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Correlative evidence for competition between *Fucus serratus* and the introduced chlorophyte *Codium fragile* subsp. *fragile* on the southwest coast of Norway

Abstract: The distribution of *Codium fragile* subsp. *fragile* and the native canopy-forming alga *Fucus serratus* was recorded at 51 sites in a 20 km long, sheltered region on the southwest coast of Norway. The purpose of the study was to examine if these species are potentially competing and how their distributions are related to wave-exposure and substrate. *Codium fragile* subsp. *fragile* was patchily distributed, a pattern which appears to have been sustained over time since its introduction to this area. It was almost always observed growing below mean low water, in the low intertidal and shallow subtidal. Both substrate type and wave-exposure influenced the vertical distribution of *C. fragile* subsp. *fragile*; growth occurred higher on the shore at sheltered sites and deeper in the subtidal on stony substrate. Its vertical range of growth overlapped with that of *F. serratus* and, when *C. fragile* subsp. *fragile* was abundant, *F. serratus* tended to grow higher on the shore and at lower abundances. This suggests that *C. fragile* subsp. *fragile* is affecting *F. serratus* in this area through competition, but only in the lower portion of the fucoid's vertical range and only at sites favorable for its own growth with regard to shelter and substrate.

Keywords: *Codium fragile* subsp. *fragile*; *Fucus serratus*; invasive species; macroalgal competition.

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Introduction

Invasive species can be defined as introduced species which are economically or ecologically harmful (Boudouresque and Verlaque 2002, Nyberg and Wallentinus 2005). Invasive species are recognized as a major threat to biodiversity (Invasive Species Specialist Group 2011), causing changes in the abundance of native species (Williams and Smith 2007), predation (Blackburn et al. 2004), interspecies interactions (e.g., Bjerknes et al. 2007), habitat structure (e.g., Sousa et al. 2009), community structure and production (Vila et al. 2011), parasite and pathogen dynamics (Telfer and Bown 2012), and hybridisation (e.g., Wu et al. 2013).

There are records of around 277 introduced species of macroalgae worldwide (Williams and Smith 2007) with 97% of these being unintentionally introduced, for example, through hull fouling, ballast water and aquaculture (Hewitt et al. 2007). Introduced macroalgae tend to have a negative effect on native macroalgal abundance and assemblages, but studies show a range of effects depending on the species, processes, or area studied (reviews in Schaffelke and Hewitt 2007, Williams and Smith 2007, Thomsen et al. 2009). Thus, it is probably too early to draw conclusions about general trends (Johnson 2007), especially as only 6% of introduced species of macroalgae have been studied for ecological impacts (Williams and Smith 2007).

Codium fragile subsp. *fragile* (Suringar) Hariot (previously subsp. *tomentosoides* [van Goor] Silva; see Provan et al. 2008) is considered one of the most invasive macroalgae in Europe (Nyberg and Wallentinus 2005, Johnson 2007). It has spread from its native range in the northwest Pacific and has become established in Europe, North America, Oceania, and South Africa (Provan et al. 2008, Guiry and Guiry 2012). It was thought to have been introduced to Northern Europe sometime just prior to 1900 (Silva 1955), but specimens have recently been identified from 1845 in Ireland (Provan et al. 2008). Thus, while the official earliest record of this subspecies in Norway is 1952 (Silva 1955), it is likely to have invaded before that, and possibly as early as 1895 (Silva 1957, Norwegian Biodiversity Information Centre 2012).

In Norway, *Codium fragile* subsp. *fragile* (hereafter referred to as *C. fragile*) grows in the infralittoral and subtidal zones (Norwegian Biodiversity Information Centre 2012) and has been recorded north to 70° 00′ N, 18° 40′ E (Stellander 1969). The fucoid *Fucus serratus* Linnaeus often forms the main canopy of the lower intertidal and infralittoral fringe zones in the northeast Atlantic (Lüning 1990). There are a number of invasive species within the Fucales (Williams and Smith 2007), and *F. serratus* itself has been unintentionally introduced to Iceland (Coyer et al. 2006) and the northwest Atlantic (Brawley et al. 2009). Due to similarities in size, branching, range, substrate requirements, winter losses, perennial nature and vertical distribution between *C. fragile* and *F. serratus* there could be potential for competition between them (Table 1). In addition, previous observations in this area suggest that *C. fragile* could have replaced *F. serratus* at some localities (Jorde 1966).

Distributions of macroalgae are influenced by competition for space, light or nutrients (Lüning 1990), but are also affected by factors such as herbivory (e.g., Norderhaug and Christie 2009), pathogens (Correa 1996), and epiphytic growth (e.g., Scheibling and Gagnon 2006). Space is often a limiting factor for algae in the low intertidal-shallow subtidal, and competition for space can involve recruiting quickly into gaps or overgrowing other algae. *Codium fragile* tends towards the former, like many other invasive macroalgae (Johnson 2007). It colonizes empty space as a result of disturbance to native algal cover, and then prevents reestablishment of the native seaweeds (see Trowbridge 1998). *Codium fragile* has been able to form large subtidal patches in this way at sites previously dominated by native kelps in the northwest Atlantic (Levin et al. 2002, Scheibling and Gagnon 2006).

Physical factors such as wave-exposure and substrate also influence macroalgal distribution (Lüning 1990, Díez et al. 2003). In more exposed areas, *F. serratus* may have lower growth rates, a shorter and later reproductive period, and consist of populations of smaller plants (Knight and Parke 1950), and for *C. fragile*, exposure reduces recruit survival (Schmidt and Scheibling 2005) and increases degree of fragmentation in winter (D'Amours and Scheibling 2007). *Fucus serratus* can tolerate moderately exposed conditions very well (Knight and Parke 1950, Johnson et al. 2012) whereas *C. fragile* grows better in areas sheltered from wave exposure (Trowbridge 1995, Bulleri and Airoldi 2005) and thus at exposed sites *F. serratus* may have an advantage.

