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Contributions of adult oligochaete emigration and immigration in a dynamic soft-sediment community

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Abstract

It is well known that adult dispersal is common in soft bottom intertidal and shallow subtidal communities. We here report on the first study that attempts to quantify the effects of both immigration and emigration on patches of soft sediment communities. Some species show adaptive emigration from the seabed, although dispersal direction, distance, and colonization success are probably strongly dependent on hydrodynamics, morphological adaptations to dispersal, and the ability to select appropriate target microsites. The naid oligochaete *Paranais litoralis* is a numerically dominant benthic species in southern New England and New York mud flats and tends to reproduce mainly or exclusively by means of budding of new individuals. When population density is high and resources in short supply, budding frequency is reduced, worms grow longer, and may emigrate from the sediment. We quantified emigration by means of a conical trap and quantified immigration with sediment dishes. We followed emigration/immigration during the typical late spring population explosion and crash cycle of worms within the sediment, which is driven by a seasonal cycle of provision and exhaustion of organic detrital food supply. Emigration was proportionally maximal either at or after the population peak, consistent with a response to food shortage. Over a span of ca. 50 m, we found no net movement in either direction along a transect, nor was emigration or immigration correlated with local density in the sediment. Nevertheless, both emigration and immigration were important in our 2004 sampling, and immigration especially had an important impact on population densities. We do not know the relative capture efficiencies of the emigration and immigration apparatus, so more needs to be done to understand the impacts of dispersal in this and other systems.
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1. Introduction

Ephemeral habitats pose unique challenges, as changing environmental conditions lead to frequent local extinctions. However, numerous organisms have the ability to live in ephemeral habitats, and populations survive despite the challenges presented. Authors have noted the benefits of dispersal ability to organisms living in frequently disturbed environments (Underwood and Fairweather, 1989; Palmer et al., 1996). Populations can survive in the face of local habitat destruction if individuals are able to move among patches, some of which permit survival and reproduction. An ultimate understanding, therefore, must be in a metapopulation context.

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In order to be able to benefit from a dispersal mechanism, however, an individual that arrives in a new patch must be able to reproduce and colonize in that new patch. As such, fast growth rates and the ability to reproduce without the benefit of a sexual partner are characteristics that will increase the benefits of dispersal. Populations of the asexually reproducing oligochaete *Paranais litoralis* in Flax Pond, Long Island, NY fit this model (Nilsson et al., 2000). Throughout the year, population abundances of *P. litoralis* undergo a very distinct cycle: they have low abundances during the winter, followed by increases in population densities during the spring. Some worms surviving from the previous summer exist at very low densities. Maximum abundances occur in late spring or early summer, until populations crash, after which densities remain low until the following year (Cheng et al., 1993), although increases in the fall occasionally occur (Kelaher and Levinton 2003).

At Flax pond, the boom-bust pattern mirrors the food availability pattern throughout the mudflat. At the start of the season, nutrient availability in the sediment is quite high. Throughout winter, organic material is likely deposited on the mudflat surface, but not consumed. Throughout the spring and summer, there is a decline in the nutritive value of the sediment as organic material is consumed by sediment feeding animals as well as by microbially mediated decomposition (Lopez and Levinton, 1987; Cheng et al., 1993). As the nutritive value of the sediment decreases, smaller populations of surface feeders can be sustained and sediment organic matter becomes more refractory (Cheng et al., 1993; Lopez and Levinton, 1987).

While this general pattern exists across the mudflat, at a smaller spatial scale, the mudflat consists of a mosaic of patches that are different across time and space (Johnson, 1970). Deposition of organic material is intermittent, and variable both qualitatively and quantitatively, as sometimes large patches of *Ulva rotundata* are found patchily on the mudflat, whereas at other times, the mudflat has patches of *Spartina alterniflora* detritus (Cheng et al., 1993). Spatial heterogeneity of particulate organic matter input results in spatially heterogeneous timing of population cycles in a salt marsh mudflat such as Flax Pond, NY (Kelaher and Levinton, 2003; Levinton and Kelaher, 2004).

Evidence from the lab supports the hypothesis that the steady decline of sediment nutritive value is likely what drives the boom-bust population pattern, as *P. litoralis* is able to respond quickly to food availability (Levinton and Stewart, 1982) but is also able to fully exploit the resources in a patch, leaving it exhausted of nutrients (Cheng et al., 1993). Lab studies have shown that seasonal differences in sediment quality are able to influence the growth rates of *P. litoralis*, as exposure to early-spring mud leads to higher population growth rates than late-season (summer) mud in *P. litoralis* (Nilsson et al., 1998; Cheng et al., 1993) and the addition of detrital material to sediment stimulates both population and somatic growth in the laboratory (Levinton and Stewart, 1988). Additionally, evidence from the field supports the idea that the pattern of change in sediment nutritive value is likely what drives the boom-bust population pattern. The temporally and spatially shifting heterogeneous pattern of nutrient availability is mirrored by subpopulations of *P. litoralis* within Flax Pond that have heterogeneous growth rates (places with highest growth rates shifted across time—Nilsson et al., 1998) and peak population sizes have been shown to exist at different times in different places across the marsh (Kelaher and Levinton, 2003). In a field experiment, Kelaher and Levinton (2003) found that detrital enrichment is the driving force in altering abundances of deposit-feeders, and that heterogeneity in detrital enrichment contributes substantially to spatio-temporal patterns of species abundance and composition.

This spatial and temporal heterogeneity of growth and nutrient conditions provides a scenario in which one can imagine that dispersal would be a valuable trait (Commito et al., 1995). While in the past it has been assumed that meiobenthic animals are bound to the sediment and as such have low rates of dispersal (Sterrer, 1973), Armonies (1988) showed that some meiobenthic animals do indeed leave the sediment in response to various physical factors, but oligochaetes were not among those animals that were capable of entering the water column. Smaller macrofauna and meiofauna have been observed to leave the sediment and swimmers may have morphological adaptations for swimming (e.g. Thistle and Sedlacek, 2004).

