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Irregular recruitment of the echinoid *Echinocyamus pusillus* and its implications for biological traits analysis

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Abstract

Size-frequency analysis of the echinoid *Echinocyamus pusillus* from six offshore areas in the southern North Sea and eastern English Channel reveal five distinct cohorts, suggesting a lifespan of five years. In all six individual areas one or more year-groups are absent, due to the unsuccessful recruitment of planktonic larvae to the seabed in some years, giving a false impression of a shorter lifespan. A relatively long lifespan and planktotrophic larval development are remarkable for such a small species, which reaches a maximum test length of 7.3 mm in the area, such traits being more typical of large-sized macrobenthic species. The feeding mode is akin to that of many meiobenthic taxa. The architecture of the test confers exceptional strength and resilience to mechanical perturbation.

Introduction

Biological trait-based approaches are increasingly being adopted as a tool by which to explore changes in ecosystem functioning (Bremner *et al*., 2003*a*, 2003*b*; Degen *et al*., 2018). Morphological, life history and behavioural traits can be used to investigate ecosystem functions and properties such as energy and nutrient cycling, production, resilience and heterogeneity (Degen *et al*., 2018). However, extensive gaps still exist in our knowledge of the natural history of species even for well-documented faunas such as the marine benthos of the UK (Tyler *et al*., 2012), and it is often necessary to resort to the application of generalized relationships, such as that between body size and age (e.g. Marine Ecological Surveys Limited, 2007) or reproductive mode (Strathmann & Strathmann, 1982), even though in specific cases these may be misleading. *Echinocyamus pusillus* (O.F. Müller, 1776) is one such example.

Echinocyamus pusillus is a very small sea urchin with an oval, flattened body typically only 1 cm in length (Picton & Morrow, 2016), although reported to reach a maximum of 15 mm (Hayward & Ryland, 1990). It is common all around the British Isles and is found from the extremely low intertidal to sublittoral depths of more than 200 m (Southward & Campbell, 2006). It has a preference for medium to coarse-grained sand (median grain size >200 µm) and reaches maximum densities in sediments with a median grain size of 500–550 µm, preferring sediments with a low mud content (maximum 10%) (Degraer *et al*., 2006). Being a very small species in very coarse sediments, its occurrence may be under-recorded due to its inconspicuousness and the methodological problems of its extraction from the sediment. The test is completely covered with fine short spines and is coloured grey to greenish, becoming completely green when injured (Southward & Campbell, 2006). The calcite test has extraordinary structural strength and skeletal integrity within the echinoids, due to the absence of supportive collagenous fibres between single plates and an internal buttress system (Grun & Nebelsick, 2018). This provides the species with exceptional resilience to physical abrasion in coarse sediments that are often unstable and mobile. Since the coarse sands and gravels which *E. pusillus* inhabits are often the target for aggregate dredging by the construction industry, the species resilience to physical abrasion is likely to be crucial to its continued persistence in these areas (Marine Ecological Surveys Limited, 2007).The high preservation potential of the tests is also responsible for their frequent occurrence in both recent and fossil (Pliocene) death assemblages.

Despite its small size, *E. pusillus* has a planktotrophic larval phase in its life history. It has separate sexes and fertilization takes place externally. The breeding season is in the summer months and the echinoplutei are found in the plankton from summer to autumn (Southward & Campbell, 2006).

Echinocyamus pusillus is a deposit-feeder, its gut content including sediment, remains of plants and bottom material (detritus), and infauna, especially foraminiferans, and *E. pusillus* itself is eaten by fish, especially by dab and haddock (Mortensen, 1927; de Ridder & Lawrence, 1982; Eleftheriou & Basford, 1989; Schückel *et al*., 2010). Haddock show a strong preferential prey selection for *E. pusillus* in the North Sea, which may be effective as a grinding element in their stomach, enhancing digestion due to its hard calcareous shell and compensating for the low nutritional value of their benthic prey (Schückel *et al*., 2010).