The aim of this study is to record the distributions of *C. fragile* and *F. serratus*, and assess their potential for

Table 1 *Codium fragile* subsp. *fragile* and *Fucus serratus* traits.

	***Codium fragile* subsp. *fragile* (Ulvophyceae, Bryopsidales)**	***Fucus serratus* (Phaeophyceae, Fucales)**
Vertical range	Low intertidal, the sublittoral, and in tide pools (Burrows 1991, Trowbridge and Todd 1999, Trowbridge and Farnham 2009)	Low-intertidal, infralittoral fringe (Knight and Parke 1950, Lüning 1990).
Temperature range	Survival from at least 0°C up to 30°C (Lüning 1984). Optimum growth at 24°C, with growth above 6°C (Hanisak 1979).	Survival from at least 0°C up to 25°C, optimum growth at 15°C (Lüning 1984). Cold tolerant (Lüning 1990).
Salinity range[a]	Maximum growth at 24‰ (Yang et al. 1997). No germination below 18‰ at 6–30°C (Hanisak 1979).	Maximum growth at 20–30‰, but grows well between 10‰ and 40‰ (Bird et al. 1979).
Nutrient and light requirements	Uses all forms of nitrogen, may be able to store nutrients (Hanisak 1979, Benson et al. 1983). Nutrient enhancement may increase spread (Trowbridge and Todd 1999). Optimum growth at 88 μmol m^{-2} s^{-1} in filamentous form, but at over 200 μmol m^{-2} s^{-1} as a spongy thallus (Yang et al. 1997, Nanba et al. 2005).	Nutrient enrichment with N and P over normal levels in Norway did not affect growth (Bokn et al. 2002). Saturation for growth is reached at a minimum of 100 μmol m^{-2} s^{-1} (Bird et al. 1979).
Growth	Fast in good conditions, e.g., summer a maximum of 9.6–12 cm per month in Nova Scotia (Scheibling and Gagnon 2006). Trowbridge (1998) recorded rates of 1–2 cm per month in spring/summer native populations (Oregon). Up to 1 m long, but usually around 20 cm (Rueness 1998).	Mean of 0.49–0.85 cm per week, impacted by shelter (British Isles; Knight and Parke 1950), and latitude; 4–7 cm per year in Trøndelag (Norway; Printz, 1926, cited in Knight and Parke 1950). Around 30–60 cm long (Rueness 1998).
Structure	Mostly dichotomously branching, coenocytic (Rueness 1998).	Dichotomously branching, parenchymatous (Graham et al. 2009).
Reproduction	Parthenogenic (Feldmann 1956, Churchill and Moeller 1972, Dromgoole 1975, Benson et al. 1983) or vegetative (Mathieson 2003).	Sexual and dioecious (Graham et al. 2009).
Winter losses	Fragmentation caused by wave-action and cold temperatures (Fralick and Mathieson 1972, D'Amours and Scheibling 2007).	Breakdown of receptacle-bearing branches after reproduction (Williams 1996).

[a] Salinity reported as parts per thousand (as per the original publications) – ppt values are approximately equivalent to salinity values on the practical salinity scale.

competition on the southwestern coast of Norway. This will involve answering the following questions: (i) Do *C. fragile* and *F. serratus* grow in the same vertical zone? (ii) What are the distribution patterns of *C. fragile* and *F. serratus*, and are they associated? (iii) Are these patterns related to wave-exposure and substrate?

Materials and methods

The study region was on the southwest coast of Norway near Bergen (60° 04′ N, 005° 13′ E to 60° 16′ N, 005° 13′ E; Figure 1). This coastline is made up of islands with irregular shorelines, with seawater from the Norwegian coastal current (Sætre 2007). The macroalgal vegetation is typical of the cold temperate northeast Atlantic biogeographic region (Lüning 1990).

Observations were made at a total of 51 sites, distributed over three areas with between 13 and 22 sites in each, all relatively sheltered from wave action (Figure 1). Within each area, there were sites with a variety of wave-exposures and substrate types. Observations were made during June and August 2011. Both *Codium fragile* and *Fucus serratus* are perennial, and no large changes in their vegetation structure or cover would be expected to take place

