constant supply of propagules into the water column.

Stage-dependent dispersal and metapopulation dynamics

Dispersal can potentially be risky, which could be why many organisms disperse large numbers of relatively inexpensive propagules (Palmer et al. 1996). The trade-off between dispersing as an adult compared to a juvenile or larvae is likely to depend on the size or stage-dependent risks associated with dispersal. If mortality is less dependent on size or stage, then releasing large numbers of small stages may be a hedge against local mortality to a particular habitat. However, if adults face a reduced risk and if upon arrival to a new shell they can release offspring in the relative safety of a protected habitat (e.g., a pen shell), then adult dispersal may be favored.

Regardless of the mechanism driving differences in stage-dependent dispersal, the persistence of amphipod metapopulations in pen shell communities could be influenced by their dispersal strategy. Pen shells are an ephemeral hard substrate (they persist approximately 1 year after the death of the bivalve; personal observations of authors), thereby forcing species that occupy shells to colonize and reproduce rapidly. Therefore, the dispersal phase, as shown in this study, can be an important component in affecting local population growth and distribution. Competition at the local scale may be important, but there was no obvious distributional signature of competition (P. Munguia, unpublished data). If competition does exist among these three species, its strength would be temporally and spatially variable, depending on local densities. Alternatively, the three amphipods could interact with the other pen shell inhabitants that form the community affecting the local and regional patterns (Munguia 2004); however, we do not have direct evidence to support this. Theoretical studies tend to focus on the competitive environment that structures species distribution and enables coexistence (e.g., Leibold et al. 2004; Amarasekare et al. 2004). For example, Amarasekare et al. (2004) suggest that in source–sink dynamics where dispersal is the key mechanism for species persistence, competitive ability is crucial in determining population growth or extinction. Our study shows not only how dispersal is important in the maintenance of spatially structured populations but how dispersal mode can be a key

mechanism that leads to population growth and species distribution. Theoretical studies should consider variation in the dispersal stage and its population benefits and consequences.

An important aspect of metapopulation theory is the connectivity among populations. With complete dispersal limitation, subpopulations are isolated from one another, suggesting a “closed” system; however, as dispersal ability increases, populations become more open, allowing individuals to reach more habitats (Loreau and Mouquet 1999; Mouquet and Loreau 2003). Typically, the mechanisms invoked to explain dispersal limitation include high propagule mortality and the ability to invade or colonize habitats. We suggest that another mechanism that can promote or diminish the connectivity among habitats is the stage of the disperser. Late-stage dispersers can seed local habitats quickly but seem to be limited in the number of habitats that are invaded. In contrast, early-stage dispersers can flood a larger range of habitats, but these populations grow slower because increases in abundance are dependent on continued recruitment from other populations.

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