

Total and opportunistic algal cover in relation to environmental variables

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Abstract

Based on a large data set from the national Danish monitoring program, spatial and temporal variability in total algal cover and in the fraction of opportunistic macroalgae was analysed in relation to environmental variables. Variations in water clarity and salinity combined with information on geographical location of sampling areas were found to explain almost 80% of the large-scale variation in algal cover between areas. As water clarity was largely regulated by concentrations of total-nitrogen (TN), and TN-concentrations by TN-input from land, total algal cover at given water depths was partly related to TN-input from land. The fraction of opportunistic algae responded predominantly to differences in salinity, the highest fractions being found in the most brackish areas. Temporal variability in algal cover and fraction of opportunists over the 14-year investigation period was much smaller than the variability between areas and could not be predicted from variations in environmental variables. In order for macroalgal cover to become a more sensitive indicator of water quality it would be necessary to either increase the sensitivity of the method or identify and include supplementary regulating factors in the model.

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1. Introduction

The distribution, composition and abundance of benthic macroalgae depend on physical, chemical and biological factors affecting growth and removal. Light climate (water clarity), nutrient concentration and salinity are three of the primary growth-regulating factors that have been documented to influence large-scale patterns of distribution and abundance of macroalgae (Duarte, 1991; Nielsen et al., 2002a,b). Macroalgal cover at specific water depths is also likely to reflect changes in water quality. The gradual reduction in light availability towards deeper water should cause a parallel decline in algal cover; the decline starting at water depths where light levels become insufficient to saturate

growth rates. Factors such as lack of suitable substratum in deep areas may, however, prevent macroalgae from colonising as deep as water clarity allows. This limitation can occur in Danish coastal waters where the bottom substrate is dominated by moraine deposits with scattered stones, which become scarcer towards deeper waters.

This pattern has been identified for macroalgal cover on stone reefs in the Kattegat, Denmark, and algal cover on stone reefs also tend to be higher in years characterised by low nutrient input and high water transparency (Dahl et al., 2001a). Similarly, the cover of eelgrass in Danish coastal waters declines gradually from intermediate water depths towards the depth limit, and in spite of considerable variation between sites, cover levels tend to be lower in areas with reduced water clarity (Krause-Jensen et al., 2003). Such patterns are also likely to exist for coastal macroalgae but have not, as yet, been investigated.

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The composition of macroalgal communities has also been found to reflect changes in environmental conditions. Macroalgal biodiversity increases with increasing water clarity and salinity and declines with increasing nutrient concentration, though other regulating factors also play a role (e.g. Nielsen et al., 1995; Middelboe et al., 1998; Middelboe and Sand-Jensen, 2004). Species richness and composition of macroalgae on intertidal rocky shores also reflect changes in water quality and may be used in the assessment of water quality under the European Water Framework Directive (Wells et al., 2006). Moreover, eutrophication affects dominance patterns between functional algal groups because increased nutrient concentrations generally stimulate growth of opportunistic algae characterised by thin, simple tissue and potentially high growth rates (Littler and Littler, 1980; Steneck and Dethiers, 1994; Duarte, 1995; Pedersen, 1995). A nutrient-generated shift towards increased dominance of opportunistic species, at the expense of large, perennial algae, has for example been identified in a long-term study in shallow waters of the Roskilde Fjord/Isefjord system in Denmark (Middelboe and Sand-Jensen, 2000) and in other coastal areas of the Baltic Sea (Schramm, 1996). The relative dominance of opportunists has been suggested as indicator of water quality in Greek coastal waters (Orfanidis et al., 2003).

The algal variables ‘total algal cover’ and ‘fraction of opportunists’ are simple and integrative variables of large ecological relevance. Therefore, it is interesting to identify how the spatial and temporal variability of these variables are regulated. Moreover, if environmental variables such as water clarity and nutrient concentration play clear regulating roles, it should be possible to use the algal variables as bioindicators of water quality. With the adoption of the Habitats and Water Framework Directives in Europe, and the Clean Water Act in the US, identification of good biological indicators of coastal water quality has gained a high priority. Whereas assessment of water quality was traditionally based primarily on physicochemical variables such as nutrient concentrations and water clarity, the European Directives demand assessment primarily on the basis of biological indicators.

This work aims to analyse spatial and temporal variations in coastal algal cover and in the fraction of opportunistic algae in relation to environmental variables.

2. Materials and methods

2.1. Algal data

Datasets on algal cover along coastal depth gradients collected under the national Danish monitoring program provide the basis for the analyses.

Algal data were collected along 186 depth gradients/sites distributed in 28 coastal areas (Table 1; Fig. 1). Data were collected annually in summer (May–September) from 1989 to 2002. The Danish counties undertook the data collection

as part of the Danish National Aquatic Monitoring and Assessment Program (DNAMAP).

Data collection followed common guidelines (Krause-Jensen et al., 1998, 2001). Samplers using SCUBA visually recorded the total erect macroalgal cover (excluding the crust-forming algae), the cover of individual algal species and the cover of hard substratum within depth intervals along the depth gradients/sites. Algal cover was estimated relative to hard substratum. Until 2000, cover was estimated as an average for a depth interval; total algal cover was assessed as a percentage (0–100%) while cover of individual species was assessed using a 5-level scale with 2 subsection scales (Table 2). From 2001, total cover as well as cover of individual species was estimated as a percentage within 3 sub-areas of 25 m² in each depth interval. Intercalibration documented that this change of method did not significantly affect mean cover levels, while it did reduce the variability between estimates (Laursen et al., 2000).

The cover data retrieved for the analysis were averaged for each 2-m depth interval. Data recorded on a cover scale were recalculated to percentage cover using the average cover of each scale class (Table 2). Only few (149) observations represented water depths larger than 12 m, and we therefore restricted the analysis to the depth range from 0 to 12 m.

All species were allocated to a functional group, using the system of Steneck and Dethiers (1994), Table 3. The functional groups 2, 2.5, and 3: filamentous algae and single-layered foliose algae are dominated by opportunistic algal species with thin thalli, fast growth rates and ephemeral life forms and are in the following referred to as ‘opportunistic algae’. The remaining groups (3.5, 4, 5 and 6) primarily include perennial species with thick, corticated, leathery or calcareous thalli and relatively slow growth rates. Microalgae (functional group 1) and crustose algae (functional group 7) were not consistently recorded in the entire dataset and were therefore excluded from analysis.

