

Recent invasion of the foraminifer *Nonionella stella* Cushman & Moyer, 1930 in northern European waters: evidence from the Skagerrak and its fjords

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Abstract: The eastern Pacific benthic foraminifer *Nonionella stella* Cushman & Moyer, 1930 was recorded for the first time in the Skagerrak (North Sea) and its fjords. In this short note we evaluate its migration, considering both dispersal by propagules and ship ballast tanks. We suggest that the predominantly southward surface currents along the western European seaboard and Morocco would impede a wide-range dispersal of *N. stella* propagules and hypothesize transportation by ship ballast tanks as the possible vector of *N. stella* immigration into northern European seas.

Keywords: biological invasions; protozoans; environmental change; benthic foraminifera; propagules

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The species inventory of Recent benthic foraminifera is considered rather static in most areas. The foraminiferal assemblage composition and population density is governed by abiotic and biotic environmental factors. In particular, seasonal fluctuations of food supply, oxygen, water turbulence and substrate properties have been reported to influence variability in species' abundances (Murray 2006). However, marginal seas and Nordic fjords with sluggish circulation have recorded pervasive faunal changes. The elimination of established faunal elements and immigration of other foraminiferal species has been recognized over the course of multi-annual to decadal variability of thermohaline water column structure or severe hypoxic events (e.g. Schönfeld & Numberger 2007; Nikulina *et al.* 2008). Recently, the propagule concept has been proposed, suggesting that gamonts of numerous species are resting in surface sediments worldwide, which represent a so-called 'propagule bank' (Alve 1999; Alve & Goldstein 2003). Propagules start to grow and reproduce when exposed to appropriate environmental conditions and may be transported passively by currents (Goldstein & Alve 2011). This concept has been used to explain the uniformity of abyssal benthic foraminiferal assemblages (Pawlowski *et al.* 2007), whereas the relevance of propagules for the dispersal of subtidal to shelf species is not sufficiently constrained to date. In addition, the introduction of alien species by ships' ballast water, sediment in ballast tanks, anchor mud, hull fouling or commercial aquaculture has been suggested as explanations for new faunal elements breaching wide biogeographical barriers (Teeter 1973; Williams *et al.* 1988; Carlton & Geller 1993; McGann & Sloan 1996; McGann *et al.* 2000; Calvo-Marcilese & Langer 2010; Schweizer *et al.* 2011).

The Skagerrak–Kattegat area hosts the highest number of introduced non-indigenous biological species recorded in Nordic waters (Weidema 2000). Some of the most extreme examples are the Pacific oyster *Crassostrea gigas*, introduced in the 1970s (e.g. Wrangé *et al.* 2010); the Japanese seaweed *Sargassum muticum* first recorded in 1984 (Christensen 1984); and the eastern American comb jelly *Mnemiopsis leidyi* first recorded in 2006 (e.g. Boersma *et al.* 2007; Jaspers *et al.* 2015). The first two were

introduced with aquaculture (Weidema 2000), whereas the latter may have been transported both in ship ballast tanks and by coastal currents (Faasse & Bayha 2006; Oliveira 2007). Another example is a diatom *Coscinodiscus wailesii*, which was introduced either with ballast waters or through oyster import in 1977 (Reise *et al.* 1999) and became a significant member of the northeastern Atlantic diatom community (Edwards *et al.* 2001).

To date there is a substantial lack of data on invasive protozoan species (Weidema 2000; Pettay *et al.* 2015), despite their documented high abundance in ship ballast tanks (Galil & Hülsmann 1997). In the present short note, we provide new data on the introduction of the eastern Pacific foraminifer *Nonionella stella* Cushman & Moyer, 1930 into the northeastern Atlantic, and evaluate the species' migration considering propagule dispersal and marine traffic.

