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Changes in small scale spatial structure of cockle *Cerastoderma edule* (L.) post-larvae

Timothy Andrew Whitton *, Stuart Rees Jenkins, Christopher Allan Richardson, Jan Geert Hiddink

School of Ocean Sciences, Bangor University, Menai Bridge, Anglesey LL59 5AB, UK

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ABSTRACT

Understanding the spatial structure of populations at different scales can help reveal the processes controlling abundance and distribution. For species with a pelagic larval stage and highly mobile post-larval stage, such as the common cockle *Cerastoderma edule*, changes in spatial distribution from settlement through to juvenile stages are likely to occur at various spatial scales influencing the population dynamics observed. To record such changes a small-scale high-resolution field survey of *C. edule* post-larvae over an area of 60 × 80 m of tidal mudflat was conducted using a spatially-explicit staggered-nested design in the Dee estuary, UK. The survey was repeated three times from initial settlement in June 2011 to March 2012. Changes in spatial structure were described using Moran's *I* correlograms and prediction mapping, with analysis of correlations between cockle cohorts and sediment composition. At the first sampling event in June 2011, when initial settlement was occurring, post-larvae were highly aggregated in patches of 10–14 m in size and 16–20 m apart. By October 2011 the post-larvae had become more evenly dispersed with some small scale (<4 m) random patchiness and a gradient in post-larval density. This spatial structure was maintained into March 2012 but with increased patchiness. At settlement post-larval density showed no correlation with adult abundance or sediment mud content, but by October 2011 and March 2012 there was a strong positive correlation with adult abundance. Such changes in spatial structure, abundance and adult association after settlement show the likely importance of small scale (metres to tens of metres) processes on post-larval survival from predation and adult interactions, thereby potentially shaping adult distributions. Small scale patchiness in post-larvae can be created at settlement; however the distribution and association with adults change over time.

1. Introduction

Understanding the spatial structure of a population is a fundamental part of understanding its ecology, and is also relevant in designing appropriate sampling strategies (Thrush, 1991; Underwood et al., 2000). In this study spatial structure is defined as the pattern of organisation of individuals in space (e.g. uniform, random and patchy) and the quantification of that pattern (size of patches and the distance between them). The scale, characteristics and temporal variability of a population's spatial structure can indicate which processes may be important in creating or altering a population's distribution (Bergström et al., 2002; McArdle et al., 1997; Underwood et al., 2000). The post-settlement period is important in determining recruitment success in many marine systems, particularly soft sediment habitats (Olafsson et al., 1994). This is largely due to high mortality from predation and other intra- and inter-specific interactions, with spatial structure likely to influence the strength of these processes (Beukema and Dekker, 2014; Clark et al., 2000). Post-larvae of soft sediment invertebrates can be highly mobile (Armonies, 1994), changing their spatial structure and influencing adult distributions (Armonies and Reise, 2003). Therefore studying spatial structure during key life stages will help define processes influencing population size and distribution in soft sediment systems.

The spatial structure of the common cockle *Cerastoderma edule* (Linnaeus, 1758), a commercially and ecologically important infaunal soft-sediment bivalve, is often highly patchy (spatially aggregated) over scales of thousands (Kraan et al., 2009) and tens of metres (Boldina and Beninger, 2013), despite living in what appears to be a spatially homogenous physical environment. The reasons for such spatial heterogeneity are not clearly understood (Kraan et al., 2009). The post-larval stages of many soft sediment invertebrates can have very high mortality rates and be very , and so this apparent under-utilisation of the available habitat is likely to be generated in this early life stage (Armonies and Reise, 2003).

The post-larval stage (defined here as the period from larval settlement until the next main settlement event) of *C. edule* is a critical period for determining a cohort's abundance and distribution, primarily through very high early post-settlement mortality (Beukema and Dekker, 2005; Jensen and Jensen, 1985) and redistribution (or secondary settlement) through bysso-pelagic migrations (Armonies, 1994). The large scale (≈ 1 km^2) settlement of *C. edule* post-larvae has been shown to be

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* Corresponding author. Tel.: +44 1248 383936.
E-mail address: t.whitton@bangor.ac.uk (T.A. Whitton).

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more restricted in extent than the adult distribution, however changes after the initial larval settlement indicate that post-larvae become more widely dispersed by resuspension in currents (Armonies, 1996; Bouma et al., 2001; Jung et al., 2006; Kraan et al., 2009; Lindegarth et al., 1995). Large scale observations suggest that initial patterns of distribution are created through passive deposition of larvae where currents are low or converge, which can be facilitated by biological structures such as mussel reefs (Donadi et al., 2013), often producing positive correlations with fine sediments (Armonies and Reise, 2003). However, there is little information about the specific spatial structure of post-larvae within the areas where they occur and how it changes through time. At small spatial scales (<100 m) Boldina and Beninger (2013) showed that juvenile *C. edule* (likely 1- and 2-group cohorts) are highly aggregated (patchy) with adults being more homogenous. However work considering small scale spatial structure of post-larval (0-group) individuals is lacking.

Over large scales the soft-sediment tidal flat can appear homogenous, but over smaller scales heterogeneity can be observed. Pools of standing water, loose algal mats (Arroyo et al., 2012; Norkko, 1998), patchiness of meiofauna and microphytobenthos (Pinckney and Sandulli, 1990) are a few examples of variables which can be heterogeneous at scales of centimetres to metres on tidal flats. Such patchiness of physical and biotic variables at small scales is likely to influence survival and fitness of post-larvae. For example the juvenile shore crab *Carcinus maenas* and juvenile brown shrimp *Crangon crangon* contribute heavily to early post-settlement mortality of *C. edule* (Beukema and Dekker, 2005; Jensen and Jensen, 1985; van der Veer et al., 1998), and their ability to locate *C. edule* post-larvae and the efficiency with which they can feed on them is likely to be influenced by the spatial structure of the post-larvae (Andresen and van der Meer, 2010; Clark et al., 2000; Thrush, 1999; Whitton et al., 2012). Predation has a large scale effect on post-settlement survival (Beukema and Dekker, 2005) but may be highly influenced in its intensity from small scale spatial patterns in their prey.