Two algal variables were analysed: (1) total cover of erect macroalgae and (2) fraction of opportunistic algae, (calculated as the summed cover of all algal species belonging to functional groups 2, 2.5, and 3 divided by the summed cover of all algal species). Data from one county showed systematic differences related to a change in sampler personnel and was therefore excluded from analysis. We also excluded data sets where the summed cover of individual species constituted <80% of the estimated total algal cover, as we suspected that species registration in these datasets might be incomplete. The dataset retrieved for analysis included 5884 observations of total algal cover and 5564 observations of cover of opportunistic algae (Table 1).

2.2. Environmental variables: climate, nutrient input and physicochemical variables

Temporal variations in algal variables were correlated with (1) climatic variations regarding wind and insolation,

Table 1
Overview of sampling areas, no. of depth gradients (dg) and no. of observations of total cover and cover of opportunistic algae over the period 1989–2002

Area	No. of dg	No. of cover obs.		
		Total (max per year)	Opportunists	
1.	Limfjorden W	11	341 (45)	289
2.	Limfjorden–Løgstør Broad	3	139 (34)	129
3.	Limfjorden C	9	471 (79)	372
4.	Limfjorden–Skive Fjord	9	219 (45)	194
5.	Limfjorden E	6	127 (17)	119
6.	Nissum Fjord	8	117 (46)	106
7.	Ringkøbing Fjord	9	65 (21)	62
8.	Århus Bay	6	347 (56)	341
9.	Åbenrå Fjord	8	554 (74)	508
10.	Augustenborg Fjord	7	331 (48)	310
11.	Flensborg Fjord	6	577 (63)	534
12.	Odense Fjord	6	310 (50)	299
13.	Kertinge Nor	4	23 (6)	23
14.	Archipelago of S. Funen	4	231 (23)	230
15.	Kalundborg Fjord	6	39 (34)	37
16.	Sejerø Bay	6	47 (34)	45
17.	Isefjord	10	86 (26)	82
18.	Roskilde Fjord	9	474 (114)	470
19.	Sealand N coast	6	173 (93)	173
20.	Nivå Bay	6	63 (30)	63
21.	Øresund	11	864 (88)	854
22.	Køge Bay	5	322 (36)	319
23.	Karrebæksminde Bay	5	73 (30)	72
24.	Karrebæk Fjord	4	27 (7)	27
25.	Dybsø Fjord	3	16 (4)	14
26.	Præstø Fjord	6	20 (10)	20
27.	Bornholm W	4	258 (56)	243
28.	Bornholm E	8	264 (53)	249
Total	186	5884 (865)	5564	

The location of areas is shown in Fig. 1.

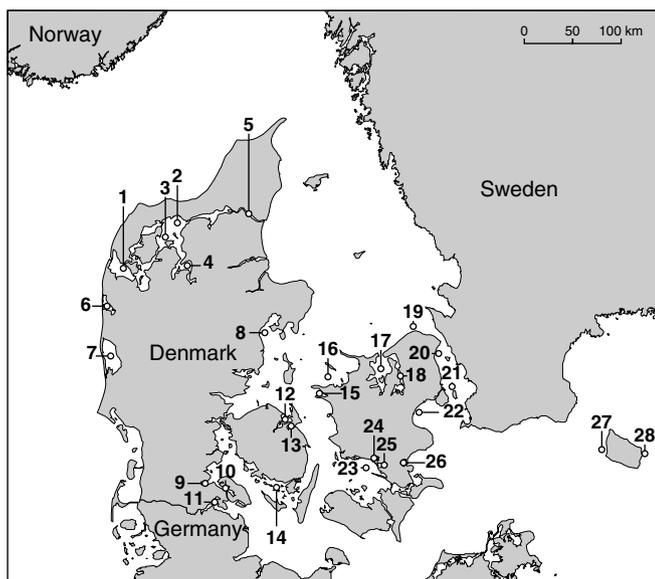


Fig. 1. Map showing the location of sampling areas. The numbers refer to the sampling areas listed in Table 1.

(2) nutrient input from Danish freshwater- and point sources, and (3) physicochemical characteristics of the water column. Insolation data with a temporal resolution

Table 2
Modified Braun–Blanquet scale used for estimating eelgrass cover

Scale level	Cover (%) range	Cover (%) average
1	0–2	1
2	2–25	13.5
2a	2–10	6
2b	10–25	17.5
3	25–50	37.5
4	50–75	62.5
5	75–100	87.5
5a	75–95	85
5b	95–100	97.5

The scale has five main levels and the possibility of subdividing levels 2 and 5. The cover range and average corresponding to each scale level are indicated.

of 30 min. were obtained from the Royal Veterinary and Agricultural University, Denmark (measured at 'Højbakkegård') from 1989 until 1999. Thereafter data representing a temporal resolution of 10 min. were obtained from NERI (measured at the 'Hans Christian Ørsted Institute'). Wind data with a temporal resolution of 10 min. were obtained from 'Sund and Belt Holding' from 1989 until 1998 (measured at Sprogø) and from 'Risø National Laboratory' (measured at Risø) from 1996 onwards. Effects of changes

Table 3
Overview of functional groups (Steneck and Dethiers, 1994)

Functional group	Examples of algal genus
1. Microalgae (single cell) ^a	Cyanobacteria and diatoms
2. Filamentous algae (uniseriate)	<i>Cladophora</i> , <i>Bangia</i>
2.5 Filamentous algae (polysiphonous or thinly corticated)	<i>Polysiphonia</i> , <i>Ceramium</i> , <i>Sphacelaria</i>
3. Foliose algae (single layer)	<i>Monostroma</i> , <i>Ulva</i> , <i>Porphyra</i>
3.5 Foliose algae (corticated)	<i>Dictyota</i> , <i>Padina</i>
4. Corticated macrophytes	<i>Chondrus</i> , <i>Mastocarpus</i>
5. Leathery macrophytes	<i>Laminaria</i> , <i>Fucus</i> , <i>Halidryx</i>
6. Articulated calcareous algae	<i>Corallina</i> , <i>Halimeda</i>
7. Crustose algae ^a	<i>Lithothamnion</i> , <i>Peyssonnelia</i> , <i>Ralfsia</i>

Note that groups 2, 2.5 and 3 are considered opportunists.

