

Climatic and environmental factors influencing occurrence and distribution of macroalgae – a fjord gradient revisited

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Abstract

During the last decades a tendency of increasing sea water temperatures and more precipitation has been seen in the North Atlantic. Increasing sea water temperatures are expected to have strong effects on coastal benthic species. Here the distributions of macroalgae, sampled at stations along a fjord during 1955-1956 and 2008-2009, are correlated to hydrographical indexes made from measurements along the fjord during the two periods. The following indexes were used: annual maximum sea temperature, minimum salinity, and salinity stress (difference between maximum and minimum salinity). In addition, changes in abundance and distribution range in the fjord were calculated for the macroalgae. The hydrographical measurements showed higher summer temperatures and reduced salinity stress due to lower winter salinity, during 2008-2009. Results from constrained ordination analyses showed that the highest variation of the macroalgal distributions along the fjord was explained by hydrographical indexes from 5 m depth, and that there were strong response differences between the algal groups. The red algae showed the strongest positive correlation with the gradient of maximum temperature, and then a negative correlation with increasing salinity stress. Many red algae also increased in abundance and occurred further into the fjord in 2008-2009. The brown algae showed the highest negative correlation with increasing salinity stress, and showed less change in abundance or range shifts along the fjord. Some species showed a strong correlation with temperature (positive or negative). The results demonstrate that both temperature and salinity changes will have an impact on cold temperate macroalgal communities.

Key words: Macroalgal community, hydrography, climate change, fjord gradient, species composition

Introduction

The coast is extensively used and densely inhabited in many regions, and under great pressure worldwide. Macroalgae dominate the vegetation in the intertidal and the euphotic zone, and the occurrence and abundance of these may consequently be strongly affected by anthropogenic activity (Walker & Kendrick 1998). Conspicuous changes in macroalgal composition and abundance are reported due to anthropogenic impact such as nutrient enrichment (e.g. Valiela et al. 1997, Middelboe & Sand-Jensen 2000, Worm & Lotze 2006, Liu et al. 2013), interactions between nutrient enrichment and grazers (Lotze & Worm 2000), and increased sedimentation (Eriksson et al. 2002, Eriksson & Johansson 2005). More recently there has been a strong focus on effects of increasing sea temperatures in coastal areas, and a number of cases with concurrent changes in macroalgae range shifts (e.g. Lima et al. 2007, Diez et al. 2012, Tanaka et al. 2012, Duarte et al. 2013) or community compositions (e.g. Husa et al. 2008, Sangil et al. 2012, Diez et al. 2012) have been reported.

Sea temperature and salinity are normally the main physical factors which determine regional and local distribution of macroalgae in euphotic coastal waters. For most macroalgal species the seasonal temperature extremes, sometimes in combination with day lengths, set biogeographical boundaries for survival, growth or reproduction (van den Hoek 1982a, b, Breeman 1988, Lüning 1990). In addition to temperature tolerance limits, most macroalgae also have optimum temperature ranges for photosynthesis and growth. For European cold-temperate algae the optimum temperature for growth is often around 15 °C, or in the range between 10 and 15 °C (Fortes & Lüning 1980). In addition to affecting survival and growth rate, temperature may also influence the functionality of macroalgae in other ways, e.g. by influencing fecundity and thereby local abundance. For example, Krueger-Hadfield et al. (2013) observed that reproductive effort in the red alga *Mastocarpus papillatus* was positively correlated with temperature. Local variation in salinity will also set physiological tolerance limits for marine macroalgae, or affect growth and functionality in several ways (Kirst 1990). In estuaries, where salinity of the surface waters varies with precipitation and fresh water run-off from land, macroalgal communities are likely to be dominated by euryhaline species with wide tolerance limits.

Variation in sea temperature and other marine physical factors is due to both natural variability and to anthropogenic activity. Inter-annual variability is typically the result of large

scale weather patterns as e.g. described by the North Atlantic Oscillation index (NAO; Hurrell et al. 2003). Anthropogenically induced variability of physical factors is to a large extent due to greenhouse gas induced climatic changes resulting in increased temperatures and precipitation (www.ipcc.ch). During the last decades increased sea temperatures and precipitation have been observed in the North Atlantic (Benestad & Melsom 2002, Lenderink et al. 2009). Both elevated temperatures and increased freshwater run-off to the sea, causing lower salinity, may be especially pronounced in estuaries. While increased precipitation may have resulted in an overall increase in freshwater run-off to estuaries, the establishment of hydroelectric power plants has caused a strong intra-annual change in freshwater run-off to many fjords in Norway. Snow melting during spring and early summer results in high fresh water run-off to the sea and causes the formation of a pronounced brackish layer in the fjords during this period. Approximately 70 % of the large river systems in Norway have now been regulated for hydroelectric power plant production (www.environment.no), with the main part being regulated after 1960 (Kaartvedt 1984). The regulation includes making basins for retaining water, and as a result of this the seasonal pattern with a pronounced peak in freshwater discharge during spring and early summer has changed in many of the fjords (Kaartvedt 1984).

Large-scale and mainly climate-driven changes have recently been observed in coastal ecosystems (e.g. Parmesan 2006, Harley et al. 2006, Aksnes et al. 2009, Iles et al. 2012, Hernández-Fariñas et al. 2014). The more long-lasting the fluctuations in the physical environment, the greater the ecosystem impacts (Sundby & Nakken 2008). The most marked ecological effects of such changes will be altered composition of trophic groups and food-webs. Thus, analyzing climate-driven changes in the composition of different trophic levels is imperative in understanding ecosystem effects, and this can only be done by utilizing historical data. Here, changes in macroalgal distributions between 1955-1956 and 2008-2009 at a total of 20 stations in Hardangerfjord have been analyzed in relation to hydrographical data from the same time periods. The data of the macroalgal distribution in 1955-1956 have previously been published in Jorde & Klavestad (1963) and the stations were reinvestigated by Husa et al. (2014), who observed an increase in number of species per station and a higher occurrence of species with a more southern distribution in 2008-2009 compared to the data from 1955-1956. Husa et al. (2014) suggested that the changes were caused by hydrographical changes, but did not provide any analyses of the macroalgal data in relation to hydrographical data. Here we have compiled data on temperature and salinity along Hardangerfjord from

1955-1956 and 2008-2009. The temperature and salinity profiles were different between the two periods, which enabled us to show significant correlations between algal distributions and environmental gradients made from the hydrographical data sets. Further, we have related the correlation patterns to changes in macroalgal abundance and distribution shifts along the fjord. By this we are able to show differences between algal groups with regard to environmental responses, and to examine in detail response differences between species.

Material and methods

Hydrography

Data describing the long-term variability of sea temperature in the Hardangerfjord region the last 60 years have been taken from the coastal monitoring station Utsira operated by the Institute of Marine Research, Norway. The Utsira station (59° 18' N, 04° 52' E) is situated approximately 25 km southwest of the outside mouth of Hardangerfjord, and the monthly mean values of temperature at 10 m depth compare well with similar averages from high frequency observations inside Hardangerfjord (Asplin et al. 2014). At the Utsira station profiles of salinity and temperature on a bi-weekly scale go back to 1942 (Sætre et al. 2003).

Salinity and temperature were measured in Hardangerfjord monthly at 0, 5 and 10 m depth at 5 stations (H3-H7) distributed along the fjord gradient (Figure 1) during 1955-1956 (Sælen 1962). These data were compared to recent data collected at irregular intervals (from every month to every four months) during 2008 and 2009, and supplemented with additional measurements from 1992 and 1993 from locations close to stations H3 and H4 (data from 5 and 10 m during the months November 1992 and June, August and September 1993). The hydrographical recordings from 2008-2009 do not include measurements from station H6. As a substitute for H6, averages of measurements collected at two new hydrographical stations placed around 8 km inside and 10 km outside station H6 were used.

The long-term trend in precipitation has been derived from monthly records of precipitation from a weather station close to station 20 (Figure 1), situated in the inner part of the Hardangerfjord area. The data are accessible from the Norwegian Meteorological Institute (eklima.met.no).

In order to evaluate the effect of hydroelectric power plant constructions in Hardangerfjord the freshwater run-off data from an unregulated river and from a nearby hydroelectric power plant at the head of Hardangerfjord in the largest fjord branch Sørfjord (Figure 1) have been compared. Data are made available by the Norwegian Water Resources and Energy Directorate (www.nve.no) (Pettersen 2008).

Macroalgae communities

The macroalgal data set used in the present study consists of presence-absence recordings of species from 20 shore stations situated from the outer part of Hardangerfjord to the innermost fjord branches. Stns. 1-15 are placed in the Hardangerfjord proper, and Stns. 16-20 in fjord branches (Figure 1). The stations were first investigated during the summers of 1955 and 1956 (Jorde & Klavestad 1963), and recently during June-July in 2008 and 2009 (Husa et al. 2014). The sampling during 2008-2009 was carried out using the methods and dredging depths as described in Jorde & Klavestad (1963). During 1955-1956 most of the stations were sampled in 1955, and in 2008-2009 seven stations were sampled in 2008 and the rest in 2009. Macroalgae were collected by hand in the intertidal around low tide and in the subtidal by dredging from a boat to depths between 5 and 21 m at each of the stations. A detailed description of the sample procedure and species identification is found in Husa et al. (2014). Taxa were identified to species when possible. Very small species, crustose species and species with uncertain taxonomic status were not included. Species introduced to Norway since 1956 were not included in the analyses.

