

# Epiphytic macroalgae mediate the impact of a non-native alga on associated fauna

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**Abstract** The introduction of a non-native, habitat-forming macroalga may have impacts on the seaweed-associated faunal community. *Codium fragile* subsp. *fragile* is a well-known and widespread algal invader that may compete with native habitat-forming macroalgae and affect ecosystem services. This alga can be abundant at semi-exposed/sheltered sites on the south-west coast of Norway, where its vertical distribution range overlaps with another canopy-forming alga, the native *Fucus serratus*. Whether these seaweeds support similar or dissimilar associated communities will influence the ecological impact of *C. fragile* subsp. *fragile*. Therefore, the richness and composition of fauna associated with these species was assessed by sampling at three localities. While the majority of taxa occurred on both *F. serratus* and *C. fragile* subsp. *fragile*, there were clear differences in community composition between them. Fauna taxa richness and community composition were also related to macroalgal epiphyte abundance, and there were a number of taxa associated to high epiphyte samples.

The results suggest that shared macroalgal epiphytes lead to higher similarity between the invertebrate communities associated with *C. fragile* subsp. *fragile* and *F. serratus*, providing correlative evidence that epiphytic macroalgae play a role in shaping the impact of this macroalga on associated fauna.

**Keywords** *Codium fragile* · *Fucus serratus* · Associated communities · Non-native species impact · Epiphyte

## Introduction

Along northern temperate coasts the dominant macroalgae tend to be habitat-forming kelps and fucoids, which are important in providing food, substratum and shelter for many species (Christie et al., 2009). While they are a direct food source for some mesoherbivores (e.g. Haavisto & Jormalainen, 2014), these tough brown algae mostly enter the food chain through decomposition (Norderhaug et al., 2003). Therefore, differences in their nutritional value may have a relatively small impact on their associated fauna; instead, the richness, composition and densities of fauna they directly support is largely determined by their structure (Hacker & Steneck, 1990; Norderhaug et al., 2002; Christie et al., 2007, 2009). Habitat structure is known to have an important influence on the faunal community in many systems (e.g. MacArthur & MacArthur, 1961; Tews et al., 2004; Hauser et al., 2006).

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When a non-native macroalga establishes in an ecosystem, it may be expected to affect the seaweed-associated faunal composition of the area if it alters the structure of the algal vegetation and the amount of available habitat space (e.g. Buschbaum et al., 2006). Most of the reported negative effects of introduced macroalgae have been on the density and abundance of native macroalgae (Williams & Smith, 2007), but effects on faunal communities have also been demonstrated (e.g. Schmidt & Scheibling, 2006; Harries et al., 2007). The impacts of non-native macroalgae on fauna have been difficult to generalise as they vary in direction and magnitude depending on a number of factors, e.g. the species in question, where it is growing, and the time of year (Wernberg et al., 2004; Buschbaum et al., 2006; Lutz et al., 2010; Gestoso et al., 2012; Engelen et al., 2013).

The non-native macroalga *Codium fragile* subsp. *fragile* (dead man's fingers, oyster thief) (previously subsp. *tomentosoides* (van Goor) Silva, Provan et al., 2008) is a branched, canopy-forming, siphonal green alga. It has spread over large areas of the world from its native range in the North-West Pacific, reaching Europe during the 1800s, North America by 1957 and Oceania by 1973 (Silva, 1955; Bouck & Morgan, 1957; Dromgoole, 1975; Provan et al., 2008). *Codium fragile* subsp. *fragile* (hereafter *C. fragile*) is considered a high-risk introduced species, ranked highly for dispersal and establishment ability (Nyberg & Walentinus, 2005), with long expected population lifetimes (Gederaas et al., 2012), the ability to compete with native seaweeds (Scheibling & Gagnon, 2006) and a high number of impact types on ecosystem services (Vilà et al., 2010). However, comparisons of associated species between native seaweeds and *C. fragile* indicate that it can support a faunal community of comparable or higher diversity than native macrophytes (Schmidt & Scheibling, 2006; Drouin et al., 2011).

In Norway, *C. fragile* has been a common seaweed in the infralittoral and upper-subtidal zones for over 60 years (Norwegian Biodiversity Information Centre, 2012). Along the south-west coast (northern North Sea), it can form locally dominant patches of canopy vegetation, typically at sheltered and semi-exposed rocky sites (Jorde, 1966; Armitage et al., 2014). These patches can extend into the low-intertidal zone usually dominated by the native canopy-forming brown alga *Fucus serratus* L. (Fig. 1), where they may compete

for space (Armitage et al., 2014). An increase in abundance of *C. fragile* at the expense of *F. serratus* could have an impact on infralittoral seaweed-associated communities. The strength of this impact will depend on whether *C. fragile* can support a similar community to *F. serratus*—a community with typically high abundance and richness of fauna and epiphytes (Hagerman, 1966; Williams, 1996; Fredriksen et al., 2005; Christie et al., 2009).

Because associated fauna are influenced by macroalgal architecture, structural similarities between *C. fragile* and *F. serratus* could shape a similar faunal community on them. Both species are canopy-forming, branch dichotomously and can become quite large, resulting in a coarse bushy structure. Both are perennial; although *C. fragile* thalli are normally reduced somewhat during the winter by fragmentation, many thalli retain intact basal branches and can quickly regrow during spring and summer. There are, on the other hand, some clear differences between the two species: *F. serratus* is parenchymatic, with flat leathery blades which are smooth but studded with some hair groups, while *C. fragile* is siphonal, with cylindrical soft branches which have an uneven surface composed of utricles set with hairs. As *C. fragile* is a green alga (Chlorophyta) and *F. serratus* is a brown alga (Phaeophyceae), they also have different production of some secondary metabolites which may influence epifauna (e.g. phlorotannin and DMSP concentrations; Amsler & Fairhead, 2005; Lyons et al., 2007). In addition, the epiphytic macroalgal community on *C. fragile* can differ from that of native seaweeds (Schmidt & Scheibling, 2006; Jones & Thornber, 2010). This may also impact the faunal community associated to the two species; for example, Eilertsen et al. (2011) found that the morphology and degree of branching of algal epiphytes strongly influenced the composition of amphipods associated with kelp.

