Spatially structured habitats challenge populations to have positive growth rates and species often rely on dispersing propagules to occupy habitats outside their fundamental niche. Most marine species show two main life stages, a dispersing stage and a sedentary stage affecting distribution and abundance patterns. An experimental study on *Corophium acherusicum*, a colonial tube-building amphipod, showed the strong influence that a source population can have on new habitats. More importantly, this study shows the effect of temporal sinks where newly established populations can show reduced growth rates if the propagule supply from a source is removed. Sink populations had a reduction in abundance and became male-biased as females left colonies. The consequences arising from short-term dispersal and temporal sinks could be due to different selection pressures at the source and sink populations. These consequences can become reflected in long-term dynamics of marine populations if we shift focus to non-random dispersal models incorporating behaviour and stage-dependent dispersal.

1. Introduction

Propagule dispersal is a critical mechanism that links spatially structured communities and maintains segregated populations. Ecological theory suggests that populations exhibiting negative growth or occurring on habitats outside the species’ fundamental niche can only be rescued via dispersing individuals coming from populations having excess propagule production [1]. Such coupling of population sources with sinks is fundamental for understanding and managing spatially structured systems [2,3] and has been applied to both terrestrial and marine systems [1,4,5]. Yet the challenge resides in incorporating dispersal behaviour with demographic and habitat qualities in spatially structured populations.

Source–sink populations can have long-term consequences arising from short-term events. For example, different dispersal abilities among individuals of different life-history stages or sexes can affect population structure in newly established habitats [6]. Differential dispersal can also cause a delay in population growth rate, which can be reflected in a temporary creation of a sink. In many systems temporal sinks can arise because of rapid shifts in habitat quality or because new populations require a constant supply of propagules until a steady growth rate is achieved [7,8]. A ubiquitous example would be invasive species, where newly invaded habitats require a steady supply of propagules before the population can become established; it is speculated that invasion success is often lower than expected because there is no constant supply of propagules to establish new populations [9,10]. Thus, temporal sinks occur either because habitats have a shift in resources or because a population requires overcoming a density threshold before becoming self-sustaining [11], yet most source–sink studies focus on permanent sinks [12].

In marine habitats, species exhibit a variety of dispersal strategies [13]. Because both the ultimate and proximate causes of dispersal vary based on a species’ life history and ecology, dispersal strategy and dispersal ability can be variable between closely related groups of species [6,14]. Species may...
disperse at different life-history stages, leading to differences in initial population sizes, population growth rates and habitat occupancy. Defining a source or a sink can be problematic in sexually reproducing species where mate availability fluctuates if sexes have different dispersing ability or if individuals use conspecific cues to identify suitable habitats. Focus on behavioural decisions and stage-dependent dispersal can help develop non-random dispersal models [15] or help explain shifts in diversity associated with spatially structured systems [16].

Here I highlight the short-term source–sink dynamics in a tube-building marine amphipod and the consequences arising from differential dispersal between sexes. If sex-biased dispersal is important [4], it should be reflected in the influence of a source population; additionally these biases could reduce population growth rate and colonization of sinks. Corophium acherusicum (hereafter Corophium) is a relatively common tube-building benthic amphipod in the Gulf of Mexico where immature and mature adults carry out dispersal and can form relatively large colonies. This species can produce between 7 and 15 offspring per female and females are iteroparous [17]. Specific objectives were to test the influence of a well-established population on a temporal sink and the effect that a temporal sink can have on newly established populations when isolated from a constant source of propagule supply. Using this amphipod as an example, I discuss the effects that temporal sinks can have on selection pressures in marine populations.

2. Material and methods

Field experiments were set up at the University of Texas Marine Science Institute marina (Port Aransas, TX, USA) during the 2009 and 2010 summers. The marina provided shelter and reduced wave action while still supplying propagules from broader spatial scales coming from both estuarine and coastal environments. PVC tiles (10 × 10 cm) commonly used in experimental studies [18] were deployed at 1.5 m depth and at least 5 m apart to create source communities. After four weeks, communities were well established and the following treatments were initiated: a source tile paired with a new tile (sink), two new tiles in close proximity to each other (electronic supplementary material, Appendix A). Newly paired tiles were facing each other approximately 5 cm apart without opposite tiles physically touching. This forced individual amphipods to swim when migrating between neighbouring tiles. Ten days after deploying the sink tiles all tiles were collected and all Corophium individuals were counted; this time length is long enough to observe the initial effect of a source.

In a second experiment, I tested the effect of isolation from a source by paired source–sink tiles created as above with a treatment of new tiles alone to monitor background recruitment to account for random colonization. After 10 days, half the source–sink tiles were split and the source removed (electronic supplementary material, Appendix A). Ten days later all tiles were collected and all amphipods counted. In both experiments, the sample size was \( n = 10 \) per treatment.