Both during 1955-1956 and 2008-2009 a pronounced gradient in macroalgal species richness was found along the fjord, with a decrease in number of species with increasing distance to the mouth of the fjord (Jorde & Klavestad 1963, Husa et al. 2014). In order to examine if species exhibited changes in range distribution along the fjord, data from the two investigations were utilized for calculating range shifts between the two studies. The distance along the fjord from the outermost to the innermost station in the longest fjord branch was 126 km. The distance was divided by number of stations along the distance (18) resulting in 18 sectors, each 7 km long, and when adding the sectors in the other fjord branches this gave an average distribution of 1.1 station per sector. The sectors were numbered, and the difference between the innermost sectors in which each of the species was recorded during the two investigations, was noted. In order to reduce the effect of randomly occurring rare species

only species recorded at more than two stations during one or both of the investigations were included.

In order to calculate concurrent changes in each species' local abundance in the fjord between the two studies, the frequencies of each species within their distribution ranges were calculated. The abundance of each species was calculated as frequency of occurrence between the innermost station where a species was present and the outermost station (Station 1). Only species recorded at more than two stations during one or both of the investigations were included. The relative change in abundance for each species was calculated as difference in frequency from 1955-1956 to 2008-2009.

In order to test if changes in macroalgal distributions between 1955-1956 and 2008-2009 could be related to hydrographical factors, the distributions during the two periods were correlated to hydrographical indexes made from measurements at the hydrographical stations H3-H7 during the two periods. The two successive years of both periods did not differ much in their extreme values of temperature and salinity, and the measurements during each period were compiled in order to make the indexes. Macroalgae have been shown to respond quickly to environmental changes (see e.g. Pedersen et al. 2008). Since hydrographical extreme values over the year are most likely to have an influence on survival or growth of macroalgae, seasonal maximum and minimum values of temperature and salinity were used in the analyses. Temperature and salinity of the surface water may be prone to big short-term variations due to day-to-day variations in e.g. rainfalls, air temperature or the horizontal advection of water masses, and consequently the recordings from 5 and 10 m depth were used to make salinity and temperature indexes. The following environmental indexes were constructed: annual maximum temperature; T(max), annual minimum salinity; S(min), and salinity stress; S(str). Salinity stress was calculated as the maximum annual difference of the salinity measurements at each hydrographical station. Annual minimum temperature was not included since it did not differ much between the two investigation periods or between the hydrographical stations. The calculated index values for each hydrographical station were then assigned to the closest shore stations. Between H7 and H6 and H6 and H5 the index values were interpolated, and the resulting values were assigned to the shore stations between each hydrographical station.

Correlations between the species' distribution in the fjord and the constructed temperature and salinity indexes during the two periods were made by using a direct gradient

analysis with constrained ordination (linear Constrained Redundancy Analysis (RDA)) (Lepš & Šmilauer 2003). Monte Carlo permutation tests with unrestricted permutations for significance were applied. CANOCO Version 4.5 for Windows was used for the analyses. Results from stations 19 and 20 were not included in the ordination analyses, since these were placed in separate fjord branches with no recent hydrographical measurements nearby. Likewise, species recorded only once during one or both investigations, and species with the same distribution during both studies or with only one more or less recording during one of the investigations, were omitted. A total of 78 macroalgae species were included in the ordination analyses; 5 Chlorophyta (green algae), 36 Phaeophyceae (brown algae) and 37 Rhodophyta (red algae) (Appendix Table 1). Separate analyses were carried out on the distributions of green, brown and red algae.

Results

Hydrography

Temperature plots from the hydrographical stations inside Hardangerfjord (H3-H7) during 1955-1956 and 2008-2009 are shown in Figure 2. While the minimum temperatures during January – March did not show big differences between 1955-1956 and 2008-2009, the temperatures during summer and early autumn were clearly higher throughout the fjord in 2008-2009 when compared to the measurements in 1955-1956. This was most evident at 0 and 5 m depth, where the maximum temperature was 4.7 °C and 4.5 °C higher respectively in 2008-2009, when compared to the measurements in 1955-1956. The difference in maximum summer temperatures between 1955-1956 and 2008-2009 was biggest in the inner part of the fjord proper (Stns. 10-14) and smallest at the innermost stations (Stns. 15-18) (Figure 2, Table 1). The observed water temperatures at 10 m depth at the coastal monitoring station Utsira outside Hardangerfjord from 1955 to 2009 are shown in Figure 3. A positive trend was evident for all quarters of the year, but the highest increase was seen during summer-autumn (2nd and 3rd quarter of the year).

Salinity measurements at H3-H7 from the fjord showed differences between the two periods. During 1955-1956 the late autumn – winter maximum salinities at stations H4-H7 were between 33 and 34 at 0 and 5 m depth, while they were between 28 and 31 during 2008-2009 (Figure 4). At the innermost hydrographical station (H3) the maximum salinity was 30.7

and 33.2 at 0 and 5 m depth respectively during 1955-1956, while during 2008-2009 it was around 27. At 10 m depth the differences between the two periods were less pronounced.

The recordings of seasonal minimum salinity during summer – early autumn in the fjord was slightly lower at 0 m during 2008-2009 than during 1955-1956 (Figure 4), and varied between 4.2 and 15.8 during 2008-2009 and 7.6 and 21.6 during 1955-1956, at the inner- and outermost hydrographical station respectively. The results also suggest more variability between monthly recordings at 0 m of salinity in 2008-2009 than in 1955-1956. At 5 m depth on the other hand, the minimum salinity recordings were much higher during 2008-2009 than during 1955-1956 in the innermost parts of the fjord (Figure 4, Table 1). The minimum salinities were 16 and 14.2 in 1955-1956, and 20.2 and 19 in 2008-2009, at stations H3 and H4 respectively. Further out in the fjord there was a tendency to slightly lower minimum salinity values at 5 m depth during 2008-2009 when compared with the results from 1955-1956. At 10 m depth only small differences in recordings of minimum salinity between 1955-1956 and 2008-2009 were found (Figure 4).

Precipitation data from Eidfjord in the inner part of Hardangerfjord showed that there has been a more than 30 % increase in the monthly mean values between 1955 and 2009 (Figure 5). The shift in the seasonal cycle of freshwater run-off into Hardangerfjord following the large river regulations is illustrated by data from the regulated river at the hydroelectric plant Oksla in the inner part of Sør fjord and from the largest nearby unregulated river system. In the unregulated river the freshwater discharge displayed a typical pattern with low values during the winter, and a spring flood and an autumn flood with peak values of around $150 \text{ m}^3 \text{ s}^{-1}$ (Figure 6). The discharge from the regulated river at the Oksla hydroelectric power plant had a more steady discharge of fresh water on around $50 \text{ m}^3 \text{ s}^{-1}$ (Figure 6) with highest discharge in the cold season.

Macroalgae communities

An overview of the changes in distribution range and abundance of the algal species is shown in Figure 7. Relatively few green macroalgae were included in the study. Of these, *Bryopsis hypnoides* showed a clear increase in both distribution and abundance, while *Codium fragile* subsp. *fragile* showed a decrease (Figure 7A). While many brown algae showed only minor changes in abundance and distribution between the two investigations, some displayed large

changes. *Acrothrix gracilis*, *Dictyota dichotoma*, *Stictyosiphon soriferus* and *Striaria attenuata* showed a pronounced increase in both abundance and distribution range, while *Dictyosiphon foeniculaceus* and *Protohalopteris radicans* showed a clear decrease (Figure 7A). There were also several species with a large negative shift in distribution ranges and little difference in abundance, e.g. *Halosiphon tomentosus*, *Battersia racemosa* and *Battersia arctica*. These occurred sparsely in the inner parts of the fjord in 1955-1956 but were not recorded in 2008-2009. Finally a few large and dominating species showed some increase in abundance without or with only a minor extension in distribution; *Desmarestia aculeata*, *D. viridis*, *Saccharina latissima*, and *Laminaria hyperborea* (Figure 7A). While *L. hyperborea* was not recorded in the fjord proper at all in 1955-1956 (Jorde & Klavestad 1963) it was recorded at the three outer stations in 2008-2009.

Most of the red algae showed an increase in both distribution range and abundance (Figure 7B), while a few showed a decrease; *Aglaothamnion tenuissimum*, *Dumontia contorta* and *Furcellaria lumbricalis*. A few others showed a decrease in abundance without a concurrent shift in distribution range; *Polyides rotunda*, *Corallina officinalis* and *Ceramium virgatum* (Figure 7B).