Once *C. fragile* has established, it can maintain dominant stands which prevent regrowth of native macroalgae (Scheibling & Gagnon, 2006). If *C. fragile* supports an associated fauna very different from native macroalgae, then an increase in its abundance could have large effects within the ecosystem (e.g. on near-shore food webs and carbon budgets; Salvaterra et al., 2013). For example, macroalgal-associated crustaceans and gastropods are important food for shallow-water fishes (Norderhaug et al., 2005). On the

**Fig. 1** A photograph of *Codium fragile* subsp. *fragile* (upper) and *Fucus serratus* (lower) in the infralittoral zone, taken from the shore at Espegrend marine biological station (Bergen, south-western Norway) in 2009



other hand, if *C. fragile* supports a similar invertebrate community to *F. serratus*, then the ecological impact of a change in their proportions may be less severe. This may be particularly important in future years as ocean warming influences the distribution of *F. serratus* (Jueterbock et al., 2013).

The aim of this study therefore is to compare the associated invertebrate fauna of *C. fragile* with that of *F. serratus*, and to examine whether it is influenced by the abundance of macroalgal epiphytes. This is done by testing the hypothesis that there are differences in invertebrate community composition, taxa richness and the densities of certain invertebrate groups between *F. serratus* and *C. fragile*. We also test if the epiphytic algae influence the associated fauna, and whether the abundance of epiphytic algae is influenced by species or surface area of the host alga.

## Methods

### Sampling

Sampling was carried out at three stations within a 50 km region on the south-west coast of Norway in June 2011. Station A was on the shore of Siglo in Fitjar (59°56.006'N, 05°12.431'E), Station B near Møsterhamn in Bømlo (59°42.675'N, 05°22.260'E) and Station C on Stussholmane in Austevoll (60°08.158'N, 05°09.675'E). This area is within the cold temperate North-East Atlantic biogeographic region (Lüning, 1990), with a mean tidal difference of 90 cm and MLW at 45 cm above chart datum

(Statens Kartverk, 2014). The area has an irregular coastline, with many areas sheltered from open sea by a barrier of islands to the west. The three stations were all moderately sheltered with hard substratum. Each station had *C. fragile* and *F. serratus* present in a patch or zone at similar depths, and Station C had the densest occurrence of *C. fragile*.

Five individuals of *C. fragile* and *F. serratus* each (hereafter referred to as the host algae) were collected at each station (a 15 m stretch of shoreline). Thalli growing at the same depths (between chart datum and 30 cm above chart datum), and with approximately similar size were preferentially chosen. Sampling was done by wading during low spring tide, while the algae were still submerged. The thalli were gently torn (*C. fragile*) or cut (*F. serratus*) free from the substrate at the base, and while still submerged were slowly transferred to a large cloth bag held open nearby (Fredriksen et al., 2005). Since the fauna in the infralittoral zone are accustomed to wave motion, this treatment would cause negligible disturbance of the seaweed-associated fauna.

### Associated organisms

Each host algal sample was soaked in and rinsed with freshwater, to stun mobile fauna. The water was filtered using a 0.5-mm plankton net, and the fauna stored in 4% formalin solution with borax. Next, all epiphytic algae (visible to the eye) were removed from each thallus and frozen. The main purpose of collecting the epiphytic macroalgae from each sample was to estimate the total abundance, but we also identified as

many as possible to the genus or species level. For each sample, we visually determined the most dominant epiphytic taxon. In cases where two taxa were similarly abundant, both were recorded as dominant. The epiphytes were checked for any fauna which had become caught in them, then dried and weighed. Total dry weight was used as the measure of abundance of epiphytic macroalgae (hereafter 'epiphytes').

The number of individuals was counted for most taxa. Those estimated to be under 0.5 mm were excluded. If a taxon was very abundant in a sample then a subsample (one-fourth of the total) was taken and the individuals counted within that to get an estimate. Nematodes and Platyhelminthes were abundant everywhere, and juvenile *Mytilus* sp. were abundantly attached to epiphytes making counting inaccurate, so were recorded as presence/absence. Fauna were identified to as low a taxonomic level as possible (most commonly to species) using Hayward & Ryland (1995) and more specialist keys or expert assistance as necessary. In some cases, it was only possible to sort the animals into higher taxonomic groups (family, order or class) due to their small size or juvenile form (e.g. juvenile gastropods and amphipods, harpacticoid copepods). If it was clear that there were multiple taxa likely present but these could not be identified, they were given a separate taxon code (e.g. ostracod 1 and ostracod 2). Because this could result in identification errors or taxa containing multiple species, an additional analysis was run only using identified species (see: Statistical analysis).

The host thalli were also examined for sessile fauna. Tube-forming polychaetes (excluding juveniles <1 mm) and other individual animals were counted, while colonial animals were recorded as presence/absence. Total bryozoan coverage of each thallus was estimated by eye using categories of cover, ranging through none (no cover); low (very few small colonies); intermediate (a few colonies to around one quarter of the thallus); high (around one half of the thallus) and very high (well over half of the thallus). In addition, if there was an obviously dominant species of bryozoan this was recorded.

#### *Codium fragile* and *Fucus serratus* samples

It was necessary to measure the size of the host thalli to allow standardisation when making comparisons. *C.*

*fragile* thalli are cylindrical and siphonal, whereas *F. serratus* thalli are flat and parenchymous, making wet or dry weight unsuitable for comparing size. Surface area was chosen instead, as it is unaffected by weight differences, reflects available habitat space and has been used before in comparing *C. fragile* to native seaweeds by Schmidt & Scheibling (2006). To estimate the surface area of the samples, a relationship between dry weight and surface area was created for each species by sampling and measuring additional *F. serratus* and *C. fragile* thalli. The surface area was measured by cutting the thalli into roughly uniform sections, then measuring the diameter (*C. fragile*) or the width (*F. serratus*) and length of these sections. The surface area of each section could then be calculated using approximations of their shape: For *C. fragile*, the surface area of a cylinder ( $(2 \times \pi \times r) \times length$ ) and for *F. serratus*, the area of a rectangle ( $2 \times (length \times width)$ ). The surface areas of the sections were summed to get total surface area of each thallus, and this was related to the dry weight using linear models (response = surface area, predictor = dry weight; *C. fragile*,  $P < 0.001$ ,  $R^2 = 93\%$ ,  $n = 9$ ; *F. serratus*,  $P < 0.001$ ,  $R^2 = 86\%$ ,  $n = 10$ ). The parameters of these models were then used with the dry weight of the host algae to get an estimate of their surface area.

