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Long-term changes in area distribution of eelgrass (*Zostera marina*) in Danish coastal waters

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Abstract

For five shallow-water eelgrass stands in Denmark, changes in area distribution over the period 1940/50s–1990s were assessed from aerial photographs. In areas where the wasting disease had decimated eelgrass meadows in the 1930s, this included determination of the time scale of recolonization. In addition, we aimed at evaluating whether fluctuations in eelgrass area distribution were related to various natural and human-induced disturbances, namely storm events, ice-cover, water temperature and nutrient loading. We found that populations affected by the wasting disease exhibited a time lag of more than 10 years before substantial recolonization began, probably reflecting long distances to seed-producing populations and extreme climatic events in the period. After the initial time lag, eelgrass area distribution increased rapidly, and a substantial recovery had taken place in the 1960s. All eelgrass populations showed marked inter-annual fluctuations. Declines were often rapid with reductions of about 60% occurring in less than 6 years. Recoveries occurred over similar time scales and documented that recolonization may take place relatively fast when suitable environmental conditions are present. Fluctuations in eelgrass area distribution tended to be larger in enclosed, protected bays as compared to open coasts, probably because enclosed sites are often more eutrophic. Changes in shallow-water eelgrass area distribution did not correlate with the available long-term records of natural and human-induced disturbance parameters. Thus, while deep-water eelgrass populations have declined markedly over the last century in response to eutrophication, long-term changes in shallow-water populations are less equivocal and seem more stochastic.

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Keywords: Seagrass; *Zostera marina*; Aerial photography; Long-term change; Recolonization; Wasting disease; Area distribution

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1. Introduction

During the last century, various natural and human-induced disturbances have caused large oscillations in the world's seagrass populations (for review see [Short and Wyllie-Echeverria, 1996](#)). The most severe, natural-induced change occurred in the 1930s, when almost the entire North Atlantic population of eelgrass (*Zostera marina*) was destroyed by the wasting disease ([Rasmussen, 1977](#)). Climatic factors may also influence seagrass distribution on both small and large scales. Heavy storms and hurricanes generate waves and currents capable of markedly reducing seagrass cover and increasing fragmentation of seagrass beds ([Fonseca and Bell, 1998](#); [Fonseca et al., 2000](#)). The waves and currents may tear off leaves and uproot entire plants ([Patriquin, 1975](#); [Williams, 1988](#); [Larkum and West, 1990](#)) as well as causing redistribution of sediment resulting in either burial of plants or exposure of roots and rhizomes ([Kirkman, 1978](#); [Kirkman and Kuo, 1990](#); [Preen et al., 1995](#)). In northern temperate sites, ice scouring may likewise destroy shallow-water eelgrass populations ([Robertson and Mann, 1984](#); [Wium-Andersen and Borum, 1984](#); [Schneider and Mann, 1991](#)). Moreover, large-scale fluctuations in water temperature have been proposed to control the distribution of eelgrass ([Rasmussen, 1977](#); [Glemarec et al., 1997](#)) possibly because high temperatures may generate a negative carbon balance ([Marsh et al., 1986](#); [Zimmerman et al., 1989](#)).

The exponential increase in nutrient input to coastal zones ([Nixon, 1995](#)) is a main cause of recent declines in the distribution of seagrasses ([Cambridge and McComb, 1984](#); [Giesen et al., 1990](#); [Short and Wyllie-Echeverria, 1996](#)). Increased nutrient levels stimulate the production of phytoplanktonic, epiphytic and drifting algae ([Borum, 1985](#); [Pedersen, 1995](#); [Nielsen et al., 2002a](#)) and the accompanying reduction in light availability leads to reduced depth penetration and abundance of seagrasses ([Duarte, 1991](#); [Nielsen et al., 2002b](#)). Eutrophication has also increased the risk of anoxic events, especially in sheltered waters with limited mixing and in periods of high water temperature ([Valiela et al., 1992](#); [Boynton et al., 1996](#)), thereby introducing a further threat to seagrass populations ([Terrados et al., 1999](#); [Holmer and Bondgaard, 2001](#); [Greve et al., 2003](#)).

