

# Interspecific competition between *Enteromorpha* (Ulvales: Chlorophyceae) and *Fucus* (Fucales: Phaeophyceae) germlings: effects of nutrient concentration, temperature, and settlement density

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**ABSTRACT:** The increased abundance of ephemeral algae and corresponding decline in perennial fucoids observed in eutrophic (nutrient-rich) waters could be caused by eutrophication-driven shifts in the competitive relationship between the 2 groups as early as the germling stage. During the initial post-settlement period germlings are exposed to large temporal variations in temperature, which may influence their performance and competitive interactions. Effects of temperature, nutrient concentration, and settlement density on the competitive relationship between germlings of *Fucus serratus* L. and *F. evanescens* C. Agardh and of the ephemeral alga *Enteromorpha compressa* (Linnaeus) Greville were examined using factorially designed culture experiments. In monocultures, germling growth of both *Fucus* species and *E. compressa* was generally stimulated by nutrient enrichment (32  $\mu\text{mol}$  nitrate/ammonia and 2  $\mu\text{mol}$  phosphate  $\text{l}^{-1}$  seawater) and high temperature (17°C compared to 7°C), and negatively related to settlement density (10 to 50 germlings  $\text{cm}^{-2}$  for *Fucus*, 30 to 130 germlings  $\text{cm}^{-2}$  for *E. compressa*). In mixed cultures, interspecific competition effects of *E. compressa* on *F. serratus* and *F. evanescens* germlings increased with increasing nutrient and temperature levels. In the nutrient-enriched cultures, interspecific competition from *E. compressa* suppressed the yield of *Fucus* spp. by 80 to 100% at 17°C, with *F. evanescens* being more suppressed than *F. serratus*, whereas the suppressive effects of *E. compressa* on *Fucus* germlings were <60% at 7°C. These results suggest that competition from ephemeral algae at early life stages may be a reason for the decline of fucoids in eutrophic waters and that reproduction at low temperatures, as in species like *F. serratus* and *F. evanescens*, may shield the vulnerable initial germling stages from the severest competition pressure by ephemeral algae.

**KEY WORDS:** *Fucus* spp. · *Enteromorpha compressa* · Germlings · Competition · Nutrients · Temperature

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## INTRODUCTION

The most widely noted floristic changes associated with eutrophication (i.e. nutrient enrichment) of coastal waters are the increased abundance of ephemeral algae and the corresponding decline or disappearance of large perennial algae such as fucoids (Fletcher 1996 and references therein). Interpretations of this phenomenon are largely based on descriptive data, water chemistry, and measurements of selected physiological traits, while the underlying mechanisms have been less explored. The observed changes in vegetation are readily attributed to

eutrophication-driven shifts in competitive relationships between these algae groups, although effects of nutrient enrichment on species interactions in seaweeds have rarely been subjected to experimental testing (Choi 2001, Worm et al. 2001). A common explanation for the observed patterns is that, if they are not directly harmed by eutrophication, perennials such as fucoids are unsuccessful in competition with more nutrient-facilitated ephemeral algae (Duarte 1995, Pedersen & Borum 1996, 1997). Large benthic macroalgae support a wide variety of associated organisms and their decline will inevitably reduce habitat and species diversity.

Along Atlantic European coasts, *Fucus serratus* L. is the dominant seaweed on lower rocky shores. Another low-shore furoid, *F. evanescens* C. Agardh, was introduced to southern Scandinavia in the 1890s (Simmons 1898) and rarely forms associations, with the exception of some eutrophic fjord systems, e.g. the inner Oslofjord, where its abundance has decreased following improved sewage treatment (Bokn et al. 1992). The abundance of *F. evanescens* thus appears to be positively associated with eutrophication, whereas that of most other furoids (including *F. serratus*) appears to be negatively related to eutrophication. Although the exact mechanisms behind the apparent nutrient-induced changes in the abundance of *F. serratus* and *F. evanescens* remain unknown, interspecific differences in autecology and competitive ability of the early post-settlement stages may contribute. *F. serratus* and *F. evanescens* reproduce at lower water temperatures than most other north European furoids (Steen & Rueness 2004), and this has been proposed as a potential mechanism that may protect the most vulnerable initial germling stages from the severest competition pressure by ephemeral algae, whose growth is reduced at low temperatures (Lotze et al. 1999, Lotze & Worm 2002). This hypothesis relies on the assumption that competition effects of ephemeral algae on furoid germlings are positively related to temperature, which has so far not been tested.

Competition arises when shared resources are limited, and is commonly detected by manipulating the density of competitors and examining the effects on growth and survival (Begon et al. 1986). Considering the diversity of designs developed for studying interspecific competition in terrestrial plants and their extensive usage (Schoener 1983, Snaydon 1991), such experimental designs have only occasionally been applied in studies of interspecific competition in seaweeds (Russell & Fielding 1974, Enright 1979, Karez & Chapman 1998, Choi 2001). Although there are some obvious differences, terrestrial plants and seaweeds share several features such as remaining fixed to the substrate and competing for similar resources (e.g. light, nutrients and space), so the same principles of competition should apply and experimental approaches be interchangeable between these groups of organisms. The 2 classical experimental approaches for studying interspecific competition in binary plant mixtures are replacement (or substitutive) and additive designs. In standard replacement designs, the performance of 2 competing species in mixed stands is compared to their performance in pure stands (de Wit 1960). In this design the mixtures are formed by serially replacing a given number of plants of one species by the same number of plants of the second species while the overall density is held constant. One major disadvantage of the replacement design is that the effects of intra- and interspecific competition are confounded, as the density

of one species is reduced while that of the other is simultaneously increased (Connolly 1986, Cousens 1996). In the additive design, the density of one species is held constant while plants of the competitor species are added (Donald 1958). As a consequence, overall plant density is always greater in mixtures than in pure stands, which confounds the effects of overall density with those of proportional density of the components (Firbank & Watkinson 1985, 1990). The shortcomings of the replacement and additive designs can be avoided by using more elaborate response-surface or bivariate factorial designs, where the density of both species is varied independently (Law & Watkinson 1987, Snaydon 1991).

Although it is more or less accepted that physical and biological factors interactively affect marine community dynamics (Carpenter 1990), there have been few experimental studies evaluating the combined effects of multiple environmental factors on species interactions at the germling stage in furoid seaweeds (Choi 2001, Worm et al. 2001). The objective of the present study was to examine interactive effects of nutrient concentration, temperature and settlement density on the competitive relationship between germlings of the furoids *Fucus serratus* and *F. evanescens* and of the ephemeral alga *Enteromorpha compressa* (Linnaeus) Greville in laboratory cultures, using bivariate factorial competition experiments. The manipulated factors were arranged in a fully crossed orthogonal factorial design, which made it possible to estimate their effects and interactions on the early life stages in each of these species and enabled cross-species comparison of responses.

