

1 **Reduced cover of drifting macroalgae following nutrient reduction in Danish**
2 **coastal waters**

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11

12 **Keywords**

13 Drift algae, Eelgrass, *Zostera marina*, Nitrogen, Nutrients, Relative exposure index

14

15 **Abstract**

16 Based on a large dataset from the national Danish monitoring programme we analysed the temporal
17 variability of drifting algae cover in shallow (1-2 m) water during a period of reduced nutrient loadings.
18 Algal cover was analysed both in absolute terms and relative to eelgrass, *Zostera marina*, cover to test the
19 hypotheses that 1) the cover of drifting algae and the relative dominance of algae versus eelgrass in shallow
20 waters have declined in parallel to reductions in nutrient levels during the last decades, and 2) spatio-
21 temporal differences in algal cover can be related to differences in nutrient conditions and environmental
22 characteristics. The cover of drifting algae was positively related to total nitrogen concentration and Secchi
23 depth, but negatively related to exposure, salinity and mean summer temperature. The cover of drifting
24 macroalgae showed significant declines over the past two decades, paralleling the reduction in nutrient
25 concentrations. The present cover of drifting algae is low (< 10%) and probably pose little threat to the
26 general distribution of eelgrass in shallow Danish waters though local accumulations may be harmful.

27 However, the ratio between drifting algae cover and eelgrass cover showed no significant trend, reflecting
28 that eelgrass cover had not increased despite the reduced levels of nutrients and drifting algae. This ratio also
29 showed no consistent relationship to water quality probably because different regulation mechanisms govern
30 drifting algae and eelgrass, and feed-back mechanisms may delay eelgrass recovery. Reduced drift algal
31 cover may be an early sign of improved ecological status while further improvements in terms of recovery of
32 eelgrass meadows have longer perspectives.

33

34 **Introduction**

35 Nutrient levels increased by a factor of 2 or more from the 1960s to the 1990s in many estuarine and
36 coastal waters as a result of increased nutrient inputs from anthropogenic activities, and changes in the
37 structure and function of coastal ecosystems as a result of eutrophication have been evident across the world
38 (Cloern 2001). Increased nutrient availability stimulates the production of planktonic microalgae and fast-
39 growing, ephemeral macroalgae with simple tissues (opportunistic macroalgae) at the expense of the larger
40 slow-growing and long-lived macroalgae and rooted macrophytes (late-successionals), but does not
41 necessarily cause systematic changes in total primary production (Borum and Sand-Jensen 1996; Valiela et
42 al. 1997; Krause-Jensen et al. 2012).

43 The abundance of opportunistic algae in Scandinavian and Baltic Sea waters generally increased
44 during the 1980s and early 90s as a result of eutrophication (Pihl et al. 1995). In bays of the Åland
45 Archipelago in the Baltic Sea, Berglund et al. (2003) reported cover of filamentous macroalgae of 14 – 35 %
46 in the late 1990s. On the Swedish west coast cover of filamentous algae between 20 and 50 % were
47 commonly observed during the 1990s (Pihl et al. 1995; Pihl et al. 1999), and there were also reports on high
48 abundances from Danish coastal waters (Thybo-Christesen et al. 1993). Seagrasses, by contrast, experienced
49 general declines during the 20th century in Scandinavia (Boström et al. 2014) and worldwide (Waycott et al.
50 2009). In Denmark eelgrass meadows thus extended deeper, covered larger areas and exhibited higher
51 abundance and productivity at the beginning of the past century than at the end, and losses have been
52 attributed primarily to the wasting disease epidemic during the 1930s and accelerated eutrophication in the
53 latter half of the century (Boström et al. 2003; Krause-Jensen et al. 2012).

54 Such shifts in primary producers entail functional changes because seagrass meadows and forest of
55 perennial macroalgae support important ecosystem functions and ecological services which are lost when
56 these ecosystems disappear (Gutiérrez et al. 2011). As opportunistic species contain less structural
57 components and more nutrients than late-successional species (Littler & Littler 1980) they are also more
58 readily grazed and decomposed, leading to faster turnover of organic matter and increased risk of oxygen
59 depletion in ecosystems dominated by opportunists compared to ecosystems dominated by late-successionals
60 (Sand-Jensen and Borum 1991, Cebrian and Duarte 1995).

61 The basis for nutrient-driven shifts in the functional composition of the vegetation is that seagrasses
62 and perennial macroalgae have relatively low nutrient requirements and high nutrient storage capacities
63 (Pedersen and Borum 1996) and therefore are good competitors when nutrients are limited (Duarte 1995). In
64 contrast, opportunistic macroalgae have limited nutrient storage capacities and high nutrient requirements,
65 but when nutrients are readily available their high surface area to volume ratios allow for high uptake rates
66 and a high proportion of photosynthetic tissue facilitates fast growth that may allow them to outgrow grazers
67 (Hein et al. 1995; Pedersen and Borum 1997; Valiela et al. 1997; Padilla and Allen 2000; Schmidt et al.
68 2012). These species, therefore, have a competitive advantage when nutrient levels are high and they may
69 cover and shade the late-successional species (Sand-Jensen & Borum 1991, Duarte 1995; Schmidt et al
70 2012). Also, poor oxygen conditions and build-up of reduced compounds, such as sulphide, inside and under
71 algal accumulations may further intensify negative effects on covered seagrass shoots (Krause-Jensen et al.
72 1996; Borum et al. 2005; Pulido and Borum 2010). Hence, the abundance of seagrasses and perennial
73 macroalgae is expected to decrease with increasing abundance of opportunistic algae, and the shift in
74 dominance from late-successional to opportunistic species has been used as a bioindicator of the ecological
75 status of estuarine and coastal waters (Orfanidis et al. 2003; Panayotidis et al. 2004; Orfanidis et al. 2011).

76 Opportunistic macroalgae often grow unattached and are, thus, subject to transportation by wind and
77 currents until they are caught in seagrass beds or by other structures or transported to deep waters (Canal-
78 Vergés et al. 2010; Rasmussen et al. 2013). In Danish coastal waters drifting *Ulva* sp., *Cladophora* sp.,
79 *Ectocarpus* sp., *Ceramium* sp., *Polysiphonia* sp. and a number of other opportunistic species are commonly
80 found accumulating in seagrass beds where they compete with seagrasses and perennial macroalgae for light,

81 nutrients and space (Pihl et al. 1995; Rasmussen et al. 2012; Rasmussen et al. 2013). The cover of drifting
82 algae as well as the ratio of drifting algae to eelgrass cover may, therefore, be a useful indicator of ecological
83 status.

84 A reduction in nutrient availability is expected to decrease the proportion of drifting opportunistic
85 algae and eventually result in increased cover of seagrasses and perennial algae. Nutrient load reductions are
86 currently being carried out in many places in response to the severe eutrophication problems and with the
87 aim of recovering the coastal ecosystems. However, only few examples of ecosystem recovery are yet
88 available (e.g., Jones and Schmitz 2009; Greening et al. 2011; Lotze et al. 2011; Orth and McGlathery 2012,
89 Tsiamis et al. 2013). A recent review concludes that partial rather than full recovery prevails, that
90 degradation and recovery typically follow different pathways as buffers act to maintain the degraded state,
91 and that recovery trajectories differ among ecosystems (Duarte et al. 2013). Recovery trajectories may
92 include marked hysteresis effects delaying or preventing the return to previous ecosystem states and
93 changing baselines e.g. in response to global warming may add to the complexity (Scheffer et al. 2001;
94 Duarte et al. 2009; Duarte et al. 2013).

95 Since the late 1980s nitrogen loadings to Danish coastal waters have been reduced by more than 50 %
96 and phosphorus loadings by 64 % primarily as a result of reduced inputs from agricultural areas and
97 improved treatment of wastewater. Surface water concentrations of total phosphorus and total nitrogen have
98 seen an associated reduction since the early and mid 1990s, respectively, both in the fjords and on the open
99 coasts, but the overall distribution of eelgrass has not yet increased (Carstensen et al. 2013; Hansen 2013).
100 However, drifting algae demanding a continuous supply of nitrogen may respond faster than eelgrass to
101 reductions in nitrogen concentrations as the coastal waters are nitrogen-limited during most of the growth
102 season (Carstensen et al. 2013; Hansen 2013).

