

# Broad-scale patterns of abundance of non-indigenous soft-bottom invertebrates in Denmark

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Received: 27 July 2008 / Revised: 16 October 2008 / Accepted: 20 October 2008 / Published online: 11 November 2008  
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**Abstract** Quantifying the broad-scale distribution and abundance of non-indigenous species (NIS) is necessary to provide accurate estimations on impacts of invasions, to prioritize research, and to guide national management. Sediment grab-sampling is a standardized method for monitoring marine benthos. In Denmark, ~45,000 grab-samples were collected from 1970 to 2005. Using these samples, we compared densities of NIS and native species among 27 broad spatio-temporal groupings. Eight known NIS and one ‘cryptogenic species’ (the polychaete *Neanthes succinea*) were found in the samples. Most were present in low abundance, but the bivalve *Mya arenaria*, likely introduced by the vikings from North America, was particularly abundant. *M. arenaria* was found in ca. 20% of all samples and was among the 10 most common species in all of Denmark. *M. arenaria*’s high abundance, high filtration capacity and

importance in food-web interactions, suggest that this species has dramatically impacted shallow coastal ecosystems in Denmark. The polychaete *Marenzelleria viridis*, the gastropod *Potamopyrgus antipodarum* and *N. succinea* were also widespread and abundant, and they too are likely to have had broad-scale impacts. In conclusion, 28% of grab-samples collected in Denmark over 35 years were affected by some degree of NIS or cryptogenic species, suggesting that centuries of human-mediated transfer of organisms has had a profound impact on the ecology of soft-bottom systems in Denmark.

**Keywords** North Sea · Baltic Sea · Non-indigenous marine invertebrates · Large-scale distribution patterns

## Introduction

The introduction and invasion of non-indigenous species (NIS) is a serious threat to biodiversity conservation (Simberloff 2005). Well known examples of high-profile invaders include rabbits in Australia and Dutch elm disease and water hyacinth in Europe and North America (Lowe et al. 2000). Marine invasions are less well documented but may match terrestrial invasions in their extent and impacts. In marine systems, NIS are constantly moved around in ballast water, on ship hulls, and by aquaculture (Verling et al. 2005), and these vectors have relocated NIS to numerous new regions, potentially with large impacts on local ecosystems (e.g. the seastar *Asterias amurensis* Lutken 1871, or the oyster *Crassostrea gigas* Thunberg 1793, Ruiz et al. 1997; Lowe et al. 2000). Ecological impacts of invasions are often inferred by assuming that the more abundant and widespread a NIS is, the more severe is its impact (Parker

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Communicated by H.-D. Franke.

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et al. 1999). However, studies where distribution and abundance of NIS can be evaluated relative to native species, are typically only done at restricted spatio-temporal scales in areas known to be infested (e.g. Stæhr et al. 2000; Thomsen et al. 2006a, b; Thomsen et al. 2007b), potentially over-estimating the importance of the NIS over broader scales. Here, we argue that large-scale quantitative assemblage studies may be particularly useful to (a) scale-up experimental results from specific locations to larger regions, (b) evaluate and compare region-to-national level importance of different NIS, (c) identify general regions and habitats most threatened by NIS, (d) prioritize national management of widespread and abundant NIS, and (e) guide future research efforts by identifying which NIS should be studied and where.

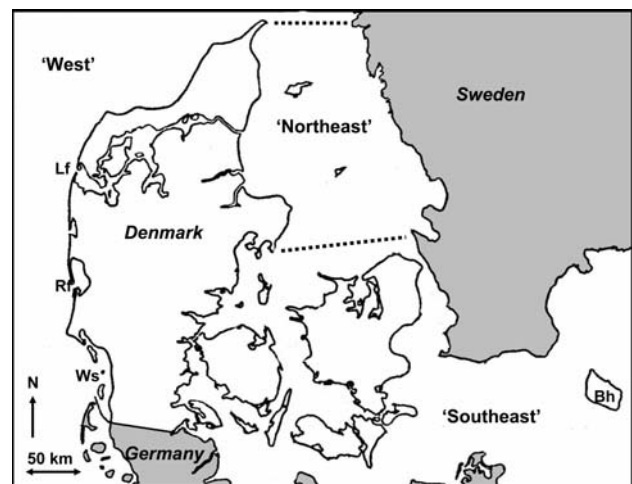
Explicitly targeting multiple NIS in broad-scale field surveys is expensive. Alternatively, NIS can be quantified from existing sampling programs where well-defined methodological practices are in place such that sampling is relatively standardized. ‘Grab-sampling’, where a device is lowered from a boat to collect a sample of a known area from the seafloor, is a prime example of such a sampling tool and grab-samples have been collected worldwide to quantify and compare assemblage structures of soft-bottom systems (Petersen 1924; Nybakken 1993). In Denmark, as part of a national monitoring program, soft-bottom invertebrate assemblages have been sampled regularly with grabs since 1970 (Josefson and Hansen 2004). Large effort has gone into identifying species and analyzing species lists with respect to anthropogenic pressures (eutrophication in particular, Conley et al. 2000; Josefson and Rasmussen 2000; Josefson and Hansen 2004). Marine invasions have however only recently caught the attention of managers and researchers in Denmark (Thomsen et al. 2007a), and these grab-samples provides a unique opportunity to assess the abundance of soft-bottom invertebrate NIS across broad temporal and spatial scales.