## MATERIALS AND METHODS

**Experimental design.** I collected furoid plants from intertidal rocks near Dröbak (59° 40' N, 10° 38' E) in the Oslofjord, Norway, on 1 March 1999 (*Fucus serratus*) and 28 May 1999 (*F. evanescens*). In the laboratory, receptacles were excised and repeatedly washed in cold tap water to remove epiphytes, then wrapped in moist paper and stored overnight in a refrigerator. The following day, zygote suspensions were obtained using standard techniques for furoids (Quatrano 1980). Zygotes of *Enteromorpha compressa* (collected in Dröbak and maintained as stock culture at the University of Oslo) were obtained by cutting gametophytic thalli into small fragments (5 to 10 mm<sup>2</sup>) and incubating the fragments in polystyrene Petri dishes containing IMR 1/2 medium (Eppley et al. 1967). Dishes were cultivated under a 16:8 h light (~50 µmol photons m<sup>-2</sup> s<sup>-1</sup>): dark cycle at 17°C to allow gamete liberation. To remove gametophytic material, *E. compressa* solutions were passed through a 45 µm filter 2 d after incubation and the filtrate was kept. The initial concentration of

zygotes was estimated using a Palmer-Maloney chamber under a stereomicroscope. By diluting the original zygote suspensions, 2 sub-suspensions varying 4-fold in zygote concentration were made for each species. A fixed volume of each species sub-suspension was seeded into plastic chambers, each with 35 quadratic plexiglass slides (9 cm<sup>2</sup>) on the floor. Mixed cultures of *Fucus* spp. and *E. compressa* were obtained by seeding zygote suspensions of both species into the same chambers.

All chambers were incubated at 12°C to allow settlement. After 1 wk incubation, the number of settlers in 4 subsections of each slide was counted under a stereomicroscope. The standardised Morisita index (Tsuji & Tsuji 1998) was used as a quantitative measure of the distribution of individuals per species per slide. The index ranges from -1 to 1, and separates regular (-1 to -0.5), random (-0.5 to 0.5), and contagious/clumped (0.5 to 1) patterns of distribution. Based on criteria such as closeness to desired density levels and non-contagious distribution of settlers, 16 slides were chosen from each density combination and placed in separate growth chambers (100 cm<sup>3</sup>). Evenly distributed monocultures and mixtures were used to avoid the confounding effects of spatial distribution on competition.

The bivariate factorial arrangement of mono- and mixed species density combinations made it possible to test interactive effects of target species density (2 levels: low and high) and competitor species density (3 levels: zero, low, and high) in both directions simultaneously, with either *Fucus* spp. or *Enteromorpha compressa* as the target species (Fig. 1). The bivariate factorial competition experiment (8 density combinations) was run at 2 temperatures (7 and 17°C, covering most of the temperature range in the species' reproduction seasons) and 2 nutrient concentrations (seawater and nutrient-enriched seawater: see below) using a crossed orthogonal factorial arrangement. This design was used in both experiments (*F. serratus* versus *E.*

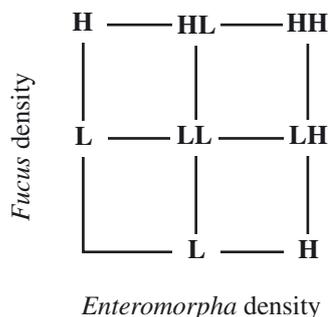


Fig. 1. Matrix showing bivariate factorial designed competition experiments, in which densities (L: low, H: high) of the 2 components (*Fucus* spp. and *Enteromorpha compressa*) are varied independently

*compressa* and *F. evanescens* versus *E. compressa*). I used 4 replicate slides for each treatment combination (32) in both experiments, giving a total of 256 slides.

The high nutrient level was obtained by enriching autoclaved seawater with 32  $\mu\text{M N}$  (nitrate and ammonia added at a ratio of 1:1) and  $\sim 2.0 \mu\text{M P}$  (phosphate), which is similar to nutrient concentrations recorded in eutrophic areas (Kristiansen & Paasche 1982). Culture medium was changed thrice a week (except for the first week during which it was left unchanged), and cultivated under a 16:8 h light:dark cycle, at 50  $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$ . Prior to each renewal of growth medium, the slides were carefully sprayed with seawater to remove necromass and dross. To reduce growth of diatoms and prokaryotes, germanium dioxide (0.2 mg l<sup>-1</sup>, a concentration recommended by Markham & Hagmeier 1982) and penicillin (2 mg l<sup>-1</sup>) were added to the cultures.

**Measurements and response variables.** After 1 mo of cultivation under experimental conditions, all slides were sampled. For each species the number of germlings in 4 subsections (with areas ranging from 0.25 to 1 cm<sup>2</sup>, depending on germling density) per slide was counted, and survivorship estimated as the proportional difference between the numbers of germlings at the end and start of the experiments. Additionally, the sizes of the parenchymatous portion (excluding rhizoids) of 10 haphazardly selected individuals per species per slide were measured. In the case of *Enteromorpha compressa*, the length of germlings was measured using a ruler, or if germlings were <1 cm long, using an eyepiece-measuring device through a stereomicroscope. In the case of *Fucus* spp., surface area projections of germlings (henceforth referred to as germling area) were measured by forcing individuals down onto a plane with a microscope slide and taking their photographs using a video camera through a stereomicroscope (Steen 2003b). The photographs were digitised and germling areas estimated using a software tool (Scion Image, available from Scion Corporation: [www.scioncorp.com](http://www.scioncorp.com)). To keep edge-effects at a minimum and equal for all slides, the positions of individuals and subsections to be sampled were kept as similar as possible, and always >3 mm away from the edge. In order to estimate total yield per species per slide at the end of the experiments, algae material was shaved off the slides, briefly soaked in freshwater to remove salt, dried at 50°C and weighed.

Competition can be measured using indices that compare the yield of plants in the presence and absence of neighbours. In 2-species mixtures, plants may compete both with conspecifics (intraspecific competition) and with conspecifics (interspecific competition), and yield suppression can be due to a multitude of possible levels of intra- and interspecific

competition. By varying the density of both species independently, as in the present experiments, it is possible to separate the effects of intra- and interspecific competition. Because plant yield in the absence of competitors often depends on environmental conditions, it is more meaningful to assess effects of competitive interactions on a relative rather than an absolute basis (Grace 1995). The relative effect of intraspecific competition ( $R_{\text{intra}}$ ) in high-density monocultures was estimated as the difference between the observed yield ( $Y_{\text{mon}}$ ) and the potential 'competition-free' yield ( $Y_{\text{pot}}$ ) that would have been produced by the same number of plants in the absence of competition, relative to  $Y_{\text{pot}}$ .

$$R_{\text{intra}} = (Y_{\text{mon}} - Y_{\text{pot}}) \times Y_{\text{pot}}^{-1} \times 100$$

The potential 'competition-free' yield ( $Y_{\text{pot}}$ ) of a species was obtained by projecting the biomass produced in a culture with density-independent growth and mortality (approximately the low-density monocultures in the present experiments) onto higher densities (Jolliffe et al. 1984). The relative effect of interspecific competition ( $R_{\text{inter}}$ ) was estimated from the difference between the yield of a species in monoculture ( $Y_{\text{mon}}$ ) and mixture ( $Y_{\text{mix}}$ ), relative to  $Y_{\text{mon}}$ , at a given plant density.

$$R_{\text{inter}} = (Y_{\text{mix}} - Y_{\text{mon}}) \times Y_{\text{mon}}^{-1} \times 100$$

These competition indices measures the relative reduction in the yield of a species due to intraspecific ( $R_{\text{intra}}$ ) and interspecific ( $R_{\text{inter}}$ ) competition on a scale from 0 (no competition) to -100 % (competitive exclusion). Positive values indicate density facilitation.

