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ORIGINAL ARTICLE

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Increasing prevalence of the marine cladoceran *Penilia avirostris* (Dana, 1852) in the North Sea

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Abstract Rising sea surface temperatures in the North Sea have had consequential effects on not only indigenous plankton species, but also on the possibility of successful colonisation of the area by invasive plankton species. Previous studies have noted the introduction and integration into the plankton community of various phytoplankton species, but establishment of zooplankton organisms in the North Sea is less well-documented. Examining continuous plankton recorder (CPR) survey data and zooplankton results from the Helgoland Roads study, the autumn of 1999 witnessed the occurrence of the marine cladoceran *Penilia avirostris* in large numbers in the North Sea. The rapid appearance of the species corresponded with exceptionally warm sea surface temperatures (SSTs). Since 1999, the species has become a regular feature of the autumnal zooplankton community of the North Sea. In 2002 and 2003, the species occurred in greater abundance than recorded before. It is suggested that increased autumn SSTs have proved favourable to *P. avirostris*, with warmer conditions contributing to the success of the species' resting eggs and aiding colonisation.

Keywords Plankton · CPR survey · North sea · Climate change · Invasive species

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Introduction

Sea surface temperatures in the North Sea over the last decade have been increasing, with six out of the seven warmest years over the last 30 years occurring in the 1990s (ICES 2000). Biological responses in the plankton community to this have been noted by Beaugrand et al. (2002), with calanoid copepod assemblages having shifted northwards by 10° and conversely, organisms favouring more boreal conditions have declined (Beaugrand and Reid 2003). In addition, the phytoplankton community structure has altered, with an increasing dominance of flagellates and dinoflagellates (Edwards et al. 2001b). These results point to a major re-structuring of the planktonic ecosystem in the North Sea, closely linked with the global warming phenomenon. The increase in sea surface temperatures (SSTs) have, in addition to affecting native species, had an influence on the success of invasive planktonic organisms. A number of warm-temperate water non-native phytoplankton species have become established in the North Sea (Nehring 1998). Here we discuss the increasing incidence and range expansion of a zooplankter, the cladoceran *Penilia avirostris*. This species (Fig. 1) is a cosmopolitan tropical/subtropical cladoceran that is found in the productive neritic zone of all tropical oceans (Marazzo and Valentin 2003), and its distribution extends north and south into warm temperate waters (Rose et al. 2004). The species occurs extensively in the Mediterranean and Black Sea and although mainly found in coastal seas, *P. avirostris* is described as a eurythermal neritic species which can survive oceanic conditions (Tokioka 1979). The distribution of *P. avirostris* is mostly restricted to waters above 18°C but can range between 12°C and 30°C (Kim and Onbe 1995), with optimum conditions for establishing large populations around 25°C. In coastal regions of the Mediterranean *P. avirostris* forms vast swarms of parthenogenetic females which appear in the summer and persist into the autumn. This habit of

Fig. 1 Photograph of *Penilia avirostris* (Photo: Frank Reiners, BSH)

parthenogenesis (without pedogenesis, which makes *Penilia* more similar to freshwater cladocera than marine cladocera; Egloff et al. 1997) would explain the sporadic and rapid expansion of the species into new areas under favourable conditions, for example the Caspian Sea, where the species entered via the Volga-Don canal in 1954 (Aladin and Plotnikov 2003). All Cladocera can reproduce parthogenetically under favourable conditions, and produce a resting egg in the female after sexual reproduction (Gieskes 1971), which sinks into the bottom sediment (Marazzo and Valentin 2003). The production of robust resting eggs (which in the cladoceran species *Cercopagis pengoi*, are known to pass undamaged through the digestive tract of herring; Antsulevich and Valipakka 2000), which require bottom water temperatures of approx. 10°C to initiate the development (Colton 1985), has undoubtedly assisted rapid range expansion, possibly by survival during ballast water transport. *Penilia avirostris* also differs from other marine cladocera in that it consumes nanoplankton, such as bacterivorous flagellates, ranging in size from 2.5 μm to 100 μm (Katechakis et al. 2004), and thus occupies a different niche (Aertebjerg et al. 2003).

