ORIGINAL ARTICLE

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Competitive ranks of three *Fucus* spp. (Phaeophyta) in laboratory experiments – testing of Keddy's competitive hierarchy model

Abstract Keddy's competitive hierarchy model describes species distribution patterns along gradients under equilibrium conditions and can potentially serve as an explanation for zonation patterns of intertidal seaweeds on rocky shores. One of the assumptions of the model is a competitive hierarchy with the top competitor occupying the benign end of the gradient. Another assumption is the consistency of competitive ranks of species in all environmental conditions included in the shared parts of species' fundamental niches. In laboratory replacement series experiments, the competitive ranks of pairs of *Fucus* species that occupy adjacent zones in the field were analysed and compared to ranks found in previous field experiments. Unattached thalli of *Fucus serratus* versus *F. vesiculosus* or *F. vesiculosus* versus *F. spiralis*, respectively, were held in aerated beakers to establish the competitive ranking of the three congeners. Each replacement series was conducted at three total densities. *F. vesiculosus* was clearly competitively dominant over *F. serratus*. In competition with *F. spiralis*, *F. vesiculosus* was only dominant at its lowest absolute input frequencies, but at higher frequencies dominance was reversed. At high densities, the total ranking was *F. spiralis* > *F. vesiculosus* > *F. serratus*, which is the opposite order to that which would be expected from Keddy's model. Although all three species thrived well under the laboratory conditions, the results did not reflect in situ competitive dominances, which may be an effect of nutrient competition in the laboratory. Keddy's assumption that competitive ranks are consistent over the whole range of fundamental niches cannot be supported for *Fucus* spp.

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Introduction

Zonation patterns as the formation of distinct bands of sessile organisms in the intertidal zone of rocky shores have fascinated scientists for many decades, leading to theories that first emphasized causal abiotic factors mediated by periodic emergence in connection with physiological competence of the organisms (e.g. Colman 1933; Doty 1946; Lewis 1961, 1964; Stephenson and Stephenson 1972). After Connell's (1961a, 1961b) pioneering work, it became evident that biotic factors such as competition and predation may be equally important in developing zonation patterns (e.g. Dayton 1971, 1975; Chapman 1973, 1974; Paine 1974; Lubchenco 1980; Underwood 1991). Although factors that influenced the upper (Schonbeck and Norton 1978; Maberly and Madsen 1990; Norton 1991) or lower (Suchanek 1978; Schonbeck and Norton 1980) limit of species were surveyed, no integrating model had been developed, until Chapman (1995) suggested that the 'competitive hierarchy model' of Keddy (1989a, 1990) could serve as an explanation for the observed patterns. One prediction of Keddy's model is that all species along a resource or environmental gradient are arranged with the best competitor occupying the most benign end of the gradient, the second best competitor occupying the zone next to the top-dominant species and less competitively dominant species following towards the unfavourable end of the gradient. In contrast, the fundamental niche of the top competitor is restricted to the conditions at the benign end, while fundamental niches of competitively inferior species include those of the more dominant ones. Keddy's model assumes that competitive dominances are consistent under various environmental conditions as long as such conditions are

included in the fundamental niches of the respective species. If it is assumed that the lower intertidal or upper subtidal zone represents the benign end of the intertidal gradient of littoral species that evolved from fully marine ancestors, Keddy's model could explain why competition precluded the seaward expansion of species' zones in the intertidal, while physiological constraints seemed to be controlling the landward expansion (e.g. Connell 1961a, 1961b; Schonbeck and Norton 1978, 1980; Lubchenco 1980; Chapman 1990). However, Keddy's model integrates only equilibrium factors, while other factors such as disturbance and predation have also been shown to be important determinants of species distribution along the shore (Underwood 1991).

To test if Keddy's model explains the observed zonation patterns of species of the brown algal genus *Fucus* on rocky shores of the North Sea, the competitive ranks and fundamental niche breadths had to be evaluated. This was done in field experiments by Karez and Chapman (1998) with the three zone-forming species of *Fucus* that occur in the intertidal of the island of Helgoland (North Sea) in the landward order *F. serratus*, *F. vesiculosus*, *F. spiralis*. Assuming that the lower intertidal is the benign end of the shore gradient, this should (according to Keddy's model) also be the order of their competitive dominances. However, replacement series competition experiments by Karez and Chapman (1998) revealed a competitive hierarchy of *F. vesiculosus* > *F. serratus* > *F. spiralis*. It is the aim of the present paper to evaluate if competitive ranks obtained in controlled laboratory experiments are consistent with the findings of the former field study.

