BERICHTE
aus dem
INSTITUT FÜR MEERESKUNDE
an der
CHRISTIAN-ALBRECHTS-UNIVERSITÄT · KIEL

NR. 293

Factors causing the zonation of three *Fucus* species (Phaeophyta) in the intertidal zone of Helgoland (German Bight, North Sea)
Testing the validity of Keddy's 'competitive hierarchy model'

DOI 10.3289/IFM_BER_293

by

Rolf Karez

Kiel 1997

Kopien dieser Arbeit können bezogen werden durch:

Institut für Meereskunde an der Universität Kiel
-Bibliothek-
Düsternbrooker Weg 20
D-24105 Kiel
Germany

ISSN 0341-8561

Diese Arbeit wurde von der Mathematisch-
Naturwissenschaftlichen Fakultät der
Universität Kiel 1996 als Dissertation angenommen.

CONTENTS

Appendix

GLOSSARY

ANOVA	analysis of variance
D1, D2, D3	initial *Fucus* germling densities in competition experiments, D1=10,000, D2=50,000, D3=100,000 shoots/m^2
df	degrees of freedom
dw	dry weight
EAD	'extended additive design' for comparisons of competition experiment treatments
fw	fresh weight
homoscedasticity	homogeneity of variances among groups, a prerequisite for ANOVA
MASD	'mixed additive/substitutive design' for comparisons of competition experiment treatments
MD	'Manly's differences', pairing of controls with treatments in analysis of grazing experiments (after Manly 1993) in which differences between food types are calculated
MR	'modified Roa' pairing of controls with treatments after Manly (1993) in which correlation between foods is preserved
NE-Intertidal	rocky intertidal flat on Helgoland ("NO-Felswatt")
P	*Fucus spiralis*
PR	'pure Roa' pairing of controls with treatments in analysis of grazing experiments in which correlation between foods is lost (after Roa 1992)
S	*Fucus serratus*
SD	standard deviation
TK	Tukey-Kramer test for multiple comparisons
V	*Fucus vesiculosus*

SUMMARY

The main objective of my study was to test the validity of the 'competitive hierarchy hypothesis' of Keddy (1989a) for a marine site. According to the competitive hierarchy model, species are arranged along resource gradients so that the competitively dominant species occupies the end of the gradient most favourable for growth. For all species along the gradient, the benign end of the gradient is physiologically optimal. Hence, fundamental niches include the fundamental niches of competitively superior species on the gradient. Species' competitive abilities decrease with increasing distance from the benign end of the gradient. The corollary is that species' fundamental niche breadths and abilities to tolerate reduced resource concentrations decrease with distance from the less benign end of the gradient. Another assumption of Keddy's model is that competitive ability is an inherent characteristic of a species and mostly independent of environmental conditions.

The competitive hierarchy model is thus a possible explanation for a growing body of evidence that upper limits of species' zones along the shore gradient are mainly set by physiological tolerances, whereas lower limits mostly are set by competitive interactions.

Fucus serratus, *F. vesiculosus* and *F. spiralis* occur in progressively higher intertidal zones on Helgoland (North Sea). I tested the following predictions of Keddy's hypothesis along the gradient of desiccation stress: 1. the competitive hierarchy is: *F. serratus* > *F. vesiculosus* > *F. spiralis*. 2. the fundamental niche breadths decrease in the order *F. spiralis* > *F. vesiculosus* > *F. serratus*. 3. Ranks of competitive ability are consistent under different environmental conditions. Modified replacement series experiments (de Wit 1960) set up *in situ* at 3 densities showed the following competitive asymmetries: *F. vesiculosus* > *F. serratus* > *F. spiralis*. Additional replacement series experiments at 3 densities in aerated 3 l beakers in the laboratory showed the competitive dominances: *F. spiralis* ≥ *F. vesiculosus* > *F. serratus*. Hence, competitive dominances depended on environmental conditions.

Transplant experiments designed to elucidate fundamental niche breadths showed that each species grew best within its native zone and not at the benign (lower) end of the shore gradient when laboratory raised germlings were used. This is in contrast to the competitive hierarchy model and supports the model of niche differentiation. Transplants of adult wild plants, in contrast, were in concordance with Keddy's model: survival of each species was highest, when transplanted to the presumably most benign zone of *F. serratus* and successively lower when transplanted to the zones above. I conclude that the competitive hierarchy hypothesis from Keddy cannot explain the zonation of *Fucus* spp. in the intertidal zone of Helgoland.

I tested a further factor that might have influence on the zonation of *Fucus* spp. along the shore gradient: preferential grazing of *Littorina* spp. In both choice and no choice experiments in the laboratory, only very small amounts of *F. serratus* were eaten by *Littorina littorea* or by *L. mariae*, the macrograzer species with highest abundances in the Helgoland intertidal zone. *F. spiralis* was highly consumed by both littorinid snails, whereas *F. vesiculosus* was consumed at an intermediate level.

In the Helgoland intertidal zone, densities of *L. littorea* are highest in the mid-intertidal zone populated by *F. vesiculosus*, slightly lower in the zone of *F. serratus* and markedly lower in the uppermost zone occupied by *F. spiralis*. Hence, in addition to competition from *F. vesiculosus*, grazing might prevent the occurrence of *F. spiralis* in the lower intertidal zones, but can not explain why *F. vesiculosus* does not occur in the zone of *F. serratus*. Due to its mainly epiphytic feeding mode, I believe that the impact of *L. mariae* is only of minor importance at the prevailing densities for the establishment of *Fucus* spp. in the Helgoland intertidal. In another feeding experiment, *L. mariae* preferred 30 mm germlings of *F. serratus* and avoided 3 mm germlings. *L. littorea* preferred the smallest germling size class in both experiments with *F. serratus* and with *F. vesiculosus*. This is in agreement with the epilithic feeding mode of *L. littorea*. I conclude from my experiments that *L. littorea* may be a major source for mortality of very young *Fucus* recruits, but that 'escapes in size' are possible at natural densities of *L. littorea*.

ZUSAMMENFASSUNG

Das Hauptanliegen meiner Arbeit war, die Gültigkeit des 'Konkurrenzhierarchien-Modells' von Keddy (1989a) für einen marinen Standort zu überprüfen. Nach diesem Modell sind Arten entlang von Ressourcen-Gradienten so angeordnet, daß die konkurrenzstärkste Art das günstige Ende des Gradienten besetzt. Dieses Ende ist physiologisch optimal für alle entlang des Gradienten vorkommenden Arten, d.h. ihre fundamentalen Nischen schließen die der konkurrenzstärkeren Arten mit ein. Im Vergleich der Arten nimmt deren Konkurrenzfähigkeit vom günstigen zum ungünstigen Ende des Gradienten ab, während die Fähigkeit ungünstige Ressourcen-Level zu ertragen und die Breite der fundamentalen Nische der Arten in dieser Richtung zunimmt. In einer weiteren Grundannahme geht Keddy davon aus, daß Konkurrenzfähigkeit ein festes Merkmal einer Art und weitgehend unabhängig von Umweltbedingungen ist.

Keddys Modell bietet somit eine Erklärung für die häufig gemachte Beobachtung, daß in der Gezeitenzone die oberen Verbreitungsgrenzen sessiler Arten durch ihr Vermögen ein Trockenfallen zu ertragen und die unteren durch Konkurrenz festgelegt werden. Dies sollte im felsigen Gezeitenbereich der Nordsee-Insel Helgoland anhand der drei dort zoniert siedelnden *Fucus*-Arten getestet werden. *Fucus serratus* besiedelt hier das nach dem Modell günstigste untere Eulitoral, *F. vesiculosus* den mittleren und *F. spiralis* den oberen Gezeitenbereich.

Ich habe die Gültigkeit folgender drei Grundannahmen des Konkurrenzhierarchien-Modells überprüft: 1. Die Konkurrenzfähigkeit weist die Rangfolge *F. serratus* > *F. vesiculosus* > *F. spiralis* auf. 2. Die Rangfolge der Nischenbreiten ist umgekehrt: *F. spiralis* > *F. vesiculosus* > *F. serratus*. 3. Die Rangfolge der Konkurrenzfähigkeit bleibt unter verschiedenen Umweltbedingungen gleich.

Modifizierte *in situ* 'Verdrängungsserien' (replacement series, de Wit 1960) in drei Gesamtdichten ergaben die folgenden Konkurrenz-Asymmetrien: *F. vesiculosus* > *F. serratus* > *F. spiralis*. Der gleiche Versuchsansatz wurde zusätzlich als Laborexperiment mit Belüftungskulturen durchgeführt. Hierbei ergab sich die Rangfolge *F. spiralis* ≥ *F. vesiculosus* > *F. serratus*. Beide Rangfolgen entsprechen nicht den Voraussagen des Konkurrenzhierarchien-Modells; sie weichen voneinander ab und entsprechen damit nicht der Annahme, daß Konkurrenzfähigkeit ein festes Merkmal einer Art ist. Zur Ermittlung der funda-

mentalen Nischen der Helgoländer *Fucus*-Arten wurden Transplantations-Experimente mit Laborkeimlingen und mit adulten Wildpflanzen durchgeführt. Verpflanzte Keimlinge gediehen am besten in der jeweiligen Zone ihres natürlichen Vorkommens. Dieses Muster entspricht eher dem Modell der Nischendifferenzierung als dem Konkurrenzhierarchien-Modell. Im Gegensatz dazu entsprach das Ergebnis des Verpflanzungsversuches mit adulten Thalli Keddys Modell: alle drei *Fucus*-Arten zeigten im unteren Eulitoral die größten Überlebens- und Wachstumsraten, die in höher gelegenen Zonen sukzessiv abnahmen.

Zusammenfassend zeigen meine Versuche, daß das Konkurrenzhierarchien-Modell die Zonierung der Helgoländer *Fucus*-Arten nicht erklären kann.

Als weiteren Faktor, der die Zonierung von *Fucus* beeinflussen kann, habe ich die Präferenz der beiden im Helgoländer Felswatt die höchsten Abundanzen aufweisenden herbivoren Schneckenarten, *Littorina littorea* und *L. mariae*, für Keimlinge der drei *Fucus*-Arten im Labor experimentell untersucht. Sowohl in Auswahl- als auch in Einzelgabe-Fraßexperimenten wurde von beiden Schneckenarten nur sehr wenig *F. serratus* und am meisten *F. spiralis* gefressen. Die Konsumption von *F. vesiculosus* erreichte ein mittleres Niveau. Die Dichte von *L. littorea* ist im Helgoländer Felswatt in der *F. vesiculosus*-Zone am höchsten, etwas geringer in der untersten, von *F. serratus* besiedelten Zone und deutlich geringer in der oberen, von *F. spiralis* besiedelten Eulitoralzone. Somit könnte ein höherer Fraßdruck durch *Littorina* spp., neben der Konkurrenzüberlegenheit von *F. vesiculosus*, die Beschränkung des Vorkommens von *F. spiralis* auf das oberste Eulitoral erklären. Die Frage, warum *F. vesiculosus* als konkurrenzstärkste *Fucus*-Art trotz des geringeren Fraßdruckes dort nicht in die *F. serratus*-Zone einwandert, kann durch meine Ergebnisse nicht erklärt werden.

In einem anderen Fraßversuch bevorzugte *L. littorea* von drei zusammen angebotenen Keimlingsgrößen die kleinste (3 mm Länge), sowohl von *F. serratus* als auch von *F. vesiculosus*. *L. mariae* zeigte eine Präferenz für die größten angebotenen Keimlinge (30 mm) von *F. serratus*. Dies spiegelt den epilithischen Beweidungsmodus von *L. littorea* bzw. den epiphytischen von *L. mariae* wieder. Nach meinen Ergebnissen sollte bei den vorherrschenden Abundanzen der Schnecken nur *L. littorea* durch Totalfraß kleiner Keimlinge einen nennenswerten Einfluß auf die Ansiedlung von *Fucus* haben, der bei der vorherrschenden Dichte von *L. littorea* aber eine Ansiedlung von *Fucus* nicht verhindern kann.

GENERAL INTRODUCTION 1

There has been much debate among benthic ecologists whether physical or biotic factors prevail in structuring intertidal communities, leading to the zonation that may be observed on many coasts. Most earlier workers believed in the absolute prevalence of abiotic impacts such as desiccation (in conjunction with light, temperature, salinity) (e.g. Colman 1933; Doty 1946; Lewis 1961, 1964; Stephenson & Stephenson 1972), followed by an increasing body of evidence for the importance of biotic effects such as competition and predation (e.g. Connell 1961a,b; Dayton 1971, 1975; Chapman 1973, 1974; Paine 1974; Lubchenco 1978). Today, the importance of both physical and biological factors seems to be generally acknowledged (Carpenter 1990; Kiirikki 1996).

In particular, several studies suggested that upper limits of intertidal species are set by physical factors while lower limits are set by biotic factors (e.g. Connell 1961a,b; Schonbeck & Norton 1978, 1980; Lubchenco 1980). A possible explanation for this pattern is the 'competitive hierarchy model' from Keddy (1989a) that will be developed below. In this study, I will test whether this model can explain the zonation of *Fucus* species along the tidal gradient of Helgoland's rocky shore.

The niche model, competition, and coexistence through niche differentiation

An early model, developed to describe species' resource demands and to explain the coexistence of species, is the 'n-dimensional niche hypervolume' of Hutchinson (1957). Each axis of this hypervolume represents an environmental condition (as e.g. temperature, salinity) or a resource (e.g. nutrients, light for plants) affecting the performance of species. A certain species may exist only on a certain section of each axis, and, therefore, only in a limited part of the hyperspace with n axes. Without any effects from other species (competition, predation), this part is the 'fundamental niche' of the species (Begon *et al.* 1990). Vandermeer (1972) even excluded intraspecific influences from the fundamental niche. Under natural conditions, other organisms may exclude the species from parts of its fundamental niche. The resulting natural occurrence is the species' 'realized niche'. Throughout the present study, 'niche' will be used in this sense of Hutchinson's model and not as in others (as reviewed by Hurlbert 1981; Aarssen 1983).

'Competition' will be defined for the purpose of this study *sensu* Keddy (1989a) as "the negative effects which one organism has upon another by consuming, or controlling access to, a resource that is limited in availability". There are other definitions of competition, emphasizing other aspects (e.g. Grime 1974; Tilman 1982; Begon *et al.* 1990), but in this study, the emphasis is on 'resources', particularly space as resource. 'Resources' will be defined here as "any substance or factor which is consumed by an organism and which can lead to increased growth rates as its availability in the environment is increased" (Tilman 1982). Differences in temporal and spatial distribution of resources may be used as criteria for a further classification of 'resources' (e.g. Keddy 1989a) but will not be considered here. For plants, it is not always easy to distinguish between conditions and resources (Begon *et al.* 1990). However, both represent axes of Hutchinson's niche model.

Competition has been classified in several ways (e.g. Schoener 1983; Keddy 1989a). One of the most common distinctions is between interference and exploitation competition (e.g. Colwell & Fuentes 1975). 'Interference competition' is competition between (two) organisms in which one physically excludes the other from a portion of habitat and hence from the resources that could be exploited there, whereas 'exploitation competition' is competition in which any adverse effects on an organism are brought about by reductions in resource levels caused by other competing organisms (Begon *et al.* 1990). Hence, the effect of interference competition is direct and that of exploitation competition more indirect through reduction of the available pool of resources (Keddy 1989a). Other classifications emphasize different aspects of competition, e.g., Goldberg (1990) pointed out that competition ability comprises competitive effect and competitive response (ability to tolerate competition), Werner (1979) distinguished pre-emptive and interactive competition. In the context of the present study, a classification of Yodzis (1986) is important (see also Keddy 1989a, Table 7.3). He emphasized the difference between competition for resources and for space. Competition for resources should, to some extent, be symmetric, since both the competitive dominant and subordinate exploit, and thus reduce, the resource level they both depend on. If community structure is produced by competition for space, the community may be 'dominance controlled', with competitive hierarchies and asymmetric competition prevailing (Keddy 1989a), or 'founder controlled', mostly depending on dispersal and colonization of its species with pre-emptive competitive dominances prevailing. In the conviction of Yodzis (1986), in contrast to other scientists (e.g. Tilman, see below), plant competition is primarily for space. However, space as a resource is a 'portmanteau' term (Begon *et al.* 1990) and for plants it is closely connected with competition for other resources (Carpenter 1990) such as light and, for terrestrial plants, with competition for nutrients through depletion zones in root competition (Wilson 1988).

Throughout this study, 'dominance' will refer, in most cases, to competitive superiority and not to abundance. Where the term is equivocal, 'competitive dominance' will be used.

Based on Hutchinson's niche model, several workers suggested that species with identical niches cannot coexist ('competitive exclusion principle', Hardin 1960; or 'Gause's principle' after works of Gause 1932, 1934, 1935) and, thus, coexisting species must differ in at least one niche axis. This is commonly termed 'niche differentiation' or, when the emphasis is on a certain resource, 'resource partitioning' (Begon *et al.* 1990). A problem with the competitive exclusion principle is that it is not falsifiable under incompletely controlled natural conditions (Keddy 1984, 1989a): If a species is excluded from a habitat by another, similar species, the niche overlap has been too great for coexistence. If species coexist despite their obvious similarity, there must be an additional niche axis, previously overlooked, in which the species differ (Shmida & Ellner 1984). Thus each outcome, exclusion and coexistence, may be explained with the same principle without a straightforward test, since it is normally impossible to consider all (nearly indefinite) niche axes. The coexistence of similar animals in the same habitat may often by explained by divergence in the food niche. For plants however, which all will need light, space, CO_2 and mineral nutrients, such an escape from competition is normally not possible (Schoener 1974; Aarssen 1983). For this reason, studies of a maximum tolerable overlap in resource utilization seem impossible for plants (Shmida & Ellner 1984). Nonetheless, plants grow in often highly diverse communities (e.g. Mitchley & Grubb 1986). Here, the paradox remains that plants must in some sense be similar if they are adapted to the same habitat, but that the widely accepted theory of competitive exclusion dictates that they must be different to coexist (Aarssen 1983).

For a niche divergence to take place through coevolution, competition must influence the species' niches in evolutionary time towards an avoidance of competition. However, this influence of historical competition is rather difficult to prove (Schoener 1974; Grace & Wetzel 1981). Connell (1980) termed this 'the ghost of the competition past' and stated that the necessary co-occurrence of competitors for coevolution is unlikely. Other causes than competition may have led to niche divergence (Connor & Simberloff 1986).

In contrast, other workers have suggested that coexistence is possible without avoidance of competition. E.g. Aarssen (1983, 1985) showed that, in addition to selection for 'ecological combining ability' (i.e. reducing fundamental niche overlap), selection for 'competitive combining ability' can promote coexistence by reducing the differences in relative competitive abilities. His line of thought is that the most severe competition must occur among (coexisting) individuals of the same species (intraspecific competition), having the most similar resource requirements and competitive abilities. If two species compete (interspecific competition), each population comprises a range of genetically different individuals. Evolution should select for the individuals most effective as competitors in both populations, thus promoting selection for enhanced competitive ability. If, at the start, mean competitive abilities were not too different, this selection may lead to coexistence because of (rather than despite) equal competitive abilities: neither species is competitively dominant enough to exclude the other.

A vast number of studies on competition has been published in the last 3 decades. Among ecologists, there has been a hot and partially rude debate about the importance of competition in community organization (e.g. Roughgarden 1983; for review see Lewin 1983). Schoener (1983) and Connell (1983) reviewed field experiments from various workers and both concluded that there is evidence for the importance of interspecific competition. In this respect it is important to discriminate between the intensity and the importance of competition (Welden & Slauson 1986). Despite the immense attention competition has received, there is still no consensus on how it structures communities.

Stress or resource gradients provide good opportunities to study competitive effects (Austin & Austin 1980; Bertness & Hacker 1994). Along gradients, environmental conditions change in some predictable manner, and responses of species may be related directly to the change in condition, in contrast to experimental units scattered over apparently homogeneous locations (Keddy 1989a). Austin (1990) distinguished 3 types of gradients: 1) indirect environmental gradients (without direct influence on growth), 2) direct environmental gradients and 3) resource gradients.