^a Microalgae and crustose algae are not represented in this investigation.

in data providers were accounted for by use of correction factors based on intercalibration. Vegetation data were related to the average insolation during the previous year (July–June) and to the average wind velocity during the previous half-year (January–June), when we expected the effect on the algae to be largest.

Data on total input of nitrogen and phosphorus were obtained from DNAMAP as monthly values for each of the years from 1989 to 2002 and algal data were related to the summed annual nutrient input of the preceding year (July–June). Atmospheric input was not included in the estimate of nitrogen input since this contribution is relatively small compared with the land-based discharges to estuaries and coastal waters.

Physicochemical variables (salinity, nutrient concentrations, chlorophyll concentrations and Secchi depths) were sampled over the period 1989–2002 in the surface waters (0–10 m) of sites situated centrally in the 28 coastal areas. Sampling and chemical analysis were performed according to common guidelines (Kaas and Markager, 1999). The sampling frequency typically varied between weekly and monthly sampling. Generally two or more algal sites were related to the same water chemistry site. Data were collected by the Danish counties under DNAMAP and stored in NERI's database for marine data (<http://mads.dmu.dk>).

2.3. Statistical analyses of algal variables

Algal cover was estimated as substratum-specific cover, which should imply that cover levels were independent of substratum composition at the sampling sites. A possible dependence on the amount of hard substratum was tested initially using a non-parametric adjustment (LOESS, Cleveland, 1979) of both total algal cover and fraction of opportunistic algae to the amount of hard substratum. This analysis led to the formulation of a model, in which the relation between algal cover and hard substratum differed for levels of hard substratum below and above 50%.

Estimates of total algal cover and of the fraction of opportunists provided observations in the range 0–100% with greater variation being expected around 50% than at 0% and 100%. Thus, for the statistical analyses, we employed the angular transformation of algal cover percentages (p , Sokal and Rohlf, 1981):

$$x = \arcsin \sqrt{p} \quad (1)$$

Variations in the transformed cover percentages (x) were described by the following generic model:

$$x = \text{area} + \text{site}(\text{area}) + \text{year} \times \text{depth interval} + \text{month} \\ + \% \text{ hard substratum}(0-50\%) \times \text{depth interval} \\ + \% \text{ hard substratum}(50-100\%) \times \text{depth interval} \quad (2)$$

The model is based on the assumption that algal cover depends on area, site/depth gradient within the area, depth-specific year-to-year variation, sampling month and substratum composition within depth intervals. The latter is expressed by a linear relation that differs between depth intervals as well as between levels of hard substratum below and above 50%. The marginal distributions for the year-to-year variation in depth-specific cover as well as for the general area-specific and site-specific cover were calculated from the model. Marginal distributions describe the variation in the various factors of the model when all variations of other factors are taken into account. Thus, one cover value representing an average for all areas and sites was calculated for each year in each depth interval given an average level of hard substratum in the depth intervals. In addition, values of average cover for the individual areas were calculated, taking into account that monitored depth intervals, substratum composition and sampling year may vary among areas. Thus, independently of differences in water depth, substratum composition and sampling year, the model provided comparable values of year-to-year variation and of spatial variation between areas.

2.4. Coupling of algal variables to environmental variables

The variation in physicochemical variables was initially separated into temporal and spatial variation using a model similar to the one described for algal variables. The model describes physicochemical variables with respect to area-specific variation, site-specific variation, seasonal variation and year-to-year variation among hydrological years, i.e. July–June. For each variable we calculated annual marginal means and area-specific marginal means.

Algal variables were related to physicochemical variables using correlation analyses and multiple regression analyses. In the multiple regression analyses, the variable with the highest explanatory power was identified and then the residuals of this regression were analysed against the remaining physicochemical variables. Supplementary variables were included iteratively as long as the new variables significantly improved the model (forward selection). The

analyses were conducted on a spatial basis to explain differences in algal parameters between coastal areas and on a temporal basis to explain differences in algal parameters between years. The annual mean values of climatic variables and nutrient input data were included as explanatory variables in the temporal analyses.

As water clarity was the main factor controlling macroalgal cover, we established a conceptual model to illustrate that algal cover could be further coupled to nutrient input and concentration mediated through water clarity. We first related algal cover to water clarity and then water clarity to concentrations of total-nitrogen ([TN]) by linear regression. Finally we related TN-concentration to TN-input from land using the following model:

$$\log([\text{TN}]) = \text{area} + \text{site}(\text{area}) + \text{TN-input} + \text{month}, \quad (3)$$

where TN-input explains the year-to-year variation in TN-concentration. This relation was analysed only for year-to-year variations and not for variations between areas because it was not possible to determine an area-specific nutrient input for relatively open areas, e.g. around Bornholm. The model relies on the coarse assumption that year-to-year variation in nutrient input has the same relative effect on nutrient concentration in all areas.

3. Results

3.1. Levels of total macroalgal cover and fraction of opportunists

Total algal cover and fraction of opportunists were modelled based on variations between areas and sites, year-to-year variation between depth intervals, seasonal variations and variations in substratum composition in depth intervals (Eq. (2)). All factors contributed significantly to explaining the variation in algal variables (F -test, $p < 0.05$).

In spite of large variability in the relation between algal cover and substratum composition, macroalgal cover increased significantly as a function of the cover of hard substratum up to levels of 40–60% hard substratum while further increases in the cover of hard substratum generally had no effect. The fraction of opportunists also varied depending on substratum composition, but was generally highest at low levels of hard substratum and then decreased as a function of the fraction of hard substratum until the latter reached levels of 40–60% (data not shown).