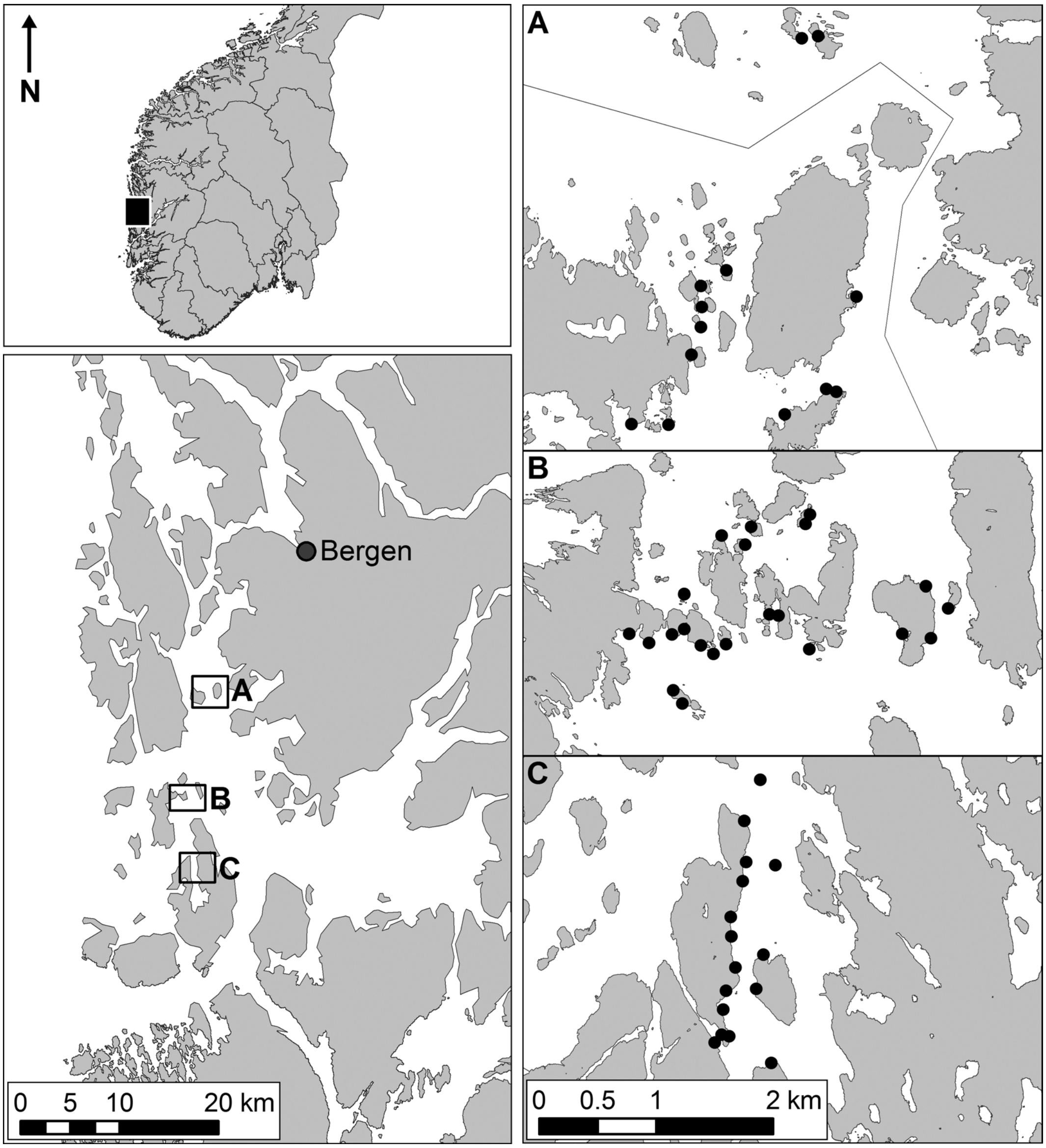

Figure 1 Location of the study. Top left is the location of the study region along the coast of Norway; bottom left shows the three areas where study sites were located; maps on the right show the locations of sites (n=51) within the three study areas.

between June and August. Possible sites on the shoreline were chosen from a distance by boat. Sites with different compositions of *F. serratus* and *C. fragile*, i.e., presence of both species or absence of one, were required in order to test possible relationship patterns between the two species. Because of this some preselected sites were discarded in order to ensure that there were sufficient sites in the different categories. In addition, only sites with hard substrate were included, and no sites facing open sea were included since *C. fragile* tends not to thrive at very exposed sites (Trowbridge 1995, Bulleri and Airoldi 2005).

Observations at each site were made around low water during spring tides using a small outboard motorboat. Observations were made along a stretch of shoreline approximately 15 m long which defined the site. The inclination was relatively high (around 20–70°) at most sites. All fieldwork was done under calm conditions and in periods with clear water and good visibility. The following field observations were made by two persons using an aquascope and a telescopic measuring rod: (i) Substrate – This was recorded as being either “rock” (solid rock face), “stones” (cobbles or boulders), or “rock, stones” (sites with a mixture). (ii) Depth of shallowest and deepest *C. fragile* and *F. serratus* to the nearest 10 cm. (iii) Distribution patterns of *C. fragile* and *F. serratus* – three main distribution patterns were observed and recorded: “zone” when the plants were in a continuous band for ≥75% of the length of the site, “patch” when the plants were growing in groups together but not as a zone, or “individuals” when the plants were mostly occurring alone among other algal species. (iv) Estimated number of *C. fragile* and *F. serratus* individuals per site, visible from the surface or using an aquascope, within categories of 0, 1–19, 20–50, or >50 plants. Because observations were made from the surface, this excluded juvenile individuals under other canopy algae. (v) Other dominant vegetation. (vi) Location (handheld GPS device, Garmin, Olathe, KS, USA).

A time record was kept for all depth measurements, which made it possible to calculate them relative to chart datum using the website of Statens Kartverk (http://www.sehavniva.no). This website provides retrospective space- and time-referenced data on observed tidal levels in Norway, based on 24 measuring stations along the coast. The heights above water were measured by placing the end of the measuring rod at water level and recording the height of the target species above the surface by sighting. Depths were measured by placing the end of the rod at the point where the target species was observed and recording the height of the water above it. In cases where it was difficult to determine the shallowest or deepest position of the two target species, more than one measurement was made. The observed lower limit of *C. fragile* could in some cases extend to more than two metres, and in these cases, the measured lower limits are probably less accurate. When small waves were present at the site, the water level was recorded by noting the midpoint of the wave amplitudes along the measuring rod.

Measuring wave-exposure directly requires measurements of many factors over time, so a cartographic measure based on Baardseth (1970) was used. On a map (Båtsportkart, Statens Kartverk Sjøkartverket, Nordeca, scale 1:50000), straight distances from a site to the nearest land were measured at 10° intervals. These lengths were summed to give a relative exposure value for each site. To ensure that this value was reliable and not affected by chance placement of the lines, the exposure of each site was measured three times, each time randomly placing the 10° lines. From these a mean was calculated and used as the exposure value in analysis. Data of wind force and direction were not included. All the sites were relatively sheltered with small wind fetches, and in addition, there is no predominant wind direction in this area. Similar methods have been used previously in projects on littoral species (e.g., Rustad 2010). A comparison of exposure values calculated with or without wind data was done by Rustad (2010) in a comparable area, and the results showed a similar ranking of the localities.

Field measures of estimated number of plants and distribution pattern were combined to categorise sites as either low or high abundance for *C. fragile* and *F. serratus* (Table 2). The field measures of number of plants were estimates, so using them with distribution pattern improves reliability. The estimated number of plants and distribution measures were also often related, since they both reflect abundance, thus combining them gives a more integrated picture of the abundance of macroalgae at each site.