The naid *P. litoralis* is macrofaunal in size and has been found to swim in the lab under conditions of low resources (Nilsson et al., 2000) suggesting that the worms emigrate in response to habitat deterioration. In Long Island, NY, mudflats it normally reproduces exclusively asexually by means of naidian paratomy. After a set of segments are added, a fission zone forms, followed by the formation of a head and splitting off of the budded individual (Martinez and Levinton, 1992). Nilsson et al. (2000) found that, under poor conditions, fission does not occur and a swimming results. Swimming *P. litoralis* are longer (having more segments) and thinner than non-migrating worms. In

addition, they have been shown to swim more actively and are better able to stay in the water column than are non-dispersers. In the lab, swimming worms were shown to select sediment that was higher in nutrients, and avoided sediment which was resource-depleted (Nilsson et al., 2000). Kelaher and Levinton (2003), however, failed to find selection in the field for sediment with higher nutritive value by immigrating *P. litoralis*. It may be that moving water prevents the sort of selection seen under still-water laboratory conditions.

In this study, we quantify the ability of *P. litoralis* to disperse in the field as measured by swimming behavior, and their ability to settle out of the water column and colonize new patches. We determined the number of worms that emerged from the sediment and swam into the water column, relative to the abundance of worms in the sediment. We also counted the number of worms that settled into new patches by the use of settlement trays of sediment. Further, we determined whether swimming and settling worms were longer than their non-swimming counterparts. We believe this to be the first study that quantitatively assesses the relative importance of emigration and immigration of adults to population dynamics of a soft-bottom macrobenthic species.

2. Methods

2.1. Study site

Flax Pond is a *Spartina*-dominated salt Marsh near Old Field Village on the north shore of Long Island, New York USA (Levinton and Bianchi, 1981; Cheng et al., 1993). Eight sites arrayed along a transect on a mud flat within Flax Pond (the same as those used and reported by Kelaher and Levinton, 2003) were sampled a number of times throughout the spring and summer of 2003 and 2004. The eight sites ran along the edge of a bay in an east to west direction, with site one nearest to the head of the bay and site eight closer to open water. In 2003, only sites 1, 2 and 3 were used, and each site contained only emergence traps. In 2004, all eight sites were used, with emergent and settlement traps placed alternatively at each site (emergence traps at odd-numbered sites, settlement traps at even-numbered sites). Sites were on average about 6 m from one another. All sites were at a similar tidal height in the mid-intertidal zone. A majority proportion of intersite variance in abundance had been previously found for oligochaetes at the spatial scale used in this study (Kelaher and Levinton, 2003).

2.2. Quantification of population density of *P. litoralis*

On each sampling date, four cores (5 cm in diameter and 5 cm deep ≈80 cm^3) were collected from within the sediment at the base of each emergence trap (for description of the emergence traps, see below). Each core was washed in a 297 μm sieve, and preserved in a 7% formalin solution. Later, the material from each sieved core was sorted under 16× magnification and all *P. litoralis* were counted, and preserved in 70% ethanol.

3. Quantification of emergence of *P. litoralis*

In order to test the hypothesis that worms in the field are able to swim into the water column, we constructed emergence traps designed to catch emigrating worms (Fig. 1). At each site where emergence traps were planted, traps were haphazardly located 0.5–1 m from each other. The traps were fashioned after those described by Thistle and Sedlacek (2004) and were constructed from pieces of PVC pipe that were 15 cm in height and had a 10 cm inner diameter. These pipe pieces were fitted with the spout (funnel like) section of a clear plastic two-liter soda bottle. Worms swimming into the water column would swim up through the narrow opening of the soda bottle, but would be unlikely to escape back down out of the funnel, and could easily be collected from the upper part of the trap. The top of the trap was enclosed with mesh, so that worms could not escape. The base of the trap, which was inserted into the sediment, was made out of pipe joint material, such that the upper part of the trap fitted snugly, but could be removed from the trap base.

Traps were placed at each of the sites on the mud flat at Flax pond. Sites were sampled seven times between March 2003 and August 2003 and five times between April 2004 and July 2004, at approximately 2–3 week

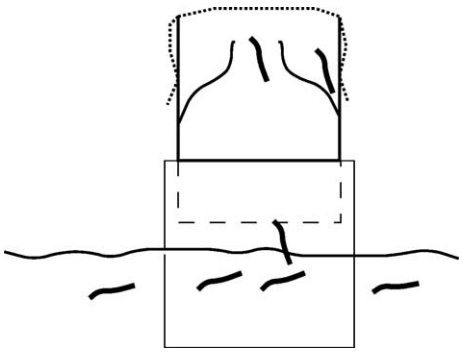

Fig. 1. Schematic cross section of the emergence traps, showing how worms might emerge from the sediment, swim upward, and be trapped in the upper part of the apparatus. Upper tube is covered by mesh.

intervals. In 2003, sites 1–3 were used, and six traps were placed at each of the sites two days previous to the sampling dates. In 2004, sites 1, 3, 5, and 7 were used. Three traps were placed at each site and worms were collected after two days. The emergence traps were then left in the field, and worms were collected again from the same traps on day four. This was done in order to allow traps to be left in the field for a longer amount of time in order to collect more worms, while at the same time, preventing worms from getting too hot, as the water was quite warm in the traps and temperatures higher than 25 °C may be lethal (Nilsson et al., 1998).

At collection times, a rubber stopper was placed in the opening of the soda bottle in order to prevent the water and animals from being lost from the trap. The trap was then removed from the base, and the water and animals collected in it were poured off, while the sediment at the base of the trap was allowed to remain intact. The collected water in the trap was brought back to the lab, where it was washed in a 90 μm sieve and *P. litoralis* were immediately counted and preserved in 70% ethanol.

3.1. Quantification of settlement of P. litoralis

In order to determine if *P. litoralis* could colonize new habitats, four sheets of Plexiglas (1000 × 600 mm), with settlement dishes affixed to them with Velcro, were placed in the field. The Plexiglas sheets were free of sediment, which ensured that worms arriving into the settlement dishes arrived in the water column and not by crawling from adjacent sediment. Settlement dishes were petri dishes (90 mm in diameter and 13 mm deep) filled with flax pond sediment. Sediment was collected approximately one week before the initial sampling date, and was frozen at −80 °C in order to kill any living animals. On the day of the experiment, the mud was thawed and sieved in a 1 mm sieve, in order to remove any large particles, and the petri dishes were filled with this mud.