Methods

Replacement series (de Wit 1960), using germlings of ca. 1 cm, were set up with pairs of *Fucus* species that occupy adjacent zones in the field, i.e. *F. serratus* versus *F. vesiculosus* and *F. vesiculosus* versus *F. spiralis*. These were established in 0:100, 25:75, 50:50, 75:25 and 100:0 mixture proportions, each at three total densities (low, medium, high) with each of the two species combinations (Fig. 1). The same monocultures of *F. vesiculosus* were used for replacement series with *F. serratus* and with *F. spiralis*. Densities were chosen to be comparable with those used in Karez and Chapman (1998), i.e. 10,000 (low), 50,000 (medium) or 100,000 (high) shoots m^{-2}, corresponding to 130, 650 or 1300 shoots per cultivation beaker of 13 cm diameter. Each experimental unit (beaker) was replicated 4-fold.

Germlings of all three *Fucus* species were cultivated in the laboratory from zygotes that were sown on ceramic tiles [for details see Karez and Chapman (1998)]. When they had grown to an average 1 cm length, they were detached gently from the tiles and distributed individually into the various mixtures and monocultures of the replacement series. In each experimental unit, the lengths of 25 randomly chosen thalli per species were measured to obtain an estimate of the initial algal biomass using a length/dry weight regression based on a separate set of measurements of 50 juveniles per *Fucus* species. Maximum starting biomass ranged from 18 mg dry weight (low density monoculture of *F. spiralis*) to 730 mg dry weight (high density monoculture of *F. serratus*). Mixtures and monocultures were kept in 3 l beakers covered with a glass lid and containing 2 l of sterile seawater. The beakers were aerated with sterile filtered air that agitated small thalli and prevented formation of clumps due to occasional contamination with bacteria. The experiment was performed in a temperature constant room at 13°C and at a photoperiod of 16 h and a light intensity of 60 µmol

