Journal of Sea Research 98 (2015) 24–32

Contents lists available at ScienceDirect

Journal of Sea Research

journal homepage: www.elsevier.com/locate/seares

Does stability in local community composition depend on temporal variation in rates of dispersal and connectivity?☆,☆☆

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ARTICLE INFO

Article history:
Received 29 March 2014
Received in revised form 31 August 2014
Accepted 5 September 2014
Available online 16 September 2014

Keywords:
Coexistence
Metacommunity
Baltic Sea
Benthic
Invertebrates
Diversity

ABSTRACT

In ecology understanding variation in connectivity is central for how biodiversity is maintained. Field studies on dispersal and temporal dynamics in community regulating processes are, however, rare. We test the short-term temporal stability in community composition in a soft-sediment benthic community by determining among-sampling interval similarity in community composition. We relate stability to *in situ* measures of connectivity (wind, wave, current energy) and rates of dispersal (quantified in different trap types). Waves were an important predictor of when local community taxa are most likely to disperse in different trap-types, suggesting that wave energy is important for connectivity in a region. Community composition at the site was variable and changed stochastically over time. We found changes in community composition (occurrence, abundance, dominance) to be greater at times when connectivity and rates of dispersal were low. In response to periods of lower connectedness dominant taxa in the local community only exhibited change in their relative abundance. In contrast, locally less abundant taxa varied in both their presence, as well as in relative abundance. Constancy in connectivity and rates of dispersal promotes community stability and persistence, suggesting that local community composition will be impacted by changes in the spatial extent over which immigration and emigration operates in the region. Few empirical studies have actually measured dispersal directly in a multi-species context to demonstrate the role it plays in maintaining local community structure. Even though our study does not evaluate coexistence over demographic time scales, it importantly demonstrates that dispersal is not only important in initial recruitment or following a disturbance, but also key in maintaining local community composition.

1. Introduction

Loss of biodiversity highlights the urgent need to better understand how community composition is maintained (Connell and Sousa, 1983; Butchart et al., 2010; Chase and Myers, 2011). In addition to species niche requirements and local environmental conditions, immigration from sources in the wider area may be equally important in maintaining diversity (Kneitel and Chase, 2004; Ricklefs, 2008; Srivastava and Kratina, 2013). Thus it has increasingly been recognized that regional processes will also influence local assemblages (MacArthur and Wilson, 1967; Hanski and Gilpin, 1997; Leibold et al., 2004). Following disturbance, dispersal will be a prerequisite allowing species to re-assemble at a site (Whitlatch et al., 1998; Norkko et al., 2010). In many systems continued dispersal after initial colonization may play an important role in maintaining community structure (Ricklefs and Jenkins, 2011; Cornell and Harrison, 2013). Dispersal can be a highly variable process that can occur at a much faster rate than the generation times of the taxa involved to the extent that a local equilibrium will rarely ever be achieved at the local scale (e.g. Lotka–Volterra models). Dispersal can impact the local assemblage (i.e. relative abundances and species richness) by changing the spatial extent over which immigration and emigration operates in the region (Hewitt et al., 1997; Lundquist et al., 2006). However, most field investigations use data taken at only one point in time and largely neglect dispersal and temporal dynamics in community regulation processes (White et al., 2006). Thus it is still unclear to what extent a local assemblage operates in isolation from the surrounding region, or is influenced by the spatial context in which it occurs (Gravel et al., 2006; Ricklefs, 2008).

In marine systems studies on dispersal have emphasised supply-side ecology (sensu Gaines et al., 1985), where dispersal is limited to episodic long-distance dispersal by larvae (Lundquist et al., 2006; Pineda et al., 2009; Cowen and Sponaugle, 2009). Demographic openness is

☆ Note: authors declare that there is no conflict of interest.
☆☆ Author contribution: all contributed to this manuscript. SV JN and AN conceived the study design, conducting fieldwork. SV conducted data analysis and wrote a draft of the manuscript, JN and AN contributed substantially to revisions.

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http://dx.doi.org/10.1016/j.seares.2014.09.001
1385-1101/

often assumed over >1000 km, so that larvae from well-mixed larval pools will disperse, survive and settle into local populations (Cowen and Sponaugle, 2009). In this view, a stochastic supply of larvae determines how dispersal-limited a site is or, conversely, how connected the site is. However, in contrast to passive particles, larval behavior may distort settlement estimates based on supply (Pineda et al., 2009). For example, upon release, larvae can also be retained within very close proximity (Osman and Whitlatch, 1998). Larval dispersal can also be very costly, incurring high rates of mortality (Pedersen et al., 2008). It has been shown that larval density may rapidly diminish with distance and time owing to advective and diffusive properties of the mixing and stirring of currents (e.g. 20–30 km, Becker et al., 2007). In addition to initial larval recruitment, many marine species also continue to disperse as post-larvae and as adults, which is relatively more frequent but tend to occur at smaller scales (Whitlatch et al., 1998). These post-larval processes may be relatively more important in maintaining community composition than site-to-site variation in initial larval recruitment that is now considered to be largely independent of local adult abundances (Pedersen et al., 2008; Caro et al., 2010; Pineda et al., 2009).

