

Spatial and temporal variation in eelgrass (*Zostera marina*) landscapes: influence of physical setting

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Abstract

The distribution of eelgrass (*Zostera marina*) was mapped from aerial photographs at three Danish sites with different levels of physical exposure by digital image analysis at 1 m × 1 m resolution. A set of indices from landscape ecology were used to quantify various components of the eelgrass landscapes such as patch shapes and landscape aggregation in photographs from 1995. Furthermore, the long-term fluctuations in the spatial distribution of eelgrass were investigated during the period 1954–1995/1999. Eelgrass landscapes exposed to wave dynamics were less aggregated with more elongated patch shapes than the sheltered eelgrass areas. The outline of the larger patches also tended to be more complex at exposed sites. Patch size distribution at all sites was highly skewed with 75–95% of the patches being < 10 m². Although the majority of the patches were small, they only constituted a small proportion of the total eelgrass area because most of the eelgrass-covered area was contained in a few, large patches. Large fluctuations in the spatial distribution of eelgrass occurred at both exposed and protected sites in the course of the investigation period. In the relatively short intervals of ~7 years between two consecutive photographs, on average 39–62% of the total eelgrass area covered in the photographs had changed (i.e., disappeared or recolonized) and the largest changes occurred at exposed sites. Overall, this study showed that shallow eelgrass populations form characteristic landscapes with a configuration that is highly related to the level of physical exposure and that the size and position of eelgrass beds changes substantially among years. © 2003 Elsevier B.V. All rights reserved.

Keywords: Seagrass; *Zostera marina*; Landscape-ecology; Spatial distribution; Sediment movement; Physical exposure

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1. Introduction

Seagrass communities form characteristic landscapes ranging from highly fragmented to almost continuous meadows covering extensive areas. The mosaic of patches shows a hierarchical arrangement of spatial structure ranging from individual shoots (centimeters), to discrete patches (meters), to seagrass landscapes (tens of meters to kilometers; Duarte and Sand-Jensen, 1990a,b; Duarte et al., 1994; Robbins and Bell, 1994; Turner et al., 1999). Most seagrass research has been concentrated on the meter scale or lower, whereas large-scale studies are few (Duarte, 1999).

Seagrass populations show extensive spatial and temporal fluctuations (Clarke and Kirkman, 1989; Robbins, 1997; Kendrick et al., 1999; Robbins and Bell, 2000) and seagrass landscape patterns are under continuous transformation due to disturbances of varying intensity and frequency (Williams, 1988; Short and Wyllie Echeverria, 1996; Fonseca and Bell, 1998; Kirkman and Kirkman, 2000). The agents of pattern formation can be categorized as either extrinsic or intrinsic depending on whether they relate to factors in the surrounding environment or result from attributes of the plants themselves. Physical disturbances are considered one of the main extrinsic factors controlling the spatial structure and species diversity of seagrass meadows (Den Hartog, 1971; Patriquin, 1975; Clarke and Kirkman, 1989; Duarte et al., 1997), and accordingly Fonseca and Bell (1998) demonstrated that seagrass cover could be successfully predicted from a wave exposure index. Wind-generated wave dynamics and tidal currents create sediment movement, which may either bury plants, expose roots and rhizomes or during heavy storms even uproot entire plants (Kirkman and Kuo, 1990; Preen et al., 1995). Plant burial was found to be an important mechanism of gap formation in a seagrass system in Tampa Bay, USA (Bell et al., 1999) and the patch dynamics of a *Zostera marina* vegetation in Rhode Island, USA was likewise thought to be controlled by sediment movement (Harlin and Thorne-Miller, 1982). Furthermore, Marbà et al. (1994) found that subaqueous dune migration in Alfacs Bay, Spain, led to periodic burial of a *Cymodocea nodosa* population. In areas with moderate to strong wave surge, migrating blowouts (i.e. vegetation-free depressions within the seagrass beds) may develop (Patriquin, 1975; Clarke and Kirkman, 1989). Other extrinsic disturbances such as ice scouring, sediment reworking by bioturbation and anthropogenic eutrophication may also be important determinants of meadow structure (Cambridge and McComb, 1984; Robertson and Mann, 1984; Duarte, 1995; Townsend and Fonseca, 1998).

Intrinsic agents of patch formation are plant growth characteristics (e.g., rhizome growth rates, rhizome branching frequency and branching angle), plant demographic processes (e.g., shoot recruitment and mortality) and competition between species (Duarte and Sand-Jensen, 1990a,b; Olesen and Sand-Jensen, 1994a,b; Vermaat et al., 1995; Marbà and Duarte, 1998). In the case of *C. nodosa* it has been observed that even small directional differences in patch growth resulted in asymmetric shapes, because patch growth accelerated as size increased and small differences were therefore enhanced as the patch elongated (Duarte and Sand-Jensen, 1990b). Fonseca and Bell (1998) described the formation of halos in large circular patches of *Halodule wrightii* and *Z. marina*, most likely arising from centrifugal expansion of the patches and increased mortality of older plants at the center of patches.

The combined action of the various extrinsic and intrinsic factors result in landscape patterns with different patch shapes. In protected areas with calm hydrodynamic conditions the patches have been observed to be predominantly circular, resulting in a pattern resembling that of leopard skin (Den Hartog, 1971). This pattern is not confined to seagrasses but is also seen in coral formations behind the outer reefs and in freshwater plants growing in stagnant waters (Den Hartog, 1971). As the area becomes more exposed, wave action and tidal currents make the seagrass patches more elongated (Den Hartog, 1971; Fonseca et al., 1983), and the patches often form a stripy zig-zag pattern (Den Hartog, 1971). The same pattern has also been observed in mussel banks in the Dutch Wadden Sea and is probably related to shuttling tidal currents (Den Hartog, 1971). The fact that these patterns are not just restricted to seagrasses strongly suggests that extrinsic factors are an important influence on the spatial configuration of seagrass landscapes.