**Statistical analyses.** Data were analysed by univariate 4-way analyses of variance (ANOVA) to test for treatment effects on germling survival and size. The independent variables temperature, nutrient concentration, target-species density, and competitor species density were considered orthogonal and fixed. The magnitude of treatment effects was estimated as the percentage of variance explained using the omega-squared ( $\omega^2$ ) measure as recommended for fixed-factor models (Howell 1992). The direction of treatment effects and interactions was interpreted graphically. Lower-order ANOVAs were performed to test for effects within subgroups of treatments, and Student *t*-tests were used for post hoc comparisons of treatment pairs without applying multiple testing adjustments (e.g. Bonferroni adjustments) of significance levels (Hurlbert & Lombardi 2003, Moran 2003).

Probability levels (p-values) were estimated by resampling (without replacement) and randomly redistributing the data over treatment levels and, for each run, recalculating the test statistic (*F*-ratio in the case of ANOVA, *t*-value in the case of *t*-tests), as described in Crowley (1992). The p-value is given by

the number of times the resampled test statistic proves to be at least as extreme as the original test statistic divided by the total number of resamplings (1000). Compared to conventional parametric procedures, which are based on the assumption that data are normally distributed, resampling techniques are independent of data distribution and are considered to give more reliable statistical estimates, especially in cases of low N where the shape of the underlying distributions cannot be determined (Crowley 1992). To ensure homogeneity of variances, as required by resampling methods involving randomisation of data across treatments, germling area data were logarithmically transformed, and survival ratios and competition indices were angular (arcsine-square-root)-transformed. Confidence intervals were constructed using the bootstrap percentile method (Dixon 2001). By this method, the 2.5 and 97.5 percentiles of the bootstrapped distribution (resampled with replacement within each level of variation) are used as the limits of a 95 % confidence interval, which correspond to the 25th and 975th largest values when 1000 resamplings are run. For the germling size measurements, where there were variation components both within and between slides, multistage resamplings were performed with the lower level (slide) nested at the higher level (treatment). All computations were done in Microsoft Excel for Windows, and the resamplings were run using an Excel macro, available from Resampling Stats ([www.resample.com](http://www.resample.com)).

## RESULTS

### Method and treatment efficacy

The standardised Morisita index ranged between -0.5 and 0.2, indicating that germlings of each species were randomly distributed on all slides in both experiments. As a result of the dilution procedure, the density of settled germlings fell into 2 significantly distinct categories for each species in both experiments (*t*-tests, *p* always < 0.001). Mean ( $\pm 95\%$  confidence limits) settlement densities were:  $10.7 \pm 0.2$  and  $40.8 \pm 0.9$  germlings  $\text{cm}^{-2}$  for *Fucus serratus*,  $11.7 \pm 0.4$  and  $49.3 \pm 1.1$  germlings  $\text{cm}^{-2}$  for *F. evanescens*, and  $31.7 \pm 0.9$  and  $124 \pm 2.9$  germlings  $\text{cm}^{-2}$  for *Enteromorpha compressa*. The reason for using a higher density range for *E. compressa* than for *Fucus* spp. is that *E. compressa* commonly recruits at higher densities than *Fucus* spp., and the densities applied were probably realistic given the natural settlement variations of these algae (Creed et al. 1996, Lotze 1998). There were no significant differences in intraspecific density between levels of subsequent treatments (competitor species density, tem-

perature and nutrient concentration) for any of the species in either experiment (3-way ANOVAs,  $p$  always  $> 0.05$ ). Comparison of the 2 experiments revealed that germling settlement density was higher (9 to 17%) in cultures of *F. evanescens* than *F. serratus*, while the settlement density of *E. compressa* germlings was higher (11 to 14%) in the *F. serratus* experiment than in the *F. evanescens* experiment. Compared to the large differences between density categories within each species (300 to 400%), the differences in settlement density categories between the 2 experiments were assumed to have negligible effects on responses, and were ignored whenever treatment effects were compared between the 2 experiments.

### Survival

The 4-way ANOVA (Table 1) showed significant 3-way interaction effects of main factors ( $T \times N \times C$  and  $T \times I \times C$ ) on germling survival in *Fucus serratus* and *F. evanescens* (Table 1). The strongest 3-way interaction was that of  $T \times N \times C$ , which explained 4 and 8% of the variation in survival of *F. serratus* and *F. evanescens* germlings, respectively. In monocultures, survival rates of germlings of both *Fucus* species were in the range of 60 to 85% (Fig. 2). The presence of *Enteromorpha compressa* had a negative effect on *Fucus* spp. germling survival in the nutrient-enriched cultures at 17°C, but had little effect at the other nutri-

ent and temperature combinations (Fig. 2). The negative effect of *E. compressa* on germling survival in the nutrient-enriched cultures at 17°C was less pronounced in *F. serratus* than in *F. evanescens*. Most of the latter species' germlings were killed by competition from *E. compressa* in the nutrient-enriched mixtures at 17°C (Fig. 2).

To test for differences in responses of *Enteromorpha compressa* germlings between the 2 experiments (*Fucus serratus* versus *E. compressa* and *F. evanescens* versus *E. compressa*) this was incorporated into the ANOVAs as a 5th factor. The responses (survival, length and biomass) of *E. compressa* germlings did not differ significantly between the 2 experiments (5-way ANOVAs,  $p > 0.05$  for all main and interaction terms involving the 5th factor), and the 2 data groups were pooled post hoc (Table 1 and Figs. 2 to 5). The 4-way ANOVA showed significant effect of nutrient enrichment and significant interaction effects of temperature and intraspecific density ( $T \times I$ ) on the survival of *E. compressa* germlings (Table 1). The presence of *Fucus* spp. (C) had no effect on the survival of *E. compressa* for any temperature, nutrient or density combinations (Table 1). Survival of *E. compressa* was generally in the range of 30 to 50%, and was lower than that of *Fucus* spp. germlings in monocultures (Fig. 2). *E. compressa* survival decreased with increasing temperature, nutrient concentration and intraspecific density, and was lowest in the nutrient-enriched high-density cultures at 17°C (Fig. 2).