The results of the ordination analyses showed strong correlations between the distributions of the species and the environmental indexes, with the gradients of maximum temperature and salinity stress (difference between maximum and minimum salinity during the year) being the most important ones. Significant correlations ($P = 0.002$) between distributions of red, brown and green algae and the environmental indexes from 5 and 10 m depth during the two periods were found. However, less of the species' distributions was explained when using the environmental indexes from 10 m depth, and the F-values of the analyses were considerably higher when using the environmental indexes from 5 m depth. Consequently the environmental indexes from 5 m depth were used in the final analyses (Table 1).

The correlations between green algae and the environmental indexes are shown in Figure 8. Only five species are included, and their distributions show the strongest associations with the salinity gradients. The results of the RDA analysis showed that around 18 % of the variation of the species' distribution could be explained by the gradient of minimum salinity and around 24 % of all the canonical axes together (F-values are 7.1 for first canonical axes and 3.8 for all). The distribution of *C. fragile* subsp. *fragile* and

Cladophora rupestris showed some degree of positive correlation with the gradient of minimum salinity (Figure 8). The negative axis of salinity stress is correlated with the one of minimum salinity for the green algae, which makes the interpretation of the analysis difficult. In addition *C. rupestris* is an intertidal species, and the environmental gradients at 5 m depth may not be representative for the salinity at 0 m. However, the decrease in abundance and range shift of *C. fragile* subsp. *fragile* and range shift of *C. rupestris* in 2008-2009 compared to 1955-1956 (Figure 7A) may be caused by greater fluctuations in salinity of the surface waters, and also an overall slight decrease in minimum salinity of the surface waters in the fjord proper during 2008-2009 (Figure 4, Table 1). *Bryopsis hypnoides* showed a positive correlation with the gradient of maximum temperature (Figure 8).

The brown algae distribution showed an overall strong negative correlation with an increasing salinity stress (Figure 9). There was also strong positive correlations between the algal distribution pattern and both maximum temperature and minimum salinity, but the significance of the first canonical axis was much higher than for all the canonical axes (F-value of the first canonical axis = 6.3 vs. 4.2 for all). The results of the RDA analysis showed that around 16.4 % of the variation of the species distribution could be explained by the gradient in salinity stress, and around 28.2 % by the all three canonical axes together. The distribution of *B. racemosa* seemed to be positively correlated with increasing salinity stress, while the distributions of *Cutleria multifida*, *S. latissima* and *Sphacelaria cirrosa* were strongly negatively correlated (Figure 9). Of these, *B. racemosa* showed a decrease in abundance/distribution in 2008-2009 when compared to the first study, while *S. latissima* and *C. multifida* showed an increase (Figure 9). A high number of species showed a positive association with the gradient of minimum salinity (Figure 9). These included large perennial algae like *Fucus serratus*, *F. spiralis*, *Halidrys siliquosa* and *Laminara digitata* and *L. hyperborea*. However, except for the occurrence of *L. hyperborea* in the outer fjord in 2008-2009 none of these showed big changes between the two surveys. In addition the distributions of some species were associated with the gradient of maximum temperature (Figure 9). *H. tomentosus*, *B. arctica*, *P. radicans*, *D. foeniculaceus* and *Asperococcus fistulosus* displayed a negative correlation with maximum temperature, while *S. attenuata* showed a strong positive correlation. In addition the distributions of *S. soriferus*, *D. aculeata* and *D. viridis* also showed some degree of positive correlation with the temperature maximum gradient. Most brown algae showing a negative correlation with maximum temperature showed a decrease in

abundance/distribution in 2008-2009 compared to 1955-1956, while those with a positive correlation showed an increase (Figure 9).

The distribution of the red algae showed a strong positive correlation with the gradient of maximum temperature, and subsequently a significant negative correlation with increasing salinity stress. The F-value of the first canonical axis was substantially higher (13.1) than the one for all the canonical axes (6.8). Around 29 % of the variation in the species distribution pattern could be explained by the gradient in maximum temperature, while around 36 % was explained by all three canonical axes together. The red algae with the best correlations with the maximum temperature gradient were *Pterothamnion plumula*, *Bonnemaisonia hamifera*, *Callithamnion corymbosum*, *Polysiphonia elongata* and *Scagelia pylaisaei* (Figure 10). Another group showed a strong negative correlation with increasing salinity stress, e.g. *Cystoclonium purpureum*, *Lomentaria clavellosa*, *Polysiphonia fucoides*, and *Chylocladia verticillata*. There was also a large group which seemed to have both a strong positive association with maximum temperature and a negative association with the salinity stress gradient, e.g; *Phycodryus rubens*, *Brongniartella byssoides*, *Bonnemaisonia asparagoides*, *Chondrus crispus*, *Rhodomela confervoides*, and *Seirospora interrupta* (Figure 10). Most of the species with a clear positive association with maximum temperature or temperature in combination with a reduced salinity stress, showed a clear increase in abundance and/or range shift in the fjord in 2008-2009. Only a few of the red algae showing a positive association with reduced salinity stress alone showed such an increase (Figure 10). The distribution of *Phyllophora pseudoceranoides* showed some positive correlation with the gradient of minimum salinity, but did not differ in abundance or distribution in 2008-2009 compared to 1955-1956. Finally there was a group of red algae which were correlated with each other but which were not well correlated with any of the environmental factors, except for a weak positive association with the gradient of minimum salinity; *C. officinalis*, *C. virgatum* and *P. rotunda* (Figure 10). These also showed a decrease in abundance in 2008-2009 when compared to 1955-1956, which may be associated with slightly lower values of minimum salinity at 5 m in the inner parts of the fjord proper in 2008-2009 compared to in 1955-1956 (Table 1).

Discussion

The strong correlations between the distributions of macroalgae and environmental indexes at 5 m depth in Hardangerfjord show that the environmental gradients of temperature and salinity in the shallow parts are most important in determining the horizontal macroalgal distribution in the fjord. It has earlier been shown that there are high densities of sea urchins (*Echinus acutus*) and relatively little algal vegetation at many places below 2-8 m depth in Hardangerfjord (Husa et al. 2014). This was also shown to be the case in 1955-1956 (Jorde & Klavestad 1963) and it seems to be a persistent situation in this fjord. However, during summer when salinity is at its lowest in the surface layer, Husa et al. (2014) observed no sea urchins above 8 m in Hardangerfjord. This suggests that the brackish surface layer during summer keeps the sea urchin density low in the shallow subtidal, and that sea urchin grazing mainly takes place below 5 m depth. Consequently, the vegetation will be undisturbed in the upper depth range where it is most exposed to seasonal temperature and salinity variations.

One of the most conspicuous hydrographical changes in Hardangerfjord in 2008-2009 compared to 1955-1956 was the higher surface temperatures during summer. Temperatures at 10 m depth outside Hardangerfjord are representative for those of Hardangerfjord at this depth (Asplin et al. 2014). Consequently the long-term trend of increasing sea temperatures observed at the monitoring station outside Hardangerfjord, especially during summer, also applies to the fjord water. The temperature variations of the upper and most brackish layer are more variable and prone to year-to-year variation in surface fluxes. However, the higher summer temperature found at all examined depths in Hardangerfjord during 2008-2009 is in accordance with a relatively warm period (last 20 years) shown by meteorological observations (<http://folk.uib.no/ngfhd/Climate/climate-t-utsira.html>).

Other differences between 1955-1956 and 2008-2009 were also evident, like lower winter salinity of the upper layers of the fjord waters and a less pronounced seasonal brackish layer in the fjord branch in 2008-2009. A long-term trend of decreasing salinity of upper layers of Norwegian fjord water has also been reported by Aksnes et al. (2009). The salinity variations of the fjord water will both be due to variations in freshwater run-off to the fjord and to variable salinity of the inflowing water from the coast. Consequently, the changes in salinity are caused by both increased precipitation in coastal areas in south Norway, and by the fact that a large fraction of the spring and autumn flood has been redistributed mainly to the winter season due to the hydroelectric power production. Around 93 % of the hydroelectrical power production made from rivers to Hardangerfjord is due to regulations made after 1955, and 72 % of this production has come from regulations of two large river

systems ending in two inner fjord branches (Johnsen et al. 2007). The data show that the hydroelectrical power production has resulted in lower fresh water run-off to Hardangerfjord during spring and summer and higher run-off during winter, when compared to the natural hydrological pattern. The less pronounced seasonal brackish layer in the fjord branch, with higher salinity values at 5 m depth in 2008-2009 compared to 1955-1956, is thus most likely due to the shift in fresh water run-off to the fjord. This, in combination with lower winter salinity, is the most likely cause for the reduced salinity stress (i.e. difference between maximum and minimum salinity during the year) in most parts of the fjord in 2008-2009, when compared to 1955-1956.