103 In this study we aimed to identify whether the abundance of drifting macroalgae and the relative
104 dominance of algae versus eelgrass in shallow coastal areas have changed during the last decades and
105 whether spatio-temporal differences in algal abundance can be related to differences in nutrient conditions
106 and environmental characteristics such as physical setting and salinity. We used a comprehensive dataset on
107 the cover of drifting macroalgae and eelgrass in shallow waters during the period 1994-2010 along with

108 associated data on nutrient levels, water clarity, salinity, temperature and exposure from the national Danish
109 monitoring programme covering a wide range of coastal ecosystems. We hypothesised that reduced nutrient
110 availability has led to a general decrease in the cover of drifting macroalgae both in absolute terms and
111 relative to eelgrass. We expected that this would be the case in fjord-systems as well as in more open coastal
112 waters and that the cover of drifting algae would be lowest in areas characterised by the lowest nutrient
113 concentrations. Moreover, we expected that high levels of wind-generated wave exposure would reduce the
114 cover of drifting algae, and that high salinity would also reduce drifting algal cover as the proportion of
115 opportunistic green algal species decreases with increasing salinity (Nielsen et al. 1995).

116

117 **Methods**

118 *Data*

119 Monitoring data on the cover of drifting macroalgae and eelgrass (*Zostera marina*) along coastal depth
120 gradients and associated data on physico-chemistry provided the basis for the analyses. As part of the Danish
121 National Aquatic Monitoring and Assessment Programme (DNAMAP) data are collected annually by local
122 departments of the Danish Nature Agency according to technical guidelines (Kaas and Markager 1998;
123 Andersen et al. 2004). Data are afterwards stored in the national database for marine data (MADS) located at
124 the Danish Centre for the Environment and Energy (DCE), University of Aarhus.

125 The dataset represented soft/sandy bottom habitats where rooted macrophytes were present. The gross
126 dataset comprised 17,442 observations of eelgrass (*Zostera marina*) and drifting macroalgae cover over the
127 period 1994-2010 and from these 1431 sets of corresponding eelgrass/macroalgae observations were
128 extracted for the analysis. The data extract represented a total of 352 vegetation sites which were divided into
129 4 area types: 'Inner fjords' (128 sites), 'Outer fjords' (129 sites), 'Open coast' (45 sites) and 'Limfjorden'
130 (50 sites) (Fig. 1). Limfjorden is a complex of connected relative shallow sub-basins in the north-western
131 part of the country. The area was treated separately as it possesses distinct features such as relatively high
132 salinity (see Table 4) and high occurrence of the invasive macroalga *Sargassum muticum*.

133 Data typically represented one annual survey of each vegetation site conducted in the period from early
134 May to late September (Fig. 2). Monitoring took place along depth gradients covering the distance from the

135 shoreline to the maximum depth of eelgrass occurrence. For this analysis, however, only data from the depth
136 interval 1-2 m were used as we wished to explore the distribution of drifting algae in shallow waters. Also,
137 this depth interval provides the most extensive dataset while minimizing the risk of edge effects with respect
138 to eelgrass depth distribution. Estimation of algal and eelgrass cover along the depth gradients (transects)
139 was done visually by SCUBA divers. Until the year 2000, cover of eelgrass, drifting opportunistic
140 macroalgae and other drifting macroalgae (i.e. detached late-successional species) were each assessed as an
141 average value per depth interval (i.e. the 1-2 m interval as used in the analysis). The observations represent a
142 corridor of ca. 1-2 m width which the diver could overview while swimming along the depth gradient.
143 Throughout the programme, drifting algae cover was estimated using a percentage scale (0-100 %) whereas
144 the early eelgrass observations (until year 2000) were assessed on a 5-level scale corresponding to 0-2%, 2-
145 25%, 25-50%, 50-75%, and 75-100% cover. From 2001, the programme was fine-tuned so that each depth
146 interval was represented by several point observations of vegetation cover rather than just one average value
147 for the depth interval, and all observations were assessed as percent cover. Intercalibration documented that
148 this change of method did not affect mean cover levels while it did reduce variability between estimates
149 (Laursen et al. 2000). Divers were asked to distinguish between drifting opportunistic algae and drifting
150 other algae. For the analyses we used the sum of the two groups, however, as divers had often not
151 distinguished between them during busy surveys and mainly reported the cover of drifting opportunistic
152 species.

153 Secchi depth and water chemistry data were sampled one to four times per month at sites in the vicinity
154 of vegetation sites, typically located centrally in the investigated basins (Fig. 1), and both samplings and
155 chemical analyses were performed according to standard guidelines (Kaas and Markager 1998; Andersen et
156 al. 2004).

157 Prior to statistical analysis, data on total nitrogen and phosphorus concentrations (total N and total P),
158 salinity and Secchi depth were aggregated into yearly estimates representing the first six month of the year.
159 This approach was chosen as nutrient and light conditions during this period was expected to best define the
160 potential for algal production and magnitude of algal cover. Summer nutrient concentrations are less useful
161 in this respect as they are generally close to the detection limit. Water temperatures were, on the other hand,

162 aggregated into yearly summer estimates (T_{summer}) representing the period May to September when maximum
163 water temperatures occur, as these are expected to exert most influence on the algae. The aggregation was
164 conducted station-wise by fitting a generalized linear model accounting for variation in sampling times and
165 intensity using the statistical software package SAS/STAT 9.2 (SAS Institute Inc, 2009).

166 A yearly relative exposure index (REI) was calculated for each station based on mean monthly wind
167 speeds (V) and frequency of winds (P) from 8 compass directions (i), as well as effective fetch in each
168 direction (i.e. the distance to the shore, F). These variables were multiplied for each compass direction and
169 then summed:

$$170 \quad REI = \sum_{i=1}^8 (V_i P_i F_i) \quad \text{Eq. 1}$$

171 Meteorological data on wind speed and direction were obtained from the Danish Meteorological
172 Institute (DMI). They were measured at 19 stations nationwide (Fig. 1) and reported as daily averages.
173 Weather data from the period from April to October were extracted for the analysis, as this is the main period
174 of drifting algae occurrence, and calculations were performed in ArcGIS according to the method by Fonseca
175 et al. (2002).

176

177 *Statistical analyses*

178 For the analyses we used two variables: ‘Total cover of drifting macroalgae’ and ‘eelgrass cover’, and
179 analysed the cover of drifting algae both in absolute terms and relative to eelgrass cover (A/E ratio). Missing
180 values were set as NULL and not included in the analysis, and as algal and eelgrass variables are in the range
181 0-100 % and greater variation was expected around 50 % than around 0 and 100 % we employed the angular
182 transformation, $y = \arcsin \sqrt{p}$ in the statistical analyses (Sokal and Rohlf 2012).

183 First, we conducted trend analyses over the study period. Changes in the slopes in the trends of the
184 yearly estimates of cover of drifting algae, A/E ratios and cover of eelgrass were tested by fitting piecewise
185 linear regression models describing the level of the variable (x_t) as a function of time (year) of the type. This
186 analysis would allow identification of possible occurrence of change points in the trends:

$$187 \quad \text{For } t < k: \quad E(x_t) = \mu + \beta t + \varepsilon$$

188 For $t \geq k$: $E(x_t) = \mu + \beta t + \delta(t - k) + \varepsilon$

189 Where t is time (i.e. year), δ is the change in the slope at time k , and k is year of the change point
190 (Carstensen and Weydmann 2012). The models were fitted by optimising the likelihood function of the
191 parameters using the PROC MODEL procedure in the software package SAS/ETS 9.2 for econometrics and
192 time series analysis (SAS Institute Inc 2008).

193 Temporal and spatial variability in drifting algal cover was related to the environmental drivers:
194 Exposure (REI), salinity (Sali), water transparency (Secchi), mean summer temperature (T_{summer}), total
195 Nitrogen (total N) and total Phosphorus (total P). Drifting algae cover was related to the physico-chemical
196 variables by fitting mixed models to the data (PROC MIXED in the statistical software package SAS/STAT
197 9.2; SAS Institute Inc 2009). Similarly, the A/E ratio was analysed as a function of the physico-chemical
198 variables by fitting a generalized linear model to the data (PROC GENMOD in the statistical software
199 package SAS/STAT 9.2; SAS Institute Inc 2009). A strong correlation between nutrient concentrations and
200 Secchi depth led to the formulation of two sets of mixed effect models.

