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ORIGINAL ARTICLE

Alien macroalgae in Denmark – a broad-scale national perspective

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Abstract

Most studies documenting the importance of alien macroalgae relative to native species are based on smaller-scale sampling programmes. Between 1989 and 2003, a Danish monitoring programme collected data on the percentage cover of macroalgae at more than 600 locations throughout the country. We examined this data set to estimate the relative abundance of alien species in the algal flora on large spatiotemporal scales, i.e. across depth ranges, regions and years. Of the 10 alien macroalgal species known to inhabit Danish coastal waters, nine were found in the survey. Most of the alien species were only present in low quantities (<1% of the entire flora). In contrast, the two most common alien species, *Sargassum muticum* and *Bonnemaisonia hamifera*, constituted 2–7% of the assemblages, depending on depth, region and year. *Sargassum muticum* was abundant from 0 to 5 m in the northwestern region, where salinity and species richness are highest, whereas *B. hamifera* was abundant in several regions in deeper waters, where the native flora is species-poor. Based on their relatively high abundance, we hypothesize that these two aliens have had the largest impact on the native communities. Of some concern is the recent introduction of *Gracilaria vermiculophylla*. This species has traits that match the conditions of Danish estuaries and may become widespread with potential negative impacts on native biota.

Key words: *Alien macroalgae, Baltic Sea,* Bonnemaisonia hamifera*, large-scale monitoring, North Sea,* Sargassum muticum

Introduction

Alien macroalgae have been found in most parts of the world. Several highly invasive species such as *Sargassum muticum* (Yendo) Fensholt, *Codium fragile* ssp. *tomentosoides* (van Goor) P.C. Silva and *Caulerpa taxifolia* (M. Vahl) C. Agardh have attracted special attention (e.g. Trowbridge 1998; Stæhr et al. 2000; Boudouresque & Verlaque 2002). For example, *C. taxifolia* has outcompeted the native flora at several locations in the Mediterranean Sea (Piazzi et al. 2001; Ceccherelli et al. 2002; Dumay et al. 2002) and *C. fragile* has been suggested to drift away with financially important oysters (Trowbridge 1998) and limit kelp recruitment (Levin et al. 2002). These alien algae often form mono-specific stands in the invaded habitats, potentially with dramatic impact on the native assemblage structure.

The ecological impacts of invasions are often inferred from distribution data under the assumption that the more abundant the alien species, the more severe the impact (Stæhr et al. 2000; Piazzi & Cinelli 2001; Boudouresque & Verlaque 2002). To document distribution, and infer impacts, autecological studies are often conducted, e.g. large-scale overviews based on qualitative (Maggs & Stegenga 1999; Reise et al. 1999; Boudouresque & Verlaque 2002; Nyberg & Wallentinus 2005) or quantitative data (Carlton & Scanlon 1985; Wikström et al. 2002). Alternatively, both alien and native species are quantified, but such time-consuming assemblage studies are typically of limited spatiotemporal scales (e.g. Piazzi et al. 2001; Thomsen et al. 2006a). We see an additional need for analyses of quantitative assemblage data at large scales to assess regional-to-national level abundance (and

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hence impacts) of introduced macroalgae, to identify "problem species" and regions and depth ranges most threatened by them, and to guide future research efforts regarding species and regions/locations to be studied.

Denmark is a small country, yet the coastline covers >7000 km and encompasses a broad range of habitats within several sounds and estuaries. Macroalgal assemblages have been regularly quantified along Denmark's coastline since 1989, as part of a national marine monitoring programme. This data set provides a unique opportunity to evaluate the importance of alien macroalgae on regional and national scales. To date, only a few studies have focused on alien macroalgae in Danish waters, and these have concerned *S. muticum* (Stæhr et al. 2000; Wernberg et al. 2001, 2004; Pedersen et al. 2005; Thomsen et al. 2006b) and *Dasya baillouviana* (S. G. Gmelin) Montagne (Nielsen & Mathiesen 2005). The objective of this study was to provide the first nationwide analysis of how abundant alien macroalgae are compared to native species, and to identify regions and depth ranges that have probably been impacted by alien macroalgae.

Material and methods

Study area

Denmark is located at the entrance to the Baltic Sea and the Danish coastal waters can be divided into several regions (Figure 1). The primary environmental factor that varies horizontally is salinity, which decreases markedly from the North Sea (34 psu) to the Baltic Sea around Bornholm (8 psu) (Wallentinus 1991). Secondary salinity gradients are also seen within most Danish estuaries. Species richness decreases dramatically along these gradients (Wallentinus 1991; Middelboe et al. 1997b). The red algae, for example, are reduced from ca. 125 species in the North Sea to ca. 25 species around Bornholm (Køie et al. 2000). The availability of hard substratum also varies spatially, ranging from a rocky coast around Bornholm to sandy beaches in western Denmark. Except for northern Bornholm, which is a granite horst, Denmark is a sedimentary basin, where hard