The frequent exposure to various kinds of disturbances keep seagrass populations in a continuous cycle of degradation and recolonization, resulting in seasonal and long-term oscillations in distribution (e.g., [Den Hartog and Polderman, 1975](#); [Olesen and Sand-Jensen, 1994a](#); [Robbins and Bell, 2000](#)). In Denmark, records of eelgrass distribution dating back to the beginning of the last century provide a unique opportunity for describing such long-term changes. In 1901, Danish eelgrass meadows covered approximately 6726 km², equivalent to 1/7 of all Danish marine waters ([Petersen, 1901, 1914](#)). In the 1930s, the wasting disease decimated these meadows leaving only the most brackish populations in the south-eastern part of the country unaffected ([Blegvad, 1935](#)) and in 1941, their distribution area was estimated at only 8% of the 1901 level ([Lund, 1941](#)). Brackish populations probably survived because the slime mold believed to cause the wasting disease ([Muehlstein et al., 1991](#)) is less pathogenic and growth conditions for eelgrass are optimal in brackish environments ([Rasmussen, 1977](#); [Short et al., 1988](#)). Recolonization of the Danish eelgrass meadows is not well investigated ([Rasmussen, 1977](#)) because no nation-wide study was undertaken until 1989 when the national Danish monitoring programme was initiated. Comparisons between historic and recent data show that eelgrass is widely distributed in Danish coastal areas once

again, although the present distribution area constitutes only about 25% of the 1901 level and many deep-water populations have disappeared (Boström et al., 2003). However, the large gap in large-scale eelgrass studies in the period 1940/50s–1990s implies that rates of eelgrass recolonization following the wasting disease and dynamics of eelgrass meadows in this period are still unknown. In this study, we use aerial photographs from the period 1940/50s–1990s to quantify the area distribution of five shallow-water eelgrass populations in order to pursue two goals: (1) Determining the size and time scales of fluctuations in eelgrass area distribution through the investigation period; for populations subjected to the wasting disease this goal includes determination of the time-scale of recolonization. (2) Identifying whether fluctuations in eelgrass area distribution are related to long-term records of natural- and human-induced disturbances.

2. Materials and methods

2.1. Study sites

Study sites were selected on the basis of a critical survey of aerial photos in the archives of the National Survey and Cadastre (KMS), Denmark, according to a predefined set of criteria: (1) Photographs should be available from the study sites throughout the period 1940/50s–1990s. (2) The sea bottom at the sites should be light in color and sandy to achieve the highest possible contrast between vegetation and background, thereby reducing errors in detecting eelgrass. (3) Sites with large mussel beds and heavy macroalgal growth were avoided since these structures can be confused with eelgrass in the image analysis. (4) The quality of the photographs should be good; i.e. no sun glint, no surface waves and high water transparency. These criteria markedly reduced the number of suitable study sites, and we ended up with five sites in estuaries and coastal areas of Kattegat and Øresund, Denmark (Fig. 1). Two of the sites, “Holmstange” and Boddum Vig (“Boddum”) are situated in Limfjorden, a 1500 km² natural channel intersecting the northern part of Jutland and connecting the North Sea with the Kattegat. A third study site is located on the outer north coast of Vejle Fjord (“Vejle”), a fourth site in Østerfjord on the island of Samsø (“Samsø”) and the final site “Amager” is situated in Øresund near the Baltic Sea.

Depending on the photographs available, the investigation period began either in 1945 or 1954 and ended in the 1990s (Table 1). The area of the study sites varied from 30 to 360 ha, the limits of each area being defined by the photograph with the smallest area cover in each time series (Table 1). All sites are shallow with maximum depths in the order of 2–3 m. The tidal range is less than 40 cm but wind causes larger fluctuations in water levels (Lund-Hansen et al., 1994). At three of the sites (Holmstange, Boddum and Vejle), eelgrass had been wiped out by the wasting disease, the Samsø-site had been only moderately affected (eelgrass present in 1933 (Blegvad, 1935) but gone in 1941 (Lund, 1941), and Amager was unaffected. The sites also differed in level of exposure to wind generated wave action (Table 1). As Kattegat and Øresund are transitional waters connecting the saline North Sea and the brackish Baltic Sea, salinity declines gradually moving from the northwestern to the southeastern part of Denmark and thus varies between the five sites (Table 1).