The level of algal variables at given water depths was modelled as an average for all areas for each of the sampling years 1989–2002 (Fig. 2, grey bars). The modelled levels of total cover at specific water depths varied from 10% to 80% but showed no consistent variation with depth and the expected reduction in cover with depth was apparent only in some sampling years (1989, 1990, 1995, 1999 and 2002). The modelled fraction of opportunistic algae at specific water depths varied between 10% and 90% during the

period 1989–2002 (Fig. 2, hatched bars). In most sampling years (except 1995, 1998–2000 and 2002) the fraction of opportunists declined as a function of water depth. In shallow water, the fraction of opportunists was similar among years, ranging from ~60% in 1993 and 1994 to 85% in 1990. In deeper water, the fraction of opportunists was low (<20%) in 1990–1994 and high (>40%) in 1995, 1998–2000 and 2002.

Area-specific levels of total algal cover and fraction of opportunists were modelled as averages for the period 1989–2002 representing an average water depth of 6 m, a substratum composed of 38% hard bottom and July as the sampling month. Modelled levels of total cover varied from <20% in an enclosed brackish embayment (Nissum Fjord) to 90–100% in some open coastal areas (Sejerø Bugt, Kalundborg Fjord, Sealand N Coast; Fig. 3A). Modelled fractions of opportunists varied from about 10% to 100% (Fig. 3B).

3.2. Environmental variables: climate, nutrient input and physicochemical variables

Insolation varied about 10% between years during the investigation period with the typical annual insolation constituting about 1300–1400 W m⁻². Most years (1990–2002) had average wind velocities of 6.5–7.5 m s⁻¹ (Table 4).

Nitrogen input from Danish freshwater and point sources to marine waters generally declined over the period 1989–2002 (Carstensen et al., 2006). Two years of very high levels (1994 and 1995) and two years of very low levels (1996 and 1997) were exceptions to this general trend. Nitrogen input from freshwater and point sources varied by a factor of 3 over the investigation period from a minimum of 40,000 tonnes (July 1995–June 1996) to a maximum of 130,000 tonnes (July 1994–June 1995). Phosphorus input was high until the mid-1990s and then declined, following the establishment of waste water plants, to around 2500 tonnes per year, corresponding to about half the level in 1990–1991 (Table 4).

Concentrations of TN and DIN (dissolved inorganic nitrogen) showed a declining trend over the period 1989–2002 though the years having the highest run-off, 1994 and 1995 also had the highest concentrations (~650 µg TN l⁻¹ and 150 µg DIN l⁻¹). The lowest concentrations were measured in 2001 (~330 µg TN l⁻¹ and 110 µg DIN l⁻¹). Concentrations of TP (total phosphorus) and DIP (dissolved inorganic phosphorus) dropped markedly from 1989 (~65 µg TP l⁻¹ and almost 25 µg DIN l⁻¹) to 1997 and then stabilised. The lowest concentrations were measured in 1999 (20 µg TP l⁻¹ and <10 µg DIN l⁻¹). Secchi depths and chlorophyll concentrations varied only moderately between years. The lowest annual average Secchi depths (5.2 m) were recorded in 1989 when chlorophyll concentrations were highest (3.75 µg l⁻¹), while highest Secchi depths (6.1 m) were recorded in 2001 when chlorophyll concentrations were lowest (2.75 µg l⁻¹, Table 4).

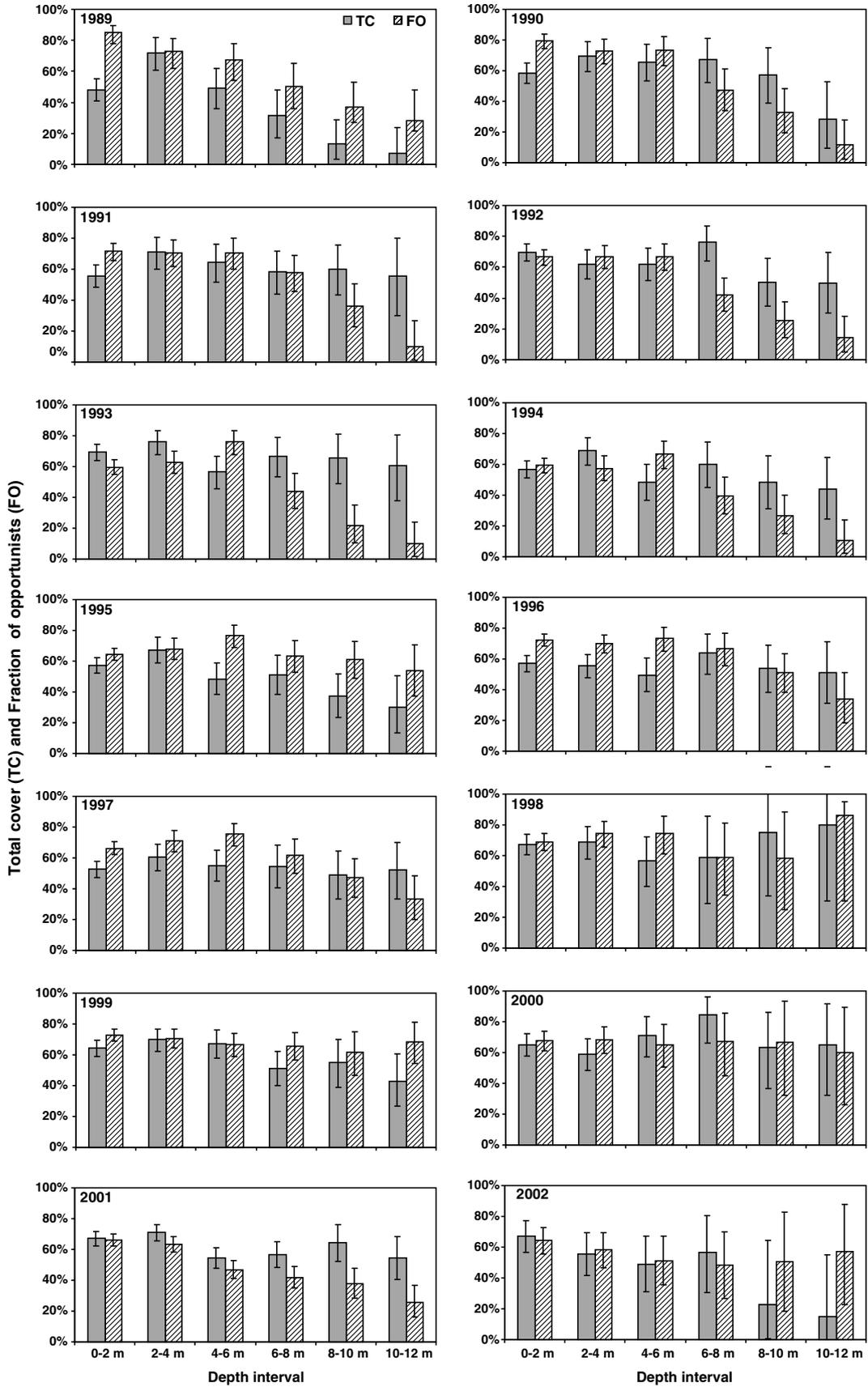


Fig. 2. Modelled total algal cover (TC, grey bars) and fraction of opportunistic algae (FO, hatched bars) in depth intervals (1989–2002). Error bars represent 95% confidence intervals.