Material and methods

The present study comprises faunal data from surface sediment samples from the Skagerrak–Kattegat and adjacent fjords taken by the authors (Appendix B) as well as a data compilation from literature and web-based resources (Fig. 1). The samples SK3 and OVS300714-7A were retrieved from Alsbäck Deep, Gullmar fjord (Fig. 1), with a Bowers & Connolly Maxicorer (8 tubes; 98 mm Ø) in August 2013 and with a Mini Muc K/MT 410 (4 tubes; 100 mm Ø) in July 2014. In 2013, the surficial sediment from the 0–1 cm level was taken, preserved in a 2 g l⁻¹ rose Bengal-ethanol solution for 8 days, and washed through 125 and 2000 µm sieves. The 125–2000 µm residue was examined wet for well-stained (living) benthic foraminifera. In 2014, the 0–3 cm sediment was taken and immediately washed with seawater through 125 and 2000 µm sieves. The 125–2000 µm residue of one core was stained in a rose Bengal-ethanol solution, washed after two months with tap water to remove the excess dye, and wet picked for well-stained foraminifera by using a Duffield–Bogorov tray (Duffield & Alve 2014). A short core (St. 10A) and a surface (0–1 cm) sample (D14-30F) were taken south of the Skagerrak–Kattegat front and

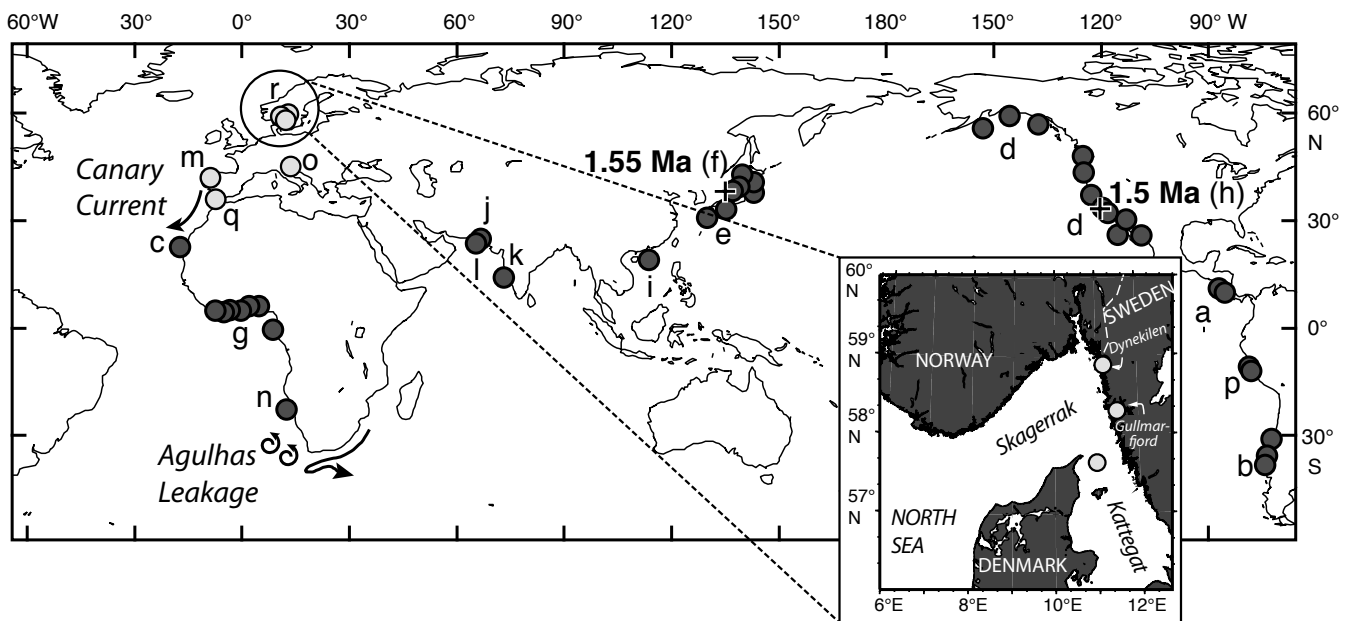


Fig. 1. Occurrence pattern of Recent *Nonionella stella* (dark grey circles), first appearances (crosses) and new findings in the northeastern Atlantic and adjacent seas (light grey circles). Compiled after (a) Bandy & Arnal (1957), (b) Ingle *et al.* (1980), (c) Lutze (1980), (d) Culver & Buzas (1985, 1986), (e) Oki (1989), (f) Kato (1992), (g) Schiebel (1992), (h) McDougall & Lagoe (1993), (i) Kuhnt *et al.* (1999), (j) Maas (2000), (k) Mazumder *et al.* (2003), (l) Erbacher & Nelskamp (2006), (m) Diz & Francés (2008), (n) Leiter (2008 unpublished), (o) Sabbatini *et al.* (2010), (p) Mallon (2012 unpublished), (q) Mendes *et al.* (2012), and (r) this study.