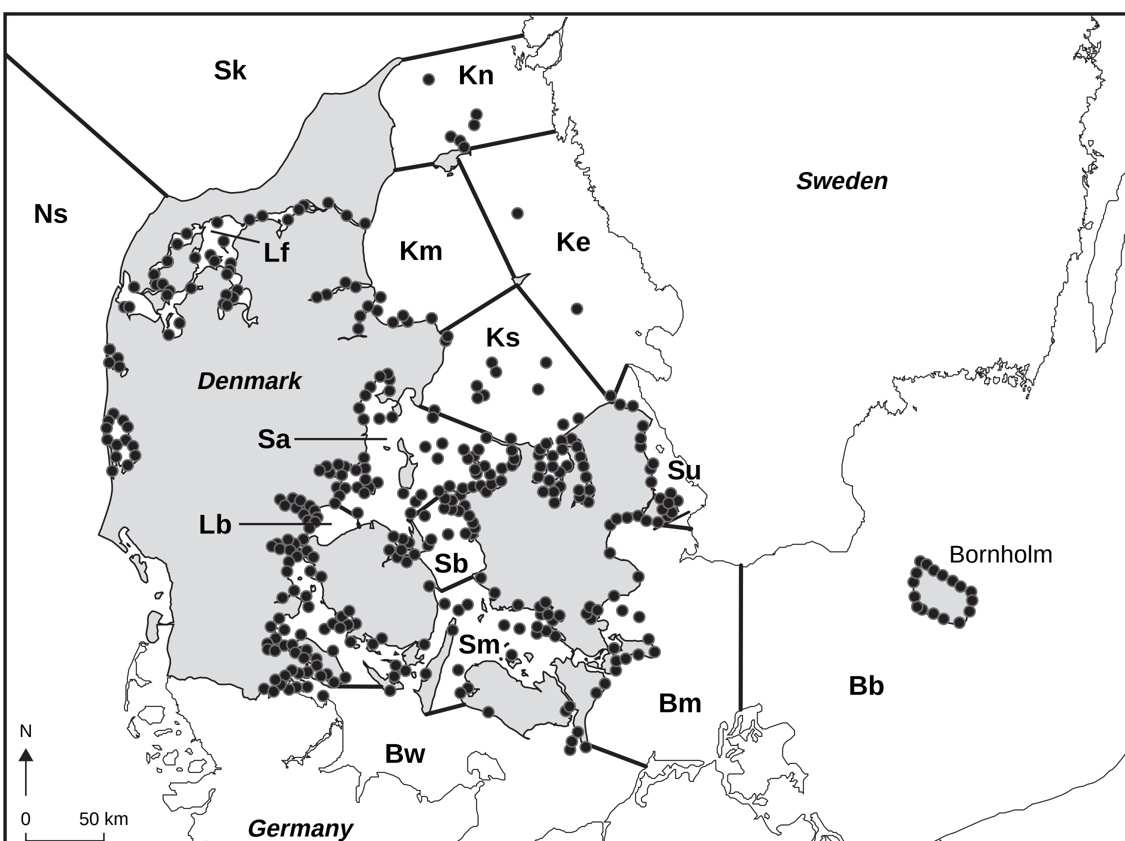

Figure 1. Map of Danish coastlines divided into regions as in Nielsen (2005). North Sea = Ns (including western fjords and inlets); Kattegat (including Limfjorden) = Kn + Ke + Ks + Km + Lf; Northern Belt Sea = Sa; Small Belt = Lb; Great Belt = Sb + Sm; The Sound = Su; Southern Belt Sea = Bw; Baltic Sea = Bm + Bb (see also Table I). Black circles correspond to sample locations. Note the lack of coastal sampling localities in the North Sea and Skagerrak, as these coastlines are sandy, wind- and wave-exposed and without attached macroalgae.

substratum for algal attachment is mainly composed of quaternary boulder reefs, scattered stones and boulders deposited by glacial activity. With the exception of the Wadden Sea, Denmark has little tidal influence, and most marine waters are therefore subtidal. Wave exposure is highest on coasts facing the predominant westerly winds, and nutrient and sediment levels are highest in inner coastal waters. Sedimentation, hydrodynamics, substrate conditions and light change dramatically with depth, causing a vertical zonation. Waters are generally turbid, with typical summer Secchi depths of 2–5 m in inner coastal waters (Conley et al. 2000), causing light limitation of photosynthesis in deeper waters. In many places, the lack of boulder reefs add a limiting factor to macroalgal distribution below 5–10 m. Interannual variation in physicochemical factors is generally much smaller than the nationwide spatial gradients [for details see Krause-Jensen et al. (in press)].

Taxonomic considerations

Ten macroalgal species are considered alien in Denmark (Wallentinus 2002; Nielsen 2005), and these include five red, four brown and one green algal species (Table I). We included the same species as aliens as Wallentinus (2002) (with "*Heterosiphonia japonica*" = *Dasysiphonia?* sp.), except that we also included *Dictyota dichotoma* (Hudson) J.V. Lamouroux, because this species was first reported in Denmark in 1939 (Lund 1940), only shortly before the first record of the alien *Fucus evanescens* C. Agardh (Lund 1949) (Table I). However, both species occur naturally in the east and north Atlantic, and their presence in Denmark could therefore potentially represent natural range expansions. The list of aliens includes two subspecies of *C. fragile*, which probably represent separate introductions (Lund 1949; Wallentinus 2002). However, with no visible macroscopic morphological differences, they are treated as a single entity in the monitoring programme, and hence in this article. Finally, it should be noted that we did not include *Mastocarpus stellatus* (Stackh. in With.) Guiry as alien, as it has been present in Danish waters for more than 100 years (R. Nielsen, pers. commun.). However, some authors argue that

Table I. Alien macroalgae in Denmark.

Species	Origin	Dispersal vector	Year Europe	Year Denmark	Distribution Denmark[a]
Rhodophyta					
Bonnemaisonia hamifera	West Pacific	Ship?	1890 (England)[b]	1900[f]	Ns, Sk, Lf, Kn, Ke, Km, Ks, Sa, Sb
Dasya baillouviana	Mediterranean	Oysters? Ship?	Natural[b]	1961[b]	Lf, Sa, Lb, Sb, Su, Bw
Gracilaria vermiculophylla	West Pacific	Oysters?	?? (France?)[g]	2003[h]	Ns, Sa
"*Heterosiphonia japonica*"	Pacific	Oysters? Ship?	1994 (Holland)[i]	2005[a]	Lf, Kn
Neosiphonia harveyi	Pacific/Northwest Atlantic	Epiphyte?	1908 (England?)[b]	1986[b]	Lf, Kn
Phaeophyta					
Colpomenia peregrina	West Pacific	Oysters?	1905 (France)[c]	1939[j]	Lf, Kn
Dictyota dichotoma	Atlantic	Oyster? Natural?	Natural[f]	1939[j]	Sk(d), Lf
Fucus evanescens	North Atlantic	Ship? Natural?	Natural[f]	1948[d]	Sk(d), Kn, Ke, Km, Ks, Sa, Lb, Sb, Su, Bw
Sargassum muticum	West Pacific	Oysters?	1960s (France?)[c]	1984[e]	Ns(d), Sk, Lf, Kn, Km, Ks(d), Su(d)
Chlorophyta					
Codium fragile ssp. *tomentosoides*	West Pacific	Oysters? Ship?	1900? (Holland)[c]	1919[d]	Ns(d), Sk(d), Lf, Kn, Ke, Km, Ks, Sa
Codium fragile ssp. *scandinavicum*	West Pacific	Oysters? Ship?	1919 (Denmark)[d]		