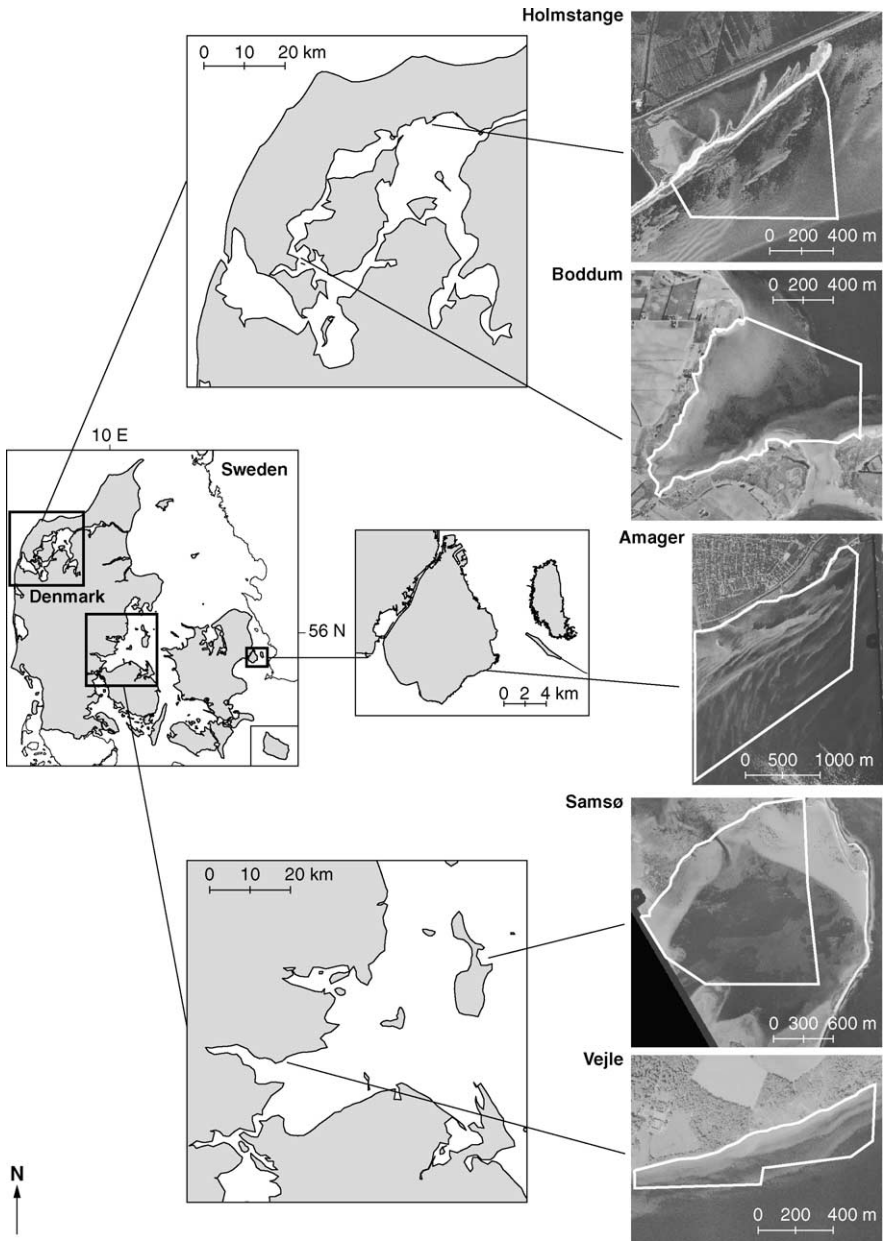


Fig. 1. Location of the five study sites.

Table 1

Basic information on the five study sites. Physical exposure is expressed as weighted effective fetch (WEF)

Study site	Area (ha)	Max depth (m)	Physical exposure (WEF)	Salinity (‰)	Wasting disease	Study period
Holmstange	66.7	2.5	36	26	+	1945–1995
Boddum	103.0	2.0	5	26	+	1954–1998
Vejle	30.2	3.0	48	24.5	+	1954–1999
Amager	396.6	3.0	100	11	—	1954–1995
Samsø	283.1	2.0	12	13–25	— ^a	1954–1999

^a Samsø was only moderately affected by the wasting disease since eelgrass was present in 1933 (Blegvad, 1935) but gone in 1941 (Lund, 1941).

2.2. Eelgrass mapping from aerial photographs

Black and white (B/W) or color contact copies of aerial photographs covering each of the five study sites were acquired from the KMS. The photographs were on the scale 1:10,000, 1:20,000 or 1:25,000 and most of them (80%) were taken in April–May. Eelgrass shoot density changes with season, but since the majority of the pictures were taken within a quite narrow time span, we assume that seasonality did not influence the results significantly. The photographs were all scanned at 800 dpi and the pixel size before resampling ranged from 0.32 m × 0.32 m to 0.79 m × 0.79 m. The B/W pictures were saved in 8-bit tagged image file format (TIFF) and the color photographs as 24-bit TIFF stored in three bands (red, green, blue) for each pixel. Color photos constituted a minor fraction (34%) of the photographs and were converted to B/W in order for the same mapping method to be used on all pictures.