Management objectives in many marine systems aim at achieving near-pristine conditions. It is therefore important to document the extent to which marine systems are affected by NIS. A broad-scale perspective is critical because the ultimate management units are at the national and international levels. Our objective was to quantify the abundance of soft-bottom macro-benthic NIS in Denmark over long time scales (decades) and across broad geographic regions. Our expectation was that, like other temperate marine systems with a long human history (Lotze et al. 2006), Danish soft-bottom systems would be markedly affected even decades ago, but also that the steadily increasing NIS pressure would be visible in the record. The intention was also for this study to set the stage for similar analyses of grab-samples collected throughout the world for large-scale comparisons between and across biogeographical regions, seas and oceans.

## Materials and methods

### Study area and soft-bottom taxa

Denmark is located between the North and Baltic Seas (Fig. 1) where salinity decreases from 34 psu in the North Sea to ca. 8 psu around Bornholm. Secondary salinity gradients are also seen within most Danish estuaries. Only the Wadden Sea has any significant tidal influence (1–2 m). The taxonomic status of benthic invertebrate NIS in Danish waters was recently reviewed by Jensen and Knudsen (2005) and we use their lists as a template for what species to include or exclude as NIS. However, it should be noted that the polychaete *Neanthes succinea* Frey and Leuckart 1847 is considered a native species in Europe (Reise et al. 1999) but this species was observed for the first time in Danish waters only in the 1940s and has therefore been suggested to be introduced to Denmark from nearby European regions (Jensen and Knudsen 2005). Because its status as a NIS is uncertain, we included *N. succinea* as a ‘cryptogenic’ species with its own level of ‘origin’ (i.e. it was not included in pooled NIS abundance estimates). Clearly, this species needs biogeographical and molecular analysis before its origin can be concluded upon (cf. Reise et al. 1999 for similar discussion on the polychaete *Nereis virens* Sars 1835). Also, the taxonomy of *Marenzelleria* species (also polychaetes) is complex, and it is likely that multiple



**Fig. 1** Geographical regions. West = North Sea + Skagerrak + Wadden Sea (Ws) + western fjords (e.g. Ringkøbing Fjord = Rf) and Limfjorden (Lf, a sound connecting the western North Sea to eastern Kattegat). Northeast = Northeastern Kattegat + Swedish waters near Kullen and Goteborg. Southeast = Southeast of Aarhus + the Belts + Inner Baltic all the way to Bornholm (Bh). West is characterized by an ‘oceanic’ influence of high salinity (western fjords and sounds can have brackish conditions), Northeast by frequent fluctuations in salinity, from fully marine to brackish conditions (depending on wind direction, currents, precipitation patterns and runoff), and Southeast by relatively constant and low salinities

sibling species have invaded the North and Baltic Seas in several independent events (Blank et al. 2004). In the present paper we refer the Danish records to *M. viridis* Verrill 1973, but note that this may represent a conglomerate of several morphologically and taxonomically very similar species.

Data collection

Grab-samples of sediments were collected by the Danish counties and The National Environmental Research Institute. The total data-set included ca. 45,000 assemblage-level samples distributed around the Danish coastline (including samples collected in Northwestern Sweden) to a depth of 300 m and covering all major open and estuarine waters. The number of stations and samples varied from year to year (Table 1). Most samples were collected in summer months and all samples were standardized to unit area before data analysis (grab-sizes varied typically between 0.0085, 0.0123, 0.0143 or 0.1 m<sup>2</sup>, but not in any confounding

way across years, regions or depth). Grab-samples normally sampled the sediment to depth of ca. 20 cm. Sediments were sieved through a 1 mm mesh, and the residual preserved in 80% ethanol. Species were identified and counted in the laboratory to provide estimates of grab-densities (converted to individuals per m<sup>2</sup>). Densities were reported as both ‘absolute’ and ‘relative’ abundances, which focus on the individual NIS and on NIS in relation to the entire grab-assemblage across all samples (rank-ordered, with the most abundant species = number 1), respectively. In addition to calculating national averages, we also calculated abundances for 27 broad combinations of temporal (1970–1984, 1985–1994, 1995–2004), spatial (West = North Sea + Skagerrak + western fjords including Limfjorden, Northeast = Northeastern Kattegat + Swedish waters near Kullen and Goteborg, Southeast = Southeast of Aarhus + the Belts + Inner Baltic, see Fig. 1) and bathymetric (≤5, 5–20, >20 m) variability. No samples were collected from the deep West in 1970–1984 resulting in 26 final groupings (i.e. only 26 groupings are shown on figures

**Table 1** Number of grab-samples and species-specific dominance rankings (no. 1 = most abundant) of NIS compared to the entire assemblage within 26 spatio-temporal groupings (no rankings could be provided for groupings where the species was not recorded at all)

Period	Region	Depth	No. of samples	Bal	Cre	Ens	Mar	Mya	Nea	Pet	Pot
1970–1984	West	<5 m	411		118			8	16	35	
1970–1984	West	5–20 m	1,341		99			12	35	66	
1970–1984	Northeast	<5	43					22			
1970–1984	Northeast	5–20 m	165					64			
1970–1984	Northeast	>20 m	884					477			
1970–1984	Southeast	<5	640					20	87		4
1970–1984	Southeast	5–20 m	240					9	117		29
1970–1984	Southeast	>20 m	44					12			
1985–1994	West	<5	5,335	59	71	187	16	12	94	124	18
1985–1994	West	5–20 m	4,734		116	147		20	59	137	
1985–1994	West	>20 m	130					6			
1985–1994	Northeast	<5	156					17	38		10
1985–1994	Northeast	5–20 m	1,441					56	0		293
1985–1994	Northeast	>20 m	1,459					261	0		
1985–1994	Southeast	<5	3,048	45				2	39	134	6
1985–1994	Southeast	5–20 m	6,391	303				13	41	273	54
1985–1994	Southeast	>20 m	1,079				301	21	250		
1995–2004	West	<5	5,249	54	114	122	11	6	47	93	25
1995–2004	West	5–20 m	2,187	209	41	75		43	32	65	
1995–2004	West	>20 m	135			160	98	48			
1995–2004	Northeast	<5	106					15	30		64
1995–2004	Northeast	5–20 m	3,056		313			31	150		295
1995–2004	Northeast	>20 m	1,619					68	265		
1995–2004	Southeast	<5	1,985			125	58	3	14	0.74	25
										134	
1995–2004	Southeast	5–20 m	5,628	186		241	344	16	40		169
1995–2004	Southeast	>20 m	1,845			244		31	78		15