One of the *F. serratus* samples was excluded from further analysis due to its very large surface area (approximately double all the other *F. serratus* samples, 8306 cm<sup>2</sup>). This was done because it is known that habitat area can influence faunal communities (e.g. Matias et al., 2010), so it was difficult to make fair comparisons with a size difference this extreme. After this exclusion, the calculated mean ( $M$ ) estimated surface area of the *F. serratus* thalli was 2842 cm<sup>2</sup> (standard deviation (SD) = 800), and of the *C. fragile* thalli was 1054 cm<sup>2</sup> (SD = 318). The relatively small surface area of the *C. fragile* thalli is mainly due to their cylindrical branches, compared to the flat branches of *F. serratus*. The mean dry weights of the host thalli were 8.39 g *C. fragile* (SD = 3.16), and 27.73 g for *F. serratus* (SD = 8.29). This method estimates the surface area of the algae at the macroscale; it does not take into account the surface area of hair groups on *F. serratus*, or the extra surface provided by the utricle structure or hairs of *C. fragile*.

## Statistical analysis

Analysis was carried out using the program R (version 3.1.0, R Development Core Team, 2014). Taxa richness and macroalgal epiphyte abundance was standardised to per 500 cm<sup>2</sup> of host algal surface area for some analyses, indicated by the prefix ‘Standardised’. A manual backwards stepwise selection procedure using p-values was followed to find minimum adequate models, and models were checked by examining diagnostic plots. Only the response variables *Epiphyte abundance* and *Standardised epiphyte abundance* required transformation (Box-Cox transformation in R package *car*; Fox & Weisberg, 2011). Mixed-effects models were used for all univariate analyses, with *Station* as a random factor; this accounted for spatial dependence between the samples from each station. These were

linear mixed-effects models (R package *nlme*; Pinheiro et al., 2015) or generalised mixed-effects models when the response variable was count data (R package *MASS*; Venables & Ripley, 2002). *R*-squared values were calculated using the package *MuMIn* (Barton, 2015).

Multivariate analyses were used to look for patterns in community composition of the epiphytic macroalgae. Bray–Curtis distances (Bray & Curtis, 1957) were calculated on the presence/absence data, and used to perform non-metric multidimensional scaling (nMDS; Shepard, 1962; Kruskal, 1964). Permutational multivariate ANOVA was used to see if there were differences in the epiphyte community by host species (adonis in R package *vegan*; Oksanen et al., 2013). Univariate analyses were then used to explore whether total epiphyte abundance was associated with the species or size of the host algae (Table 1). Because the

**Table 1** Table of statistical analyses carried out to examine the relationships between fauna, host algae and epiphytic macroalgae

Response	Predictors	Method	Test statistic	<i>P</i> value	<i>R</i> <sup>2</sup>
Epiphytic macroalgae					
Epiphyte community	Host species	Permutational MANOVA	$F_{1,27} = 3.21$	0.01	0.11
Std. epiphyte abundance	Host species	LME	$F_{1,25} = 11.4$	0.002	0.25 (0.37)
Epiphyte abundance	Surface area ( <i>C. fragile</i> )	LME	$F_{1,11} = 17.5$	0.002	0.56 (0.56)
	Surface area ( <i>F. serratus</i> )		$F_{1,10} = 0.01$	NS	–
Associated fauna					
Std. taxa richness	Host species	GLMM	$t_{25} = -7.12$	<0.001	0.21 (0.21)
	Epiphyte abundance		$t_{24} = 0.02$	NS	–
Taxa richness	Host species	GLMM	$t_{23} = 4.72$	<0.001	0.07 (0.07)
	Epiphyte abundance		$t_{23} = -2.70$	0.01	
Invertebrate community	Host species	Permutational MANOVA	$F_{1,26} = 9.99$	<0.001	0.25
	Epiphyte abundance		$F_{1,26} = 4.61$	<0.001	0.11
Amphipod density	Host species	GLMM	$t_{24} = -3.48$	0.002	0.05 (0.11)
	Epiphyte abundance		$t_{24} = 3.01$	0.006	
Copepod density	Host species	GLMM	$t_{24} = -4.00$	0.001	0.03 (0.05)
	Epiphyte abundance		$t_{24} = 3.38$	0.003	
Gastropod density (adult)	Host species	GLMM	$t_{24} = -2.99$	0.006	0.11 (0.24)
	Epiphyte abundance		$t_{24} = 5.02$	<0.001	
Gastropod density (juv)	Host species	GLMM	$t_{24} = -2.32$	0.03	0.01 (0.01)
	Epiphyte abundance		$t_{24} = 3.95$	0.001	

Methods include linear mixed-effects models (LME), generalised linear mixed-effects models (GLMM) and multivariate analysis of variance (MANOVA). “Community” refers to the Bray–Curtis distance matrix; *Std.* standardised by surface area; *NS* not significant and removed from the model; *juv* juveniles. No corrections have been applied to *P* values. Where two *R*<sup>2</sup> values are given, the first is the marginal *R*<sup>2</sup> (the variance explained by fixed factors) while the second in parentheses is the conditional *R*<sup>2</sup> (variation explained by both fixed and random factors; in this case, including Station)

surface area of the *F. serratus* thalli was generally larger, the relationship between surface area and epiphyte abundance was analysed separately for the *C. fragile* and the *F. serratus* data to see if the epiphyte abundance was related to the surface area within each host species.

For the fauna, univariate methods were used to examine various relationships between taxa richness, densities of certain groups, epiphyte abundance and the host species (Table 1). Taxa richness was analysed both as standardised and unstandardized to give an indication of what influence standardising abundances by area had on the conclusions.