Methods

The Continuous Plankton Recorder (CPR) survey has extensive spatio-temporal coverage of the North Sea (51°N–60°N, 2°W–12°E), spanning over 40 years and over 36,000 samples. The CPR survey provides a unique long-term dataset of plankton abundance in the North Atlantic and North Sea, using 'ships of opportunity' on regular routes to tow the CPR at about 10 m depth. Each sample represents 18 km of tow and approximately 3 m^3 of filtered seawater (John et al. 2002), with a mesh size of 270 μm. Sampling from the Helgoland Roads study area (approximately 54°N 7°E) was conducted using a ring trawl device on an oblique haul, with a mesh size of 500μm, with the plankton samples preserved in formalin (Greve et al. 2004).

Results

The earliest record for *P. avirostris* in the North Sea was in 1947, found by Ministry of Agriculture Fisheries and Food fishery vessels (Cattley and Harding 1949), this was followed by nearly a 50 year absence until October 1990, when the species was recorded in the Helgoland Roads area (Table 1). *Penilia avirostris* is typically recorded in the CPR survey in waters south of the Bay of

Table 1 Monthly mean abundance of *Penilia avirostris* at Helgoland Roads (54°11′18″N 7°54 E)

	1990	1993	1994	1998	1999	2001	2002	2003	2004
January	0	0	0	0	0	0	0	0	0
February	0	0	0	0	0	0	0	0	0
March	0	0	0	0	0	0	0	0	0
April	0	0	0	0	0	0	0	0	0
May	0	0	0	0	0	0	0	0	0
June	0	0	0	0	0	0	0	0	0
July	0	0	0	0	0	0	0	0	1.15
August	0	0	0	0	0	0	0	0.33	3176.4
September	0	0	0	0	9.15	1.25	0.36	1.00	83.67
October	0.60	0.31	2.55	0.80	272.00	55.60	6.50	22.75	16.17
November	0	0	0.26	0	20.58	9.60	0.75	0.40	2.76
December	0	0	0	0	0	2.67	0.18	0	0

Biscay, in the late autumn months, with a large abundance found in Spanish and Portuguese coastal waters. Previous to the 1990s appearances, the species was found further north in the southern region of the Celtic Sea in 1983. During the 1990s *P. avirostris* has occurred on a few occasions in the North Sea; during September and October in 1994, 1995, and 1997, but then in much greater abundance post-1999. Figure 2 shows the CPR samples in the North Sea that *P. avirostris* have been recorded on, from 1960 to 2003. It is apparent from Fig. 2 that the species has been more frequently recorded in 2002–2003 than in previous years.