Settlement dishes were placed on the mud flat at sites 2, 4, 6, and 8 within Flax Pond five times throughout the spring and summer of 2004, at the same time as the swimming traps were placed in the field. The settlement plate sites were interspersed between the emigration trap sites, which were odd numbered. The whole design therefore consisted of eight sites separated by ca. 6 m, alternating emergence traps combined with coring, and colonization trays. Four days before the collection dates, the plexiglass sheets were placed in the field. Settlement plates were left in the field for four days in order to leave enough time for settlement to occur, while minimizing the opportunity for settling worms to reproduce, as under laboratory conditions, a new worm will mature and produce its first asexual offspring within approximately four days (Nilsson et al., 1998). Of course, it is possible that large worms arrived and divided while in the settlement dishes. We did not notice any obvious erosion of sediment from the colonization trays after the four-day period.

On the collection dates, settlement dishes were removed from the Plexiglas sheets, and brought back to the laboratory, whereupon the sediment in each plate was sieved on a 120 μm mesh and the remaining material was preserved in a 7% formalin solution, and later sorted under 16× magnification. Alternatively, some dishes were sorted immediately. Upon counting, all *P. litoralis* were preserved in 70% ethanol solution. While in the first sampling period, in order to repeat the methods of Levinton and Kelaher (2004) we sorted all material in the greater than 90 μm fraction, we never found any animals in the <120, >90 μm fraction, and very few in the <297 μm greater than 120 μm fraction. We therefore decided to sort only that material in the greater than 120 μm fraction.

3.2. Statistical analyses for quantification of swimming, settling and source populations

A two-way ANOVA (Sokal and Rohlf, 1995) with the main effects of time and site was performed on results for each of the three collection methods (i.e. sediment, swimming or settling) in order to determine if numbers of worms varied across time or space. When no interaction was found, but there was a significant main effect, comparisons among means were done using the GT-2 method (Sokal and Rohlf, 1995) to determine which sites and sampling times were significantly different from one another.

In order to determine if the numbers of swimmers, settlers or source population worms changed differently across time, a two-way ANOVA with the main effects of time and collection method was performed. The interaction between collection method (within sediment, emerging worms = swimmers, or settling worms) and time was evaluated to determine if the changes in numbers across time were different for swimming, within-sediment, or settling worms, or if the changes were proportionally similar to one another.

3.3. Correlations of swimmers and source populations

In order to determine how closely related the numbers of swimming worms were to the numbers of

worms found in the sediment from which they swam, we determined the ranked correlation between numbers of swimming and sediment worms among sites. Ranks were used because of the large temporal changes in overall abundance. Numbers of worms in either the swimming or sediment condition were therefore effectively ranked in order to remove the effect of time, and Spearman's coefficient (r_s) (Sokal and Rohlf, 1995) was used to determine to what extent the numbers of swimming worms were correlated with the numbers of worms found in the sediment.

3.4. Spatial correlations of swimmers, settlers and source populations

In order to determine whether worms tended to swim in the eastward direction (toward the head of the bay) or in the westward direction, we evaluated the ranked correlation between sites of origin (swimming or sediment) and sites of destination (settling). Two different correlations were calculated for each comparison; 1) the correlation between origin and destination sites with destination to the east of the origin (i.e. toward the head of the bay) and 2) the correlation between origin and destination sites with destination sites to the west of the origin sites. Fig. 2 shows a simple schematic of the design. Again, Spearman's coefficient (r_s) was used to evaluate correlations. If the correlation was greater in one direction than the other, we inferred that the overall direction of movement was greater in that direction.

3.5. Impact of immigration and emigration on growth rate and numbers of individuals in a patch

In order to determine the overall impact of immigration and emigration on an individual patch at any time, we estimated the numbers of individuals that left a patch over the entire interval between sampling times. In order to do this, we calculated the area of the polygon under the curve for swimmers and settlers between each time period. We then estimated the numbers of individuals that would have been in the patch had there been no immigration or emigration at each sampling date by subtracting the numbers of individuals estimated to have entered the patch, and adding the number that was estimated to have left the patch over the time interval previous to the sampling date to the numbers of individuals found at each sampling date. We also calculated the growth rates of the populations over each time interval both using the original numbers, and those estimated to occur without immigration or emigration.

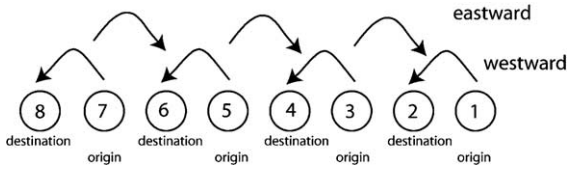

Fig. 2. Schematic of the east/west correlation analysis. Correlation between origin and destination sites was evaluated by ranking the origin and destination sites by numbers of individuals across all time periods. For the eastward direction, the origin sites 3, 5 and 7 were paired with the destination sites 2,4 and 6, respectively. There were thus three sites, and five times, giving 15 data points in the correlation. For the westward direction, the origin sites 1, 3, 5 and 7 were paired with the destination sites 2,4,6 and 8, respectively. There were thus four sites, and five times, giving 20 data points in the correlation.

3.6. Worm size

To test the hypothesis that swimming worms were on average longer than non-swimming worms, the average number of segments of *P. litoralis* was determined at each time of sampling for swimming, and source population worms in 2003 and settling and source population worms in 2004. Number of segments was thought to be a practical measure of length, especially because the preserved worms experienced different degrees of curling. Worms were chosen at random from each of the three conditions, and the number of segments was counted under 50× magnification. A *t*-test (Sokal and Rohlf, 1995) was performed in order to compare differences in numbers of segments between swimming and sediment worms in 2003, and settling and sediment worms in 2004.

3.7. Sediment analysis

Sediment cores were collected from each of the eight sites used in this experiment. Cores were dried in an oven overnight to remove the moisture content, and were weighed. The <62 μm (silt–clay) fraction was sieved from each core, and the remaining material was dried overnight in the oven again. The remaining material was weighed, in order to determine the percentage of material that was silt and clay.