Clear differences between the three macroalgal groups with regard to responses to the environmental factors were observed in the present study. As a group the red algal species showed a high degree of correlation with the maximum temperature gradient. Many species with higher abundances and increased range distributions in 2008-2009 compared to 1955-1956 showed a high degree of association with the maximum temperature gradient, demonstrating a positive effect on many red algae of the high summer temperatures in 2008-2009. The study involved very few green algae, since only taxa identified to species were included in the analyses. Except for *Bryopsis hypnoides*, the green algae were not affected by a higher summer temperature in 2008-2009 compared to 1955-1956. The brown algae showed some positive response to the higher temperatures in the fjord during 2008-2009, but less than the red algae. This is in accordance with a generally higher warm water affinity of red algae compared to brown algae (Price et al. 2006, Santelices et al. 2009). A likely consequence of higher sea temperatures in cold temperate zones is therefore that a number of red algal species may become locally more abundant. However, the results of the present study show that the reduced salinity stress during summer in 2008-2009 also had a strong positive effect on the occurrence of many red algae.

In estuaries, like Hardangerfjord, salinity may be more important than temperature in influencing the macroalgal composition, and e.g. salinity is known to influence the ratio between red and brown algae (Munda 1978, Middelboe et al. 1997, Schubert et al. 2011). Red algae seem to be generally more sensitive to salinity than brown algae (Kain & Norton 1990), and hypoosmotic treatment has for example been shown to affect the photosynthesis in red algae more negatively than in brown algae (Kirst 1990). Based on compilations of field data collected along salinity gradients Kain & Norton (1990) suggested that a salinity around or slightly below 20 was a critical lower tolerance limit for many red algae. In the present study

the salinity stress was the second most important environmental index explaining the distribution of red algae, but relatively few red algae showed a positive response to the reduced salinity stress alone. The combination of high summer temperature and reduced salinity stress seemed to have a more pronounced positive effect on red algae. The combined effects of salinities and temperatures on macroalgal growth have seldom been tested, however Hanisak (1979) found that the green alga *Codium fragile* subsp. *fragile* had a wider salinity tolerance when growing under optimum temperatures.

As a group the brown algae showed less change than the red algae, and also less response to the increase in temperature in 2008-2009 compared to 1955-1956, even though some species showed a strong correlation with the maximum temperature gradient. The strong positive correlation between the temperature gradient and distribution of *Striaria attenuata*, and its increase in distribution and abundance during 2008-2009 can be attributed to the relatively high summer temperatures since it has a high upper temperature limit of survival (Peters & Breeman 1992). Some brown algae showed a clear decrease in occurrence in 2008-2009 compared to 1955-1956, and for some this decrease can be connected to the higher temperature in 2008-2009. *Battersia arctica* has a clear northern distribution (Prud'homme van Reine 1982, Guiry & Guiry 2014) and could be expected to decline with an increase in summer temperature, and the sporophytic stage of *Halosiphon tomentosus* has been shown not to grow at a temperature above 15 °C (Sundene 1963). The apparently complete disappearance of the brown algae *Dictyosiphon foeniculaceus* and *P. radicans* from the area is on the other hand strange, since both species have been recorded much further south in Europe than the location of the present study area (Peters & Breeman 1992, Prud'homme van Reine 1982) and they should thus be expected to tolerate summer temperatures above 15 °C. A slightly higher abundance of *Saccharina latissima* was found in 2008-2009 compared to 1955-1956, associated with less salinity stress. Consequently, the results of the present study suggest that summer temperatures up to 18-19 °C do not seem to affect *S. latissima* negatively, while Andersen et al. (2013) showed that temperatures above 20 °C are detrimental.

The members of Fucales were more related to the salinity gradients than the temperature gradient, but their abundance and distribution range were relatively unaltered in 2008-2009 compared to 1955-1956. This can be attributed to the fact that the members of Fucales are adapted to the littoral zone habitat with extreme short time variations in salinity. The distributions of most brown algae with a pronounced increase in abundance or

distribution range during 2008-2009 were associated with a decrease in salinity stress, either alone or in combination with increased summer temperature or an increase in the minimum salinity. However, we cannot rule out that other environmental factors, not included in the analyses here, can also be responsible for the observed changes in the vegetation. For example, *Laminaria hyperborea* occurred in the outer part of the fjord in 2008-2009, and its distribution showed some positive correlation with the gradient of minimum salinity in the study. However, the minimum salinity in the main fjord is slightly lower in 2008-2009 than in 1955-1956, which makes it seem unlikely to have caused the recent entrance of *L. hyperborea* in the fjord. The occurrence of *L. hyperborea* is on the other hand normally associated with high wave-exposure (Kain 1971), and the appearance of *L. hyperborea* in the outer part of the fjord in 2008-2009 may thus possibly be due to recent changes in wind patterns causing more waves in the outer area. Another example is *Battersia racemosa*, which appeared to have a clearly positive association with increasing salinity stress and was not found in 2008-2009. This species normally occurs in sandy littoral pools (Proud'homme van Reine 1982) where salinity can vary much over short time spans. In the former study of the algal vegetation in Hardangerfjord it was found on a few localities in the infralittoral fringe of the innermost parts of the fjord proper and the fjord branches (Jorde & Klavestad 1963). The decrease of this species in Hardangerfjord may be due to low competitive abilities in a presently less stressful habitat.

When comparing the results of the present study with those of a study from the coastal area north of Hardangerfjord (Husa et al. 2008), some species appear to have increased in abundance recently according to both studies (Table 2). However, except for two species where the increase in Hardangerfjord can be attributed in full or partly to high summer temperatures (*Phycodrys rubens* and *Pterothamnion plumula*), the increase in abundance of these species in Hardangerfjord is associated with a reduction in salinity stress in 2008-2009 when compared to 1955-1956. One of the reasons why they have become more common in Hardangerfjord may be that there has been an increase in propagule pressure coming from the coastal area outside the fjord. E.g. *Dictyota dichotoma* and *Rhodophyllis divaricata* have their northern limit of distribution in South Norway (Brattegard & Holthe 1997) and are considered to have a warm-water affinity. While their abundance increase on the coast of Norway can be due to higher sea water temperatures (Husa et al. 2008), their distribution within the fjord may still be limited by salinity stress.

Recently, there has been a lot of focus on the effects of increased sea temperatures and concurrent range shifts of seaweeds (e.g. Müller et al. 2009). Migration northwards of warm temperate macroalgae, or extinction of cold temperate/Arctic species in the southern part of their distribution ranges, will probably require increased sea water temperatures over a longer period of time. In Brittany Gallon et al. (2014) observed a complex pattern of red algae responses to a warming over two decades, with many warm-water red algae declining in occurrence and cold-water species increasing. On the other hand the results of the present study show that local and episodic temperature increase of 3-5 °C will have a clear, positive effect especially on many red algal species present in the cold temperate Atlantic zone. Climate effects may however also involve community ecological shifts in competitive interactions and/or grazing intensity (Harley et al. 2012), which make predictions about changes in macroalgal distributions difficult. The results of the present study also show that a positive effect of higher summer temperatures on many red algae in estuaries could to some degree be associated with a mitigation of salinity stress. Since a pronounced climate change in the North Atlantic most likely will bring about a further increase in both precipitation and sea temperatures, the combined effects of sea temperature and salinity changes on the macroalgae vegetation in estuaries could be more important than effects of temperature changes alone.

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Table 1. Overview of environmental indexes based on measurements from 5 m depth at hydrographical stations H3-H7, used in ordination and RDA analyses of macroalgal species' distribution at shore Stns. 1-18. Index values for the two periods are indicated by suffix 55-56 and 08-09. Changes in maximum temperature ($\Delta T(max)$), salinity stress ($\Delta S(str)$) and salinity minimum ($\Delta S(min)$) between 2008-2009 and 1955-1956 are shown. Locations of the hydrographical stations H3-H7 in relation to shore stations are indicated. Indexes are interpolated between H7 and H6 and H6 and H5.

Hydrographical station:	H7							H6			H5			H4	H3	H3		
Station:	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18
T(max) 55-56	14	14	14	14	14.1	14.1	14.1	14.1	14.1	13.7	13.7	13.7	13.3	13.3	14.1	14.7	14.7	14.7
T(max) 08-09	16.8	16.8	16.9	17	17.1	17.2	17.3	17.4	17.4	17.6	17.6	17.6	17.8	17.8	16.4	15	15	15
$\Delta T(max)$	2.8	2.8	2.9	3	3	3.1	3.2	3.3	3.3	3.9	3.9	3.9	4.5	4.5	2.3	0.3	0.3	0.3
S(str) 55-56	3.6	3.6	5.1	6.6	8.1	9.6	11.1	12.6	12.6	13.3	13.3	13.3	14	14	17.9	17.1	17.1	17.1
S(str) 08-09	5.9	5.9	6.4	6.9	7.4	7.9	8.4	9	9	10.3	10.3	10.3	11.6	11.6	10.3	7.3	7.3	7.3
$\Delta S(str)$	2.3	2.3	1.3	0.3	-0.7	-1.7	-2.7	-3.6	-3.6	-3	-3	-3	-2.4	-2.4	-7.6	-9.8	-9.8	-9.8
S(min) 55-56	24.2	24.2	23.6	23	22.4	21.8	21.2	20.6	20.6	20	20	20	19.4	19.4	15	16	16	16
S(min) 08-09	23.7	23.7	23.2	22.7	22.2	21.7	21.2	20.8	20.8	18.9	18.9	18.9	16.9	16.9	19	20.2	20.2	20.2
$\Delta S(min)$	-0.5	-0.5	-0.4	-0.3	-0.2	-0.1	0	0.2	0.2	-1.1	-1.1	-1.1	-2.5	-2.5	4	4.2	4.2	4.2

Table 2. Macroalgae showing a clear increase in abundance both in Hardangerfjord (this study) and the coastal area outside Hardangerfjord (Husa et al. 2008). The environmental index with the strongest association with each species' distribution is given (S(str) = salinity stress, T (max) = maximum summer temperature, R = red algae , B = brown algae).