201 Model 1: $y = REI + Sali + Secchi + T_{summer}$

202 Model 2: $y = REI + Sali + \ln(totalN) + \ln(totalP) + T_{summer}$

203 The analyses were conducted for the entire dataset as well as for the four individual area types. The
204 choice of two different models (i.e. mixed and linear) for the analyses was for technical reasons, as the two
205 models give similar results when all parameters are fixed. Also, Wilcoxon each pair analysis was used to test
206 for differences in A/E ratios among area types as homoscedasticity could not be achieved, and linear
207 regression of annual means was conducted to test for temporal trends in the physico-chemical variables.

208

209 **Results**

210 *Temporal trends*

211 Surveys of drifting algae and eelgrass were performed primarily in the summer months from June to
212 September with a substantial peak in the number of observations in August (Fig. 2). Across years and area
213 types the average cover of drifting algae showed a seasonal variation ranging from less than 1 % cover in

214 March to 23 % cover in August (Fig. 2). Cover increased considerably from March to April, remained high
215 throughout the summer when most observations were done and decreased rapidly in October (Fig. 2). During
216 the 1990s, average cover of drifting macroalgae was generally high with a peak of 40-60% cover in the
217 fjords during the years 1995-96 (Fig. 3). Since then algal cover has declined significantly in all area types i.e.
218 inner fjords, outer fjords, Limfjorden and open coasts (linear regressions, $p < 0.05$, Table 1) with reductions
219 of 74-99 % from the 1994-1996 average to the 2008-2010 average in all area types. After year 2000, algal
220 cover has been relatively low for all area types with average values ranging from 0.3 % in Limfjorden to 8.6
221 % on the open coasts (Fig. 3). Despite the steep drop in drifting algal cover occurring in the late 1990s we
222 did not find any significant changes in the slope of the regression lines for any of the area types during the
223 17-year period.

224 Eelgrass cover showed overall declining trends in the outer fjords and in Limfjorden (Table 2). In the
225 inner fjords there was no significant trend in eelgrass cover throughout the study period, and on the open
226 coast there was no significant trend from 1994 to 1998, but a significant decrease in cover from 1998 to
227 2010. Eelgrass cover in the inner fjords averaged 15.3 % throughout the study period with a peak of 35.7 %
228 in 1999. In both the outer fjords and Limfjorden eelgrass cover peaked at about 50-60 % in 1994-95, but
229 declined during the latter parts of the 1990s and has since year 2000 varied between 10 and 30 % with an
230 average of about 22 %. On the open coasts the pattern is similar to outer fjords and Limfjorden except that
231 cover declined from an average of 32 % in the mid-1990s to less than 10 % after year 2000.

232 The A/E ratio gives an indication of whether the benthic vegetation is dominated by drifting
233 macroalgae or eelgrass. For inner fjords and open coasts the ratio was generally above 1 (average 3.8 and
234 2.8, respectively) indicating dominance by algae. For outer fjords the ratio was above 1 just as often as below
235 (average 1.3) and only Limfjorden was significantly different from the other area types with values generally
236 below 1 (average 0.6) (Wilcoxon each pair, $p < 0.004$) (Fig. 4). There was no significant trend in A/E ratios
237 for the inner fjords, the open coasts or Limfjorden (linear regressions, $p > 0.24$), however, for the outer fjords
238 the A/E ratio decreased significantly from 1994 to 2010 (linear regression, $p = 0.0023$) (Table 3, Fig. 4).

239

240 *Algae cover controls*

241 Both physical and chemical parameters were highly variable and, as could be expected, values overlapped
242 between area types (Table 4). Average concentrations of total N and total P decreased slightly from inner
243 fjords to outer fjords and further out onto the open coasts, and this decline was associated with an increase in
244 Secchi depth. Limfjorden was somewhat different with higher levels of total N and correspondingly low
245 Secchi depth. Limfjorden also had the highest salinity due to the westwards opening to the saline North Sea.
246 For the other area types, salinity counter-intuitively decreased from the inner fjords to the open coasts (Table
247 4), reflecting that the majority of the open coastal areas included in the study were located in the south
248 easterly part of the country closest to the brackish Baltic Sea (Fig. 1). Mean summer temperatures were all
249 around 14 °C, but tended to be slightly lower on the open coasts compared to the fjords. REI was lowest for
250 the inner fjords and highest for the open coasts as expected.

251 Total N concentrations showed a significant decline from 1994 to 2010 across all four area types
252 (Table 4). Within individual area types, each covering only part of the range in environmental conditions, we
253 found similar reductions in total N for all area types except for the inner fjords. Secchi depth and exposure
254 similarly declined across all area types and also declines were significant for most of the specific area types
255 except for Secchi depth in Limfjorden and exposure in the inner fjords. Total P declined only in the outer
256 fjords and salinity and mean summer temperature showed no significant trends either within or across the
257 four area types (Table 4).

258 Across all area types, the cover of drifting macroalgae was positively related to total N and Secchi
259 depth (analysed in separate models due to correlations between the two) and negatively related to REI,
260 salinity and T_{summer} (Fig. 5, Table 5). When analysed separately for each area type algal cover was similarly
261 related to some of the environmental variables. Algal cover was generally positively related to nutrient
262 concentrations, but data suggested that the limiting nutrient differed between area types with algal cover
263 being related to total N in the outer fjords, to total N and total P in Limfjorden and to total P in the inner
264 fjords. For the open coasts, the model indicated a negative relationship between algal cover and total P along
265 with a strong positive effect of Secchi depth (Table 4), the apparently negative effect of total P possibly
266 being an artefact caused by cross correlations between explanatory variables, such as tP and salinity. Algal
267 cover was generally negatively related to salinity and T_{summer} . REI showed a negative relation to algal cover

268 in inner fjords, but a positive relation in the outer fjords and no significant relationships along the open
269 coasts or in Limfjorden.

270 The A/E ratio for all area types combined showed no significant relationship with either total N, total
271 P or Secchi depth across area types, but was negatively related to REI (Fig. 6, Table 6). For the individual
272 area types, the model gave contrasting results with respect to Secchi depth and salinity showing positive
273 relations to A/E-ratio in the outer fjords but negative relations in inner fjords and on the open coast. The A/E
274 ratio was negatively related to mean summer temperature in both the outer fjords and on the open coast.
275 Nutrient concentrations were only significantly related to the A/E ratio on the open coast with a positive
276 relation to nitrogen and a negative to phosphorus. For Limfjorden none of the explanatory variables came out
277 significant.

278

279 **Discussion**

280 *Trends and controls of drifting algae*

281 This study illustrates that the cover of drifting macroalgae in shallow (1-2 m) Danish coastal waters
282 has been significantly reduced from the mid-1990s till 2010. During the 1990s, average summer algal cover
283 ranged from 11 to 37 % for the four areas types with peaks of up to 48 and 62 % cover in the fjords in 1995-
284 96. After year 2000 average algal cover has dropped to less than 10 % in all four area types investigated.
285 Algal cover showed, as hypothesized, a positive relationship with nutrient concentrations, and the reduction
286 in algal cover paralleled the general reduction in nutrient loadings (Hansen 2013) and nitrogen
287 concentrations during the past two decades (Table 4). Hence, the results strongly suggest that reduced
288 nitrogen inputs can have an immediate positive effect on the amount of drifting algae in eutrophic coastal
289 areas, even though significant correlations do not document a cause-effect relationship. The analyses showed
290 no sign of change points in slope over the study period so the changes were not abrupt from one year to the
291 next but were better described as a gradual decline.

292 The analyses further indicated that nitrogen was overall the most limiting nutrient for algal growth as
293 it was positively related to algal cover in the overall dataset (Table 5). The more detailed analyses for
294 specific area types suggested that correlation between algal cover and nitrogen concentration was most

295 pronounced in the outer fjords while phosphorus correlated best in the inner fjords, and the two nutrients in
296 combination correlated with algal cover in Limfjorden. Though nitrogen is generally the most limiting
297 nutrient in marine areas, it is not uncommon that estuaries and coastal marine ecosystems that have been
298 heavily loaded with nutrients show a combination of nitrogen and phosphorus limitation, phosphorus
299 limitation being most likely in the spring and at the transition between fresh and saline waters (Conley et al.
300 2009; Howarth et al. 2011). As better light conditions also stimulated the cover of drifting algae (Table 5)
301 there is, apparently, a tradeoff between the stimulating effect of nutrients on algal growth and the
302 impoverished light conditions resulting from high nutrient levels.