Seagrass communities show many analogs to terrestrial vegetation. On the landscape scale, both form mosaics of patches and as seagrasses occur in shallow water their distribution can be assessed by techniques normally applied in terrestrial ecology (i.e., aerial photographs and satellite images). Terrestrial ecologists have derived a number of indices for detecting and describing patterns of land use and habitat change and many of these are readily applicable to seagrass landscapes (Robbins and Bell, 1994; McGarigal and Marks, 1995 and references therein). Frederiksen et al. (2003) used aerial photographs to assess fluctuations in overall area cover of eelgrass over the last 50 years and found that significant changes in eelgrass area had occurred in the intervals of around 7 years between photographs. Here, we assess how these changes occurred spatially and determine whether the spatial distribution of eelgrass in exposed and protected sites differs. The present study has two main purposes: (1) to use indices derived from terrestrial landscape ecology to describe differences in landscape configuration (patch complexity, elongation of patches, landscape aggregation) and landscape composition (patch size distribution) between the areas; (2) to examine long-term changes in the spatial distribution of shallow-water eelgrass populations in three areas with different levels of physical exposure. We hypothesize that the increased wave action in exposed sites results in less aggregated populations, more complex patch shapes and large changes in eelgrass cover as compared to protected areas.

2. Materials and methods

2.1. Study sites

Three study sites (Vejle, Amager and Samsø) with different levels of physical exposure were selected for this study (Frederiksen et al., 2003). Located on the north coast of Vejle fjord, the study site Vejle is exposed to southwesterly to southeasterly winds. The coastal profile is quite steep in that a depth of 3 m is reached over a distance of 250 m. The water circulation in the fjord is controlled by meteorological factors, but the predominant situation is an incoming current on the north side and an outgoing one on the south side (Christiansen et al., 1991). The study site at Amager is exposed to southwesterly to easterly winds and the prevalently north-going current results in high water exchange in the area. The coastal slope is gentle (6 m depth is reached about 2000 m from shore) providing a large area suitable for

eelgrass growth. The third study site Samsø is the most protected site, being sheltered from waves in all directions. The area is shallow with water depths of no more than 2 m and the deepest parts are located in the center of the area.

2.2. Wave exposure computations

The measure of wave exposure was based on a calculation of weighted effective fetch (WEF) modified from a model developed by the [Beach Erosion Board \(1972\)](#). The study sites were normalized by giving the most physically exposed site (i.e., the site with the highest WEF) the value 100 and then relating the remaining sites to that value. Amager was the most exposed (WEF = 100), Vejle was intermediate (WEF = 48) and Samsø was the most protected site (WEF = 12). For more details, see [Frederiksen et al. \(2003\)](#).

2.3. Acquisition and rectification of photographs

The analysis of landscape structure and long-term changes in spatial distribution of eelgrass was based on aerial photographs acquired from the National Survey and Cadastre (KMS) on the scales 1:10,000, 1:20,000 or 1:25,000. Most of the photographs (66%) were in black and white and only the most recent photographs were in color. For the analysis of landscape structure color photographs were used but in the analysis of long-term change in spatial distribution we converted color photographs to black and white in order to use the same mapping method on all photographs. Detailed information on scanning and rectification is presented in [Frederiksen et al. \(2003\)](#).

2.4. Analysis of landscape structure

We used a number of indices derived from the terrestrial landscape ecology to describe landscape configuration (patch shape, landscape aggregation) and landscape composition (patch size and patch area distribution). None of the acquired photographs were originally taken for the purpose of mapping vegetation, but color photographs from 1995 were of a high quality and available from all sites and were therefore used in the landscape analysis. By using color photographs the accuracy of eelgrass mapping was enhanced because these photos contain information in three bands (red, green and blue) compared to only one in black and white photographs. This extra information was applied in a maximum-likelihood classification analysis using the [CHIPS software \(CHIPS Development Team, 2003\)](#). A detailed description of the maximum-likelihood classification algorithm can be found in [Jensen \(1996\)](#). Briefly, the classification procedure uses statistics (covariance matrix) derived from a set of training data to calculate the probability of a given pixel belonging to a given class (sand, eelgrass, other vegetation, etc.). Training data are pixels specified by the interpreter as belonging to a given class. In the mapping procedure, each pixel is assigned to the class to which it has the highest probability of belonging. The accuracy of the maximum-likelihood classification was tested by comparing mapping results with a new set of training data (control data), and between 90 and 93% of the pixels specified to be eelgrass in the control data were classified as such in the three locations. This accuracy describes how well the pixels specified as eelgrass by the interpreter are classified as

such by the maximum-likelihood algorithm. As no ground truth data exist for the historical photographs used, it was not possible to assess how well the mapping results matched the actual eelgrass cover.

To be able to describe the composition and configuration of the landscape, the eelgrass area was divided into distinct patches. The outline of patches was based on the 4N method (Elkie et al., 1999), where 4N refers to the number of directions in which the program searches for neighboring pixels of a similar kind. This method includes orthogonally and not diagonally positioned pixels. Patches extending beyond the outer borders of the study area were included in the calculations but only the fraction of the patch within the limits of the study area was analyzed.

The following (dimensionless) indices were used in the analysis.

2.5. Aggregation index (AI)

This index measures the level of aggregation of the pixels representing eelgrass (He et al., 2000; Mladenoff and DeZonia, 2001):

$$AI = \frac{\text{total adjacent edges of the eelgrass class with itself}}{\text{maximum possible adjacent edges of the eelgrass class with itself}}$$

Each pixel has four edges and maximum aggregation (AI = 1) is achieved when all pixels of a class are completely aggregated into a single square patch. The aggregation index was calculated in APACK (Mladenoff and DeZonia, 2001)

2.6. Related circumscribing square (SQUARE)

This index describes the “elongatedness” of patches by comparing the area of the patch with the area of the smallest square that circumscribes the patch (McGarigal and Marks, 1995):

$$SQUARE = 1 - \frac{a_{ij}}{a_{ij}^s}$$

where a_{ij} = area (m^2) of patch ij and a_{ij}^s = area (m^2) of the smallest circumscribing square around patch ij . SQUARE = 0 for square patches and approaches 1 for elongated, linear patches one pixel wide. The Related Circumscribing Square index was calculated by the Patch Analyst (Elkie et al., 1999) and Spatial Analyst extensions for ArcView (ESRI GIS and Mapping Software).