in the Dynekilen Fjord (Fig. 1; Appendix A) in June 2013 and September 2014, respectively, by using a Gemini corer (2 tubes, 80 mm Ø). The D14-30F sample was freeze-dried, washed over 63 and 1000 µm sieves and dry picked for total foraminiferal faunas. The core St. 10A was sliced in 1 cm intervals down to 10 cm, preserved and stained with a rose Bengal-ethanol solution for 2 weeks, washed over 63 and 1000 µm sieves, and dry picked for living (stained) foraminifera. The variety of methods used primarily reflects the different study purposes: teaching (SK3, D14-30F), collection for physiological experiments (OVS300714-7A) and a microhabitat study (St. 10A).

Study material is stored at the University of Gothenburg (G113-091; st.10A; D14-30F) and at GEOMAR, Kiel (SK3; OVS300714-7A).

Nonionella stella occurrence in northern Europe

Nonionella stella was discovered in the living fauna >125 µm fraction in surface sediment samples SK3 and OVS300714-7A from Alsbäck Deep, Gullmar Fjord, in August 2013 and July 2014. Furthermore, we found abundant living *N. stella* in the >63 µm fraction of surface sediments from the Skagerrak–Kattegat front area sampled in June 2013. Living specimens were recorded down to 10 cm in the sediment (Appendix A). In addition, in September 2014 *N. stella* was discovered as a dominant species (11%) of the total foraminiferal fauna >63 µm in surface samples from Dynekilen Fjord at 37 m water depth. All specimens were bright green and included younger individuals (Pl. 1, figs 9–10). The ecological parameters (sediment type, temperature, salinity and oxygen concentration) at which *N. stella* occurred at all three locations are given in Appendix B.

Recent geographical distribution and ecology

Nonionella stella is a free-living, calcareous, thin-walled and shallow infaunal foraminiferal species common in the oxygen minimum zones of the eastern Pacific since the early Pleistocene (Bandy & Arnal 1957; Phleger 1964; Bandy *et al.* 1965; Ingle *et al.* 1980;

Resig 1990; Kato 1992; Bernhard & Bowser 1999; Murray 2006; Mallon, J. 2012, unpublished PhD Dissertation, Christian-Albrechts-Universität zu Kiel. <http://d-nb.info/1020284048/34>). The species occurs from mid-shelf to bathyal depths and is particularly frequent in anoxic basins off California. Despite its relatively high respiration rates (Geslin *et al.* 2011), *Nonionella stella* usually lives in 0–2 cm sediment depth in dysoxic to anoxic (0–15 µmol l⁻¹ O₂) microhabitats (Bernhard *et al.* 1997, 2000). The species stores high amounts of nitrate in the cytoplasm to be used as the final electron acceptor under anoxic conditions (Risgaard-Petersen *et al.* 2006). It is also known to sequester chloroplasts from diatoms (Grzymski *et al.* 2002) and uses these plastids for denitrification (Bernhard *et al.* 2012).

Though oxygen minimum zones also exist in the Atlantic Ocean, they usually do not reach anoxic conditions (Stramma *et al.* 2010). Indeed, there are only three records of living *Nonionella stella*: from the Namibian Shelf (Leiter, C., 2008, unpublished Dissertation Ludwig-Maximilians-Universität München. edoc.ub.uni-muenchen.de/9551/1/Leiter_Carola.pdf), the Gulf of Guinea (Schiebel 1992) and the NW African shelf off Cape Barbas (Lutze 1980). In the western tropical, northwestern and northeastern Atlantic this species is almost absent. This has been proven by our own studies and an extensive literature survey including material collected in the northeastern Atlantic during 1913–2004 (Schönfeld 1997, 2002; Murray 2006, online appendix; Dorst & Schönfeld 2013 and references therein). There are, however, two recent records of *Nonionella stella* from the Iberian seas deserving attention. Firstly, in 1997–98 the species was recognized in surface sediments from Ria de Vigo (Diz & Francés 2008). *Nonionella stella* occurs there at water depths of >30 m and shows a patchy distribution with high abundances in September under upwelling conditions. The other record is from the outer shelf in the northern part of the Gulf of Cadiz where the species dwells with variable proportions in sandy muds at 50–100 m water depths (Mendes *et al.* 2012). Again, it occurs in patches with occasionally high abundances under temporary upwelling. In both Ria de Vigo and the Gulf of Cadiz, this species was not recorded in earlier studies of Recent foraminifera (Colom 1952; Van Voorthuysen 1973; Ubaldo & Otero 1978; Levy *et al.* 1995; Schönfeld 2002).