303 Cover of drifting macroalgae was furthermore related to salinity and mean summer temperature with
304 algal cover being higher in areas or years with low salinity or low summer temperatures. The negative effect
305 of summer temperature may be due to limited growth under extreme temperatures ($> 20\text{-}25\text{ }^{\circ}\text{C}$) (Taylor et al.
306 2001), but it is also possible that warm summers are connected with low precipitation and, hence, low supply
307 of nutrients during summer months. High temperatures earlier in the year when temperatures are below
308 optimum for algal growth may, conversely, stimulate algal growth if sufficient nutrients are available (Taylor
309 et al. 2001). A general warming is, therefore, likely to cause increased variability in algal cover over the year
310 and a change in the 'baseline' of algal cover at a given site, but with the effect depending on nutrient
311 availability. We did, however, not identify any trend in mean summer water temperature to indicate general
312 warming during the study period.

313 Opportunistic algae generally have a high tolerance towards low salinities ($< 6\text{-}8\text{ PSU}$) reflected in
314 increased abundance of green algae along the salinity gradient from the north sea towards the inner Baltic
315 Sea (Nielsen et al. 1995; Middelboe et al. 1997; Middelboe et al. 1998) and a larger fraction of opportunistic
316 to late-successional algae at decreasing salinity (Taylor et al. 2001; Krause-Jensen et al. 2007). Opportunistic
317 algae often proliferate in inner fjords near freshwater outlets where salinity is low and nutrient supply is high
318 (Kopecky and Dunton 2006). In this study, however, salinity generally increased from inner fjords towards
319 the open coastal areas located towards the brackish Baltic Sea which may explain why algal cover was
320 higher in the outer fjords compared to the inner fjords in spite of higher nutrient levels in the inner fjords.

321 The cover of drifting algae was, as hypothesized, negatively related to wind-generated exposure
322 (REI) when the entire dataset was considered, but not in all analyses of individual area types (Table 5).
323 Probably this reflects that the range of exposure in individual area types becomes too narrow and the dataset
324 too limited to explain variations in algal cover at the coarse spatio-temporal scale applied. However, drifting
325 algae are often transported by wind and currents and correlations between exposure and algal biomass,
326 showing that algae often accumulate in sheltered areas, have been found in other studies from similar
327 locations sampled at a finer spatio-temporal scale (Pihl et al. 1999; Berglund et al. 2003; Rasmussen et al.
328 2013).

329 Whereas algal cover in Danish waters has been reduced over the past decades, there are no signs of
330 reductions in cover along the nearby Swedish west coast, and blooms of the filamentous chlorophytes, *Ulva*.
331 *sp.* and *Cladophora sp.* as well as of the phaeophyte *Ectocarpus siliculosus* are still common during summer
332 months (Jephson et al. 2008; Risinger 2012). This system, however, is suggested to be controlled by a
333 combination of bottom-up control by nutrients and top-down control by grazing (Jephson et al. 2008;
334 Moksnes et al. 2008). Macroalgal blooms appear mainly in regions where overexploitation of large predatory
335 fish populations, primarily Atlantic cod, *Gadus morhua*, have resulted in high numbers of intermediate
336 predators and high predation rates on mesoherbivore grazers (Pihl et al. 1999; Persson et al. 2008; Andersson
337 et al. 2009; Baden et al. 2010; Baden et al. 2012). In Danish coastal waters there are very few studies on the
338 grazer communities, but top-down control of opportunistic algae in an interaction with bottom-up control has
339 been shown locally (Geertz-Hansen et al. 1993).

340

341 *Trends and controls of the ratio of drift algae to eelgrass cover*

342 Blooms of opportunistic macroalgae have often been connected with increased mortality of
343 seagrasses and loss of seagrass beds (den Hartog 1994; Olyarnik and Stachowicz 2012), and on the Swedish
344 west coast where eelgrass distribution has been reduced by about 60 % opportunistic algae are considered a
345 main cause of the decline (Pihl et al. 1999; Baden et al. 2003). A reduction in the abundance of opportunistic
346 algae is, therefore, expected to carry an increase in eelgrass cover, though the response may be slow (Duarte
347 1995). In the present study, however, the significant reduction in the abundance of drifting algae was not

348 mirrored by a decrease in the ratio of drifting algae to eelgrass, except for the outer fjords. This was due to
349 parallel declines in eelgrass cover during the past two decades (Table 2, Hansen 2013). The apparent lack of
350 recovery of eelgrass indicates that either 1) there is a lag-period or resilience against the recovery of eelgrass
351 following the reduction in cover of drifting algae or 2) the distribution of eelgrass in shallow Danish waters
352 is limited by other factors than opportunistic macroalgae, which may be the case under the present low levels
353 of macroalgal abundance. While feed-back mechanisms e.g. related to the capacity of seagrasses to stabilize
354 sediments and trap particles tend to create resilience in dense eelgrass meadows, sparse meadows lose this
355 capacity and increased resuspension of sediments may initiate feed-back mechanisms leading to further loss
356 of eelgrass and resilience of the non-vegetated regime (van der Heide et al. 2011; Krause-Jensen et al. 2012;
357 Carstensen et al. 2013). The decline in eelgrass across the study period might be related to such feed-backs.

358 Though the recent average cover of drifting algae is low compared to the levels of the 1990s, high
359 levels are still found locally where the algae may exert negative effect on the eelgrass meadows in which
360 they tend to accumulate (Rasmussen et al. 2013). Also, as eelgrass seedlings are particularly vulnerable to
361 both mechanical and biogeochemical stress imposed by algal accumulations even low amounts of drifting
362 macroalgae may delay the spread of eelgrass by increasing seedling mortality (Valdemarsen et al. 2010;
363 Rasmussen et al. 2013). It should also be noted, that in spite of the low absolute levels, drifting algae, in fact,
364 had higher cover than eelgrass in inner fjords and on the open coasts (A/E ratios often above 1; Fig. 4).
365 Limfjorden, by contrast, had low absolute and relative cover of drifting macroalgae possibly due to
366 competition with the introduced macroalga *Sargassum muticum*, which is the most dominant alga in
367 Limfjorden today but is absent from most other Danish coastal areas likely due to their lower salinity (Stæhr
368 et al. 2000; Thomsen et al. 2006). Den Hartog (1997) suggested that *Sargassum* may be able to replace
369 eelgrass under certain conditions and we cannot exclude that it has such effects in parts of Limfjorden.

370 Overall, the A/E-ratio showed no relationship to either Secchi depth or nutrients as we had expected.
371 We believe that this may be because algae and eelgrass are subject to different control mechanisms. This
372 complicates the interpretation of changes in their ratio which could result from changes in either or both of
373 the variables and for various reasons. Also it should be noted that a direct relationship resulting from a

374 trapping effect of drifting algae in eelgrass beds could potentially complicate any trends in their ratio. Ratios
375 are, thus, inherently more difficult to interpret than variables investigated one by one.

376

377 *The importance of the scale of study*

378 The most distinct relationships between drifting algal cover and environmental variables were
379 obtained when analysing all areas combined rather than conducting separate analyses for different area types
380 (Table 5). The overall analysis thus identified correlations between algal cover and total N, Secchi depth,
381 REI, salinity and mean summer temperature whereas this was not the case for all the area-specific analyses.
382 The overall analysis makes maximum use of the strengths of the dataset which lies in the large number of
383 data covering marked gradients in both explanatory variables and response variables and multiple
384 combinations of these. This large scale approach to some extent overcomes the obvious limitations of the
385 dataset related to yearly observations at a limited number of sites in each coastal area, which do not capture
386 the large seasonal variation in algal cover nor the large spatial variation within areas due to e.g. local
387 accumulation of algae by wind and currents (Salomonsen et al. 1999; Berglund et al. 2003; Rasmussen et al.
388 2013). The large-scale gradients of the full dataset also have the potential to address relationships between
389 algae and physico-chemical factors in spite of the limitation that water chemistry sites are generally situated
390 centrally in the basins rather than next to vegetation sites and therefore do not offer a detailed description at
391 the small scale.