The objective of this study is to establish some of the major life history traits relating to the function of this species, in particular its lifespan or time taken to reach maximum size, which can be established by cohort growth analysis.

Materials and methods

Quantitative samples of *Echinocyamus pusillus* were collected at six offshore sites licensed for aggregate extraction in the southern North Sea and eastern English Channel (Figure 1, Table 1) in May and June 2005 as part of a broader research programme investigating the ability of benthic communities to recover from aggregate extraction (Marine Ecological Surveys Limited, 2007). The bottom sediments comprised coarse mixtures of sand and gravel, occasionally with a small mud component, and water depths ranged from 18–49 m (Table 1). Ten 0.1 m^2 Hamon grab samples of sediment were taken randomly within each site, sieved over a 0.5 mm mesh sieve, gently eluted to remove excess fine sediment and preserved in formalin for further separation and analysis in the laboratory. Test-length measurements to the nearest 0.1 mm were made under a binocular microscope using an eyepiece graticule calibrated with a stage micrometer. Size-frequency analysis requires a reasonably large number of specimens, and all specimens from all 10 samples taken from a particular area have been combined to establish the size-frequency distribution. Areas where less than 20 specimens were recorded, across the 10 samples, have been excluded from this analysis.

Several computer packages such as ELEFAN, SLCA, MULTIFAN and MULTIFAN-CL are available to identify modes in size-frequency distributions (see Van der Meer *et al.*, 2013 and references therein) but these are based on the assumption that the sizes in each age class are normally distributed, which is intuitively invalid. If recruitment occurs over a period of time and the recruits then begin to grow and suffer mortality then we would expect a right-skewed size distribution for that cohort (i.e. with the mode to the left of the distribution). In practice, if cohorts are clear they can be identified by eye without the need for computationally cumbersome techniques, and this approach has been adopted here. A further problem arises when attempting to estimate the number of year classes in the population in that the local recruitment of many benthic species is erratic (see e.g. Buchanan & Warwick, 1974) and in some years may be particularly strong while in others it may be weak or there may be a complete recruitment failure.

Results

Figure 2 shows that, for all areas combined, there are clearly five cohorts present, giving a maximum age of five years. The smallest cohort, with a modal length of 1.5 mm, can be assumed to be almost one year old, since samples were collected in May/June and spawning and planktonic larval development takes place in the summer–autumn (Southward & Campbell, 2006). The maximum length attained is just 7.3 mm, at Area 461. Clearly, the five cohorts are not all well represented in all areas and interpretation of the data from one area alone could be quite misleading. In Area 461 there appears to be a single cohort of large animals which would suggest an annual species with a rapid growth rate. Size-frequency data from Areas 452 and 460 would be interpreted as having 2 cohorts (but these are not of equal size in the two areas), with a lifespan of two years. Areas 458 and 483 would be interpreted as having three cohorts, with a lifespan of three years, whilst data from Area 430 are more difficult to interpret but suggest a lifespan of at least two years.