Discussion

The question of how *P. avirostris* appeared initially in the North Sea is debatable. Hydroclimatic changes during the 1990s have undoubtedly assisted in the rapid expansion of *P. avirostris*, particularly raised SSTs in the North Sea (Becker and Pauly 1996). The well documented rise in SST and the increased incursion of oceanic water has led to large scale changes in the plankton community of the North Sea. It is interesting to note that *P. avirostris* was found in the southern North Sea in 1990 (Helgoland Roads time-series), the same time as an exceptionally large pulse of warm high salinity water entered the North Sea (Lindley et al. 1990; Edwards et al. 1999). Another large pulse of warm high salinity water also entered the North Sea during 1997/1998. This event signalled the arrival of warmer, more saline waters from further south in the Atlantic with salinity values approaching the highest ever observed this century and a high sea-surface temperature anomaly. The species is known to require specific temperatures to proliferate and the autumnal months of 1999, 2002 and 2003 have been exceptionally warm, allowing rapid expansion of *P. avirostris* . Sea surface temperatures in September 1999 were 2–4°C above the long-term mean (ICES 2000) and bottom temperatures exceeded 19°C. Other studies recorded *P. avirostris* in large numbers in 1998 and 1999, in the Helgoland Roads area (over 1,000 individuals m^{-3} in October 1999), and in Norwegian waters (Båmstedt et al. 1998). In 2000 and 2001, when SSTs were lower, abundance also fell, and it was recorded infrequently in the North Sea (absent from the Helgoland Roads area in 2000, Table 1) in the CPR survey and other surveys (Aertebjerg et al. 2003). Data from the CPR survey for 2002 indicate that *P. avirostris* had appeared further north, west of the Orkney Isles, and in greater abundance than previously recorded, in conjunction with an increase in sea surface temperatures (over 3°C, Bundesamt für Seeschifffahrt und Hydrographie, Germany) during autumn months. Work by Aertebjerg et al. (2003) also noted an increase in *P. avirostris* in 2002, in the Kattegat, where the species was the dominant mesozooplankter in the autumn months. Other cladocerans recorded in the CPR survey, *Podon* spp. and *Evadne* spp., have not responded as *P. avirostris*, with both

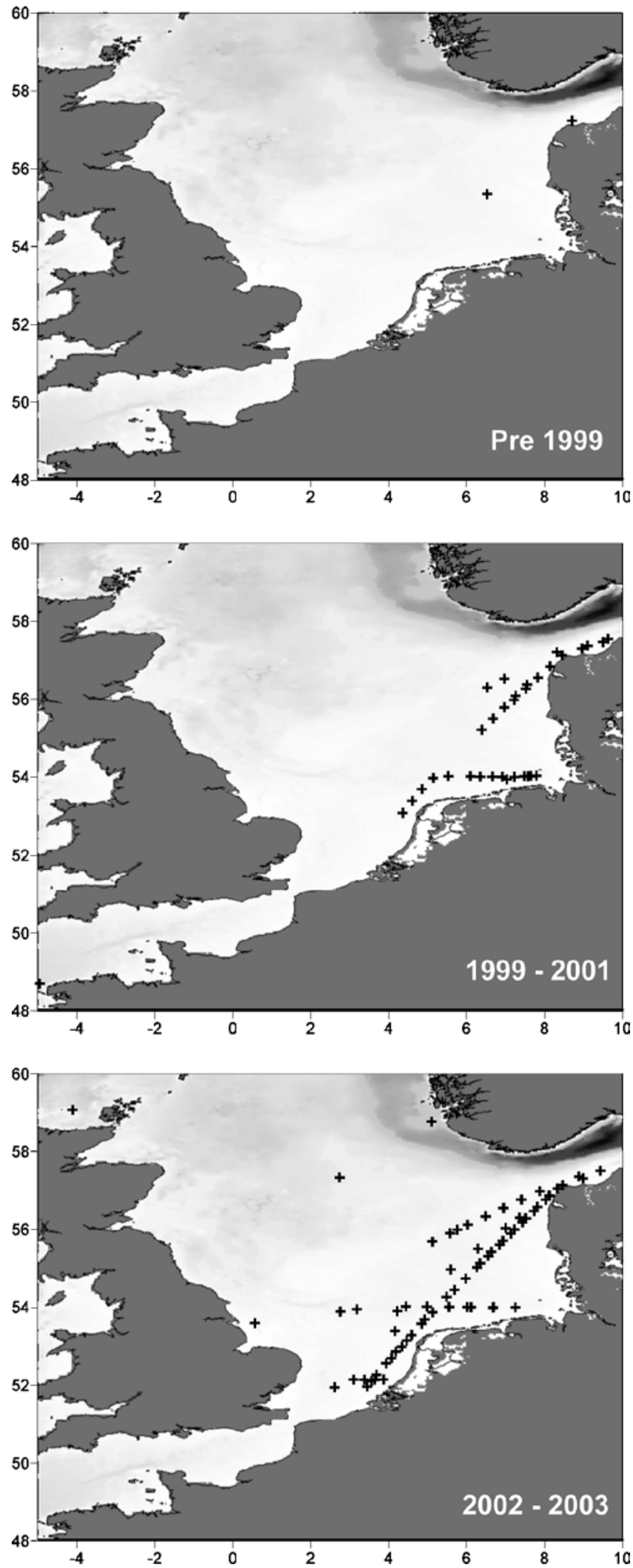

Fig. 2 Map of *Penilia avirostris* distribution from the CPR survey, marked with years

genera remaining highly variable throughout the last 40 years (data not shown).