[a]Nielsen (2005).
[b]Maggs & Stegenga (1999).
[c]Reise et al. (1999).
[d]Lund (1949).
[e]Christensen (1984).
[f]Køie et al. (2000).
[g]Rueness (2005).
[h]Thomsen et al. (2005b).
[i]Stegenga (1997).
[j]Lund (1940).
Distribution abbreviations (cf. Figure 1): Ns, North Sea; Sk, Skagerrak; Lf, Limfjorden; Kn, Kattegat north; Ke, Kattegat east; Ks, Kattegat south; Km, Kattegat mid; Sa, sea around Samsø; Lb, Small Belt; Sb, Great Belt; Sm, Smålandshavet between Sealand and Lolland; Su, The Sound; Bw, Baltic west; Bm, Baltic around Møn; Bb, Baltic around Bornholm; (d), only observed as drift alga.

it has been introduced to Denmark on ship hulls (Køie et al. 2000). *Mastocarpus stellatus* is, like *D. dichotoma* and *F. evanescens*, naturally occurring in the eastern Atlantic and none of these species are therefore typical "exotic invaders". Also, *M. stellatus* has only been observed in very low abundances four times in the entire Danish National Monitoring Programme (see below) and its inclusion would then not have influenced the general results (Table II). The 10 alien species correspond to ca. 1–3% of native taxa, both on a total species basis and within each algal division (159 red, 126 brown, 91 green algae; Nielsen 2005).

Sampling data

Algal surveys were conducted as part of the Danish National Monitoring Programme. Algal assemblage structure was quantified from a total of more than 600 locations (Figure 1, geo-coordinates can be downloaded at http://www2.dmu.dk/1_Viden/2_Miljoetilstand/3_vand/4_mads_ny/). Sampling areas

Table II. Summary of monitoring data of macroalgal assemblages in Denmark 1989–2003. The total data set consisted of 9738 samples, with a total of 290 algal taxa, of which nine species were aliens, corresponding to 3.10% of the species. The table presents all the samples subdivided into "Depth", "Region" or "Year" groupings. The percentage of alien species was calculated as the number of alien species (not shown) divided by the number of all recorded taxa. The percentage cover of all algae (% cover per sample) is the summed cover of all taxa (not shown) divided by the number of samples for a specific grouping. Note that some values exceed 100%, indicating multiple vertical layers of algae. The percentage cover of alien species was calculated as the summed cover of alien species (not shown) divided by the summed cover of all taxa (not shown).

Group	Samples	All taxa	% alien species	% cover per sample	% alien cover
Depth (m)					
0–2	3037	182	4.95	58	3.31
2–4	2338	184	3.80	87	6.96
4–6	1624	192	3.65	95	3.72
6–8	1144	193	2.07	93	1.54
8–10	700	172	1.74	93	1.15
10–12	428	171	1.75	96	1.14
12–14	170	162	1.85	108	2.17
14–16	124	160	1.25	102	3.27
16–18	84	122	0.82	78	1.91
18–20	46	115	0.87	84	2.55
20–22	22	82	1.22	91	6.32
22–24	14	70	1.43	105	0.14
24–26	6	25	4.00	20	0.83
26–28	1	9	11.11	108	0.00
Region					
North Sea	236	17	0.00	10	0.00
Kattegat	1822	252	3.17	96	11.10
Northern Belt Sea	1724	205	2.44	94	4.21
Small Belt	3077	114	4.39	73	1.22
Great Belt	1121	145	2.07	81	0.38
Southern Belt Sea	78	56	1.79	107	0.36
The Sound	729	116	0.86	100	0.41
Baltic Sea	951	81	1.23	59	0.00
Year					
1989	637	156	3.85	74	2.40
1990	664	183	3.83	74	3.42
1991	781	194	3.61	82	4.61
1992	836	192	3.65	84	4.52
1993	920	213	3.29	85	4.59
1994	863	189	3.70	82	2.07
1995	870	168	3.57	76	2.89
1996	821	181	3.87	72	2.19
1997	783	136	5.15	82	3.58
1998	334	111	6.31	88	8.94
1999	809	131	5.34	96	4.41
2000	382	129	2.33	62	1.27
2001	509	131	6.11	88	5.68
2002	52	64	3.13	89	0.59
2003	477	120	7.50	88	3.03

were selected to represent a broad range of coastal and stone reef algal habitats of Denmark. As the North Sea and the Skagerrak coasts are generally sandy and lack vegetation, these areas were not included in the programme. Within each area, sampling locations were distributed randomly.

Some areas, e.g. the stone reefs, have been sampled regularly since the start of the monitoring programme in 1989, whereas other areas have been sampled only occasionally. Many coastal areas were surveyed every summer until 1997, but thereafter surveys were typically conducted every second summer (1999, 2001, 2003) and only on locations where hard substratum was represented. This study included data from 1989 to 2003 and encompassed on average 222 locations per year. Most surveys were conducted during midsummer and sampling time did not vary much between years. Over the years, 71–97% of the observations represented June–August, and 91–100% May–September.