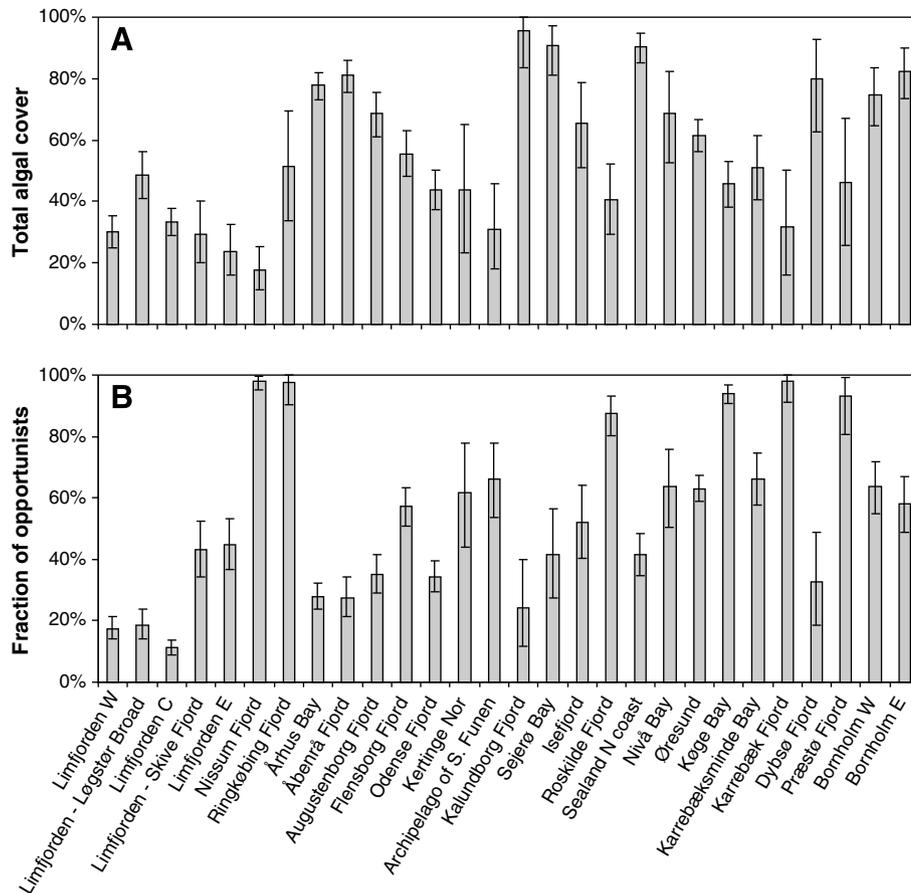


Fig. 3. Total macroalgal cover (A) and fraction of opportunistic algae (B) calculated as averages for each sampling area. Averages are modelled over all depth intervals (0–12 m) and all years (1989–2002). Error bars show 95% confidence intervals.

Table 4

Temporal and spatial variation in meteorology, nutrient input and physico-chemistry in Danish coastal areas characterised by average and range (min max) of annual means (14 years) and area-specific means (28 coastal areas)

Independent variables	Annual variation	Area-specific variation
Insolation (W m^{-2})	1343 (1211–1442)	
Wind (m s^{-1})	6.9 (6.1–7.8)	
TN load (10^3 tonnes)	89.7 (41.3–137.0)	
TP load (10^3 tonnes)	3.4 (2.1–5.5)	
Salinity (psu)	17.9 (17.2–18.9)	17.0 (5.1–28.3)
TN ($\mu\text{g l}^{-1}$)	559 (472–650)	633 (254–1951)
DIN ($\mu\text{g l}^{-1}$)	104 (76–145)	146 (20–509)
TP ($\mu\text{g l}^{-1}$)	44 (32–64)	46 (17–105)
DIP ($\mu\text{g l}^{-1}$)	14.1 (9.1–24.2)	17.0 (0.7–51.0)
Chlorophyll (mg chl l^{-1})	3.3 (2.8–3.8)	4.0 (1.2–26.2)
Secchi depth (m)	4.9 (4.5–5.2)	5.2 (1.0–13.2)

Annual values (1989–2002) represent means over all coastal areas (second column) and area-specific values represent means over all years (third column). Area-specific means were available for physico-chemistry only.

The level of physicochemical variables varied markedly between areas. The range of mean concentrations of total phosphorus was ~ 30 – $100 \mu\text{g TP l}^{-1}$, phosphate concentrations ~ 0 – 50DIP l^{-1} , total nitrogen concentrations ~ 250 – $2000 \mu\text{g TN l}^{-1}$ and inorganic nitrogen concentrations ~ 25 – $500 \mu\text{g DIN l}^{-1}$. Average Secchi depths ranged from

1 to 13 m and chlorophyll concentrations from ~ 2 to $25 \mu\text{g l}^{-1}$ (Table 4).

3.3. Total macroalgal cover in relation to environmental variables

Total macroalgal cover was generally highest in the areas having clearest waters and lowest concentrations of DIN, TN, TP and chlorophyll (all significantly correlated with cover). Macroalgal cover correlated best with Secchi depth and TN ($r = 0.69$ for both variables). When Secchi depth was used as the independent variable in a linear regression, the residuals of the regression were significantly related to salinity if data from Limfjorden were excluded (Fig. 4). As Limfjorden behaved differently from other areas, the following overall model was established:

$$\text{Total cover} = -0.386 + 0.0407 \times \text{Secchi depth} + 0.0205 \times \text{salinity} - 0.419 \times L, \quad (4)$$

where $L = 1$ indicates that data were collected in Limfjorden and $L = 0$ that data were collected elsewhere.