The Spatial Analyst extension was only applicable to polygons. The mapping results were therefore converted to polygons using the cityblock method, which follows the edges of the pixels in order to preserve the raster-based nature of the eelgrass maps.

2.7. Shape index (SI)

The shape index measures the complexity of the eelgrass patch shape (Forman and Godron, 1986) by comparison to a standard shape (square) of the same area and

therefore involves no size dependency problems:

$$SI = \frac{0.25P}{\sqrt{A}}$$

where P and A are perimeter and area of the patch, respectively. $SI = 1$ when the patch is square (a square is the simplest patch shape due to the square nature of the pixels) and increases without limit as the patch shape becomes more irregular. This index overcomes the problem of the simple perimeter–area ratio, where an increase in patch size will cause a decrease in the perimeter–area ratio when keeping the shape constant (Forman and Godron, 1986). The shape index was calculated by the Patch Analyst (Elkie et al., 1999) extension for ArcView.

The shape index and the related circumscribing square index are both affected by the scale of the study. As the area decreases to the resolution of the eelgrass maps (1 m^2), the indices invariably approach 1 and 0, respectively, and patches in the $1\text{--}10 \text{ m}^2$ size category were therefore excluded from the analysis.

2.8. Analysis of long-term changes in area distribution

The rectified black and white photographs were analyzed manually because brightness levels changed significantly within and between photographs causing variation in the gray tones corresponding to eelgrass. Each photograph was divided into smaller sub-areas with similar brightness levels, and pixels representing eelgrass were identified. The sub-areas were finally merged and the resulting raster map was filtered using a mode filter, which converts highly isolated pixels with high possibility of being misclassifications to the most frequently occurring pixel in the filter kernel.

After the mapping procedure, eelgrass maps from two subsequent sampling years were overlaid and areas where eelgrass had declined, increased or remained unchanged in the intervening period were identified. To quantify the changes between two consecutive mappings we calculated an index of relative change to express the spatial changes. This index describes the proportion of the total area covered by eelgrass that was either lost or gained from year 1 to year 2:

$$\text{index of relative change} = \frac{\text{loss} + \text{gain}}{\text{loss} + \text{gain} + \text{common}}$$

Loss, Gain and Common refer to the area (m^2) of eelgrass that disappeared, was formed or remained in the same position, respectively, from year 1 to year 2. If no change occurred, the index was 0 and if all eelgrass had changed the value was 1.

Change detection by overlaying two classification results (post-classification comparison) is very sensitive to methodological errors in the rectification and the mapping process (Rutchev and Velcheck, 1994; Jensen, 1996). Positional errors introduced during rectification can displace eelgrass patches several meters from one year to another and thereby introduce false changes. We estimated the potential error by displacing the total eelgrass area in an east-west direction by a distance determined by the mean RMS error (1 m at Amager and Samsø, 6 m in Vejle). This area was then overlaid the original mapping result and the

Table 1

Percentage of the total eelgrass area affected by a displacement determined by the mean rectification error (RMS)

Station	Mean RMS rectification error (m)	Percentage of total area affected by displacement, average (range)
Samsø	1.0	5.0 (3.6–7.3)
Amager	1.2	7.2 (3.8–9.7)
Vejle	5.9	31.2 (26.9–36.9)

The analysis is based on three photographs from each study site.

area affected by displacements determined (Table 1). Three photographs from each study site were included in this analysis. At Samsø and Amager, the influence of the rectification error was low (5 and 7%, respectively), but at Vejle, where the mean RMS was about six times larger than at Samsø and Amager, on average 31% of the total eelgrass area might have been displaced without any real spatial change having occurred. We found this error to be too high for reliable analyses and Vejle was therefore excluded from detailed investigations of spatial changes. The previous estimates only apply to situations with no net change in total eelgrass cover. When the eelgrass cover changes substantially between years as in this study, the influence of displacement errors become less important. To illustrate this point classification results from two different years were overlaid as in the original analysis, but an additional rectification error was introduced by displacing the eelgrass by the mean RMS distance in both photographs. Though we displaced the eelgrass in the two photographs in opposite directions in order to cause the largest possible change they influenced the index of relative change by less than 2% (Table 2). It must be emphasized that the original index value is already influenced by rectification errors and that the new estimate only reflects the additional displacement.

The mapping process introduces additional errors in the spatial change detection because the relative gray tone threshold defining eelgrass may differ between years. The precision of the interpreter was tested as discussed in detail in Frederiksen et al. (2003). In short, a time series containing both low- and high-quality photographs was analyzed according to the procedures described above. Furthermore, a maximum and a minimum estimate of the eelgrass area cover were made to assess the possible range of cover the given year. The maximum estimate included areas with very sparse eelgrass cover (bright pixels) that might easily be mistaken for other features such as dark sand. The minimum estimate only included the darkest pixel values representing the most distinct and dense eelgrass areas. The eelgrass areas of the original mapping results ranged from –2.6 to +6.6% relative to the

Table 2

Potential influence of rectification and mapping errors on the index of relative change

Station	Total displacement (m)	Maximum influence of rectification errors on index of relative change, average (%)	Maximum influence of mapping errors on index of relative change, average (%)
Samsø	2	1.7	14.1
Amager	2	1.9	5.3

The analysis is based on three photographs from each study site.

mean of the corresponding minimum–maximum interval. To illustrate the effect of mapping errors on the index of relative change the average of this interval was either subtracted or added to the eelgrass area in the 2 years included in the change detection, respectively. The influence of this error turned out to be highest at Samsø (14%; Table 2).

In conclusion, the analysis of spatial changes is affected by considerable methodological errors. At Samsø and Amager our estimates of the combined rectification and classification error ranged from about 7–16%. At Vejle, we found the potential influence of the rectification errors to be too high to make reliable analyses and conclusions. Comparisons of long-term spatial changes between exposed and protected eelgrass landscapes are therefore based only on the results from Amager and Samsø, and Vejle is only used to emphasize our conclusions.