Table 2 *Codium fragile* subsp. *fragile* and *Fucus serratus:* Categorization of sites where the species were present (*C. fragile* n=36; *F. serratus* n=47) into low and high macroalgal abundance, determined by field estimates of number of individuals per site and of distribution pattern. Values are the number of sites with each combination for each species; C=*C. fragile*, F=*F. serratus*. Because the vertical distributions of *C. fragile* and *F. serratus* varied, it was possible for a site to have large numbers and zones of both species.

Field measures	1–19 plants	20–50 plants	>50 plants
Individual	Low (C=10, F=3)	Low (C=1, F=0)	–
Patch	Low (C=3, F=6)	Low (C=4, F=11)	High (C=11, F=4)
Zone	–	High (C=0, F=4)	High (C=7, F=19)

The program R (version 3.0.2, R Core team 2013) was used for statistical analyses. Significance for p-values was set at 0.05. A Kruskal-Wallis test was used to test for a relationship between wave-exposure and substrate. Substrate and wave-exposure were then used as predictor variables in binary logistic regression analysis (R package MASS; Venables and Ripley 2002) to test for a relationship between them and the abundance of *C. fragile* (the response variable – with levels "low" or "high" abundance). Sites where *C. fragile* was absent were grouped into the "low" abundance category. The model was developed using a forward selection procedure; each predictor was tested singly in a model, then models which had predictors with a significant relationship to the response variable were compared to each other by dividing the estimated standard errors by the p-values. Binary logistic regression was used firstly because the response variable was binary ("low" or "high" abundance of *C. fragile*), and secondly because this method allows the inclusion of a random factor. This random factor, "Area", was included in the model to account for possible dependency between observations, because the sites are grouped into three areas (Figure 1).

Next, the depth distribution of *C. fragile* was investigated. A linear mixed-effects model (R package nlme; Pinheiro et al. 2011) was used to see if the predictors, substrate and wave-exposure, were related to the lower limits of *C. fragile* (the response variable). Again, the random factor "area" was included. The same was then done for the upper limits of *C. fragile*. These models were developed using a standard backwards selection procedure, where Akaike's information criterion was used to compare models. One outlying observation was removed from the upper limits analysis, as it was far outside the range of the other data and was having an exaggerated effect on the analysis (45 cm below chart datum – the rest of the observations were between 5 and 50 cm above chart datum).

The same methods were then used for the two response variables, *F. serratus* abundance and lower depth limits. However, in these models, an extra predictor, *C. fragile* abundance, was included along with substrate and wave-exposure.

All of the linear models were checked for violation of assumptions, and two of the response variables required transformation. The lower limits of *F. serratus* showed heteroscedasticity which was corrected by square-root transformation. The lower limits of *C. fragile* showed problems with both heteroscedasticity and normality of errors, and a Box-Cox transformation was applied. Transformation improved both problems, but there was still some non-normality. Therefore, a nonparametric test (Kruskal-Wallis test) was also carried out to confirm that the conclusions drawn from the linear model were reliable. The result of the binary logistic regression analysis testing for a relationship between *F. serratus* and *C. fragile* abundance (Response: *F. serratus* abundance, Predictor: *C. fragile* abundance) was also compared to a nonparametric test using the same variables (Fisher's exact test on a 2×3 contingency table of abundance) to check if the simpler analysis gave the same conclusions. Plots with confidence intervals were constructed using R package BradleyTerry2 (Turner and Firth 2012). Ninety-five percent confidence intervals (CIs) for means of upper and lower limits were calculated using ordinary nonparametric bootstrapping (R package boot; Davidson and Hinkley 1997, Canty and Ripley 2013), because much of these data were not normally distributed.

Results

The most common substrate was rock (29 sites), followed by stones and rock,stones (11 sites each). The cartographic wave-exposure of the sites ranged from 24 to 634 (mean of 225) with the majority of sites at the more sheltered end of this range; 38 out of 51 sites had values under the midpoint of the observed range (305). Substrate and exposure were not significantly associated (Kruskal-Wallis test, p=0.23). In all analyses, the standard deviation of "area" was always small compared to the standard deviation of residuals, indicating that little of the overall variation was due to differences between the three areas.

Current distribution of *Codium fragile* subsp. *fragile*

The abundance of *Codium fragile* was significantly related to substrate, but not to exposure (Table 3). There was a significantly greater chance of finding high abundance of *C. fragile* at sites where stony substrate was present (Figure 2). This was supported by our observations that at six of the 11 sites where there was both rock and stony substrate present, *C. fragile* was only observed as a patch on the stony part, remaining at low abundances on the solid rock within the same site (pers. obs.). The lower limits of *C. fragile* were also related to substrate but not to exposure, being deeper at sites with stones rather than rock (Table 3; Figure 3). On the other hand, there was a significant relationship between the upper limits of *C. fragile* and

Table 3 *Codium fragile* subsp. *fragile* and *Fucus serratus:* Statistical analyses, with response variables in bold, and predictors listed underneath. "Method" indicates statistical method used: BinaryLR, Binary logistic regression; Kruskal, Kruskal-Wallis test; LME, linear mixed-effects model; Fisher, Fisher's exact test on contingency tables. Comparisons of levels of a predictor variable (e.g. "Rock vs. Stones" within "Substrate") indicate whether there is a difference in the response variable between those levels. p-Values are rounded to 3 decimal places; those in bold are significant. Significance for multiple tests has not been corrected.