In Figure 1a (top) the realized niches of 4 species along a gradient are shown. This pattern of distribution is observed in field under the influence of other competing species. If these other species are removed experimentally, the target species may fully occupy its fundamental niche. Two distinct patterns of fundamental niches may result from such a release experiment. The first is the model of niche differentiation as described above (Figure 1a, left). Competition in the course of evolution has driven the species' fundamental niches to separate sections of the gradient (alternatively, a species may have invaded a new habitat and occupied a free sector, Connell 1980). In this way the species avoid competition and, thus, competitive exclusion by competitively dominant species. Present competition only sets the exact limits of the realized niches, since fundamental niches overlap at their margins.

The competitive hierarchy model

A second model explaining the pattern of realized niches along gradients was proposed by Keddy (1989a, 1990): the 'competitive hierarchy model'. This model will be the central subject of the present study.

For this model, the outcome of the release experiment is the 'competitive hierarchy' (Figure 1a, right). Here, the gradient has a more benign end (+) and a less favourable end of low resource level (-). In the introduction of his model, Keddy (1989a, p. 73) explicitly developed the model with <u>resource</u> gradients, but he also used the term 'environmental gradient' in the same paragraph. All species compete for the same end of the gradient. This is occupied by the competitively dominant species that excludes the other species to successively less favourable parts of the gradient. The fundamental niches of subordinate species include those of species with higher competitive abilities ("niche inclusion", see Colwell & Fuentes 1975). Keddy (1989a) gives three assumptions for his model:

1. "[I]t is assumed that the species in the community have inclusive niches; i.e. the gradient is a gradient of resource quantity, with all species having best performance (size, growth rate and reproductive output) at the same end of the gradient."

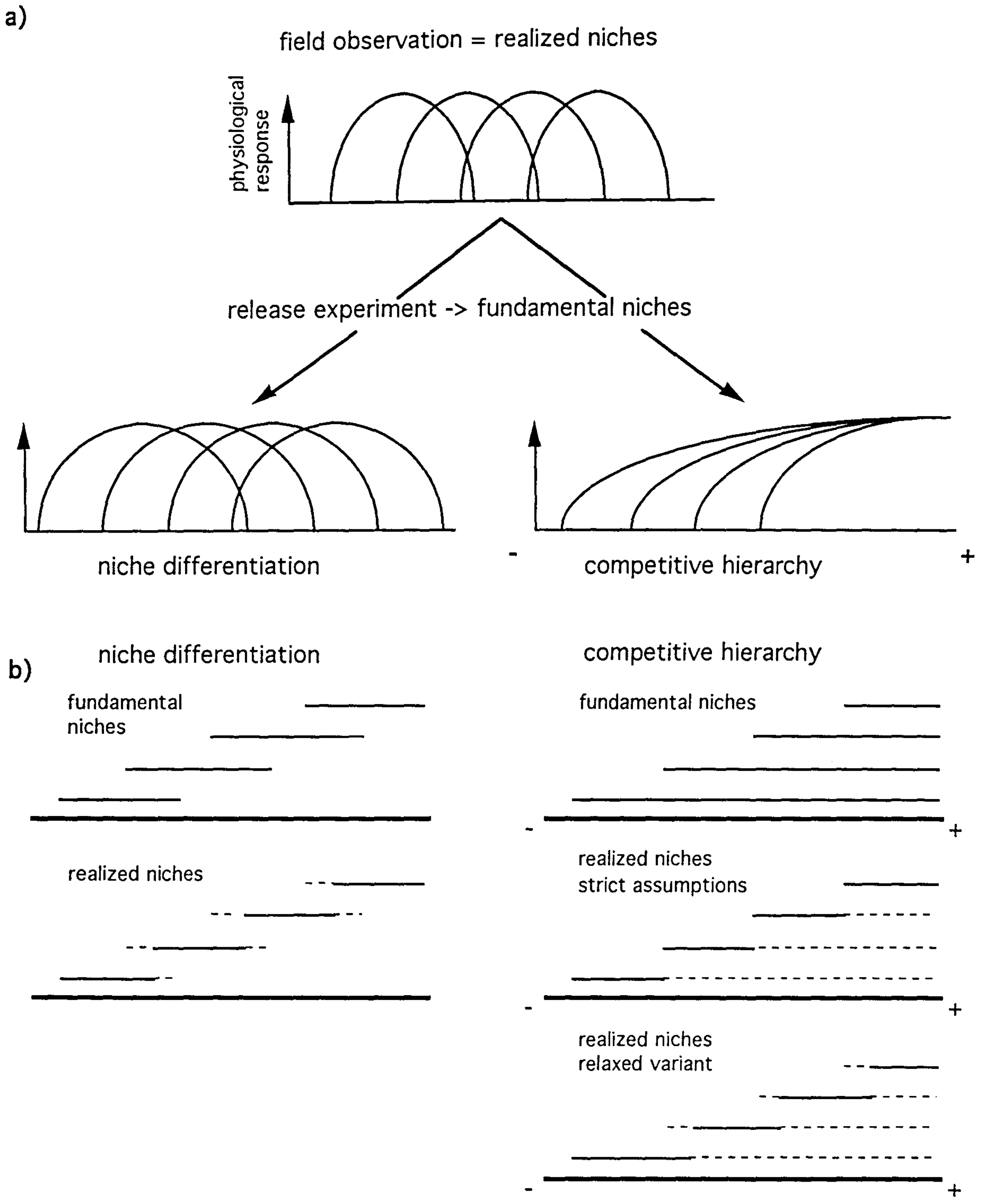


Figure 1: Two models explaining species distribution along resource gradients. a) Upper graph: physiological response curves of 4 species realized in the field. Removal of neighbours may lead to the pattern explained by niche differentiation (lower left) or by the competitive hierarchy hypothesis (lower right). b) Fundamental and realized niches of the models. Realized niches for strict competitive hierarchies are given and those for the relaxed variant proposed by Keddy (1989a). For further explanations see text. Modified after Keddy (1989a).

2. "[T]he species vary in competitive ability in a predictable manner and [...] competitive ability is an inherent characteristic of a species, perhaps having something to do with rates of resource acquisition and capacity to interfere with neighbours."

3. "[C]ompetitive abilities are negatively correlated with fundamental niche width, perhaps because of an inherent trade-off between ability for interference competition and ability to tolerate low resource levels."

Assumption 2. is again described by Keddy (1989a) in that "competitive ability is an inherent trait of a species rather than a trait which is strongly dependent upon the environment".

The model suggests that the transition from a competitive dominant to the next subordinate species occurs at the exact point where the dominant's fundamental niche ends. Keddy (1989a) proposed a relaxed variant of the model where the competitive ability of the dominant species is weakened at the (left-hand in Figure 1a, right) border of the fundamental niche so that at some earlier point it can be excluded by the subordinate. Figure 1b shows the patterns of realized and fundamental niches from the discussed models.

Hence, in Keddy's model, present competiton is at work and setting the species' limits along gradients. Unlike the model of niche differentiation, Keddy's model may be tested in a straightforward manner: zoned species along a gradient should show transitive ranks in their competitive abilities and, in reverse order, in the widths of their fundamental niches. According to the second of Keddy's assumptions these ranks should be consistent among different environmental conditions (environments). Keddy and his co-workers provided much evidence for the competitive hierarchy hypothesis from their own work. In most cases, the surveyed gradient was a gradient parallel to the shoreline of Canadian lakes. Mediated by wave exposure gradients exist between sheltered bays with rich organic content, high nutrient levels of soil (= low stress *sensu* Grime 1974), high plant biomass and low disturbance and exposed sites with infertile soils of coarser grain structure, low plant biomass, with high levels of stress and disturbance (Keddy 1984; Wilson & Keddy 1985, 1986a,b). It should be noted that this gradient is a very complex one. However, even on gradients of, for example, only one mineral nutrient, interactions with other factors (ion balances) may produce effective complex gradients (Austin &

Austin 1980). In his studies with lakeshore plant communities, Keddy found no evidence that niche differentiation ('specialization', Keddy 1984) led to species' coexistence. He found that most species had highest biomasses at the same (high fertility) end of the gradient (Wilson & Keddy 1985), that the competitive abilities of species from the high fertility end were highest (Wilson & Keddy 1986b) and that diffuse competition was greatest there (Wilson & Keddy 1986a). In the following years, Keddy found that plant biomass (and height) is a trait that often explains competitive dominance (Gaudet & Keddy 1988; Keddy 1989b). He came to the conviction that in plant communities consistent hierarchies of competitive ability prevail (Keddy & Shipley 1989; Shipley 1993; Shipley & Keddy 1994) rather than intransitive networks as known from e.g. bryozoan assemblages (e.g. Buss & Jackson 1979; Karlson & Jackson 1981; Russ 1982). For hierarchies to develop, competitive interactions have to be asymmetric (Keddy & Shipley 1989; Shipley & Keddy 1994). Keddy *et al.* (1994) partly confirmed that hierarchies of competitive effects (*sensu* Goldberg 1990) were mostly consistent between different environments, although in single species pairs there were some reversals. Recently, Keddy recommended looking for general patterns of plant traits rather than compiling more and more single species pairs observations (Keddy 1992), and he co-operated in an intercontinental experiment designed to test one of Keddy's (and others') assumptions that competition intensity increases with habitat productivity, which could only partly be confirmed (Reader *et al.* 1994).

All these briefly reviewed works are closely connected to predictions that derive from the competitive hierarchy model. But along gradients only can the hierarchies lead to coexistence. In more homogeneous habitats, species richness must be maintained by other forces. Here, disturbance is thought to prevent that the competitive dominant species eventually excludes all other species (Keddy 1984; Wilson & Keddy 1986b; and see below).

In addition to the evidence from Keddy's experiments, there are some observations supporting the competitive hierarchy model from other gradients such as the depth gradient of ponds (Grace & Wetzel 1981) and salt-marshes (Snow & Vince 1984; Bertness 1991a,b), although, in some cases, the gradient may not be simply a function of tidal height for the latter (Pennings & Callaway 1992).

The competitive hierarchy model, as depicted by Keddy (1989a), suggests a simple gradient. However, in practice, Keddy did experiments on a complex gradient, and these led to the development of his model. Two of the factors that changed along the lakeshore gradient he studied were disturbance and stress. Presumably to include disturbance more explicitly, Keddy (1989a,

1990) extended his competitve hierarchy model by connecting it to Rosenzweig & Abramsky's (1986) 'centrifugal community organization model'. From a central habitat, several gradients (as in the competitive hierarchy hypothesis) radiate to peripheral habitats with different kinds of stress or disturbance (Figure 2a).

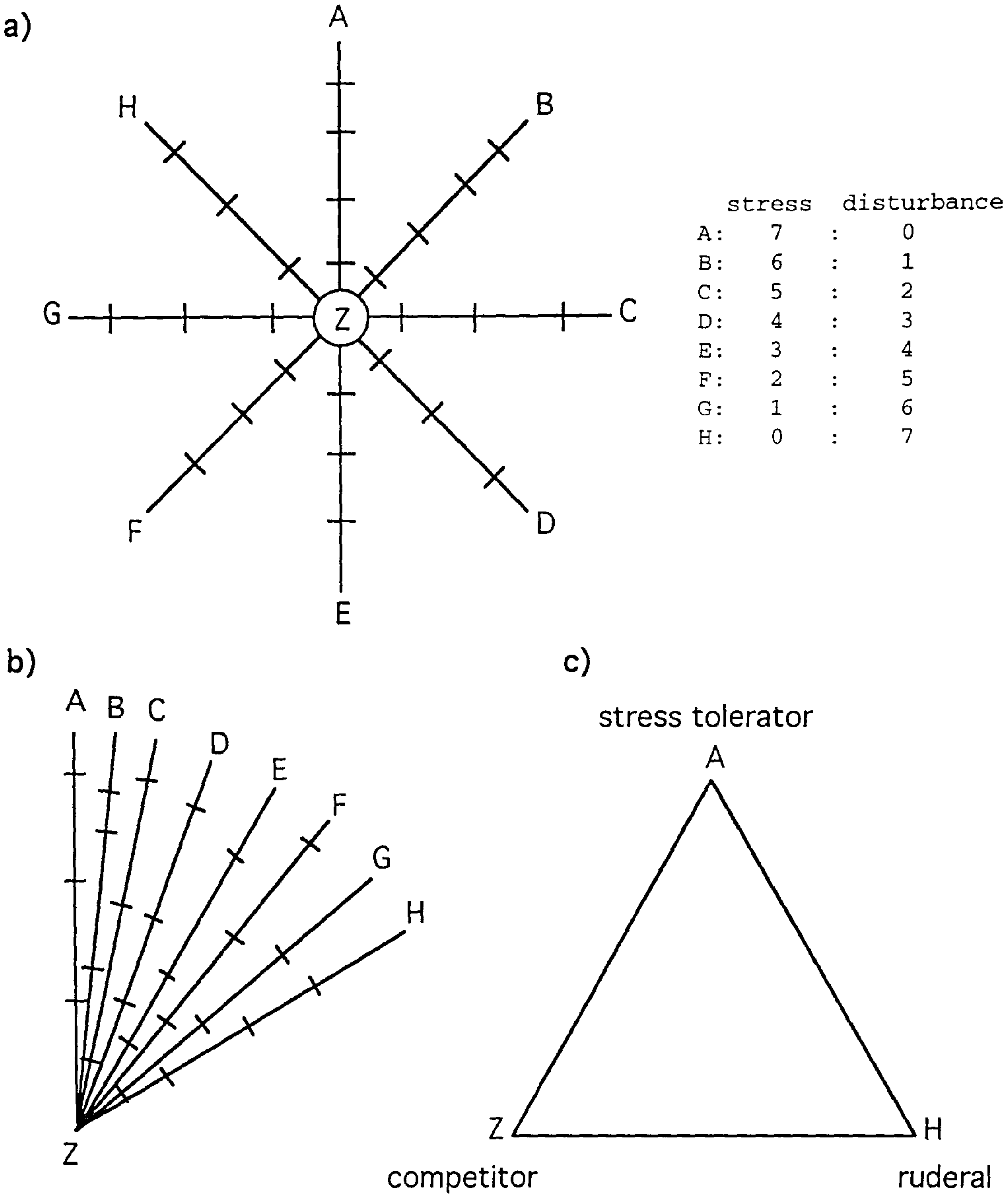
Other ecological models explaining species distribution

Keddy's centrifugal extension of the competitive hierarchy hypothesis very much resembles the triangular model earlier developed by Grime (1974, 1977). Grime proposed the evolution of three distinct plant "strategies" (the controversial term "strategy" was later changed to "life history trait" by Grace 1991):

1. 'competitors': plants with effective capture and utilization of light, water, mineral nutrients and space and with an elevated leaf canopy and lateral spread, adapted to habitats with low levels of stress and disturbance.
2. 'stress tolerators': adapted to low resource levels and other factors hindering a rapid accumulation of biomass as desiccation, acid soils or shading. In contrast to both other "strategies", stress tolerators have low potential relative growth rates. Therefore, biomass is predicted to be too valuable to be lost to herbivores without defenses.
3. 'ruderal': plants with high growth rates and a capacity for rapid seedling establishment and growth, adapted to productive habitats that are disturbed frequently (physically or by herbivores) leading to a loss of biomass.

While the three "strategies" are the extremes, most plants will show features of all three trait syndromes to some extent. The triangular model was created for and tested with terrestrial plants by Grime. Steneck & Dethier (1994) modified and extended it as an application to functional groups of marine algae.

While the triangular model of Grime has been hotly debated (e.g. Loehle 1988; Steneck & Dethier 1994; Grime 1995; Steneck 1995), partly against another popular model from Tilman (see below), Keddy's competitive hierarchy hypothesis seems to have achieved less attention (but see Wilson & Tilman 1991; Chapman 1995; Worm & Chapman in prep.). This may be because of the apparent resemblance to Grime's model (Figure 2a-c), however, differences exist giving the competitive hierarchy hypothesis the status



	stress		disturbance
A:	7	:	0
B:	6	:	1
C:	5	:	2
D:	4	:	3
E:	3	:	4
F:	2	:	5
G:	1	:	6
H:	0	:	7

Figure 2: Centrifugal extension of Keddy's (1989a) 'competitive hierarchy model' in comparison with Grime's (1974, 1977) triangular model. a) The centrifugal model with a central habitat (Z) that is included in the niches of all species that occupy sections on gradients from Z to 'peripheral' habitats (A-H). Peripheral habitats differ in their degrees of stress and disturbance. When peripheral habitats are ranked in their stress:disturbance ratio, they may be arranged as in b). When peripheral habitats are connected, the line depicts one side of Grime's model triangle c): the gradient from stressful (A) to disturbed (H) habitats. For further explanations see text.

of a separate model. For example, Grime (1974) classified plants and fitted them into his model according to certain traits such as relative growth rate, canopy height, lateral spread, litter accumulation etc. According to their potential for the three strategies, species will populate and succeed in certain habitats. Keddy's model is explicitly concerned with environmental gradients and the distribution of species along them. His model is more operational, predicting the occurrence of a species from its fundamental niche and competitive ability in relation to those of other species, thus emphasizing the action of competition. However, although certain traits are recognized to be correlated with competitive ability in both Grime's and Keddy's models, both neglect the mechanism of competition. This is included in, and is, in fact, the basis of, Tilman's 'resource competition model' (Tilman 1981, 1987a). For Tilman, competitive dominance is defined as the ability to maintain a population at a lower resource level than competing species. In Tilman's conviction, species differ in their relative abilities in competing for different resources, i.e. under certain conditions, two species can coexist, if one is the best competitor for one resource, the second species for a second resource. Thus, Tilman's approach is explicitly concerned with the measurement of resource concentrations, in contrast to Grime's and Keddy's models.

The origin of Tilman's model comes from his work with phytoplankton, where it has been confirmed in further studies (Tilman 1981; Sommer 1983; for periphyton: Sommer 1996), but, with later extensions, it is now also meant to apply to terrestrial plants (Tilman 1985; Tilman & Wedin 1991). Some controversies in the persisting debate between Grime and Tilman (Grime 1988; Tilman 1987b, 1989; Campbell *et al.* 1991; Wilson & Tilman 1991) lie in their different definitions of 'competition' (Grime 1988; Grace 1990, 1991). For example, competitive dominant species *sensu* Grime are 'resource capture specialists' adapted to habitats of high resource supply (= low stress), while in the opinion of Tilman, the dominant species is able to utilize and tolerate lower resource concentrations at equilibrium, i.e. when resources have been reduced. For Grime's model, abilities to compete for different resources are positively correlated, since a plant will need more than one resource for maintaining high growth rates. For Tilman, species have negative correlations among abilities to compete for different resources and competitive dominance depends on the special concentrations and ratios of different resources (Grace 1991).

Equilibrium *versus* non-equilibrium models

The pure competitive hierarchy hypothesis (along one resource axis) is an equilibrium model, i.e. it is a model for, theoretically, undisturbed habitats. In its centrifugal extension (see above) disturbance is included. It remains unclear from Keddy's introduction of the model (Keddy 1989a, 1990) if there are, theoretically and practically, gradients between highly disturbed and undisturbed sites included in his extended centrifugal model that only have minimum stress. Such gradients would be similar to the bottom side of Grime's triangle (Figure 2c), representing habitats with potential high fertility (high resource levels). It is hard to imagine, and it is largely unexplained by Keddy, how along such a gradient the inverse rankings of competitive ability and fundamental niche breadth could be formed. However, for more homogeneous habitats (without established gradients), there is a prevailing non-equilibrium view of community organization (e.g. Connell 1978; Huston 1979; Paine & Levin 1981). Physical and biotic (predation) disturbance are thought to prevent the eventual total dominance (expressed as space monopolization) of the top competitor (by providing gaps in space limited systems) and, at a medium level, thus maintaining high diversity and coexistence of species (Paine 1966; Levin & Paine 1974; Menge & Sutherland 1976; Huston 1979; Paine & Levin 1981). Other such factors may be spatial (Ives 1995) and temporal heterogeneity of resources or different life-forms or timing of reproduction (Shmida & Ellner 1984; Benedetti-Cecchi & Cinelli 1996). In this respect, approaches emphasizing the generation of diversity (e.g. selection for annually recurring and thus predictable generation of free space) and those maintaining diversity (e.g. through preventing exclusion by the top competitors) through disturbance have to be distinguished (Huston 1979).