Multivariate analyses were also used to study the community composition of the counted invertebrates, using the same methods as for the epiphytic macroalgae. Here, distances were calculated on log-transformed standardised taxa abundances. To see if there were particular taxa which were significantly associated to (a) one of the host species or (b) samples with above-median epiphyte weights, permutation tests on group-equalised point-biserial correlations were carried out ( $r_{pb}^g$ ; multipatt in R package *indicspecies*; De Cáceres et al., 2010). The faunal nMDS was run a second time on a data subset which only included taxa identified to species (37 species). This was done to check if artificial similarity between the samples had been created by potentially having more than one species present in a taxon unit; but this was not indicated as the nMDS analyses were similar (PROTEST,  $m_{12}^2 = 0.26$ , correlation = 0.86,  $P = 0.001$ ).

Lastly, the fauna and epiphyte ordinations were compared using a Procrustes rotation and PROTEST (Gower, 1971; Jackson, 1995). This showed whether patterns in epiphyte composition were matched by patterns in faunal composition.

## Results

### Epiphytic macroalgae

The composition of epiphytic macroalgae was significantly different between the *C. fragile* and *F. serratus* samples (Table 1). The epiphyte which was most common (present in the most samples) and dominant (most abundant in the most samples) was the same on both, *Pylaiella/Ectocarpus* spp. (present on 15/15 *C. fragile* samples, and 12/14 *F. serratus* samples). On *F.*

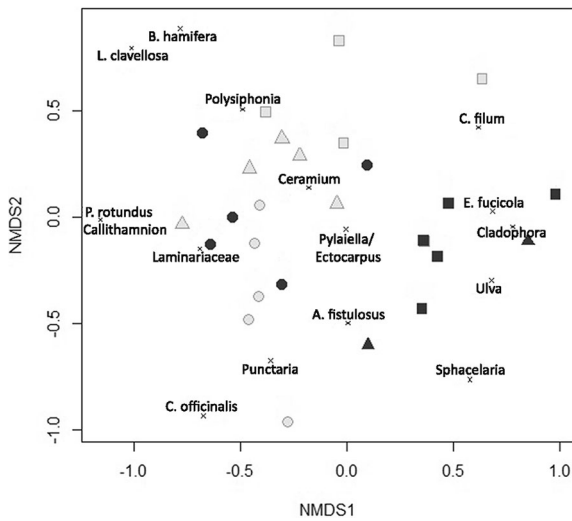
*serratus*, *Cladophora* spp. was the second most common, followed by *Elachista fucicola* and *Ceramium* spp. (all dominant in two to four samples). On *C. fragile*, common epiphytes were *Ceramium* spp., *Polysiphonia* spp. and small individuals of the Laminariaceae (all dominant in 2–3 samples). The host species appeared to have more similar epiphyte communities at station A than at B or C (Fig. 2). A full list of the epiphytic macroalgae is provided in Appendix Table A2 in supplementary material.

The mean abundance of epiphytes on *C. fragile* was 1.55 g (SD = 1.53; 13 taxa), and on *F. serratus* was 1.41 g (SD = 1.35; 12 taxa). Although the abundance per sample was thus similar, the smaller surface area of the *C. fragile* thalli meant that standardised epiphyte abundance (abundance per 500 cm<sup>2</sup> of host algal surface area) was significantly higher on *C. fragile* ( $M = 0.66$  g, SD = 0.53) than *F. serratus* ( $M = 0.27$  g, SD = 0.28; Table 1). Epiphyte abundance was positively related to surface area in the *C. fragile* samples, but not the *F. serratus* samples (Table 1).

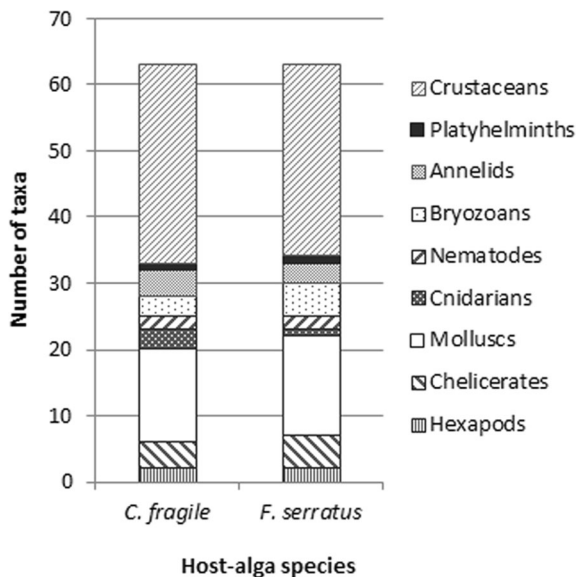
### Associated fauna

A total of 77 fauna taxa were recorded (Appendix Table A1 in supplementary material), with 63 in the *C. fragile* samples and 63 in the *F. serratus* samples. There were 49 taxa which we present on both *C. fragile* and *F. serratus*, and approximately half of the taxa unique to one host alga were only present as single individuals or in one sample. The number of taxa from each phylum/subphylum was strikingly similar between the two host species, with both dominated by crustaceans and molluscs (Fig. 3). Standardising by surface area had quite a large effect on relationships to faunal taxa richness: per sample taxa richness was significantly higher on *F. serratus* (30.8 taxa per sample (SD = 6.0) compared to 23.1 (SD = 5.8) on *C. fragile*), but standardised taxa richness was significantly higher on *C. fragile* (11.6 taxa (SD = 3.2) compared to 5.7 (SD = 1.3) on *F. serratus*). In addition, per sample taxa richness was significantly related to the abundance of epiphytic macroalgae, while standardised taxa richness was not (Table 1; Fig. 4).