Response and predictor variables	Method	F- or t- value	p-value
***C. fragile* abundance** (n=51)			
Substrate	BinaryLR		
Rock vs. Stones		$t_{46}=-3.44$	**0.002**
Rock vs. Rock, stones		$t_{46}=3.02$	**0.004**
Stones vs. Rock, stones		$t_{46}=-0.44$	0.660
Exposure	BinaryLR	$t_{45}=0.08$	0.936
***C. fragile* lower limit** (n=36)			
Substrate	Kruskal		**0.009**
Substrate	LME	$F_{2,31}=4.95$	**0.010**
Rock vs. Stones		$t_{31}=-2.94$	**0.006**
Rock vs. Rock, stones		$t_{31}=-2.53$	**0.017**
Stones vs. Rock, stones		$t_{31}=-0.43$	0.672
Exposure	LME	$F_{1,30}=0.491$	0.489
***C. fragile* upper limit** (n=36)			
Substrate	LME	$F_{2,29}=0.025$	0.974
Exposure	LME	$F_{1,31}=4.17$	**0.050**
***F. serratus* abundance** (n=51)			
C. fragile abundance	Fisher		**0.031**
C. fragile abundance	BinaryLR		
Absent vs. High		$t_{46}=-2.47$	**0.017**
Absent vs. Low		$t_{46}=-1.68$	0.099
High vs. Low		$t_{46}=0.98$	0.333
Substrate	BinaryLR		
Rock vs. Stones		$t_{44}=0.613$	0.543
Rock vs. Rock, stones		$t_{44}=0.668$	0.102
Stones vs. Rock, stones		$t_{44}=1.159$	0.253
Exposure	BinaryLR	$t_{45}=1.01$	0.316
***F. serratus* lower limit** (n=47)			
C. fragile abundance	LME	$F_{2,41}=9.85$	**<0.001**
Absent vs. High		$t_{41}=3.12$	**0.003**
Absent vs. Low		$t_{41}=-1.14$	0.261
High vs. Low		$t_{41}=-4.71$	**<0.001**
Substrate	LME	$F_{2,39}=1.15$	0.328
Exposure	LME	$F_{1,41}=6.92$	**0.009**

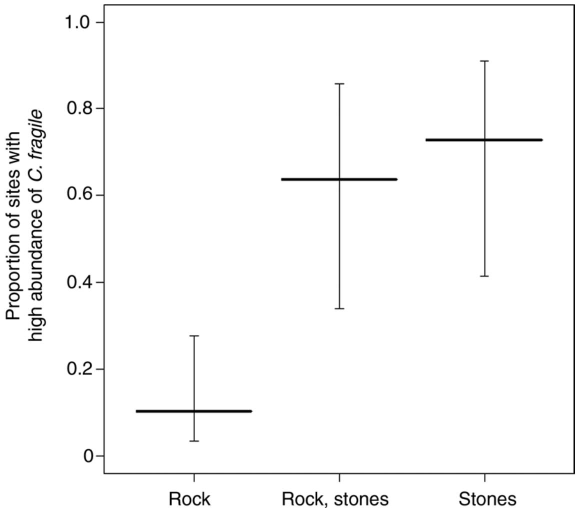

Figure 2 *Codium fragile* subsp. *fragile:* Proportion of sites with high abundances of *C. fragile* on different substrate types, with 95% confidence intervals ("Rock" n=29; "Rock, stones" n=11, "Stones" n=11).

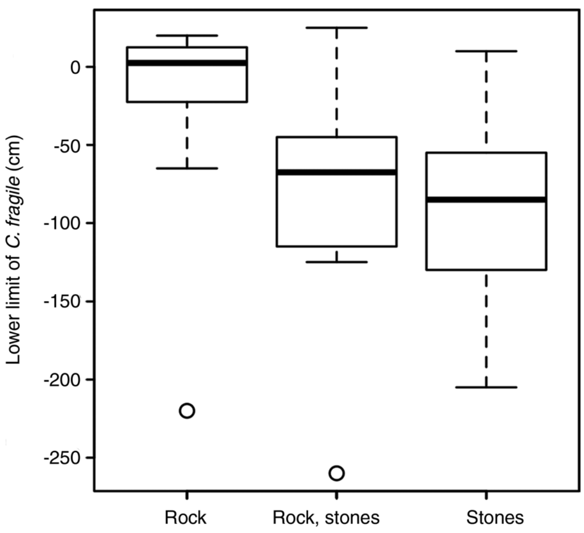

Figure 3 *Codium fragile* subsp. *fragile:* Lower limits of growth (relative to chart datum) on different substrate types ("Rock" n=16; "Rock, stones" n=10, "Stones" n=10). Upper and lower limits of boxes represent upper and lower quartiles of the data, while middle horizontal line is the median. Lines extending vertically from the boxes show the spread of remaining data, excluding the observations shown as open circles; these are values outside the upper and lower quartiles by over 1.5×the interquartile range, i.e., unusual observations.

wave-exposure but not substrate, with the upper limits being lower at more exposed sites (Table 3; Figure 4).

At rock sites, the dominant subtidal vegetation beneath the lower limit of *C. fragile* tended to be one of the native kelps *Laminaria digitata* (Hudson) J.V. Lamouroux or *Saccharina latissima* (Linnaeus) C. E. Lane, C. Mayes, Druehl and G. W. Saunders, with the native brown alga *Halidrys siliquosa* (Linnaeus) Lyngbye also present at 6 sites. At sites with stones ("stones" or "rock, stones"), *Saccharina latissima* or *Laminaria digitata* also tended to form dominant subtidal cover next to or beneath *C. fragile* patches. However, little or no kelp was observed at two sites. At these two, along with five more of the stony sites, ephemeral filamentous brown algae were observed covering any space within patches of *C. fragile*.

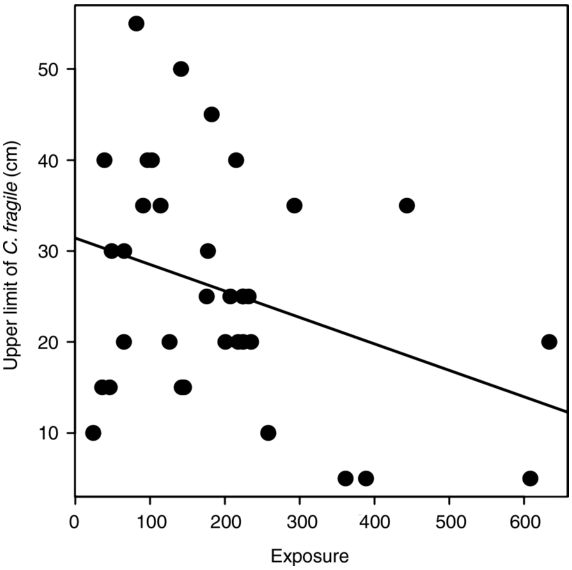

Figure 4 *Codium fragile* subsp. *fragile*: Relationship between the upper depth limit of growth (relative to chart datum) and cartographic wave-exposure (n=35).