Table 1. *Fucus serratus* (*F. ser.*), *F. evanescens* (*F. eva.*) and *Enteromorpha compressa* (*E. com.*). Results of 4-way analysis of variance (ANOVA) of treatment effects on survival and size in germlings after 1 mo treatment. Magnitudes of explained variance ( $\omega^2$ ) for significant treatment effects ( $p < 0.05$ ) and residuals are given as percentages. Size was recorded as area for *Fucus* spp., and as length for *E. compressa*. Data for *E. compressa* was pooled from 2 experiments (*F. serratus* vs *E. compressa* and *F. evanescens* vs *E. compressa*). Residual df = 72 (*F. serratus*, *F. evanescens*), 168 (*E. compressa*). Residual MS = 0.008 (*F. serratus* survival), 0.008 (*F. evanescens* survival), 0.003 (*E. compressa* survival), 0.001 (*F. serratus* size), 0.003 (*F. evanescens* size), 0.002 (*E. compressa* size)

Source of variation	df	Survival						Size					
		<i>F. ser.</i>		<i>F. eva.</i>		<i>E. com.</i>		<i>F. ser.</i>		<i>F. eva.</i>		<i>E. com.</i>	
		F	$\omega^2$										
Temperature (T)	1	59.7	(12)	347	(20)	222	(46)	286	(10)	1174	(18)	5024	(60)
Nutrients (N)	1	98.1	(20)	310	(18)	18.7	(4)	113	(4)	781	(12)	1131	(13)
Intraspecific density (I)	1	23.5	(5)	18.7	(1)	37.1	(8)	1068	(37)	452	(7)	1413	(17)
Competitor density (C)	2	26.6	(11)	103	(12)	1.32		300	(21)	522	(16)	0.33	
$T \times N$	1	49.5	(10)	348	(20)	3.05		115	(4)	883	(14)	560	(7)
$T \times I$	1	2.57		1.25		12.0	(2)	9.04	(<1)	3.66		98.8	(1)
$N \times I$	1	2.28		0.57		1.60		5.76	(<1)	18.1	(<1)	0.04	
$T \times C$	2	17.9	(7)	79.7	(9)	0.31		126	(9)	397	(12)	0.42	
$N \times C$	2	21.6	(9)	71.3	(8)	0.65		94.5	(7)	338	(10)	1.22	
$I \times C$	2	1.25		0.74		0.74		2.04		7.35	(<1)	0.33	
$T \times N \times I$	1	0.01		0.84		2.02		6.02	(<1)	16.9	(<1)	0.84	
$T \times N \times C$	2	10.9	(4)	67.0	(8)	0.44		50.4	(3)	261	(8)	0.04	
$T \times I \times C$	2	3.05	(1)	3.70	(<1)	0.94		4.53	(<1)	11.9	(<1)	0.62	
$N \times I \times C$	2	1.98		1.86		0.38		7.55	(<1)	0.04		0.45	
$T \times N \times I \times C$	2	0.21		2.52		0.26		1.20		3.06		1.44	
Residual			(20)		(5)		(40)		(3)		(1)		(2)

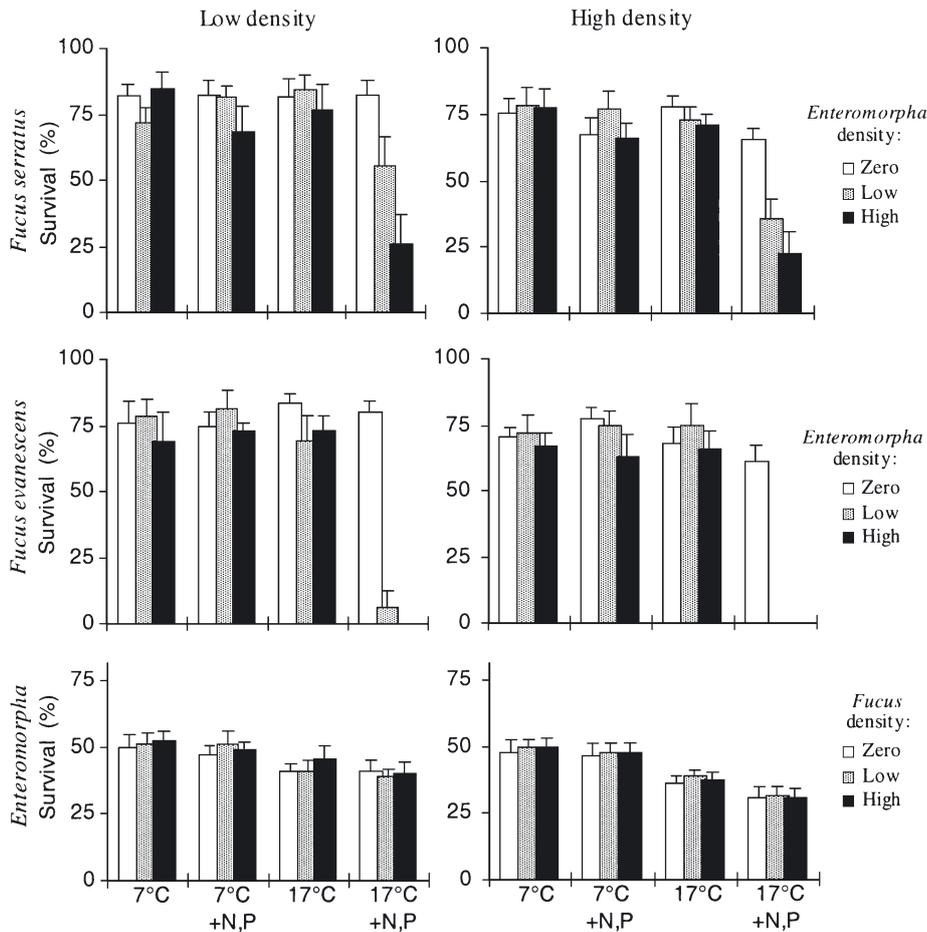


Fig. 2. *Fucus serratus*, *F. evanescens* and *Enteromorpha compressa*. Mean survival of germlings at low and high settlement densities in monocultures and mixtures after 1 mo treatment at 7 and 17°C, in seawater and N + P-enriched seawater. For *E. compressa*, data of 2 experiments was pooled (*F. serratus* vs *E. compressa* and *F. evanescens* vs *E. compressa*). Error bars: upper 95% confidence limits

### Germling size

There were significant 3-way interaction effects of main factors ( $T \times N \times I$ ,  $T \times N \times C$  and  $T \times I \times C$ ) on germling area in both *Fucus* species, and a significant 3-way interaction of  $N \times I \times C$  on germling area in *F. serratus* (Table 1). The strongest 3-way interaction was that of  $T \times N \times C$ , which explained 3 and 8% of the variation in germling area in *F. serratus* and *F. evanescens*, respectively. In monocultures, the germling area of both *Fucus* species generally increased with increasing temperature and nutrient level and decreased with increasing intraspecific density (Fig. 3). The effect of nutrient concentration on *Fucus* spp. germling area increased with increasing settlement density, and in the low-density monocultures nutrient enrichment increased the germling area significantly more in *F. evanescens* than in *F. serratus* at both temperatures tested (Fig. 3, *t*-tests, *p* always < 0.05). *Fucus* spp. germling area decreased with increasing density of *E. compressa*; and this effect increased with increasing temperature and nutrient level, and depended on *Fucus* spp. germling density and species (Fig. 3).