*Bal* balanus improvisus, *Cre* crepidula fornicata, *Ens* ensis americanus, *Mar* marenzellaria viridis, *Mya* mya arenaria, *Nea* neanthes succinea, *Pet* petricola pholadiformis, *Pot* potamopyrgus antipodarum

and tables). The database contained 1,543 taxa, including 422 taxa registered on taxonomic levels above the species level (e.g. Polychaete indet.).

## Results

Of the 1,121 species recorded eight were NIS and one cryptogenic (*N. succinea*), corresponding to <1% of the full species list. NIS and cryptogenic species accounted for 3.9% of all individuals, and at least one NIS or cryptogenic species was found in 28% of the samples. The tunicate *Styela clava* Herdman 1882 was only found in four samples (0.01 ind m<sup>-2</sup>, rank 964), and due to its low abundance and lifestyle (sessile hard-substratum species) its distribution was not analyzed further. Half of the NIS have been known from Danish waters for more than a century, the other half are more recent introductions (one of them being *S. clava*). These two groups are here classified as ‘old’ and ‘new’ NIS and represent a (somewhat arbitrary) point in time to separate species that have had long vs. short time to disperse in Danish waters.

Of the old NIS, the bivalve *Petricola pholadiformis* Lamarck 1818 and gastropod *Potamopyrgus antipodarum* Gray did not show any clear temporal trends (Figs. 2, 3). *P. pholadiformis* was found with an overall mean density of 0.7 ind. m<sup>-2</sup> and was rank no. 262 of all Danish soft-bottom invertebrates on the entire data-set. In 1970–1984 it was found in West (≤20 m), in 1985–1994 in West and Southeast (≤20 m) and in 1995–2004 again in West (≤20 m) and Southeast (≤5 m). This NIS had highest abundances in 1970–1984 in West (5–20 m) where it was ranked 66. *P. antipodarum* was much more common with an overall mean density of >40 ind. m<sup>-2</sup> and was ranked 24 overall. In 1970–1984 it was registered in Southeast (≤20 m), in 1985–1994 in West (≤5 m) and Northeast (≤20 m), and in 1995–2004 in both West (≤5 m), Northeast (at all depths) and Southeast (≤20 m). This species was particularly common in 1970–1984 and 1985–1994 in Southeast (≤5 m) where it was found with very high densities and was ranked respectively number 4 and 6, i.e. was amongst the 10 most abundant soft-bottom species. The third old NIS, the barnacle *Balanus improvisus* Darwin 1854, had a mean density of 2.3 ind. m<sup>-2</sup> with rank 152, but was only found in the last two time periods and with increasing abundances (Figs. 2, 3). In 1985–1994 it was found in West and Southeast (≤20 m) and in 1995–2004 in the same two regions (but only at 5–20 m in Southeast). This NIS was most common in 1985–1994 in West (≤5 m), where it was ranked 45. The last of the old NIS, the bivalve *Mya arenaria* Linnaeus 1758, was by far the most common of any NIS. *M. arenaria* was observed in all 26 spatio-temporal groupings, was found in 21% of all samples, with an