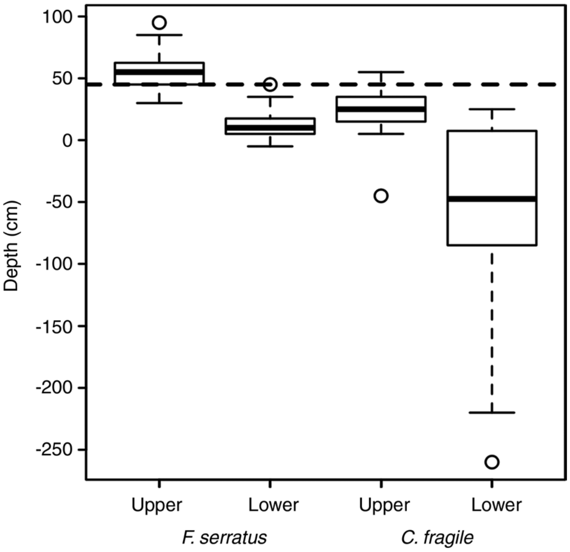

Figure 5 *Codium fragile* subsp. *fragile* and *Fucus serratus:* Upper and lower limits of growth, relative to chart datum (n=36 for *C. fragile* and n=47 for *F. serratus*). Broken horizontal line is level of mean low water for Bergen (45 cm above chart datum). Box plots as in Figure 3.

Relationship between *Fucus serratus* and *Codium fragile* subsp. *fragile* distributions

Fucus serratus occurred most often as patches or zones and rarely as individual plants, while *Codium fragile* occurred commonly in a patchy distribution, and least often as a zone. In this study, approximately equal numbers of sites had low and high abundances of each alga (Table 2). *Codium fragile* was nearly always observed growing in the subtidal zone, extending up into the infralittoral fringe. Its mean upper limit was 24 cm (upper CI=28 cm, lower CI=17 cm) above chart datum, while its lower limits were more variable, with a mean of -54 cm (upper CI=-33 cm, lower CI=-81 cm). The mean upper limit of *F. serratus* was 56 cm (upper CI=61 cm, lower CI=53 cm), and the mean lower limit was 12 cm (upper CI=16 cm, lower CI=9 cm) (Figure 5).

There was a higher probability of *F. serratus* abundance being low at sites where the abundance of *C. fragile* was high than at sites where *C. fragile* was absent (Table 3, Figure 6). No significant relationship was found between abundance of *F. serratus* and substrate or wave-exposure. The lower limit of *F. serratus* was also significantly related to *C. fragile* abundance (Table 3, Figure 7). The lower limits of *F. serratus* were significantly higher at sites with high abundances of *C. fragile* than at sites with low or absent *C. fragile*. The mean lower limit of *F. serratus* at localities with high *C. fragile* abundance was 21 cm above chart datum (upper CI=26 cm, lower CI=15 cm), whereas the mean when *C. fragile* was absent and low was 8 cm (upper CI=10 cm, lower CI=5 cm). The lower limit of *F. serratus* was also related to wave-exposure, and was significantly higher at more sheltered sites (Table 3, Figure 7).

Discussion

Current distribution of *Codium fragile* subsp. *fragile*

Codium fragile is patchily distributed in this area, establishing in some sites as the dominant canopy but failing to establish in large numbers or to spread to others and is absent at a number of seemingly suitable sites. The same observation was made in the late 1940s in Norway (Fægri and Moss 1952), and was attributed to *C. fragile* still being in the process of dispersing into new areas. However, *C. fragile* has now been present here for so long that this explanation is inadequate. Distribution of *C. fragile* populations is also patchy in Scotland (Trowbridge and Todd 1999) and New Zealand, where presence/absence was not related to wave-exposure, bare space, herbivores or other algae and many physically suitable sites close to existing populations were not colonized (Trowbridge 1995). Thus, a patchy distribution seems to be a feature of *C. fragile* distribution in some places, rather than indicating spreading from a point of introduction.

Codium fragile was almost always observed growing below mean low water and into the subtidal zone. This

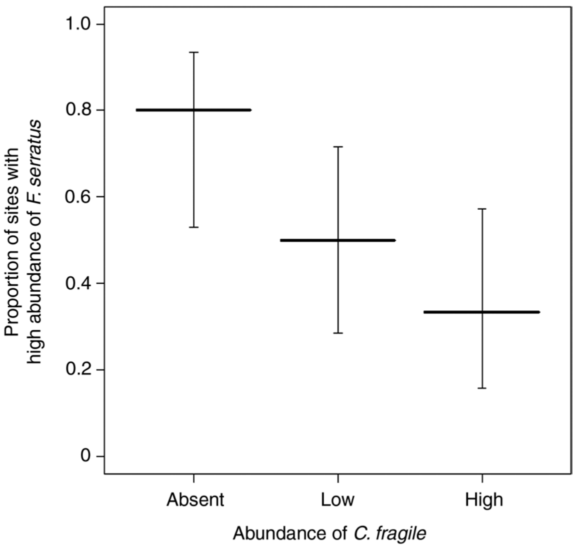

Figure 6 *Codium fragile* subsp. *fragile* and *Fucus serratus*: Proportion of sites with high abundances of *F. serratus* at different abundances of *C. fragile*, with 95% confidence intervals (*C. fragile* abundance level: "Absent" n=15, "Low" n=18, "High" n=18).