CHIPS for Windows software (CHIPS development team) was used for rectification and mapping of the photographs. All photographs were rectified to a single photogrammetric reference (Orthophotos from 1995 covering all parts of Denmark, reported accuracy about 2 m). Between 10 and 53, ground control points distributed over as large a part of the photograph as possible were used to create a deformation model for the rectification (Table 2). Model accuracy was determined by running the control point coordinates through the model and comparing the calculated (X_{calc} , Y_{calc}) and original positions (X_{orig} , Y_{orig}). The distance

Table 2

Information on rectification and model error. Control points were used to create a deformation model for rectification of aerial photos. The model error is expressed as the RMS (root mean square) distance (m) between original and modelled positions of control points

Study site	Control points (no.)			Model error, RMS distance (m)	
	Min	Max	Mean	Max	Mean
Holmstange	12	28	20	20.9	2.9
Boddum	10	21	17	18.4	3.6
Vejle	10	22	14	26.0	5.9
Amager	10	53	37	5.0	1.2
Samsø	11	26	18	3.3	1.0

between the points represents the model error and can be calculated as the root mean square (RMS) distance:

$$\text{RMS} = \sqrt{(X_{\text{calc}} - X_{\text{orig}})^2 + (Y_{\text{calc}} - Y_{\text{orig}})^2}$$

The maximum and the mean RMS value for each study site are shown in Table 2. Finally, the photographs were all resampled to a pixel size of 1 m × 1 m using a bilinear technique, and were now ready for image analysis.

Ground truth information for the eelgrass mapping process was obtained by surveys conducted at each study site in April and May 2000—the same time of year where most of the photographs were taken. By video filming several transects under water, the different gray tones of the aerial photographs could be related to features such as eelgrass, algae or mussel beds at the study site. At the same time, information on depth and GPS position were recorded on a computer providing data for a simple depth model made in the program SURFER (Golden Software).

Although automated techniques exist (Kendrick et al., 2002), we decided to analyze the photographs manually, because brightness levels varied significantly within and between photographs, causing variation in the gray tones corresponding to eelgrass. Each image was divided into smaller sub-areas with similar brightness levels and classified separately. Contrast stretching was applied whenever necessary and eelgrass was defined as pixels with gray tones below a certain threshold value. Finally, the results from all sub-areas in the image were merged and the mapping result was filtered by a mode filter to convert highly isolated pixels with high possibility of being misclassifications or “noise” to the most frequently occurring pixel value within a filter kernel. The most recent pictures were classified first in order to use the information provided by the ground truth surveys to enhance mapping accuracy.

We determined the accuracy of the mapping process by creating a maximum and minimum estimate of eelgrass cover in addition to the normal mapping procedure. This test was performed on the photo series from Holmstange, which included both high- and low-quality photographs. In the maximum estimate, we decreased the gray tone threshold to include even sparse eelgrass at the risk of including other features such as dark sand in the process. The minimum estimate included only the darkest pixel values representing the most distinct and dense eelgrass areas and therefore leaves large areas of eelgrass out of the mapping. The eelgrass areas of the original mapping results ranged from −2.6 to +6.6% relative to the mean of the corresponding min–max interval. Hence the interpreter succeeded in using the same relative threshold for eelgrass quite accurately throughout the investigation period. The actual error is therefore much smaller than indicated by the minimum–maximum interval (shown as error bars on the figures) as long as it comes to detecting relative changes between years and not absolute areas.

2.3. Data on climate and nutrient loading

Wind measurements from the period 1953–1999 were obtained from the Danish Meteorological Institute (DMI). Wind data from Kastrup represented the nearby Amager site while wind data from Ålborg represented the nearby sites Boddum and Holmstange. The remaining two eelgrass sites (Samsø and Vejle) were situated in between the two wind

stations and were tested for relations to both. The wind speed was measured for the three sites. We used wind speeds >15 m/s to represent hard weather conditions, while wind speeds >20 m/s represent storm events.