The above results could suggest that *P. avirostris* has shifted northwards in its distribution in response to increased SSTs. The appearance of *P. avirostris* in the 1990s appears to have heralded the successful colonisation of the North Sea by the species, with a peak in abundance in 1999 and subsequently in 2003 (with a further increase in abundance in 2004 in the Helgoland Roads survey, Table 1), whereas previous occurrences do not appear to have established a viable population. The data for 2003 suggests an ongoing expansion of the species' distribution, with an appearance further north than previously recorded. The continued success of *P. avirostris* is likely due to the high temperatures of the North Sea during recent years, particularly autumnal SST.

Anthropogenic introduction is also a possible vector of the species, although determining whether the species was anthropogenically introduced via ballast water transport, or has shifted northwards as a response to changes in SST, would be difficult. Genetic studies of molecular markers are able to localize the point of origin of an invading species and genetic analysis of cladoceran lineages have been carried out (Herbert and Cristescu 2002), the results of which show that the pace of modern 'invasions' are nearly 50,000 times higher than historical levels. The North Sea has some of the busiest shipping lanes in the world—in 1996 alone approximately 270,000 ships entered the North Sea and English Channel area (QSR 2000). This volume of traffic, much of it international in origin or destination, has increased the potential for transport of non-indigenous marine organisms in ballast water. Successful invasions by non-indigenous phytoplankton species include *Odontella sinensis* (1908) and *Coscinodiscus wailesii* (1977) into the North Sea (Nehring 1998; Edwards et al. 2001a), both of which have established themselves successfully into the phytoplankton community and are recorded regularly in the CPR survey. The introduction of zooplankton into the North Sea by ballast water is not so apparent, although work by Gollasch et al. (2000) has shown that not only can certain zooplanktonic organisms survive transport, but actually flourish in ballast water. Accidental zooplankton introductions have occurred in the Baltic, approximately 100 non-indigenous species have been recorded, although less than 70 species have established reproducing populations (Leppakoski et al. 2002), the most likely vector for invasion has been ballast water (in conjunction with tank sediment), with 38 of the species from transoceanic origin (half of which survived transport across the Atlantic). It is fortuitous that *P. avirostris* does not appear to be detrimental to the plankton ecosystem, particularly populations of other cladocera (by occupying another ecological niche by feeding on nanoplankton), and may even provide a food source for higher trophic levels, such as *Cercopagis pengoi* and *Bosmina coregoni* in the Baltic, which are the main prey of herring and other planktivorous fish species during the latter part of the year (Antsulevich and Valipakka 2000).

The presence of *P. avirostris* in increasing numbers and wider distribution in the North Sea points towards a significant change in the aquatic ecosystem, and is a clear response to changes by a species that can exploit ideal conditions very rapidly. Results for 2003 have suggested the pattern of advance is continuing, with unprecedented numbers of the species being recorded in the southern North Sea. The noted shift in the phytoplankton community (Edwards et al. 2001b) towards a dominance of dinoflagellates and naked flagellates could be an additional benefit to the species, with its main food source being nanoplankton such as flagellates. How the species arrived initially in the North Sea is open to debate, with a northwards shift in response to increased SSTs and anthropogenic introduction via ballast water both possible. Irrespective of this, the continuing increase in SSTs will see the further spread and increase in abundance of the species, defining the species as indicative of climate change.

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