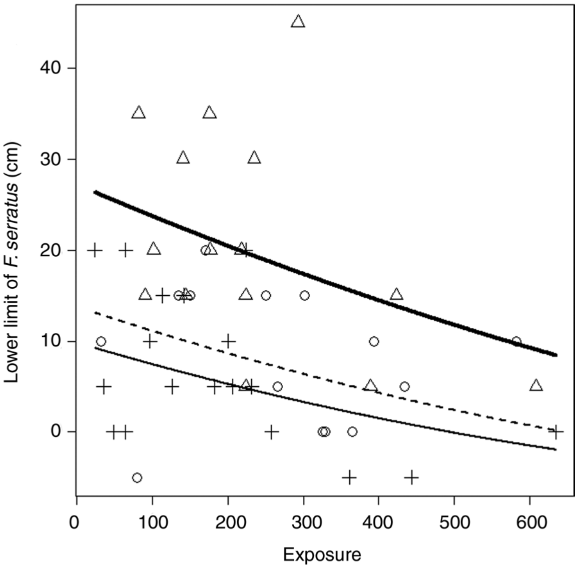

Figure 7 *Codium fragile* subsp. *fragile* and *Fucus serratus:* Lower depth limits of *F. serratus,* relative to chart datum, plotted against cartographic wave-exposure with points coded according to abundance of *C. fragile* (circle: "Absent", n=14; cross: "Low", n=18; triangle: "High", n=15). Thick line indicates relationship of *F. serratus* lower limit to wave-exposure at sites where *C. fragile* abundance was high. Thin line indicates this relationship where *C. fragile* was low, and the broken line is where *C. fragile* was absent (these two were not significantly different from each other). Regression lines are drawn based on back-transformed model parameters.

fits fairly well with other observations from the northeast Atlantic, which report *C. fragile* growing in both the lower littoral zone (in tide pools and on rock surfaces) and the sublittoral zone (Burrows 1991, Trowbridge and Todd 1999, Trowbridge and Farnham 2009). According to Chapman (1999), the northeast and northwest Atlantic differ in that *C. fragile* tends to form small intertidal populations in the northeast Atlantic but subtidal populations in the northwest Atlantic. However the results of the present study do not support this, as *C. fragile* was observed both in the infralittoral fringe and in large subtidal patches. This is similar to other observations of its distribution in the northwest Atlantic (low intertidal and subtidal, Carlton and Scanlon 1985; subtidal, Mathieson 2003, Scheibling and Gagnon 2006), and from the native range of *C. fragile*, where it grows in the subtidal (Chavanich et al. 2006).

The distribution of *C. fragile* showed some clear patterns in relation to wave-exposure and substrate. At more exposed sites, its upper limit of growth was deeper, which may be due to damage or dislodgement by the waves near the surface. This is expected since *C. fragile* does not cope well with wave-exposure; at more exposed sites, individuals grow less "bushy" and can become fragmented with wave action (Dromgoole 1975, D'Amours and Scheibling 2007), and they tend to grow larger and more densely and to survive better in sheltered conditions (Bulleri and Airoldi 2005). If open-ocean sites had been included in the present study, one might also expect a relationship between *C. fragile* abundance and wave-exposure. However, in the relatively sheltered areas studied, *C. fragile* abundance was not related to wave-exposure. This suggests that under suitable shelter conditions other factors become important in determining abundance, one of which is likely to be substrate. The lower limits and abundance of *C. fragile* were related to substrate type, with *C. fragile* growing deeper and at higher abundances at sites with stony substrate present. *Codium fragile* can grow on many different types of substrate, such as on solid or loose rock, artificial surfaces, and in soft bottom areas through attachment to shells and eel grass rhizomes (Dromgoole 1975, Carlton and Scanlon 1985, Garbary et al. 2004, Chavanich et al. 2006), but this study indicates that stones somehow provide *C. fragile* with better conditions than an even rock surface. The causes of this were not investigated, but one potential explanation is herbivory: Scheibling et al. (2008) suggested that the impact of gastropod grazing on *C. fragile* may be substrate dependent, because settling in cracks between rocks allows macroalgal germlings to escape some herbivory (Lubchenco 1980). Alternatively, Bulleri and Airoldi (2005) found positive facilitative effects of mussel beds on *C. fragile* at exposed sites, where the rugged substrate of the mussels provided shelter for the basal parts of *C. fragile* thalli from wave action. It may be that the large stones in this area are providing similar benefits.

Recently, in southern Norway, the kelp *Saccharina latissima* has declined by 40–80%, with losses mostly occurring at sheltered sites (Moy and Christie 2012). This is probably due to a combination of high summer temperatures, eutrophication and siltation, which have favored a shift to ephemeral algae (Moy and Christie 2012). Since availability of bare space can limit *C. fragile* recruitment (Bulleri and Airoldi 2005), this decline could be an important factor in providing opportunities for *C. fragile* in the subtidal. A reduction in native kelp may allow *C. fragile* to establish in gaps, after which cover can be maintained at physically suitable sites, i.e. sheltered and stony locations. Even in its native range *C. fragile* tends to become dominant only where the canopy-forming species have been disturbed, remaining as an understorey alga at undisturbed sites (Chavanich et al. 2006). The expansion of *C. fragile* has previously been linked to unrelated changes in the distribution of native species, e.g. decline in *Zostera marina* Linnaeus abundance due to disease (Fægri and Moss 1952). Thus, disturbance of native competitors may be an important explanatory factor in the success of *C. fragile* (Trowbridge 1998, Trowbridge and Todd 1999). Indeed, more generally, it may be that many invasive species' expansions are concurrent with unrelated declines in native competitors (Gurevitch and Padilla 2004).