Data on ice-cover in open waters for the period 1906–1998 were provided by the Danish Navy (SOK, 1999). Open waters are the last to freeze over compared to more or less enclosed bays, and hence the use of open-water data gives the best indication of periods of ice-cover at all five study sites.

Daily measurements of water temperature in the period 1941–1998 (except 1976) at a depth of 1 m at Vilsund in Limfjorden were supplied by DMI. Monthly means were calculated and the average temperature of the warmest month was identified for each year in the study period. Yearly fluctuations in mean monthly surface-water temperature are generally synchronous in Danish waters with local differences of only a few degrees (Rasmussen, 1977). Hence water temperatures from Vilsund can be used to describe the relative year-to-year changes for all five study sites.

Data on nutrient loading were based on reports of the total amount of fertilizers sold per year in Denmark (data from Statistics Denmark). A nitrogen budget for the Danish farming industry has demonstrated a relatively strong correlation between fertilizer consumption and the nitrogen surplus that eventually ends up in the environment, and hence suggests that fertilizer consumption is a reasonable indicator of the general nutrient load to the coastal waters.

2.4. Calculation of exposure index

We calculated the weighted effective fetch (WEF) at the study sites based on the following model (modified from Beach Erosion Board, 1972):

$$\text{WEF} = \sum Fwf$$

where F is the weighted fetch, i.e. distance (km) to the nearest coast, for each of eight compass directions, w the average maximum wind speed per month and f the frequency of observations at a given wind direction. In the calculation of F , the fetch was measured for each of the eight compass directions, each including four additional directions (± 11.25 and $\pm 22.5^\circ$):

$$F = \sum D_i \frac{\cos i}{5}$$

where D_i is the length of each of the five fetch lines for each compass direction and i the angle between compass direction i and each of the additional fetch lines. Calculations of WEF are based on data on wind frequency and speed measured every 3 h in the period 1995–99 at Kastrup Airport situated about 4 km from the Amager study site. Finally, the study sites were normalized by giving the most physically exposed station (i.e., the station with highest WEF) the value 100 and relating the remaining stations to that value.

2.5. Data analysis

We used the coefficient of variation (CV) as a measure of the variability in eelgrass area distribution and the linear regression analysis to assess temporal trends in eelgrass area distribution at each site.

The distribution area of eelgrass in each study site was correlated to environmental factors of the previous year. Similar combined analyses including all study sites were performed based on relative levels of eelgrass area distribution (Rel. area) calculated as:

$$\text{Rel. area}_{\text{site } x}(\%) = \frac{\text{area}_{\text{site } x, \text{ year } x}}{\text{mean}_{\text{area site } x, \text{ all years}}} \times 100$$

As the wasting disease markedly influenced many of the sites until around 1970, correlation between eelgrass area distribution and environmental variables was tested for the period 1970–1990s. The limited number of data points at each study site and the lack of site-specific environmental data excluded more sophisticated analyses such as multiple regression.

3. Results

3.1. Changes in eelgrass area distribution

The populations severely affected by the wasting disease in the 1930s (Holmstange, Boddum and Vejle) showed slow initial recolonization in the 1940s/early 1950s before substantial recolonization took over in the late 1950s/1960s (Fig. 2). At Holmstange, only slight changes occurred in the 1940s and early 1950s, but from 1954 to 1959 the eelgrass area increased about nine times from 1.1 to 9.7 ha (Fig. 2A). Vejle did not show significant recolonization until the 1960s when the eelgrass area increased from 1.7 to 5.0 ha (Fig. 2C). At Boddum, the first record of significant recolonization was in 1975, but since no data are available from the 1960s, it could have taken place much earlier (Fig. 2B).

The two areas where little or no damage was seen as a result of the wasting disease (Samsø and Amager) both exhibited high eelgrass cover right from the beginning of the investigation period in the 1950s (Fig. 2D and E). According to local inhabitants, extensive eelgrass populations were present at Samsø already in the 1940s, and a low-quality aerial photograph from 1945 (not meeting the criteria for image analysis) supports this statement. In the 1950s and 1960s, Amager, which was unaffected by the wasting disease, showed the highest levels of eelgrass area cover of the entire investigation period (Fig. 2D).

After the generally high levels in the 1960s and early 1970s, eelgrass area distribution declined in the late 1970s and early 1980s at many sites. At Samsø, the decline started already in the 1950s or 1960s, with an 18% reduction from 1954 to 1969, and continued through the 1970s. Holmstange, Boddum and Amager also experienced marked declines of 25, 44 and 50%, respectively, in the 1970s, while the populations in Vejle remained unchanged.