4. Results

4.1. Quantification of populations of P. litoralis in the sediment

The number of *P. litoralis* found in the sediment per day was variable across site and time (2003 data,

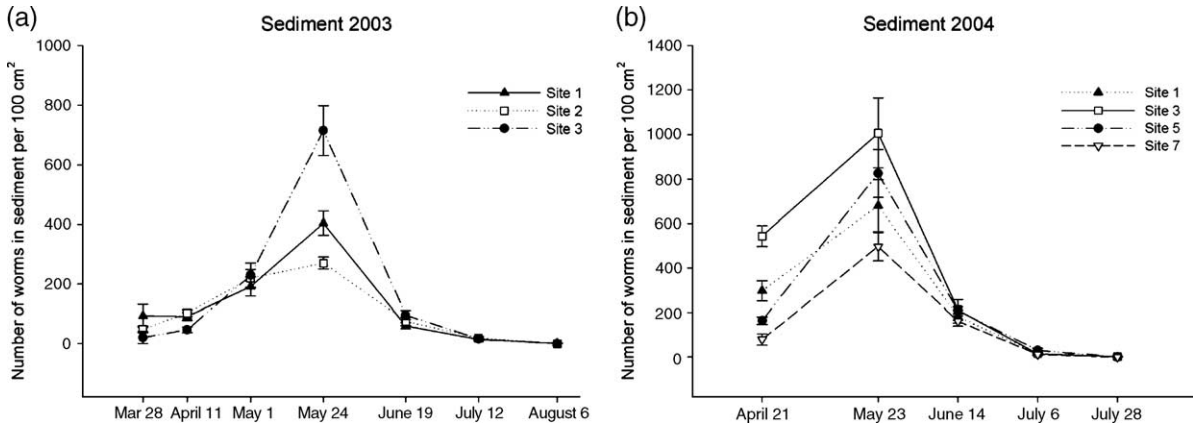

Fig. 3. Numbers of worms found in the sediment at each site and time in (a) 2003 and (b) 2004.

ANOVA: site by time interaction: $F=11.858$, $p \ll .001$; 2004 data, ANOVA: site by time interaction: $F=3.585$, $p \ll .001$). Fig. 3 shows the numbers of sediment worms across time in different sites. While there is a significant site by time interaction, the general pattern of increase in numbers of worms throughout the spring months followed by their decline can be seen. In 2003, the numbers of worms increased throughout the spring, reached a peak and then dropped off. A similar pattern was found in 2004, with a strikingly similar time of the population peak, although this conclusion is obviously constrained by the time between samplings.

4.2. Quantification of emergence of P. litoralis

In 2003 (Fig. 4) there were no significant differences in numbers of swimmers (as estimated by worms caught in the emergence traps) across site or time, and no significant interaction between the two. In 2003, the overall pattern, as shown by means over all sites (Fig. 6), seems to show that the numbers of swimming worms increased throughout the spring, and peaked in the time period following the peak abundances. In 2004 (Fig. 4), the numbers of swimming *P. litoralis* were extremely variable over space and time (ANOVA: site by time interaction: $F=3.789$, $p \ll .001$). Overall, however, an increase was followed by a decline, with peak numbers of swimmers coincident with peaks in abundance of worms within the sediment (Fig. 6).

4.3. Quantification of settlement of P. litoralis

The number of *P. litoralis* found settling out of the water column into settlement dishes was variable across time and sites (ANOVA: time by site interaction: $F=8.330$, $p \ll .001$). In 2004 (the only year for which we have data), the numbers of swimming worms increased throughout the spring, and peaked in the same time period as the abundances of worms in the sediment (Figs. 5 and 6).

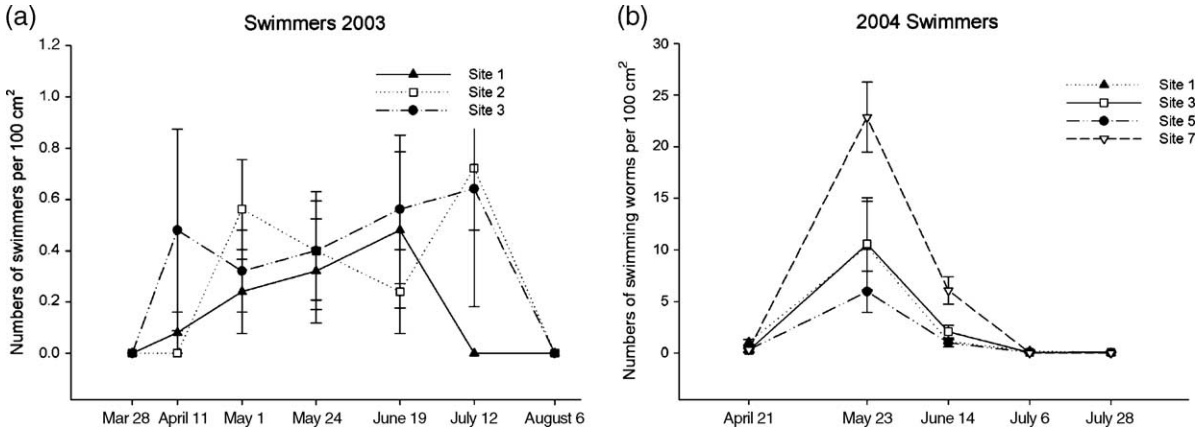

Fig. 4. Numbers of swimming worms per day found in (a) 2003 and (b) 2004.

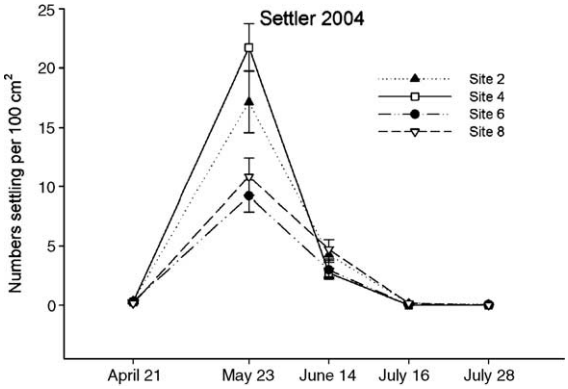

Fig. 5. Number of settling worms found in 2004.

4.4. Quantification of patterns of swimming, settling and source populations

The pattern of swimmers and settlers across time (Fig. 6) is not simply proportional to the numbers of worms found in the source population, as the numbers of worms varied significantly by collection method and time (For 2004 data, ANOVA: collection method (sediment and settlers) by time interaction: $F=53.37$, $p \ll .001$; collection method (sediment and swimmers) by time interaction: $F=20.02$, $p \ll .001$. For 2003 data collection method (sediment and swimmers) by time interaction: $F=19.91$, $p \ll .001$). However, there was no significant interaction between time and the collection methods of swimmers and settlers in 2004, indicating that the patterns of swimming and settling were very similar.