Testing the competitive hierarchy model

It should be clear from the above short and by no means exhaustive review of models which include 'competition' as a structuring agent that there is no consensus among ecologists about the validity of the models and even definitions of terms differ among models and among the special viewpoints of researchers (e.g. Grace 1991). Some models persist over years untested except, in the better cases, by their modellers until they become established in ecological theory merely by habituation (Loehle 1987). Explicit and unbiased model testing is therefore important and will be the main objective of the present study. I will test whether the predictions of Keddy's competitive hierarchy hypothesis can explain macroalgal zonation along the tidal gradient of the island of Helgoland (German Bight, North Sea). As mentioned above, there is much evidence that, in the intertidal zone, the upper limits of macroalgae are set by physical factors while the lower limits are due to competition. This is in striking correspondence with the predictions from the competitive hierarchy hypothesis, when the upper intertidal is interpreted as the stressful end, the lower intertidal as the benign end of the gradient for these originally marine organisms (Chapman 1995). However, although the application of the model perhaps may be extended from macroalgae to animals in some cases (e.g. barnacles; Connell 1961a,b), there are contradicting examples for macroalgae (Schonbeck & Norton 1978; Hawkins & Hartnoll 1985; Chapman & Johnson 1990).

I used the three species of the brown algal genus *Fucus* that dominate the Helgoland rocky intertidal zone (for a more comprehensive description see below). These form distinct zones on many of Helgoland's seawalls, with *Fucus spiralis* L. in the upper intertidal zone, *F. vesiculosus* L. at mid tidal level and *F. serratus* L. populating the lower shore. Other organisms form additional zones, but the usage of these fucoids is ideal for the experiments, because they are easily distinguished when adult but can be similarly treated during experimentation, they have similar life histories, have been cultivated frequently and are rather robust.

The three assumptions of Keddy's model (see above) may be used to formulate hypotheses that can be experimentally tested. Firstly, the ranking of competitive abilities has to be tested for the *Fucus* species. The lowermost occurring species, *F. serratus*, should be the competitive top dominant, the uppermost species, *F. spiralis*, the subordinate of the three *Fucus* species. It is dangerous to infer competitive dominances from descriptive studies or census data only (Schoener 1974; Abramsky *et al.* 1986; Pfister 1995), only controlled experiments manipulating species densities and falsifiable null-hypotheses can reveal competitive relationships safely (Paine 1977; Connor & Simberloff 1986; Underwood 1990). This will be done in the present study under two different environmental conditions (laboratory and field), thus testing Keddy's assumption of competitive ability as a characteristic of a species, independently of conditions. Lastly, the niche breadths must be surveyed. Keddy's hypothesis predicts that their ranks are inversely correlated with the competitive abilities. Hence, the fundamental niche of *F. serratus* should be the smallest, that of *F. spiralis* the widest, while that of *F. vesiculosus* should be intermediate.

From the models described above, only Keddy's competitive hierarchy hypothesis will be tested explicitly. However, when the fundamental niches of *Fucus* spp. are surveyed, the pattern typical for niche differentiation as shown in Figure 1a (left) may emerge. This does not seem likely because of the general tendency of many intertidal studies indicating that lower distribution limits of intertidal seaweeds are set by biotic effects. Further, such a pattern would only show the outcome, but not the underlying causes leading to niche differentiation, competition being only one among others. For the proof of niche differentiation occurring due to competition other rigorous tests are necessary (Connell 1980) and these were not done in this study. Further, in this study only the effect and strength of competitive interactions will be surveyed, not the mechanisms.

General questions of the present study and corresponding predictions of the competitive hierarchy model were:

- What is the competitive hierarchy of Helgoland *Fucus* species? Does it fit to the predictions of the 'competitive hierarchy model' (Keddy 1989a)?

  $H_{0\text{-}1}$: competitive dominance: *F. serratus* > *F. vesiculosus* > *F. spiralis*

- Is this hierarchy consistent under different environmental conditions (included in the species' fundamental niches)?

  $H_{0\text{-}2}$: hierarchy in field = hierarchy in laboratory

- Which are the fundamental niche breadths of Helgoland *Fucus* spp. (referring only to the Helgoland intertidal)? Does niche breadth ranking follow the predictions of the competitive hierarchy model?

  $H_{0\text{-}3}$: fundamental niche breadths: *F. serratus* < *F. vesiculosus* < *F. spiralis*

- Is this ranking consistent for different life stages of *Fucus* spp.?

  $H_{0\text{-}4}$: niche breadth rank of germlings = niche breadth rank of adults

Any rejection of the above hypotheses would mean a contradiction of the validity of the competitive hierarchy model for the Helgoland *Fucus* species.

Herbivory as another factor that may cause zonation

As shown in many studies, webs of competition and predation (including herbivory) influenced by physical factors such as wave exposure and desiccation determine the distribution of fucoids in patterns that may vary considerably between coasts (for review see Chapman 1995). Although some of these patterns are quite consistent, for most evidence there is some contradicting evidence and "there is a danger that everything revealed will become site specific" (Chapman 1995). This may be very true for the Helgoland intertidal, where some of the key species are absent that greatly influence other European rocky coasts (barnacles, limpets; see site description below). For the Helgoland intertidal, Janke (1986, 1990) showed that grazing by snails of the genus *Littorina* represents the predation most likely to have an additional influence on the distribution of *Fucus*. Germlings of *Fucus* may be the crucial life stage for the development of a canopy in being most susceptible to littorinid grazing (e.g. Lubchenco 1983). In the present study, feeding preference experiments with *Fucus* germlings and *Littorina* will shed light on grazing as factor that does not necessarily change monotonically along the intertidal gradient (e.g. Barker & Chapman 1990).

In this study, anwers will be sought for the following questions:

- Is there an escape in size for the *Fucus* species subjected to greatest grazing pressure (*F. serratus*, *F. vesiculosus*) from the most effective grazers (*Littorina littorea*, *L. mariae*)? Are smaller germlings preferred to larger?

  $H_{0\text{-}5}$: equal consumption of three size classes of *Fucus* germlings (for all 4 *Fucus* - *Littorina* combinations)

- Can selective consumption of certain *Fucus* species by *Littorina* spp. explain zonation patterns? Is there a feeding preference?

  $H_{0\text{-}6}$: equal consumption of similarly sized germlings of *Fucus* species

Structure of this thesis

The next three chapters (2-4) will be concerned with the experiments performed in this study. In particular, chapter 2 is concerned with competition experiments to elucidate the competitive ranks of Helgoland *Fucus* species (see $H_{0\text{-}1}$ and $H_{0\text{-}2}$). Chapter 3 will deal with the fundamental niche breadths of Helgoland *Fucus* species surveyed in transplant experiments (Ho-3 and Ho-4). Chapter 4 will include littorinid grazers and examine their preferences among *Fucus* germlings of a certain length or species (Ho-5 and Ho-6). Several methods of statistical analysis will be applied to the data for comparison of their utility. This comparison will mostly be presented as an appendix. Chapters 2-4 will have their own introduction, description of experimental designs, results and a short summary of the results.

Finally, chapter 5 will summarize and discuss the findings of the foregoing chapters.

1.1 Description of the study site

The distribution of Helgoland's marine fauna and flora has been surveyed in various ways (e.g. Lüning 1970; Kornmann & Sahling 1977; Karez 1991; Jacobs 1993; summarized by Harms 1993). The NE rocky intertidal zone of Helgoland ("Nordost-Felswatt", hereafter "NE-Intertidal", Figure 3) is the only part of the island's shoreline where the sea reaches up to the natural red sandstone cliff without protection by seawalls, except from a few shelves left unsheltered for rock-breeding seabirds. The special physiognomy of the NE-Intertidal and its species distribution have been described by Janke (1986), who also, for this site, performed the most thorough and important experiments in respect to the present study (Janke 1989, 1990).

From the cliff seaward, a flat rocky terrace follows with a horizontal extension of >300 m from MHW to MLW, with a difference in vertical level of 2.4 m (Janke 1990). Thus, the mean angle of gradient is less than 0.5°. Along the whole stretch, the NE-Intertidal is sheltered from western storms by a seawall ("N-Mole", see Figure 3). Spring low tides occur in early morning and evening hours. Hot midday conditions affect the lower intertidal organisms only when low tides coincide with southeastern storms. Genuine tidepools, surveyed in studies of many other coasts (Lubchenco 1982; Chapman 1990b; Metaxas *et al.* 1994; Benedetti-Cecchi & Cinelli 1996; van Tamelen 1996), are absent from the rocky flat. Parallel to the N-Mole, grooves cut through the rock. These originate from the broken up layers of sandstone that eroded differentially. The bias of the layers runs NE-wards, right-angled to the grooves, reaching a difference in height of a few deci-

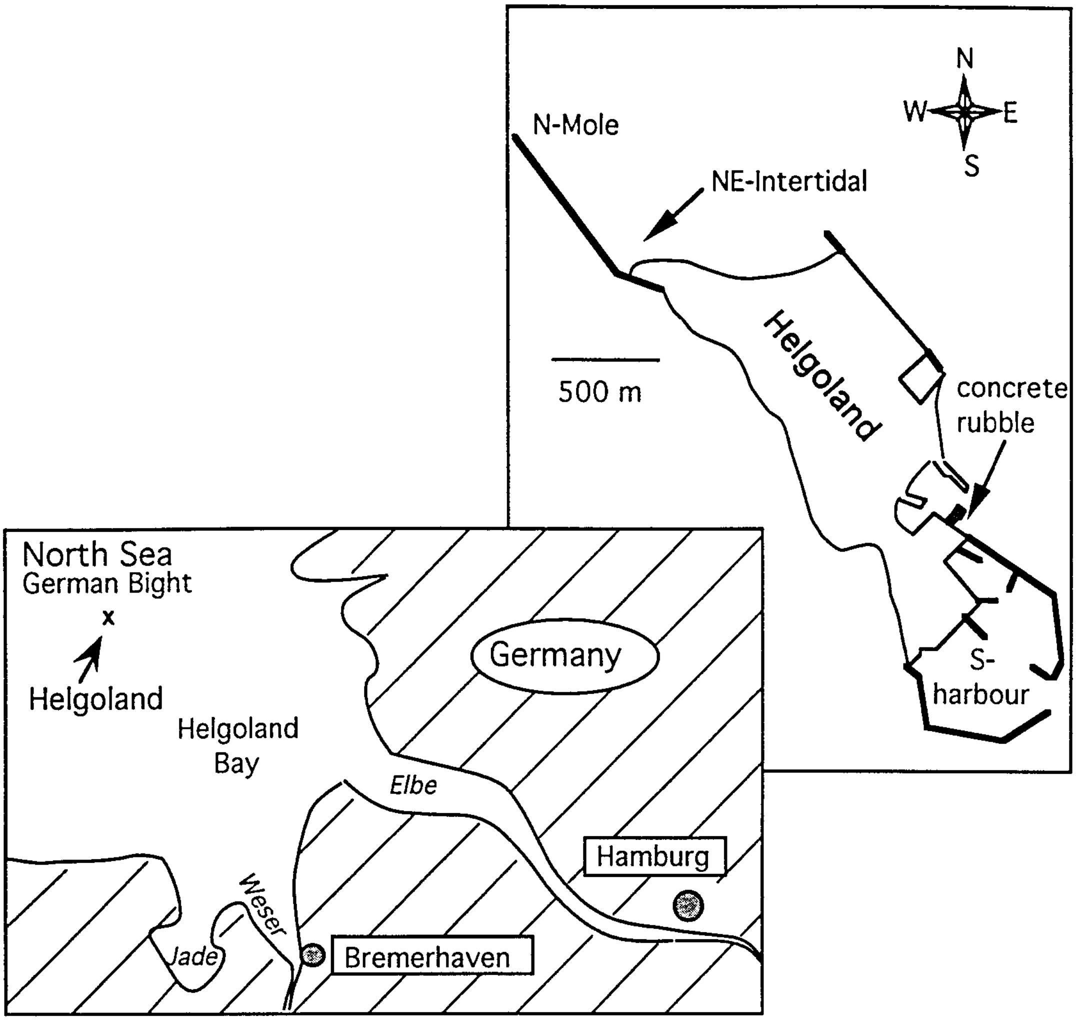


Figure 3: Map of the island of Helgoland and its location in the German Bight (North Sea). Sites of experiments were the rocky flats of the NE-Intertidal, the N-Mole and an intertidal field of concrete rubble (indicated with an arrow).

meters on horizontal distances of ca. 0.5 - 5 m. This pattern of grooves distorts the normal zonation, leading to two tidal gradients: a large scale gradient along the land-sea axis and a small scale gradient, right-angled to the former. Small scale distributions of macroalgae have been described elsewhere (Janke 1986), here only zonation patterns of the most conspicuous macroalgae along the large scale gradient will be considered.

Some of the grooves retain enough water during most low tides to allow, near the lower end of the large scale intertidal gradient, growth and survival of *Corallina officinalis*. On the layers' surfaces in the lower intertidal zone, adjacent to subtidal stands of *Laminaria digitata*, a dense canopy of *Fucus serratus* begins, extending landwards over ca. half of the regularly emergent area. It is accompanied by an understorey population of *Chondrus crispus*, that does not form an own belt in the lowermost intertidal zone as on North-American Atlantic shores (see below), and *Cladophora rupestris* patches. The main canopy of *Fucus serratus* is rather dense with a leaf area index (LAI) of >>1. Landwards, the *F. serratus* canopy becomes more scattered with a lower LAI. Dense patches of *Mytilus edulis* populate the tops of the sandstone slabs. *F. vesiculosus* alone or together with *F. serratus* builds patches of sparse canopies. In the uppermost zone of the main NE-Intertidal, plateaus of rocks more recently fallen from the cliff are often populated by a dense mixed canopy, mostly of *F. vesiculosus* and *F. spiralis* and, in a few cases, *F. serratus*. The area surrounding these boulders is populated from ca. March to September by dense stands of green ephemeral algae, mainly *Enteromorpha* spp. (Janke 1986). On big concrete blocks of the eastward extents of the NE-Intertidal, *F. spiralis* (and still higher *Porphyra* spp.) forms a distinct zone. The typical zonation pattern of *Fucus* spp. (landwards *F. serratus* - *F. vesiculosus* - *F. spiralis*), conspicuous on most of Helgoland's seawalls and the main subject of this study, is only with difficulties discernible in the main NE-Intertidal.

Ascophyllum nodosum is absent from the NE-Intertidal, presumably due to the semi-exposed character of the site (Janke 1986) or due to the brittle substratum. In the more sheltered southern harbour, it forms a dense canopy. The overwhelming dominance of *F. serratus* in the lower intertidal zone is in contrast to other coasts. E.g. on N-Atlantic coasts of America, this zone is often dominated by *Chondrus crispus* that is competitively dominant and less susceptible to grazing there (Lubchenco 1980; Worm & Chapman in prep.). Lubchenco (1980) suggested that in Europe grazing by limpets and ice scouring remove *Chondrus* crusts and, thus, facilitate the establishment of *F. serratus*. However, several findings contradict this contention for Helgoland: Janke (1990; or see review of Chapman 1995, p. 26) found no evidence for a competitive superiority of *Chondrus* over *Fucus*. Helgolands coasts are normally not affected by ice and limpet grazing. *Fucus* itself is affected by ice scouring (McCook & Chapman 1993; Kiirikki 1996), although is has high regenerative abilities (McCook & Chapman 1992). However, in the experiments of the present study, *Chondrus* was not included.

The grazer guild consists mainly of *Littorina* spp. and small crustaceans, while limpets, a major structuring force on e.g. many British coasts (Southward & Southward 1978; Hawkins 1981), are absent from the Helgoland intertidal.

Another contrast to many other coasts (e.g. Hartnoll & Hawkins 1985) is the absence of dense barnacle populations from the main NE-Intertidal. This is presumably due to the brittle consistence of the red sandstone, since they settle on other substrata in Helgoland's intertidal zone, e.g. on concrete and PVC frames of Janke's (1990) enclosure cages (pers. observation). Lubchenco (1983) showed that barnacles may be important for the establishment of fucoids.

More comprehensive descriptions of the distribution of Helgoland's intertidal species are given by Markham & Munda (1980), Janke (1986) and some of the studies summarized by Harms (1993).

COMPETITION 2

2.1 Introduction

Experimental detection and estimation of competition

Substitutive designs - replacement series

There are several ways of performing experiments to detect and measure competition. One of the designs used most frequently in botany is the replacement series (de Wit 1960). It was first proposed for use in agricultural research and was used extensively for crop experiments (e.g. Spitters 1983a,b). Its main use is in comparing pairs of species (Cousens 1991) and, as such, has also become an important tool in ecology (e.g. Fowler 1982; Chapman 1990a; Chapman & Johnson 1990).

In a replacement series experiment, the performance of two competing species in mixed stands is compared to their performance in monocultures. The original de Wit design comprises a monoculture of a species A and several plots in which individuals of A are replaced successively by individuals of a species B (Figure 4). The last plot is a monoculture of species B. All these plots have the same total density.

Plots in replacement series are set up with young stages of plants (seedlings or seeds in agriculture). Some unit of starting condition is fixed (e.g. number of seeds) or measured (dry weight of seedlings; for each species in mixtures) and all plots are grown under the same conditions. At the termination of the experiment, the same unit is estimated and surviving individuals (of each species in mixtures) are counted.

The classical analysis of replacement series experiments is the replacement series graph (e.g. de Wit 1960; Khan *et al.* 1975; Lobban & Harrison 1994). Here, the yield of each component is plotted against its mixture proportion (Figure 4, bottom). When the yield increases linearly with the mixture proportion, this is an indication of no interaction and the plot is a line connecting the origin with the yield of the species' monoculture (Figure 4, bottom

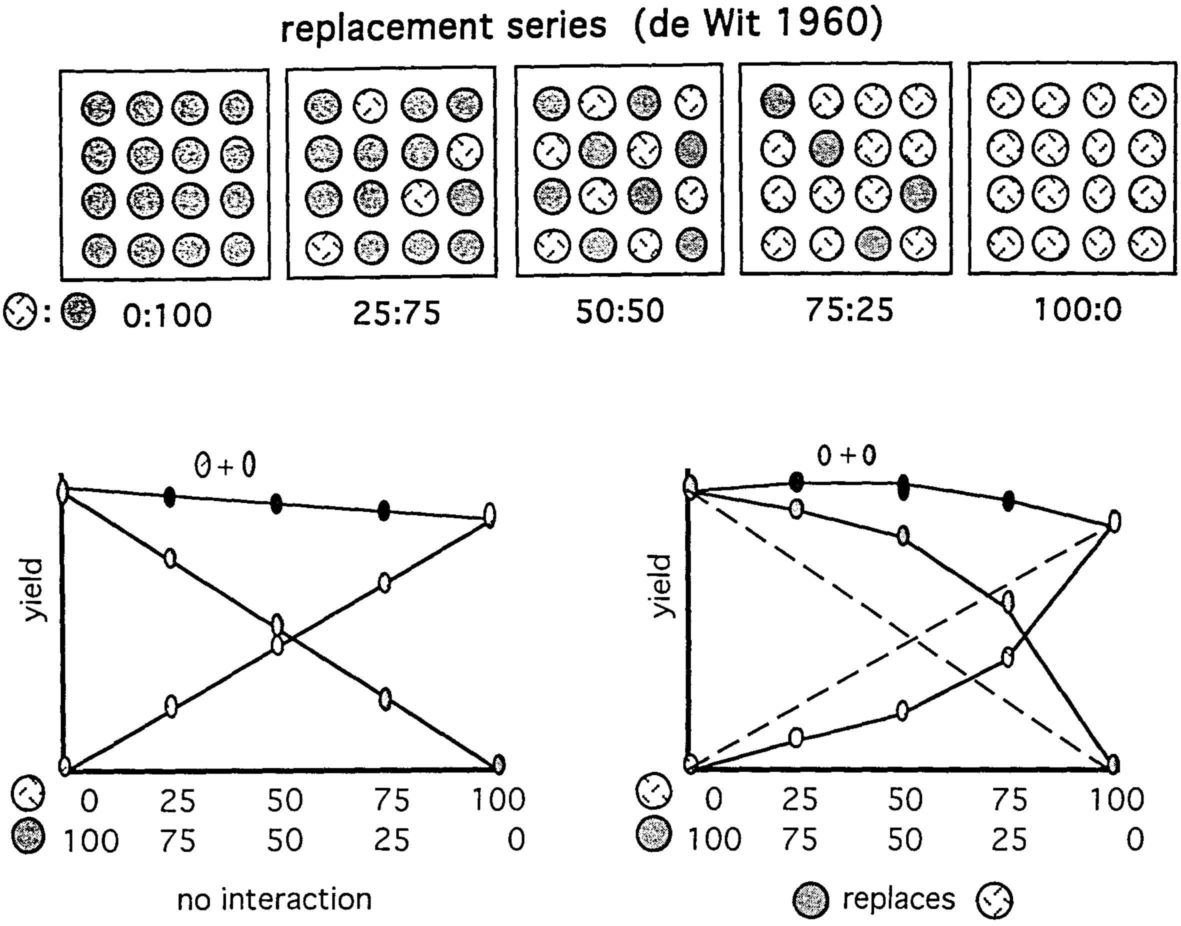


Figure 4: Design of a replacement series experiment (top), replacement series graphs (bottom). With constant total density, individuals of a monoculture of the shaded species (top, left) are replaced by individuals of another (open circles) species for further treatments. Two possible outcomes analysed by replacement series graphs (bottom): no competitive interaction (left) or competitive dominance of the shaded species (right).

left). These lines are the 'expected yields' to which realized yields from replacement series experiments can be compared (e.g. Willey & Rao 1980; Jolliffe *et al.* 1984). If the yield of one species is suppressed below this line in all mixtures, while the yield of the other species is elevated in all mixtures, the second species will outcompete the first (Figure 4, bottom right).