The 1980s and 1990s were characterized by large fluctuations, especially at the sites of low and medium exposure in Limfjorden (Holmstange and Boddum) and at Samsø. Thus, at Holmstange and Boddum, the eelgrass area more than tripled from 1986 to 1992. This trend continued at Holmstange while Boddum experienced a 58% decline from 1992 to 1998. At Samsø, the eelgrass area declined by 55% from 1988 to 1993 and did not increase noticeably the following years. At the more exposed sites, Vejle and Amager, the eelgrass area distribution was quite stable except for the low 1995 level in Vejle (Fig. 2C).

Eelgrass area distribution thus showed marked inter-annual variations at all study sites. When calculated for the entire investigation period, coefficients of variation (CV) around

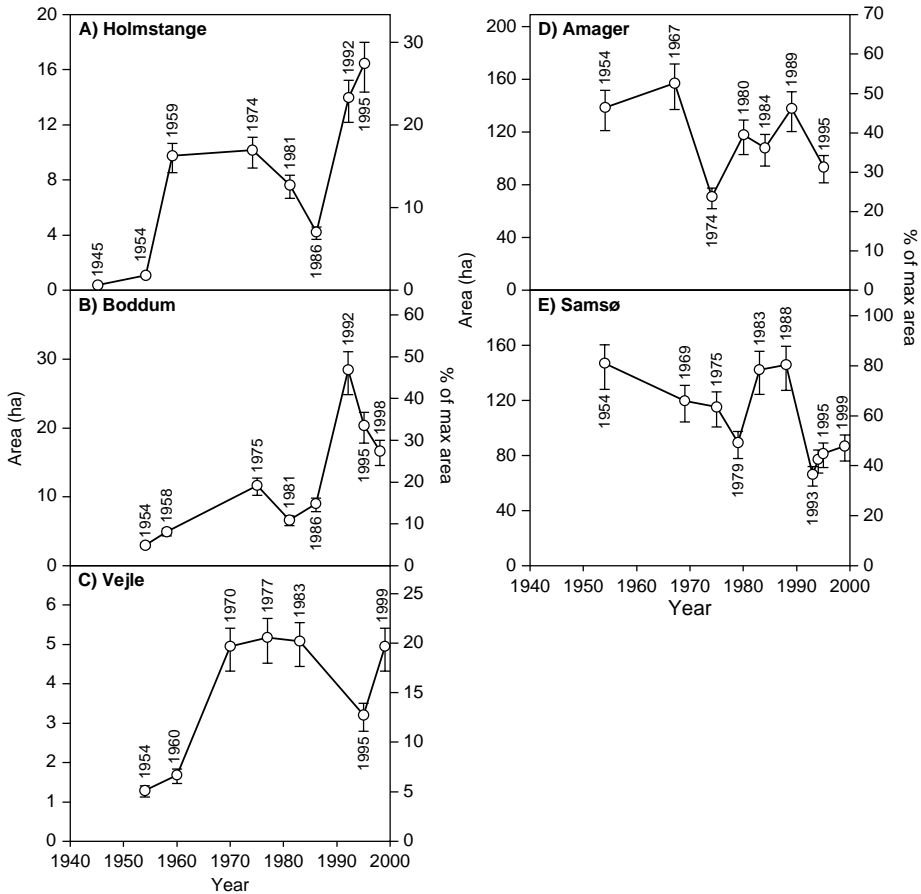


Fig. 2. Long-term changes in eelgrass area distribution at (A) Holmstange, (B) Boddum, (C) Vejle, (D) Amager and (E) Samsø. Error bars indicate maximum error of interpretation (see text). Eelgrass area distribution is illustrated on both an absolute hectare scale and a relative scale indicating the percentage of the total colonizable area (found by overlaying all mapping results and tracking the outer boundary of the total eelgrass area).

the mean area distribution ranged from 25 to 73%, the largest variations occurring in sites subjected to the wasting disease (Table 3). In the period after major recolonization had taken place (1970–1990), CV's ranged from 18 to 47%. The variation in eelgrass area cover tended to be larger in the most protected bays than in more exposed sites (Tables 1 and 3) but the differences were not significant (correlation analysis 1970–1990s: $P = 0.30$, $r^2 = 0.34$).