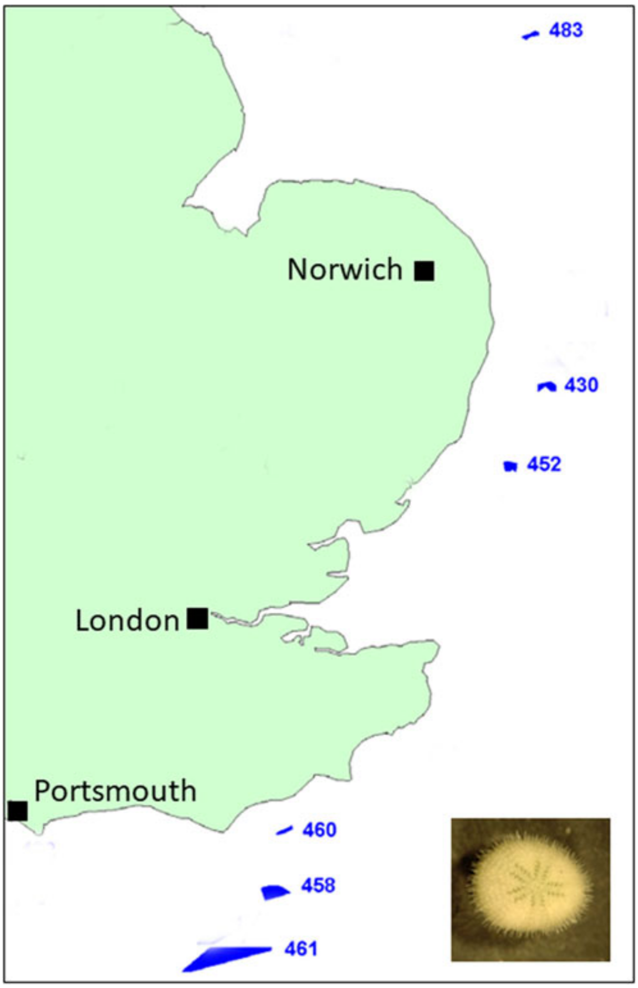

Fig. 1. Map of SE England showing locations of the six sampling areas. Inset: photograph of a living specimen of *Echinocyamus pusillus*.

Discussion

In the present study size-frequency distributions have only been established for a single point in time and so the annual nature of the size modes is equivocal. However, cohort growth analysis has been widely used in field programmes directed towards the estimation of annual production of marine benthic macrofaunal species in UK waters (Buchanan & Warwick, 1974; Warwick & Price, 1975; Warwick *et al.*, 1978; Price & Warwick, 1980; Warwick & George, 1980; George & Warwick, 1985). Such studies typically result in a time series of size-frequency distributions, from which the demographic parameters of recruitment, growth rates and mortality rates can be derived (Crisp, 1984; Van der Meer *et al.*, 2013). A time series of size-frequency distributions is used to follow the progression of size-modes over time so that it is possible to determine whether the size modes are annual or not, since it is conceivable that modes could result from a series of discrete spawnings over time periods shorter than a year, or annual modes might be missing due to recruitment failure. Thus, if a species is only present in one or two areas, the data must be interpreted with caution since the size modes may not represent successive years. However, in all the studies of benthic species cited above these size modes have proved to be annual, and therefore this is assumed to be the case for *Echinocyamus pusillus*.

This analysis is predicated on the assumption that the settlement timing and post-settlement growth rates are similar in all areas. The composition of each size cohort in the combined

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Table 1. Sediment composition in sampling areas as Folk classification categories (Folk, 1954), with sampling date in 2005 and water depth (m)

Area	Sediment	Date	Depth
483	Sandy gravel (6), gravelly sand (3), sand (1)	26 May	21–25
430	Gravelly sand (5), muddy sandy gravel (3), sandy gravel (2)	29 May	29–35
452	Sandy gravel (5), muddy sandy gravel (3), gravelly sand (1), gravelly muddy sand (1)	30 May	23–29
460	Sandy gravel (4), gravel (3), gravelly sand (2), sand (1)	1 June	18–32
458	Gravelly sand (5), sandy gravel (5)	1 June	41–43
461	Sandy gravel (4), gravel (3), gravelly sand (2), sand (1)	1 June	43–49

Number of grab samples comprising each sediment type in parentheses.

graph comprises individuals from more than one area (except for the oldest). The first cohort comprises individuals from all areas except 461, being particularly strong in area 483. The second cohort also comprises individuals from all areas except 461, being particularly strong in area 452. The third cohort comprises individuals from all areas, the fourth from areas 452, 460 and 461 only and the fifth from area 461 only. The most logical scenario is therefore that the overall pattern results from varying recruitment success in different areas with roughly the same settlement time and growth rate in each. A possible alternative explanation of the combined distribution might be that there are fewer year classes than five but settling at very different times and growing at very different rates in individual areas. The two areas of highest urchin abundance, 483 and 452, each provide a clear indication of only two cohorts and would lead to the conclusion of a two-year lifespan, but if this were the case it would imply *very* different settlement times and/or growth rates in the two areas, which are only some 150 km apart in the same sea area and have a very similar sediment type. This would also contradict data from the other areas, where more than two cohorts were typically observed. Furthermore, while there are small differences among areas in the size range of individuals within each year class, if these differences had been larger they would have blurred the clear separation of classes.