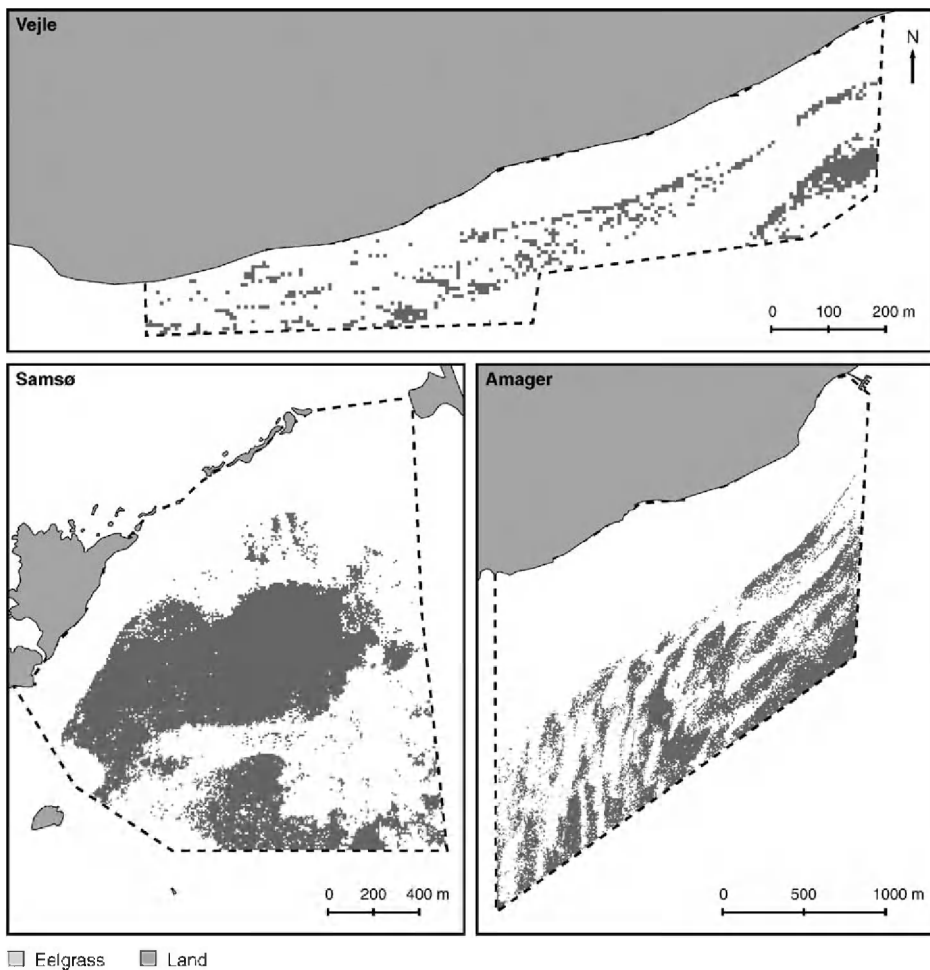


Fig. 1. Mapped eelgrass distribution in 1995 at the three study sites.

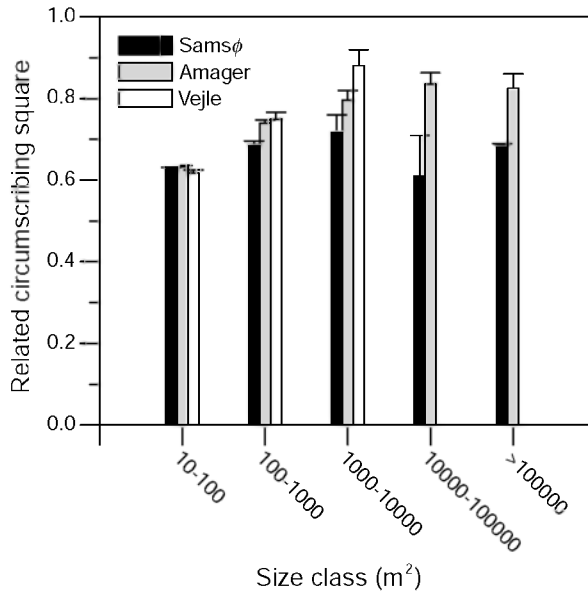


Fig. 2. Related circumscribing square index of patches in various size classes at Vejle, Amager and Samsø. The index ranges from 0 and 1, where high values indicate elongated patches and low values indicate more circular patches. Mean values \pm S.E. are shown.

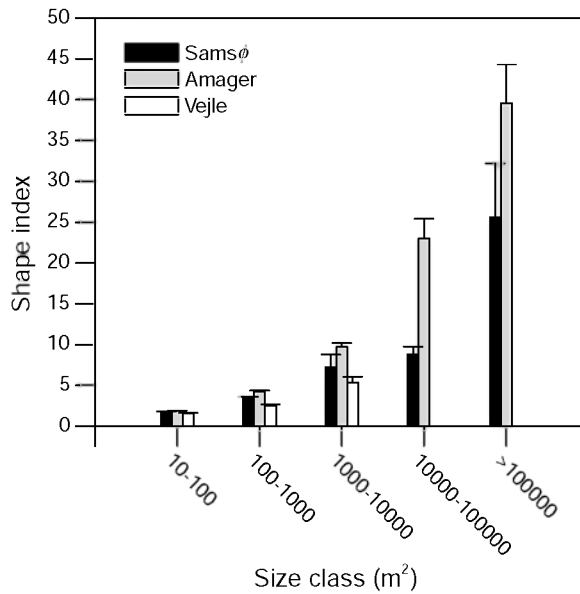


Fig. 3. Shape index of patches in various size classes at Vejle, Amager and Samsø. The shape index is 1 for patches with simple forms (square) and increases indefinitely, as the patch shape becomes more irregular. Mean values \pm S.E. are shown.