Species:	Environmental index:
<i>Acrothrix gracilis</i> (B)	S(str) (negatively correlated)
<i>Cystoclonium purpureum</i> (R)	S(str)(negatively correlated)
<i>Delesseria sanguinea</i> (R)	S(str) (negatively correlated)
<i>Dictyota dichotoma</i> (B)	S(str) (negatively correlated)
<i>Phycodrys rubens</i> (R)	T (max) (positively)/ S(str) (negatively)
<i>Pterothamnion plumula</i> (R)	T (max) (positively correlated)
<i>Rhodophyllis divaricata</i> (R)	S(str) (negatively correlated)

Legends

Figure 1. Map of the area with stations for macroalgal sampling (1-20) and hydrographical stations (H3-H7).

Figure 2. Temperature recordings at 0, 5 and 10 m depth at stations H3 to H7 during 1955-1956 and 2008-2009. The data plots for H6 in 2008-2009 are averages of measurements from two new hydrographical stations, placed 8 inside and 10 km outside the H6.

Figure 3. Time series of temperature ($^{\circ}\text{C}$) at 10 m depth from the coastal monitoring station Utsira split into the four quarters of the year (January-March, upper left; April-June, upper right; July-September, lower left; October-December, lower right). The linear trend is increasing for all periods.

Figure 4. Salinity recordings at 0, 5 and 10 m depth at stations H3 to H7 during 1955-1956 and 2008-2009. The data plots for H6 in 2008-2009 are averages of measurements from two new hydrographical stations, placed 8 inside and 10 km outside the H6.

Figure 5. Monthly precipitation (mm) from observations at the weather station in Eidfjord, in the inner part of the Hardangerfjord region (eklima.met.no).

Figure 6. Daily river runoff ($\text{m}^3 \text{s}^{-1}$) during the years 2008 and 2009 from the unregulated river Sandvenvatn (black line) and from the hydroelectric power plant Oksla (blue line) at the head of Sjørfjorden.

Figure 7. Changes in range distribution and relative abundance in brown and green algae (A) and red algae (B) between 1955-1956 and 2008-2009. Negative values represent range shifts towards the mouth of the fjord, or a decrease in abundance within the range of distribution compared to the first study. Name abbreviations shown in Appendix Table 1.

Figure 8. Ordination of the green (G) algal distribution, and the environmental factors **T(max)** (maximum summer temperature), **S(min)** (minimum salinity recordings) and **S(str)** (maximum variation in salinity) at the hydrographical stations H3-H7 in Hardangerfjord during the two investigations. Names of species with increase in abundance $\geq 30\%$ and/or distribution range ≥ 6 sectors between 1955-1956 and 2008-2009 are underlined, names of species with decrease are framed. Name abbreviations shown in Appendix Table 1.

Figure 9. Ordination of the brown (B) algal distribution, and the environmental factors **T(max)** (maximum summer temperature), **S(min)** (minimum salinity recordings) and **S(str)** (maximum variation in salinity) at the hydrographical stations H3-H7 in Hardangerfjord during the two investigations. Names of species with increase in abundance $\geq 30\%$ and/or distribution range ≥ 6 sectors between 1955-1956 and 2008-2009 are underlined, names of species with decrease are framed. Name abbreviations shown in Appendix Table 1.

Figure 10. Ordination of the relationship between the red (R) algal distribution, and the environmental factors **T(max)** (maximum summer temperature), **S(min)** (minimum salinity recordings) and **S(str)** (maximum variation in salinity) at the hydrographical stations H3-H7 in Hardangerfjord during the two investigations. Names of species with increase in abundance $\geq 30\%$ and/or distribution range ≥ 6 sectors between 1955-1956 and 2008-2009 are underlined, names of species with decrease are framed. Name abbreviations shown in Appendix Table 1.

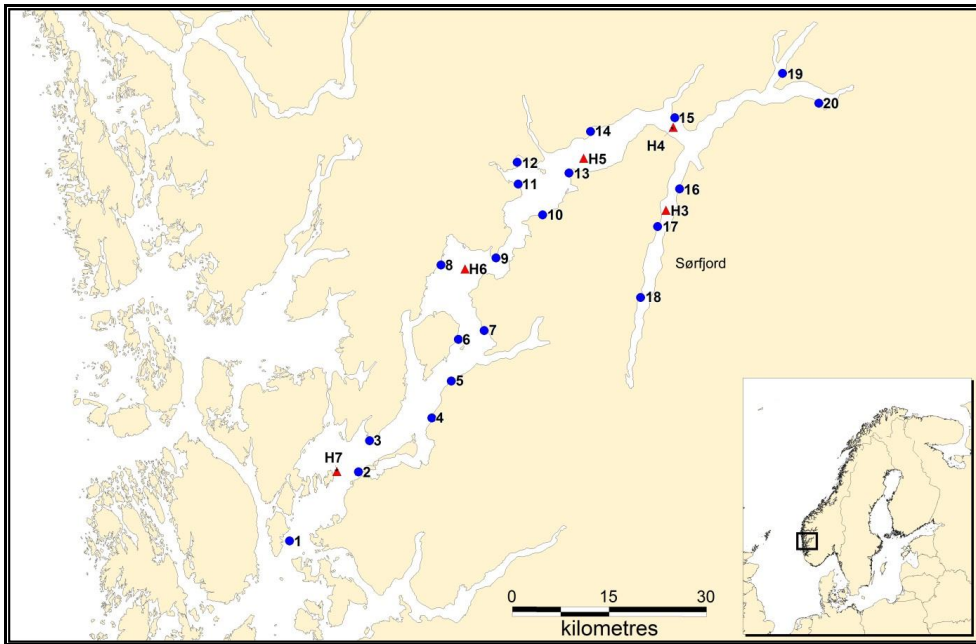


Figure 1.

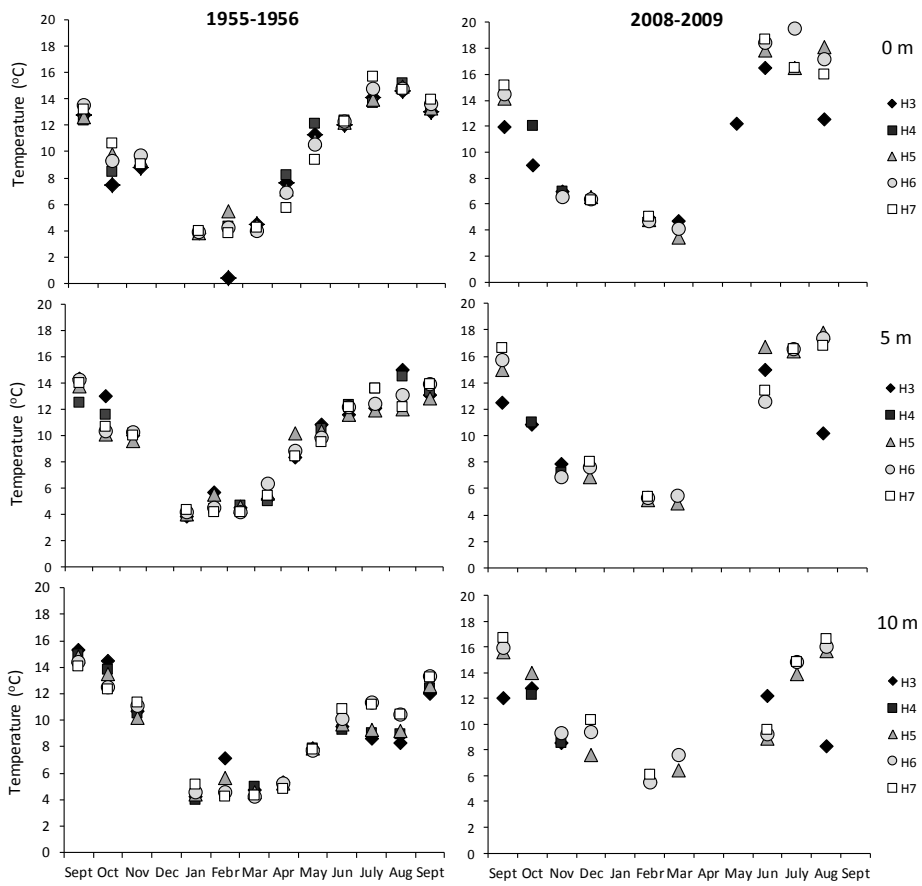


Figure 2.