The 4-way ANOVA (Table 1) showed that the effect of temperature on the length of *Enteromorpha compressa* germlings depended on nutrient concentration and intraspecific density (significant  $T \times N$  and  $T \times I$  interactions, explaining 7 and 1% of the variation in length, respectively). The presence of *Fucus* spp. germlings (*C*) did not significantly affect the length of *E. compressa* germlings at any temperature, nutrient or density treatment (Table 1). Increasing temperature had a strong positive effect on the length of *E. compressa* germlings, and this effect was most pronounced in the nutrient-enriched cultures at the low-density level (Fig. 3). Nutrient enrichment increased the mean length of *E. compressa* germlings by ~20% at 7°C, and by ~150% at 17°C.

### Yield and competition indices

The monoculture yields of *Fucus* spp. and *Enteromorpha compressa* generally increased with settlement density (Fig. 4). *E. compressa* monoculture yields were always higher than those of *Fucus* spp. and this

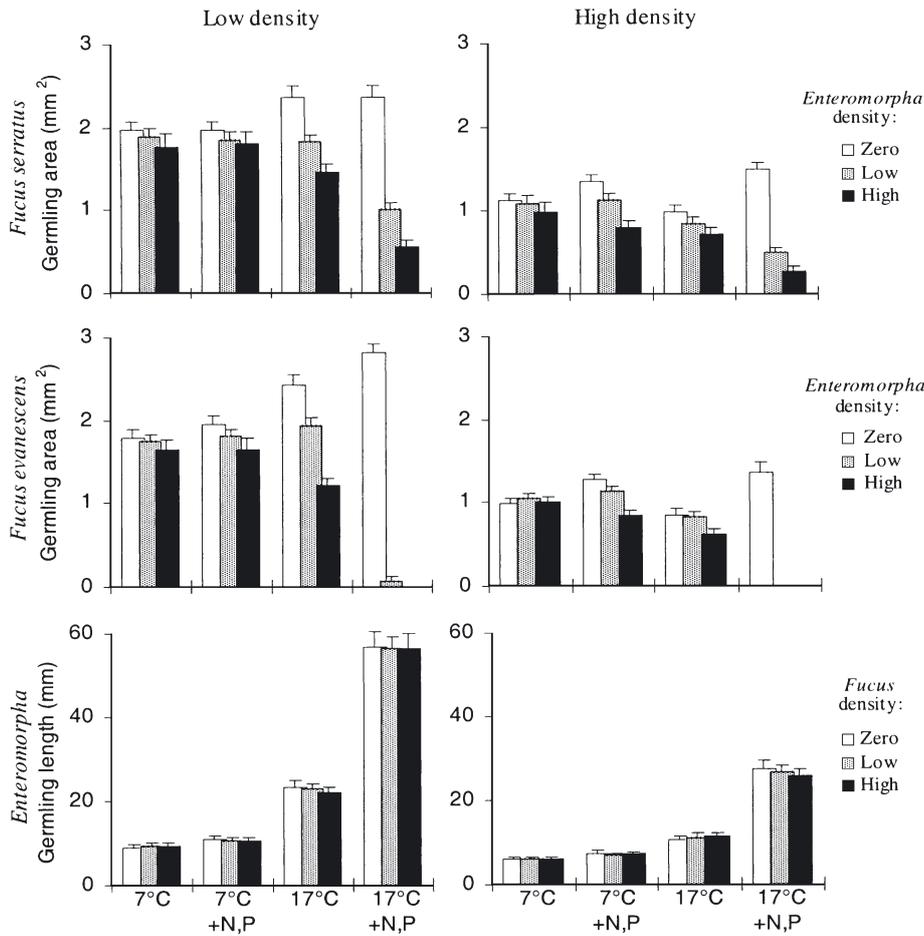


Fig. 3. *Fucus serratus*, *F. evanescens* and *Enteromorpha compressa*. Mean size of germlings at low and high settlement densities, in monocultures and mixtures after 1 mo treatment at 7 and 17°C, in seawater and N + P-enriched seawater. Note different response variables for *Fucus* spp. (germling area) and *E. compressa* (germling length) graphs. Further details as for Fig. 2

difference increased with increasing temperature and nutrient concentration. While the monoculture yield of *Fucus* never differed by more than 100% between any combinations of temperature and nutrient concentration at any settlement density, *E. compressa* yield increased by ~600% when temperature and nutrient levels were both increased. Fig. 4 shows the species monoculture and mixture yields (at the highest competitor density level) plotted against settlement density, along with the projections of 'competition-free' yield. The vertical distance between the 'competition-free' yield projection and observed monoculture yield describes the absolute yield depression due to intraspecific competition, and the vertical distance between a species' monoculture and mixture yields measures the absolute yield depression due to interspecific competition. At the high settlement density, the vertical distance between the 'competition-free' yield projection and a species' mixture yield represents the total absolute yield depression due to competitive interactions, including both intra- and interspecific effects.

Intraspecific competition increased with increasing settlement density (Fig. 4), and the relative effects of

intraspecific competition in the high-density monocultures of both *Fucus* species and *Enteromorpha compressa* increased significantly with increasing temperature and decreasing nutrient concentration (Fig. 5, 2-way ANOVAs, p always < 0.05). In mixed cultures, the relative interspecific competition effects of *E. compressa* on *Fucus* spp. germlings increased significantly with increasing temperature and nutrient levels (Fig. 5, 2-way ANOVAs, p always < 0.05). In the nutrient-enriched mixtures cultivated at 17°C, interspecific competition from *E. compressa* reduced the yield of *Fucus* spp. by 80 to 100%, with the yield of *F. evanescens* being significantly more reduced than that of *F. serratus* at all density combinations (*t*-tests, p always < 0.05). For the other temperature and nutrient combinations, the relative yield reductions of *Fucus* spp. caused by interspecific competition from *E. compressa* were always less than 70%, and competition responses did not differ significantly between the 2 *Fucus* species at 7°C (*t*-tests, p always > 0.05). Neither of the *Fucus* species had any negative effect on the yield of *E. compressa* in mixtures at any temperature, nutrient and density combination (Figs. 4 & 5).