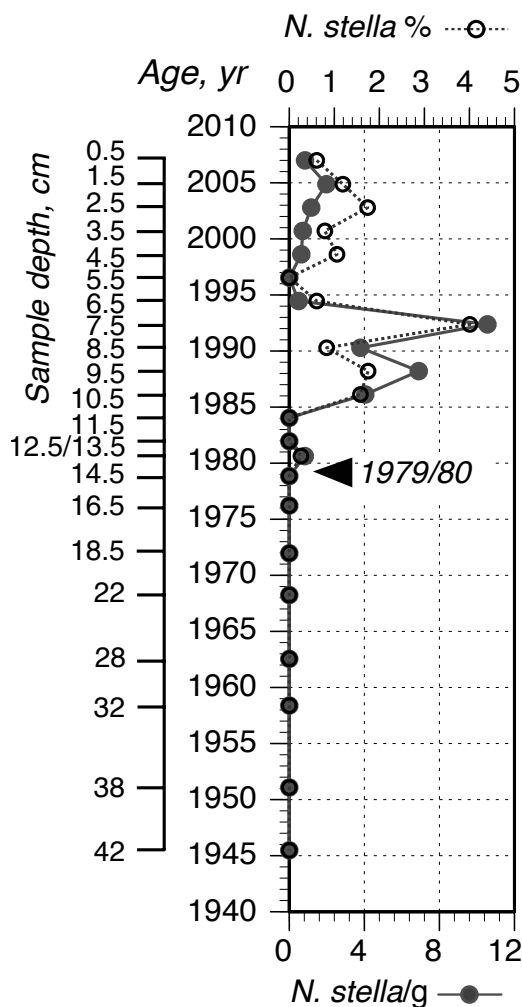


Fig. 2. Downcore abundance of *Nonionella stella* and the chronology for core G113-091 from Gullmar Fjord (Polovodova Asteman & Nordberg 2013). The age model is based on sediment accumulation rates obtained by ^{210}Pb for the core GA113-2Aa from the same location (Filipsson & Nordberg 2004). The black triangle is a relative age marker, which represents a decline in foraminiferal species common for the Skagerrak–Kattegat area (aka *S–K fauna*) and an increase in *Stainforthia fusiformis*, both dated to *c.* 1979/80 (Nordberg *et al.* 2000).

Furthermore, *N. stella* was first recorded in the northern Adriatic Sea in 2006 (Sabbatini *et al.* 2010), but was not found there in extensive foraminiferal distribution studies until 1991 (Daniels 1970; Jorissen 1988; Cimerman & Langer 1991).

Nonionella stella has not been reported from either Gullmar Fjord, Dynekilen or the Skagerrak before. However, there was an earlier record documented by a scanning electron microscope image of a specimen from Gullmar Fjord identified as '*Nonionella turgida*' by Gustafsson & Nordberg (2001, pl. 1, fig. 4). The morphology of the specimen is clearly distinguishable from that of *N. turgida* Williamson, 1858 (see discussion below). The specimen was collected at their site G116 close to Alsbäck Deep in Gullmar Fjord between August 1993 and December 1994. Similar *Nonionella* morphotypes were not reported by Höglund (1947), who studied surface samples from Gullmar Fjord taken in 1927. It is conceivable that *Nonionella stella* immigrated to the area between the late 1920s and early 1990s. We therefore re-examined samples from core G113-091, which was taken near Alsbäck Deep in 2009 (Polovodova Asteman & Nordberg 2013), and has an age model based on ^{210}Pb -dated sedimentation rates and relative age markers established for core GA113-2Aa from the same location (Filipsson & Nordberg 2004). *Nonionella stella* appears for the first time in