First, I tested the effect of a source on a newly established habitat by comparing amphipod abundance on lone tiles against new tiles that had a source population nearby with a \( t \)-test (experiment 1). Next, a one-way ANOVA compared the effect of a sink on amphipod populations by comparing new lone tiles with isolated sinks and sinks next to a source (experiment 2). This last test used abundance and sex ratios as dependent variables; tiles that were not colonized by Corophium (\( n = 4 \)) were omitted from the sex-ratio analysis. Finally, well-established populations were compared in both isolated old tiles and old source tiles associated with a sink to observe population recovery (experiment 2; electronic supplementary material, Appendix B).

3. Results

Corophium populations establish relatively fast and by four weeks an average of 112 individuals occurred on source tiles (electronic supplementary material, Appendix B), with the largest population having 281 individuals. However, in a 10-day period extremely few individuals colonized the new tiles, unless these new tiles were in close proximity to a source tile (figure 1; \( t \)-test, \( t = 3.24, p = 0.005 \)).

When sink habitats were isolated from their source, Corophium populations were immediately affected relative to those sinks that remained paired with sources. Isolation caused populations to decrease threefold (\( F_{2,18} = 6.73, p = 0.007 \); figure 2a) and sex ratios became male-biased (\( F_{2,14} = 5.33, p = 0.019 \); figure 2b) as fewer females occurred in isolated sinks.

4. Discussion

The relationship between source and sink populations can have strong repercussions on population viability and trait quality [5]. Most studies exploring source–sink dynamics focus on long time scales with the aim of understanding rescue events and colonization probability [4,12,19,20]. Yet, marine populations such as the amphipod in this study can be strongly affected by temporal source–sink dynamics often leading to individuals rapidly sorting themselves among neighbouring habitats [21,22]. Similar to the model presented by Amarasekare [15], this non-random dispersal can have strong effects on population and community structure by segregating individuals and species among habitats.

Results from this experiment highlight the effects of source populations on temporal sinks created by recently established populations. Corophium’s colonial lifestyle coupled with the differential dispersal between males and females causes a strong shift to male-dominated populations if sinks are decoupled from their source during the early stages of colony formation. This rapid shift in population structure can have strong implications on the quality of propagules within the temporal sink and can delay population growth rate if sinks become isolated from sources. By reducing the number of available females, males have stronger competition for access to mates resulting in strong selection at the temporal sink,
which can affect gene flow [23] even if the population recovers. This outcome is similar to the founder effect observed in marine crab and fish metapopulations [9,23]. However, the mechanisms that trigger differential dispersal and temporal sinks in marine species require further exploration.

Spatially structured populations can differ in growth rates or traits [5]. These implications translate to different selection pressures arising from each habitat, whether it is a source or a sink (table 1). The evolutionary (ultimate) causes of dispersal have been the focus of much theoretical work, and hypothesized drivers of dispersal include kin competition, inbreeding, resource competition and environmental stochasticity [24]. This often results in trade-offs between dispersal and life-history traits such as reproduction or growth. Trade-offs between dispersal ability and reproduction have been studied extensively in insect systems [4,25,26], though are relatively unstudied in marine organisms. The differential dispersal and behavioral decisions of migrating individuals can have repercussions at both short- and long-term scales. In a marine mesocosm study, dispersal did not increase abundance of mesograzers within habitat patches that were resource-limited [27]. Here, Corophium can recover to large population sizes, but only when there is weak competition for space which depends on the propagule supply of other sessile species [16,21].

Sources and sinks have been studied at population (e.g. genetic diversity, genetic quality, population structure), community (e.g. species diversity) and ecosystem (e.g. resource heterogeneity) scales, which all depend on the dispersal stage [6] and can have consequences for community composition, diversity and ecosystem function [21,27]. A temporal scale warrants attention given the short-term effects arising from temporal sinks and the effects of dispersal and quality of source populations on selection. In contrast to terrestrial systems or most models [19], many marine populations disperse in large pulse events [18] reflecting strong temporal source–sink dynamics.

Dispersal has often been considered and modeled as a single, unconditional process in which some constant fraction of the population disperses during each generation independent of conditions being experienced by that generation. In most cases, however, dispersal is a conditional process that depends on each disperser’s experiences [24]. As the proximate causes of dispersal vary, so too will the consequences of dispersal.

Acknowledgements. I would like to thank K. Duszak and C. Heron for field assistance, and M. Leibold, B. Walther and W. White for stimulating conversations.

Data accessibility. Data are available in the supplementary material.

References