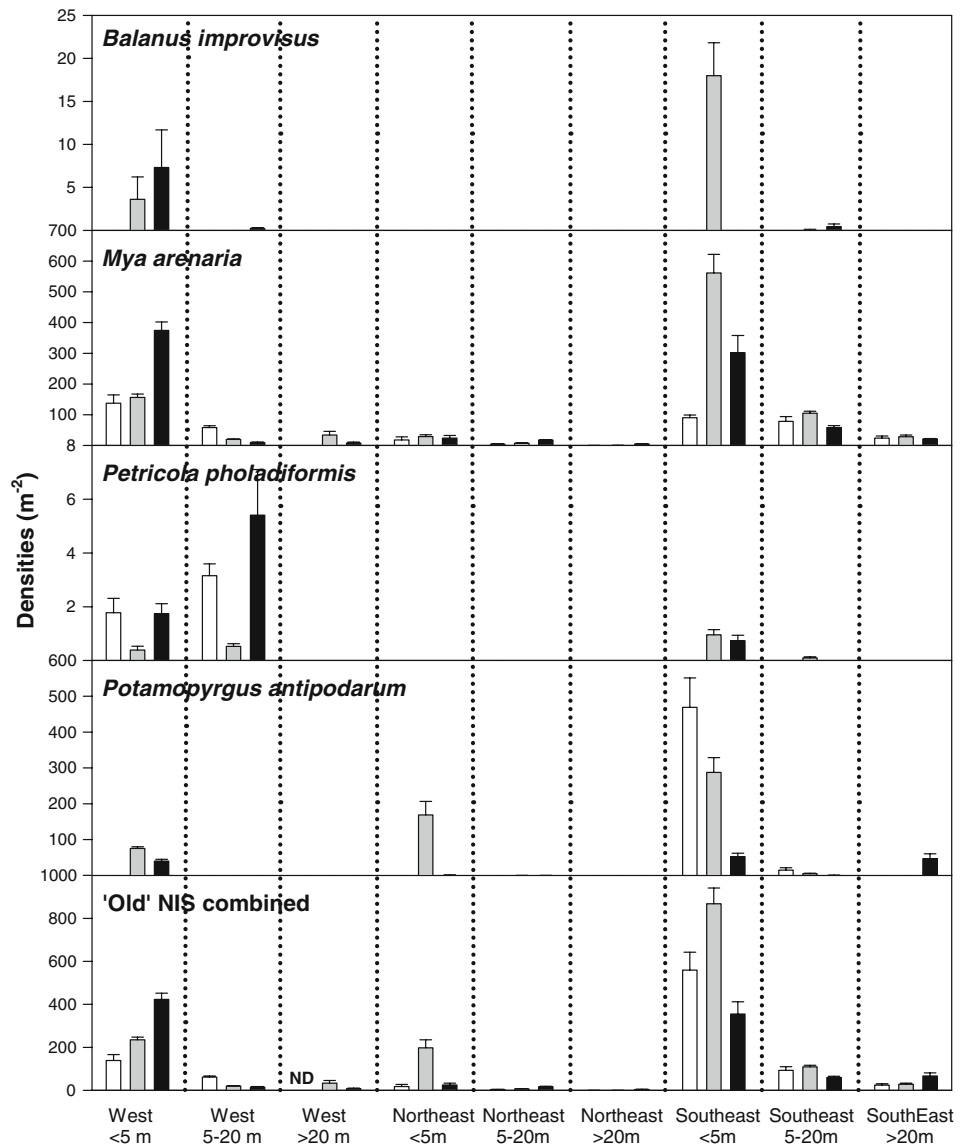
overall mean density of 131.5 ind. m<sup>-2</sup>. Overall, *M. arenaria* was the 9th most abundant soft-bottom invertebrates based on all 45,000 samples. *M. arenaria* was particularly abundant in shallower waters, and was the second most abundant species in Denmark in Southeast (≤5 m). The combined abundances of all old NIS showed variable temporal patterns; some depth strata and regions were increasingly impacted by NIS (e.g. Northeast >20 m), some groupings had highest impact in the mid-time interval (e.g. West >20 m), and a single grouping had decreasing impacts over time (West ≤20 m). These patterns were primarily driven by fluctuations in two highly abundant NIS, *M. arenaria* and *P. antipodarum*.

Of the new NIS the gastropod *Crepidula fornicata* Linnaeus 1758 was found in all three time periods, but without any clear temporal trends (Figs. 2, 3). *C. fornicata* had a mean density of 0.9 ind. m<sup>-2</sup> and was ranked 234. In 1970–1984 it was registered in West (≤20 m), in 1985–1994 in West (≤20 m) and in 1995–2004 in West (≤20 m) and Northeast (5–20 m). *C. fornicata* was most common in 1995–2004 in West (5–20 m) where it was ranked 41. The two other new NIS, the bivalve *Ensis americanus* Gould 1870 and *M. viridis*, were only found in the last two time periods, clearly with highest abundances in the last period (Figs. 2, 3). *E. americanus* had a mean density of 0.4 ind. m<sup>-2</sup> and was ranked 331. In 1985–1994 it was found in West (≤20 m) and in 1995–2004 in both West and Southeast (all depth). *E. americanus* was most common in 1995–2004, in West (5–20 m) being ranked 75. *M. viridis* had a mean density of 25.4 ind. m<sup>-2</sup> (rank 30). It was found in both time periods in both West (≤5; ≤5 and >20 m) and Southeast (>20 m; ≤20 m). *M. viridis* was most common in 1995–2004, in West ≤5 m with densities of 152.8 ind. m<sup>-2</sup> and was ranked 11. In contrast to the old NIS the new NIS, when added together, generally increased in abundances in most regions and depth intervals. This pattern was driven by all three invaders in West; *C. fornicata* at intermediate depth, *E. americanus* in intermediate and deep water, and *M. viridis* in shallow and deep water.

Finally, the cryptogenic *N. succinea*, was found in all three time periods with increasing abundances and in increasing number of regions and depth intervals (Figs. 2, 3). *N. succinea* had a density of 9.7 ind. m<sup>-2</sup> and was ranked 61. In 1970–1984 *N. succinea* was registered in West and Southeast (≤20 m), in 1985–1994 in West (≤20 m), Northeast (≤5 m) and Southeast (all depth) and in 1995–2004 in almost all regions and depths (except >20 m in West). *N. succinea* was most common in 1995–2004, particularly in Northeast ≤5 m where it was the 14th most common soft-bottom invertebrate (Fig. 3).

Summing old and new NIS demonstrated that the spatio-temporal groupings most impacted by NIS, with total NIS densities of >300 ind. m<sup>-2</sup>, were shallow water regions

**Fig. 2** Densities of ‘old’ NIS (>100 years in Danish waters, ±SE), for 26 broad spatio-temporal groupings (cf. Table 1). *White bars* correspond to 1970–1984 samples, *grey bars* to 1985–1994 samples and *black bars* to 1995–2004 samples. Note the different scales on Y-axis and that no samples were collected from >20 m at West in 1970–1984



from the West and Southeast. This pattern was primarily driven by high abundances of the two old and very abundant invaders, *M. arenaria* and *P. antipodarum* (Fig. 4).