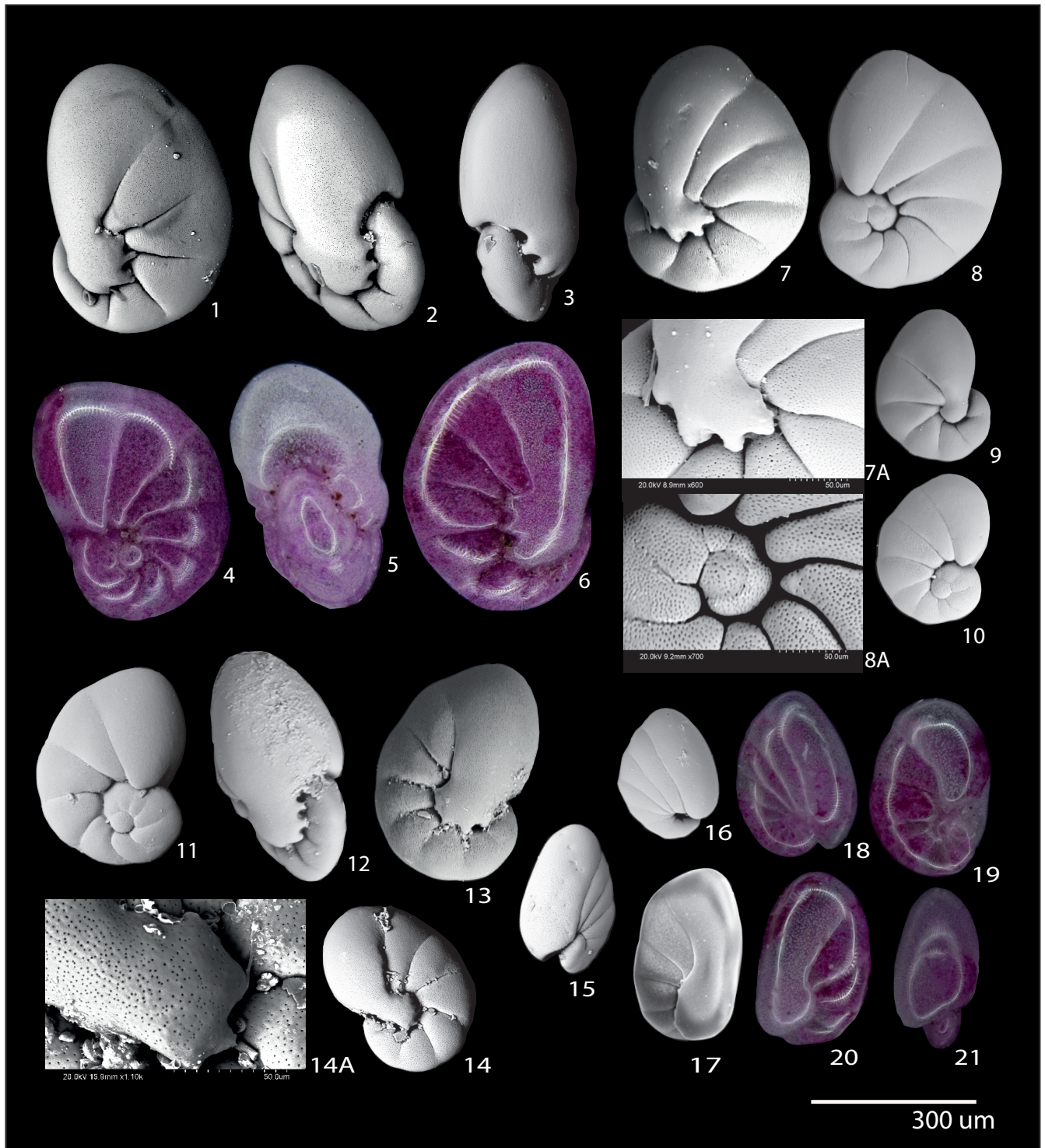
sample 10–11 cm, corresponding to *c.* 1985 and is present in higher abundances between *c.* 1985 and 1995 (Fig. 2). The first occurrence seems to follow after a severe hypoxic event ($<44\ \mu\text{mol l}^{-1}\ \text{O}_2$) in 1984, and the highest abundances co-occur with the following episodes of severe hypoxia in the winters of 1987–88, 1988–89, 1990–91 and 1994–95 (Filipsson & Nordberg 2004).