Surveys on offshore stone reefs were conducted exclusively by a team of three experienced divers and algal specialists. Surveys along the coasts were much more numerous and involved a larger and more diverse group of divers from the various counties and private companies. In order to make the surveys as homogeneous as possible, all surveys followed the same guidelines, which contained detailed instructions and specifications (Krause-Jensen et al. 2001). Moreover, diver intercalibration and training exercises were undertaken (Middelboe et al. 1997a). However, because the divers did not all have the same experience and taxonomic expertise, differences in the quality of the surveys were unavoidable and some misidentifications of inconspicuous taxa are possible. Of the introduced species, particularly *Neosiphonia harveyi* (J. Bailey) M.-S. Kim, H.-G. Choi, Guiry & G.W. Saunders (= *Polysiphonia harveyi* in Wallentinus 2002), *Bonnemaisonia hamifera* Hariot and recruits of *F. evanescens* can be difficult to separate from native species and their abundances were therefore likely estimated with less certainty (probably underestimated). Divers who were not taxonomic experts may not have identified these species as aliens or may have had difficulties in the field distinguishing the cover of these species from that of neighbouring native species.

For algal surveys, divers visually estimated the percentage cover of each macroalgal species within 2 m depth intervals (0–2, 2–4, 4–6, 6–8 m, etc.), along depth gradients extending from the coast until the deepest algal record. In the following, a sample refers to observations within a 2 m depth interval, whereas a location refers to the group of samples located along the same depth gradient. Depth was measured with dive computers and incorporated both atmospheric and tidal effects. Algal cover was estimated relative to hard substratum. Until 2000, cover was estimated as an average for a depth interval according to an abundance scale. From 2001, cover was estimated directly as percentages within three subareas of 25 m^2 in each depth interval. Intercalibration documented that this change in method reduced the variability between estimates without significantly affecting mean cover (Laursen et al. 2000). We converted the abundance scale to percentages, as used by Stæhr et al. (2000), before analysis. Visual cover estimates are less precise than biomass collections, but are preferable when large areas must be surveyed repeatedly at low cost (Meese & Tomich 1992). Species that could not be identified in situ were typically collected and brought to the laboratory and identified using microscopic analyses, and in some cases taxonomic experts were consulted for identification.

All algal data were reported to the National Environmental Research Institute and stored in the database "MADS". The entire data set consisted of 9738 samples, i.e. specific combinations of locality, depth and year. Before analysis, genus and species names were standardized according to Nielsen (2005). After taxonomic standardization, the MADS database contained 290 taxa, including 38 taxa registered on a higher taxonomic level than species (mainly genus level, e.g. *Antithamnion* sp.). Data were extracted from MADS according to: (a) 14 vertical depth intervals, (b) eight horizontal regions and (c) 15 individual years (Table II). Within each of these groupings, cover estimates for each species were summed and the relative abundance of each species calculated as the summed cover of the given species divided by the summed cover of all species within each grouping. In addition, rank-ordered abundances are also presented, with the most abundant species in Denmark corresponding to number 1. Some groupings were based on a relatively low number of samples and are therefore less general compared with groupings with more samples. For example, all depth intervals "deeper than 16 m", "The Southern Belt Sea", and "2002" were based on less than 100 samples (Table II).

Results

Nine of the 10 alien macroalgal species known to occur in Denmark were recorded in the data from the MADS database (the last, "*Heterosiphonia japonica*" was found in the 2005 survey), and their percentage cover corresponded to 3.75% of the total cover of all macroalgae along the entire Danish coastline (calculated from the entire 9378 assemblage samples). Overall, *Sargassum muticum* was the most abundant alien species (1.38%, rank 19), followed by *Bonnemaisonia hamifera* (0.96%; rank 26), *Dictyota dichotoma* (0.56%; rank 40), *Dasya baillouviana* (0.35%; rank 49), *Codium fragile* (0.24%; rank 54), *Fucus evanescens* (0.10%; rank 70), and *Colpomenia peregrina* Sauvageau, *Gracilaria vermiculophylla* (Ohmi) Papenfuss and *Neosiphonia harveyi* (all <0.10%; ranks 112, 196 and 201, respectively). In comparison, >40% of the total cover of algae in Denmark was made up of only seven native species. These included *Ectocarpus siliculosus* (Dillwyn) Lyngbye (9.55%), *Ceramium virgatum* Roth (*as C. rubrum* in the database, potentially a complex of several corticated *Ceramium* species) (8.67%), *Phycodrys rubens* (Linnaeus) Batters (5.38%), *Polysiphonia fucoides* (Hudson) Greville (5.13%), *Furcellaria lumbricalis* (Hudson) J.V. Lamouroux (4.56%), *Fucus vesiculosus* Linnaeus (3.92%) and *Coccotylus truncatus* (Pallas) M.J. Wynne & J.N. Heine (3.24%).

Depth distribution of alien species

The summed abundance of all alien species was highest at 2–4 m (6.96% of the entire assemblage) and 20–22 m depth (6.32%) and lowest between 22 and 28 m depth (0.00–0.83%, Table II). The deepest record of an alien species was *B. hamifera* (24–26 m), followed by *C. fragile* (14–16 m), *D. baillouviana* (12–14 m), *S. muticum* (6–8 m), *C. peregrina*, *D. dichotoma* and *N. harveyi* (4–6 m) and finally *G. vermiculophylla* and *F. evanescens* (0–2 m) (Figure 2). Most individual alien species were more abundant and had highest ranks from 0 to 4 m (Figure 2). For example, *S. muticum* was among the 20th most abundant algae, both at 0–2 and 2–4 m depth (1.5 and 3.3% relative cover). In contrast, *B. hamifera* was among the 25 most abundant species at all depths deeper than 2 m, with a relative cover of 6.3% of the entire assemblage at 20–22 m. *Codium fragile* and *D. baillouviana* were also found relatively deep, remaining among the 115 most common taxa down to 16 and 14 m, respectively.