Fig. 1 Design of replacement series conducted with *Fucus serratus* versus *F. vesiculosus* (*top*) and *F. vesiculosus* versus *F. spiralis* (*bottom*) in aerated beakers at three total densities (low = 130, medium = 650, high = 1300 thalli per beaker). Each treatment was replicated 4-fold. The same monocultures of *F. vesiculosus* were used to complete replacement series with *F. serratus* and with *F. spiralis*
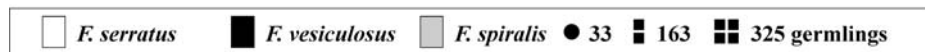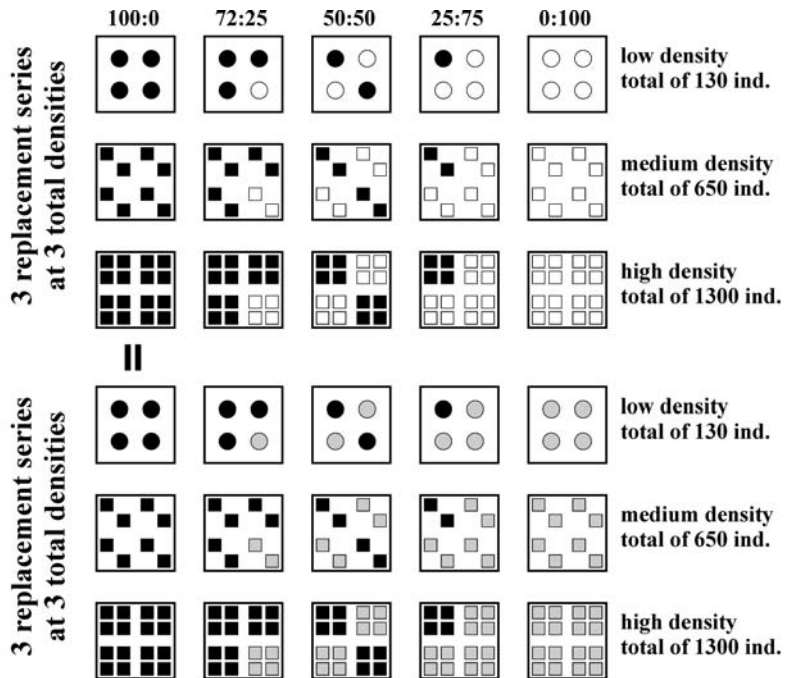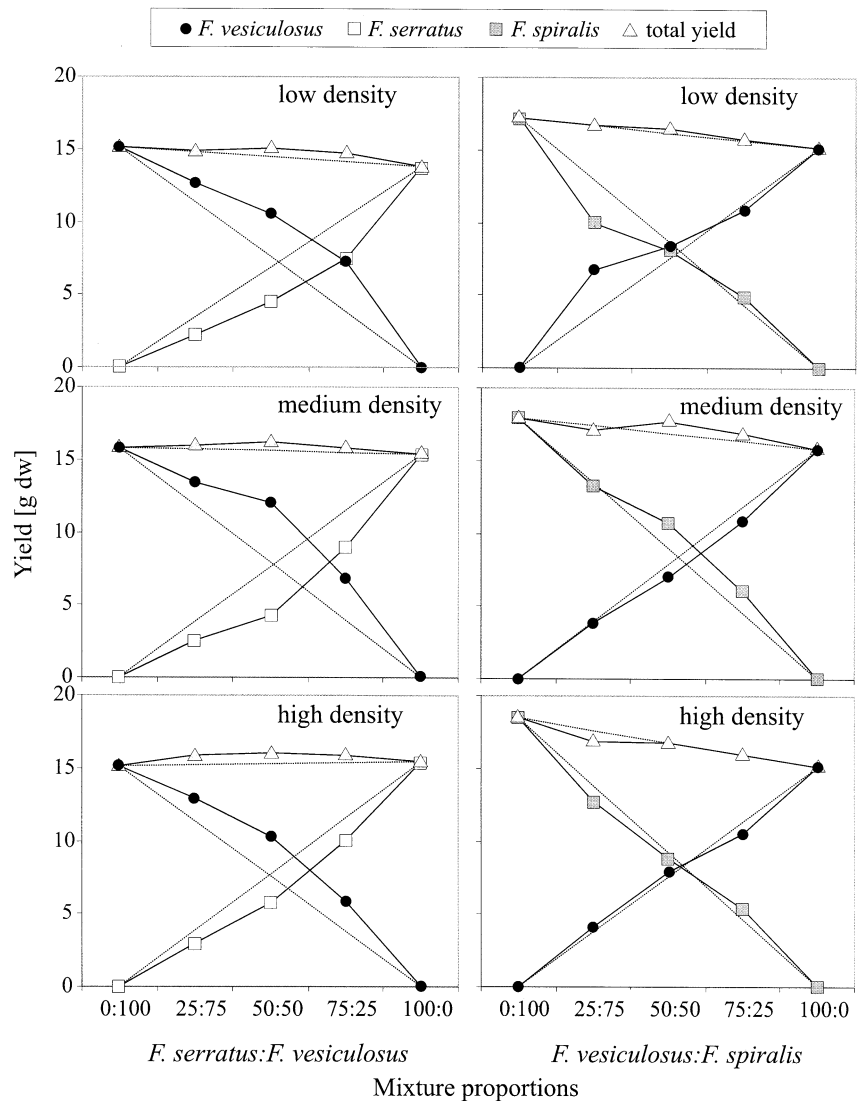
Fig. 2 Replacement series graphs from competition experiments with *F. serratus* versus *F. vesiculosus* (*left*) and *F. vesiculosus* versus *F. spiralis* (*right*) in aerated beakers at three total densities (low = 130, medium = 650, high = 1300 plants per beaker). Mean values of four replicates. *Stippled lines* indicate expected yield

● *F. vesiculosus*   □ *F. serratus*   ▨ *F. spiralis*   △ total yield

photons m^{-2} s^{-1}. Beakers were arranged randomly after every exchange of culture medium. The culture medium was exchanged every 10 days in the first 4 weeks of the experiment. After thalli on average had grown to >2 cm length, medium was exchanged every 4 days. By that time it was possible to pour the contents of a beaker through a sieve (1 mm mesh) and to rinse algae with running tap water without losing them. The beaker was cleaned of bacteria and exudates with a paper tissue soaked with ethanol and rinsed thoroughly with tap water. During the first 4 weeks, the culture medium was half-strength Provasoli enriched seawater (Starr and Zeikus 1987), afterwards full strength and during the last 3 weeks double strength enrichment was used. The experiment was performed for 116 days, and was terminated when a few thalli showed necrosis. In total ca. 0.03 mol nitrogen (as nitrate) were added to each beaker during the experiment. At harvesting, mixtures were separated by species. Final biomass was determined as collective dry weight of individuals of each species from each experimental unit after 3 days at 60°C.

