

NOTE

What an introduced species can tell us about the spatial extension of benthic populations

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ABSTRACT: In the late 1970s the American jackknife *Ensis americanus* (syn. *E. directus*) was introduced into the North Sea. The history of its dispersal along the coast is used to derive an estimate of the species' mobility. On average, the population spread by 125 km per year to the north and, at the same time, by 75 km per year to the west, against the residual currents. Therefore, recruitment in a given area may depend on larvae produced some 125 km upstream while the offspring produced in the study area may recruit another 125 km downstream. As a consequence, the population dynamics cannot be explained from single-site sampling and even studies on local effects need knowledge of the population dynamics on a large spatial scale to distinguish between general trends and local peculiarities. For *E. americanus* in the North Sea a minimum longshore extension of the sampling area of some 250 km is suggested. Provided other benthic species with pelagic larvae have similar dispersal capabilities, community studies need a similar spatial scale. This implies that the number of distinguishable major communities is very limited in the coastal North Sea. To overcome the logistic difficulties in studying a sufficiently large area, a permanent network of institutes engaged in benthic population and community dynamics is recommended.

KEY WORDS: Benthos · Population dynamics · Population structure · Spatial scale · North Sea

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Population studies on benthic species in sedimentary environments have been performed for a long period of time (e.g., Möbius 1877). Nevertheless, there is nearly no information about the spatial scales that need to be sampled to obtain reliable estimates of population parameters. Usually, samples are collected somewhere in the (presumed) centre of a population. However, this can only adequately reflect the population composition if the age stages and sexes are uniformly distributed. Particularly in species dispersing by planktonic larvae the spatial patches of juveniles may

often deviate from those of adults, resulting in habitat partitioning among age groups. Examples are all marine species that have nursery areas, e.g., the bivalves *Chlamys opercularis* (Cadée 1968) and *Macoma balthica* (Beukema 1993), lugworms *Arenicola marina* (Flach & Beukema 1994), shrimps *Crangon crangon* (Janssen & Kuipers 1980), and bottom-feeding fish such as *Pleuronectes platessa* (Kuipers 1977). In these cases, sampling needs to cover the entire area occupied by any age group, otherwise the population estimates only reflect the situation in the sampled site and not the state of the population. In addition, since the spatial distribution of a population may vary over time, the entire range of habitats that potentially may be occupied needs to be included in sampling.

The dimensions of the area used by a population depends on the mobility of individuals. The term 'mobility' includes the dispersal capabilities of larvae and later stages as well as passive redistribution of benthic stages. The latter may occur from resuspension during sediment disturbance with consecutive transport of the organisms by the currents (e.g., Thiébaud et al. 1996, Olivier & Retière 1998, Armonies 2000). Adequate scaling of the study area relative to the mobility of species also turned out to be decisive for the detection of density-dependent processes in populations (Ray & Hastings 1996, Young & Ebert 1996).

Unfortunately our knowledge of the mobility of specimens is very limited, although it might also indicate the kind of population structure we have to expect. If mobility is rather low, the specimens are most likely organised in separate populations, with a very limited exchange of organisms among them. Increasing mobility will lead to increasing exchange of organisms among the sub-populations of a metapopulation (Hanski 1999). Finally, high mobility may be indicative of a population distributed across a large area, and a patchy distribution within this area (Thomas & Kunin

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1999). Usually, such patchiness may reflect resource heterogeneity, disturbances, or the capacity for reaching all suitable sites.

As a rare exception in marine invertebrates, there is some information about the mobility of razor clams *Ensis americanus* (Binney, 1870). This species is a well-known inhabitant of the lower intertidal and shallow subtidal along the entire North American Atlantic coast between Labrador and Florida (Theroux & Wigley 1983). In the late 1970s it was introduced into the North Sea, presumably as larvae in the ballast water of a ship crossing the Atlantic (Von Cosel et al. 1982). Analysing the history of its dispersal along the coastal North Sea gives an idea of its mobility. In this species, development includes a planktonic larva, and duration of the planktonic larval phase is 10 to 29 d, depending on temperature (Loosanov & Davies 1963). This is within the range of 2 to 6 wk assumed typical for completion of planktonic larval development in temperate invertebrates (Thorson 1961, Scheltema 1986). Postlarval specimens up to 55 mm shell length are capable of byssus-drifting (Essink 1985, and references therein). On the other hand, like other *Ensis* species *E. americanus* has an excellent burying capacity (Swennen et al. 1985, Schiedek & Zebe 1987). Therefore, it may not be very susceptible to passive dislocation during sediment disturbance and the dispersal capabilities of *E. americanus* may be amidst the range of other macrobenthic species in the North Sea with a pelagic larval phase. Similar dispersal capabilities of benthic

species with pelagic larvae are expected for other shelf sea areas (e.g., Mileikovsky 1968, Scheltema 1986) though modulated by the velocity of local currents.