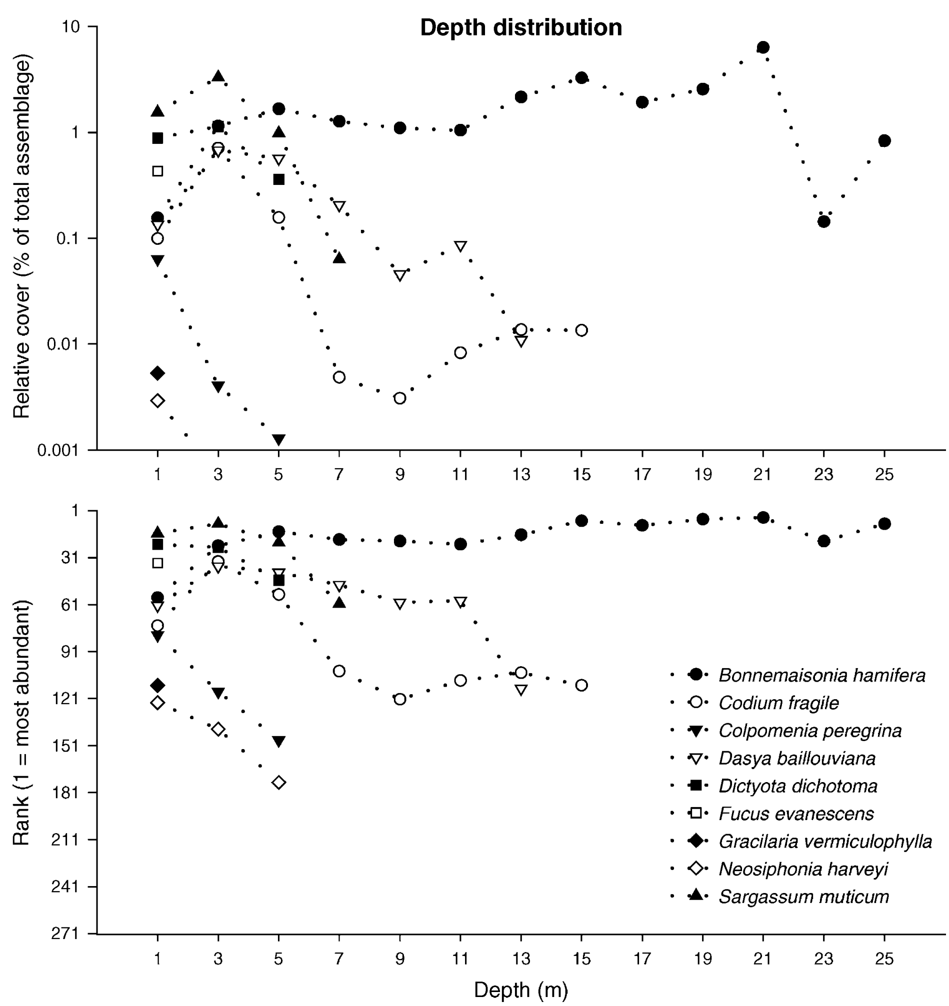

Figure 2. Depth distribution patterns of alien macroalgae in Denmark. A lacking symbol means that the species was not observed in that depth interval (years and localities were pooled). Note log-scale for relative cover values.

Distribution of alien species among regions

We found a general decrease in importance of alien species from 11.12% in the Kattegat region to less than 0.5% in the less saline regions from the Great Belt to Bornholm (Figure 3). The high abundance of alien macroalgae in the Kattegat region was due to a high abundance of *S. muticum* (6.27%), *D. dichotoma* (2.51%), *B. hamifera* (1.21%) and *C. fragile* (1.07%). The relatively high abundance in the Northern Belt Sea was mainly due to *B. hamifera* (3.49%) and *D. baillouviana* (0.66%) (Figure 3). No alien algae were found in the North Sea, but this region was only represented by a low number of samples (236) collected in shallow turbid and brackish estuaries (Nissum Bredning and Ringkøbing Fjord) with few algal taxa (17) and low total cover values (Table II). Thus, *B. hamifera* had the most general distribution, being found in all regions except the North Sea, followed by *D. baillouviana* and *F. evanescens* (the Kattegat to Great Belt). *Codium fragile* was only found in the Kattegat and the Northern Belt Sea, *C. peregrina* and *N. harveyi* in the Kattegat and Small Belt. *Sargassum muticum*, *D. dichotoma* and *G. vermiculophylla* had the most restricted distribution, only being found in the Kattegat (the two former) or the Northern Belt Sea (the latter).

Temporal distribution of alien species

The summed abundance of all alien species fluctuated between 0.59% (2002) and 8.94% (1998) of the entire algal assemblages, with typical values ranging between 2 and 4% per year. The two extreme values match years of relatively low sampling effort (Table II). Neither the abundance of a single alien species nor the total group of aliens showed any clear trends of increase or decrease, as relative abundance or in rank-order (Figure 4), e.g. *D. baillouviana* constituted more than 1% of the entire flora in both 1991 and 2001 but had much lower values in all other years. *Sargassum muticum*