At harvest, thalli were counted in several of the low density beakers, where individual thalli had grown to a larger size than in higher density beakers. At higher densities, the majority of thalli remained small. Although it was feasible to separate species for almost all thalli, at the higher densities it was not possible to distinguish thalli that remained small from broken off adventive shoots of several larger thalli. In a small number of cases, a few plants escaped during the maintenance procedure of the cultures. So, in the end, there were still about 1300 genets in the high density beakers, and determination of individual weight [as in Karez and Chapman (1998)] was not feasible.

Data were analysed graphically with replacement series graphs and input-output ratio diagrams, and by calculating relative crowding coefficients (Khan et al. 1975). In replacement series graphs, the yield of each species is compared to the 'expected yield', i.e. the yield that could be expected with no interaction, when a linear increase with mixture proportion is assumed (cf. Willey and Rao 1980; Jolliffe et al. 1984; stippled lines in replacement series graphs of Fig. 2). If one species produces a higher yield in comparison to the expected yield in all mixtures, while the other species remains below its expected yield, the first species is competitively dominant to the second (Khan et al. 1975; Lobban and Harrison 1994). In input:output graphs, the output ratio of both species is plotted against their input ratio for each mixture and compared to the bisecting line. If a certain input ratio leads to a lower output ratio, the species in the ratio's denominator performs better relative to that in the numerator, and it can be predicted that the latter species will be outcompeted. Relative crowding coefficients (K_{ij}) are calculated as the ratio of individual crowding coefficients (K_i/K_j) of two species i and j with $K_i = (y_{i,\text{mix}} / \text{init}_{i,\text{mix}}) /$

$(y_{i,mon} / init_{i,mon})$ where y is the final yield and init the initial mass in mixed (mix) or monocultures (mon). A $K_{ij} > 1$ means that species i succeeds relative to species j, if $K_{ij} < 1$ then species j succeeds, while $K_{ij} = 1$ indicates a neutral outcome (Khan et al. 1975).

Only replacement series of species pairs that occupied neighbouring zones in the intertidal were employed. To estimate the whole ranking of competitive dominances, i.e. also *F. serratus* versus *F. spiralis*, and to compare inter- with intraspecific effects, selected treatments from each series were analysed with t-tests. The effect of conspecific individuals (in monocultures) on target individuals was compared to that of congeneric individuals (in mixed cultures). Firstly, for each total density and each species from each species combination, 25% of individuals from a monoculture were declared as target individuals (by dividing the total yield by 4). This yield was compared to the yield of the same species in a 1:3 mixture with a congener, i.e. under interspecific versus intraspecific competition. In a second set of analyses, half of the individuals were declared as target individuals (by dividing total yield by 2) and their yield was compared to the yield of the same number and species in a 2:2 mixture with a congener. In total, 24 *t*-tests were performed. The probability levels were not Bonferroni-adjusted, because the aim was to show the general pattern by which the yield of a certain target species is, e.g., elevated by a certain congener and suppressed by another. This analysis provides an indication of the variation in the data that is not obtained by the classical methods alone.

Results

During the course of the experiment, size distributions of plants became skewed to the right, i.e. with few large and many small plants. The largest thalli (up to 12–16 cm length) were not agitated by the air bubbles and accumulated at the bottom of the beakers. At harvest, a few large plants filled most of the volume of the beakers, while the smaller plants accumulated beneath them at the bottom of the beakers. In high density treatments, many plants only achieved lengths of approximately 2 cm.

Despite the small size of many thalli, identification was possible in most cases with reference to thalli in monoculture. Each of the three *Fucus* species developed distinctive morphologies that were used for identification. *F. serratus*, in comparison to *F. vesiculosus*, was serrated (if bigger), had a broader thallus with distinct dark spots and only 1–2 (if any) new shoots from the base, while the latter species was narrower, lacked the distinct black spots and could develop several new shoots. *F. spiralis*, in comparison to *F. vesiculosus*, was broader, had a slightly undulated rim, was distally more lobed and more greenish translucent. Only in a few cases of very small individuals was identification impossible. However, these normally only consisted of 1–2 cm midrib and contributed negligibly to total yield.