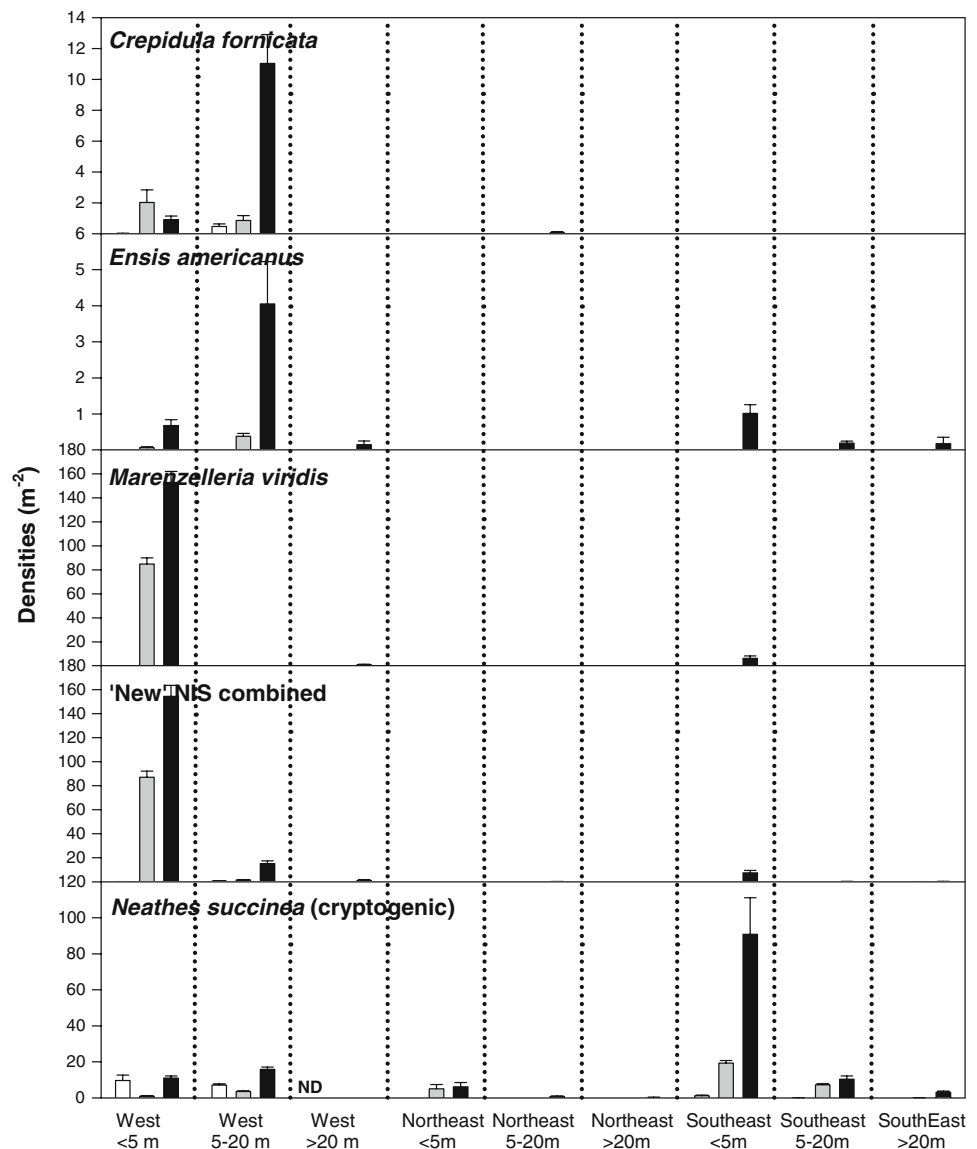
**Discussion**

We used a large dataset, collected using a relatively standardized sampling methodology, to quantify the abundance of marine benthic NIS in Danish soft-bottom systems. NIS were found in 28% of all samples, documenting the ubiquity of invader impacts in Danish soft-bottom systems. Shallow waters are particularly impacted with total NIS densities routinely reaching >300 ind. m<sup>-2</sup>, and one NIS, *M. arenaria*, was found in high abundance at all time intervals, depth, and geographical regions.

**General spatio-temporal patterns**

The distribution of benthos in Danish coastal waters varied between years, regions and depth intervals. Many key drivers could contribute to these patterns of distribution, including hydrodynamic conditions, nutrient input, water temperature, solar irradiance, salinity, sedimentation, sediment characteristics, hypoxia events and biotic interactions such as competition and predation (Conley et al. 2000; Josefson and Hansen 2004). Superimposed on this environmental variability are patterns relating to time of NIS introduction, and dispersal and colonization capability. Here, we did not attempt to relate temporal variation in abundances to environmental causes (work in progress), but taking the invasion history into account; our results suggest an increasing abundance, particular of the new NIS. Thus, the three new NIS and

**Fig. 3** Densities of ‘new’ NIS (<100 years in Danish waters,  $\pm$ SE) and cryptogenic species (*N. succinea*) for 26 broad spatio-temporal groupings (cf. Table 1). White bars correspond to 1970–1984 samples, grey bars to 1985–1994 samples and black bars to 1995–2004 samples. Note the different scales on Y-axis and that no samples were collected from >20 m at West in 1970–1984