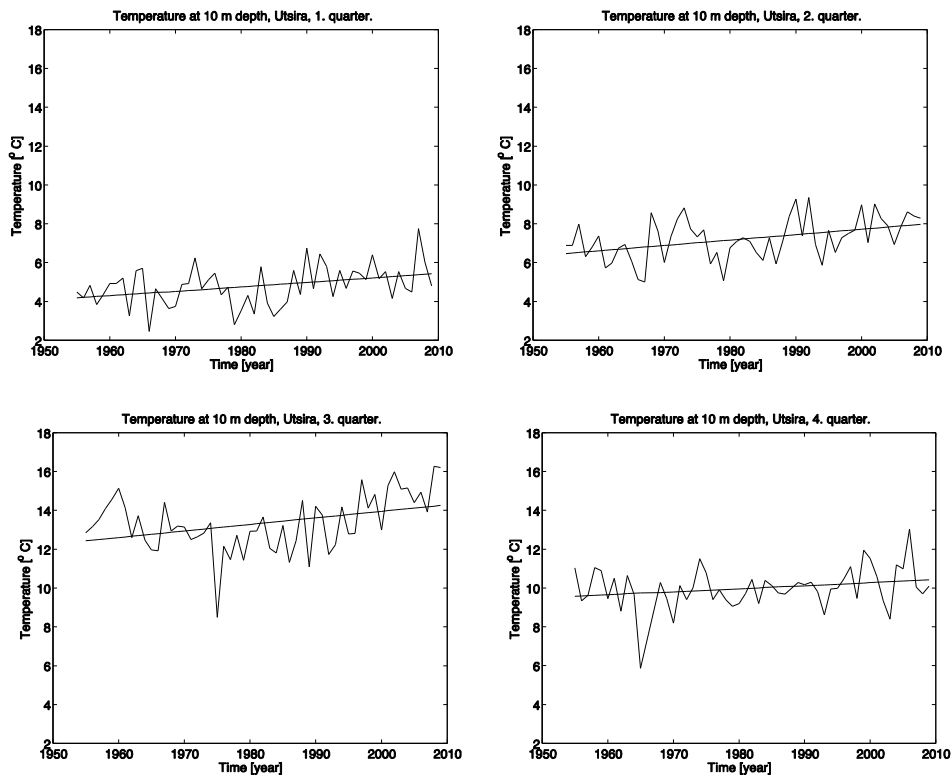


Figure 3.

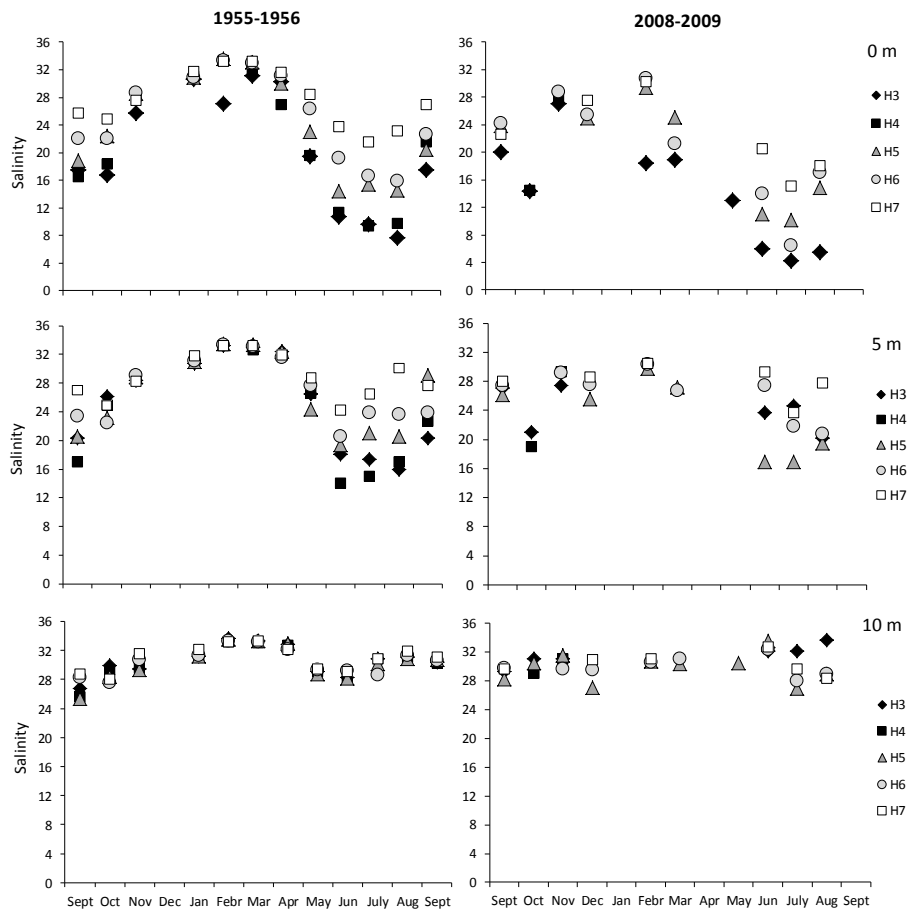


Figure 4.

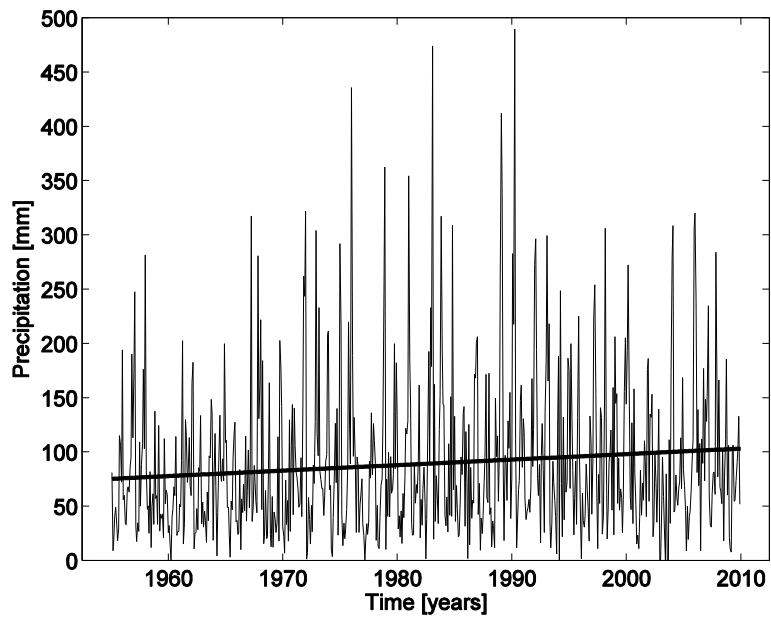


Figure 5.

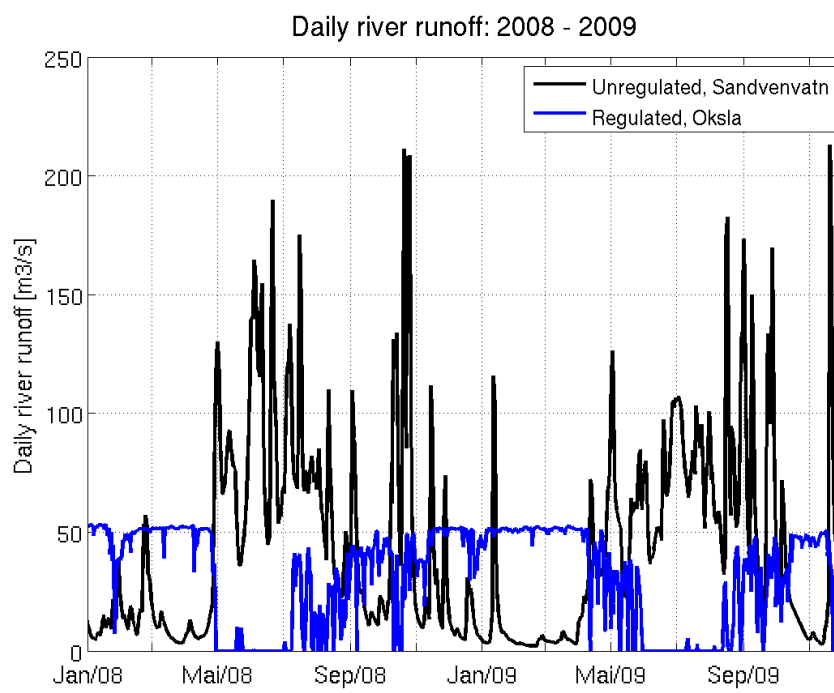


Figure 6.