Transient advance to European waters during the late Holocene

There is also evidence for a late Holocene appearance of *N. stella* off western Iberia (Martins *et al.* 2006, 2007). Both papers refer to a sediment core from the Galician mud deposit, which goes back to 4.8 ka. However, in their dataset these authors lump together three *Nonionella* species, which with absent census data make it difficult to estimate true *N. stella* abundances. *Nonionella stella* is mentioned to co-occur with *N. turgida* and both were slightly more abundant during *c.* 2200–1200 years BP. In an earlier paper, Martins & Gomes (2004) mention the occurrence of this species in three other cores from the Galicia and northern Portuguese margin. They explicitly say that *N. stella* occurs only in fossil assemblages with abundances of less than 11% in the $>63\ \mu\text{m}$ fraction. Surprisingly, less than 300 km further south, Bartels-Jónsdóttir *et al.* (2006a, b) did not record *N. stella* in a core from very similar sedimentary environments of the Tagus Prodelta covering the last 2.2 ka, nor did they recognize the species in the living fauna from surface samples taken in April 2002. Unless more detailed information is available, it appears likely that *N. stella* immigrated to the western Iberian margin during the mid- to late Holocene, disappearing again between 200 and 750 AD, during the Dark Ages, when climatic conditions were colder than today. The earlier, Holocene invasion could be facilitated or at least promoted by an episodically, narrow, warm, northward Iberian Poleward Current, which extends to 400 m depth and may even reach the southern Bay of Biscay in autumn and winter (Haynes & Barton 1990; Garcia-Soto *et al.* 2002). Today, autumn is not the time of high primary production, food flux to the seafloor and subsequent reproduction of opportunistic benthic foraminiferal species off western Iberia. The Iberian Poleward Current and its southern tributaries may once have been a persistent, perennial phenomenon under different climatic conditions in the past (e.g. Mojtahid *et al.* 2013), and a proliferation of *N. stella* propagules may have been possible north up to the Bay of Biscay.

Taxonomy and morphology

Discerning *Nonionella stella* from the often co-occurring *Nonionella turgida* has proven difficult. We strictly followed J.A. Cushman's definition and determined only those specimens as *N. stella* (Pl. 1, figs 1–14) that exhibited a hand-shaped, lobate extension of the final chamber covering the umbilicus with clearly developed finger-like processes over the sutures (Cushman & Moyer 1930). In *N. turgida*, the extension is straight, often parallel to a previous chamber (Pl. 1, figs 16, 18) or rounded and drop-shaped (Pl. 1, figs 17, 20). Furthermore, the largest specimens of *N. turgida* are about half the size of *N. stella* in our samples, and the coloration of rose Bengal-stained specimens is light rose in *N. stella* and dark ruby-red in *N. turgida*. The California form of *N. stella* has a more rounded test with fewer and broader chambers (Cushman 1939, pl. 9, fig. 10; Bernhard & Bowser 1999, fig. 1A), whereas in our samples most *N. stella* are slightly elongated (Pl. 1). Cushman (1939) also illustrated specimens as *N. turgida* characterized by a big drop-shaped extension of the last chamber with voids between less developed fingers (see Cushman 1939, pl. 9, figs 2–3). This might have caused the confusion in the literature about the species concept of *N. stella*. Furthermore, the distinction from another closely related species, *Nonionella pulchella* Hada, 1931, should be noted. *N. pulchella* has far more chambers in the last whorl than *N. stella*, and the test is



Explanation of Plate 1. **figs 1–14.** Scanning electronic microscope (SEM) images and light micrographs of *Nonionella stella*: **1–3**, SEM of *N. stella* from surface sediments (0–3 cm) in Gullmar Fjord on the Swedish west coast (location G113); **4–6**, micrographs of *N. stella* from Gullmar Fjord (location OVS300714-7A); **7–8**, *N. stella* from Dynekilen Fjord (location D14-30F) (**7A**, enlargement of the umbilical area covered by finger-shaped processes shown in **7**; **8A**, enlargement of the spiral side shown in **8**); **9–10**, young individuals of *N. stella* from Dynekilen Fjord, identified as *Nonionella* sp., **11–14**, living (stained) *N. stella* from Skagerrak–Kattegat front (location St. 10D, 0–1 cm) (**14A**, enlargement of the umbilical area showing numerous diatom frustules concentrated around the umbilicus). **figs 15–21.** SEM images and light micrographs of *Nonionella turgida*: **15–17**, *N. turgida* from Skagerrak–Kattegat front (location St. 10D, 0–1 cm); **18–21**, *N. turgida* from Gullmar Fjord (location OVS300714-7A).

more compressed than in the latter species. In *N. pulchella* (Cushman 1939, pl. 9, fig. 11) the sutures on the umbilical side are curved while they are straight in *N. stella*. The umbilical extension of the last chamber is bow-shaped and thin in *N. pulchella*, whereas it is straight and somewhat inflated in *N. stella*.