At all three total densities, *F. vesiculosus*, when mixed with *F. serratus*, yielded more dry weight than expected (Fig. 2, left column), while *F. serratus* yielded less than expected. The pattern is consistent over all three total densities. From this it can be concluded that *F. vesiculosus* is competitively superior to *F. serratus*. In mixtures of *F. vesiculosus* with *F. spiralis* (Fig. 2, right column), the outcome was more variable and revealed an input-frequency dependent pattern. At high input frequencies of
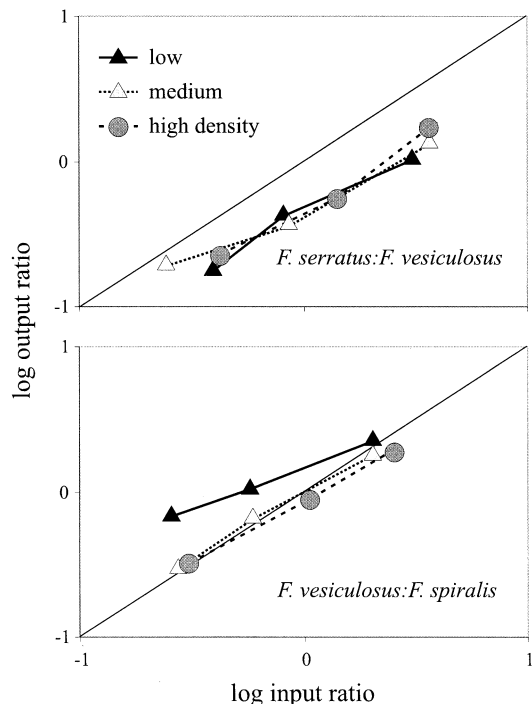

Fig. 3 Ratio diagrams from replacement series experiments with *F. serratus* versus *F. vesiculosus* (*top*) and *F. vesiculosus* versus *F. spiralis* (*bottom*) in aerated beakers at three total densities (low = 130, medium = 650, high = 1300 plants per beaker). The logarithm of the output ratio of dry weight is plotted against the log input ratio of dry weight. Mean values of four replicates. The line with unit slope indicates stable conditions where output ratios equal input ratios

F. vesiculosus, this species yielded less than expected, while *F. spiralis* yielded more. Though not very pronounced, this pattern was consistent at the three experimental densities. Conversely, at low input frequencies of *F. vesiculosus* the outcome was dependent on the total density. At low density, *F. vesiculosus* accumulated more and *F. spiralis* less biomass than expected. At medium and high density, neither species significantly deviated from the expected yield. In all six replacement series, the total yield deviated only slightly from the expected yield. For *F. serratus* versus *F. vesiculosus* mixtures, however, total yield is slightly hump-shaped, indicating weak mutual stimulation. It seems clear that the environment (beaker) of this laboratory experiment had a limiting maximum capacity for algal biomass that was about 15 g/beaker for *F. serratus*-*F. vesiculosus* mixtures and about 17 g/beaker for *F. vesiculosus*-*F. spiralis* mixtures. In all mixtures, a gain in yield of one species must have been compensated for by a loss of yield in the other species. Therefore, the curves for both species in mixtures are mirror images to each other.

In input:output diagrams (Fig. 3), all *F. serratus:F. vesiculosus* ratios lay below and parallel to the line with unit slope. This pattern is indicative of unstable mixtures, and predicts that *F. serratus* would be outcompeted. For mixtures of *F. vesiculosus* and *F. spiralis*, again a