In contrast to the view that there is no space monopolization by *C. fragile* in the northeast Atlantic (Schaffelke and Hewitt 2007), we observed *C. fragile* forming dominant subtidal canopy vegetation. However, it was only dominant at certain sites, and these observations were all restricted to the relatively sheltered areas studied. In addition, since this study was carried out at just one point in time, it is not known what the longevity of these patches is – whether they continue to dominate or eventually become replaced by native species again. This lack of information is an issue brought up in other work on *C. fragile* (e.g., Drouin et al. 2012) and should be addressed in future work as it is central to understanding what the impacts of *C. fragile* will be in the long-term.

Relationship between *Fucus serratus* and *Codium fragile* subsp. *fragile* distributions

Fucus serratus was very common, growing in the lower intertidal and infralittoral fringe zones as normal for this species (Knight and Parke 1950). There was an overlap between the depth ranges of *Codium fragile* and *F. serratus* in the infralittoral fringe, with *F. serratus* then extending up into the intertidal and *C. fragile* deeper into the subtidal. As they are growing within the same vertical limits and at the same sites, this indicates there is potential for competition, but only in the infralittoral fringe.

High *C. fragile* abundance was associated with *F. serratus* growing at lower abundances, and, along with low-wave exposure, was associated with the lower limits of *F. serratus* being higher. Although the observed shift was only 13 cm, this represents a reduction of almost a third of the vertical range of *F. serratus* at sites where *C. fragile* is highly abundant. Depending on the slope of the shore, this shift can be a broad zone, detectable even using our relatively coarse measurement methods.

Wave-exposure, the upper limits and abundance of *C. fragile*, and the lower limits of *F. serratus* were all linked, but because this is a correlative study, we cannot say which is the driving force. Upper limits and abundance of *C. fragile* could be lower at exposed sites due to invasion resistance by *F. serratus*; lower limits of *F. serratus* at sheltered sites could be higher due to competition with *C. fragile*; or a third factor could be at work. An experimental approach is required to distinguish between these explanations. Having said this, *F. serratus* grows faster, larger, and has a longer reproductive period at sheltered sites (Knight and Parke 1950); thus, shelter is not expected to reduce its vertical distribution. This supports the second interpretation of relationships; favorable conditions for *C. fragile* at sheltered sites allow it to compete more effectively. This is not unlikely given that the lower limits of other fucoid species are determined by competition, while upper limits are determined by physical characteristics of the littoral zone (Lubchenco 1980, Schonbeck and Norton 1980). Recently, a decrease in effective population size and allelic richness of *F. serratus* has been shown in Norway (Coyer et al. 2008). Competition with *C. fragile* may result in additional stress for *F. serratus* in this area.

The competitive ability of *F. serratus* seems to vary depending on situation. Based on correlative work, it appears to compete well against *F. distichus* and kelp in its introduced range (Ingólfsson 2008, Johnson et al. 2012) and against *F. vesiculosus* in an area of range expansion (Arrontes 2002). In its native range, on the other hand, removal experiments have indicated that *F. vesiculosus* can be competitively superior (Jenkins et al. 1999), and that the lower limits of *F. serratus* can be determined by competition with kelp (Kain and Jones 1975). Differences in competitive ability may be due to the vertical height/depth range studied or other unexamined factors, for example *F. serratus* may be competitively superior or inferior against the same competitor species depending on life stage (Choi and Norton 2005a). Thus, it is difficult to assess the competitive ability of *F. serratus* against *C. fragile* without experimental work.

A number of biological or physical factors, other than direct competition, could be contributing to the distribution patterns observed. Competition is rarely only between two species, and other factors such as facilitative effects (Jenkins et al. 1999, Choi and Norton 2005b), herbivory (Lubchenco and Gaines 1981) and nutrient levels can all influence competitive relationships in macroalgae (Olson and Lubchenco 1990). *Codium fragile* may be grazed by gastropods when it is newly recruited or damaged (Scheibling et al. 2008) and can be limited when specialist herbivore densities are high (sacoglossan opisthobranchs; Trowbridge 2002), but generalist intertidal herbivores are unlikely to control *C. fragile* populations (Trowbridge 1995). Other herbivores, such as urchins (Scheibling and Anthony 2001, Sumi and Scheibling 2005), or the gastropod *Littorina obtusata* which can graze on *F. serratus* (Jenkins et al. 1999), may facilitate *C. fragile* by preferentially grazing competitor species. However, grazing by *L. obtusata* tends to occur in the midlittoral zone (Jenkins et al. 1999), and large-scale urchin grazing is restricted to northern Norway (Norderhaug and Christie 2009). In addition, we did not observe urchins or large abundances of other mesograzers during fieldwork.

Conclusion

These results suggest that localities which are sheltered and have stony substrate provide good conditions for the growth of *Codium fragile* subsp. *fragile*, allowing it to reach high abundances and grow over a greater depth range than at rock sites. In this situation *C. fragile* may supersede *Fucus serratus* in the infralittoral fringe where their ranges overlap, with the lower limit of *F. serratus* shifting up the shore. While the present study shows correlative evidence of a competitive relationship between the two species, an experimental study is needed to prove this. However, the results are consistent with many observations of invasive macroalgae competing with and having a negative effect on native macroalgal species (Parker et al. 1999, Schaffelke and Hewitt 2007, Thomsen et al. 2009). In the northwest Atlantic, however, it has been shown that *C. fragile* is dependent upon disturbance to the closed kelp canopy for establishment within the kelp bed (Scheibling and Gagnon 2006). Whether *C. fragile* can supersede existing *F. serratus* vegetation in the infralittoral fringe or if *C. fragile* is dependent on a decrease in *F. serratus* cover in order to occupy the substratum is not known, and an experimental setup is needed to test this. In the same way, the competitive interactions between *C. fragile* and kelp species could be tested at the deeper end of the *C. fragile* depth range, given the observations of its vertical range in this study. The patchy distribution of *C. fragile* has persisted for many years along this coastline (Fægri and Moss 1952), but because *C. fragile* has a higher optimum temperature for growth than both *F. serratus* and the native kelps (Table 1, Lüning 1990), it may acquire a competitive advantage in possible future periods of higher sea surface temperatures.

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