The percentage of the population in the sediment that swam is shown in Fig. 7. There is a distinct pattern of increase in percentage of swimming worms following the peak in abundances in 2003. In 2004, the percentage of swimming worms was higher throughout, and remained high after the peak in source population. The final data point in 2004 is a fraction based on very small numbers, and as such is very unstable.

4.5. Spatial correlation of swimmers, settlers and source populations

In 2003, there was very little correlation between numbers of worms in the source population and numbers of worms that emerged from that population within sites (Spearman's coefficient: $r_s=0.159$). In 2004, the correlation was also very low ($r_s=0$). The correlations between numbers of worms in the origin and destination sites in either the eastward or westward directions were all quite low (swimming westward: $r_s=0.197$, swimming eastward: $r_s=-0.056$, settling westward: $r_s=-0.126$, settling eastward $r_s=0.316$).

4.6. Impact of emigration and immigration on growth rates and numbers of individuals in patch

The overall effect of immigration and emigration on the size of an average population at any one time (as calculated by adding or subtracting the total numbers of worms that were found swimming and settling throughout any one time period to the source count at each sampling date) is shown in Fig. 8. In 2003, when there were very few swimmers found throughout the experiment, the numbers of individuals predicted to be found without emigration are not very different from those that we observed. In 2004, the numbers of worms predicted to be in the population with neither immigration nor emigration were very similar to those numbers that we observed. In 2004, at the time of peak abundance, the numbers that are predicted to occur without immigration are about 30% smaller than the numbers that we observed, and the numbers that are

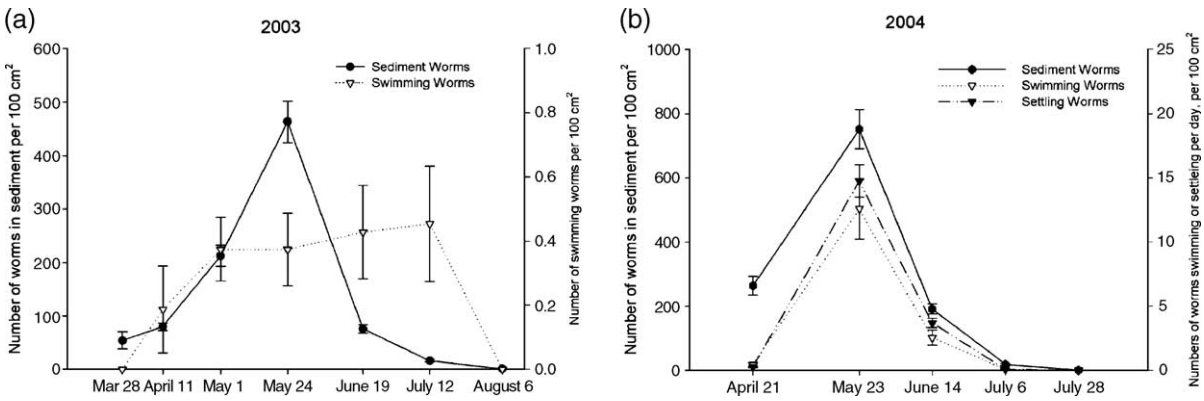

Fig. 6. Numbers of swimming, settling and source population worms averaged across sites at each time period in (a) 2003 and (b) 2004.

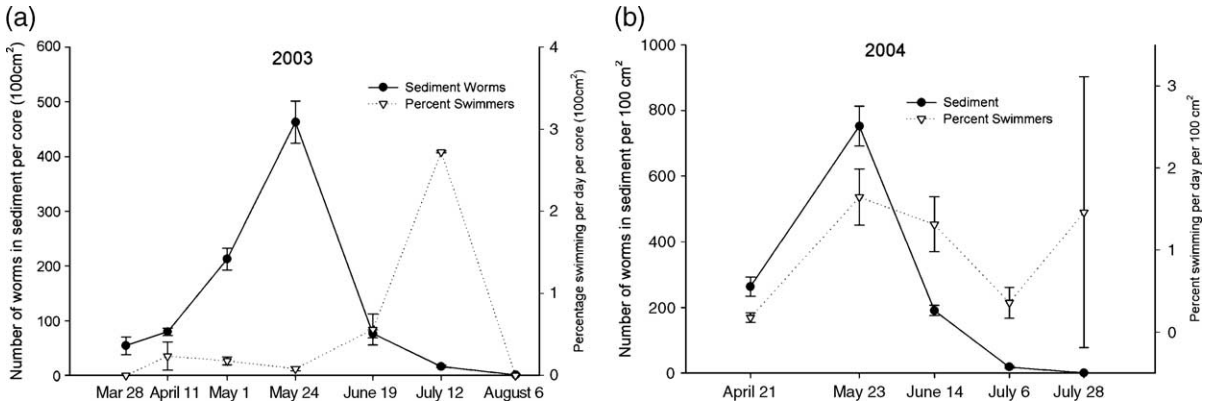

Fig. 7. Average percentage of source population (worms in the sediment) that swam into the water column at each time period in (a) 2003 and (b) 2004.

predicted to occur without emigration are about 30% larger.

The population growth rates calculated from the above numbers of worms in source populations at each time period (both the numbers predicted to occur without immigration or emigration, and those numbers we observed) are shown in Fig. 9. In 2003 (for which we only have the emigration data) the predicted and observed growth rates were similar throughout the first three time periods, in which the population was