The combined size distribution charts suggest that *E. pusillus* is very slow growing in the studied areas, taking five years to reach the small maximum size of 7.3 mm. The somewhat larger size elsewhere may either mean that it grows faster in these areas or lives longer. Although this species is reported to attain a greater size of 15 mm (Hayward & Ryland, 1990), there is no primary citation to support this value, although it is also attributed to Degraer *et al.* (2006) by WoRMS Editorial Board (2019). One of us (BP) has counted many thousands of individuals of this species throughout the UK, and never encountered specimens this large, and the 10 mm of Picton & Morrow (2016) is probably more realistic. The slow growth rate may be due in part to the low organic content of the coarse sediments that it inhabits, and also to its feeding behaviour which is potentially expensive energetically. The feeding mechanism is atypical for clypeasteroids because the coarse sediment particles are too large relative to the body size to be ingested whole. Sediment particles with attached food material are selected and transported by the suckered podia to the mouth, where particles are held in place and slowly rotated by the free margin of the peristomial membrane, while the teeth strip away diatoms and organic debris (Telford *et al.*, 1983). This mode of feeding is thus akin to that of many

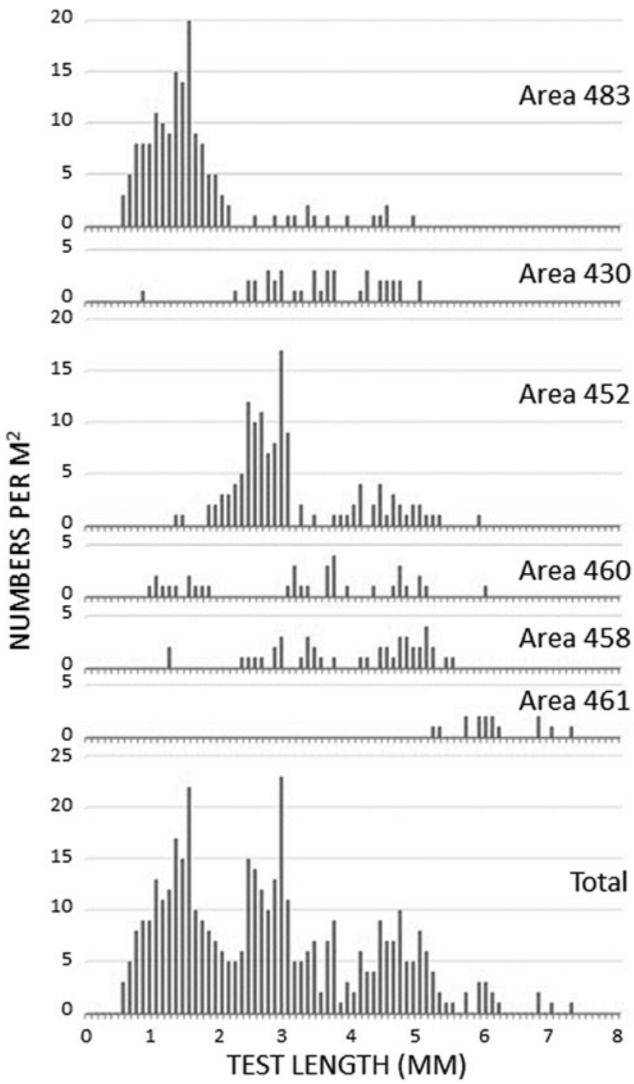

Fig. 2. Size-frequency histograms of *Echinocyamus pusillus* test length in the six individual areas and in all areas combined.

meiobenthic taxa that feed by scraping the biotic films from sediment particles, e.g. many nematodes (Wieser, 1953) and harpacticoid copepods (Marcott, 1977).