Dispersal of *Ensis americanus* along the coastal North Sea. In the North Sea, a first population of 1 yr old specimens was found in 1979 at the mouth of the River Elbe estuary (Von Cosel et al. 1982). The species rapidly spread along the continental coastline of the North Sea, presumably as pelagic larvae and byssus-drifting post-larvae. Local studies on age composition indicated that *Ensis americanus* had reached the island of Sylt (about 125 km from the first findings) in 1979, and by 1982 it had passed the Skagerrak area (about 500 km from the first findings; Essink 1985, 1986). This equals an average dispersal of 125 km yr⁻¹ in the northward direction, i.e., with the residual currents of the eastern North Sea. In the westward direction dispersal was against the residual currents. Nevertheless, *E. americanus* had reached the Ems estuary by 1981 and the island of Texel (300 km from the first findings) no later than 1982 (Essink 1985, 1986). This equals an average dispersal of 75 km yr⁻¹ (Fig. 1). In the case that Von Cosel et al. (1982) had actually missed 1 yr of study, i.e., the species had already been introduced into the North Sea in 1977, the estimated average dispersal rates of *E. americanus* would be less (ca 100 km northwards and 60 km towards the west). The temporal course of dispersal along the coastline fits the hypothesis of a single introduction of *E. americanus* into the North Sea but cannot exclude the possibility of multiple imports of the species. This may be tested by genetic analyses.

In the coastal North Sea, the direction and velocity of the currents are highly variable. Daily average velocities between 0.02 and 0.1 m s⁻¹ (i.e., 1.7 to 8.6 km d⁻¹) are common while stormy weather may increase the current velocities up to 0.3 m s⁻¹ (roughly 25 km d⁻¹; BSH 2000, Dick pers. comm.). Therefore, the observed annual dispersal of 125 or 75 km may be well explained by a 20 d duration of the larval phase and rather calm weather, or by a few days with stormy weather, which results in faster currents. In addition, *Ensis americanus* is capable of secondary dispersal by byssus-drifting, as may be generally the case in bivalves (Sigurdsson et al. 1976). Byssus-drifting *E. americanus* were about 7 times more abundant in the water column during night than during daylight (Armonies 1992), indicating that they performed vertical migrations between the sediment and the water column. This may result in unidirectional transport over much larger spatial scales than is expected for non-migrating particles in tidal waters (Hill 1991).

Highest abundances were recorded between mid-intertidal and shallow subtidal areas, often in a rather mobile sediment (Beukema & Dekker 1995, Armonies & Reise 1999). Byssus-drifting specimens were also

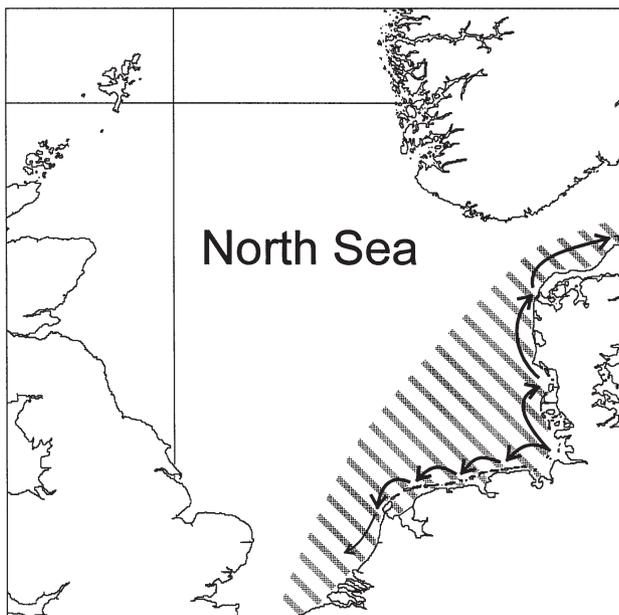


Fig. 1. *Ensis americanus*. Presumed annual stages of clam dispersal in the North Sea (arrows) and the potential dimension of a 'coastal continental benthic community' (hatched area)