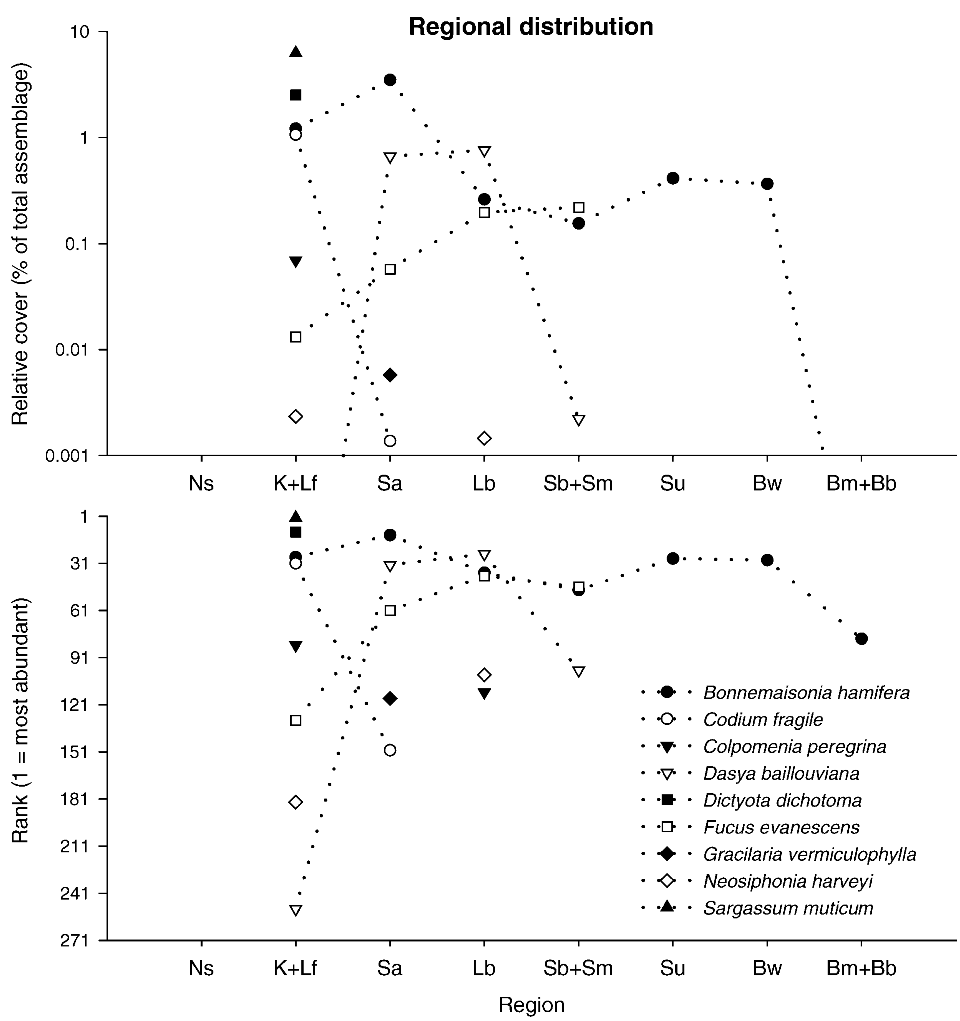

Figure 3. Regional distribution patterns of alien macroalgae in Denmark. A lacking symbol means that the species was not observed in that region (years and depth were pooled). Note log-scale for relative cover values. Cf. Figure 1 for regional abbreviations.

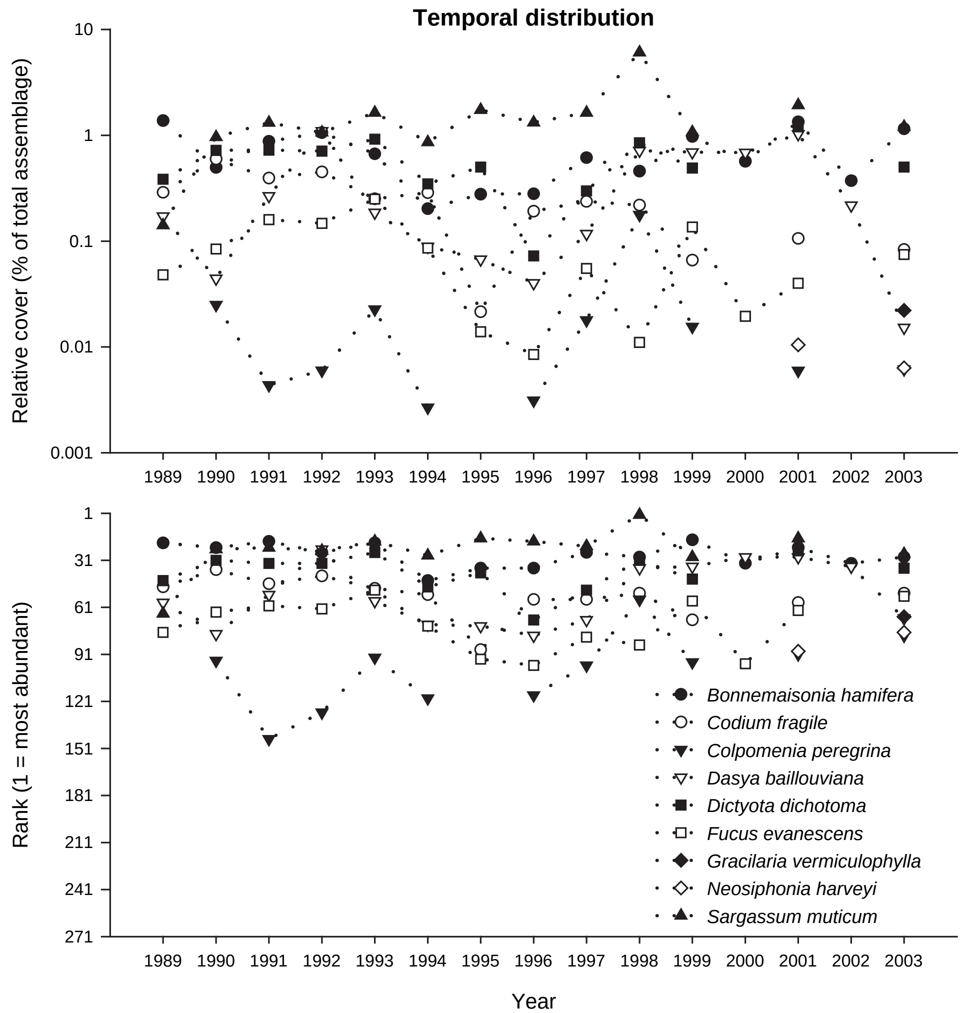

Figure 4. Annual distribution patterns of alien macroalgae in Denmark. A lacking symbol means that the species was not observed in that year (depth and localities were pooled). Note log-scale for relative cover values.

was the most abundant alien alga in all years except 1989 (*B. hamifera* was the most abundant), 1992 (*D. baillouviana*) and 2000 (*B. hamifera*). *Sargassum muticum* was particularly abundant in 1998, when it covered more than 6% of the entire flora and was the second-most abundant alga, only superseded by the *C. virgatum* complex.