Fig. 4 Comparison of intra-versus interspecific effects in selected treatments from 2×3 replacement series experiments with *Fucus* spp. at three total densities. Generally the yield (g dry weight) of a certain portion of individuals from a monoculture is compared to the yield of the same number of individuals in mixed cultures. In the *left column*, these individuals represent 50% of total density in mixtures, in the *right column* 25%. For each data set, the *first row* represents effects on *F. serratus*, and the *second row* effects on *F. vesiculosus* from the *F. serratus – F. vesiculosus* replacement series, while the *third row* represents the effects on *F. vesiculosus*, and the *last row* effects on *F. spiralis* from the *F. vesiculosus – F. spiralis* replacement series. Left of each symbolized treatment, the mean yield (±sd) of the encircled target individuals is given. Means are normally based on four replicates and compared with a *t*-test (t_6 and *P* value), in some cases (t_5) one replicate was missing in one of the compared means. Percentages indicate the reduction or elevation of yield of target plants in mixed culture in relation to their yield in monoculture. Refer to Fig. 1 and text for further explanation
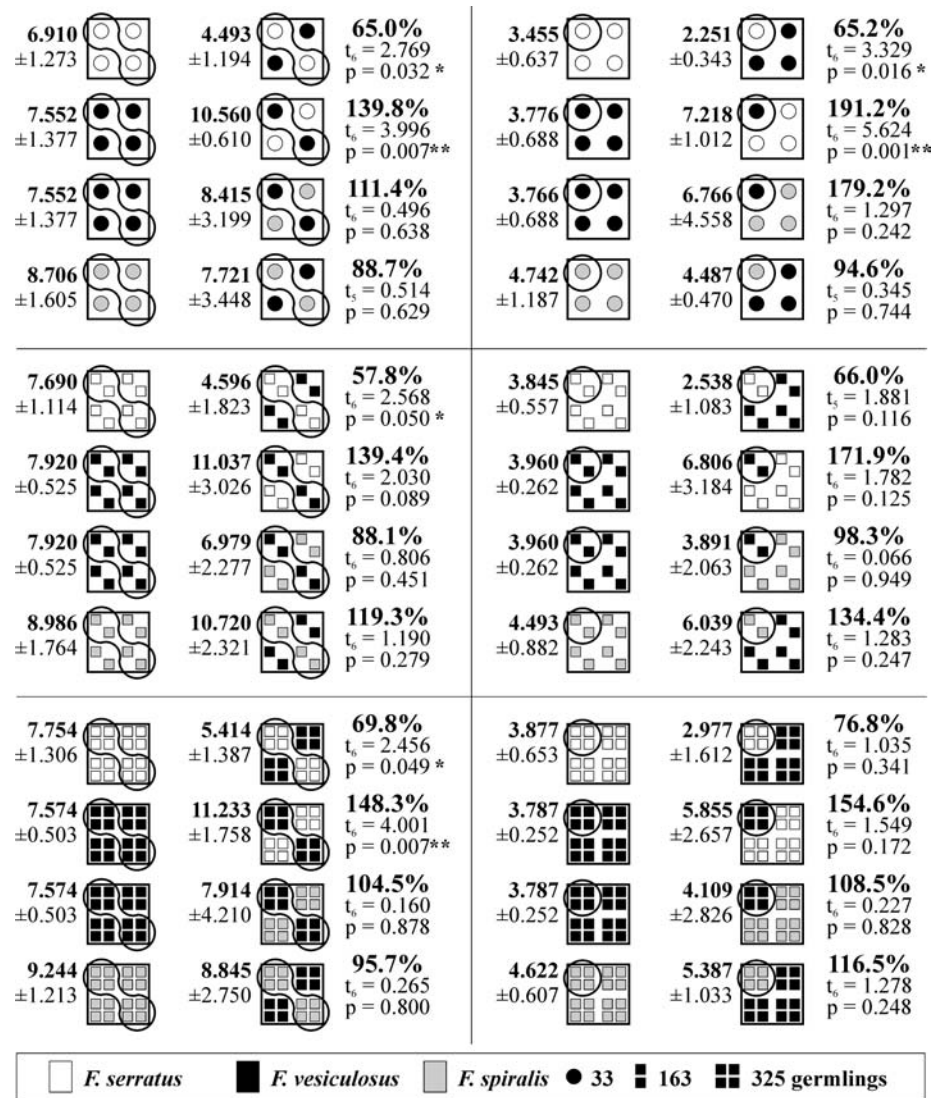
competitive dominance of *F. vesiculosus* could be seen only at the low density treatments in low input frequencies of *F. vesiculosus*. For both higher density series, input ratio was the same as output. These results indicate that competition in mixtures of *F. vesiculosus* and *F. spiralis* would stabilize at high frequencies of *F. vesiculosus*. At low absolute frequencies, *F. vesiculosus* would outcompete *F. spiralis*.