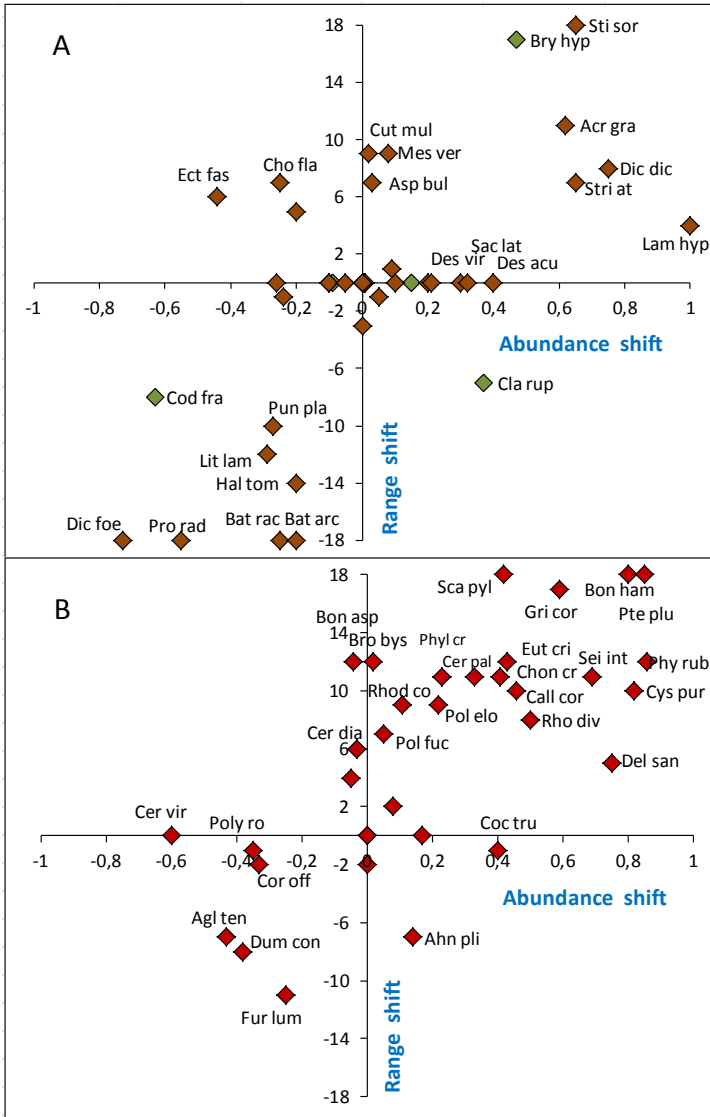


Figure 7.

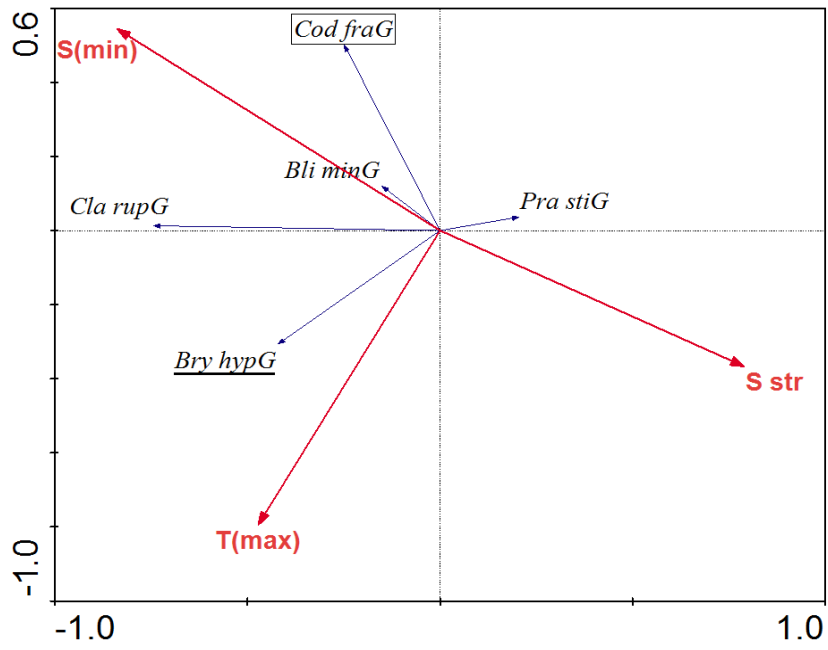


Figure 8.

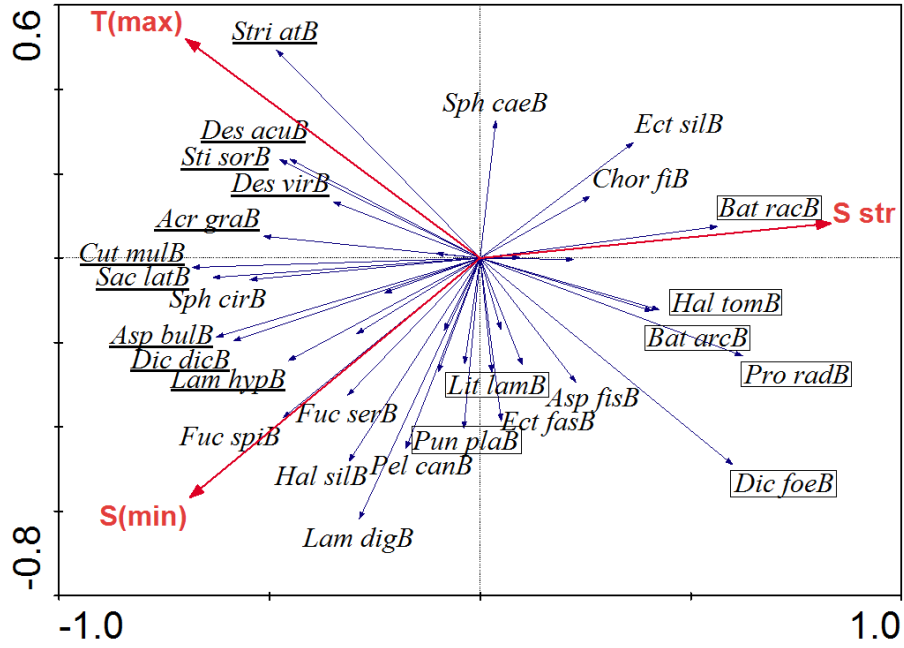


Figure 9.

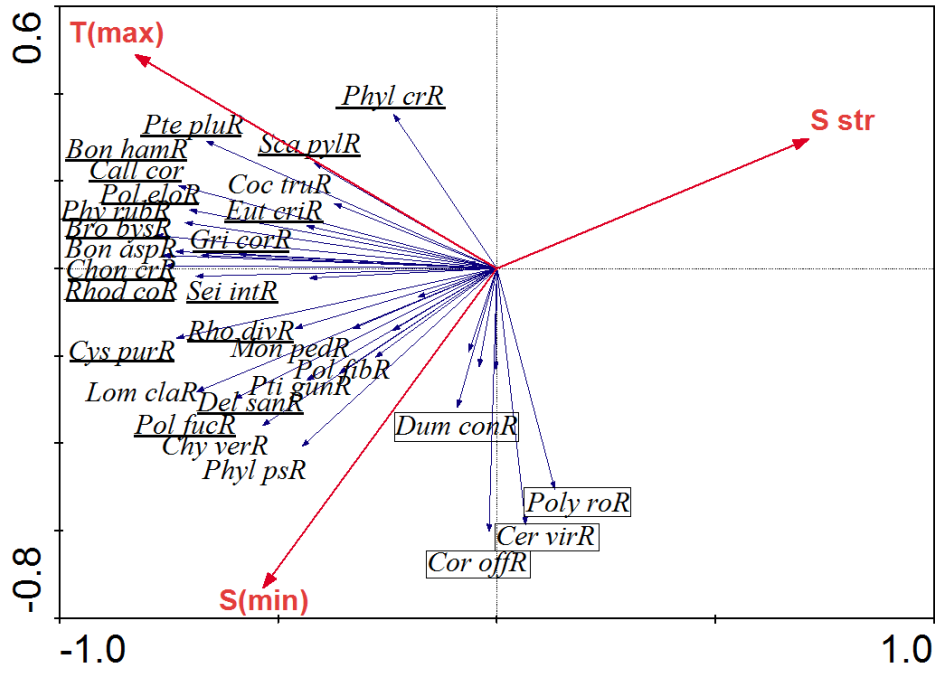


Figure 10.