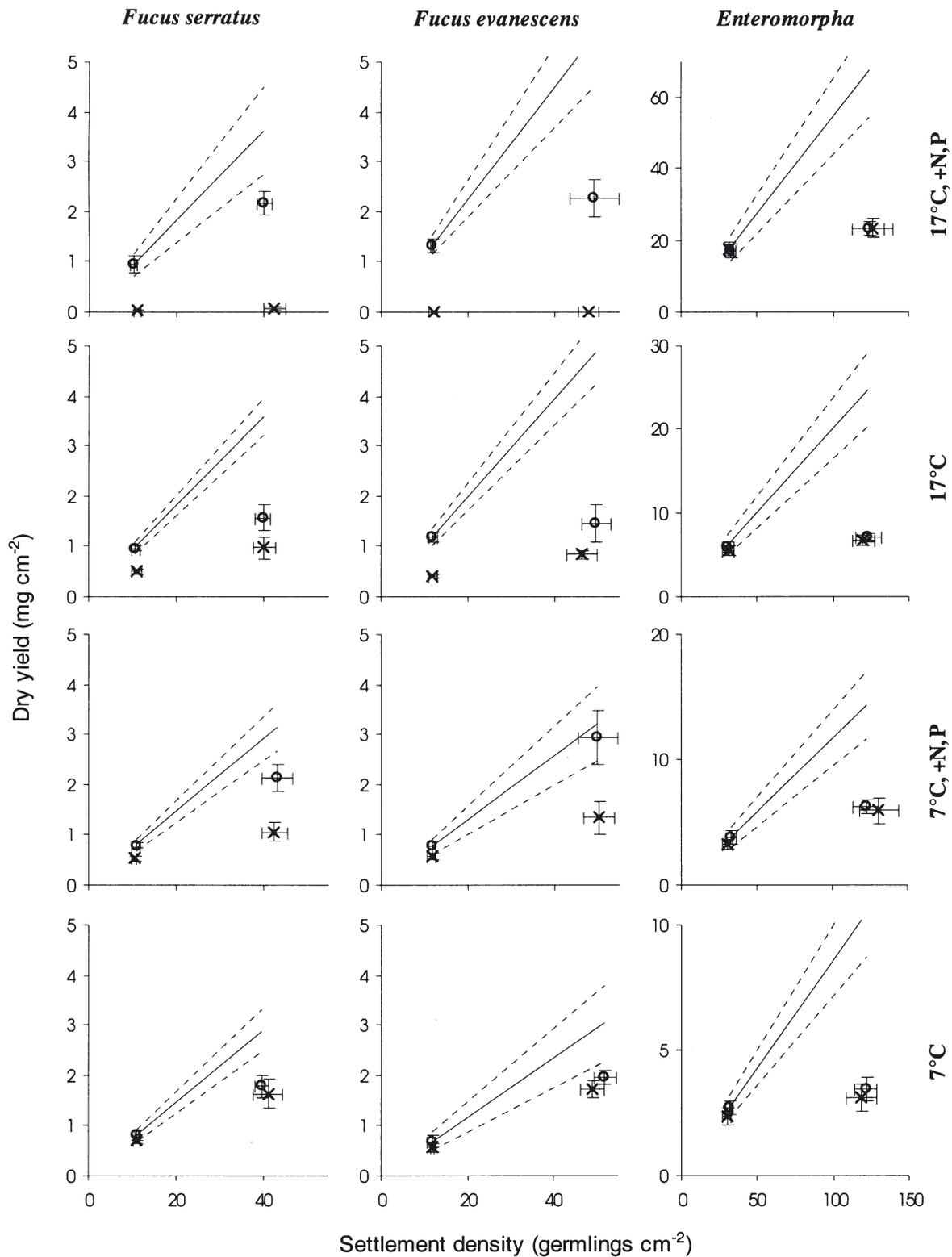


Fig. 4. *Fucus serratus*, *F. evanescens* and *Enteromorpha compressa*. Mean dry yield in monocultures (●) and high competitor density mixtures (×) as a function of settlement density after 1 mo treatment at 7 and 17°C in seawater and N + P-enriched seawater. Linear diagonal projections represent estimated mean potential dry yield that would have been produced in a 'competition-free' environment (continuous lines) and its 95% confidence limits (dashed lines). Note scale differences between graphs. Further details as for Fig. 2