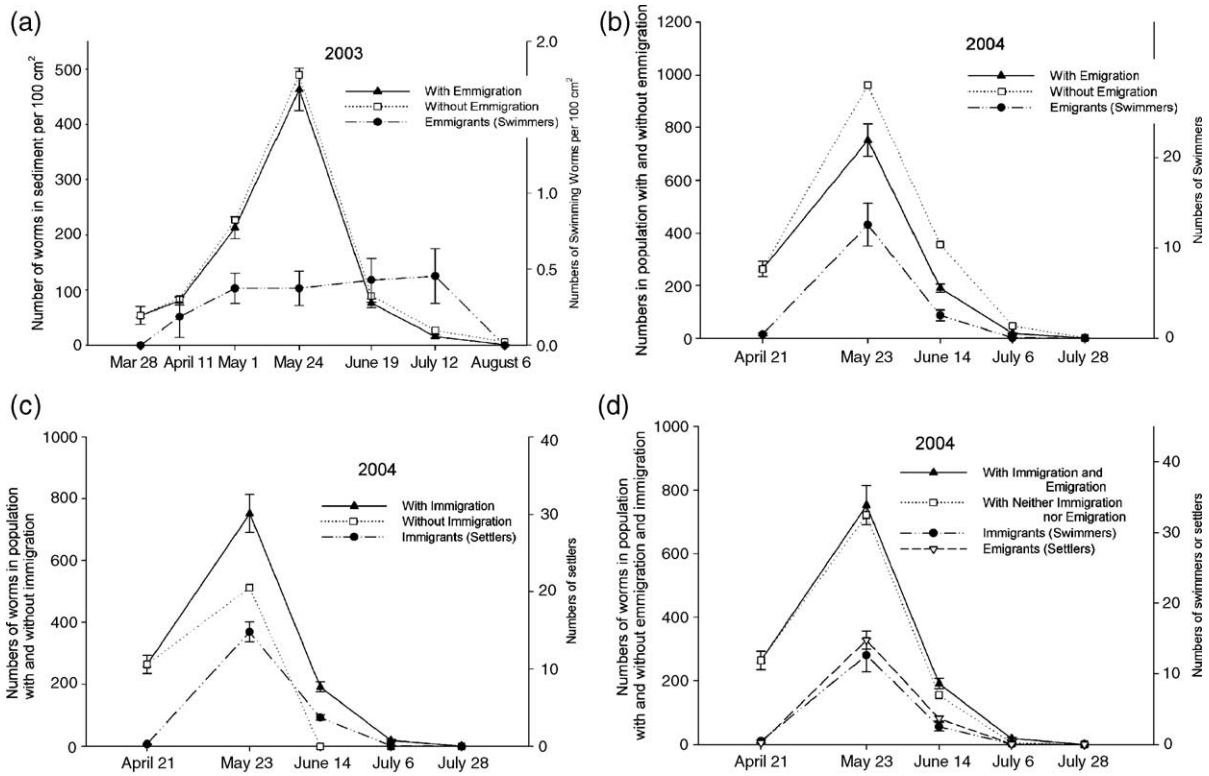

Fig. 8. Effect of emigration and immigration on population sizes. Also shown are the numbers of swimmers and settlers that were collected at each time period. (a) The numbers of emigrants and numbers of source with and without emigrants in 2003; (b) Numbers of emigrants and numbers of source with and without emigrants in 2004; (c) Numbers of immigrants and numbers of source with and without immigrants; (d) Both the numbers of immigrants and emigrants and the numbers of worms that were in the sediment given these numbers, and the numbers that would have been found had there been no immigration or emigration.

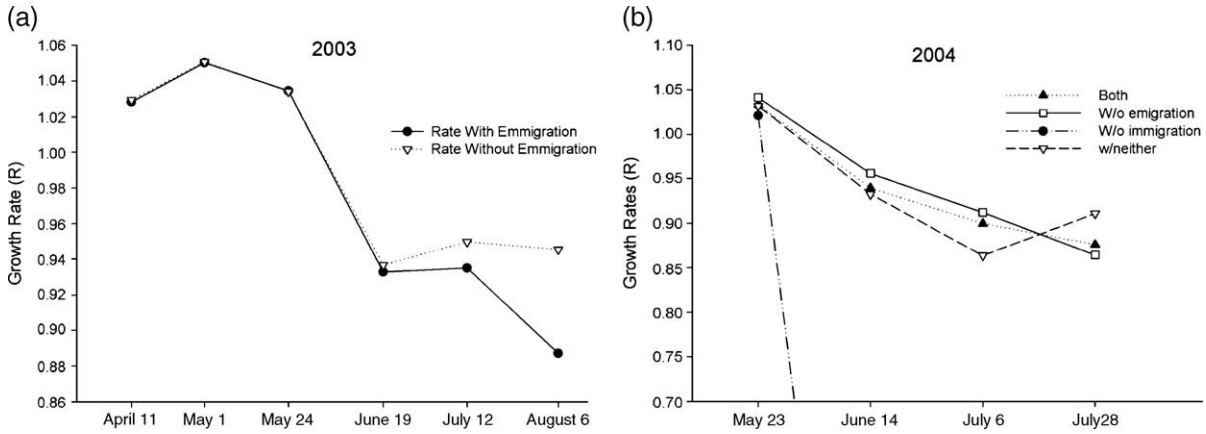

Fig. 9. Observed and predicted growth rates of average populations across time, with and without emigration in (a) 2003 and (b) 2004, and with and without immigration in 2004. Observed growth rates of *Paranais* (in 2003: "with emigration" and in 2004: "both") are those that occurred in the presence of both immigration and emigration. The growth rates predicted to occur in the absence of immigration, or with neither immigration nor emigration (2004 only) and those predicted to occur in the absence of emigration (2003 and 2004) are also shown.

growing. However, when the growth rate declined, and the population began to decrease, the growth rate was noticeably affected by emigration. After an initial drop in growth rate, the predicted growth rate leveled off, and remained at 0.95, while the observed growth rate continued to decline.

In 2004, we were able to predict what the growth rates would be if there were neither immigration nor emigration. Similar to what happened in 2003, in the time period between the May and June sampling dates, the growth rate changed from being greater than one to being less than one. However, whereas in 2003, after this decline in growth rates, the removal of emigration had a large negative effect on the growth rate, in 2004, it did not. The removal of immigration alone, however, did have a large negative effect on the growth rate. The removal of both emigration and immigration did not have a large effect on the growth rates, as the worms that were lost by emigration were replaced by immigration.

4.7. Body length

There were differences between swimming and sediment worms in 2003, and settling and sediment worms, in 2004. In all cases, the worms that were settling or swimming had significantly more segments than those which were found in sediment. In 2003, swimming worms were on average 5 segments longer than non-swimming worms and, in 2004, worms found in settlement trays were on average 7 segments longer than those found in the sediment. The average numbers of segments across all sites and times are shown in Fig. 10.