Taxa composition was significantly different between *C. fragile* and *F. serratus* (Table 1), which is reflected in the grouping of the samples by host alga

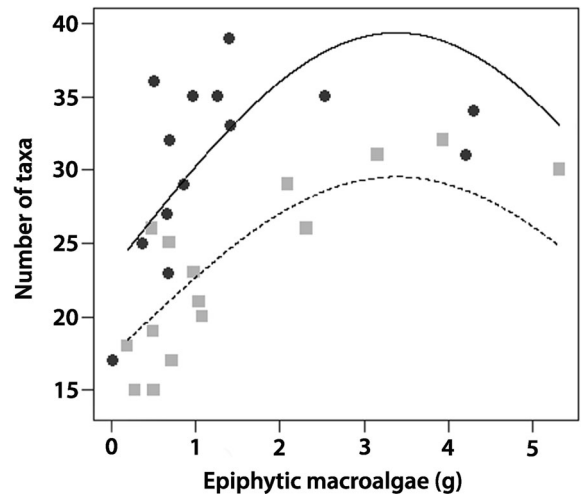


**Fig. 2** nMDS plot of the algal epiphyte community, using Bray–Curtis distances on presence/absence data (stress = 0.13). Samples of *Fucus serratus* are denoted by black symbols and *Codium fragile* subsp. *fragile* by grey symbols (station A = circles; B = triangles; C = squares;  $n = 29$ ). The grey crosses show the centroids of the occurrence of each taxon; full taxa names can be found in Appendix Table A2 in supplementary material



**Fig. 3** Taxa richness of each phylum/subphylum on *Codium fragile* subsp. *fragile* ( $n = 15$ ) and *Fucus serratus* ( $n = 14$ )

in the nMDS plot (Fig. 5). The densities of amphipods, harpacticoid copepods, and gastropods were all highest on *C. fragile* (Table 1; Fig. 6), and there were 11

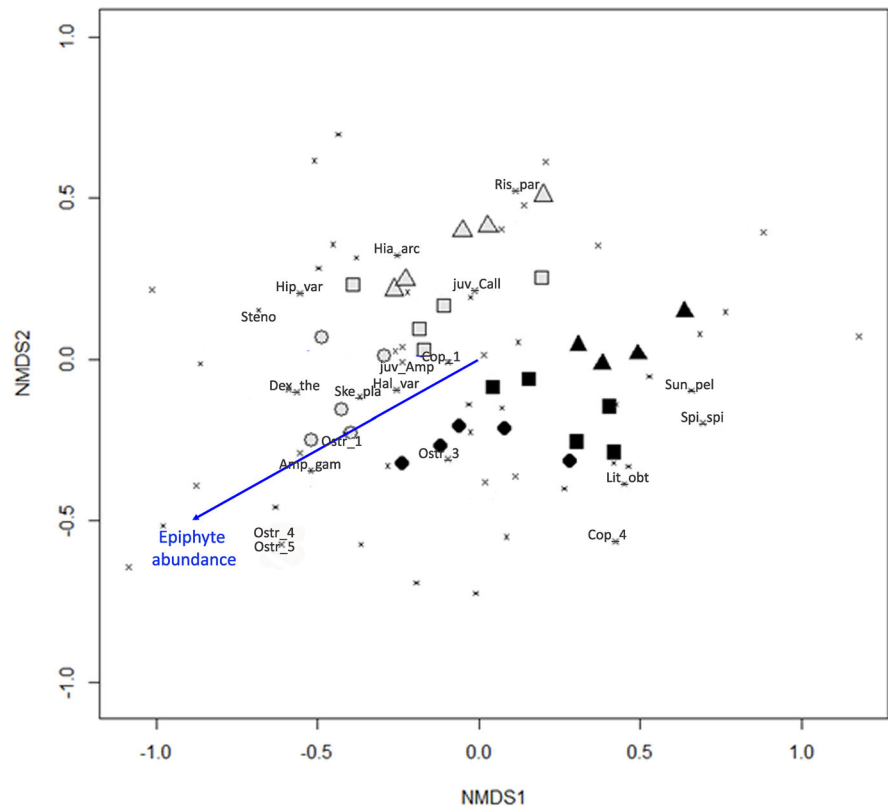


**Fig. 4** Relationship of per sample taxa richness to epiphyte abundance by host species [*Codium fragile* subsp. *fragile* (grey squares, dashed line)  $n = 15$ ; *Fucus serratus* (dark circles, solid line)  $n = 14$ ]

taxa which were significantly associated with either *C. fragile* or *F. serratus* (Table 2; Fig. 5). Taxa which were abundant ( $>1$  individual per  $500\text{ cm}^2$ ) but showed no particular association to *F. serratus*, *C. fragile* or high epiphyte abundances were juvenile snails, mites of the suborder Oribatida, the amphipod *Calliopos laeviusculus* and the small gastropod *Pusillina sarsii*.

There were also clear differences in colonial organisms between the two host algae (Appendix Table A1 in supplementary material). On *C. fragile*, bryozoan coverage was ‘low’ for one thallus (one small colony of *Electra pilosa*) and ‘none’ on the other fourteen, while *F. serratus* had thalli of low (2 thalli), intermediate (8 thalli) and high coverage (4 thalli) (data not shown). All bryozoans in the *C. fragile* samples were present in tiny amounts, and were not observed growing on the thallus itself; rather they were either unattached or on species associated with *C. fragile*. The most common and dominant bryozoans on *F. serratus* were *Electra pilosa*, followed by *Membranipora membranacea* and *Flustrellidra hispida*. *Alcyonidium gelatinosum* also occurred commonly but was never dominant (Appendix Table A1 in supplementary material). The hydrozoan *Dynamena pumilla* was commonly present on both host algae, but was observed mostly at low abundances in *C. fragile* samples and unattached to the thallus, whereas on *F.*

**Fig. 5** nMDS plot of the quantified faunal community, using Bray–Curtis distances on log-transformed abundances (stress = 0.15). Symbols as in Fig. 2. Taxa with significant associations are labelled (see Table 2). The vector displays increasing epiphyte abundance



*serratus* it was observed growing attached and at higher abundances (data not shown).

#### Influence of epiphytic algae on associated fauna

The invertebrate community composition was also related to abundance of epiphytic macroalgae (Table 1). This can also be seen in the nMDS plot, where the distance between *F. serratus* and *C. fragile* narrows in the direction of increasing epiphyte abundance (Fig. 5), indicating that these samples had more similar communities. There were 9 taxa which were specifically associated to samples with high epiphyte abundances (Table 2). In addition, densities of amphipods, harpacticoid copepods and gastropods all increased significantly with increasing epiphyte abundance (Table 1; Fig. 6).