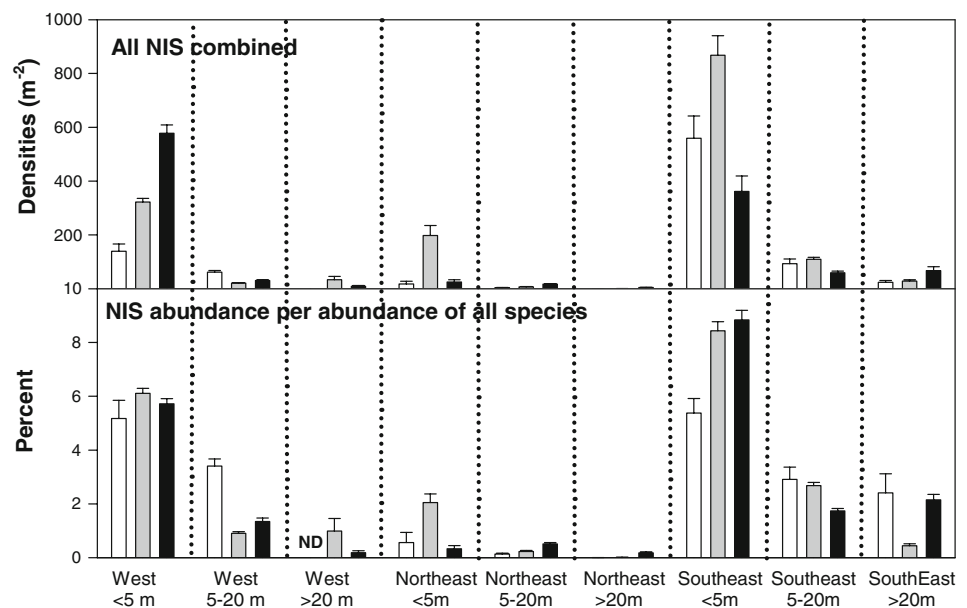


also the cryptogenic *N. succinea* appear to be spreading. This contrasts the old NIS which has had a long opportunity for secondary dispersal into suitable habitats throughout Denmark. Most of the new NIS are eurohaline and tolerant to sedimentation and anoxia (see later), and they will most likely continue their spread into other Danish estuaries and become even more abundant. Most NIS were found at shallow depths in West, suggesting that (a) this grouping is exposed to high propagule pressure (e.g. secondary introductions via the English Channel and the North Sea) (Lockwood et al. 2005), (b) that the declining salinity through the Northeast is a barrier to stenohaline marine organisms (e.g. *Crepidula fornicata*) (Leppakoski et al. 2002), and (c) that elevated wave disturbance and primary production in West create space and food for invaders (Mack and Antonio 1998).

#### Species-specific patterns

*Mya arenaria* has a remarkable invasion history. The species is of Pacific origin, but dispersed to Atlantic North America and Europe in the Miocene before becoming extinct in Europe, probably due to climatic changes (Strasser 1998). It was likely re-introduced from North America by the vikings ca. 1,000 years ago, potentially as a food source (Petersen et al. 1992; Strasser 1998; Behrends et al. 2005). *M. arenaria* is characterized by a large size, relatively fast growth rate, high burial capacity affecting sediment characteristics, high water filtration rates affecting water-column characteristics and by being an important food source for fish and birds (Hansen et al. 1996; Riisgard and Seerup 2003). The high abundances, wide distributions and ‘ecosystem engineering’ characteristics of *M. arenaria* (Palacios et al. 2000) suggest that this species has had a

**Fig. 4** Summarized densities of NIS for 26 spatio-temporal groupings (cf. Table 1,  $\pm$ SE). White bars correspond to 1970–1984 samples, grey bars to 1985–1994 samples and black bars to 1995–2004 samples



large impact on the present-day ecosystems not only in Denmark, but potentially throughout invaded locations in Europe. Another important NIS, *M. viridis*, is today, only 15 years after its first recording, abundant in several shallow fjords, with  $>140 \text{ ind. m}^{-2}$  at shallow depths in the West, a dramatic invasion as also observed in the Gulf of Riga (Cederwall et al. 1999) and other locations in the southern Baltic Sea (Bastrop and Blank 2006). Impacts in the Baltic include competition with native infauna and increased benthic chlorophyll levels, probably via excretion of waste products that facilitate growth of benthic diatoms (Kotta and Olafsson 2003; Neideman et al. 2003). The success of *Marenzelleria* species has been attributed to a high tolerance to low salinity, sedimentation, anoxia and nutrient enrichment (Blank et al. 2004). We expect the invasion to continue, as the polychaetes are given the opportunity to disperse to estuaries throughout Denmark. A third successful species, *N. succinea*, is cryptogenic, and is generally not considered introduced in Europe (Reise et al. 1999). *N. succinea* has increased dramatically in abundance and distribution since its first observation in Denmark in the 1940s (Jensen and Knudsen 2005). Still, historical, biogeographic and molecular analyses are needed to clarify why this conspicuous species was not observed in Denmark until the 1940s. If these analyses suggest a natural distribution in Denmark, alternative explanations are needed to explain its late first description and dramatic population expansion. Thus, natural range expansion from nearby regions could have co-occurred with climatic changes and eutrophication and thereby both facilitated new arrivals and increased ecological performance. For example, *N. succinea* is an eurohaline predator that is known to be resistant to hypoxia (Sagasti et al. 2000), important traits in eutrophic brackish

waters. We are not aware of any impact studies of *N. succinea*, but with an average density of  $>70 \text{ ind. m}^{-2}$  in shallow water, this species is likely an important trophic link between small consumers and top-predators such as fish. *P. antipodarum* is a freshwater and estuarine species in its native New Zealand. It is tolerant to environmental stressors such as ammonia pollution and anoxia (Alonso and Camargo 2003), making it robust to environmental conditions in Danish coastal ecosystems. Large impacts have been documented in invaded freshwater systems in Europe and North America, including competition with native snails, altering biogeochemical cycles and increasing secondary production (Hall et al. 2003, 2006). *P. antipodarum* is common at shallow depths in both the Southeast and West, where high abundances match the brackish conditions of the Southeast and estuaries and semi-enclosed lagoons in West. Given the high abundances at shallow depths and its known impacts on invaded freshwater systems, we expect this fast growing gastropod to have a major impact on secondary productivity and trophic transfers in Danish brackish waters.