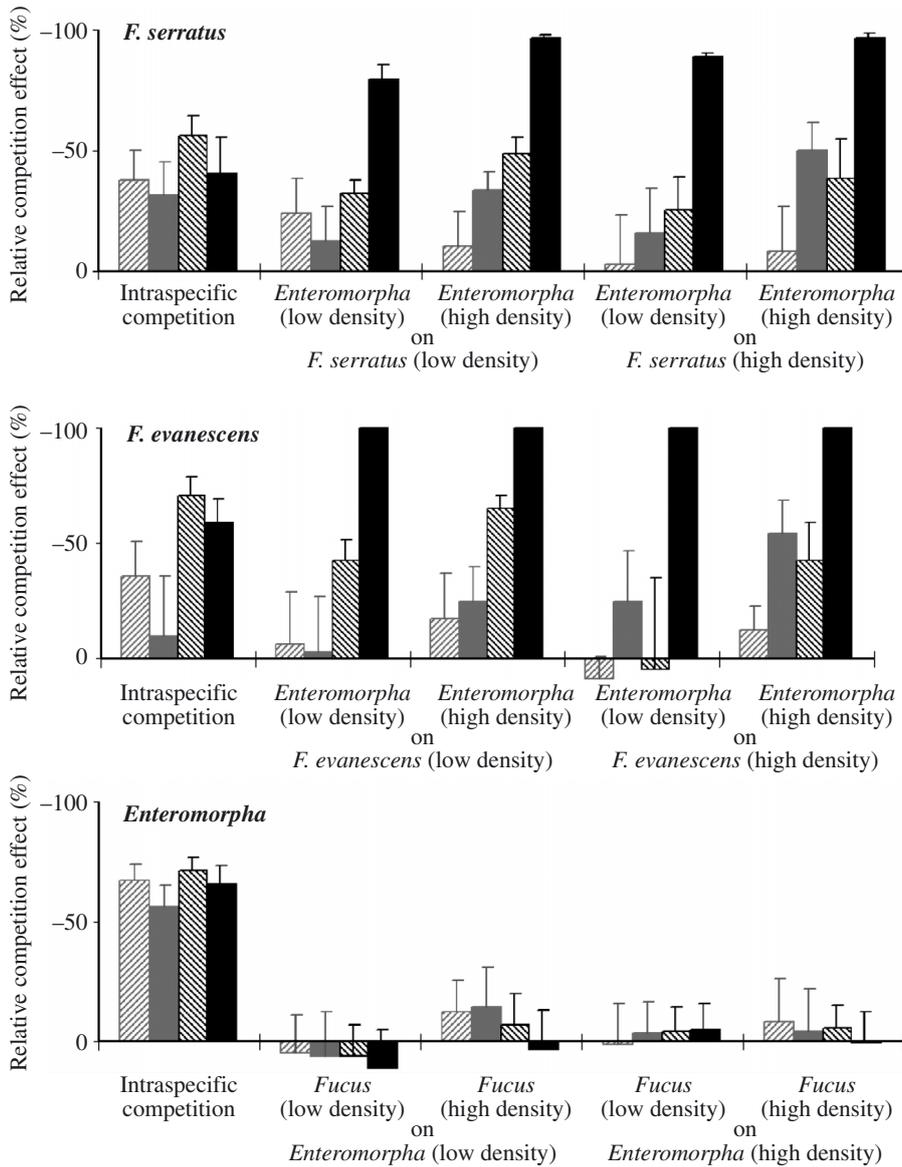


Fig. 5. *Fucus serratus*, *F. evanescens* and *Enteromorpha compressa*. Mean relative intraspecific and interspecific competition effects for various target species and competitor species density-combinations in cultures after 1 mo treatment in seawater (hatched bars) and N + P-enriched seawater (filled bars), at 7°C (grey bars) and 17°C (black bars). Relative competition effects were estimated as percentages on scale of 0 (no competition) to -100% (competitive exclusion), whereas positive values indicate density facilitation. Further details as for Fig. 2

**DISCUSSION**

Nutrient enrichment of shallow coastal waters alters the composition of macroalgae communities so that fast-growing ephemeral algae replace slow-growing macrophytes such as fucoids. The decline of fucoids in eutrophic waters may be caused by direct negative effects of nutrient enrichment, and experiments have shown that survival and attachment ability of germlings in species like *Ascophyllum nodosum* (L.) Le Jolis and *Fucus vesiculosus* L. are negatively related to nutrient concentration (Choi 2001, Bergström et al. 2003). However, nutrient enrichment had no direct negative effect on either of the *Fucus* species tested in the present experiment, and the decline of *F. serratus* in eutrophic areas is probably caused by other factors.

Although fucoid algae could be negatively influenced by secondary factors often associated with eutrophication, such as toxic wastes (Wikström et al. 2000) and increased sedimentation (Chapman & Fletcher 2002, Eriksson et al. 2002, Berger et al. 2003), their decline has commonly been attributed to competitive displacement by ephemeral algae. According to this hypothesis, ephemeral algae should benefit more from nutrient enrichment and/or be less negatively affected by other factors associated with eutrophication than the declining fucoids. The results of the present study support this hypothesis, as growth of *Enteromorpha compressa* germlings was significantly more stimulated by nutrient enrichment than growth of *F. serratus* and *F. evanescens* germlings. These results agree with observations indicating that ephemeral green algae have

higher nutrient requirements for growth than *Fucus* species (Pedersen & Borum 1996, 1997). Such responses do not necessarily correlate with algal morphology, as thin foliaceous forms like *E. compressa*, with a high surface/volume ratio, should be better equipped to derive nutrients from the water when availability is low than the coarser multilayered furoids. However, compared to ephemeral algae, furoid seaweeds have a better nutrient storage capability, with efficient internal nutrient recycling (Duarte 1995, Pedersen & Borum 1996), and form hairs which increase the algae's surface area and nutrient uptake ability when availability is low (Steen 2003a).

Ephemeral algae may negatively affect furoids through direct competitive interactions or by blocking the settlement of germlings (Berger et al. 2003). The early post-settlement period is probably a critical phase, as the minute furoid germlings may easily become overgrown and outcompeted by fast-growing ephemeral algae. In the present experiments, growth and survival in germlings of *Fucus serratus* and *F. evanescens* were negatively affected by interspecific competition from *Enteromorpha compressa*, and the magnitude of this effect depended on nutrient concentration, temperature and settlement density. This is the first time that competitive interactions between *E. compressa* and these 2 *Fucus* species have been experimentally demonstrated, and the results show that nutrient enrichment, mediated by temperature, tilts the competitive relationship in favour of *E. compressa* as early as the germling stage. These results agree with those of Worm et al. (2001), who found that nutrient enrichment increased the negative effect of *Enteromorpha* spp. on *F. vesiculosus* germlings (but not adults) in field experiments in the Baltic Sea.

In the nutrient-enriched monocultures at 17°C, *Enteromorpha compressa* accumulated 10 times more biomass than *Fucus* spp. after 1 mo of treatment (Fig. 4), and interspecific competition from *E. compressa* suppressed *Fucus* spp. germlings by 80 to 100% when the species were mixed together under these conditions (Fig. 5). In the nutrient-enriched monocultures kept at 7°C, *E. compressa* accumulated 2 to 4 times more biomass than *Fucus* spp. and the suppressive effect of *E. compressa* on *Fucus* spp. germlings in mixtures never exceeded 60%. This suggests that reproduction at low water temperatures (7°C) may prove beneficial for furoids in eutrophic areas by shielding the most vulnerable germling stages from the severest competition with ephemerals like *E. compressa*. Germlings of *F. serratus* and *F. evanescens* are produced early in the year, and have a high growth potential at 7°C (~75% of that at 17°C, Fig. 3), and may have reached a resistant stage before competition from ephemeral algae intensifies as the season progresses and the temperature

rises. Despite being rapidly overgrown and competitively suppressed by ephemeral algae such as *E. compressa* during the early stages of substrate colonisation, furoid germlings may persist and resume their growth when competition from the ephemeral algae becomes less intense as water temperature decreases in the autumn. Nevertheless, to succeed in the long-term, the furoid germlings must at least survive the intense competition pressure from ephemeral algae during summer, and the chances of surviving this wave of ephemeral competition will probably depend on the developmental status of the germlings, which again depends on the timing of reproduction. Avoiding the hardest competition from ephemeral algae appears to be particularly important for young *F. evanescens* germlings, as few survived competition from *E. compressa* in the nutrient-enriched mixtures at 17°C, which resembles summer temperatures in Norwegian shallow coastal waters ([www.efan.no/Tempgraph](http://www.efan.no/Tempgraph)).