392

393 *Conclusion*

394 In conclusion, we show that the general cover of drifting macroalgae in shallow (1-2 m) Danish
395 coastal waters has been significantly reduced following reductions in nutrient loadings during the past
396 decades. The present levels of drifting algae are low in all area types and probably pose little threat to the
397 general distribution of eelgrass in Danish coastal waters. Locally, aggregations of algae may, however, still
398 limit eelgrass survival and delay re-colonisation. The ratio of drift algae to eelgrass cover did not change
399 across the study period, reflecting that eelgrass cover had declined in spite of reduced drift algal cover,
400 probably because recovery is delayed by feed-back mechanisms related to e.g. more unstable sediments

401 when eelgrass cover is low. Reduced drift algal cover may, thus, be a first indication of improved ecological
402 status while further improvements in terms of recovery of eelgrass meadows have longer perspectives.

403

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583

584 **Figure captions**

585

586 **Fig. 1** Map of Denmark showing locations of monitoring sites for eelgrass and algae cover (Vegetation), as
587 well as stations for water chemistry and meteorological data

588

589 **Fig. 2** Seasonal distribution of algal cover and monitoring observations. Cover is the average for all area
590 types over the period from 1994 to 2010 and error bars show SE.

591

592 **Fig. 3** Temporal trends in the cover of drifting macroalgae in the period from 1994 to 2010 for four coastal
593 area types: Inner fjords, outer fjords, open coasts, and Limfjorden which is treated separately. Dotted lines
594 represent plus and minus SE, and the dashed line is a linear regression line from trend analyses

595

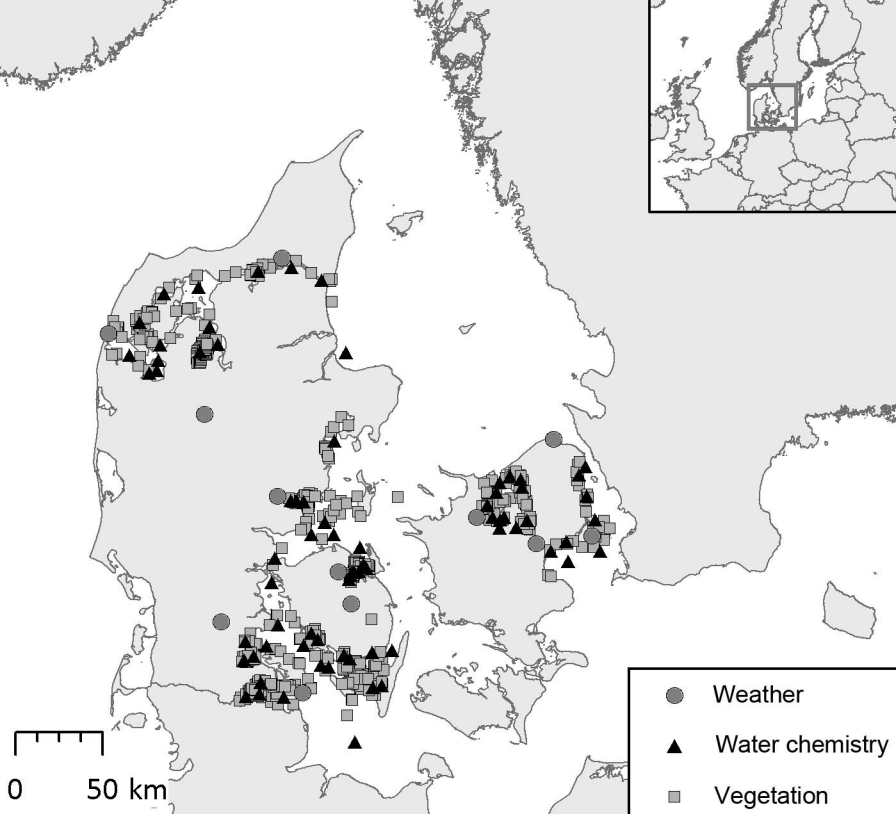
596 **Fig. 4** Temporal trends in the ratio of drifting macroalgae cover to eelgrass (*Zostera marina*) cover (A/E
597 ratio) in the period from 1994 to 2010 for four coastal area types: Inner fjords, outer fjords, open coasts and
598 Limfjorden which is treated separately. The solid horizontal line marks the value 1 where cover of algae and
599 eelgrass are equal and the dashed line in the Outer fjords pane is a linear regression line from trend analyses.
600 The gap in the Limfjorden pane in 1996 is due to a lack of data. Note the logarithmic scale on the y-axis

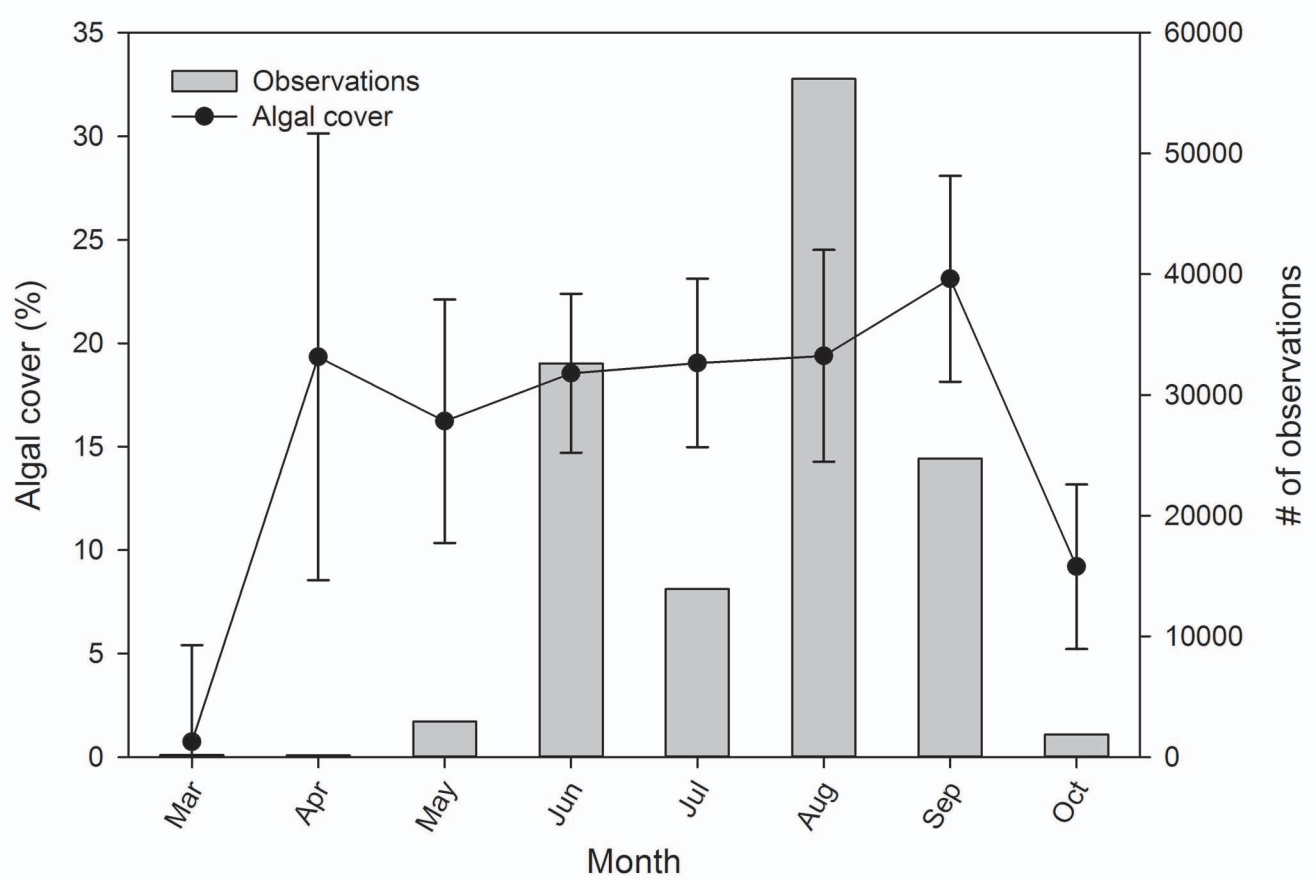
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602 **Fig. 5** Single observations of drifting macroalgae cover plotted against relative exposure (REI), salinity (ppt),
603 total nitrogen (μM) and mean summer temperature ($^{\circ}\text{C}$). Data are for all area types and individual points
604 represent individual years in the period from 1994 to 2010 showing the large variation between sites and
605 years