#### Less common NIS and sampling bias

The data presented are not representative for all benthic NIS and have several types of potential bias. First, grab-samples can only be collected in soft-bottom systems, excluding boulder fields, rocky coasts and seagrass beds. In addition, grab-samples are difficult to collect in very shallow water (e.g.  $<1 \text{ m}$ ) and under stormy conditions. Grab-samples may also have different collection efficiencies for different sediment textures and in the presence of biogenic structures (e.g. reefs, large shells). Furthermore, fewer

samples have been collected from deep waters, the early sample period and the North West region. This implies that rare NIS are more likely to be missed from these groupings. Finally, and most importantly, highly mobile NIS (e.g. the decapod *Eriocheir sinensis* Milne-Edwards 1854) are often missed by the grab. For example, the abundance of *E. americanus*, introduced to the North Sea in the late 1970s (Jensen and Knudsen 2005), is probably substantially underestimated due to its capacity for fast and deep burial. It is relatively common in the West, and has recently been observed in the Southeast, indicating tolerance to low salinities and therefore a potential to inhabit most regions in Denmark. Its disjunct distribution (absent from the Northeast) may be attributed to a lack of dispersal rather than adverse environmental conditions. This, in turn, suggests that Southeast populations have bypassed the entrance to the Baltic Sea either via ballast water transport or via The Kiel Canal. *E. americanus* share several of the characteristics of *M. arenaria*; it can occur in high densities in the Wadden Sea, it is large and it has a high filtration capacity (Armonies and Reise 1998). It is therefore likely it will have considerable impacts on biogeochemical processes and biological interactions in the near-future. A relatively uncommon NIS is *P. pholadiformis* which was probably introduced with oysters >100 years ago (Jensen and Knudsen 2005) and therefore has had ample time to disperse between regions. However, *P. pholadiformis* exhibits high substratum selectivity, primarily burrowing into hard clays or limestone (Alexander et al. 1993) and is therefore only found in low abundances in Denmark.

### Perspectives

Most of the benthic soft-bottom NIS in Denmark are thought to be secondary introductions which have dispersed from founder populations in neighboring countries (Jensen and Knudsen 2005). It is therefore unlikely that a national action program could have prevented these introductions, highlighting the need for international collaboration and regulation. The primary introductions for many of the founder populations in adjacent and nearby countries have been via oyster-transplantations or by fouling of ship hulls (Jensen and Knudsen 2005). Future introductions can to some extent be controlled, as the oyster-industry is increasingly controlled, new antifouling agents are developed and oceanic ballast water exchange become increasingly utilized. In a recent companion paper we analyzed ~10,000 samples for introduced macroalgae in Denmark (Thomsen et al. 2007a). We found that Danish macroalgal assemblages have been invaded by ca. 10 NIS, and that two species, *Sargassum muticum* (Yendo) Fensholt 1955 and *Bonnemaisonia hamifera* Hariot 1891, constituted a large part of the algal flora. Collectively, these two large-scale distribution

studies document a substantial influence of NIS throughout Danish benthic assemblages, although the influence of animal invaders on stone reefs remains unknown. Still, marine NIS must be recognized as a fundamental human-associated influence which, in concert with other and better described anthropogenic pressures, impact marine ecosystems in Denmark and elsewhere.

Finally, it is important to emphasize that grab-samples have been collected throughout the world, bridging >50 years of monitoring programs and scientific investigations across institutions, nations and biogeographic regions. Today, retrospective analysis of such grab-samples presents a rare opportunity to investigate the temporal trajectory and spatial extent of marine invasions in soft-bottom systems throughout the world and at many levels of hierarchical scales. No similar globally available data-set and based on a single relatively standardized methodology, exist for any other marine group of organisms or habitat. Our study should therefore be straightforward to duplicate in other regions. We suggest to utilize already existing grab-based datasets for more detailed distributional studies, to compare broad-scale patterns between seas, oceans and biogeographic regions, and, in conjunction with demographic research and manipulative experiments, to test for ecological impacts and theories of invasions (e.g. ‘propagule pressure’, ‘diversity-resistance’ or ‘invasional meltdown’ theories, Simberloff and Von Holle 1999; Lockwood et al. 2005).

**Acknowledgments** Mads Thomsen was supported by the Danish Research Academy. We thank colleagues from the Danish counties and The National Environmental Research Institute, who collected this enormous dataset.

### References

- Alexander RR, Stanton RJ, Dodd JR (1993) Influence of sediment grain-size on the burrowing of bivalves—correlation with distribution and stratigraphic persistence of selected neogene clams. *Palaios* 8:289–303
- Alonso A, Camargo JA (2003) Short-term toxicity of ammonia, nitrite, and nitrate to the aquatic snail *Potamopyrgus antipodarum* (Hydrobiidae, Mollusca). *Bull Environ Contam Toxicol* 70:1006–1012
- Armonies W, Reise K (1998) On the population development of the introduced razor clam *Ensis americanus* near the island of Sylt (North Sea). *Helgol Meeresunters* 52:291–300
- Bastrop R, Blank M (2006) Multiple invasions—a polychaete genus enters the Baltic Sea. *Biol Invasions* 8:1195–1200
- Behrends B, Hertweck G, Liebezeit G, Goodfriend G (2005) Earliest Holocene occurrence of the soft-shell clam, *Mya arenaria*, in the Greifswalder Bodden, Southern Baltic. *Mar Geol* 216:79–82
- Blank M, Bastrop R, Rohner M, Jurss K (2004) Effect of salinity on spatial distribution and cell volume regulation in two sibling species of *Marenzelleria* (Polychaeta : Spionidae). *Mar Ecol Prog Ser* 271:193–205
- Cederwall H, Jermakovs V, Lagzdins G (1999) Long-term changes in the soft-bottom macrofauna of the Gulf of Riga. *Ices J Mar Sci* 56:41–48