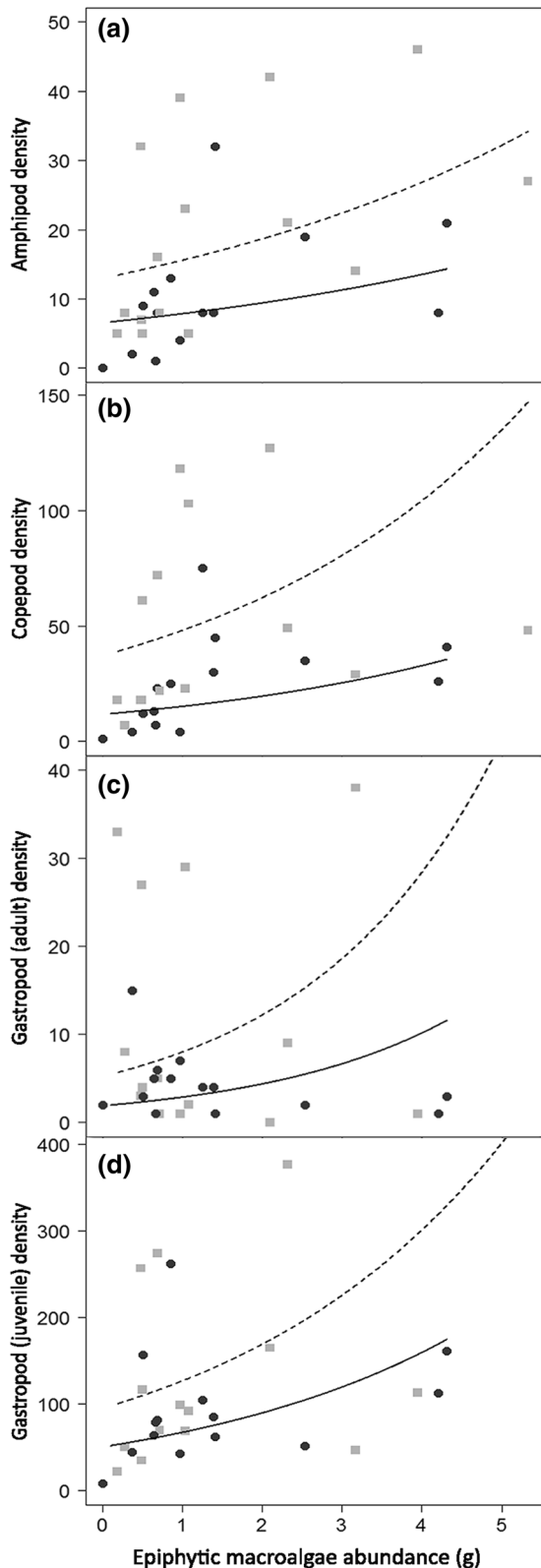
The composition of the fauna was also related to the composition of epiphytic macroalgae (PROTEST,  $P = 0.001$ ). The epiphytes were most similar between the two host species at station A (Fig. 2), and these

samples also showed the greatest community similarities with regard to the counted invertebrates (Fig. 5). However, the correlation between the two compositions was not particularly high ( $m_{12}^2 = 0.76$ , correlation = 0.48). This indicates that while the association between the communities was significantly more similar than random, there was not a tight match between the epiphyte and faunal composition of the samples.

#### Discussion

There were clear differences in the invertebrate communities associated with *C. fragile* and *F. serratus*. However, the differences were reduced in the samples which had abundant and similar epiphytic macroalgae. The results of this study thus indicate that algal epiphytes are important in mediating the impact of *C. fragile*, through making its faunal community more similar to the native host alga.





**Fig. 6** The relationship between epiphytic macroalgal abundance and the density of amphipods (a), harpacticoid copepods (b), adult gastropods (c), and juvenile gastropods (d), by host species (*Codium fragile* subsp. *fragile* (grey squares, dashed line)  $n = 15$ ; *Fucus serratus* (dark circles, solid line)  $n = 14$ ; densities as individuals per 500 cm<sup>2</sup> of host alga). Three values are excluded from these plots in order to have visually useful axes scales, all *C. fragile*: 393 copepods in (b); 82 gastropods in (c); 1077 gastropods in (d)

#### Causes and effects of community similarities

It is known that the structure of the epiphytic algae is a main factor which may attract or deter certain fauna (Hacker & Steneck, 1990; Wahl & Hay, 1995; Eilertsen et al., 2011). In the present study, the most abundant and dominant epiphytes on both host species were uniseriate annual brown algae (*Pylaiella/Ectocarpus* spp.), which have a fine filamentous structure. This is probably why total epiphyte abundance had a homogenising effect on the overall composition of associated invertebrates.

This homogenising effect is supported by the fact that there were a number of taxa which were associated to high epiphyte samples, regardless of host species identity. Fine filamentous algae may trap detritus in their complex structure (Gibbons, 1988), which can attract small detritus-feeding invertebrates. Many of the taxa associated to samples with much epiphytic algae are known to be epiphyte-associated or detritus-feeding e.g. *Ampithoe* spp. (Skutch, 1926; Norderhaug et al., 2003; Norderhaug, 2004), Ostracoda (Hagerman, 1966 and references therein), *Halocladius varians* (Garbary et al., 2005), and harpacticoid copepods (Hall & Bell, 1988; Meyer & Bell, 1989; Hall & Bell, 1993).

The fact that these organisms occur on both *F. serratus* and *C. fragile* (depending on their epiphytic macroalgal load) is important when considering the impact of *C. fragile* on food webs. Ostracods, harpacticoid copepods, and small amphipods are important prey items for common small fish such as the two-spot goby, *Gobiusculus flavescens* (Potts et al., 1990). Harpacticoid copepods can also form part of the diet of juvenile cod, *Gadus morhua* (Keats et al., 1987). This provides a link between small macroalgal-associated fauna and wider food webs, since *Gobiusculus flavescens* is a common prey for larger gadoids in the coastal zone (Fosså, 1991).