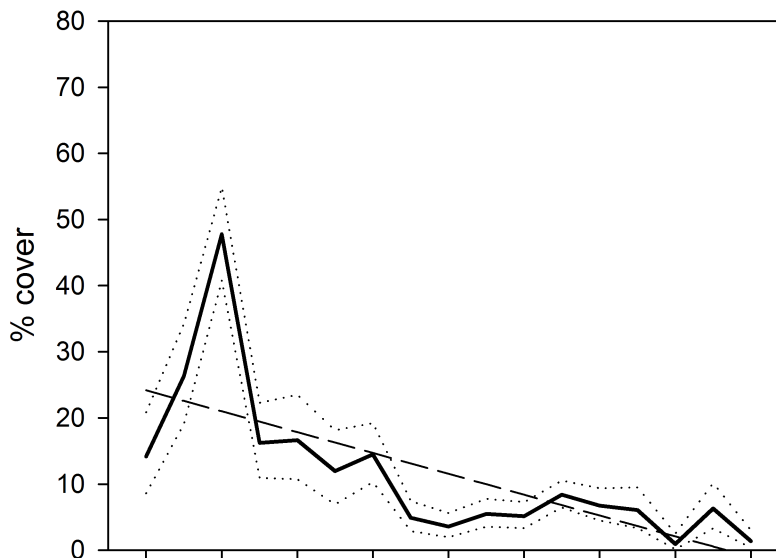
606

607 **Fig. 6** Ratio of drifting macroalgae cover to eelgrass (*Zostera marina*) cover plotted against relative exposure
608 (REI). Data are for all area types and individual points represent individual years in the period from 1994 to
609 2010 showing the large variation between sites and years. Note the logarithmic scale on the y-axis