Regarded over the entire investigation period, sites subjected to the wasting disease showed a positive trend in eelgrass area distribution, significant for Holmstange and Boddum (linear regression, $P < 0.05$, Fig. 2A and B, Table 3). In contrast, areas unaffected by the wasting disease showed a negative long-term trend, significant for Samsø (linear regression, $P < 0.05$, Fig. 2e, Table 3). The three populations affected by the wasting disease also generally cover a smaller fraction (up to 21, 28 and 47% in Vejle, Holmstange and Boddum,

Table 3

Temporal trends in area distribution of eelgrass meadows. Coefficients of variation (CV) of eelgrass area distribution in the entire period 1940/1950–1990 and in the period after marked recolonization had taken place (1970–1990)

Study site	CV (all years)	CV (1970–1990)	<i>r</i>
Holmstange	73	47	0.76*
Boddum	69	52	0.77*
Vejle	45	18	0.63
Amager	25	24	−0.403
Samsø	29	30	−0.65*

Long-term trends in eelgrass area distribution are represented by the correlation coefficient (*r*) between year (1940–1990) and area.

* $P < 0.05$.

respectively) of the total colonizable area than do the unaffected sites Samsø and Amager (up to 81 and 53%, respectively, Fig. 2).

3.2. Environmental variables and their relation to eelgrass area distribution

The period before 1975 was generally more windy than the subsequent period although the occurrence of storms was relatively evenly distributed over the investigation period (data not shown). Wind speeds >15 m/s were observed on average 53 times per year in 1953–1975 as compared to 16 times per year in 1976–1999, while wind speeds >20 m/s were observed 2.1 and 1.4 times per year, respectively, in the same periods. Some of the most severe storms occurred in October 1967, November 1973, 1981, 1984 and 1985 and in January/February 1990.

The last century experienced several ice winters. In the late 1930s/early 1940s winters were very cold, the coldest of the century being in 1941/42, when open waters were ice-covered for 71 days. Ice winters also occurred in 1955/56, 1962/63, 1969/70, 1978/79, 1981/82, 1984/85, 1986/87 and 1995/96 (data not shown).

The average water temperature of the warmest month ranged from 15.9°C in 1964 to 21.6°C in 1997 with a mean of 18.1°C . The warmest period was 1988–1997 but temperatures were also high in the 1940s, the late 1960s and early 1970s (data not shown).

The use of nitrogen fertilizers in Denmark increased dramatically in the period 1950–1980 and in spite of a slight decrease during the 1990s, the level was still at nearly 300,000 t N per year in 1997 (data not shown).

None of the available physicochemical factors correlated significantly with the area distribution of eelgrass in the individual sites or with the relative distribution area of eelgrass across study sites.

4. Discussion

4.1. Aerial photography and image analysis as assessment tools

Aerial photography in combination with image analysis has become an increasingly common tool for identifying changes in area distribution of seagrasses (e.g., Robbins, 1997;

Kendrick et al., 1999; Kendrick et al., 2000). The techniques have developed rapidly over the past few years, and when high-quality photos and solid ground truth information are available, automated techniques have proved quite successful (Kendrick et al., 2002) and more sophisticated analyses and modelling can be made (e.g. Moore et al., 2000; Kelly et al., 2001; Lathrup et al., 2001). The techniques are generally most reliable in shallow waters since light attenuation reduces the contrast between eelgrass and background sediments at greater water depths and renders interpretation difficult. Reliability problems may also arise in areas with dark structures such as macroalgae, stones and mussels that can be mistaken for eelgrass. In the present study, we decided to apply manual image analysis rather than automated techniques because not all the historic photos had the quality necessary for a reliable automated interpretation. Tests of the manual interpretation technique demonstrated a reliability satisfactory for assessing relative changes in area distribution between years since the interpreter used approximately the same relative threshold for identifying eelgrass in all photos (the area interpreted as eelgrass varied only -2.6 to $+6.6\%$ relative to the mean of the interval defining the maximum possible error of the eelgrass estimates. Also, in the present study, we used only shallow sites with bright, sandy sediments providing a clear contrast to eelgrass meadows. Hence, the marked long-term fluctuations in area distribution of eelgrass (Fig. 2) reflect genuine changes.