In input-output ratio diagrams (Khan *et al.* 1975) log ratio of output weights (or seed numbers etc.) is plotted against log ratio of input weights (or seed numbers etc.) of two competing species i and j (Figure 5). Hence, the ratio of the yields of two species i and j is compared to the ratio of the biomasses at the outset of the experiment.

In mixtures whose data points lie on the line of unit slope, ratios of output equal input ratios, hence, these mixtures will be stable (Fig. 5a). If the data points lie above the line of unit slope, all input ratios (i:j) lead to a higher output proportion of i. Through time, this will lead to competitive elimination of j (Figure 5b). Species i will go to extinction, if data points lie on a line below and parallel to the line of unit slope (Figure 5c).

Mixtures, whose data points lie on a line with a slope between 0 and 1 that intersects the line of unit slope will stabilize in the intersecting point through time, since low input proportions of i lead to higher output proportions, while high input of i leads to low output (Figure 5d). Other possible outcomes are not dicussed here (but see Khan *et al.* 1975 and Chapman 1986).

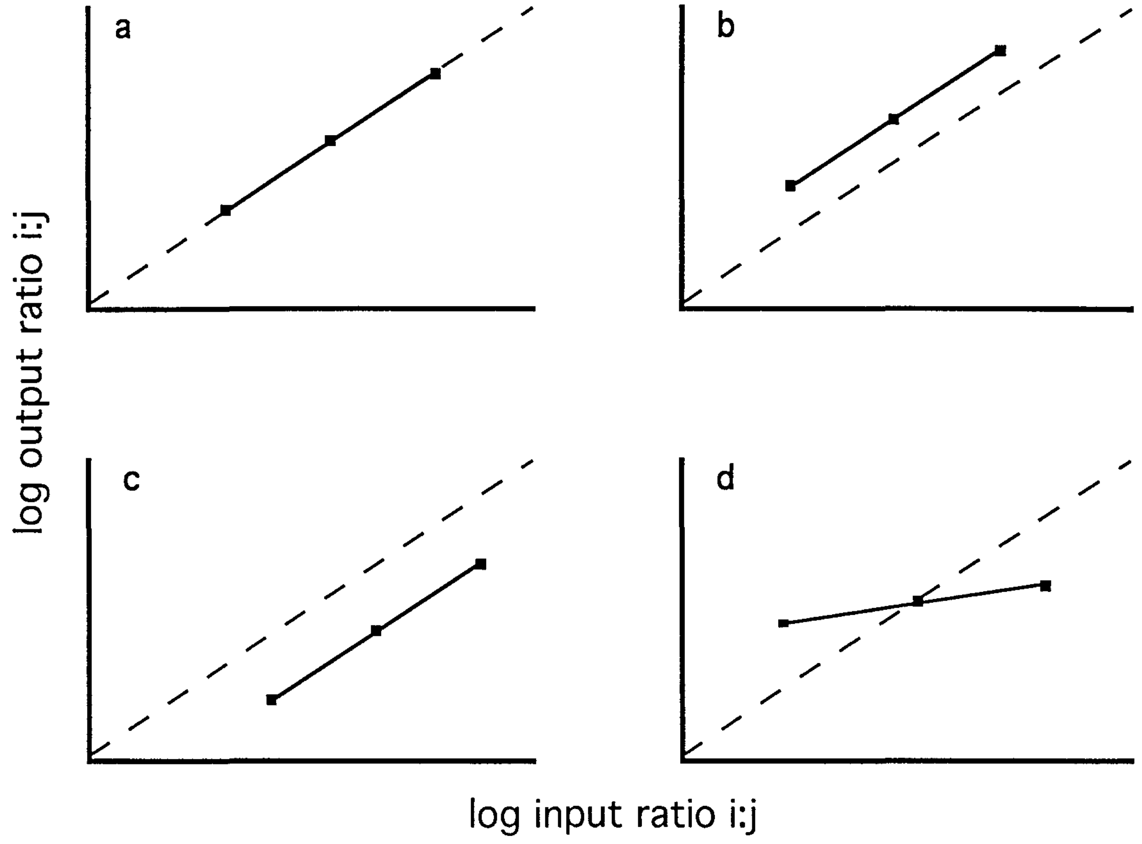


Figure 5: Theoretical results of replacement series experiments expressed as ratio diagrams. a) All input ratios lead to the same output ratios, hence all mixtures of i and j are stable through time. b) All, low and high, input ratios lead to higher output ratios (i:j), hence species j will go to extinction c) All input ratios lead to lower output ratios, hence species i will go to extinction. d) Low input ratios lead to high output ratios and vice versa, hence mixtures will eventually stabilize at the intersection with the line of unit slope.

From the data obtained with the replacement series design, many indices may be calculated (review e.g. in Cousens & O'Neill 1993). I use here the relative crowding coefficient.

The individual crowding coefficient K_i (Khan *et al.* 1975) is calculated for species i as:

$$K_i = \frac{\omega_i / \sigma_i}{\omega_{i0} / \sigma_{i0}}$$

where ω_i is the per plant yield in mixed culture, σ_i is the initial per plant mass in mixed culture, ω_{io} the per plant yield in the corresponding monoculture and σ_{io} the inital per plant mass in monoculture. Hence, the individual crowding coefficient is the ratio of the growth in mixed culture to the growth in monoculture on a per plant basis. $K_i<1$ indicates suppression of growth in mixed cultures, $K_i>1$ elevation of growth.

From individual crowding coefficients K_i and K_j of two species i and j grown together in replacement series, the relative crowding coefficient K_{ij} is calculated as:

$$K_{ij} = \frac{K_i}{K_j}$$

If $K_{ij}=1$, the two species are equal in their interaction. If $K_{ij} >1$, then species i succeeds relative to species j, if $K_{ij}<1$, species j succeeds.

Authors that developed replacement series and its analyses 20-30 yr ago (e.g. de Wit 1960; Khan *et al.* 1975) worked mostly with agricultural plants and seeds were the measured unit at the onset and at termination of the experiments. Since seeds vanish to produce seedlings which grow into new plants that produce new seeds, the final number of seeds is a synonym for 'yield'. If the starting unit is biomass of small seedlings, the measured unit at the termination of the experiment should be 'final biomass' rather than yield (final biomass minus starting biomass), since starting biomass is still included in final biomass. However, normally starting biomass is less than 1% of final biomass and errors due to usage of the wrong unit will be negligible.

A serious disadvantage of replacement series is that they are analysed only by visual evaluation of the graphs (Khan *et al.* 1975). It is not possible to compare differences in individual yield from all treatments (as shown in Figure 4), because the effects of two factors cannot be separated: the increase in the proportion (density) of one species and the simultaneous decrease of the proportion of the other species.

Additive designs

In additive designs the density of one species is held constant, while that of the other is varied. The performance of the first species is then compared under different competition regimes. Additive designs are also well suited for agronomic objectives (Cousens 1991) and in many studies the effect of varying weed densities on a fixed crop density has been analysed (Cousens 1985; Cousens *et al.* 1988). Underwood (1986) proposed an additive design that allows the evaluation of intra- and interspecific effects (Table 1 and Figure 6). The treatments of this design can be compared in an ANOVA (as indicated in Table 1).

Table 1: Additive experiment to compare intra- and interspecific competition between two species. d_i and d_j are monoculture densities of species i and j, respectively. (Modified after Underwood 1986.)

plot no.	**1**	**2**	**3**	**4**	**5**
species i	d_i	d_i+d_j	d_i	-	-
species j	-	-	d_j	d_i+d_j	d_j

intraspecific competition in species i: compare 1 with i's at density d_i in 2
intraspecific competition in species j: compare 5 with j's at density d_j in 4

interspecific competition (j on i): compare i's in 3 with 1
interspecific competition (i on j): compare j's in 3 with 5

Both replacement series and additive designs have their drawbacks and have been criticized for them (Cousens 1991). Critics of replacement series emphasized the confounding of intra- and interspecific effects, since the density of one species is reduced and that of the other elevated simultaneously (Underwood 1986). Some authors have stated that the results of replacement series

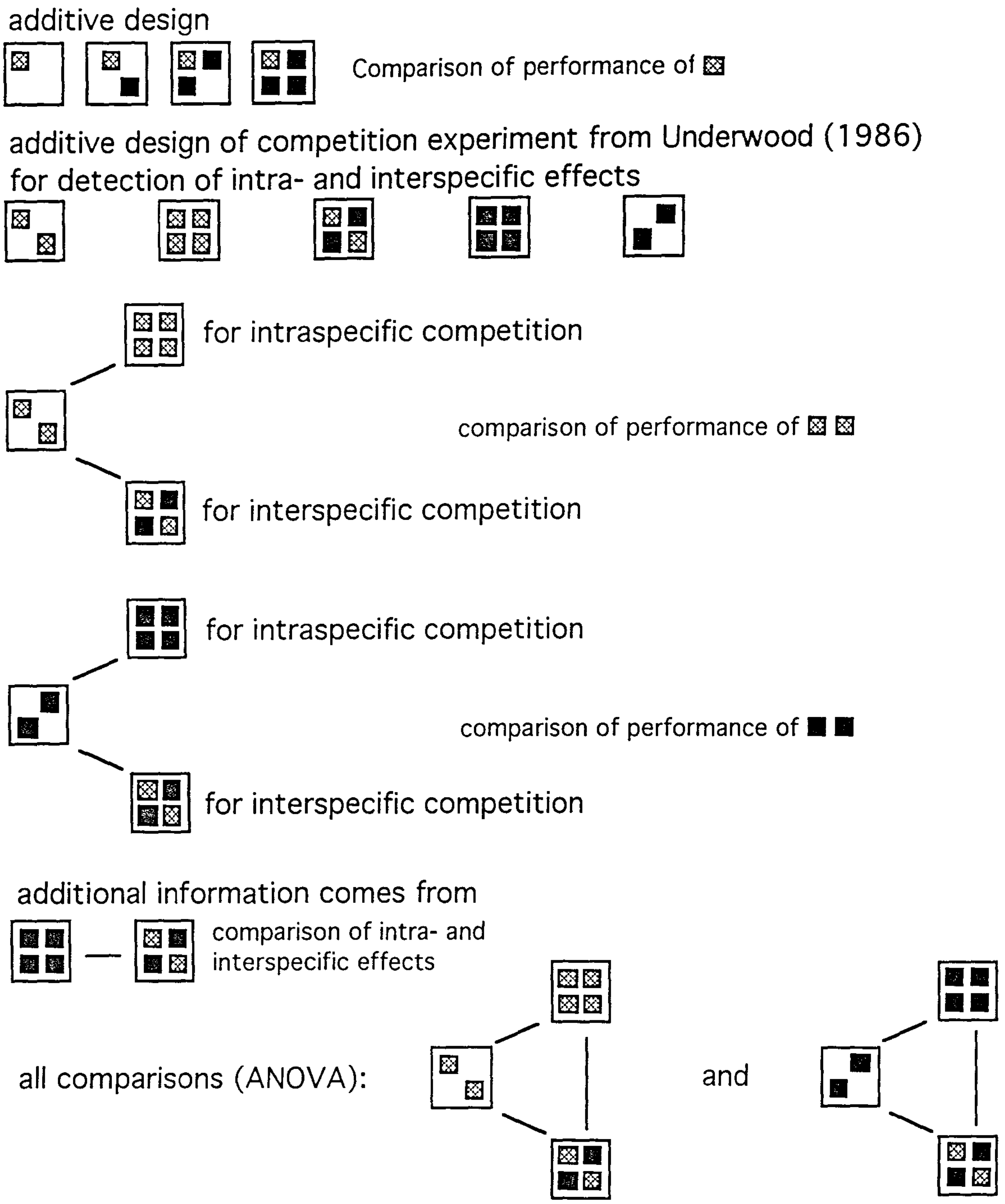


Figure 6: Additive design of competition experiments. Density of one species is held constant (crossed areas), while that of another (black areas) is varied (top). Additive design after Underwood (1986) to detect intra- and interspecific competition (middle) plus additional (substitutive) comparison as performed in the present study ('extended additive design', EAD, bottom). For further information see text.

are valid only for the total density used in the experiment and must not be generalized (Inouye & Schaffer 1981; Connolly 1986; Firbank & Watkinson

1990). Taylor & Aarssen (1989) pointed out that some workers did not ensure that single species densities (i.e. the density of only one of the two component species) were high enough to achieve constant final yield, when grown alone at that density, a prerequisite for competition experiments in their opinion.

Additive designs have been criticized, because total density and proportion vary together (Begon *et al.* 1990; Firbank & Watkinson 1990; Cousens 1991). In simple additive experiments, where the yield of a constant number of individuals of one species is compared, when grown together with different amounts of another species, it is not clear that yield suppression is due to interspecific effects by a competitive dominant rather than increased total density, i.e. an effect 'any' additional plant would have. In Underwood's (1986; see Table 1 and Figure 6) design it is possible to compare the intraspecific effects of additional plants of the same species to the interspecific effect of the same number of plants from a second species. Underwood compares both treatments to a 'control' (plots no. 1 and 5 in Table 1). The direct comparison of plot 2 with 3 (for species i) and plot 3 with 4 (for species j) is avoided by Underwood, presumably because of his disapproval of substitutive designs, but it is done here.

In the present study, replacement series were done at three total densities to meet the criticism of Inouye & Schaffer (1981) and successive authors. Certain treatments from the three parallel replacement series can be assembled into an additive design, analysable with ANOVA. Hence, in a combination of additive and replacement series design the shortcomings of both methods were overcome. I did not explicitly test wether the treatments achieved constant final yield. With analyses of self-thinning effects (see below), information should be obtained, as to whether monospecific treatments behaved according to the -3/2 power law and whether mortality was due to self-thinning. This should provide the information required to show that Taylor & Aarssen's (1989) suggestions (see above) were met in the experiments.

Other designs

A combination of additive and substitutive designs can be used to produce 'response surfaces'. These are either derived from 'addition series', when several replacement series with various total densities are performed simultaneously, or from factorial designs with a series of additive designs at different total densities (Cousens 1991). Both include a wide range of frequencies and total densities. For the addition series, these are of the same (triangular) form as in Figure 7. From the results, surfaces can be calculated that describe the complete range of outcomes of competition between two species. Additive designs and replacement series merely take "slices" through this surface (Firbank & Watkinson 1990). Addition series and response surfaces have been used in terrestrial plant studies more recently (Spitters 1983a; Firbank & Watkinson 1985; Law & Watkinson 1987), but, depending on the particular objectives, they may be unnecessarily complex (Cousens 1991). In the current study, the three replacement series formed in effect an addition series (albeit with rather few points on the surface spread out by the density axes of two species, see Figure 7). However, response surfaces were not calculated since I was only interested in competitive dominances rather than in yield responses under all possible mixture proportions and densities. Competitive dominances are best analysed by replacement series (Cousens 1991). These were performed at three total densities only to meet the criticism referring to density dependence of results (see above) and to have the possibility of comparing the outcomes of two analyses: classical replacement series methods *versus* additive design analysis similar to the design proposed by Underwood (1986; see below and Table 1).

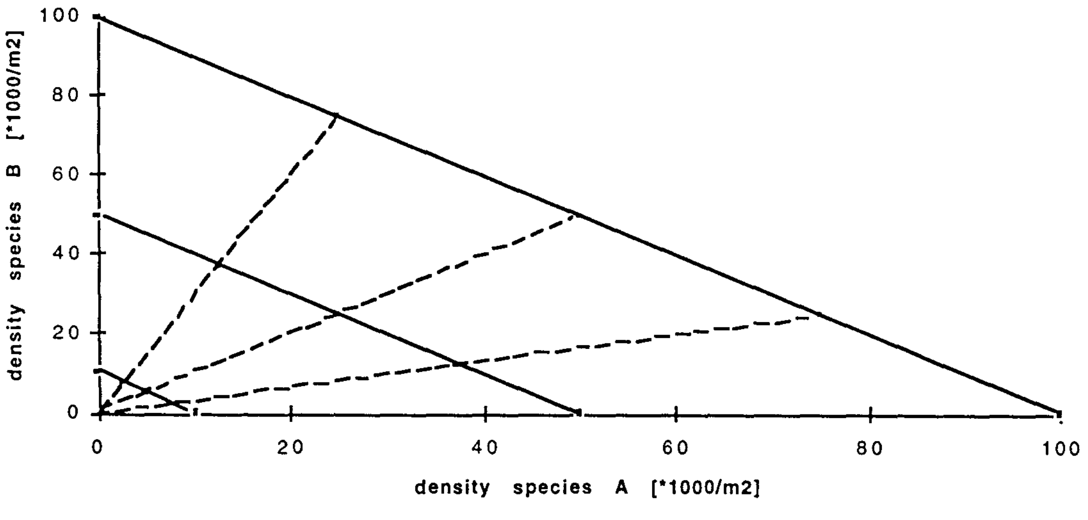


Figure 7: Densities of two species in a replacement series experiment as performed with Helgoland *Fucus* spp. Fixed mixture proportions (dashed lines and axes) were used at three total densities (=three replacement series experiments: solid lines).

While the above designs are implemented with plant stands artificially constructed by the experimenter, two other experimental designs are mainly concerned with detection of competition in established plant communities. 'Phytometers' (bioassays) are plants that are introduced into different communities. Their performance is measured with respect to the density and species composition of neighbours and may be compared with transplants to sites where other species were removed (Keddy 1989a). This design was used e.g. by Wilson & Keddy (1986a) to measure the intensity of competition along a lakeshore gradient.

In 'removal experiments' a species A is removed from stands were it grows together with another species B (or a more diverse community; e.g. Fowler 1981; Silander & Antonovics 1982). The performance of B from removal plots is then compared to control plots, where A was not removed. There are certain problems with this design, e.g. it is applicable only to species mixtures and thus excludes situations with monospecific stands (Keddy 1989a; Campbell *et al.* 1991).

This review of designs for competition experiments is by no means exhaustive.

Self-thinning and density-competition effect

In even aged monospecific populations, individual small plants will first grow as though without neighbours, but sooner or later, depending on density, plants will interfere and compete for the same resources (nutrients, light, space). At high densities three major effects of intraspecific competition have to be distinguished: the reduction of mean plant weight due to the 'competition-density effect', mortality due to 'self-thinning' and shifts in population structure (Firbank & Watkinson 1990).