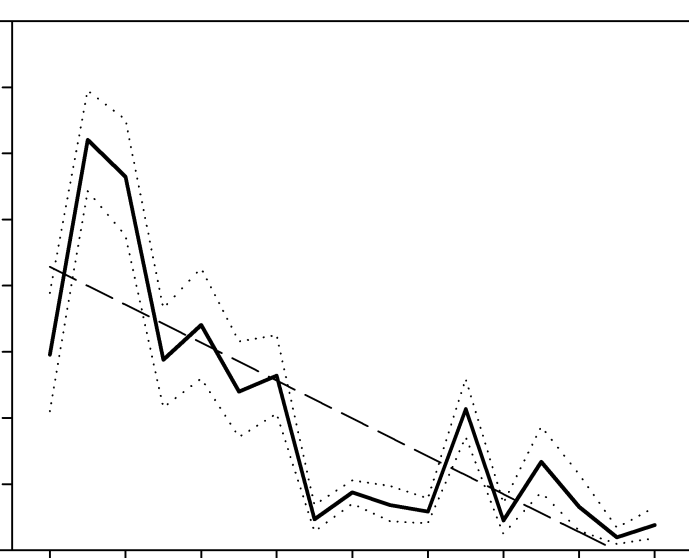




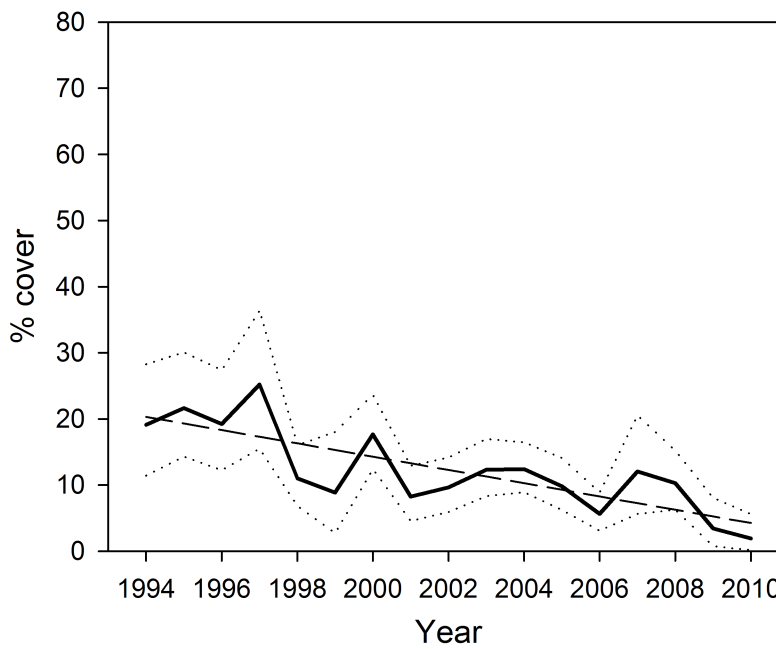
Inner Fjords



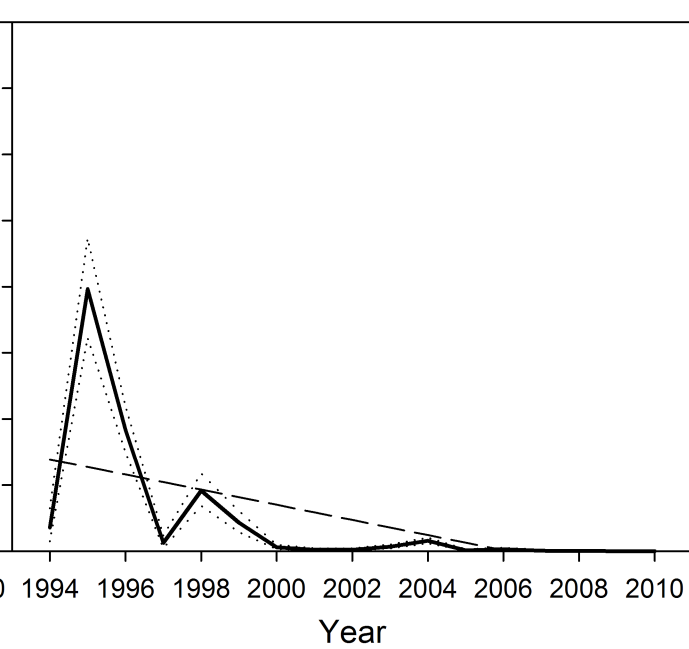
Outer Fjords



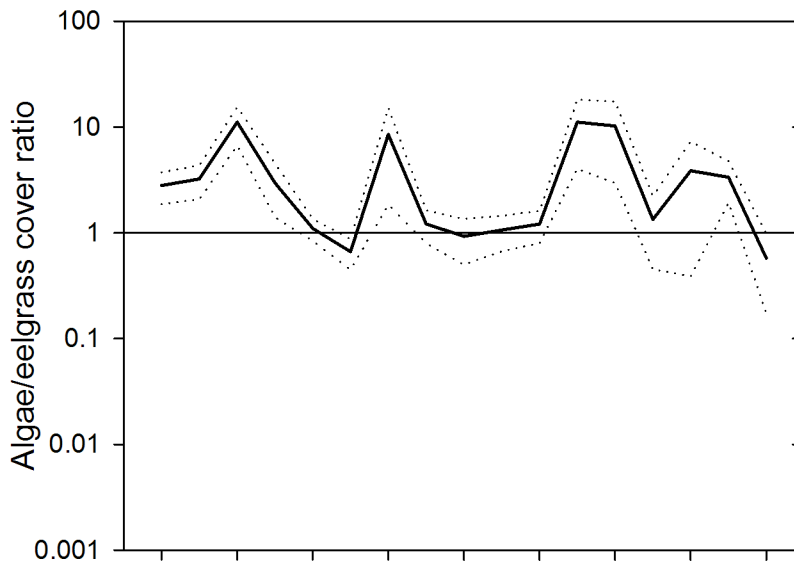
Open Coast



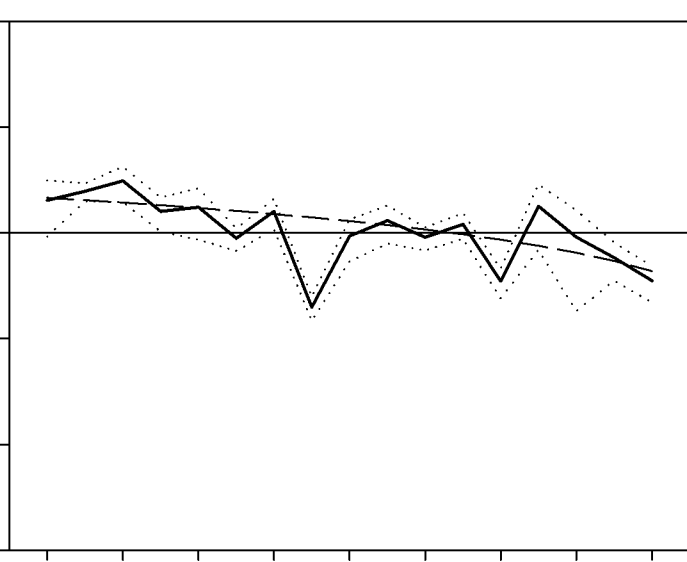
Limfjorden



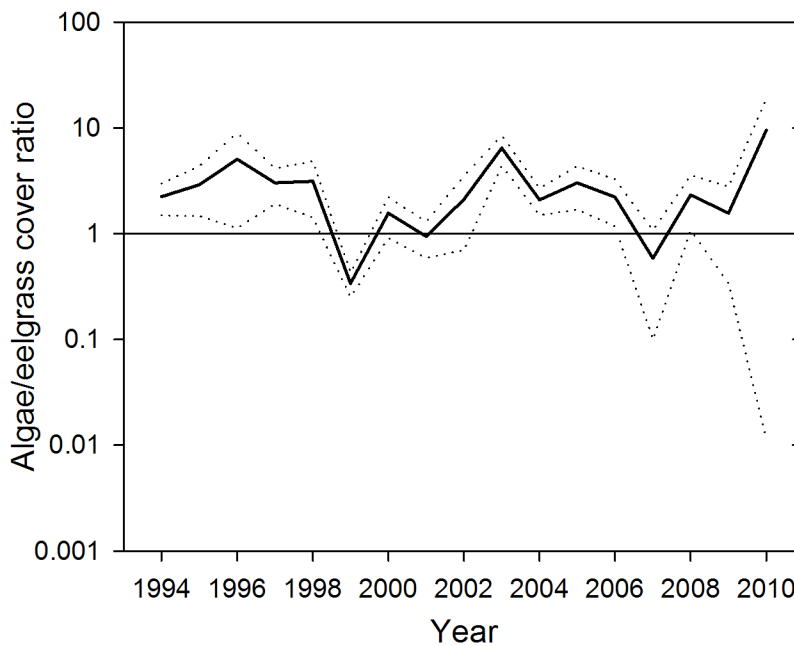
Inner Fjords



Outer Fjords

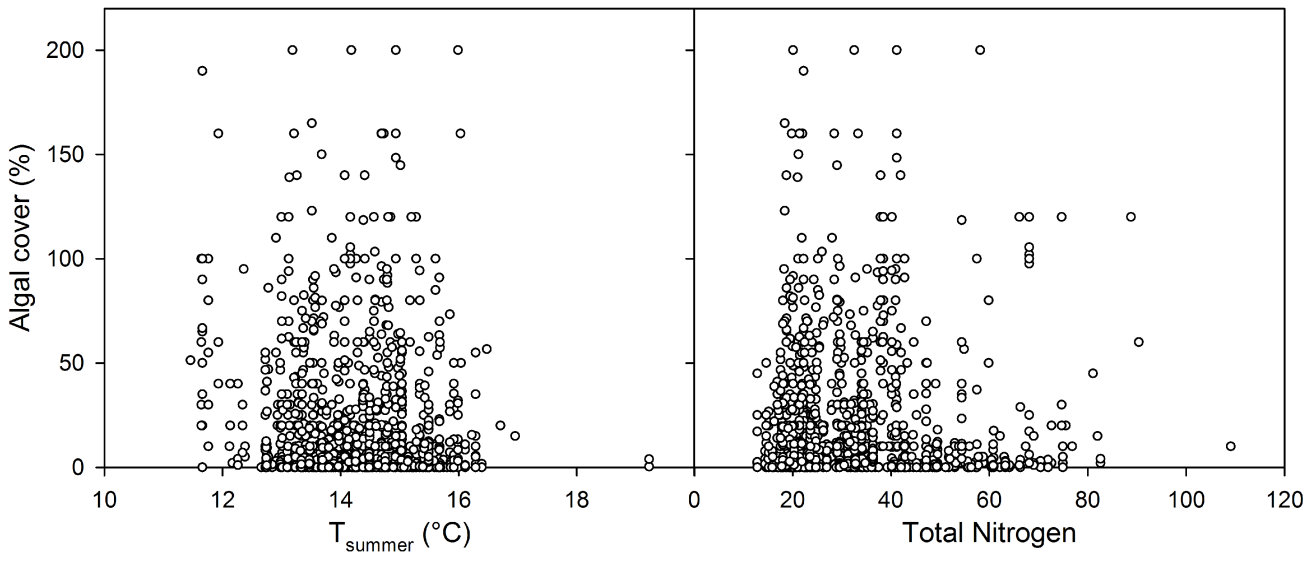
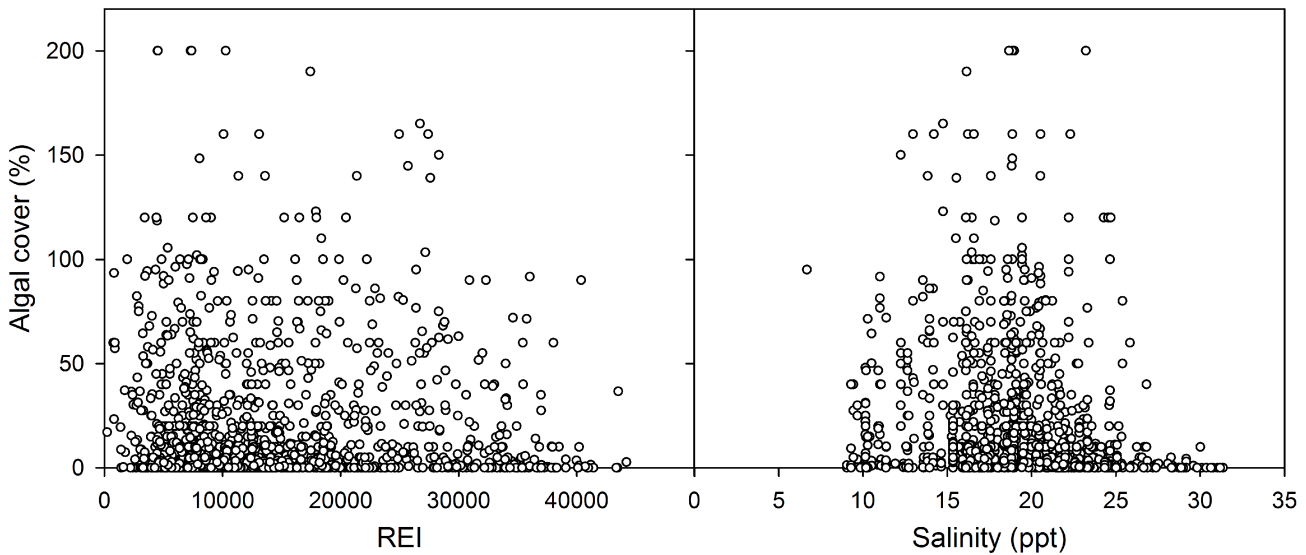


Open Coast



Limfjorden





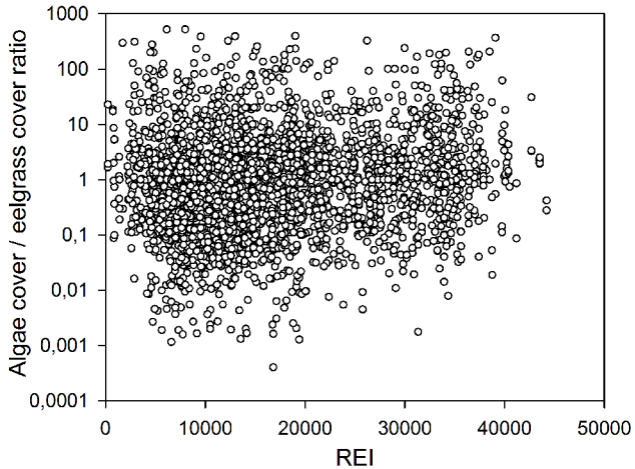


Table 1: Slopes of stepwise linear regression models describing yearly average cover of drifting algae. Arrows indicate direction of trend; ↗: significantly ($p \leq 0.05$) increasing cover, ↘: significantly ($p \leq 0.05$) decreasing cover, →: no significant changes in cover.