This model explained 79% of the variation in total cover (Fig. 4). On average, total macroalgal cover increased by 4% when Secchi depths increased by 1 m and by 2% when

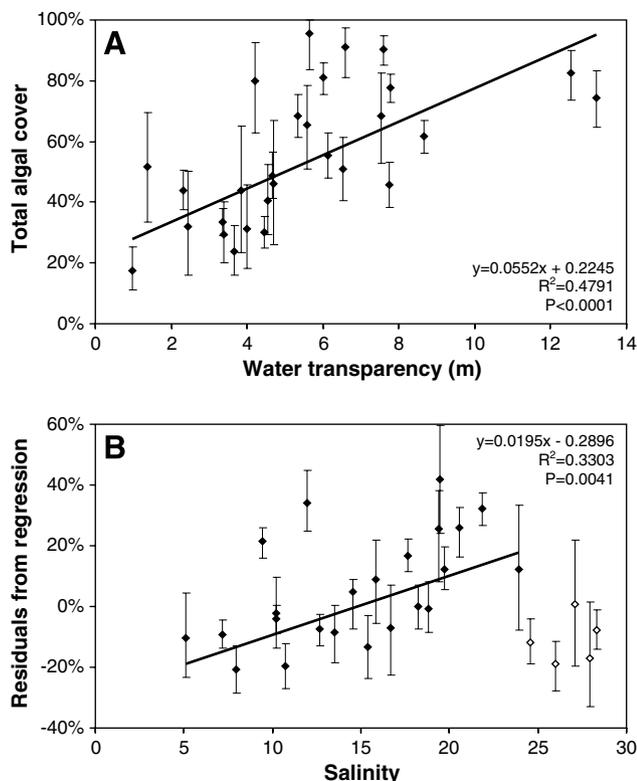


Fig. 4. Total macroalgal cover as a function of Secchi depth (A) and residuals of this regression as a function of salinity (B). The plotted data represent area-specific levels of total macroalgal cover and error bars represent 95% confidence intervals. The relations are analysed using weighted linear regression in which cover values are weighted against the reciprocal of the variance of the estimated cover values (BLUE – Best Linear Unbiased Estimation). Open symbols represent observations from Limfjorden, which are not included in the regression.

salinity increased by 1. Areas in Limfjorden had 42% lower cover than other areas if the relation between cover, Secchi depth and salinity established primarily for the remaining areas was extrapolated to the salinity levels of Limfjorden (Fig. 4).

Table 5

Temporal correlations between annual averages of total macroalgal cover in depth intervals and independent variables

Independent variables	Depth interval						
	0–2 m	2–4 m	4–6 m	6–8 m	8–10 m	10–12 m	
Insolation	0.0673	–0.2879	–0.0111	0.5872	–0.0775	0.0524	
Wind	–0.1407	0.1394	–0.1397	0.0224	–0.6019	–0.5035	
TN load	0.0749	0.5632	0.0587	–0.1260	–0.2433	–0.3175	
TP load	–0.1029	0.3720	0.2583	0.2318	–0.1475	–0.4054	
Salinity	0.0065	0.0910	0.1240	0.4062	0.2742	0.3780	
Chlorophyll	0.2007	–0.0143	0.0739	0.6086	–0.1472	–0.0726	
DIN	–0.2293	0.2391	–0.0090	–0.1702	–0.5181	–0.4794	
DIP	–0.1415	0.1261	0.2233	0.4250	–0.0106	–0.2641	
TN	–0.2315	0.2440	–0.0719	0.0605	–0.4568	–0.3955	
TP	–0.1155	0.1417	0.1464	0.4628	–0.0182	–0.2382	
Secchi depth	–0.0618	–0.1533	–0.1942	–0.4149	0.2648	0.4217	

Observations are weighted against the reciprocal of the variance of the estimated cover values. Significant correlations, as identified by *t*-test, are accentuated in bold. Confidence limit 95%.

Only 4 of 66 temporal correlations between depth-specific levels of total cover and independent variables were significant at the 95% confidence level (Table 5). The correlations showed no systematic pattern and the correlation between chlorophyll and algal cover at 6–8 m depth was the opposite of that expected. The number of significant correlations corresponded to what should be expected if cover values and environmental variables were independent.

3.4. Fraction of opportunistic algae in relation to environmental variables

The fraction of opportunistic algae showed a significantly negative relation to salinity, being highest in the most brackish areas (Fig. 5). Salinity explained 73% of the variation in the fraction of opportunists and no other physicochemical variables contributed to explaining the variations.

Year-to-year variations in the fraction of opportunistic algae in various depth intervals showed no systematic

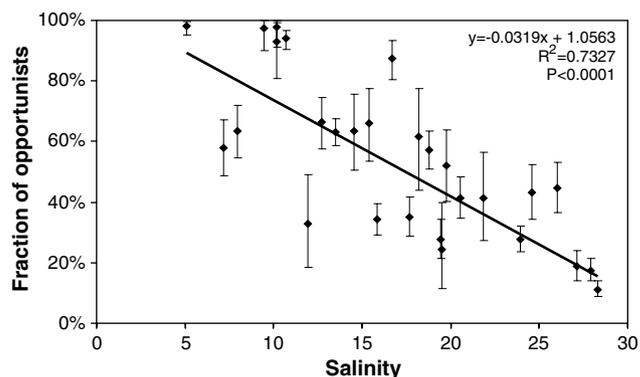


Fig. 5. Fraction of opportunistic algae as a function of salinity. The plotted data represent area-specific values and error bars represent 95% confidence intervals. The relations are analysed using weighted linear regression in which cover values are weighted against the reciprocal of the variance of the estimated cover values (BLUE – Best Linear Unbiased Estimation).