3. Results

3.1. Landscape variables

The spatial distribution patterns of eelgrass, as analyzed from the 1995 photographs, differed among the 3 study sites (Fig. 1). The total area colonized by eelgrass varied from $32 \times 10^3 \text{ m}^2$ at Vejle to $907 \times 10^3 \text{ m}^2$ at Amager and $817 \times 10^3 \text{ m}^2$ at Samsø. At Amager, a characteristic pattern of multiple elongated eelgrass beds separated by sandbars was observed. At Vejle a similar but simpler pattern was found with eelgrass growing mainly in two elongated belts parallel to the coastline. The eelgrass population at Samsø was not confined to belts and the patches were more circular in shape. The analyses on landscape configuration and composition further illustrated these observations. The AI showed that the eelgrass vegetation at the most protected site Samsø was less fragmented than the exposed popu-

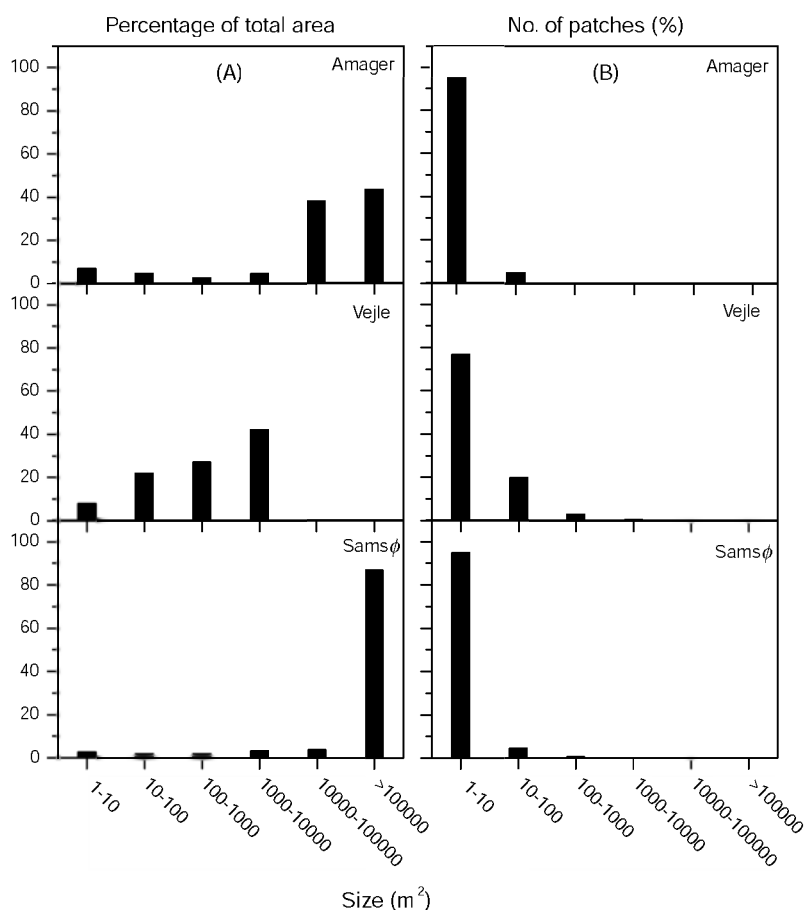


Fig. 4. Patch statistics of the three study sites. The figure shows the frequency distribution of total eelgrass area (A) and the numbers of patches (B) contained in the various size classes.

lations at Amager and Vejle (AI for Vejle, Amager and Samsø respectively 0.81, 0.83 and 0.95). The related circumscribing square index showed a clear tendency towards the large patches ($>100\text{ m}^2$) being more elongated at the two exposed sites Amager and Vejle than at Samsø (Fig. 2) In the smaller size categories, there was no difference between protected and exposed sites but the small patches were generally more square/circular than large patches at both the protected and exposed sites. The complexity of patch shapes determined by the shape index was higher at the exposed site Amager than at the protected Samsø site (Fig. 3).