**Table 2** Taxa with a significant ( $P < 0.05$ ) association to a host algal species, or to higher epiphyte weight samples, according to a group-equalised point-biserial correlation coefficient ( $r_{pb}^g$ )

	Taxa (and code)	Association coefficient
<i>Codium fragile</i> subsp. <i>fragile</i>	<i>Hippolyte varians</i> (Hip_var)	0.56
	<i>Hiattella arctica</i> (Hia_arc)	0.51
	Family Stenothoidae (Steno)	0.49
	<i>Dexamine thea</i> (Dex_the)	0.44
	Family Alopeiidae juveniles (juv_Call)	0.40
	<i>Rissoa parva</i> (Ris_par)	0.40
	Harpacticoid copepod 1 (Cop_1)	0.36
<i>Fucus serratus</i>	<i>Littorina obtusata/fabalis</i> (Lit_obt)	0.64
	<i>Spirorbis spirorbis</i> (Spi_spi)	0.52
	Harpacticoid copepod (Cop_4)	0.45
	<i>Sunampithoe pelagica</i> (Sun_pel)	0.34
Above-median epiphyte abundance	Juvenile amphipods	0.56
	<i>Halocladius varians</i> (Hal_var)	0.48
	Ostracoda 3 (Ostr_3)	0.41
	Ostracoda 4 (Ostr_4)	0.41
	Harpacticoid copepod 1 (Cop_1)	0.40
	<i>Ampithoe gammaroides</i> (Amp_gam)	0.38
	Ostracoda 1 (Ostr_1)	0.37
	Ostracoda 5 (Ostr_5)	0.34
	<i>Skeneopsis planorbis</i> (Ske_pla)	0.28

The ‘above-median epiphyte abundance’ group consisted of 8 *C. fragile* and 7 *F. serratus* samples. Taxa ID codes are given in brackets; only the taxa with counted abundances (65 taxa) were included in the analysis

In both *C. fragile* and *F. serratus*, taxa richness rose with epiphytic algal abundance. Whether this is due to increased habitat size, heterogeneity, or complexity cannot be answered by this study, as all of these factors are thought to influence taxa richness in various systems (e.g. Kerr & Packer, 1997; Lomolino, 2000; Hauser et al., 2006; Matias et al., 2010). With very high abundances of epiphytic macroalgae, the number of taxa levelled out or even decreased. In these high epiphyte samples, which were dominated by the fine filamentous genera *Pylaiella/Ectocarpus* and *Ceramium*, there may have been fewer taxa due to avoidance by invertebrates with relatively large body size compared to the interstitial space (Hacker & Steneck, 1990; Kelaher, 2003). The same trend in richness could be seen in both host species, indicating that it is a real effect. However, because epiphyte weight was related to surface area in *C. fragile*, some of the increase in taxa richness with epiphyte weight may partially be due to increasing surface area in that

host species. It should also be noted that the curvature of this relationship was strongly influenced by a few samples with very high amounts of algal epiphytes. In general, more samples with high abundances of algal epiphytes would be desirable to verify the relationships indicated in this study.

Not all of the community similarities between *C. fragile* and *F. serratus* were related to epiphytic macroalgae. The structure and shape of a macroalga is very important in determining the composition of associated mobile faunal communities (Christie et al., 2009); even artificial structures may be readily colonised by similar species if their structure is similar to the host alga (Edgar, 1991; Norderhaug et al., 2002; Kelaher, 2003; Christie et al., 2007). *C. fragile* has a coarsely branched three-dimensional structure like *F. serratus*, thus it provides a somewhat similar structural habitat. This may allow it to support many similar species, despite being a comparatively new addition to the flora.

Our study supports this, as *C. fragile* had many taxa shared with *F. serratus*, not all of which were epiphyte-associated. These seaweeds seem to have similar functional roles, and both house a high density of molluscs and crustaceans which are important food for small fishes in shallow coastal areas (Norderhaug et al., 2005). This is in accordance with other studies which have found that *C. fragile* can support many species of fauna (Schmidt & Scheibling, 2006; Drouin et al., 2011), and that introduced macroalgae in general do not have severe negative effects on diversity (e.g. Johnson, 2007; Thomsen et al., 2009; Engelen et al., 2013). Few taxa were completely absent from one of the host species, a pattern which has also been seen in other comparisons of non-native and native algae (e.g. Viejo, 1999; Wernberg et al., 2004; Engelen et al., 2013), and native macroalgae compared to each other (Fredriksen et al., 2005).

#### Causes and effects of community dissimilarities

It is known that *C. fragile* can provide a good, year-round habitat for epiphytic macroalgae, potentially due to the rough microstructure of its surface (Jones & Thornber, 2010). On *F. serratus* however, algal epiphyte abundance was comparatively low and showed no relationship to surface area. Former studies have shown that the epiphyte community of *Fucus* sp. may be greatly influenced by mesograzing activity, which can remove specific or overall epiphytic algal growth (Råberg & Kautsky, 2008; Leidenberger et al., 2012). The vagile fauna on *F. serratus* contained a number of specialised mesograzers in higher densities than *C. fragile*, e.g. the *Littorina obtusata/fabalis* group (Watson & Norton, 1987) and *Idotea granulosa* (Leidenberger et al., 2012). The overall mesoherbivorous grazing on the epiphytic algal growth on the *F. serratus* individuals may therefore have been more efficient in keeping the epiphytic growth under control than on the *C. fragile* individuals.

The composition of algal epiphytes was also different on *C. fragile* and *F. serratus*. The commonness of red algal epiphytes on *C. fragile* can be related to its rough surface, which may efficiently trap rhodophyta spores (Wilson 1978, cited in Trowbridge, 1998). In the present study, we found that the composition of the faunal community was related to the composition of algal epiphytes present, but only weakly. The weakness of this association should be

interpreted with caution, because the algal data were only presence/absence and many of the host algae were dominated by the same algal taxa. This limits our ability to draw conclusions about the effect of epiphyte community composition on faunal composition. An experiment comparing the fauna on host thalli with manipulated and quantified epiphytic algal communities is needed to answer this fully.