While the distribution of *Fucus serratus* and several other furoid species appears to be negatively related to eutrophication, observations indicate a positive relationship between eutrophication and the distribution of *F. evanescens* (Grenager 1957, Bokn & Lein 1978, Bokn et al. 1992). If the success of *F. evanescens* in eutrophic waters depended solely on a favourable reproductive season to avoid competition from ephemeral algae, then *F. serratus*, whose reproduction starts earlier in the year and at lower water temperatures than that in *F. evanescens* (Steen & Rueness 2004), should be facilitated too. There are several factors that might induce such interspecific differences in responses to eutrophication. A contributing factor could be that germlings of *F. evanescens* are less negatively affected by competition with ephemeral algae than *F. serratus*. However, the results obtained here did not support this, as the competition responses of the 2 *Fucus* species differed little when cultivated at 7°C, and *F. evanescens* germlings were even more affected than *F. serratus* germlings by interspecific competition from *E. compressa* in the nutrient-enriched mixtures at 17°C. In southern Scandinavia, *F. evanescens* is largely confined to harbour areas where abundance of other furoids (e.g. *Ascophyllum nodosum*, *F. vesiculosus*, *F. serratus*) is low (Wikström et al. 2002), and where *F. evanescens* may have no competition from other furoid species. As demonstrated here and in previous studies (Steen 2003a, Steen & Scrosati 2004), the growth of *F. evanescens* germlings is more stimulated by nutrient enrichment than that of *F. serratus* germlings, and this may increase the competitiveness of *F. evanescens* in eutrophic areas.

Whereas *Enteromorpha compressa* exerted considerable competition pressure on *Fucus* spp. germlings, *Fucus* spp. did not affect the growth and survival of

*E. compressa* germlings at any treatment combination. It may be argued that the use of a higher settlement density range for *E. compressa* in these experiments will give this species a competitive advantage. However, competition was also asymmetrical in the *Fucus* spp. (high-density)–*E. compressa* (low-density) mixtures where *Fucus* spp. germlings (40 to 50 germlings  $\text{cm}^{-2}$ ) initially outnumbered *E. compressa* germlings ( $\sim 30$  germlings  $\text{cm}^{-2}$ ). This asymmetrical competition relationship might be attributable to the different growth forms of these algae. Competitive dominance is generally believed to be positively correlated with plant size, since a larger plant creates a larger depletion zone for resources, especially light (Grime 1977, Schmitt et al. 1986, Keddy et al. 2002, but see Olson & Lubchenco 1990 and Worm & Chapman 1998 for exceptions). After 1 mo of treatment, *E. compressa* germlings were from 4 times (unenriched monocultures at 7°C) to >15 times (nutrient-enriched monocultures at 17°C) longer than those of *Fucus* spp. germlings. Although my experimental design did not allow complete separation between light and nutrient competition, the frequent changes of growth medium probably ensured that competition for nutrients was low. The positive relationship between nutrient concentration and competition effects of *E. compressa* on *Fucus* spp. further indicates that interspecific competition was less intense for nutrients than for light. In the mixed-species cultures, nutrient enrichment, mediated by temperature, appeared merely to modify the interspecific competition for light by facilitating the growth of one species (*E. compressa*) more than the other (*F. serratus* or *F. evanescens*). As a result, shading effects were strongly 1-sided. *E. compressa* shaded *Fucus* spp. germlings increasingly with increasing temperature and nutrient concentration, whereas *Fucus* spp. germlings had minimal shading effects on *E. compressa* regardless of treatment. On the other hand, germlings appeared to compete more intensely for nutrients than light in monocultures, as nutrient enrichment decreased the intensity of intraspecific competition. Because they have similar growth forms, light competition will probably be more symmetrical among conspecifics than among contraspecifics as diverse as *Fucus* spp. and *E. compressa*.

On the shore, *Enteromorpha compressa* and *Fucus* species often settle in dense aggregates (Creed et al. 1996, Lotze 1998, Arrontes 2002), where germlings are likely to be affected by both intra- and interspecific competition. In the present experiments the magnitude of intra- and interspecific competition effects depended on the settlement density of germlings. In treatments where intra- and interspecific competition effects were comparable (high-density monocultures versus low target-species density mixtures), intraspe-

cific competition had a stronger negative effect on *Fucus* spp. germlings than interspecific competition from *E. compressa* at the low nutrient level, whereas interspecific competition had more effect at the high nutrient level at 17°C. For all 3 species examined here, intraspecific competition increased with increasing settlement density, probably because the resources available per individual were more limited at the higher densities. These results agree with previous findings for furoid germlings (Creed et al. 1997, Choi 2001, Steen 2003b, Steen & Scrosati 2004), and suggest that growth can be density-dependent during the early stages of substrate colonisation. As the germling densities used in the present experiments appear to be at the lower range of settlement densities observed for these species in the field (Creed et al. 1996, Lotze 1998), competition effects may be more devastating in field situations than the results obtained in this study suggest.

In monocultures, survival of *Enteromorpha compressa* germlings was always lower than that of *Fucus* spp. germlings, even in the cultures where settlement density of *E. compressa* was lower. This difference could be caused by a higher degree of self-shading and crowding-induced mortality among *E. compressa* germlings, as they accumulated more biomass than *Fucus* spp. at all treatment combinations (Fig. 4). Effects of density and biomass accumulation on the survival of algae germlings will probably depend on growing conditions. On the shore, members of densely populated algae associations may have better protection from physical stress and a higher chance of survival than more solitary individuals (Bertness & Leonard 1997, Bertness et al. 1999, Choi 2001). Species of *Enteromorpha* and *Fucus* have different life-form strategies, and the high germling mortality of the ephemeral algae will probably be compensated for by a high reproductive output (Lotze 1998, Lotze et al. 1999, 2000, 2001).

The ecological relevance of results obtained from short-term laboratory experiments will always be difficult to predict for the larger spatial and temporal scales in the field, and ideally all ecological studies should be performed *in situ*. On the shore, a multitude of environmental variables (e.g. competition, grazing, resource supply, water chemistry, hydrodynamics, climatic conditions, physical disturbances) may affect macroalgae in patterns varying over several spatial and temporal scales (Åberg & Pavia 1997, Menge 1997, Burrows & Hawkins 1998). However, because of the complexity and variability of such systems it is difficult to identify the contributions of single mechanisms and estimate factorial interactions directly on the shore. Even in cases where it is possible to use natural gradients or manipulate factors on the shore, their contribu-

tion may be obscured by the presence of unidentifiable and uncontrollable covariates, that may vary systematically in parallel with the investigated factors and mediate their effects. Forces operating in the microclimate inhabited by newly settled germlings will probably be particularly hard to identify and manipulate under inadequately controlled conditions. Moreover, some of the factors examined here (i.e. temperature and nutrient concentration) are extremely difficult to manipulate and control in the field without introducing other confounding elements. Laboratory experiments provide greater opportunities for both controlling and manipulating these factors independently and for estimating their effects on target organisms more precisely. The results obtained in the present study provide new information of the potential mechanisms behind the displacement of furoids by ephemeral algae in eutrophic waters, and experimentally demonstrate that competition between these algae can be interactively modified by nutrient concentration, temperature and settlement density as early as the germling stage. Effects on germling performance and interactions will ultimately have consequences at higher levels of organisation in marine macroalgae communities.

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