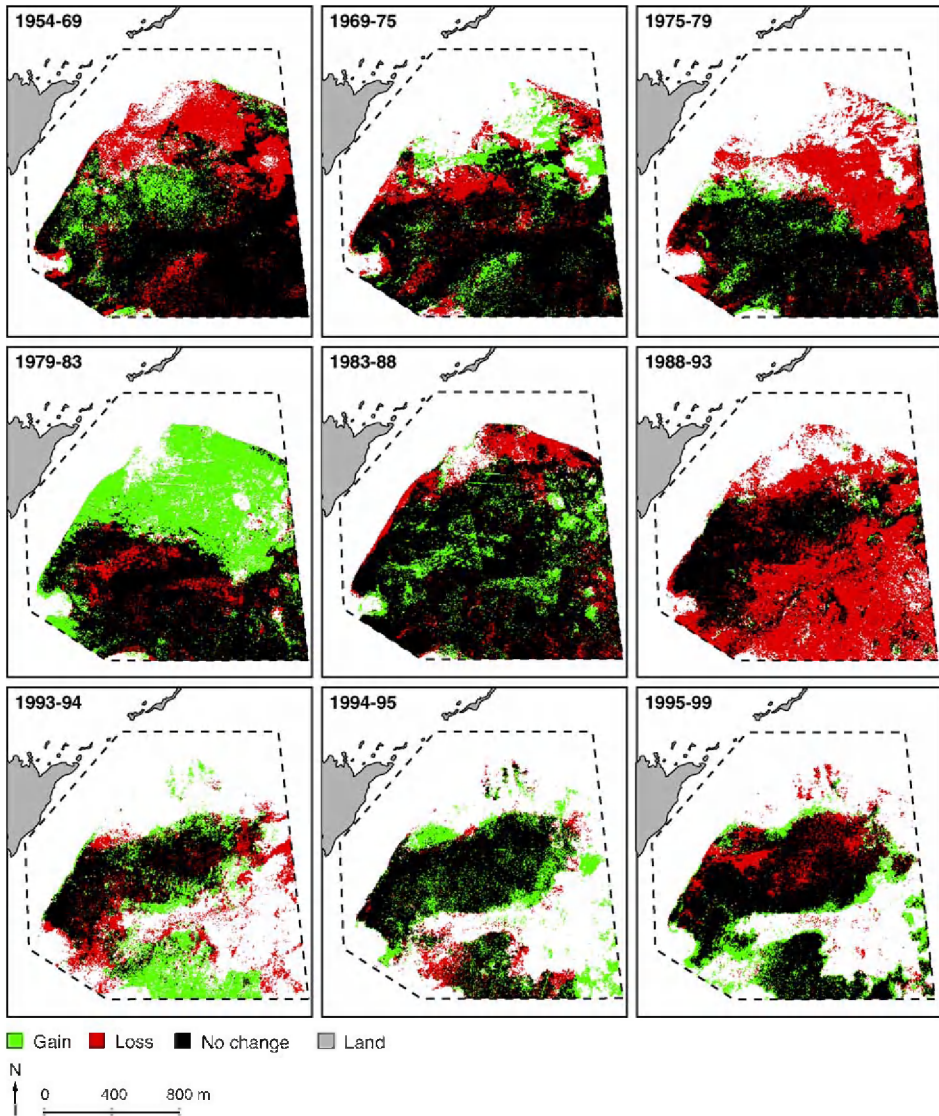


Fig. 5. Changes in spatial distribution of eelgrass at Samsø.

This was only the case in the two largest size classes, where Vejle was not represented. In the medium size classes Vejle seemed to have less complex patch shapes whereas no major differences between the three sites were observed in the small size classes.

The frequency distribution of patch size was highly skewed, with 75–95% of the patches being $<10\text{ m}^2$ (Fig. 4). Vejle, however, also had relatively high proportions of patches in the $10\text{--}100\text{ m}^2$ category. Although the majority of the patches were small, these only constituted a small proportion of the total eelgrass area because most of the eelgrass area was contained in few, large patches (Fig. 4). At Samsø, 87% of the total eelgrass area was contained in patches $>100,000\text{ m}^2$ and at Amager 38 and 43% of the eelgrass grew in the patch size categories $10,000\text{--}100,000$ and $>100,000\text{ m}^2$, respectively. This tendency was less pronounced in Vejle, where medium sized patches covered relatively large areas. Vejle

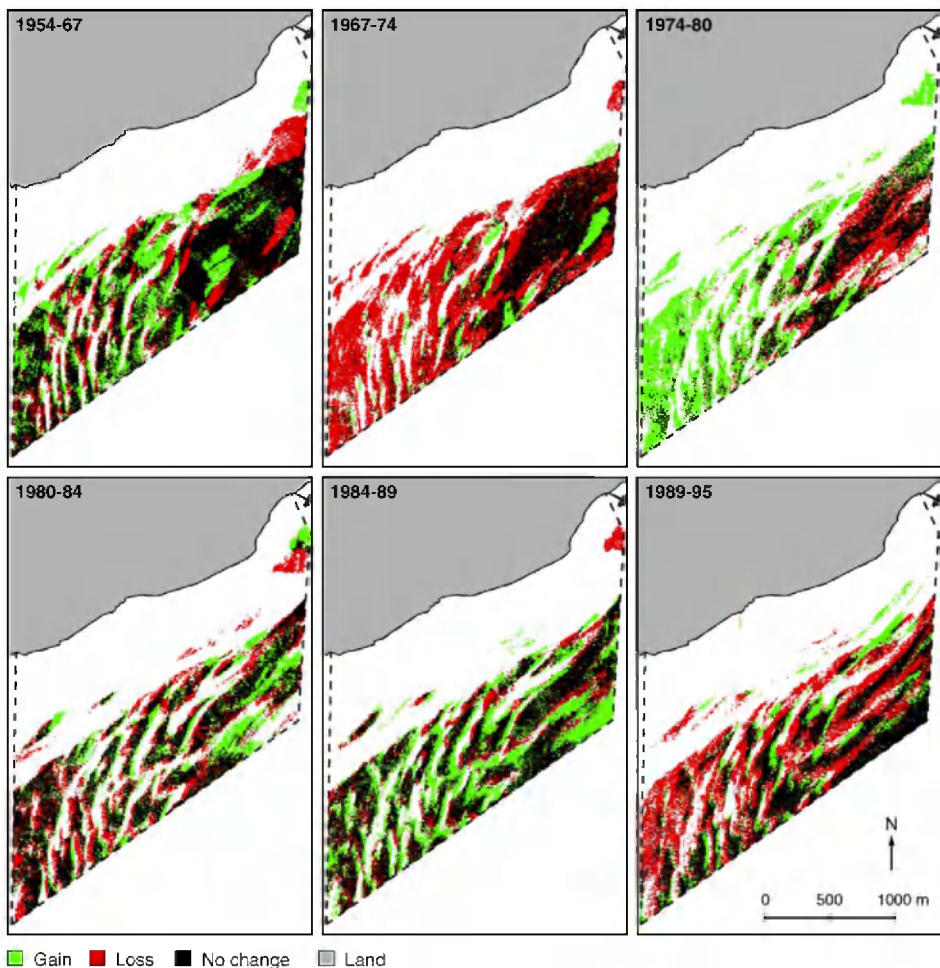


Fig. 6. Changes in spatial distribution of eelgrass at Amager.

had no patches in the largest size classes because the total eelgrass area constituted only $32 \times 10^3 \text{ m}^2$.

3.2. Temporal changes in spatial distribution

Large losses and gains occurred in the relatively short time periods between two consecutive mappings at all three sites (Figs. 5–7). The average index of relative change in eelgrass area distribution was significantly higher (*t*-test, $P < 0.01$) at the exposed Amager site (0.62) as compared to the protected Samsø site (0.39, Fig. 8). Spatial changes at Vejle were likewise very large.