For comparison, limited data are available on growth rates of two larger heart urchins from offshore sediments in this area. *Echinocardium cordatum* (Pennant, 1777) in the southern part of the North Sea off the Dutch coast has been shown, by an analysis of annual growth rings on the ventral plate, enigmatically to grow fastest in sediments with the lowest organic content (Duineveld & Jenness, 1984). It reaches a maximum length of 43 mm at more southern sites and 33 mm further north, but a longevity of 10 years is the same in all areas. On the other hand, *Brissopsis lyrifera* (Forbes, 1841) in the finer offshore sediment off the Northumberland coast has a lifespan of four years, reaching a maximum size of 60 mm. The four-year-old individuals breed in November–December and do not survive to breed a second time (Buchanan, 1967; Buchanan & Warwick, 1974). The feeding mode of this species is more typical of irregular echinoids, the fine organic sediment being ingested whole.

The results of this study indicate that *E. pusillus* has an unusual combination of functional traits. Planktotrophic larval development is prevalent in larger-bodied macrobenthic species (no meiobenthic species have planktonic larvae) and is unusual in a species of this size. According to the body sizes recorded in the WoRMS database (WoRMS Editorial Board, 2019),

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E. pusillus has the smallest body size (length) of all the 37 infaunal genera with planktotrophic larval development listed as occurring in offshore sand and gravel sediments in 20 areas around the UK (Marine Ecological Surveys Limited, 2007). For such a small species, it also has an unusually long lifespan.

On the basis of functional trait analysis it has been concluded that *E. pusillus* is robust with respect to its potential recoverability from anthropogenic disturbance caused by offshore aggregate extraction (Marine Ecological Surveys Limited, 2007). This will obviously also apply to disturbance by benthic fishing. Although recovery from aggregate extraction has been found to require much longer periods than from benthic fishing (Foden *et al*., 2010), the latter activity takes place over very much wider areas both in UK waters and globally, and the sediments in which *E. pusillus* lives are particularly vulnerable to scallop dredging (Kaiser *et al*., 2006). In a study of the effects of fishery exclusion on the benthos in the areas of offshore wind farms in the Belgian part of the North Sea, *E. pusillus* showed increases in abundance in the no-fishery areas, supporting its potential for recovery from trawling activities (Coates *et al*., 2016). *Echinocyamus pusillus* has been assigned to AMBI ecological group I, species very sensitive to organic enrichment and disturbance (Borja *et al*., 2000), but AMBI has been shown to be a poor indicator for detecting the physical impacts of aggregate extraction, there being no increased abundance of opportunistic species as a result of the extractions, and is similarly not useful in other naturally stressed communities (Muxika *et al*., 2005).

Of the traits relevant to the resilience and recoverability from physical disturbance, size, fecundity, lifespan, age at maturity, larval development mode and adult mobility have been considered the most important (Marine Ecological Surveys Limited, 2007). Fecundity and age at maturity for *E. pusillus* remain unknown and so it is not possible to predict mortality in the plankton or immediately after settlement. However, the numbers of specimens in the successive year classes found in the study area imply an increasing mortality rate with increasing size, presumably mainly as a result of predation by demersal fish, with none surviving beyond their fifth year.

To complete our knowledge of the demographics of this species, more data clearly need to be gathered. A time series of sampling at one or more locations, perhaps also exploring the possibility of analysing test skeletal features for ageing, would substantiate (or otherwise) the annual nature of the cohorts described in the present study. Analysis of the age at reproductive maturity, fecundity and frequency of spawning, concurrently with sampling of larvae in the plankton would substantially enhance our understanding of the functioning of this important and enigmatic species in the benthic ecosystem and its relevance as an indicator of ecological condition.

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