For the calculation of crowding coefficients, the number of surviving plants is needed. Here, I used the initial number of plants that remained in the beakers as genets, although they may have developed several ramets (shoots). For *F. serratus-F. vesiculosus* mixtures, all relative crowding coefficients (K_{sv}) were < 1 (Table 1), which is indicative of competitive dominance of *F. vesiculosus* over *F. serratus*. For *F. vesiculosus-F. spiralis* mixtures, relative crowding coefficients (K_{vp}) are > 1 only at the two lowest input ratios and low density of *F. vesiculosus*: in all other treatments the crowding coefficients were ≤ 1. This indicated a weak dominance

of *F. spiralis* for all but the mixtures with lowest *F. vesiculosus* frequency, where *F. vesiculosus* dominated.

The analysis of selected treatments from each replacement series with t-tests also showed a clear dominance of *F. vesiculosus* over *F. serratus* (Fig. 4). In every case, substituting conspecific individuals of *F. serratus* with *F. vesiculosus* (first row of each set in Fig. 4) resulted in a decrease of the mean yield to 58–77%, while in every case the yield of *F. vesiculosus* was elevated by 40–90% in the presence of *F. serratus* (second row of each set in Fig. 4). Significant differences between intra- and interspecific effects on yield of target individuals were only found for selected treatments from the *F. vesiculosus-F. serratus* replacement series. For *F. vesiculosus-F. spiralis*, the percentages of yield shifts ranged from 1% to 79%. There was not the same pattern over all densities. At low density, *F. spiralis* was more suppressed by *F. vesiculosus* than vice versa, at medium density this dominance pattern was reversed, and at highest density both cases occurred. In every data set, the yield of *F. vesiculosus* is more

Table 1 Relative crowding coefficients (*K*) from replacement series competition experiments with *Fucus serratus* vs *F. vesiculosus* or with *F. vesiculosus* vs *F. spiralis*. For each species combination, three replacement series were employed, i.e. at low (130 plants per beaker), medium (650) and high (1300) density. Mean values of 4 replicates. Values >1 for e.g. K_{sv} (*F. serratus* on *F. vesiculosus*) indicate competitive dominance of *F. serratus*, while $K_{sv} < 1$ indicates dominance of *F. vesiculosus* and $K = 1$ means no competitive interaction (Khan et al.1975). K_{vp} is the coefficient for effects of *F. vesiculosus* on *F. spiralis*

	Density	Mixture proportions		
		25:75	50:50	75:25
F. serratus:F. vesiculosus				
K_{sv}	Low	0.49	0.56	0.36
	Medium	0.95	0.50	0.43
	High	0.60	0.43	0.52
F. vesiculosus:F. spiralis				
K_{vp}	Low	2.08	1.42	0.86
	Medium	0.92	0.94	0.76
	High	1.00	0.80	0.74

suppressed by *F. spiralis* than by *F. serratus*. In every case, *F. vesiculosus* suppressed the yield of *F. serratus* to a lower relative amount than it suppressed *F. spiralis*. It can therefore cautiously be concluded that *F. spiralis* would be competitively superior to *F. serratus* in a replacement series with these species.

In summary, analyses with both classical methods (replacement series graphs, input:output diagrams, relative crowding coefficients) and *t*-tests unequivocally showed a competitive dominance of *F. vesiculosus* over *F. serratus*. In competition with *F. spiralis*, *F. vesiculosus* is the superior competitor only at low absolute frequencies of *F. vesiculosus*. At higher total densities and/or higher proportion of *F. vesiculosus*, competitive ability is balanced or *F. spiralis* is the competitive dominant species. Monocultures of *F. spiralis* developed the highest yields in terms of dry weight.

Discussion

In an experiment with the same replacement series design as the present study, but using attached *Fucus* spp. in situ in the *F. serratus* zone of the Helgoland rocky intertidal zone, Karez and Chapman (1998) found a clear competitive ranking of *F. vesiculosus* > *F. serratus* > *F. spiralis*. In the present study, the competitive ranking was *F. spiralis* ≥ *F. vesiculosus* > *F. serratus*. The competitive ranking of *F. spiralis* versus *F. serratus* was not tested experimentally, because the species normally do not live in adjacent zones in the field [but see Munda and Kremer (1997)]. The dominance of *F. spiralis* over *F. serratus* can be inferred from the stronger reduction of yield when *F. vesiculosus* competed with *F. spiralis* than with *F. serratus* (cf. Fig. 4). These results are surprising, especially since *F. spiralis* endures long periods of emergence in its natural habitat in the intertidal [e.g. Dring and