The 'competition-density effect' describes the plastic response (reduced mean weight) of plants to high densities. Mathematical formulations (e.g. Hutchings & Budd 1981; Firbank & Watkinson 1990) describe relationships between mean plant weight and density for populations of different densities, but after the same period of growth (Hutchings & Budd 1981). The self-thinning rule, in contrast, describes the trajectory of a single population through time, after it had begun to suffer mortality from crowding. Relationships between density and mean plant weight are then

$$w = Kd^{-3/2} \qquad \text{or} \qquad \log w = \log K - 1.5 \log d$$

where w is mean plant weight, d is density and K a constant. This formulation is often referred to as the '-3/2 power law' and has been thought of as the only real law in plant ecology by some authors (J. Harper cited in Hutchings 1983). Here, capacity of plastic response to competition of individual plants is exceeded and they die. In a log density - log mean plant weight plot, plant populations are thought to increase in mean plant weight through time until they approach the line described by the formula above of -1.5 slope and an intersect with the ordinate at log K. Then populations will travel along this line to higher mean plant weights and lower densities.

The -3/2 power law has been applied to a wide range of terrestrial plant populations and there seemed to be generality not only in the slope of -3/2, but most values for log K lay between 3.5 and 4.3 (e.g. calculated for published data by White 1980). Firbank & Watkinson (1990) proposed a log K of 5.0 as parameter for an upper boundary line of all self-thinning lines.

Although the precise answer as to why the slope is -3/2 is uncertain (Hutchings 1983; Begon *et al.* 1990), several authors (Hutchings & Budd 1981; Westoby 1984; Whittington 1984; Norberg 1988) have theoretically derived the slope from considerations of the spatial relatonship between mass (volume, dimension to the power 3) and area (dimension to the power two, but the inverse has to be used, since density is 'per area').

By fitting data from the literature, Cousens & Hutchings (1983) extended the self-thinning rule to monospecific seaweed stands and again proposed the line with the equation $\log w = 4.3 - 1.5 \log d$ as a boundary condition, above which combinations of mean plant weight and density may not occur.

Westoby (1984) suggested that log biomass rather than log mean plant weight should be used for self-thinning plots, because mortality of small plants might apparently increase mean weight drastically, even if none of the surviving plants has grown at all. Weller (1987) showed that density and mean plant weight are not independent and proposed for this reason that total plot biomass should be used instead of mean plant weight. Despite his criticism of regression analysis as method most authors used to derive their self-thinning lines, and despite his evidence that there might not be only one general self-thinning line, successive authors have stayed with established methods of analysis (e.g. Martínez & Santelices 1992).

Additionally Westoby (1984) has emphasized that "average plants hardly exist". From the start of growth, variations among phenotypes and genotypes lead to alterations in the frequency distribution of plant weight (Hutchings & Budd 1981). From normal distribution, weight frequencies become more positively skewed and often achieve log-normality, where a few individuals account for most ot the population biomass ('size hierarchies', e.g. Martínez & Santelices 1992). Eventually, further development of skewness is prevented by the death of smallest plants of the population, which suffer most from competitive stress (Hutchinson & Budd 1981; Weiner & Thomas 1986).

Size inequalities may be expressed by the Gini coefficient as recommended by Weiner & Solbrig (1984) and Weiner & Thomas (1986).

2.2 Material & methods

2.2.1 Replacement series experiment in the field

Censuses of natural *Fucus* germling density in the Helgoland intertidal zone

Censuses in the Helgoland intertidal zone of subjectively "dense" stands of *Fucus* spp. were done in order to obtain adequate experimental densities. At the beginning of March 1993 numbers were assigned to 20 patches of *Fucus* germlings. Seven of them were chosen randomly and algae from 5 small areas (5x5 cm^2, coordinates with random number tables) of each were scraped from the rock and brought to the laboratory. Densities of samples and size class frequency distributions from subsamples were estimated. Maximum density for one small area was >2,800,000 germlings/m^2 at a length of 1.2 mm (median). It was not possible to determine the species of *Fucus* safely.

The census was repeated in Juli 1993, when germlings had grown. Patches of *Fucus spiralis* juveniles (1-2 cm length) revealed densities up to 70,000 shoots/m^2. Since experimental size of fucoids was 1-1.5 cm, this density was considered to approximate natural (maximum) density, although only *F. spiralis* seems to establish such dense stands of juveniles (pers. observations and see Schonbeck & Norton 1979a; but see Creed *et al.* 1996b for similar data for *F. serratus*).

Replacement series experiment

For experimental estimation of competition the replacement series design (de Wit 1960, see 2.1) was used. Here, the original design was extended by using 3 replacement series with 3 total densities.

Experimental densities of D1=10,000, D2=50,000 and D3=100,000 shoots/m^2 were chosen for the experiment so that the highest field density for fucoid germlings of the experimental size (see above) and a range on either side were included (Figure 7).

Following the established protocol, plots of replacement series were set up with young stages of plants. In the present work, the replacement series experiments were done with mixtures of *Fucus* species living in contiguous zones in the Helgoland intertidal zone: *Fucus serratus* (S) in mixture combination with *F. vesiculosus* (V), mixture combinations of *F. vesiculosus* and *F. spiralis* (P), and monocultures of all three species. Mixture proportions of 25:75, 50:50 and 75:25% were used (as shown in Figures 4 and 7 and Table 2). Each configuration was replicated 5 times.

For a test of the applicability of the competitive hierarchy hypothesis, it was not necessary to test competitive interactions between *F. spiralis* and *F. serratus* directly. This may have been desirable, since on sandstone blocks in the upper intertidal zone both species may occur in close proximity, although they occur separatedly on more clearly zoned seawalls. However, limited facilities made the performance of such experiments impossible.

Sampling and preparation of algal material

Shoots of all three Helgoland species of *Fucus* were cultivated from zygotes in the laboratory on unglazed backsides of ceramic tiles (15x15 cm^2).

To obtain germlings, fertile plants were collected in the NE-Intertidal (*F. serratus* and *F. vesiculosus*) or from concrete blocks in front of the eastern seawalls (*F. spiralis*) of Helgoland (Figure 3). For the dioecious *F. serratus* and *F. vesiculosus*, sexes were separated. The conceptacles of male plants are orange when ripe. Green conceptacles were either females or unripe males. Sex of green receptacles was determined microscopically.

Separation of sexes was done to control the ratio of male and female plants sampled in the field and of the ratio of released male and female gametes.

Table 2: Configurations of treatments used in replacement series. Relative (%) and total (N) frequencies per 10x10 cm^2. Total densities D1= 10,000; D2=50,000; D3=100,000 shoots/m^2. V = F.ves. = *Fucus vesiculosus*; S = F.ser. = *F. serratus*; P = F.spir. = *F. spiralis*. Each configuration was replicated 5fold. The same monocultures of *F. vesiculosus* were used for S:V- and V:P-replacement series.

Abbreviation	total dens.	F.ser. %	F.ves. %	F.spir. %	F.ser. N	F.ves. N	F.spir. N
V:P 0:4	D1	-	0	100	-	0	100
V:P 0:4	D2	-	0	100	-	0	500
V:P 0:4	D3	-	0	100	-	0	1000
V:P 1:3	D1	-	25	75	-	25	75
V:P 1:3	D2	-	25	75	-	125	375
V:P 1:3	D3	-	25	75	-	250	750
V:P 2:2	D1	-	50	50	-	50	50
V:P 2:2	D2	-	50	50	-	250	250
V:P 2:2	D3	-	50	50	-	500	500
V:P 3:1	D1	-	75	25	-	75	25
V:P 3:1	D2	-	75	25	-	375	125
V:P 3:1	D3	-	75	25	-	750	250
V:P 4:0 = S:V 0:4	D1	0	100	0	0	100	0
V:P 4:0 = S:V 0:4	D2	0	100	0	0	500	0
V:P 4:0 = S:V 0:4	D3	0	100	0	0	1000	0
S:V 1:3	D1	25	75	-	25	75	-
S:V 1:3	D2	25	75	-	125	375	-
S:V 1:3	D3	25	75	-	250	750	-
S:V 2:2	D1	50	50	-	50	50	-
S:V 2:2	D2	50	50	-	250	250	-
S:V 2:2	D3	50	50	-	500	500	-
S:V 3:1	D1	75	25	-	75	25	-
S:V 3:1	D2	75	25	-	375	125	-
S:V 3:1	D3	75	25	-	750	250	-
S:V 4:0	D1	100	0	-	100	0	-
S:V 4:0	D2	100	0	-	500	0	-
S:V 4:0	D3	100	0	-	1000	0	-

Fertile tips (receptacles + non-reproductive tissue) of *Fucus* thalli were cut to convenient segments of ca. 15 cm length and brushed thoroughly under running seawater to remove adhering contaminant algae. Brushed receptacles were submerged in tap water for 10-15 min, dried lightly with tissue paper and stored in covered trays for at least one night and up to 5 d at 10° C to stimulate later gamete release (e.g. Quatrano 1980; Kremer 1981).

For the following steps, only sterile seawater was used (heated for at least 3 h in a steambox (Fa. Fritz Goessner, Hamburg) in 12 l Nalgene® bottles). Receptacles were rinsed with sterile seawater to remove discharged adhering antheridia or oogonia. Thalli were suspended in an inverted position in funnels (sediment funnels with drainage taps) filled with sterile seawater and illuminated from above with a halogen (Osram Power-Star HQI-TS 150 W ND2) lamp (Wright & Reed 1990). Over a period of up to 5 h, gametes were discharged and accumulated at the bottoms of the funnels. By this means, spermatozoids and eggs (sedimented at bottom of funnel) were obtained from *F. serratus* and *F. vesiculosus*, and zygotes (sedimented) from monoecious *F. spiralis*. Gametes and/or zygotes were withdrawn from the bases of the funnels leaving contaminating mucus and diatoms in the upper layers of seawater.

For dioecious *Fucus* spp., a quantity of spermatozoid suspension was mixed with the eggs and and left for 30 min for fertilization to proceed. Zygotes were washed 4 times with sterile seawater to remove mucus and unopened gametangia.

Six ceramic tiles (15x15 cm^2, with drilled central hole) were placed faceside down in plastic trays (30x50x6 cm^3). Before installation, the unglazed backsides of tiles were cleaned of glaze spots. Trays were filled with boiling water to kill algal spores and to saturate tiles with water. Unsaturated, dried tiles tend to release air bubbles, interfering with zygote settlement. After 10 min, hot tap water was removed, tiles were submerged in sterile seawater and moved to constant temperature rooms at 13° C and 16:8 h illumination (60 μmol photons/m^2/s). A suspension of zygotes was poured into each tray and agitated by filling the tray with additional sterile seawater immediately afterwards. In this way, zygotes were dispersed evenly and sank to the surface of the ceramic tiles where they attached and germinated.

Zygotes of *Fucus serratus* and *F. vesiculosus* were sown on ceramic tiles from the end of February to April 1993. Later in spring, extensive deterioration of receptacles occurred. Zygotes of *F. spiralis* were sown from the beginning of April to May 1993. *F. spiralis* normally becomes fertile in April on Helgoland (Kornmann & Sahling 1977).

Cultivation of *Fucus* for the experiment

Germlings were grown to a length of approximately 1 cm at 13° C and 16:8 h illumination (60-80 µmol photons/m^2/s). Water was changed every week. Fifty-percent strength Provasoli enrichment was added to the seawater (Starr & Zeikus 1987). To bottles containing 12 l sterile seawater 0.4 ml of a saturated GeO_2 solution were added to obtain a concentration of 0.18 mg/l as recommended by Markham & Hagmeier (1982). Markedly higher concentrations (ca. 5 mg/l), tested at a few cultures heavily contaminated with diatoms, induced apical necrosis as described by McLachlan *et al.* (1971), presumably a consequence of distorted cell wall organization (Yang 1993). Fucoids treated with high concentrations of GeO_2 were not used in experiments, though they seemed to grow normally when the treatment with high concentration ceased.

Growth rate was low, since only low levels of light could be supplied to the large amount of algae. To avoid shading, trays were not covered. With uncovered trays, contaminating algae entered the cultures. Diatoms occurred regularly, but their rate of cell division was kept low by the addition of GeO_2 (see above). Green algae and blue green algae often became established at the water surface level on the walls of the trays. When green algae (e.g. *Enteromorpha* spec.) contaminated experimental surfaces, tiles were removed from the cultures, if necessary, whole trays were removed. To ensure sufficient algae at the end for the experiment, cultures were started with ca. 100 tiles each bearing *F. serratus* and *F. spiralis* and ca. 160 tiles of *F. vesiculosus*, since the latter species was needed for both mixtures.

In August 1993 most of the juveniles had reached a length of 1 cm.

Assembling the replacement series experiment

To "harden" laboratory-grown juveniles, tiles bearing plantlets were exposed to field conditions for 1 wk. In August 1993 171 *Fucus* bearing ceramic tiles (45 S, 45 P, 81 V) were fixed inside 19 exclosure cages bolted to the red sandstone of the Helgoland NE-intertidal zone at the level at which *Fucus serratus* occurs. Each cage was constructed with enough space for 9 ceramic tiles (3x3, for construction see Figure 8).

Tiles were returned to the laboratory after the hardening exposure and ca. half were cut with a diamond saw into 1 cm^2 segments. Damaged or very small and/or too dense juveniles were removed from tile fragments. Shoots

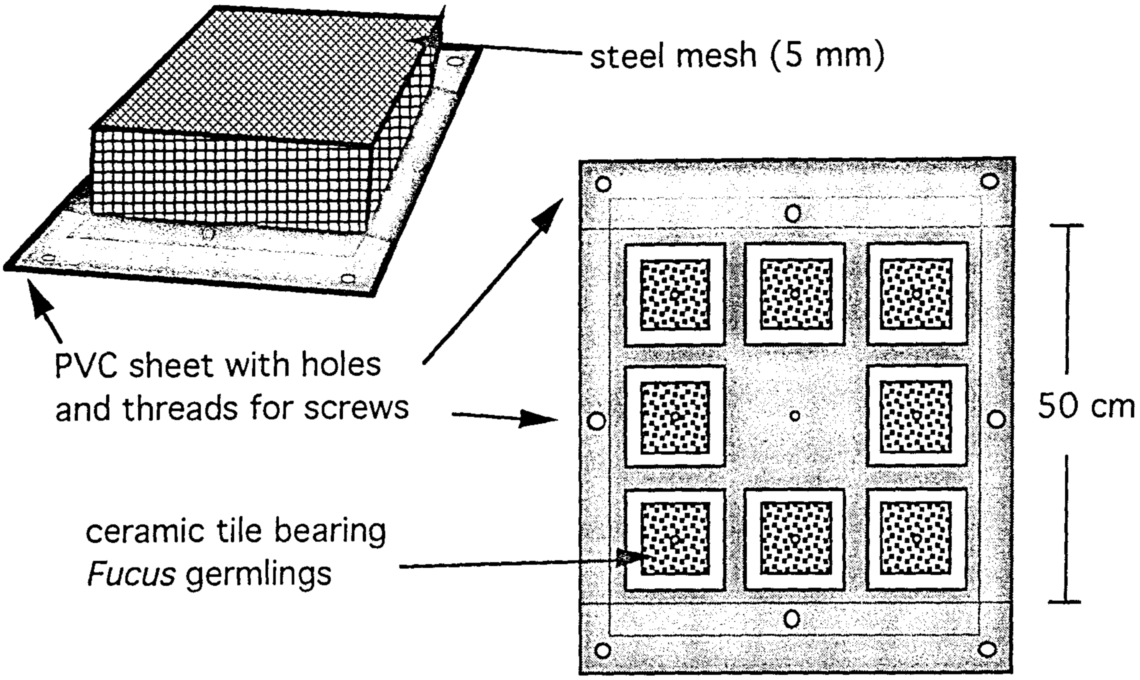


Figure 8: Construction of exclosure cages used for the competition experiment in the Helgoland NE-Intertidal. PVC sheets were bolted to the red sandstone. A cage with steel meshed sides and top (5 mm mesh of 1 mm wire) and a maximum of 9 ceramic tiles were fixed to the PVC sheet.

remaining on each tile fragment were counted. Tile fragments were arranged to form the distinct mixture proportions of the replacement series (see above). An abbreviation of the species name was carefully inscribed on each tile fragment with a pencil.

The central 100 cm^2 portions of the unglazed backsides of another unused set of ceramic tiles (15x15 cm^2) were covered with a layer of 'Sea goin' Poxy Putty' (Permalite, Newport Beach, USA). The labelled tile fragments bearing juveniles were pressed into the glue in a regular dispersion pattern. In mixture plots, the 2 species were mixed as homogeneously as possible. The glue was pushed over the edges of the tile fragments. Afterwards, experimental tiles were covered with wet paper towels and kept in warm air, while the glue hardened. Tiles were then stored in tanks with running seawater for one day to flush out toxic materials. Afterwards, tiles were stored in plastic trays, until all assembly was complete.

Lengths of 25 randomly chosen individuals of each species were measured on each experimental tile. Using a custom random-generator program, experimental tiles were assigned spaces randomly within 17 cages installed in the field. No more than one of five replicates was permitted in one exclosure cage. Installation was completed in the field on 1993/09/03. Experimental units, their abbreviations and the frequencies of the species in mixed and monocultures are listed in Table 2.

There were no tests for cage artefacts in this experiment. The procedural controls which are normally used in cage experiments (e.g. fully meshed cage, roof only, no cage) concern other objectives, and were not necessary in this case. The purpose of caging was to completely prevent littorinid grazing and was not designed to vary grazer density (to zero) for a test of grazer effects as in other experiments. It is assumed that interaction of cages with treatments is constant. As one of the assumptions of the competitive hierarchy model is that competitive dominances do not vary under different environmental conditions as long the fundamental niches of the species are met, even the experiments with cage artefacts are a genuine tests of the competitive hierarchy model.

Maintenance of competition experiment in the field

After installation of the experiment (in September), *Fucus serratus* plants surrounding the cages started to become fertile again. Data of the dispersal capability of *Fucus* range from 20 cm (Chapman 1989, 1990a) for *F. spiralis* to 2.5 m for *F. serratus* (Arrontes 1993). Hence *Fucus* plants should have been removed in a circle of >2 m around the exclosure cages. The Helgoland intertidal belongs to a national park, so a removal of another several m^2 algal cover would not have been desirable. As a compromise, the fertile tips of all *Fucus* plants that reached into a circle of 3 m around the cages were cut off with pruning shears regularly. Experiments by McCook & Chapman (1992) indicated a high regeneration ability in *Fucus*. At the end of the experiment only a few newly settled fucoids with a maximum length of about 5 mm were found on the ceramic tiles.

In the winter months, sediment was removed from the cages every 1-2 wk, when tides allowed access to the area. Cages were doused with seawater. Occasionally filamentous algae that had settled on the parts of the tiles not covered with glue and that accumulated sediment were scraped away.

In spring, *Enteromorpha* sp., *Ulva* sp. and *Porphyra* sp. settled on the tiles and elsewhere inside and on the cages. Large thalli of green algae were removed carefully from the tiles with forceps. Cages were brushed regularly, but it was found more effective to torch the algae that settled on the steel mesh.

On 1994/06/05, when fucoids on some plots had reached a length that surely influenced neighbouring experimental tiles, the experiment was terminated and tiles were returned to the laboratory.

Data collection

Prior to installation, the lengths of 25 randomly chosen individal *Fucus* juveniles (from each species in mixtures) were measured from each plot. The lengths and dry weights were measured for 50 juveniles of each species not used in the replacement series. With polynomial regression equations the lengths (L, in cm) of the juveniles on the experimental plots give an estimate of the average mass (in mg) of individual shoots and, with knowledge of the density, of the total starting biomasses of each *Fucus* species in each plot.

$$\begin{aligned}
\mathrm{mass}_{F.serr.} &= 4.516547 * L^2 - 1.916924 * L + 0.539507 && R^2 = 0.99 \\
\mathrm{mass}_{F.ves.} &= 3.616290 * L^2 - 2.033939 * L + 0.995531 && R^2 = 0.98 \\
\mathrm{mass}_{F.spir.} &= 2.552320 * L^2 + 4.453475 * L - 2.060086 && R^2 = 0.91
\end{aligned}$$

At the end of the experiment the remaining shoots were separated to species, censused and their lengths and dry weights measured individually. Dry weight was obtained by drying (at 60° C for 3 d) thalli that had been rinsed in tap water.