The higher densities of amphipods, harpacticoid copepods and gastropods on *C. fragile* are potentially linked to epiphyte abundance. A positive relationship between densities of small mobile fauna and the abundance of structurally complex epiphytic algae has often been found (e.g. Hall & Bell, 1988, 1993; Martin-Smith, 1993; Christie et al., 2009; Eilertsen et al., 2011). Thus, compared to *F. serratus*, higher algal epiphyte abundances per unit area in *C. fragile* probably allow it to support higher densities of these animals, as well as epiphyte-associated taxa such as ostracods and insect larvae. An expansion of *C. fragile* beds might therefore result in an infralittoral community with relatively higher densities of these groups per unit area than *F. serratus* beds. This effect would be enhanced by the positive relationship between thallus size and epiphytic algal load in *C. fragile*. As stated previously, these types of invertebrates are important prey items for small fish so this could have further impacts on food webs.

There were a few taxa associations which show no obvious sign of a mediating influence of epiphytic macroalgae. For example, the shrimp *Hippolyte varians* and the gastropod *Rissoa parva* were associated with *C. fragile*. This may have some ecological impact, as the small fishes *Ctenolabrus rupestris* and *C. exoletus* (wrasse) are specialist predators on small gastropods such as *Rissoa parva*, while *Hippolyte varians* is preyed on by cod, *Gadus morhua* (Norderhaug et al., 2005). In addition, the small amphipods *Dexamine thea* and family Stenothoidae were associated with *C. fragile*. This may be related to the hairs and utricles on its surface, which small appendages can cling to (Eilertsen et al., 2011). The rough surface may also be why small individuals of the bivalve *Hiatella arctica*, which normally lives in crevices in rock (Hayward & Ryland, 1995), were associated to *C. fragile*. A special association between *F. serratus* and the amphipod *Sunampithoe pelagica* also seems to exist. We have observed this species living between flat *F. serratus* fronds which it has glued together;

something that would not be possible with *C. fragile* thalli.

*Fucus serratus* was clearly a more suitable habitat for sessile fauna such as bryozoans, the hydrozoan *Dynamena pumila*, and the polychaete *Spirorbis spirorbis*. One possible explanation for this is that *C. fragile* may have reduced perennial habitat available for settlement due to winter fragmentation. However, older parts of the thallus often survive the winter intact in this area (pers. obs.) and could be colonised year-round, as observed with epiphytic algae by Jones & Thornber (2010). A perhaps more fitting explanation is that the two host algae are in different taxonomic groups with different secondary metabolites, and *F. serratus* has a comparatively smooth surface while *C. fragile* has utricles and hairs (see in e.g. Silva, 1957). This is likely to influence the sessile fauna as their settlement is affected by the shape of substrata and chemical cues. For example, convex surfaces are unattractive for bryozoans (Ryland, 1959), and chemical extracts from *F. serratus* can prompt settlement of the polychaete *Spirorbis spirorbis* (Williams, 1964) and the bryozoans *Flustrellidra hispida* and *Alcyonidium polyoum* (Crisp & Williams, 1960). The close association of sessile fauna to the algae they live on may make them slower to adapt to new invading species. Interestingly though, there may be regional differences in this; it has been suggested that the colonisation of *C. fragile* by *Membranipora membranacea* is increasing over time in the Gulf of Maine (Harris & Jones, 2005) but we have not observed this, despite *M. membranacea* being common here.

Because of the strong connection between *F. serratus* and bryozoans, *Dynamena pumilla* and *Spirorbis spirorbis*, a change in the relative abundances of *C. fragile* and *F. serratus* would likely lead to a change in abundance of macrophyte-associated suspension feeders. This could have further effects on the ecosystem because these animals feed on dissolved organic matter and plankton, thus are important contributors to energy transfer from pelagic to benthic food webs (Gili & Coma, 1998). Bryozoans may capture dissolved organic carbon released by the macroalgae they grow on, making it available to higher trophic levels (De Burgh & Fankboner, 1978), and hydroids can regulate zooplankton production by ingesting large numbers, despite their relatively small biomass (Barange & Gili, 1988; Gili & Hughes, 1995).

Nudibranchs, aplacophorans and pycnogonids are among the predators of hydroids (Gili & Hughes, 1995), with some nudibranchs particularly specialised on certain bryozoan species (Chadwick & Thorpe, 1981).

## Conclusion

This study adds to the body of work indicating that *C. fragile* can support a similar richness of associated fauna to native macroalgae and macrophytes (Schmidt & Scheibling, 2006; Jones & Thornber, 2010; Lutz et al., 2010; Drouin et al., 2011), and suggests that an increase in abundance of *C. fragile* would be unlikely to lead to major biodiversity losses in associated fauna. This fits with the general trend of non-native macroalgae tending to have neutral or positive effects on fauna communities (Thomsen et al., 2016). However, the differences observed here indicate that changes in the relative abundance of *C. fragile* and *F. serratus* would lead to changes in community composition. *Fucus*-associated taxa and suspension feeders would likely be negatively affected by an increase in *C. fragile*, while epiphyte-associated taxa might increase in density during the summer, with potential effects on coastal food webs. The influence of epiphytic macroalgae indicates that changes in associated fauna resulting from an increase of a non-native alga, its 'impact', will be modified by its suitability as substratum for native epiphytes. We therefore suggest that the three-factor relationship between fauna, host alga and epiphytic macroalgae must be considered when assessing or predicting the impact of a non-native macroalga on associated fauna.

As the epifaunal community associated with *C. fragile* changes in composition throughout the year (Schmidt & Scheibling, 2006), a limitation of this study is that it only examined the fauna in summer when seasonal epiphytic macroalgae are abundant and *C. fragile* is growing. During the winter, epiphytic algae are at lower abundances and *C. fragile* loses some branches through fragmentation, which may influence its suitability as habitat. Suggested further work includes carrying out similar work in different seasons to investigate this, as well as experimentally manipulating abundances of different epiphytic algal species to untangle the causes of the patterns seen in this study.

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