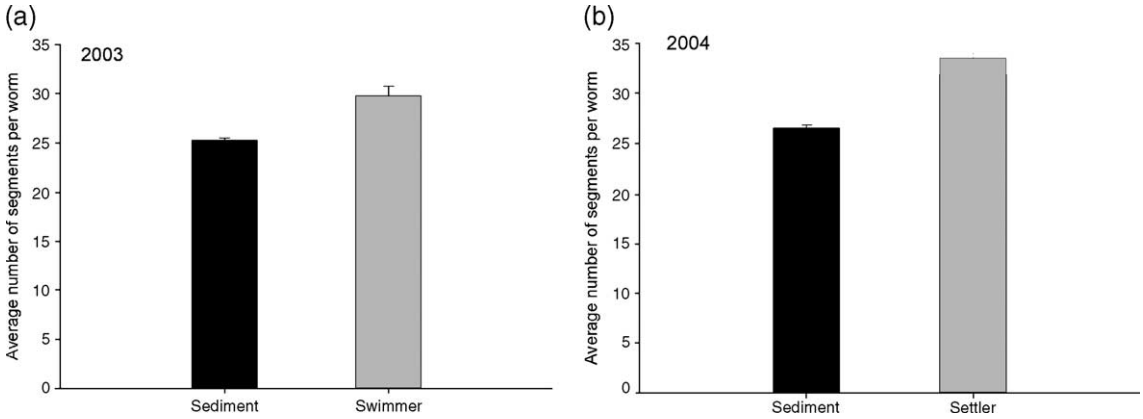

Fig. 10. Average number of segments in (a) sediment and swimming worms in 2003; and (b) sediment and settlement worms in 2004.

Table 1
Sand silt content across the eight sites sampled in 2004

	Site 1	Site 2	Site 3	Site 4	Site 5	Site 6	Site 7	Site 8
Percent silt	36%	47%	77%	41%	37%	16%	12%	17%

4.8. Sediment

There was a gradient across the sites of sediment size. Silt–clay content was less in the eastern sites (Table 1).

5. Discussion

Our previous work (Levinton and Stewart, 1988; Cheng et al., 1993) demonstrated a seasonal cycle of population growth and decline of surface and near-surface feeding oligochaetes and polychaetes, which appears to be driven by a cycle of late winter supply of detrital food followed by consumption and severe food decline into early summer. Studies of the food value of sediment and uptake of radiolabeled organic matter demonstrate that the sediment has less food at the surface as the spring progresses (Cheng et al., 1993). In summer, population densities of surface deposit feeding polychaetes are very low, which is probably a reflection of high temperature and previous consumption of labile particulate organic matter. The mobile surface-feeding deposit feeder *Ilyanassa obsoleta* moves toward patches and consumes surface detritus, which reduces food at the surface and reduces spatial heterogeneity (Levinton and Kelaher, 2004). On the other hand, movement of the surface feeding gastropod *I. obsoleta* also results in negative effects on small surface-feeding polychaetes and oligochaetes (Kelaher et al., 2003). Spatial heterogeneity of surface and near surface deposit feeders results therefore from the opposing forces of localized population growth and recruitment and movement by mobile deposit feeders (Levinton and Kelaher, 2004).

Strong spatial heterogeneity of population densities is also explained by asynchronies of population cycling in different patches just a few meters apart (Kelaher and Levinton, 2003). Presumably there are localized differences in timing and amount of detrital supply in the winter but this has only been confirmed by qualitative observations and biotracers of spatial patchiness of degrading stands of seaweeds such as *Ulva* sp. (Levinton and McCartney, 1991; Kelaher and Levinton, 2003). The dominant naid oligochaete *P. litoralis* has been observed in the laboratory to react to high local population density by failing to reproduce asexually, adopt a swimming behavior, and emigrate from the sediment (Nilsson et al., 2000). In the lab, swimming worms are able to select high food quality sediment (Nilsson et al., 2000), but this selectivity was not observed in colonization experiments in the field (Kelaher and Levinton, 2003).

It is well known that movement by adults is common in soft sediments and may be a major explanation for spatial and temporal variation in abundance. Movement can be divided into three stages: (a) adaptive emigration and passive dispersal by erosion; (b) saltation or lifting into the water column with transport; and (c) eventual deposition, perhaps aided by microhabitat selectivity. *Hydrobia* snails, for example, respond to high density by increased movement and swimming (Levinton, 1979). As a consequence, local abundance of *Hydrobia* sp. may vary by an order of magnitude over just a few days (Armonies and Hartke, 1995). Emigration of soft sediment organisms may also occur in response to colonization of space competitors or biological disturbers (DeWitt and Levinton, 1984). The extensive studies of Thistle and Sedlacek (2004) show extensive emigration from the sediment by meiofauna and those harpacticoid copepod species that emigrate have morphologies distinct from those others that emigrate less. The phenomenon of secondary settlement of recently recruited molluscs does not involve density-dependent emigration, but does result in adaptive use of ephemeral sites and eventual redistribution of benthos to other habitats (e.g., Bayne, 1964; Armonies, 1992).

Erosion and deposition of benthic animals are also common and cannot be excluded from our study system. A reasonable strategy by which an organism could successfully colonize a new patch may combine active behavior and passive drift, as an animal actively swims into the water column, is then passively transported with the current, and then actively swims down to test the sediment (Andre et al., 1993; Commito et al., 1995; Palmer, 1988; Palmer et al., 1996). The first study of passive dispersal known to us demonstrated that the settling velocity of juvenile dwarf tellin clams *Tellina agilis* resembled the settling velocity of the sand in which they were found (Gilbert, 1968). Settling, therefore, may not necessarily involve adaptive selectivity; such movement is found in a wide variety of soft-bottom shallow-water benthos (Palmer and Gust, 1985; Palmer et al., 1996).

We are able to confirm that the specialized emigration change in behavior and size that has been identified in the lab (Nilsson et al., 2000) occurs to some extent in the field. Swimming worms both actively emerge from the sediment into the water column, and leave the water column and return to the sediment. This specialized

behavior is consistent with a response to spatially and temporally asynchronous food and population dynamics throughout the Flax pond mudflat (Kelaher and Levinton, 2003). Dispersing worms are able to leave an unsuitable patch when necessary and survive and reproduce in a suitable one nearby. Given the negative results on field selectivity (Kelaher and Levinton, 2003) the benefit of dispersal may only be determined by random movement or systematic movement perhaps to quieter water where sediment may be richer in organic matter. This idea, while tantalizing, was not verified by our study of unidirectional movement. Worms did not move in the direction, for example of higher silt–clay content, which might be expected if movement were controlled strictly by hydrodynamic conditions. In freshwater tidal marsh mud flats, oligochaetes have also been found to emigrate from the sediment, with differences in dispersal ability among species (Fung and Levinton, 2005). Oligochaetes from several genera exhibit helical swimming, which probably aids in emigration from the bottom (Drewes and Fourtner, 1993; Drewes, 1999). No evidence, however, relates these movements to conditions within the source population or sediment.