In shallow soft-sediment habitats, rates of post-larval dispersal can be particularly high, often due to a higher frequency of waves and currents, and species not being permanently attached to their substrate (Armonies, 1994; Hewitt et al., 1997; Norkko et al., 2001). It has repeatedly been demonstrated that this is not a purely passive process, as many species are able to burrow deeper or actively emerge, thus regulating their subsequent transport along the bottom as bedload (Armonies, 1994; Lundquist et al., 2006). In tidal systems, many post-larval benthic invertebrates, even those lacking a planktonic larval stage (up to 40–60% of taxa, Grantham et al., 2003), have been observed to be passively transported or to actively swim higher up in the water column (Martel and Chia, 1991; Armonies, 1994; Valanko et al., 2010a). Dispersal of post-larvae and adults will involve movement from one area to another, and thus impacts both the assemblage from which the individual emigrates and into which it immigrates. Importantly, rates of dispersal may vary between species and/or community location depending on source area abundances, as well as on species-specific dispersal behavior, capability and scale (Jacobson and Peres-Neto, 2010; Valanko, 2012).

For marine ecologists a major challenge still lies in extrapolating beyond single-species populations to assess the relative importance of dispersal processes for a whole community (i.e. maintaining biodiversity; Todd, 1998). Following Holling (1973) and Connell and Sousa (1983), persistence is defined here as the continued presence of a particular species assemblage at a site, whereas stability refers to the degree of constancy in numbers, or relative abundance of organisms. Large temporal fluctuations in rates of dispersal may cause species to be temporarily variable in their occurrence, increasing temporal turnover. Rare species may be more sensitive to changes in relative rates of immigration and emigration, potentially lowering local species richness and increasing temporal turnover. Assessment of changes in community composition can be conducted using time-lag analysis (Collins et al., 2000). In this approach similarity in community composition at increasing time lags is used to determine the degree of temporal variability and the potential for clear patterns of change over time. Such studies must be carried out at an appropriate temporal scale, with the minimum time period suggested to be at least one complete turnover of individuals in a population (Connell and Sousa, 1983). For shallow benthic invertebrates local populations can complete 50% turnover in individuals within 18 h in a 0.25 m^2 area (Norkko et al., 2001) and thus present a useful platform within which to address issues related to measuring rates of dispersal and investigating the short-term stability in community composition. To date a number of studies (e.g. Hewitt et al., 1997) have addressed compositional stability of benthic invertebrate communities, yet very few studies have related it to in situ measures of connectivity and rates of dispersal. Studies also often lack temporal replication, which has limited the ability to determine causal relationships. This is partly due the logistic difficulties associated with tracking multispecies movement, where often dispersal measures available are highly simplified and distant from ecological reality (Travis and French, 2000; Jacobson and Peres-Neto, 2010). Rates of dispersal may be high and thus a challenge for benthic ecologist is to determine the extent to which biodiversity is structured by temporal variability, and also to quantify and explain stability in diversity (richness and relative abundances) in the face of this change.

In this study we test short-term stability of a soft-sediment invertebrate community based on an 18-day period by monitoring community composition (abundance, richness and dominance) every 48 h. We consider a time scale that is shorter than the generation times of the taxa involved, and thus ensure that demographic processes affecting local assemblage composition are minimal. We use between-sampling interval similarity in community composition (Bray–Curtis coefficients) as our measure of stability and apply a time-lag analysis to investigate patterns of temporal variability (Collins et al., 2000). We relate stability to connectivity (wind, wave, current energy) and rates of dispersal (quantified in different trap types). We predict that if the local assemblage operates in isolation from the surrounding region that it is embedded in, then connectivity and rates of dispersal should not be related to changes in the local assemblage and remain stable. If it, however, is influenced by the spatial context in which it occurs, then changes in the local assemblage will depend on rates of dispersal and connectivity. Our a priori prediction was that constancy in connectivity and rates of dispersal would promote community stability and persistence. We also investigate species contribution to changes in local community composition. We predict that species' contribution to change over periods of low connectedness will depend on the species' dominance in the local community. Locally more abundant species will not be as dependent on immigration and will therefore be relatively less likely to go locally extinct (i.e. emigration without immigration).

2. Methods

2.1. Study site

The study was conducted in a shallow (5.7 m) sandy sub-littoral habitat in south-western Finland (59° 49′N: 23° 10′E). At site 5, replicate sampling locations were designated for monitoring along a 50 m transect (10 m apart) running in an along-shore direction. The region's coastline varies in the degree of shelter from islands, relative to openness to wind-induced wave energy from a dominant SW direction (Soomere, 2008, Fig. 1). The region has no regular tides and weather conditions in the region vary on a synoptic-scale of about 5–10 days (Soomere et al., 2008). A study period of 18-days was thus chosen to include sufficient temporal variation in connectivity (by waves and currents, Fig. 2ab). At the same time, our study period was short enough to avoid other sources of variation in the benthic invertebrate community (e.g. mortality, reproduction, growth of juveniles, seasonality). Between 2 and 20 August 2007, we monitored nine consecutive 48 h sampling intervals for connectivity (wind, waves, currents), rates of dispersal (measured in different trap-types), and changes in local assemblage composition at the site (beginning and end of each 48 h; T0–T9; Figs. 1 and 2). At each interval, all sampling was carried out within 30 min using SCUBA. Over the study period salinity was 5.8 and temperature 18 °C at 5 m depth. Sampling interval 8 (16–18.7.2007) was not sampled due to a storm event.

Dominant taxa in the local assemblage at the site were Ostracoda, Oligochaeta, the bivalve *Macoma balthica*, the polychaete *Marenzelleria* spp. and the Gastropoda *Hydrobia* spp. (see Table 3). The local assemblage was analyzed in two complementary ways, first by identifying taxa to the lowest practical/possible level, and secondly by further dividing taxa that exhibited large size differences into size categories. The size-split divisions were made to investigate if temporal stability