4.2. *Recolonization after the wasting disease*

We found that eelgrass populations that were practically wiped out by the wasting disease in 1930–1940 showed a time lag of more than 10 years before substantial recolonization began. As only few stands had survived the wasting disease, the initial recolonization must have relied primarily on seeds and to a lesser extent on vegetative dispersal. Eelgrass seeds have a negative buoyancy that makes the majority settle close to the mother plant, but rafting of detached flowering shoots may transport a fraction of the seeds over long distances (Phillips and Backman, 1983; Orth et al., 1994). Long distances to the nearest seed-producing stands were probably the primary limiting factor to initial recolonization. Also, seedling mortality is generally high (Olesen and Sand-Jensen, 1994b), and extreme climatic events involving hard winds and severe ice winters in the period following the wasting disease may have further increased mortality. The initial recolonization may have been further delayed by changes in sediment composition towards coarser material less suitable for eelgrass growth during the period without eelgrass (Rasmussen, 1977).

After the slow initial recolonization, the eelgrass area increased rapidly, and large recoveries had taken place in the 1960s. Thus, recolonization proved to be a self-accelerating process as described by Hemminga and Duarte (2000). Several mechanisms operate in this process. The large and rapid increases in eelgrass area distribution suggest that seed dispersal played a significant role, and vegetative growth of scattered shoots not visible in the aerial photographs may also have contributed. Though vegetative growth from the edge of existing eelgrass patches is a rather slow process averaging 16 cm per year in Danish populations, patchy areas with more edge for vegetative growth recolonize faster than do continuous meadows (Olesen and Sand-Jensen, 1994b). The mutual protection among neighbouring plants reduces shoot mortality (Duarte and Sand-Jensen, 1990) and the rising number of seed-producing plants in the area increases the formation of new shoots and patches. More

and larger patches further increase self-protection and stability of the population (Olesen and Sand-Jensen, 1994b; Ramage and Schiel, 1999). In the 1960s, about 30 years after the wasting disease, the shallow eelgrass meadows had recolonized substantially. Similarly recolonization times have been observed in *Zostera* species in Australia and the Netherlands (Verhagen and Nienhuis, 1983; Larkum and West, 1990). These field observations lie within the range of eelgrass recolonization times predicted by models (Duarte, 1995). In comparison, the large Mediterranean seagrass species *Posidonia oceanica* requires centuries for recolonization due to slow rhizome elongation rates and rare sexual reproduction (Duarte, 1995; Meehan and West, 2000). Small, fast-growing seagrass species, on the other hand, recover within just one or a few years (Duarte, 1995).

4.3. Trends and patterns in eelgrass area distribution

All study sites showed large fluctuations in eelgrass area distribution during the investigation period. The fact that the fluctuations were sudden and large rather than gradual suggested that they were largely governed by stochastic factors.

The fluctuations tended to be larger in more protected bays than along open coasts (Table 3). This difference probably results from the more eutrophic conditions often prevailing in protected areas in combination with more stagnant waters allowing extreme temperatures to develop. Prolonged periods of warm and stagnant waters in eutrophic areas may generate sudden anoxic events with dramatic effects on eelgrass as well as on other flora and fauna (Valiela et al., 1992; Boynton et al., 1996; Greve et al., 2003). The warm summers of 1992 and 1994 thus affected many Danish eelgrass meadows negatively (Rask et al., 2000) and may also have triggered the decline of eelgrass at Samsø in 1993 as well as the decline in Boddum and in the two exposed sites Vejle and Amager in 1995. The protected eelgrass populations seemed more vulnerable than exposed populations to the unfavorable conditions of the 1990s since eelgrass area distribution remained low at both Boddum and Samsø while it returned to its original level at Vejle in 1999 and was unaffected at Holmstange.

The stochastic occurrences of hard winds and storms as well as severe ice winters may also have caused some of the sudden reductions in eelgrass area distribution although no such relations were revealed in our limited data set.

While deep-water eelgrass populations have declined markedly over the last century (Olesen, 1993; Boström et al., 2003), our results demonstrate that temporal trends of shallow-water populations are less equivocal. Areas unaffected by the wasting disease showed a negative long-term trend in eelgrass area distribution while the sites subjected to the wasting disease showed an overall positive trend, in spite of declines in the 1980s and 1990s (Table 3). These patterns may imply that growth conditions for eelgrass have become less favorable during the investigation period. Unfavorable conditions during the past few decades may also have prevented the meadows affected by the wasting disease from reaching their maximum potential distribution area. Only studies covering longer time series or more sites can reveal, if these speculations hold true. Still, the large potential recolonization rates of eelgrass documented in this study suggest that shallow-water and possibly also more deep-water populations may recolonize relatively fast when suitable environmental conditions are present.

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