Table 6
Temporal correlations between annual averages of relative cover of opportunistic algae in depth intervals and independent variables

Independent variables	Depth interval					
	0–2 m	2–4 m	4–6 m	6–8 m	8–10 m	10–12 m
Insolation	–0.0002	0.2329	0.5598	–0.0086	–0.2050	–0.3396
Wind	–0.4257	–0.1276	0.4687	0.0218	0.0997	0.0790
TN load	–0.4815	–0.4034	0.1330	–0.1500	–0.1422	0.0102
TP load	0.0150	–0.0585	0.3389	–0.1548	–0.3743	–0.4020
Salinity	–0.0529	0.2401	0.2880	–0.2735	–0.4459	–0.4885
Chlorophyll	–0.1948	–0.0063	0.5566	–0.1051	–0.4039	–0.4339
DIN	–0.2660	–0.0531	0.4822	0.2634	0.1694	0.2016
DIP	0.2741	0.1832	0.4531	–0.1447	–0.4614	– 0.5862
TN	–0.3579	–0.0833	0.6526	0.1420	–0.0638	–0.0990
TP	0.1395	0.0770	0.4598	–0.1974	–0.5067	– 0.6340
Secchi depth	0.1890	0.1869	–0.3517	0.1132	0.1859	0.1852

Observations are weighted against the reciprocal of the variance of the estimated cover values. Significant correlations, as identified by *t*-test, are accentuated in bold. Confidence limit 95%.

correlation at the 95% confidence level with any of the independent climate variables, nutrient input variables or physicochemical variables (Table 6). The few significant correlations seemed incidental as a consequence of the many simultaneous statistical tests.

3.5. Coupling of algal variables to nutrient concentration and nutrient input

As total algal cover was related to Secchi depth and salinity, it was relevant to test whether total algal cover could be further coupled to nutrient input and nutrient concentrations. Similar analyses were irrelevant for the fraction of opportunistic algae as this variable was related predominantly to salinity. Following the conceptual model, algal cover should correlate with nutrient input and nutrient concentrations mediated through water clarity. This was found to be the case, as mean Secchi depths declined exponentially as a function of increasing mean concentrations of TN in the investigated areas, with almost 90% of the total variation in Secchi depth being explained solely

by TN (Fig. 6). Data from Bornholm were excluded from this relation as the Baltic Sea is characterised by high concentrations of DON (dissolved organic nitrogen) and low concentrations of PON (particulate organic nitrogen) which generate a light climate differing markedly from that of the other areas. Correlations between Secchi depth and other nutrient concentrations (DIN, DIP, TP) were markedly weaker and we therefore assumed that TN was the main factor regulating Secchi depths.

TN concentrations were modelled based on seasonal variations, differences between areas and sites, and year-to-year variation as determined by TN input from land (Eq. (3)), and the model explained 75% of variations in TN concentrations (*F*-test, $p < 0.05$). On average, TN concentration changed 3% for each 10,000 tonnes change in N input. These calculations are coarse averages and serve to illustrate principles for coupling nutrient input to algal cover.

4. Discussion

4.1. Total macroalgal cover in relation to water quality

The investigation demonstrated that total macroalgal cover responded to differences in water quality and salinity between Danish coastal areas. Variations in water clarity and salinity combined with information on whether or not an area was located in Limfjorden could explain almost 80% of the variation in area-specific mean cover levels. A stepwise procedure relating water clarity to concentrations of TN, and TN to nutrient input from land, illustrated principles for relating nutrient input to algal cover and for ‘translating’ a nutrient input scenario to corresponding levels of algal cover in areas where nutrients regulate water clarity. These results confirm existing evidence that increased nutrient input shifts the balance between benthic and pelagic primary producers by stimulating the production of pelagic algae which subsequently shade the benthic

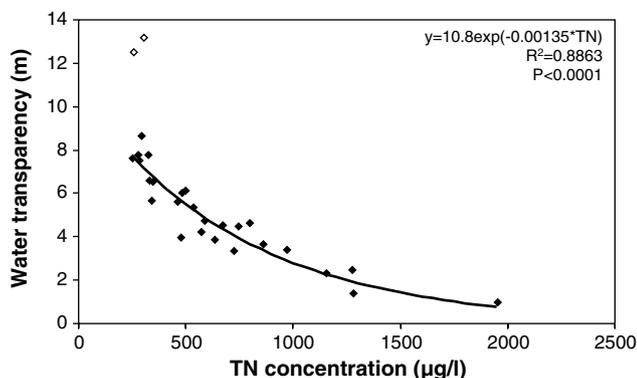


Fig. 6. Area-specific Secchi depths plotted against average area-specific TN concentration. Data from Bornholm (empty circles) were excluded due to high concentrations of DON and low concentrations of PON generating a light climate differing markedly from that of the other areas.

community (e.g. Duarte, 1995; Pedersen, 1995; Borum and Sand-Jensen, 1996).

While algal cover reflected differences in water quality between areas, it did not reflect year-to-year variations in water quality. This is most likely due to the fact that the range in water quality variables was much larger between areas than across the investigation period. Secchi depths thus varied by a factor of 13 between areas (1–13 m), but only by a factor of 1.2 between years (5.2–6.1 m). Therefore, a given algal variable is much more likely to reflect spatial than temporal differences in water quality. In order for algal cover to reflect temporal changes in water quality and become a sensitive indicator of water quality it would be necessary to reduce the unexplained variation in cover. This would require either an increase in the sensitivity of the method (e.g. reduced sampler effects, more replicates, sampling on more homogeneous substrata) or identification of supplementary factors causing the variation, and inclusion of these factors in the models.

It is likely that deeper-growing and more light-limited coastal algal communities would have responded more clearly to changes in water quality. Total algal cover did not decline markedly as a function of water depth within the investigated depth range (0–12 m, Fig. 2), indicating that the algal community was not strongly light limited. On stone reefs in Danish coastal waters, by contrast, algal cover in the depth range 10–22 m responded significantly to changes in water quality over the same investigation period (Dahl et al., 2001a). Apart from including deeper algal communities, the algal investigations on stone reefs differ from those along the coasts by representing more uniform substrata and by being conducted exclusively by a team of three experienced divers.

4.2. Fraction of opportunists in relation to water quality

Contrary to our hypothesis, the fraction of opportunists was neither related to water quality when analysed across areas nor when analysed over the 14-year investigation period. Instead, the fraction of opportunists responded to differences in salinity between areas, being highest in the most brackish areas.