Both swimming and settling *P. litoralis* were found to be significantly longer (having more segments) than their non-swimming counterparts. While this morphological change is interesting hydrodynamically (longer and thinner worms experience more drag than shorter and wider ones of the same volume—Nilsson et al., 2000), it also may offer some advantages in a worm's ability to colonize a new patch and establish a new population. Many clonal organisms reproduce asexually under favorable conditions, but on the onset of unfavorable conditions reproduce sexually to form a dispersal stage. At Flax pond, however, *P. litoralis* does not appear to undergo sexual reproduction (Nilsson et al., 1998; Levinton and Stewart, 1988; Martinez and Levinton, 1992; Cheng et al., 1993). Rather, dispersers are asexual individuals with a larger than average number of segments, suggesting that dispersing individuals postpone fission in unfavorable conditions until they find a suitable sediment after settling (Nilsson et al., 2000). This addition of segments, and delay of fission in response to bad conditions could prepare worms to reproduce once they hit the suitable patch. However, Nilsson et al. (2000) were unable to find any difference between swimmers and non-swimmers in terms of numbers of offspring per worm.

Nilsson et al. (2000) showed that a number of life history traits in *P. litoralis* were different across asexual clones (specifically, life span and fecundity). Similarly, it would be interesting to determine whether or not there is a genetic component toward swimming behavior, i.e., do some clones swim more frequently than others, and could such an analysis be used to determine the consequences of swimming on fitness.

Nilsson et al. (2000) found that swimming worms tended to appear when the population in a laboratory microcosm was at its peak and on the verge of crashing. This point seemed to be a "point of no return", in that addition of food past the time of the peak would not result in population recovery, at least at temperatures greater than or equal to 20 °C. In our field studies, we found that peaks of emigration coincided with the population peak sampling period (2004) or followed the peak (2003). This timing is consistent with the notion that the emigration is a response to low food or other poor conditions corresponding to high population density.

The timing by which a worm leaves a patch is very important, as leaving before the time of depleted resources decreases the number of offspring it may produce before taking the chance of being swept out to sea, or exposing itself to predation, as the water column provides little protection as compared to the relatively structured benthos (Robertson and Howard, 1978; Martinelli and Coull, 1987). However, not leaving when necessary is equally dangerous, as a worm that remains in a nutrient-deficient patch and starves for a long time will never again reproduce (Levinton and Stewart, 1988; Nilsson et al., 1998). Our data indicate that worms are not simply swimming in proportion to the numbers in the source population, but are actually timing their migration. The interaction between time and collection method for both swimming and sediment and settling and sediment indicates that the shape of the swimming and settling curves are significantly different as compared to the shape of the source population curve (See Fig. 6). Worms appear to delay their swimming until or after the temporal peaks in population numbers. In 2003, swimming worms peaked in arrival after peak population densities, when resources were becoming depleted. In 2004, the numbers in Fig. 6 show sustained immigration and emigration behavior, even while the source populations crashed.

In 2004, the numbers of worms that settled or swam over an entire time interval were in fact large as compared to the total number of worms in the sediment. Fig. 8 shows that the population density that would have been found in the sediment had there been no immigration was about 30% less, and those calculated without emigration are about 30% larger than those numbers that we actually found, which included immigration and emigration. However, when the two

processes are both excluded (Fig. 8d) the predicted numbers are very similar to those that we observed as the two processes appeared to compensate for one another. While one might predict that emigration should exceed immigration, as many worms that emerge from the sediment might be lost to predation or currents, we did not find this to be the case. While swimming worms had to swim about seven centimeters into the water column in order to make it into an emigration trap, swimming worms only needed to swim about two centimeters into the water column in order to land in an immigration trap. As such, the increased numbers of worms found immigrating over that predicted given the numbers of emigrating worms could in fact be due to the increased efficiency of the immigration versus the emigration traps. It is also possible that the general area we sampled, which is at the head of a small bay, was a cul de sac and trapped worms in the area.

In 2003 (using only the emigration data), there is a drop in growth rate with emigration toward the end of the experiment (Fig. 9a). However, when we added the worms lost by emigration, the growth rate ceased to decline. It appears from these data that a large contributor to the decline in growth rate is due to emigration. In 2004, immigrants make a large contribution to population growth rate. When the numbers of immigrants are removed, there is a large drop in growth rate (in fact, the growth rate declines to zero without the input from immigration). However, when we removed both immigration and emigration, the growth rates are similar to those that we observed.

While average growth rates and population sizes of *P. litoralis* show that the loss of emigration can be balanced by the gain of immigration, as the average population sizes and growth rates are not changed by immigration and emigration when the two processes are added together, it is important to remember that there is spatio-temporal heterogeneity throughout the marsh. In each biologically relevant patch, immigration does not simply replace the net loss of emigration. If so, there would be no biological advantage to immigration. Dispersal is advantageous when worms are moving to new locations throughout the marsh. While at present we are unable to say that worms in fact respond directly to food availability, as it is unclear how peak emigration rates relate to peak abundances in food availability, and we do not have evidence that worms are able to settle in favorable spots, we can at least imagine a scenario in which individual worms can benefit from the heterogeneous nutrient conditions throughout the marsh.

6. Conclusion

We found evidence for the ability of *P. litoralis* to disperse into the water column, and that immigration and emigration did indeed appear to affect population sizes and growth rates. As populations decline due to a reduction of resources in different areas throughout the marsh, some worms undergo a morphological change by adding segments (Nilsson et al., 2000), and leave the sediment. While peak abundances may be followed by, or coincident with peaks in emigration, there does not appear to be any correlation between abundance of worms in source populations and nearby swimmers. Further, evidence was found to suggest that migrating worms are able to colonize new patches. Overall, our results demonstrate that both emigration and immigration have to be quantitatively accounted in studies of population dynamics of even quiet-water mudflats. This study, we believe, is the first to quantify both processes on a local population of soft-bottom benthos. Given our collateral evidence from freshwater tidal marsh flats, we expect this degree of dispersal-driven population dynamics to be a widespread phenomenon. Differences in emigration abilities among species have obvious implications as well for community composition.

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