Appendix Table 1. Species from 20 stations in Hardangerfjord, with name abbreviations. Nomenclature follows Guiry & Guiry (2014). *species not included in CANOCO analyses

Taxon	Abbrev.		
CHLOROPHYTA			
<i>Blidingia minima</i> (Nägeli ex Kützing) Kylin	Bli min	<i>Cutleria multifida</i> (J.E. Smith) Greville, (Turner) Greville	Cut mul
<i>Bryopsis hypnoides</i> J.V. Lamouroux	Bry hyp	<i>Desmarestia aculeata</i> (L.) Lamouroux	Des acu
<i>Bryopsis plumosa</i> (Hudson) C. Agardh	Bry plu*	<i>Desmarestia viridis</i> (Müller) Lamouroux	Des vir
<i>Cladophora rupestris</i> (Linnaeus) Kützing	Cla rup	<i>Dictyosiphon foeniculaceus</i> (Hudson) Greville	Dic foe
<i>Codium fragile</i> subsp. <i>fragile</i> (Suringar) Hariot	Cod fra	<i>Dictyota dichotoma</i> (Hudson) Lamouroux	Dic dic
<i>Prasiola stipitata</i> Suhr ex Jessen	Pra sti	<i>Ectocarpus siliculosus</i> (Dillwyn) Lyngbye	Ect sil
<i>Ulva lactuca</i> Linnaeus	Ulv lac*	<i>Ectocarpus fasciculatus</i> Harvey	Ect fas
		<i>Elachista fucicola</i> (Velley) Areschoug	Ela fuc
PHAEOPHYCEAE		<i>Fucus serratus</i> Linnaeus	Fuc ser
<i>Acrothrix gracilis</i> Kylin	Acr gra	<i>Fucus spiralis</i> Linnaeus	Fuc spi
<i>Ascophyllum nodosum</i> (L.) Le Jolis	Asc nod*	<i>Fucus vesiculosus</i> Linnaeus	Fuc ves*
<i>Asperococcus bullosus</i> J.V. Lamouroux	Asp bul	<i>Halidrys siliquosa</i> (L.) Lyngbye	Hal sil
<i>Asperococcus fistulosus</i> (Hudson) Hooker	Asp fis	<i>Halosiphon tomentosus</i> (Lyngbye) Jaasund	Hal tom
<i>Battersia arctica</i> (Harvey) Draisma, Prud'homme & H.Kawai	Bat arc	<i>Haplospora globosa</i> Kjellman	Hap glo*
<i>Battersia racemosa</i> (Greville) Draisma, Prud'homme & H.Kawai	Bat rac	<i>Hinkcsia sandrina</i> (Zanardini) Silva	Hin san*
<i>Chaetopterus plumosa</i> (Lyngbye) Kützing	Cha plu	<i>Laminaria digitata</i> (Hudson) Lamouroux	Lam dig
<i>Chorda filum</i> (L.) Stackhouse	Chor fi	<i>Laminaria hyperborea</i> (Gunnerus) Foslie	Lam hyp
<i>Chordaria flagelliformis</i> (Müller) C.Agardh	Cho fla	<i>Litosiphon laminariae</i> (Lyngbye) Harvey	Lit lam
<i>Cladostephus spongiosus</i> (Hudson) C.Agardh	Cla spo*	<i>Mesogloia vermiculata</i> (Smith) Gray	Mes ver
		<i>Pelvetia canaliculata</i> (L.) Decaisne & Thuret	Pel can*
		<i>Protohalopterus radicans</i> (Dillwyn) Draisma, Prud'homme & H.Kawai	Pro rad

<i>Punctaria plantaginea</i> (Roth) Greville	Pun pla
<i>Pylaiella littoralis</i> (L.) Kjellman	Pyl lit*
<i>Saccharina latissima</i> (L.) C.E. Lane, C. Mayes, Druehl & G.W. Saunders	Sac lat
<i>Scytosiphon lomentaria</i> (Lyngbye) Link	Scy lom
<i>Spermatochnus paradoxus</i> (Roth) Kützing	Spe par
<i>Sphacelaria cirrosa</i> (Roth) C.Agardh	Sph cir
<i>Sphacelaria nana</i> Nägeli ex Kützing	Sph nan*
<i>Sphacelaria plumula</i> Zanardini	Sph plu*
<i>Sphaceloderma caespitulum</i> (Lyngbye) Draisma, Prud'homme & H.Kawai	Sph cae
<i>Spongonema tomentosum</i> (Hudson) Kützing	Spo tom
<i>Stictyosiphon soriferus</i> (Reinke) Rosenvinge	Sti sor
<i>Stictyosiphon tortilis</i> (Ruprecht) Reinke	Sti tor
<i>Striaria attenuata</i> (C. Agardh) Greville, (Greville) Greville	Stri at
<i>Tilopteris mertensii</i> (Turner) Kützing	Til mer
RHODOPHYTA	
<i>Aglaothamnion tenuissimum</i> (Bonnemaison) Feldmann-Mazoyer	Agl ten
<i>Ahnfeltia plicata</i> (Hudson) Fries	Ahn pli
<i>Bonnemaisonia asparagoides</i> (Woodward) C. Agardh	Bon asp
<i>Bonnemaisonia hamifera</i> Hariot	Bon ham
<i>Brongniartella byssoides</i> (Goodenough & Woodward) Schmitz	Bro bys
<i>Callithamnion corymbosum</i> (Smith) Lyngbye	Call cor
<i>Ceramium diaphanum</i> (Lightfoot) Roth	Cer dia

<i>Ceramium virgatum</i> Roth	Cer vir
<i>Ceramium tenuicorne</i> (Kützing) Wærn	Cer ten
<i>Ceramium pallidum</i> (Nägeli ex Kützing) Maggs & Hommersand	Cer pal
<i>Chondrus crispus</i> Stackhouse	Chon cr
<i>Chylocladia verticillata</i> (Lightfoot) Bliding	Chy ver
<i>Coccotylus truncatus</i> (Pallas) Wynne & Heine	Coc tru
<i>Compsothamnion thuyoides</i> (J.E.Smith) Nägeli	Com thy*
<i>Corallina officinalis</i> Linnaeus	Cor off
<i>Cystoclonium purpureum</i> (Hudson) Batters	Cys pur
<i>Delesseria sanguinea</i> (Hudson) Lamouroux	Del san
<i>Dilsea carnosus</i> (Schmidel) Kuntze	Dil car*
<i>Dumontia contorta</i> (Gmelin) Ruprecht	Dum con
<i>Euthora cristata</i> (C. Agardh) Kützing	Eut cri
<i>Furcellaria lumbricalis</i> (Hudson) Lamouroux	Fur lum
<i>Gelidium spinosum</i> (Gmelin) Silva	Gel spi*
<i>Griffithsia corallinoides</i> (L.) Trevisan	Gri cor
<i>Hildenbrandia rubra</i> (Sommerfelt) Meneghini	Hil rub*
<i>Lomentaria clavellosa</i> (Turner) Gaillon	Lom cla
<i>Lomentaria orcadensis</i> (Harvey) Collins ex Taylor	Lom orc*
<i>Mastocarpus stellatus</i> (Stackhouse) Guiry	Mas ste*
<i>Monosporus pedicellatus</i> (Smith) Solier	Mon ped
<i>Palmaria palmata</i> (L.) Kuntze	Pal pal*
<i>Phycodrys rubens</i> (L.) Batters	Phy rub

<i>Phyllophora pseudoceranooides</i> (Gmelin) Newroth & Taylor	Phyl ps
<i>Phyllophora crispa</i> (Hudson) Dixon	Phyl cr
<i>Plumaria plumosa</i> (Hudson) Kuntze	Plu plu*
<i>Polyides rotunda</i> (Hudson) Gaillon	Poly ro
<i>Polysiphonia elongata</i> (Hudson) Sprengel	Pol elo
<i>Polysiphonia fibrillosa</i> (Dillwyn) Sprengel	Pol fib
<i>Polysiphonia fucooides</i> (Hudson) Greville	Pol fuc
<i>Polysiphonia stricta</i> (Dillwyn) Greville	Pol str
<i>Porphyropsis coccinea</i> (J. Agardh ex J.E. Areschoug) Rosenvinge	Por coc*
<i>Ptilota gunneri</i> Silva, Maggs & Irvine	Pti gun
<i>Pterothamnion plumula</i> (Ellis) Nägeli	Pte plu
<i>Pterosiphonia parasitica</i> (Hudson) Falkenberg	Pte par*
<i>Rhodomela confervoides</i> (Hudson) Silva	Rhod co
<i>Rhodomela lycopodioides</i> (L.) C. Agardh	Rhod ly*
<i>Rhodophyllis divaricata</i> (Stackhouse) Papenfuss	Rho div
<i>Scagelia pylaisaei</i> (Montagne) M.J. Wynne	Sca pyl
<i>Seirospora interrupta</i> (Smith) Schmitz	Sei int
<i>Schmitzia hiscockiana</i> Maggs & Guiry	Sch his*
<i>Spermothamnion repens</i> (Dillwyn) Rosenvinge	Spe rep*
<i>Vertebrata lanosa</i> (L.) T.A. Christensen	Ver lan*