abundant in the water column above upper intertidal sediments but the specimens did not permanently settle there (Armonies 1998). The deepest locality of *Ensis americanus* so far encountered in the North Sea is 26 m (Mühlenhardt-Siegel et al. 1983, but see Niermann 1997 for occurrence of *Ensis* sp. at 39 m depth). However, along the US Atlantic coast this species can occur down to 100 m depth (Theroux & Wigley 1983). Thus, *E. americanus* has the potential to occupy the entire German Bight in the North Sea unless the combination of reduced oxygen concentration in the bottom water layer (Hickel et al. 1989) and the clam's limited tolerance to hypoxia (Schiedek & Zebe 1987) restrict it to the shallow coastal zone without a thermohaline stratification.

Conclusions for macrobenthic population studies.

In order to understand (and in the long run, predict) local population dynamics of *Ensis americanus*, information is needed on the number of offspring produced up to 125 km in an upstream direction and 75 km in a downstream direction because this may determine the larval supply to the locality under interest. This means that a local reduction of larval production may result in low recruitment somewhere up to 125 km away, thus spatially separating causes and consequences. The offspring of a studied locality, in turn, may recruit somewhere between 75 km upstream and 125 km downstream. Combining both ranges, we arrive at a longshore range of some 250 km of coastline. According to the currently known bathymetric distribution, the studied area should expand between mid-tide level and ca 30 m depth, which is equivalent to about 60 km in the continental North Sea. Thus, an adequately scaled study on the population dynamics of *E. americanus* in the North Sea needs a sampling area of about 15 000 km² (or 12 000 km² if the species was already introduced in 1977).

Ensis americanus was not selected as an example because of its outstanding dispersal capabilities, but its introduction simply represented an unintended, large-scale experiment on dispersal. Though factors like the time of reproduction, rate of development, patterns of vertical migration, and seasonal changes in the velocity and direction of the currents may add substantial variability to the horizontal transport of larvae (Scheltema 1986), similar spatial scales are expected to be appropriate for population studies on other macrobenthic species with planktonic larvae. A recent example is the spread of the mussel *Mytilus galloprovincialis* invading coastal waters in South Africa, which showed a yearly increase in the range of 55 to 97 km to the northeast and 12 to 29 km to the southwest (McQuaid & Phillips 2000). On the other hand, a much smaller area (possibly tens of km) may suffice for population studies on species with a short planktonic larval phase.

Effects on community studies. In studies on a community level, adequate scaling may be of similar importance because community features such as numerical abundance or biomass are often strongly dominated by a few species, at least in temperate zones. Particularly when dealing with 'major communities' ('communities that are of a sufficient size and completeness of organisation that they are relatively independent; that is, they need only to receive sun energy from the outside and are relatively independent of inputs and outputs from adjacent communities'; Odum 1971, p. 140), inadequately sizing the study area relative to the mobility of the dominant species would result in unreliable estimates for the entire community dynamics.

Community studies often aim to detect temporal changes in community composition. If the studied area is small relative to the mobility of the specimens there is no way to find out if a detected change really indicates a temporal change in the community, or a spatial shift of some members of the community. The *Ensis americanus* example demonstrates that such a spatial shift may easily cover a distance of tens of km, at least in species with planktonic larvae. As a rule of thumb I propose that the minimum extension of the study area should enclose the annual dispersal capability of the dominant species in either direction. Since *E. americanus* may be a dominant species in the benthos of the entire continental coastal North Sea (M. Strasser pers. comm.), it is concluded that community studies also demand for a minimum longshore extension in the range of 250 km.

Long-distance dispersal of benthic species with planktonic larvae should result in a high degree of similarity of the benthic fauna in the continental North Sea. This was indeed observed during North Sea-wide comparisons (e.g., Glémarec 1973, Dyer et al. 1983, Adams 1987, Basford & Eleftheriou 1988, Künitzer et al. 1992; Fig. 1) and was explained by similar environmental conditions within this area (e.g., a high seasonal variability of temperature compared to other parts of the North Sea). Wide ranges of dispersal of benthic species provide another (though not necessarily alternative) explanation. In addition, dispersal may contribute to the spatial synchrony in population dynamics over large spatial scales (e.g., Beukema & Essink 1986, Beukema et al. 1988, 1996) although the effects of environmental correlation and dispersal may not be purely additive (Kendall et al. 2000).