Geostatistics are increasingly used in Mar. Ecol. to quantify spatial pattern and structure in species distributions (Fortin et al., 2006; Legendre and Fortin, 1989; Liebhold and Gurevitch, 2002). This group of statistical analyses is of particular use for understanding spatial structure because it treats distance as a continuous variable and uses information from almost all of the samples taken (Cole, 2009). It can be a powerful tool if sampling is appropriately designed. In this study a Staggered Nested Design was used (SND). In this design samples are placed at increasing distances apart from each other, nested along a transect or area which is then replicated (Cole, 2009; Cole et al., 2001). This approach has advantages over the more widely used hierarchical nested design for investigating spatial variability at our scale of interest (Cole, 2009). Geostatistical analysis such as Moran's *I* correlograms allows the interpretation and quantification of the spatial structure of a variable (Fortin et al., 2006; Kraan et al., 2009; Legendre and Fortin, 1989).

In this study it is hypothesised that the initial small scale spatial structure at settlement is likely to be patchy owing to passive nature of the settlement process, but will change due to large scale processes, such as drifting, which will reduce densities and create a more uniform distribution. In this study the objective was to record and quantify how the spatial structure of a single cohort of post-larval *C. edule* changes from initial settlement to the following post-winter period over a small spatial scale (metres to tens of metres). Repeated sampling using a spatially explicit design allowed the observation of the spatio-temporal structure of post-larval distribution. Similar observations on the sediment properties and distribution of adult *C. edule* helped to establish possible drivers for the observed changes in post-larval distributions.

2. Methods

2.1. Study site

Sampling was conducted on the Thurstaton cockle bed in the Dee estuary, UK. The Dee estuary drains the river Dee into Liverpool Bay (Irish Sea) and is macro-tidal with a range of 7–8 m at the mouth (Moore et al., 2009). The Thurstaton cockle bed is located on an intertidal mud and sand bank situated on the eastern side of the estuary, which drains in a north westerly direction running parallel with the shore line (Fig. 1). This cockle bed is intensively fished for cockles (>20 mm in size) when densities are high enough, from July until the total allowable catch has been harvested. During the study period no fishing was undertaken.

2.2. Sampling design

2.2.1. Settlement monitoring at the study location

The initial settlement of *C. edule* can be spatially highly concentrated. To determine a suitable study location with high densities of post-larvae, a large scale survey of post-larval abundance was conducted across the Thurstaton cockle bed on May 3rd, 2011 (Fig. 1A). A 64 mm diameter core was taken to a sediment depth of 15 mm at each of 18 stations distributed among 3 transects (each was 1.2 km long), which were placed parallel to the estimated low, mid and high shore levels of the shore (Fig. 1). This survey was then repeated on September 16th 2011 to reveal how post-larval abundances may have changed. One of the sampling stations (Fig. 1) was chosen as the area for the small scale spatial sampling (Fig. 2) as it had high numbers of post-larvae and was furthest from potential disturbance by human activity and a large drainage channel (Fig. 1). Separate to the small spatially explicit sampling design this location was monitored by sampling with a 64 mm diameter core on 3rd May, 7th June, 21st July, 1st August, 16th September, 10th October 2011 and 7th March 2012 to record changes in size frequency and density of *C. edule* post-larvae during the study period. Post-larval shell length of *C. edule* at the time of initial settlement ranges between 350 and 1000 μm (Fig. 3). Sieves with a mesh size 500, 350, 255 and 125 μm mesh size were used to help separate *C. edule* post-larvae from the sediment and other fauna.

2.2.2. Staggered nested design spatial sampling

A small scale spatially explicit Staggered Nested Design (SND) was used (Fig. 2) on three occasions (June and October 2011 and March 2012) over an area of 4800 m^2 to allow robust geostatistical analysis of cockle post-larval distribution over scales from metres to tens of metres. A SND provides good replication at a variety of small distance bins for detailed geostatistical analysis. The sampling area was divided into twelve equal squares and each allocated 20 m long transects which were oriented in a random direction by random selection from 45, 91, 135, 180, 225, 270, 315, and 360° to avoid biassing the spatial structure through any natural gradients (Fig. 2). The initial design had five samples at exponentially increasing distances of 0, 0.1, 0.6, 3.4 and 20 m along each transect, totalling 60 sample stations for the whole survey (Fig. 2). After the first sampling event on June 7th 2011 two extra points were added along each transect at 7.55 and 11.70 m for the two subsequent sampling events (Fig. 2) to increase the replication at small to medium distances. A 29% increase in sampling effort from the two extra points yielded a 50% increase in data available for geostatistical analysis for each sample set (number observations in each distance bin, mean = 109, min = 36, max = 220).

2.2.3. Sampling procedure

A combination of a GPS unit, navigation compass and a tape measure was used to locate each transect and associated sample locations. Sampling of *C. edule* post-larvae was conducted to cover possible spatial structure changes during what were predicted to be important time periods. These were in June 2011 when settlement was taking place to capture the distribution of settling larvae, in October 2011 by which time settlement patterns may have changed and then in March 2012 following the winter period during which mortality might be expected to be high. Adults were also sampled in October 2011 and March 2012 using a quadrat. Sediment samples were taken in October for particle