- Conley DJ, Kaas H, Moehlenberg F, Rasmussen B, Windolf J (2000) Characteristics of Danish estuaries. *Estuaries* 23:820–837
- Hall R, Tank JL, Dybdahl MF (2003) Exotic snails dominate nitrogen and carbon cycling in a highly productive stream. *Front Ecol Env* 1:407–411
- Hall RO, Dybdahl MF, VanderLoop MC (2006) Extremely high secondary production of introduced snails in rivers. *Ecol Appl* 16:1121–1131
- Hansen K, King GM, Kristensen E (1996) Impact of the soft shell clam *Mya arenaria* on sulfate reduction in an intertidal sediment. *Aquat Microb Ecol* 10:181–194
- Jensen KR, Knudsen J (2005) A summary of alien marine benthic invertebrates in Danish waters. *Oceanol Hydrobiol Stud* 34:137–162
- Josefson A, Hansen JLS (2004) Species richness of benthic macrofauna in Danish estuaries and coastal areas. *Glob Ecol Biogeogr* 13:273–288
- Josefson AB, Rasmussen B (2000) Nutrient retention by benthic macrofaunal biomass of Danish estuaries: importance of nutrient load and residence time. *Est Coast Shelf Sci* 50:205–216
- Kotta J, Olafsson E (2003) Competition for food between the introduced polychaete *Marenzelleria viridis* (Verrill) and the native amphipod *Monoporeia affinis* Lindstrom in the Baltic Sea. *J Sea Res* 50:27–35
- Leppakoski E, Gollasch S, Gruszk P, Ojaveer H, Olenin S, Panov V (2002) The Baltic—a sea of invaders. *Can J Fish Aquat Sci* 59:1175–1188
- Lockwood JL, Cassey P, Blackburn T (2005) The role of propagule pressure in explaining species invasions. *TREE* 20:224–228
- Lotze HK, Lenihan HS, Bourque BJ, Bradbury RH, Cooke RG, Kay MC, Kidwell SM, Kirby MX, Peterson CH, Jackson JBC (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. *Science* 312:1806–1809
- Lowe S, Browne M, Boudjelas S (2000) 100 of the world's worst invasive alien species. *Aliens* 12:S1–S12
- Mack MCD, Antonio CM (1998) Impacts of biological invasions on disturbance regimes. *TREE* 13:195–198
- Neideman R, Wengren J, Olafsson E (2003) Competition between the introduced polychaete *Marenzelleria* sp. and the native amphipod *Monoporeia affinis* in Baltic soft bottoms. *Mar Ecol Prog Ser* 264:49–55
- Nybakken JW (1993) Marine biology—an ecological approach. HarperCollins College Publishers, New York
- Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham MJ, Kareiva PM, Williamson MH, Von Holle B, Moyle PB, Byers JL, Goldwasser L (1999) Impact: toward a framework for understanding the ecological effects of invaders. *Biol Invasions* 1:3–19
- Palacios RL, Armstrong DA, Orensanz JM (2000) Fate and legacy of an invasion: extinct and extant populations of the soft-shell clam (*Mya arenaria*) in Grays harbor (Washington). *Aquat Cons Mar Fresh Ecosyst* 10:279–303
- Petersen JCG (1924) A brief survey of the animal communities in Danish waters, based upon quantitative samples taken with the bottom sampler. *Am J Sci* 7:343–354
- Petersen KS, Rasmussen KL, Heinemeier J, Rud N (1992) Clams before Columbus? *Nature* 359:679
- Reise K, Gollasch S, Wolff WJ (1999) Introduced marine species of the North Sea coast. *Helgol Meeresunters* 52:219–234
- Riisgard HU, Seerup DF (2003) Filtration rates in the soft clam *Mya arenaria*: effects of temperature and body size. *Sarsia* 88:415–428
- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Am Zool* 37:621–632
- Sagasti A, Schaffner LC, Duffy JE (2000) Epifaunal communities thrive in an estuary with hypoxic episodes. *Estuaries* 23:474–487
- Simberloff D (2005) The politics of assessing risk for biological invasions: the USA as a case study. *TREE* 20:216–222
- Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? *Biol Invasions* 1:21–32
- Stæhr P, Pedersen MF, Thomsen MS, Wernberg T, Krause-Jensen D (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. *Mar Ecol Prog Ser* 207:79–88
- Strasser M (1998) *Mya arenaria*—an ancient invader of the North Sea coast. *Helgol Meeresunters* 52:309–324
- Thomsen MS, McGlathery K, Tyler AC (2006a) Macroalgal distribution pattern in a shallow, soft-bottom lagoon, with emphasis on the nonnative *Gracilaria vermiculophylla* and *Codium fragile*. *Estuar Coast* 29:470–478
- Thomsen MS, Wernberg T, Stæhr PA, Pedersen MF (2006b) Spatio-temporal distribution patterns of the invasive macroalga *Sargassum muticum* within a Danish Sargassum-bed. *Helgol Mar Res* 60:50–58
- Thomsen MS, Wernberg T, Stæhr PA, Krause-Jensen D, Risgaard-Petersen N, Silliman BR (2007a) Alien macroalgae in Denmark—a national perspective. *Mar Biol Res* 3:61–72
- Thomsen MS, Stæhr P, Nyberg CD, Krause-Jensen D, Schwærter S, Silliman B (2007b) *Gracilaria vermiculophylla* in northern Europe, with focus on Denmark, and what to expect in the future. *Aquat Invasions* 2:83–94
- Verling E, Ruiz GM, Smith LD, Galil B, Miller AW, Murphy KR (2005) Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proc Royal Soc London SB Biol Sci* 272:1249–1257