We argue that only an integrative view that considers morphology, size and staining pattern accurately identifies the species unless genetic analyses of topotypic specimens and intergrade morphotypes from other areas are available, which would then establish other differential characters in morphology.

Constraints on the immigration to northern European waters

When *Nonionella stella* evolved in 1.55 Ma in the northern Pacific (Kato 1992), the Isthmus of Panama was already closed (Fig. 1). Dispersal to the sporadic occurrences in the eastern Atlantic Ocean would have been possible by propagules only through the Agulhas Leakage around the Cape of Good Hope. Indeed, *N. stella* has been recorded from the oxygen minimum zones of the northern Indian Ocean (Maas 2000; Mazumder *et al.* 2003; Erbacher & Nelskamp 2006) and has been recognized underneath the upwelling off Namibia (Leiter, 2008 unpublished). A further proliferation to the western African Margin and further north to the Iberian shelf could only be facilitated by northward subsurface and surface currents in the north-eastern Atlantic. An alternative route by the South Equatorial, Guyana, Caribbean Current and Gulf Stream seems unlikely because *N. stella* has never been found in the Caribbean (Murray 2006, online appendix). The predominant surface current direction along the western European seaboard and Morocco is southwards (Fig. 1: Canary Current). Unless a perennial Iberian Poleward Current prevails, this would largely impede a further northward dispersal of propagules. A closer look at the occurrences of *N. stella* off Iberia reveals, however, that they are all under the main shipping routes or, in the case of Ria de Vigo, directly under the Vigo Bay Anchorage. The same applies to the Skagerrak–Kattegat boundary, where intense shipping activity prevails. There are numerous examples of other invertebrates transported to the North Sea and Kattegat by ships' ballast tanks during the last century (Reise *et al.* 1999). We therefore hypothesize marine traffic and, in particular, ballast water and sediment as the possible vector of *N. stella* immigration into northern European seas and its recent, secondary introduction to the Iberian shelf and rias. The successful recruitment of *N. stella* is favoured by local environmental conditions, such as the seasonal upwelling off Iberia, high diatom production and thus chlorophyll availability at the Skagerrak–Kattegat front or periods of strong hypoxia in Gullmar Fjord. Most likely, local dispersal and interchange between Gullmar Fjord, Dynekilen and the Skagerrak is also effected by the propagules.

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Appendix A. Occurrence of living (stained) *Nonionella stella* in a sediment core from Station 10A at the Skagerrak–Kattegat front

Core depth (cm)	<i>Nonionella stella</i>			
	Counts	%	individuals/sample	Population density (individuals/10 cm ³)
0–1	39	11.6	439	21.8
1–2	190	53.7	3109	154.7
2–3	274	80.1	4110	204.5
3–4	180	54.4	579	28.8
4–5	152	46.9	152	7.6
5–6	195	46.1	195	9.7
6–7	48	—	48	2.4
7–8	17	—	17	0.8
8–9	4	—	4	0.2
9–10	3	—	3	0.1

For coordinates, water depth and ecological parameters see Appendix B.

Appendix B. Ecological parameters for habitats of *Nonionella stella* in northern Europe

	Dynekilen Fjord	Gullmar Fjord	Skagerrak–Kattegat front
Location	D14-30F	SK3/OVS300714-7A	Station 10A
Latitude	59.0015°N	58.3230°N	57.6828°N
Longitude	11.1951°E	11.5479°E	10.9675°E
Water depth (m)	37	117 and 120	31
Sampling date	September 2014	August 2013/July 2014	June 2013
Sediment type	mud	mud	sand
Oxygen (µmol l ⁻¹)	277	136/44	303.7
Temperature (°C)	4.9	6.1/7.0	8.6
Salinity (PSU)	30.8	34.9/34.0	33.6

Temperature, salinity and oxygen were measured in near-bottom waters at the moment of sampling.

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