Even though the population at Samsø showed the lowest index of relative change, it still exhibited substantial changes. These changes occurred mainly in the northern and shallowest part of the study site, but in the 1980s and 1990s, major changes were also observed in the southern and eastern areas. A large eelgrass area was lost in the northern part of the study site between 1975 and 1979 but had recovered to a large extent 4 years later in 1983. From 1988 to 1993, an even larger eelgrass area disappeared, and in 1999 eelgrass was still absent from the deeper, central parts of the investigation area. In the western parts of the study site eelgrass was present in all photographs during the 45-year study period. The maps of long-term changes in spatial distribution indicated that the entire study area, in contrast to the exposed sites, was potentially suitable for eelgrass growth. The only exception was the

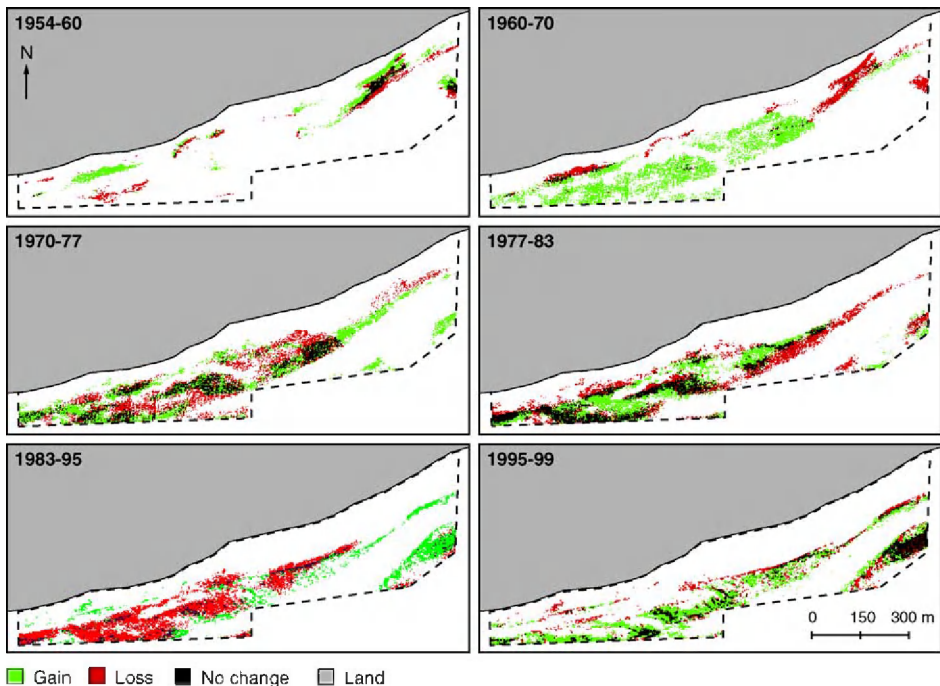


Fig. 7. Changes in spatial distribution of eelgrass at Vejle.

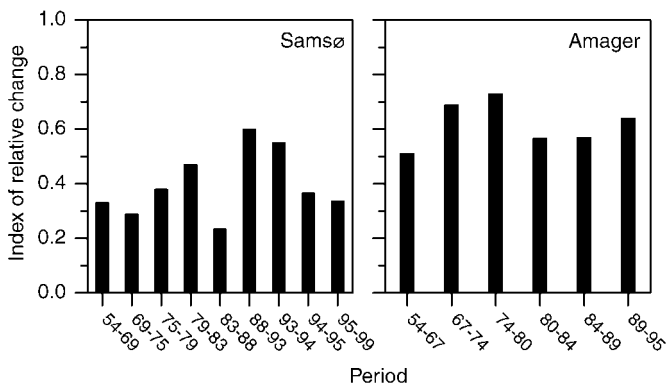


Fig. 8. Index of relative change at Amager and Samsø. The figure shows the proportion of the total eelgrass area investigated in both years that was either lost or recolonized in the intervening period.

extremely shallow (<0.4 m) zone along the northern and western periphery of the study area (Fig. 5).

At Amager, the characteristic pattern of multiple elongated eelgrass beds separated by sandbars was seen throughout the investigation period (Fig. 6). Many of the sandbars and eelgrass belts, especially in the western parts, were not parallel to the shore line but positioned at an angle of $\sim 45^\circ$ to the coast. A large proportion of the eelgrass disappeared from 1967 to 1974 but almost the same pattern of alternate eelgrass belts and sandbars emerged again after the substantial recolonization that took place from 1974 to 1980. There was a general tendency towards eelgrass meadows in the western part of the study area moving slowly in a northeasterly direction. This movement was mediated by the fact that eelgrass loss predominantly occurred along the western edges of the patches, while new growth took place along the opposite eastern edges (Fig. 6). At Vejle, the position of the eelgrass belts likewise changed markedly, and eelgrass was rarely present at the same positions at two consecutive samplings (Fig. 7).

4. Discussion

4.1. Landscape structure

From visual examination alone it is clear that the spatial patterns of seagrass cover differed between the three study sites. The use of indices from terrestrial landscape ecology made it possible to quantify these differences, allowing more detailed comparisons of the study sites. The protected site, Samsø, contained the most aggregated eelgrass vegetation, probably because it was less exposed to perturbations from physical disturbance factors. Despite the large difference in degree of exposure among the study sites the aggregation values were relatively high (>0.8), indicating that on the 1-m scale of investigation, eelgrass landscapes are highly continuous. Aggregated populations are probably more resistant to physical disturbances than patchy populations, because the homogeneous root/rhizome matrix stabilizes

the sediment and less patch edge is exposed to damage from waves or tidal current (Fonseca, 1996; Ramage and Schiel, 1999). Outside aggregated areas, eelgrass is more vulnerable and probably has a higher risk of being destroyed (Ramage and Schiel, 1999).

The related circumscribing square index showed more elongated patches at the two exposed sites compared to the protected Samsø site. This phenomenon was restricted to patches larger than 100 m² and it was probably the presence of sandbars at the exposed sites that influenced the shape of large patches. Sandbars generated by wave action (Komar, 1976) prevent seagrasses from expansion through burial of shoots (Marbà et al., 1994) and eelgrass growth was therefore restricted to the area between the sandbars (Frederiksen, personal observations). At Samsø, the absence of sandbars allows eelgrass patches to develop in all directions. Patches in the small size classes showed no difference in related circumscribing square index between exposed and protected study sites, and small patches generally appeared more circular than large patches. Small, newly formed patches are circular by nature since they arise initially from a single shoot, and if no disturbance factors act on a patch, the vegetative expansion should occur at the same rate in all directions (Den Hartog, 1971; Duarte et al., 1994). This theoretical situation can easily be disrupted in natural populations by the coalescence of patches and by extrinsic disturbance factors such as bioturbation (Townsend and Fonseca, 1998).