Discussion

We have documented the presence of alien macroalgae in the Danish algal flora, and on this general level, the alien component can be considered relatively small. Of the 10 alien species in Danish waters, two have become dominant in specific regions and depth intervals: *S. muticum* dominates the algal assemblage shallower than 6 m in northwestern Denmark, whereas *B. hamifera* is common in many regions, particularly at water depths deeper than 6 m.

Of the alien species, *S. muticum* and *B. hamifera* were the most abundant and based on their relatively high abundances within specific regions and depth intervals, we hypothesize that these two aliens have had the largest impact on the native communities. *Sargassum muticum* was particularly abundant in 1998. However, a closer inspection of the sampled localities showed that this was a year with relatively higher sampling effort in northwestern Denmark (Limfjorden), an area where it has been particularly common since first recorded in 1984 (Christensen 1984; Stæhr et al. 2000; Thomsen et al. 2006b). This demonstrates the importance of sampling localities relatively evenly across all regions each time a monitoring event is executed. It has already been suggested that *S. muticum* locally has caused decreased abundance of slower growing perennial species due to competition for space (Stæhr et al. 2000), altered biogeochemical cycling (Wernberg et al. 2001; Pedersen et al. 2005), and increased abundance of filamentous algae and epifauna (Wernberg et al. 2004; Thomsen et al. 2006b). However, whereas *S. muticum* has invaded habitats with relatively high diversity (Stæhr et al. 2000), *B. hamifera* dominates in habitats that are light stressed and with naturally low diversity (Table II). Unfortunately, fewer field data exist on *B. hamifera*, probably because *B. hamifera* is relatively inconspicuous and mainly occurs at depths (Breeman et al. 1988), were experimentation is logistically more challenging.

The remaining alien species generally accounted for less than 1% of the entire algal flora, but this does not imply that they are unimportant all over Denmark. Obviously, each species may be more important at specific combinations of depth and locality. For example, *D. dichotoma* constituted almost 3% of the entire flora in the Kattegat region, and it can indeed be very common in warm summer months on scattered stones in shallow water in Limfjorden (Stæhr et al. 2000; Thomsen et al. 2006b), where it can monopolise space (Thomsen, Wernberg & Stæhr). However, we are not aware of any studies that have documented impacts of *D. dichotoma* on native flora. *Fucus evanescens* was not found in high quantities in the monitoring programme, but can be locally abundant, particularly in wave-protected harbours, where it is shown to be associated with an impoverished epibiota compared with native *Fucus* species (Wikström et al. 2002; Wikström & Kautsky 2004). However, it should be emphasized that *D. dichotoma* and *F. evanescens* both occur naturally in the east Atlantic and their recent appearance in Danish waters can potentially be by natural dispersal. *Codium fragile* was also found in low quantities, in contrast to the more invasive populations in the west Atlantic (Carlton & Scanlon 1985; Trowbridge 1998), where it has been suggested to cause a reduction in abundance of native *Laminaria* species (Levin et al. 2002). *Neosiphonia harveyi*, *D. baillouviana*, *C. peregrina* and *G. vermicullophylla* were also only observed in low quantities, suggesting that these species have minor nationwide impact at present.

Most alien species had the highest relative abundance at water depths shallower than 8 m, probably reflecting the high turbidity of Danish waters (Conley et al. 2000) and apparently a lower capacity of the aliens to compete with the native assemblages in deeper waters. Only *C. fragile*, *D. baillouviana* and *B. hamifera* were found deeper than 8 m. *Codium fragile* is already known to be an efficient light absorber (Ramus 1990) and we hypothesize the same to be true for the two latter species as well. These three "deep-water" species are probably also sediment resistant, as net sedimentation typically increases with depth in turbid waters and has been shown to determine assemblage structure at depth in the Baltic Sea (Eriksson & Johansson 2003, 2005). However, data on sediment resistance are still lacking for most macroalgae. It is noteworthy that today *B. hamifera* is among the most abundant algae in Denmark at all depths deeper than 4 m, but still no ecological impact studies have yet been conducted.

The monitoring data showed a strong decrease in importance of alien species from the near-marine northwestern Kattegat to more brackish regions from the Great Belt to Bornholm in the Baltic Sea. Thus, the salinity gradient is probably a barrier for many established alien macroalgae, and acts as a filter for new marine stenohaline algae entering the Kattegat strait attached to ship hulls (Olenin & Leppäkoski 1999). The monitoring data generally match the presence–absence distribution data presented in Nielsen (2005) (Table I), indicating that the intensive sampling programme is efficient in detecting most introduced species in most regions. The only alien species that are found regularly in the Danish part of the Western Baltic are *D. baillouviana* and *F. evanescens*, suggesting high salinity tolerances, which ultimately are a prerequisite for any invader to have a nationwide impact in Denmark (most recently unattached fragments of *G. vermiculophylla* have been found in the Bay of Kiehl; D. Schories, pers. commun.; Schories & Selig 2006). *Bonnemaisonia hamifera* occurs in the Belts and *C. fragile* in the southern Kattegat, suggesting intermediate salinity tolerances. The remaining species (*S. muticum*, *N. harveyi*, *C. peregrina*, *D. dichotoma*, "*H. japonica*") have been found in the saltier Limfjorden and the Kattegat, and as these species (except "*H. japonica*") have existed in Denmark for more than 20 years they are less likely to spread into the more brackish regions. For *S. muticum*, it has been shown that the early life stages cannot survive salinities below 15 psu (Steen 2003), thereby preventing the establishment of long-term stable populations in the Belt Seas. Thus, even though drifting fragments and entire individuals attached to mussels and small stones can be common in the Belt (Thomsen, Wernberg & Stæhr), these arrivals eventually die out. It should be noted that *S. muticum* and *C. fragile* are positively buoyant and have large adult thalli (i.e. large drag), making these invaders highly susceptible to inter-regional drift (Johnson & Richardson 1977; Dromgoole 1982).