Statistical analyses

Replacement series graphs

Replacement series graphs were drawn by plotting final yield of each component species of a replacement series experiment against its proportion in mixtures. This was done for each starting density (D1-D3) from both species mixtures (*F. serratus* with *F. vesiculosus* and *F. vesiculosus* with *F. spiralis*). Deviation from linearity was assessed visually.

Crowding coefficients

Individual and relative crowding coefficients (see 2.1) were calculated from initial dry weight of seedlings and final biomass. Initial weight was calculated with polynomial regression equations as indicated above.

Crowding coefficients were calculated for mixtures of *F. serratus* with *F. vesiculosus* and mixtures of *F. vesiculosus* with *F. spiralis*. They were calculated for each density (D1-D3) separately.

Input-output ratio diagrams

In input-output ratio diagrams (Khan *et al.* 1975) $\log(\omega_i/\omega_j)$ is plotted against $\log(\sigma_i/\sigma_j)$, with ω_i = final biomass per plant of species i and σ_i = initial dry weight of species i. Initial biomass was calculated with polynomial regression equations from lengths of 25 individuals of each species per experimental unit. Input-output diagrams were plotted for mixtures of *F. serratus* with *F. vesiculosus* and for mixtures of *F. vesiculosus* with *F. spiralis* for each total density separately.

Comparison of intraspecific and interspecific interactions in additive designs

As indicated above (2.1), in substitutive designs of competition experiments such as the replacement series, individuals of one species are 'replaced' by individuals of a second species in the different plots (Figure 4). The total density is the same in all plots. In contrast, in additive designs, the density of one species is held constant while that of the other is varied (Firbank & Watkinson 1990). Such a design can be used to compare the effects of intra- and interspecific competition on individuals of a species i (Underwood 1986; Table 1, Figure 6). The competition experiment performed here had a replacement series design, but some plots can also be analysed according to the additive design shown in Figure 6. Figure 9 shows an application of the additive design from Underwood (1986) to replacement series performed with *F. serratus* and *F. vesiculosus*. The same was done for the replacement series experiments with mixtures from *F. vesiculosus* and *F. spiralis*. As indicated above an additional comparison was included in the experimental design of Underwood. This full design will be called 'extended additive design' and abbreviated EAD.

Differences in yields of one species under different competitive conditions were tested for significance with 1-way ANOVA. Student-Newman-Keuls test, that has been proposed by Creese & Underwood (1982) and Underwood (1986) for *post hoc* comparisons of Underwood's design, was not used following recommendations of Day & Quinn (1989). They recommended Tukey's test that was used here.

Extra information on intra- and interspecific effects can be drawn from comparisons of yields from incomplete additive designs shown in Figure 10. Comparisons A and B are concordant with parts from Underwood's (1986) additive designs. Comparisons C and D correspond to the "additional" comparisons shown in Figure 9 (i.e. comparison of substitutive experimental units).

These selected treatments from replacement series experiments will be referred to as 'mixed additive substitutive design' (MASD) hereafter.

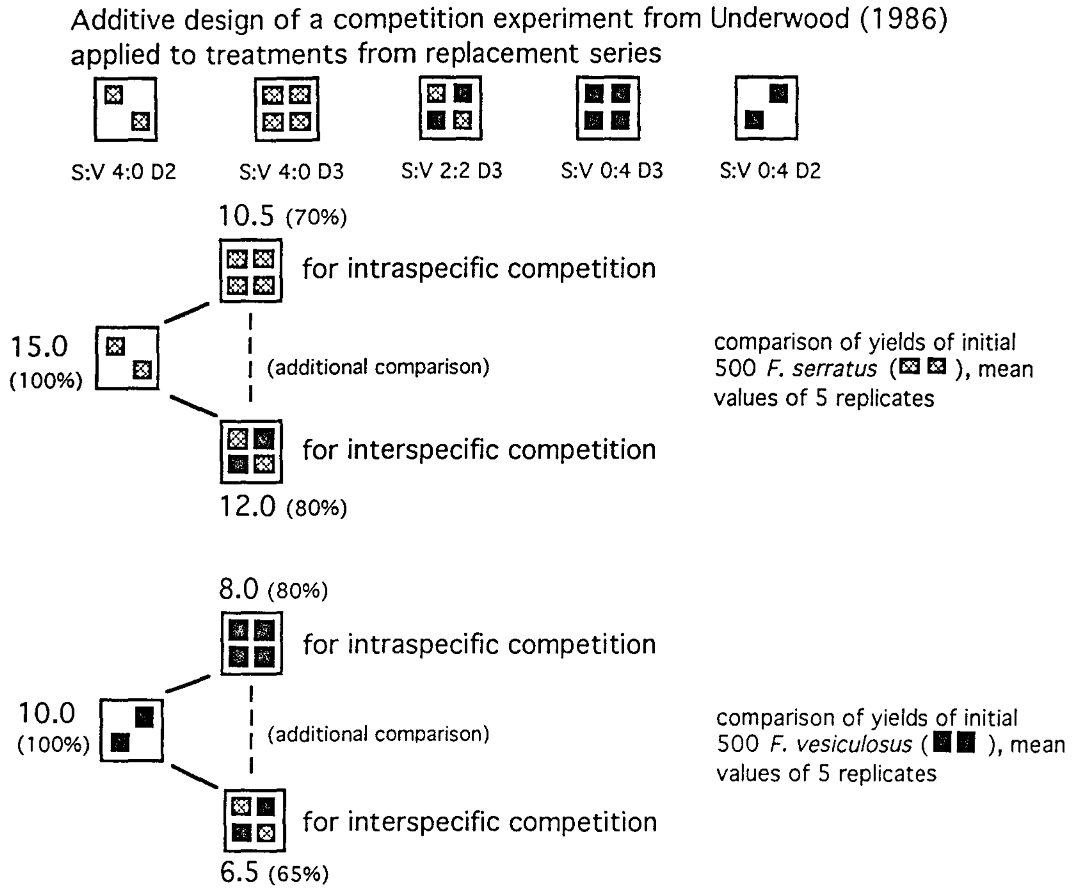


Figure 9: Application of the 'extended additive design' (EAD, compare Figure 6) to certain treatments from the replacement series experiments performed in the present study. As example, treatments from replacement series with *F. serratus* and *F. vesiculosus* are given (top, one crossed area symbolizes 250 *F. serratus*, one black area 250 *F. vesiculosus*). Comparisons of (theoretical) mean yields are shown. As example, a theoretical competitive asymmetry *F. serratus* > *F. vesiculosus* is given: yield of *F. serratus* is reduced by intraspecific competition more (to 70%) than by interspecific competition (to 80%), while *F. vesiculosus* is stronger affected by interspecific competition (to 65% yield compared to 80%).

Prior to ANOVA, homoscedasticity of data was tested with Cochran's test. When necessary, data were log-transformed to achieve homoscedasticity.

To obtain the ranking predicted by the competitive hierarchy hypothesis, competition should be asymmetric. In the opinion of Keddy, competition is asymmetric in two-species pairs when the dominant species is more negatively impacted by intraspecific competition compared to interspecific competition and the subordinate species suffers more from interspecific effects (Shipley & Keddy 1994).

For example, in Figure 9, *F. serratus* would be competitively dominant over *F. vesiculosus* with the imaginary percentages of yield as given in brackets (i.e. relative to the yield of the low density monoculture).

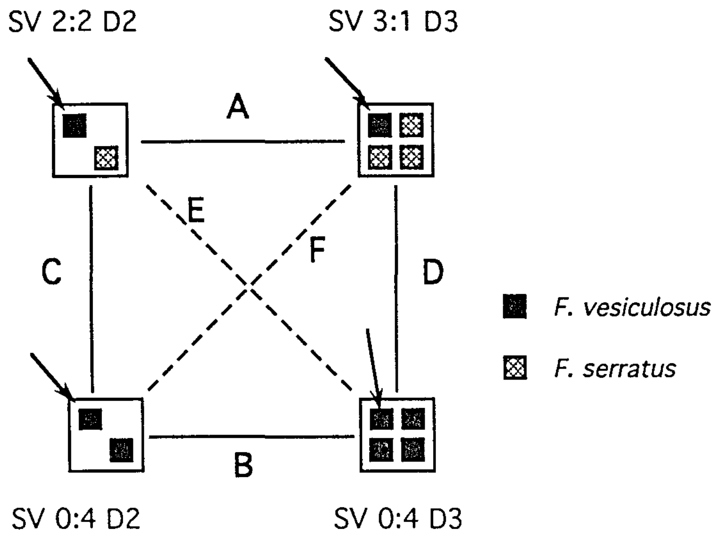


Figure 10: Additional additive and substitutive comparisons ('mixed additive substitutive design', MASD) between certain treatments from replacement series experiments, analysable with ANOVA. An example is presented here where the intra- and interspecific effect on the yield of an initial 250 *F. vesiculosus* germlings (symbolized as black area indicated with an arrow) is given. 'A' compares the interspecific effect of additional 500 *F. serratus*, 'B' the intraspecific effect of additional 500 *F. vesiculosus*. 'C' and 'D' depict substitutive comparisons between intra- and interspecific effects at D2=500 and D3=1000 shoots/10x10 cm^2, respectively. E, F: included in 'unplanned comparisons' in one-way ANOVA but irrelevant, since total density and species combination are changed simultaneously. For meaning of abbreviations (e.g. "SV 0:4 D3") see Table 2.

Gini coefficients

Gini coefficients, as recommended by Weiner & Solbrig (1984), were calculated for monospecific *Fucus* stands to detect whether self-thinning led to a decrease in size inequality. Bendel *et al.* (1989) found the Gini coefficient to be more robust than the moment skewness coefficient and the coefficient of variation.

Gini coefficients (G) were calculated as

$$G = \frac{\sum_{i=1}^{n}\sum_{j=1}^{n}\left|x_i - x_j\right|}{2n(n-1)\bar{x}},$$

where x_i and x_j are dry weights of individual plants, as recommended by Weiner (1985) and Bonan (1988) as an unbiased estimate and being related by multiplication with the factor (n-1)/n with formulas given by others (Bendel *et al.* 1989). The Gini coefficient ranges between 0 and 1, 0 indicating perfect equality and 1 inequality.

2.2.2 Replacement series experiment in the laboratory

Experimental design and maintenance of the experiment

The replacement series design used in this experiment has been described in detail in 2.1. The same species mixtures and mixture proportions were used as in the field experiment (2.2.1). The cultivation of juvenile fucoids was as described in section 2.2.1, except that in the laboratory experiment, algae were not hardend in the field.

Plantlets of ca. 1 cm length were scraped from the ceramic tiles on which they had been cultivated. They were arranged to form the portions of mixtures or monocultures of the replacement series. The lengths of 25 randomly chosen thalli were measured to obain with a length-dry weight-regression an estimate of the starting algal mass. In this competition experiment, algae were cultivated in 3 l preserving jars containing 2 l of sterile seawater. The density per base area was the same as in the competition experiment in the field. The diameter of a jar was 12.9 cm, hence e.g. 130 thalli were used to obtain the lowest density (D1) of 10,000 shoots/m^2. The jars 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 16:8 h L:D (160 µmol photons/m^2/s). The jars were rearranged randomly after every change of water. This was done every 10 d in the first 4 wk of the experiment, then, when thalli had grown, water was changed every 4 d. By that time it was possible to pour the content of a jar into a sieve (1 mm mesh) and to rinse algae with running tap water without losing them. The jar was cleaned of bacteria and exudates with a paper tissue soaked with ethanol and rinsed with tap water thoroughly. To the 2 l of sterile seawater, GeO_2 (0.18 mg/l) and Provasoli enrichment (Starr & Zeikus 1987) was added. The amount of Provasoli enrichment was increased from 20 ml to 40 ml in the course of the experiment, corresponding to 1/2 and full Provasoli formula, respectively.

The experiment was run from 1993/11/06 until 1994/03/01 (113 d). Each experimental unit was replicated twice. The entire experiment was repeated from 1994/10/01 to 1995/01/01 (120 d), again with duplication. The experiments in 1993 and 1994 were conducted as similar as possible.

Data collection and statistical analyses

At harvesting, the species were separated from mixed cultures. Dry weight was estimated after 3 d at 60° C for each species from each jar. For jars of lowest density (D1) in the first experiment at run the lengths of individual shoots were estimated. Since no algae were lost in this experiment, and every thallus produced on average 7-9 shoots (depending on species) during cultivation, it was not possible to measure algae individually from higher density jars.

2.3 Results

2.3.1 Replacement series experiment in the field

Replacement series graphs

Replacement series graphs for mixtures of *Fucus serratus* and *F. vesiculosus* are shown in Figure 11 (left). At none of the 3 densities I found a linear relationship between yield and mixture proportion. Yields of *F. vesiculosus* were elevated in all mixed cultures, while yields of *F. serratus* were depressed. Hence, for *F. vesiculosus*, the curves are totally (D2) or partially (D1 and D3) convex, those of *F. serratus* are of a concave shape. This outcome indicates that *F. vesiculosus* succeeds at the expense of *F. serratus* (Khan *et al.* 1975).

In replacement series graphs of *F. vesiculosus-F. spiralis* mixtures (Figure 11, right), curves of *F. vesiculosus* have a convex shape (partially at D1 and D3),

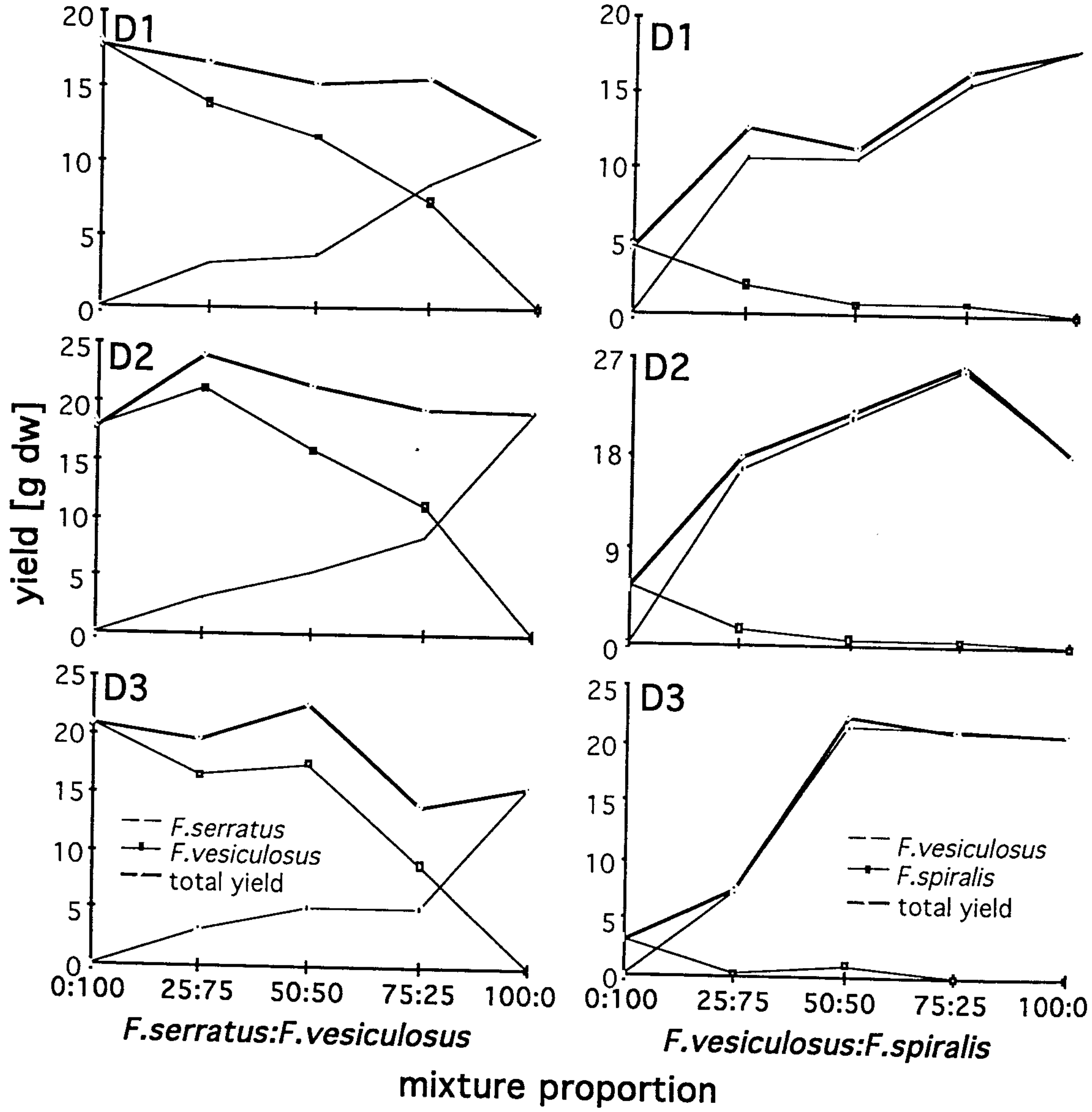


Figure 11: Replacement series graphs from replacement series experiments with *Fucus serratus* and *F. vesiculosus* (left) or with *F. vesiculosus* and *F. spiralis* (right) at three total densities (D1=100, D2=500, D3=1000 initial shoots per 10x10 cm^2). Mean values of 5 replicates.

while those of *F. spiralis* are concave indicating that *F. vesiculosus* succeeded at the expense of *F. spiralis* (Khan *et al.* 1975). *F. spiralis* performed poorly in most plots. In mixtures of 250 *F. spiralis* with 750 *F. vesiculosus* (V:P 3:1 D3), in only one of five replicates was there any survival of a few thalli of *F. spiralis.*

Thus, *F. vesiculosus* is competitively dominant over both other *Fucus* species according to field experiments.

Crowding coefficients

All but one individual crowding coefficients for *Fucus serratus* K_S were <1 (Table 3). This means that growth of *F. serratus* was depressed in mixtures (compared with its monocultures). All individual crowding coefficients except one for *F. vesiculosus* K_V from the same mixtures were >1, indicating, that growth of *F. vesiculosus* was elevated in these mixtures. All values of K_V were

Table 3: Individual and relative crowding coefficients from replacement series experiments with *Fucus serratus* and *F. vesiculosus* at three densities (D1-D3). Experiments were performed in the intertidal of the island of Helgoland. Mean values of 5 replicates. $K_{serratus}$ and $K_{vesiculosus}$ are individual crowding coefficients. K_{SV}= relative crowding coefficient *F. serratus* on *F. vesiculosus.* K_{VS}= relative crowding coefficient *F. vesiculosus* on *F. serratus.*

		F. serratus : F. vesiculosus		
	density	**25:75**	**50:50**	**75:25**
$K_{serratus}$	D1	0.90	0.60	1.02
	D2	0.67	0.65	0.53
	D3	0.51	0.79	0.91
$K_{vesiculosus}$	D1	1.08	1.25	1.70
	D2	1.30	1.41	1.81
	D3	1.48	0.96	1.78
K_{SV}	D1	0.83	0.48	0.60
	D2	0.52	0.47	0.29
	D3	0.35	0.82	0.51
K_{VS}	D1	1.20	2.10	1.66
	D2	1.94	2.15	3.44
	D3	2.89	1.22	1.95

bigger than the corresponding K_s, hence all relative crowding coefficients K_{vs} were >1, all $K_{sv}<1$. This means that *F. vesiculosus* succeeded relatively to *F. serratus* in all mixtures (Khan *et al.* 1975).

In replacement series experiments with *F. vesiculosus* and *F. spiralis* individal crowding coefficients for *F. vesiculosus* K_v were >1 and K_p <1 for *F. spiralis* for all but 2 mixtures (Table 4). All K_v were bigger than corresponding K_p, as consequence K_{vp}s>1 and K_{pv}s<1 for all mixtures. This means, that *F. vesiculosus* succeeded relative to *F. spiralis*, confirming the above analysis using replacement series graphs.