Thus, the entire 'coastal continental North Sea' may be inhabited by a single major benthic community stretching over several hundreds of km, with some local variations of species composition according to sediment types (Salzwedel et al. 1985). This is not an unlikely spatial scale. Studying the continental shelf

area west of Norway, Mileikovsky (1968) argued that rather constant exports of larvae from the continental shelf may lead to the formation of bathyal and abyssal 'pseudopopulations' 100 to 500 miles offshore that can only exist permanently by being regularly replenished by larvae settling out of the surface current. For the crab *Cancer magister* in the California current the spatial scale of dispersal was estimated to be roughly 100 to 200 km (Botsford et al. 1998). On the other hand, Gaylord & Gaines (2000) suggested that the colliding areas of nearshore ocean currents have the potential to constrain a species' geographic range even when suitable habitat outside this range is abundant. Besides the rather continuous latitudinal changes of community composition, such currents might delimit the 'continental North Sea' benthos community in the English Channel, i.e., at its southern limit, and at the same time at its northern limit in the Skagerrak area.

Because of the high variability of currents in the coastal North Sea (BSH 2000) benthic species with planktonic larvae are unlikely to exist in spatially isolated populations. This may only be expected under particular hydrographic conditions (e.g., Verdier-Bonnet et al. 1997) or in species confined to estuaries that are unable to survive current-driven transport across a fully marine area. Instead, in many species mobility may be high enough for more or less regular exchange of organisms between local (sub-) populations connecting a metapopulation complex. Hanski (1999) stated that if all local populations have a substantial risk of local extinction, long-term survival is possible only at the metapopulation level. In the coastal North Sea, a 'substantial risk of local extinction' may derive from the high variability of the environment, with gales disturbing vast areas, a long lasting ice-cover during cold winters in onshore areas, or oxygen depletion below stratified waters during warm summers in offshore areas. Thus, the variability of the environment may select for species with a high mobility, hence a high capacity for colonisation of disturbed areas. In some species with a very high mobility the entire continental North Sea may even represent the distributional area of a single population with a patchy distribution according to environmental heterogeneity. In conclusion, studies on benthic community dynamics in the coastal North Sea should be carried out on a spatial scale no less than 250 km across.

Recommendations for future research. Certainly the above estimates of the dispersal capacity in *Ensis americanus* bear some sources of error, e.g., deriving from the limited number of sites that were available for reconstruction of dispersal or the general problem to record a species when abundance is low. However, the velocity of the tidal currents in the coastal North Sea (commonly 1.7 to 8.6 km d⁻¹ during calm weather; BSH

2000) suggests that larval dispersal over tens of km per week should be rather common. Therefore, the need to study far larger spatial scales than has hitherto been done is expected to hold true even if the estimated 15 000 km² for *E. americanus* may be too high. However, because of the usual limitations of resources, sampling of a sufficiently large area may be beyond the capacity of any single institute. Comparable problems in sizing fish populations have been overcome by internationally coordinated programs over decades, e.g., the ICES International Bottom Trawl Surveys.

A similar network of institutes engaged in the study of benthic population or community dynamics in the continental North Sea is proposed. During the past decades this has been done several times; however, only during limited periods and for a restricted purpose (e.g., the ICES North Sea benthos survey in 1986, Kunitzer et al. 1992, Basford et al. 1993). What is needed in the future is some *permanent* collaboration of institutes with standardised sampling programs. As an example, existing monitoring programs could be replaced by standardised sampling of some transects perpendicular to the coastline. Assuming a distance between transects of 50 km some 24 transects could cover the continental North Sea between the English Channel and the northern tip of Denmark. This might render satisfactory spatial resolution for some species but might be insufficient for others (e.g., Beukema et al. 1996). Alternatively, a higher number of transects might be sampled with a reduced or selective taxonomic resolution, for example by restricting the number of taxa evaluated at the species level, and centrally storing the 'rest' of the samples in case resources become available for additional analyses. Another sampling strategy might be regular zigzag cruises from the English Channel alongshore towards the Skagerrak, run by a coordinated program of the coastal states.

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