One reason for the lack of coupling between water quality and fraction of opportunistic algae could be that all species grouped here as ‘opportunists’ may not necessarily show similar responses to increased nutrient concentration in coastal Danish waters. Though most of the species belonging to this group have potentially high growth rates (Steneck and Dethiers, 1994), unfavourable light levels (in e.g. the deeper depth strata), unfavourable salinity levels or losses due to grazing or physical disturbance could prevent some of the species from reaching high abundance in the nutrient-rich areas. A recent mesocosm experiment showed no overall increase in the abundance of opportunistic algae along an artificial eutrophication gradient, but instead demonstrated a change in composition of opportunistic algae from dominance of corticated filamen-

tous red algae to dominance of thin foliose green algae (Karez et al., 2004). Middelboe and Sand-Jensen (2000) also found an increase in the fraction of opportunistic green algae and a decline in large perennial brown algae in shallow water following increases in nutrient concentrations in a Danish estuary over a 50-year period.

The lack of response of the fraction of opportunists to year-to-year changes in water quality in this study may also reflect that the cover of opportunists is highly variable because the algae have fast growth rates and are easily removed by waves. An annual estimate of cover, therefore, incorporates much inaccuracy, which may obscure responses to the modest changes in water quality over the study period.

Though our study found no coupling between the fraction of opportunists and water quality at the spatial scale of ‘coastal areas’ this does not exclude that coupling may exist at smaller spatial scales e.g. along nutrient gradients within the coastal areas or in regions without salinity gradients. In Greek coastal waters, cover of opportunistic algae versus cover of late successional species including seagrasses and perennial macroalgae has been suggested as an indicator of water quality (Orfanidis et al., 2001, 2003). Our study shows that this variable is not a useful indicator in Danish coastal waters when all opportunists are considered together and their abundance calculated as an average for entire estuaries/coastal areas.

4.3. Algal cover and fraction of opportunists in relation to salinity

Salinity was strongly related to total algal cover as well as to the fraction of opportunistic algae. Variations in salinity explained about half of the variation in algal cover and almost 75% of the variation in the fraction of opportunists between areas. It seems natural to assume that the salinity effect may conceal a nutrient effect because inner parts of estuaries receive nutrient-rich freshwater from land. However, in the existing data sets, this traditional estuarine effect was confounded by a large-scale gradient in salinity and nutrients, as the brackish Baltic water is less nutrient-rich than the saline North Sea and Skagerrak waters.

The positive effect of salinity on total algal cover may be related to the fact that far more species are adapted to high salinity than to brackish conditions. The number of macroalgal species thus declines markedly along the Baltic gradient from a maximum of 325 species in the northern Kattegat to <100 species in the Bothnian Bay (Nielsen et al., 1995). Larger diversity could have a positive effect on total algal cover because the many species representing various life forms and forming a multi-layered community should be able to exploit the incoming light more efficiently and thus be more productive and dense than a less diverse community (Spehn et al., 2000). But large diversity is not a universal prerequisite for high cover; e.g. *Fucus vesiculosus*

often has a high cover in the brackish areas of the Baltic Sea where few algal species grow.

The negative effect of salinity on the fraction of opportunists may be related to the fact that many perennial red and brown algal species are excluded while many green opportunistic species cope well in low salinities (Nielsen et al., 1995). A factor contributing to this pattern may be that grazing control of opportunistic species like *Ulva lactuca* by benthic invertebrates may increase at increasing salinity (Geertz-Hansen et al., 1993). Moreover, if high salinities are coupled to high levels of exposure, it may cause opportunistic, free-floating algae to be washed away. The marked negative relation found between salinity and the fraction of opportunists in this study suggests, that in regions with large salinity gradients, salinity may have a stronger regulating role than previously acknowledged. Effects of salinity could be overlooked and instead misinterpreted as pure nutrient effects in areas containing a traditional estuarine gradient where high nutrient levels are correlated with low salinities.

4.4. Supplementary regulating factors

Our models demonstrated that total algal cover increased whereas the fraction of opportunists declined, as hard substratum became more abundant. This pattern occurred in spite of the fact that algal cover was estimated relative to the suitable hard substratum and suggests that unstable substratum fractions were included in the divers' estimates of suitable substratum. Perennial, slow growing algae may not be able to colonise the small stones before they are removed again by wave action, whereas opportunistic algae may establish on the small stones due to their high growth rates (Littler and Littler, 1984). Stone reef algal communities on large stones are also denser and have larger proportions of perennial species than those on gravel (Dahl et al., 2001b). It is also possible that physical processes such as sand scour or sedimentation may reduce algal cover in areas with low levels of hard substratum. Walker and Kendrick (1998) thus identified habitat alienation e.g. through sedimentation as a major threat to marine macroalgal biodiversity.

The algal community in Limfjorden deviated significantly from the overall pattern of total algal cover between areas. Areas located in Limfjorden had lower total algal cover than the remaining areas, assuming a linearly increasing relationship with salinity. The most likely reason is that Limfjorden is exposed to intense mussel dredging, with major parts of the fjord being dredged regularly at intervals of a few years. This disturbance is likely to reduce total algal cover as the substratum is scraped and turned upside down and in the long term, hard substratum cover is reduced.

Part of the variation in algal data was not explained by the included variables and may have been caused by other regulating mechanisms. For example, differences in the level of wind-generated wave exposure may cause variations in algal cover in very shallow water as it has been

shown for eelgrass (Fonseca and Bell, 1998; Krause-Jensen et al., 2003). Fauna effects such as competition for space by blue mussel and grazing, e.g. by sea urchins, may also contribute to regulating algal cover (e.g. Chapman, 1981; Ste-neck et al., 2002). Finally, the variation in data may be due in part to sampler effects but the data did not allow a thorough correction for these.

In conclusion, we found that total macroalgal cover responded to large-scale spatial differences in water clarity, salinity and geographical characteristics while the fraction of opportunists responded to differences in salinity. None of the algal variables responded to the smaller interannual changes in selected environmental factors. The developed models can predict relative effects on algal cover and fraction of opportunists of changes in the identified regulating factors, but cannot predict precise levels of the algal variables. A higher sensitivity of future models would require either an increased sensitivity of sampling methods and/or identification and inclusion of supplementary regulating factors.

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