Table 4: Individual and relative crowding coefficients from replacement series experiments with *Fucus vesiculosus* and *F. spiralis* at three densities (D1-D3). Experiments were performed in the intertidal of the island of Helgoland. Mean values of 5 replicates. $K_{vesiculosus}$ and $K_{spiralis}$ are individual crowding coefficients. K_{vp}= relative crowding coefficient *F. vesiculosus* on *F. spiralis*. K_{pv}= relative crowding coefficient *F. spiralis* on *F. vesiculosus*.

		F. vesiculosus : F. spiralis		
	density	**25:75**	**50:50**	**75:25**
$K_{vesiculosus}$	D1	1.90	1.30	1.24
	D2	1.42	1.81	1.89
	D3	1.02	1.07	1.19
$K_{spiralis}$	D1	0.57	0.70	1.01
	D2	1.03	0.61	0.68
	D3	0.44	0.47	0.15*
K_{vp}	D1	3.34	1.85	1.23
	D2	1.37	2.98	2.77
	D3	2.30	2.30	7.93*
K_{pv}	D1	0.30	0.54	0.81
	D2	0.37	0.34	0.36
	D3	0.44	0.44	0.13*

* in 4 of 5 replicates of this treatment (V:P 3:1 D3) none of the *F. spiralis* survived. Here final biomass only of the experimental tile with surviving plants of *F. spiralis* was used for calculation of crowding coefficients.

Input-output ratio diagrams

At each of three densities, the *F. serratus*:*F. vesiculosus* ratio diagram is a line that falls below the line of slope 1.0, parallel to this line (Figure 12a). Hence,

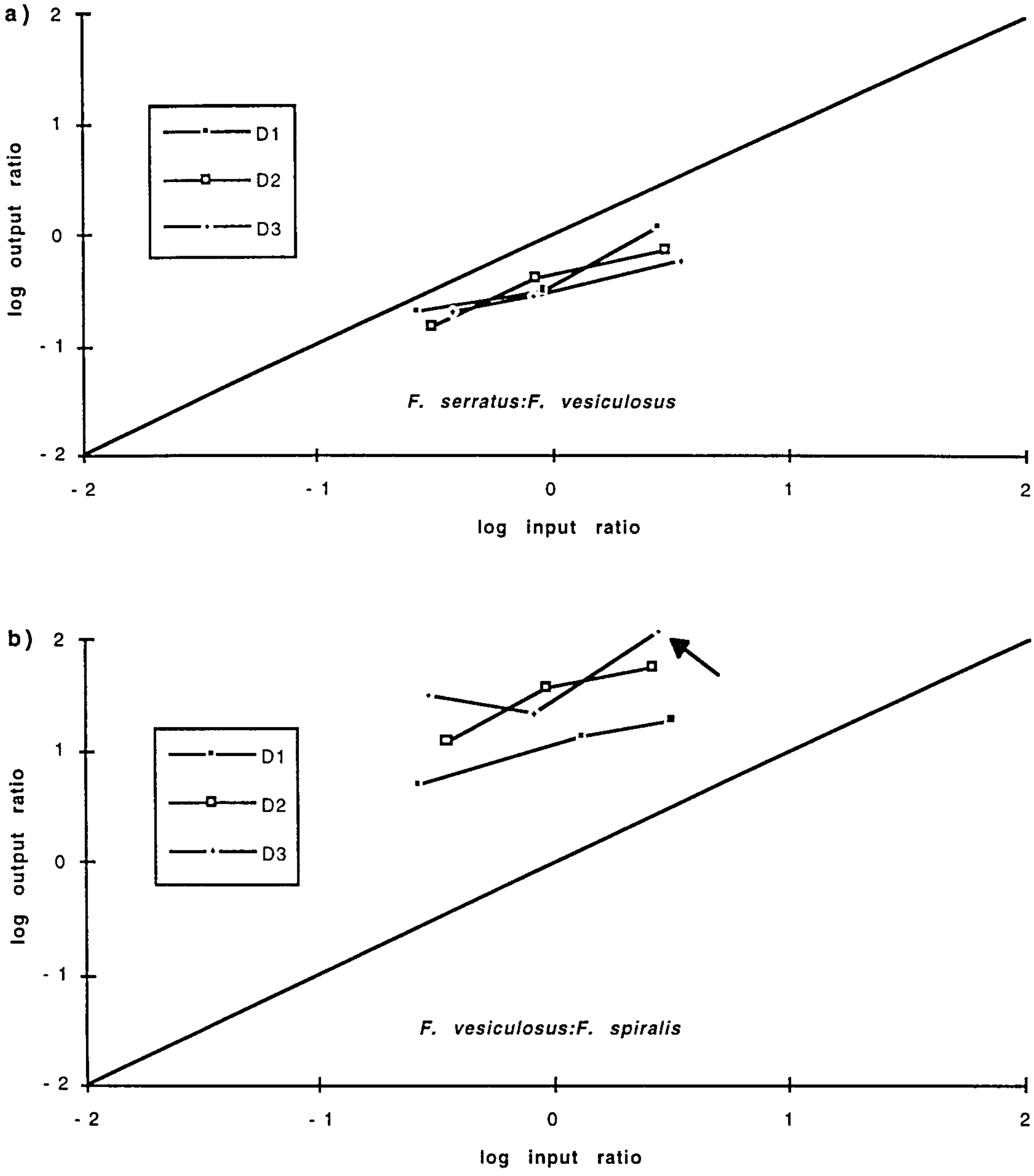


Figure 12: Ratio diagrams from replacement series experiments with a) *Fucus serratus* and *F. vesiculosus* or b) *F. vesiculosus* and *F. spiralis* at three total densities (D1=100, D2=500, D3=1000 initial shoots per 10x10 cm^2). The logarithm of the output ratio [a): *F. serratus*:*F. vesiculosus*, b): *F. vesiculosus*:*F. spiralis*] is plotted against the log input ratio. Mean values of 5 replicates.

all output ratios are less than input ratios. This configuration is indicative for unstable mixtures and predicts that *Fucus serratus* would be driven to extinction by *F. vesiculosus* (Khan *et al.* 1975).

Ratio diagrams from *F. vesiculosus*:*F. spiralis* replacement series at D1 and D2 form lines more or less parallel and above the slope 1.0 (Figure 12b). At the highest density (D3) only mean value data for mixtures V:P 1:3 and V:P 2:2 can be shown. At the mixture proportion V:P 3:1, in only 1 of 5 replicated plots a few thalli of *F. spiralis* survived. The data point (labelled with an arrow in Figure 12b) comprises only the inital weight and final biomass from the single positively yielding replicate for *F. spiralis*. All data points for *F. vesiculosus*-*F. spiralis* mixtures lie above the line of unit slope, hence, in all mixtures more biomass of *F. vesiculosus* was gained per initial mass at the expense of *F. spiralis* and, through time, *F. spiralis* would go to extinction.

Thus, the analysis through input-output diagrams is in accordance with the graphical analysis and with crowding coefficients.

Comparison of intraspecific and interspecific interactions in additive designs

Information on intra- and interspecific effect was obtained from a few plots of the replacement series experiments that fit to the design suggested by Underwood (1986) (EAD) and shown in Table 1.

Additional information was drawn from comparisons of single treatments from the replacement series, in which the yield of 250 thalli, initially sown per 100 cm^2 and grown under different intra- or interspecific conditions, was compared (MASD).

Effects on *F. serratus* (from *F. serratus*-*F. vesiculosus* mixtures)

A comparison of mean yields of 500 *F. serratus* (input frequency per 100 cm^2) is shown in Figure 13a. One-way analysis of variances (ANOVA) indicated highly significant ($p<0.001$) differences between mean yields (Table 5). *Post hoc* multiple comparisons of means with Tukey-Kramer test (TK) at $\alpha=0.05$ revealed significant differences between both double total desity treatments and the control plot. Hence, both intra- and interspecific competition had a significant influence on total yield of 500 *F. serratus*. Interspecific competition by *F. vesiculosus* reduced yield (5.12 g) to less than a third of control

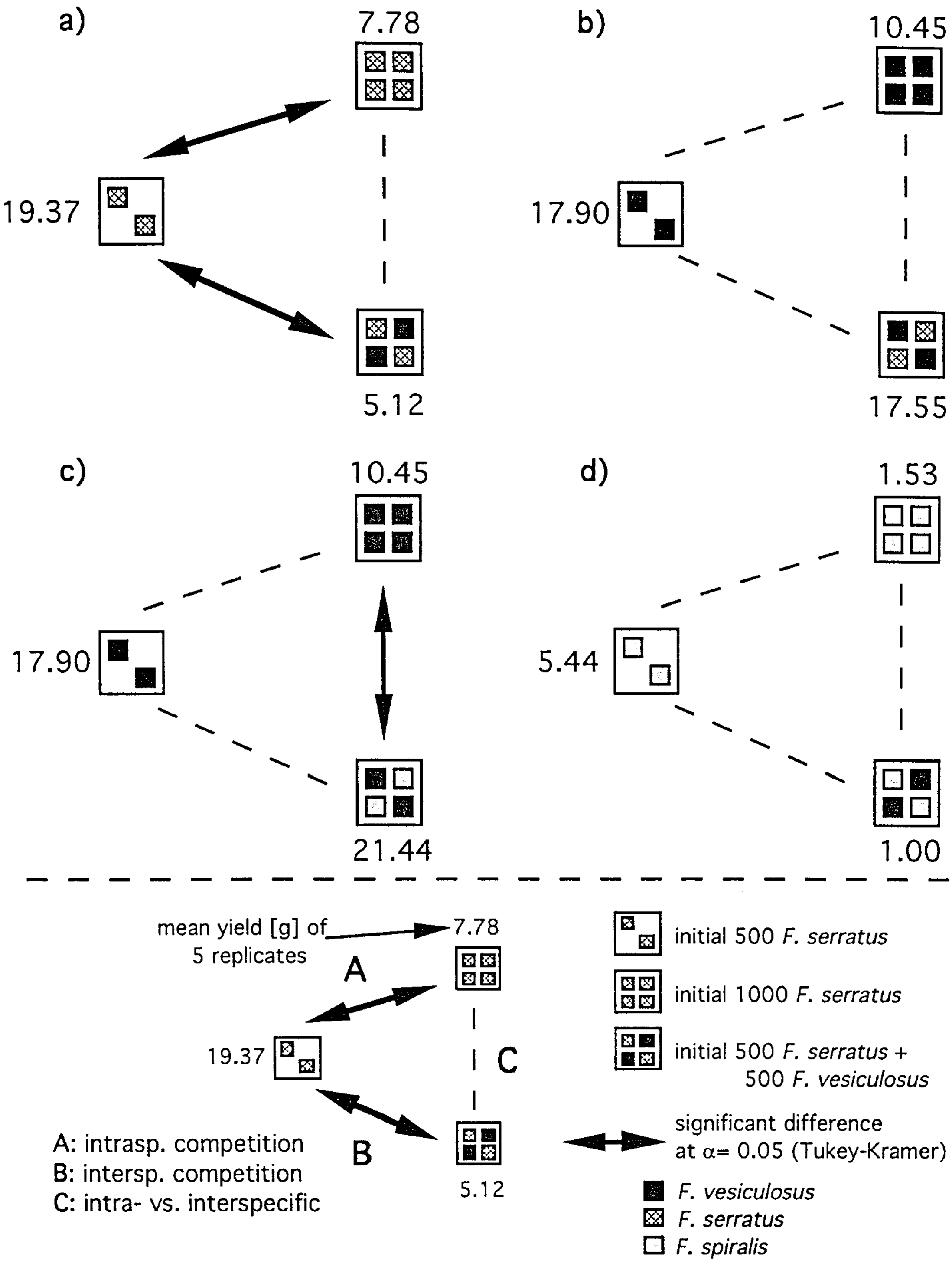


Figure 13: Comparisons (ANOVA) of certain treatments from replacement series according to the 'extended additive design' (compare Figures 6 and 9). a)-d) Effects on (an initial) 500 germlings. a) Effects on *F. serratus*, b) on *F. vesiculosus* from *F. serratus-F. vesiculosus* replacement series. c) Effects on *F. vesiculosus*, d) on *F. spiralis* from *F. vesiculosus-F. spiralis* replacement series. Mean values of 5 replicates. Arrows indicate significant differences with Tukey-Kramer *post hoc* tests at α=0.05.

yield (19.37 g). Yield reduction due to intraspecific effects (to 7.78 g yield) was not that pronounced, but nonetheless significant. Differences between intra- and interspecific effects were not significant at α=0.05 (TK).

Additional information comes from MASD-comparisons shown in Figure 14a and Table 6. An interspecific effect of *F. vesiculosus* on *F. serratus* can be seen in the reduction of yield of 250 *F. serratus* when grown with 250 vs. 750 *F. vesiculosus* (6.36 g vs. 3.23 g), though this difference was not statistically significant. When grown together with another 250 vs. another 750 *F. serratus* the yield of 250 initially sown *F. serratus* was depressed significantly (9.69 g vs. 3.89 g). Differences of intra- and interspecific effects on *F. serratus* were pronounced only at the lower total density. At the lower density, the yield of 250 *F. serratus* was more depressed by inter- than by intraspecific competition. At D3, the effect of intraspecific competition matched that of interspecific competition.

Effects on *F. vesiculosus* (from *F. serratus*-*F. vesiculosus* mixtures)

ANOVA and TK tests revealed no significant differences between treatment means for inter- and intraspecific (EAD) effects on *F. vesiculosus* from replacement series experiments with *F. vesiculosus* and *F. serratus* (Table 7 and Figure 13b). Yield reduction due to interspecific competition was very

Table 5: EAD: Comparison of intraspecific effects of *F. serratus* (S) and interspecific effects of *F. vesiculosus* on *F. serratus*. Mean yields of 5 replicates.

source of variation	df	MS	F	p	conclusion
500S in diff. treatm.	2	287.2	14.45	0.0006	***
error	12	19.9			

Table 6: MASD: Comparison of intraspecific effects of *F. serratus* (S) and interspecific effects of *F. vesiculosus* on *F. serratus*. Mean yields of 5 replicates.

source of variation	df	MS	F	p	conclusion
250S in diff. treatm.	3	128.3	7.81	0.0020	**
error	16	87.6			

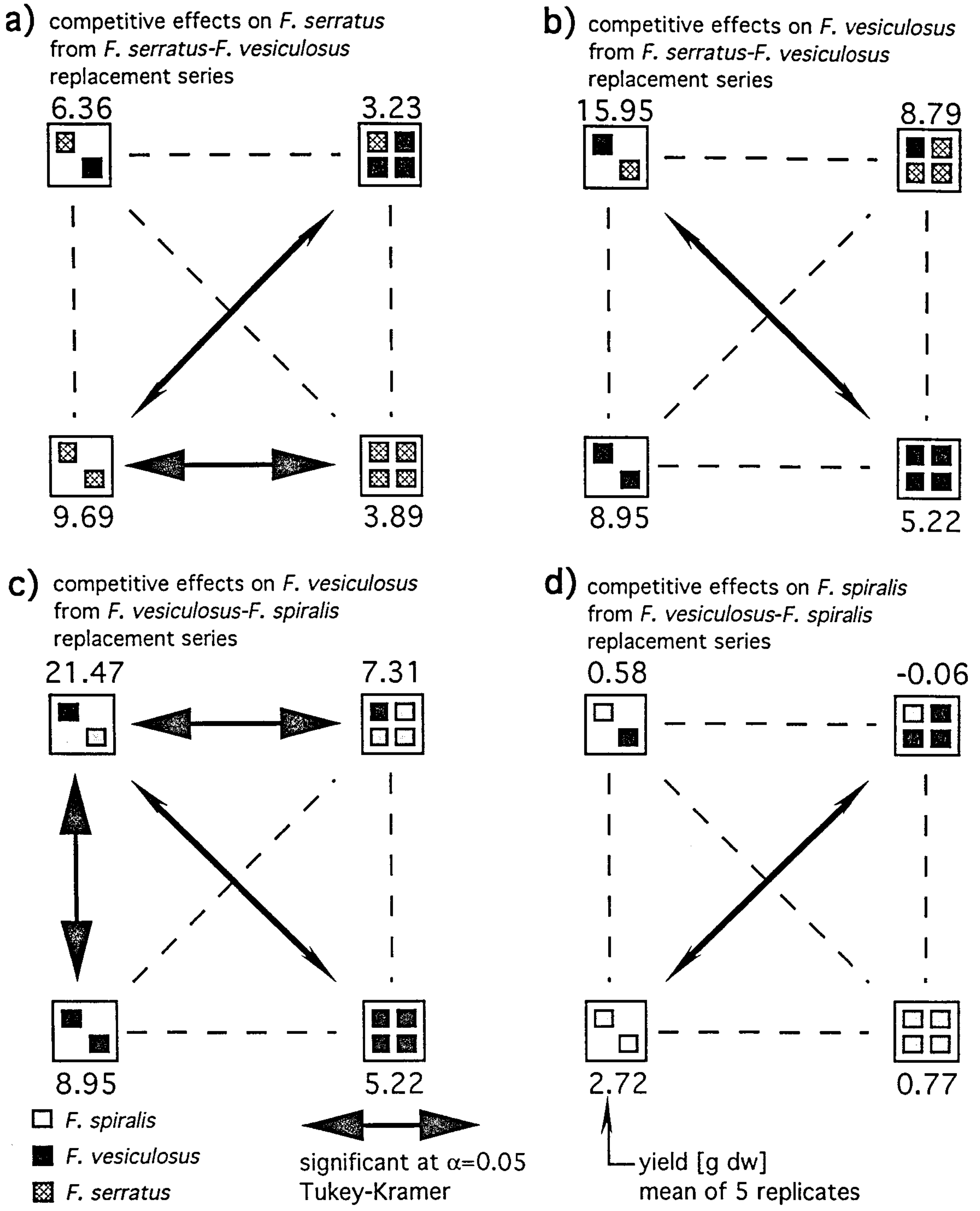


Figure 14: Results of 'mixed additive/substitutive design'-comparisons (MASD) from certain treatments of replacement series experiments performed with *Fucus serratus* and *F. vesiculosus* (a+b) or with *F. vesiculosus* and *F. spiralis* (c+d). Data are yields of an initial 250 *F. serratus* (a), 250 *F. vesiculosus* (b+c) or 250 *F. spiralis* (d) under different intra- or interspecific conditions (mean values of 5 replicates). Arrows indicate significant differences in Tukey-Kramer *post hoc* tests at α=0.05 done subsequently to ANOVA. For further explanations see Figure 10 and text.

low (17.55 g vs. 17.90 g in control). Yield of *F. vesiculosus* was reduced to 10.45 g when grown together with another 500 individuals of *F. vesiculosus*, but this intraspecific effect was not significant.

ANOVA of MASD-comparisons (Figure 14b and Table 8) revealed significant differences ($p<0.01$), but TK test showed, that this significance was based on an irrelevant comparison (compare Figure 10). Although partly pronounced, none of the differences in yield of meaningful comparisons was significant at $\alpha=0.05$ (TK). MASD-comparisons showed an interspecific effect of *F. serratus* on *F. vesiculosus* (250 V grown in mixture with 250 *versus* 750 S). Intraspecific competition reduced yield of 250 *F. vesiculosus* (grown with 250 V: 8.95 g, with 750 V: 5.22 g) but this difference was not significant.

Comparisons of intra- with interspecific effects revealed a stronger reduction (assumed, since there is no control) in yield for intraspecific competition. At the lower density (D2), the yield of 250 *F. vesiculosus* seemed to be elevated when grown with 250 *F. serratus* compared to the monospecific plot with additional 250 *F. vesiculosus* (15.95 g and 8.95 g, respectively).