Patch complexity (as expressed by the shape index) influences the rate of seagrass colonization by determining the rate of patch expansion by vegetative growth (Olesen and Sand-Jensen, 1994b). The index showed that patches larger than 100–1000 m² exhibited a higher complexity at Amager. Here, the eelgrass vegetation was widely interspersed with unvegetated areas, causing patches to become highly convoluted. At Samsø, eelgrass was predominantly confined to well-defined areas with dense eelgrass cover surrounded by unvegetated areas. The other exposed site Vejle did not have patches in the largest size classes, but in smaller size classes the patch shapes were slightly less complex than at the two other sites. Therefore, we cannot determine whether patches at exposed sites are generally more complex than at protected sites. The continuous physical disturbance at exposed sites should intuitively result in more complex shapes, but on the other hand, a protected site might better allow seedlings and small patches to survive outside the large patches and the subsequent coalescence of these patches might equally result in complex shapes.

The largest proportion (76–95%) of patches was smaller than 10 m² though small patches constituted only a small proportion of the total eelgrass area. Predominance of smaller patches appears to be typical of shallow-water seagrass populations as studied here, and studies working on smaller scales have also shown that the majority of patches are generally <1 m² (Duarte and Sand-Jensen, 1990b; Olesen and Sand-Jensen, 1994b; Vidondo et al., 1997; Ramage and Schiel, 1999). A large proportion of small patches are indicative of rapid patch formation and mortality (Olesen and Sand-Jensen, 1994b; Vidondo et al., 1997). These patches have probably been formed from seeds dispersed from nearby patches and are important for further colonization of the area. Formation of many small patches instead of few large ones could increase the rate of areal expansion by subsequent vegetative growth significantly because small patches have a larger circumference relative to their size (Olesen and Sand-Jensen, 1994b). On the other hand, small patches are subject to higher mortality than large patches because mutual protection and patch maintenance are more efficient in large patches (Duarte and Sand-Jensen, 1990b; Olesen and Sand-Jensen, 1994b). Eelgrass

populations with a large proportion of the total area contained in large patches should therefore be more resilient to physical disturbances. However, this is only true if the impact of the disturbance factor is spatially variable. A situation where the entire area is affected by some sort of stress factor (e.g. widespread sedimentation, increased turbidity) the total seagrass population is affected, and patch size will not influence survival.

4.2. Long-term changes in spatial distribution

Historical photographs provide important information on seagrass distribution from the period before extensive seagrass research started. However, the use of these photographs has some limitations because they were not taken for the purpose of vegetation mapping and ground truth information is limited. At Amager and Samsø, the methodological errors were reasonable and fell in the same range, and most often the spatial configuration and size of the eelgrass area changed so much between years that these errors did not influence the overall conclusions. The considerable rectification errors in Vejle prevented a detailed analysis of long-term changes at this site. More sophisticated methods that reduce the methodological errors are available (Jensen, 1996), but these methods generally require photographs of high quality with little variation in brightness levels (i.e. the gray tones representing eelgrass should be the same all over the photograph).

The eelgrass landscapes changed extensively during the ~45-year investigation period and the spatial changes were greatest at the more exposed sites at Amager ($P < 0.01$) and Vejle. This seems to be in contrast to observations of Frederiksen et al. (2003) who found that fluctuations in total eelgrass area cover were largest at protected sites. It is very important, however, to distinguish between changes in total eelgrass area and spatial changes. We found high indices of relative change even during periods with relatively constant seagrass cover. At Amager, for instance, the area cover of eelgrass was quite stable in the 1980s (Frederiksen et al., 2003), but about 55 % of the eelgrass changed between two consecutive mappings. The mechanism behind is probably that extrinsic disturbance factors constantly change growth conditions in the exposed areas and keep the populations in a state of continuous recolonization. Eelgrass patches may thus be constantly moving even in periods where a constant total eelgrass area distribution suggests stable conditions in the population. This situation was observed at Amager where a complex system of alternating eelgrass belts and sandbars is found. The maps showed that the eelgrass belts migrated in a northeasterly direction (Fig. 6) and a survey study found the sandbars migrating in the same direction (Binderup et al., 1999). Outer sandbars feed the inner sandbars with sediment and substantial transportation of sand thus occurs along the sandbars (Binderup et al., 1999). This sediment movement most likely led to either burial or erosion on the western edges of the eelgrass patches and new growth mainly occurred in the eastern parts. As an attempt to estimate the migrating speed of these sandbars, we randomly measured eelgrass loss at the western patch edges from 1980–1984. Assuming that the same sandbars were present in both 1980 and 1984 we estimated a migration of 10–50 m towards the northeast during this period. Some of the change may be due to methodological artifacts as discussed above, but since the direction was the same during the various years and the migrating distance was quite long, most of the change is believed to be genuine. Marbà et al. (1994) described a similar situation in Alfacs Bay, Spain where sand dunes migrated 13 m per year leading

to periodic burial of *C. nodosa*. The speed of dune migration was thus in the same range in the two places but the size of the sandbars was greater at Amager.

In conclusion, both the general spatial configuration of the three eelgrass landscapes and the long-term changes in spatial distribution seem strongly related to the physical setting of the areas. At the exposed sites, Amager and Vejle, sediment movements were considerable and seemed to be a major factor in the formation of the observed landscape patterns and patch shapes. At the protected site, Samsø, the influence of wave dynamics and sediment movements was limited, and the observed pattern was probably more a result of other extrinsic disturbances, such as ice scouring or eutrophication-related phenomena (see Frederiksen et al., 2003). The large scale of the study allowed us to detect patterns that would have been missed on smaller scales and the integration of indices derived from landscape ecology was a useful tool offering the potential for future large-scale research on seagrasses.

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