Brown (1982)], while in the laboratory it showed the highest biomass of the three *Fucus* species under conditions of permanent submergence. In the field, the other congeners generally grow to a higher maximum length, which is often seen as a trait for competitive dominance in plants [e.g. Gaudet and Keddy (1988); Keddy (1989b)]. A possible explanation may be that the experimental *Fucus* thalli were nutrient-limited in the laboratory experiment. The total supply of nitrogen (as nitrate) during 116 days was 0.03 mol/beaker. The tissue nitrogen content (% of dry weight) of *F. vesiculosus* was found to be up to 3.5% (Pedersen and Borum 1997) or even up to 4–6% (Schramm et al. 1988), that of *F. spiralis* up to 2.04% or 2.85% with addition of nitrate or ammonium, respectively (Topinka and Robbins 1976), and that of *F. serratus* 2.8% (R. Karez, unpublished data, mean of eight individuals sampled in July on Helgoland). Calculating the nitrogen demand of 15 g *F. serratus* in monoculture beakers, with an assumed 2.5% tissue nitrogen content, results in a value of 0.029 mol, which is similar to the added amount but assumes that all nitrogen supplied was used to form the final biomass. Losses of nitrogen, however, certainly occurred as a notable amount of debris and bacteria accumulated in the beakers between medium changes. In addition, the formation of hyaline hairs was frequently observed, however not permanently. Hyaline hairs are an indication of the adaptation of *Fucus* spp. to nutrient-limitation by increasing surface area for uptake (Hurd et al. 1993). In the light of nutrient competition, the ranking of competitive abilities is not surprising. It has been found that the rate of nutrient uptake is correlated with the time fucoid species are truncated from the nutrient supply during emergence (Hurd and Dring 1990, 1991) and that *F. spiralis* has a much higher maximum nitrogen uptake rate and a lower k_s compared to *F. vesiculosus* (Wallentinus 1984). Thus, a dominance ranking *F. spiralis* > *F. vesiculosus* > *F. serratus*, as found in the laboratory experiments of the present study, would be in agreement with the expected pattern under nutrient competition. It seems that under space (light) competition in the field, competitive dominances between *F. vesiculosus* and *F. spiralis* differ from those under nutrient competition in the laboratory. The assumption of consistent ranks under various environmental conditions from Keddy's (1989a) competitive hierarchy model must therefore be rejected for the conditions chosen in the present study. Light competition also played a role in the laboratory experiment. These effects were probably mitigated by stirring up the smallest thalli, leading to a better light supply. However, it seems unlikely that this mechanism can reverse competitive dominances. Under field experiment conditions, *F. vesiculosus* was very clearly dominant over *F. spiralis*. Under nutrient-limited laboratory conditions, this dominance is only found in a reduced form at the lowest absolute input frequencies of *F. vesiculosus*, but reversed at higher frequencies.

The replacement series design has been criticized for various reasons (Harper 1977; Connolly 1986; Under-

wood 1986; Herben and Krahulec 1990; Silvertown and Dale 1991; review in Jolliffe 2000) but has been regarded as a useful design to assess competitive ranks in two-species interactions (Firbank and Watkinson 1990; Cousens 1991; Cousens and O'Neill 1993). One of the criticisms is a possible dependency of the outcome on the total density used in an experiment (Inouye and Schaffer 1981; Taylor and Aarssen 1989). For the latter reason, I employed three total densities that included maximum densities of small germlings found in the field [see Karez and Chapman (1998)]. Several studies found consistent ranks for various total densities (Fowler 1982; Cousens and O'Neill 1993; Karez and Chapman 1998; review in Jolliffe 2000). However, in the present study, the competitive ranks in the replacement series of *F. vesiculosus* versus *F. spiralis* were density-dependent. This emphasizes that this potential flaw of the design has to be met by employing several total densities.

In conclusion, competitive ranks found in laboratory replacement series experiments with nutrient-limited unattached *Fucus* thalli in aerated beakers deviated from the predictions of the competitive hierarchy model. Furthermore, they did not reflect competitive ranks under field conditions. Keddy's assumption of consistent competitive ranks under varying conditions must be rejected for the set of environmental conditions chosen to compare with the previous study by Karez and Chapman (1998).

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