Most alien macroalgae have been in Denmark for many decades (e.g. *C. fragile*, *D. dichotoma*, *F. evanescens*, *C. peregrina* for more than 40 years; Table I) and have therefore had ample time to disperse naturally within and between regions. The alien species combined showed temporal fluctuations in percentage cover between less than 1% and almost 9% of the entire algal assemblages, but none of the alien species showed any continuous increase or decrease, neither as relative abundance nor in rank-order, suggesting a distribution pattern in a near steady-state condition (although a 15 year time series is relatively short for invasive species to manifest themselves on large scales). However, climate change and alterations in anthropogenic pressures imply that any of these species potentially could reach pest status at specific locations in the future. For example, it is possible that the warm-temperate species, *D. baillouviana* (Nielsen & Mathiesen 2005) and *D. dichotoma* (Bolser & Hay 1996) may become increasingly abundant if surface water temperature increases, and there are indications that this is already happening for *D. baillouviana*, which has been observed at several new locations in the last few years (Nielsen & Mathiesen 2005).

The most recent introductions, *G. vermiculophylla* (Thomsen et al. 2005b) and "*H. japonica*" (Nielsen 2005), had the opportunity for dispersal within Denmark for such a short time that it is still difficult to assess their importance. However, knowledge on their ecology provides the basis for qualified guesses of their future spreading potential in Danish coastal areas. "*Heterosiphonia japonica*" has been found in several European countries, is relatively tolerant to light and temperature fluctuations and can re-attach to substratum from fragmented laterals (Bjærke & Rueness 2004; Husa et al. 2004; Husa & Sjøtun 2006). However, it grows poorly at salinities below 15 psu (Bjærke & Rueness 2004) and is therefore unlikely to invade the lower salinity regions of Danish waters. *Gracilaria vermiculophylla* has been found in several European countries and both at the east and west coasts of North America (Rueness 2005; Thomsen et al. 2005a), suggesting an ongoing global dispersal. *Gracilaria vermiculophylla* is tolerant to low light, high sedimentation, salinity and temperature fluctuations (Rueness 2005; Nyberg 2006; Thomsen & McGlathery 2006a,b). In addition, *G. vermiculophylla* can grow in salinities down to 2 psu, can be found attached and reproductive at localities well below 20 psu, and has an efficient recruitment and an ability to re-grow from fragments (Nyberg 2006; Thomsen & McGlathery 2006a,b). These traits suggest that this species could become very abundant, particularly in the numerous shallow, turbid, low-energy Danish estuaries.

There are no generally agreed acceptable levels of introduced species. Invasions may even be considered beneficial in some instances, for example where a large canopy species (e.g. *S. muticum*) replaces smaller species or invades areas of low algal abundance such that the invader can act as a foundation species that facilitates other species (Bruno et al. 2003) by providing habitat for associated invertebrates and epiflora (Wernberg et al. 2004; Bulleri et al. 2006). Nevertheless, global biological homogenization will probably also be the end result in these positive cases. Therefore, it is relevant to consider possible measures to reduce further introduction and spreading of aliens.

Most of the alien species in Denmark are secondary introductions that have dispersed from founder populations in neighbouring countries, and the introductions of *F. evanescens* and *D. dichotoma* could represent recent natural range expansions. Thus, it is unlikely that an isolated national prevention and eradication programme could have hindered the introduction of alien macroalgae to Denmark. The primary introductions to other European countries have been via oyster transplantations, by ship-hull fouling or ballast water (Wallentinus 2002). Further introductions can to some extent be controlled, as the oyster industry is increasingly using spat from hatcheries (Drinkwaard 1999), anti-fouling agents increase in efficiency and if the treatment of ballast water becomes standard. When first established, there is little chance of eradication, unless the invasion is observed early, in a restricted area, or where large financial management costs are accepted (Williams & Schroeder 2004; Glasby et al. 2005). In general, we do not believe eradication to be an option for the alien macroalgae in Denmark, because many species have been established for a long time and are widespread; there are no traditions for such management actions in Denmark; and marine eradication programmes generally have limited success. For example, attempts to eradicate *S. muticum* in southern England were without success, because of the species' high recruitment and regeneration capacity (Critchley et al. 1986). Theoretically, it may be possible to eradicate "*H. japonica*", as this species has only been observed in a few places in Limfjorden, but given its widespread distribution in Norway (Husa et al. 2004), repeated introductions are likely. Eradication would already be very difficult for *G. vermiculophylla*, given its high abundance in the Wadden Sea and Horsens Fjord, as well as the neighbouring northern Kattegat coast of Sweden (M. S. Thomsen, pers. observ.). In addition, thalli of these species break easily and grow fast from small fragments (Husa & Sjøtun 2006; Nyberg 2006; Thomsen & McGlathery 2006b), making it virtually impossible to ensure that the entire population in a specific location is removed.

Based on this large-scale analysis, we suggest the following key areas for future research: (a) detailed distributional studies, particularly of *B. hamifera*, *G. vermiculophylla*, *D. bailloviana* and "*H. japonica*", species we know little about from Scandinavian waters, but which could potentially have a large ecological impact at present or in the near future (e.g. see Stæhr et al. 2000; Husa et al. 2004), (b) multi-factorial experiments of species-specific characteristics, such as growth and photosynthesis, under various combinations of different salinities, light levels, temperature, sedimentation, nutrient levels and grazing pressure (e.g. see Nyberg & Wallentinus 2005; Thomsen & McGlathery 2006b), (c) impact studies that test for both obvious direct and cryptic indirect effects, using addition (but only in already invaded locations) and removal methods (e.g. see Levin et al. 2002) on any of the alien species, (d) a comparison of our results with other large-scale regions and countries to test how general our large-scale findings are (we are not aware of any other similar large-scale analysis), and (e) repetition of the present and similar large-scale studies at regular time intervals to follow dispersal and large-scale spatiotemporal fluctuation patterns of the aliens.

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