Area type	Interval	Direction of slope	Slope	Std Err	t Value	Pr > t
Inner fjords	1994-2010	↘	-1.58	0.42	-3.76	0.0019
Outer fjords	1994-2010	↘	-2.86	0.57	-5.05	0.0001
Open coasts	1994-2010	↘	-1.00	0.20	-5.03	0.0002
Limfjorden	1994-2010	↘	-1.14	0.43	-2.68	0.0170

Table 2: Slopes of stepwise linear regression models describing yearly average cover of eelgrass. Arrows indicate direction of trend; ↗: significantly ($p \leq 0.05$) increasing cover, ↘: significantly ($p \leq 0.05$) decreasing cover, →: no significant changes in cover.

Area type	Interval	Direction of slope	Slope	Std Err	t Value	Pr > t
Inner fjords	1994-2010	→	-0.46	0.38	-1.22	0.2414
Outer fjords	1994-2010	↘	-1.94	0.39	-4.94	0.0002
Open coasts	1994-1998	→	-3.16	1.62	-1.94	0.0747
	1998-2010	↘	-1.89	0.43	-4.38	0.0007
Limfjorden	1994-2010	↘	-2.00	0.46	-4.34	0.0007

Table 3: Slopes of the stepwise linear regression models describing yearly average levels of cover of drifting algae / cover of eelgrass (A/E-ratio). Arrows indicate direction of trend; ↗: significantly ($p \leq 0.05$) increasing ratios, ↘: significantly ($p \leq 0.05$) decreasing ratios, →: no significant changes in ratio.

Type	Interval	Direction of slope	Slope	Std Err	t Value	Pr > t
Inner fjords	1994-2010	→	-0.04	0.19	-0.19	0.8504
Outer fjords	1994-2010	↘	-0.11	0.03	-3.68	0.0023
Open coast	1994-2010	→	0.07	0.11	0.67	0.5139
Limfjorden	1994-2010	→	-0.06	0.05	-1.22	0.2416

Table 4: Physical and chemical parameters used in the analyses. Mean values and 10 and 90 percentiles (in parenthesis) of relative exposure index (REI), salinity (Sali), Secchi depth (Secchi), summer water temperature (T_{summer}), total nitrogen (tN) and total phosphorus (tP). Parameters were calculated as seasonal averages (see methods section) and table values represent mean and range of the yearly estimates for area types over the period 1994 to 2010. Brackets show results of linear regression analysis on temporal changes in yearly means. Numbers are slopes and asterisks indicate significance level (*, $p < 0.05$; **, $p < 0.005$; ***, $p < 0.001$). NS indicates no significant change from 1994 to 2010.

Area type	REI	Sali (ppt)	Secchi (m)	T_{summer} ($^{\circ}\text{C}$)	tN (μM)	tP (μM)
All areas	15396 (5686 – 30127) [-298***]	19.5 (13.6 – 25.1) [NS]	5.6 (3.4 – 7.9) [-0,08*]	14.3 (13.1 – 15.5) [NS]	33.4 (18.1 – 57.4) [-1.0*]	0.9 (0.6 – 1.2) [NS]
Inner fjords	9137 (4083 – 14566) [NS]	20.1 (16.5 – 24.3) [NS]	5.3 (3.7 – 7.3) [-0.07*]	14.3 (13.1 – 15.6) [NS]	37.5 (18.0 – 58.1) [NS]	1.0 (0.6 – 1.3) [NS]
Outer fjords	15750 (7162 – 28376) [-165***]	18.5 (15.9 – 21.4) [NS]	5.7 (4.2 – 6.9) [-0,04*]	14.4 (13.2 – 15.5) [NS]	28.4 (18.7 – 40.2) [-1.1***]	0.8 (0.6 – 1.2) [-0,01*]
Open coasts	22705 (11668 – 36025) [-549**]	14.8 (10.2 – 21.7) [NS]	7.3 (5.5 – 9.2) [-0,12*]	13.6 (12.8 – 14.5) [NS]	20.8 (17.3 – 24.9) [-0.3*]	0.7 (0.5 – 0.9) [NS]
Limfjorden	15893 (7013 – 26418) [-321*]	26.0 (23.4 – 29.2) [NS]	3.7 (2.7 – 5.2) [NS]	14.8 (13.8 – 15.7) [NS]	53.5 (37.5 – 82.6) [-2,6***]	1.0 (0.9 – 1.2) [NS]

Table 5: Analysis of the cover of drifting macroalgae as a function of physical and chemical parameters. Parameter estimates and statistical results of two models. Model 1 including relative exposure index (REI), Salinity (Sali), summer temperature (T_{summer}) and Secchi depth (Secchi). Model 2 including REI, Sali, T_{summer} , total nitrogen (tN) and total phosphorus (tP). Only significant ($p < 0.05$) parameters are shown. Dashes indicate parameters not included in the model.

Area type	REI		Sali (ppt)		T_{summer} ($^{\circ}\text{C}$)		Secchi (m)		ln tN		ln tP	
	Est.	p	Est.	p	Est.	p	Est.	p	Est.	p	Est.	p
All areas												
Model 1	-3.3E-6	0.0007	-0.019	<0.0001	-0.033	0.0010	0.026	0.0002	–	–	–	–
Model 2			-0.025	<0.0001	-0.059	<0.0001	–	–	0.121	0.0005		
Inner Fjords												
Model 1	-5.5E-6	0.0010	-0.024	<0.0001					–	–	–	–
Model 2	-4.3E-6	0.0178	-0.027	<0.0001	-0.037	0.0005	–	–			0.153	<0.0001
Outer Fjords												
Model 1	5.0E-6	<0.0001							–	–	–	–
Model 2	8.3E-6	<0.0001			-0.023	0.0094	–	–	0.204	<0.0001		
Open Coasts												
Model 1			-0.039	<0.0001	-0.071	<0.0001	0.071	<0.0001	–	–	–	–
Model 2			-0.036	<0.0001	-0.106	<0.0001	–	–			-0.219	<0.0001
Limfjorden												
Model 1			-0.013	<0.0001	-0.039	<0.0001			–	–	–	–
Model 2					-0.026	0.0003	–	–	0.159	<0.0001	0.252	<0.0001

Table 6: Analysis of the cover of drifting macroalgae vs. eelgrass (*Zostera marina*) cover (A/E-ratio) as a function of physical and chemical parameters. Parameter estimates and statistical results of two models. Model 1 including relative exposure index (REI), Salinity (Sali), summer temperature (T_{summer}) and Secchi depth (Secchi). Model 2 including REI, Sali, T_{summer} , total nitrogen (tN) and total phosphorus (tP). Only significant ($p < 0.05$) parameters are shown. Dashes indicate parameters not included in the model.

Area type	REI		Sali (ppt)		T_{summer} (°C)		Secchi (m)		ln tN		ln tP	
	Est.	p	Est.	p	Est.	p	Est.	p	Est.	p	Est.	p
All areas												
Model 1	-1.0E-4	0.028							-	-	-	-
Model 2	-1.0E-4	0.028					-	-				
Inner Fjords												
Model 1							-1.974	0.0131	-	-	-	-
Model 2							-	-				
Outer Fjords												
Model 1			0.716	0.0058			1.210	0.0105	-	-	-	-
Model 2					-1.187	0.0325	-	-				
Open Coasts												
Model 1			-1.261	<0.0001	-4.465	0.0086	-1.924	0.0356	-	-	-	-
Model 2			-0.978	0.0040			-	-	24.37	0.0034	-14.46	0.0195
Limfjorden												
Model 1									-	-	-	-
Model 2							-	-				