In summary, the yield of *F. serratus* was significantly reduced by intraspecific competition but was even further reduced by interspecific competition from *F. vesiculosus*. *F. serratus* had a less pronounced interspecific effect on *F.*

Table 7: EAD: Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. serratus* (S) on *F. vesiculosus*. Mean yields of 5 replicates.

source of variation	df	MS	F	p	conclusion
500V in diff. treatm.	2	88.4	1.78	0.2100	n.s.
error	12	49.6			

Table 8: MASD: Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. serratus* (S) on *F. vesiculosus*. Mean yields of 5 replicates.

source of variation	df	MS	F	p	conclusion
250V in diff. treatm.	3	100.8	5.92	0.0065	**
error	16	17.0			

vesiculosus. Low density of *F. serratus* even seemed to favour growth of *F. vesiculosus*. Intraspecific effects in *F. vesiculosus* are pronounced, albeit not statistically significant. According to Shipley & Keddy's (1994) definition, the competitive relationship between *F. vesiculosus* and *F. serratus* is asymmetric, the former being the dominant species. Hence, the findings of data analysis in an additive design are in agreement with those of substitutive replacement series.

The mean yields of plots from *F. vesiculosus-F. spiralis* replacement series experiments were used to detect intra- and interspecific competition in these species.

Effects on *F. vesiculosus* (from *F. vesiculosus-F. spiralis* mixtures)

For effects on *F. vesiculosus* none of the treatments differed significantly from control mean yield (EAD, Table 9 and Figure 13c). Significant differences demonstrated by 1-way ANOVA ($p<0.05$) were between plots for intra- and interspecific effects. Nonetheless, there was a pronounced reduction in yield due to intraspecific competition (17.90 to 10.45 g, as shown above for *F. serratus-F. vesiculosus* replacement series, since the same monoculture plots of *F. vesiculosus* were used for both replacement series).

When grown together with the same amount of *F. spiralis* the yield of 500 *F. vesiculosus* thalli (inital density per 100 cm^2) was elevated (17.90 to 21.44 g). This effect was not significant when compared to the control, but direct comparison of yields of *F. vesiculosus* suffering from intra- and interspecific competition, respectively, showed a significant difference.

In contrast, additional MASD-comparisons (Table 10 and Figure 14c) revealed a significant reduction in yield of 250 *F. vesiculosus* when grown with 750 instead of 250 *F. spiralis* (21.47 and 7.31 g, respectively $p=0.0001$).

Intra- and interspecific effects were significantly different at total density D2, in that yield of 250 *F. vesiculosus* was less when grown with 250 additional *F. vesiculosus* (8.95 g) as opposed to 250 additional *F. spiralis* (21.47 g). At D3 (250 V with 750 V *versus* 750 P), yield of 250 *F. vesiculosus* suffering from intraspecific competition was less than that of 250 suffering from interspecific competition from *F. spiralis*, but this difference was not significant.

Table 9: EAD: Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. spiralis* on *F. vesiculosus*. Mean yields of 5 replicates.

source of variation	df	MS	F	p	conclusion
500V in diff. treatm.	2	157.5	4.35	0.0381	*
error	12	36.3			

Table 10: MASD: Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. spiralis* on *F. vesiculosus*. Mean yields of 5 replicates.

source of variation	df	MS	F	p	conclusion
250V in diff. treatm.	3	267.6	24.55	0.0001	***
error	16	10.9			

Effects on *F. spiralis* (from *F. vesiculosus-F. spiralis* mixtures)

None of the effects on *F. spiralis* was significant, although both treatments reduced yield strongly in comparison with control mean yield (EAD-comparisons. Table 11 and Figure 13d). Still, statistics only very closely failed to reveal significant differences, since differences in 1-way ANOVA were nearly significant (p=0.066) and differences in TK test were close to critical differences for interspecific effects (diff.=4.4, crit. diff=4.9).

Tukey-Kramer tests were used to compare differences between means after ANOVA of MASD-comparisons (Figure 14d). The only significant differences were from irrelevant comparisons (comparison between treatments with different species and different total density; Table 12). Yield was reduced both by intra- and interspecific competition. Interspecific competition by *F. vesiculosus* had a stronger effect than intraspecific competition.

In summary, yield of *F. vesiculosus* was depressed due to intraspecific competition, but elevated when grown together with *F. spiralis* in 50:50 mixture, while yield of *F. spiralis* was reduced both by intra- and interspecific competition, the latter having the stronger effect. The elevation of yield of *F. vesiculosus* in the presence of *F. spiralis* is quite remarkable. *F. spiralis* must provide *F. vesiculosus* with some positive stimulation (facilitation; Khan *et al.* 1975).

All analyses unequivocally showed competitive dominance of *F. vesiculosus* over *F. spiralis.*

Table 11: EAD: Comparison of intraspecific effects of *F. spiralis* (P) and interspecific effects of *F. vesiculosus* on *F. spiralis.* Mean yields of 5 replicates.

source of variation	df	MS	F	p	conclusion
500P in diff. treatm.	2	29.4	3.43	0.0663	n.s.
error	12	8.6			

Table 12: MASD: Comparison of intraspecific effects of *F. spiralis* (P) and interspecific effects of *F. vesiculosus* on *F. spiralis.* Mean yields of 5 replicates. Prior to analysis of variances, data were log-transformed to obtain homoscedasticity.

source of variation	df	MS	F	p	conclusion
250P in diff. treatm.	3	2.3	5.66	0.0077	**
error	16	0.4			

Demographic parameters (self-thinning)

Data for log mean weight of monocultures were plotted against log density for all three *Fucus* species (Figure 15a-c). Despite the criticism of Weller (1987), this was done for comparison with relevant literature data. Boundary lines with intercepts of 4.3 (Cousens & Hutchings 1983) and 5.0 (Firbank & Watkinson 1990) were drawn for the same reason. Monospecific stands of *F. vesiculosus* clearly were not restricted to the area underneath the boundary lines (Figure 15b). Half of the monocultures of *F. serratus* crossed the boundary lines, too. Only stands of *F. spiralis*, whose mortality had been greater, seem to be restricted by the "one overall line", proposed by Firbank & Watkinson (1990).

When stands of *Ascophyllum nodosum* exceeded their boundary line with an intercept at 4.3, Cousens & Hutchings (1983) suggested calculating geometric

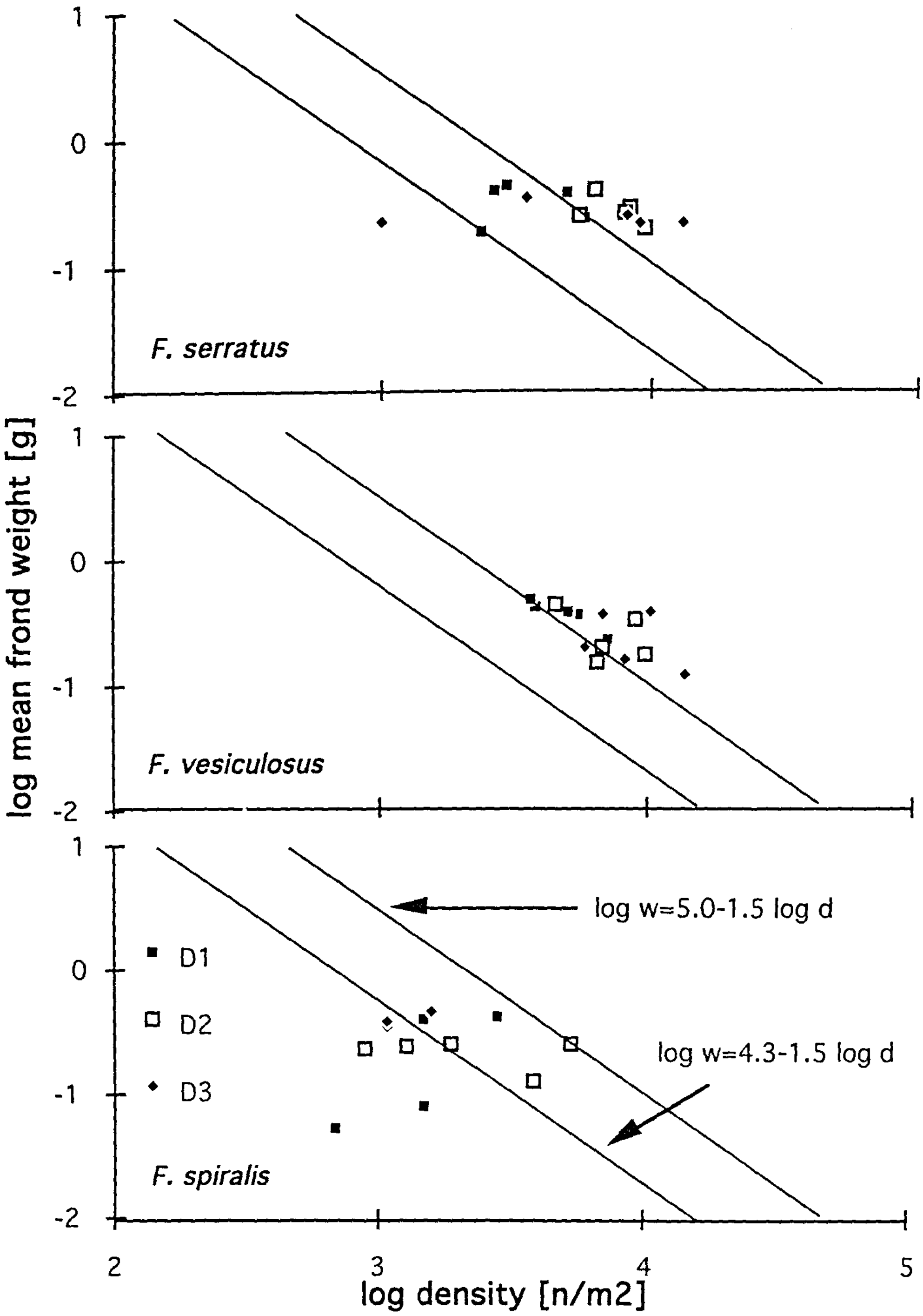


Figure 15: Test whether data of final density and (arithmetic) mean plant weight of monocultures from replacement series apply to the self-thinning rule. Two commonly used boundary lines from the literature are given, the upper intersecting the ordinate at 5.0, the lower at 4.5. Monocultures of a) *Fucus serratus*, b) *F. vesiculosus* and c) *F. spiralis*. For further explanation see text.

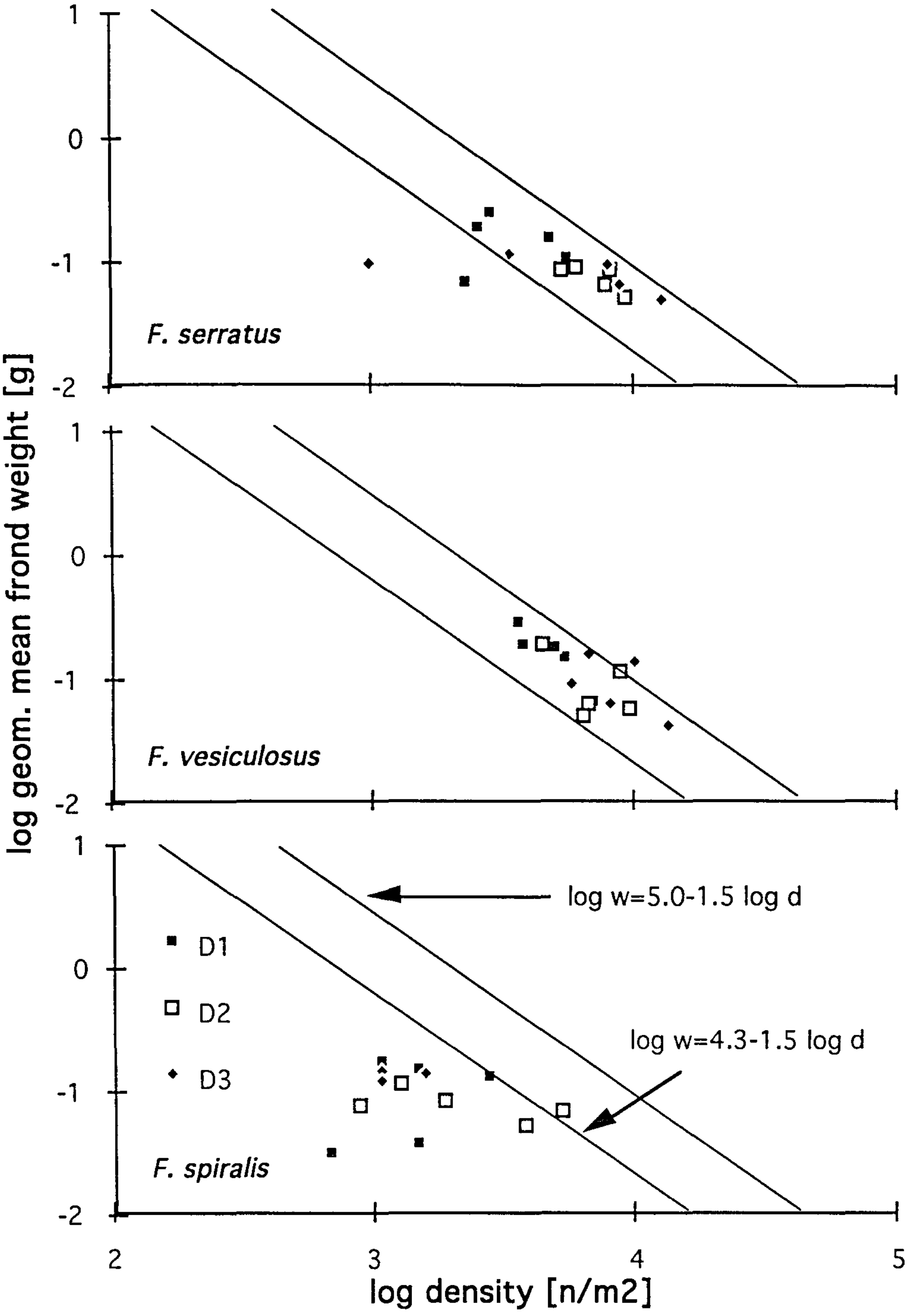


Figure 16: Test whether data of final density and (geometric) mean plant weight of monocultures from replacement series conform to the self-thinning rule. Two commonly used boundary lines from the literature are given, the upper intersecting the ordinate at 5.0, the lower at 4.5. Monocultures of a) *Fucus serratus*, b) *F. vesiculosus* and c) *F. spiralis*. For further explanation see text.

means rather than arithmetic means. Their boundary line is still exceeded by geometric means of weights of *F. serratus* and *F. vesiculosus* in the present investigation, but, using geometric means, monospecific stands of these species seem to be restricted by Firbank & Watkinson's (1990) overall boundary line (Figure 16).

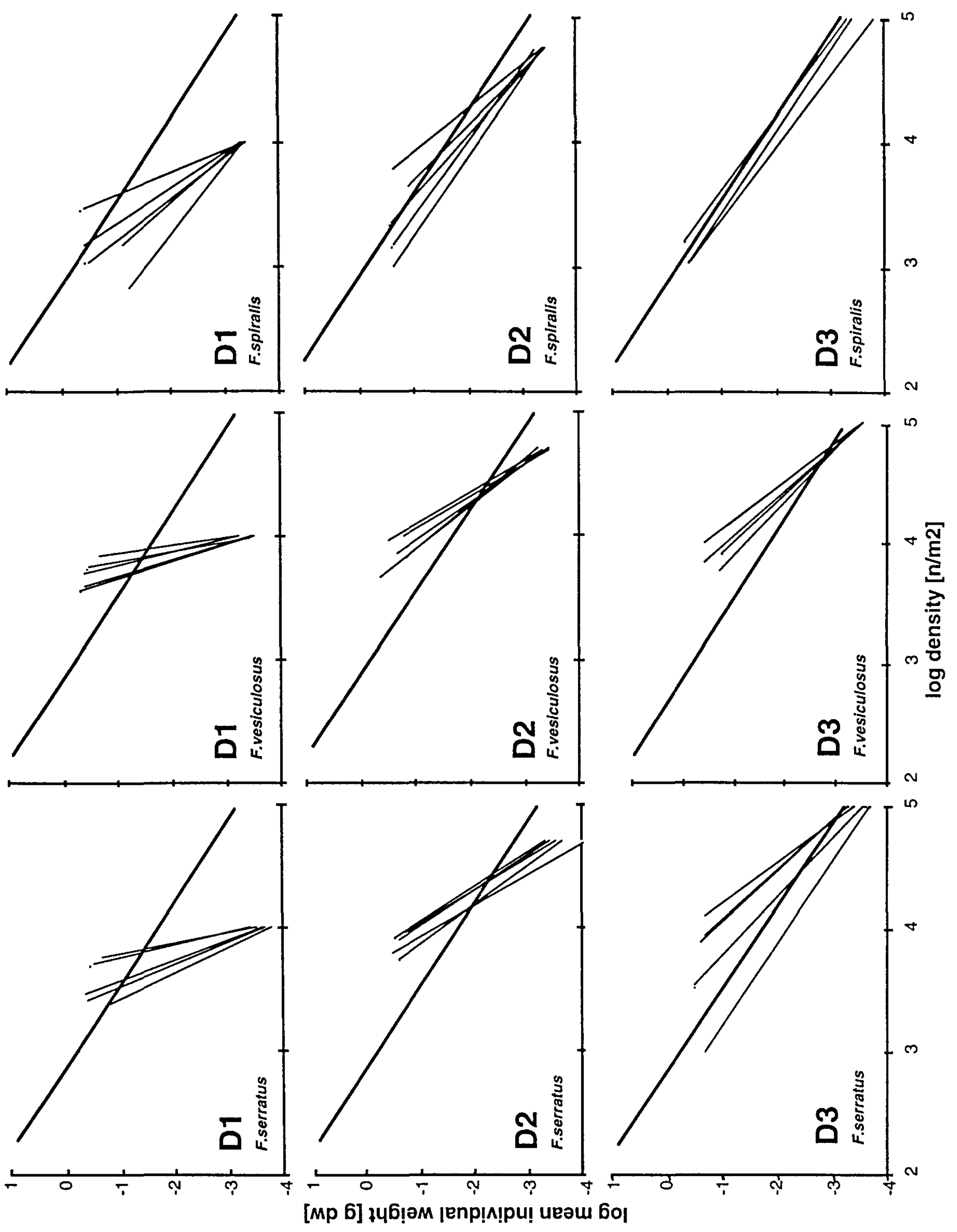
Trajectories in Figure 17 show the increase in mean plant weight and the decrease in density for all monospecific experimental units. Treatments with higher initial density had a relatively higher mortality (decrease in density) leading to trajectories more parallel to the self-thinning line (with log K = 4.3) drawn for comparison. This pattern was consistent for all three *Fucus* species.

Figure 18 was drawn for comparison of log N - log mean weight and log N - log biomass graphs, the latter suggested by Westoby (1984) and Weller (1987). Here the means of five replicated plots were used. There is no difference in the pattern, when biomass is used instead of mean plant weight.

Gini coefficients for final dry weights of all three *Fucus* species from monospecific treatments are plotted in Figure 19a against the logarithm of final density per m^2. Regression lines explain only 16-17% of variation for *F. serratus* and *F. spiralis*. Only data for *F. vesiculosus* had a significant coefficient of determination ($R^2 = 0.7$). All three species showed a trend of decreasing Gini coefficients with decreasing density, most pronounced for *F. vesiculosus*. This is indicative of an increasing equality of dry weight frequency distributions with decreasing density. Gini coefficients ranged from 0.45 to 0.73 for *F. serratus*, from 0.48 to 0.70 for *F. vesiculosus* and from 0.50 to 0.75 for *F. spiralis*.

In Figure 19b, Gini coefficients are plotted against the logarithm of mean plant dry weight which is a form of expression normally used in the literature (e.g. Weiner & Thomas 1986; Martínez & Santelices 1992). *F. vesiculosus* and *F. serratus* showed a trend of decreasing inequality with increasing mean weight, but only the regression of *F. vesiculosus* data was significant ($R^2=0.53$).

Figure 17: (next page) "Trajectories" of log mean plant weight *versus* log density of monocultures from replacement series. Left: *F. serratus*, middle: *F. vesiculosus*, right: *F. spiralis*. A commonly used self-thinning line with ordinate intersection at 4.3 is given for comparison. Stands



'self-thinned' from three different (D1-D3) inital densities of small plants (data points at lower right of each graph) to final lower densities of bigger plants (upper left). Data points from single treatments.

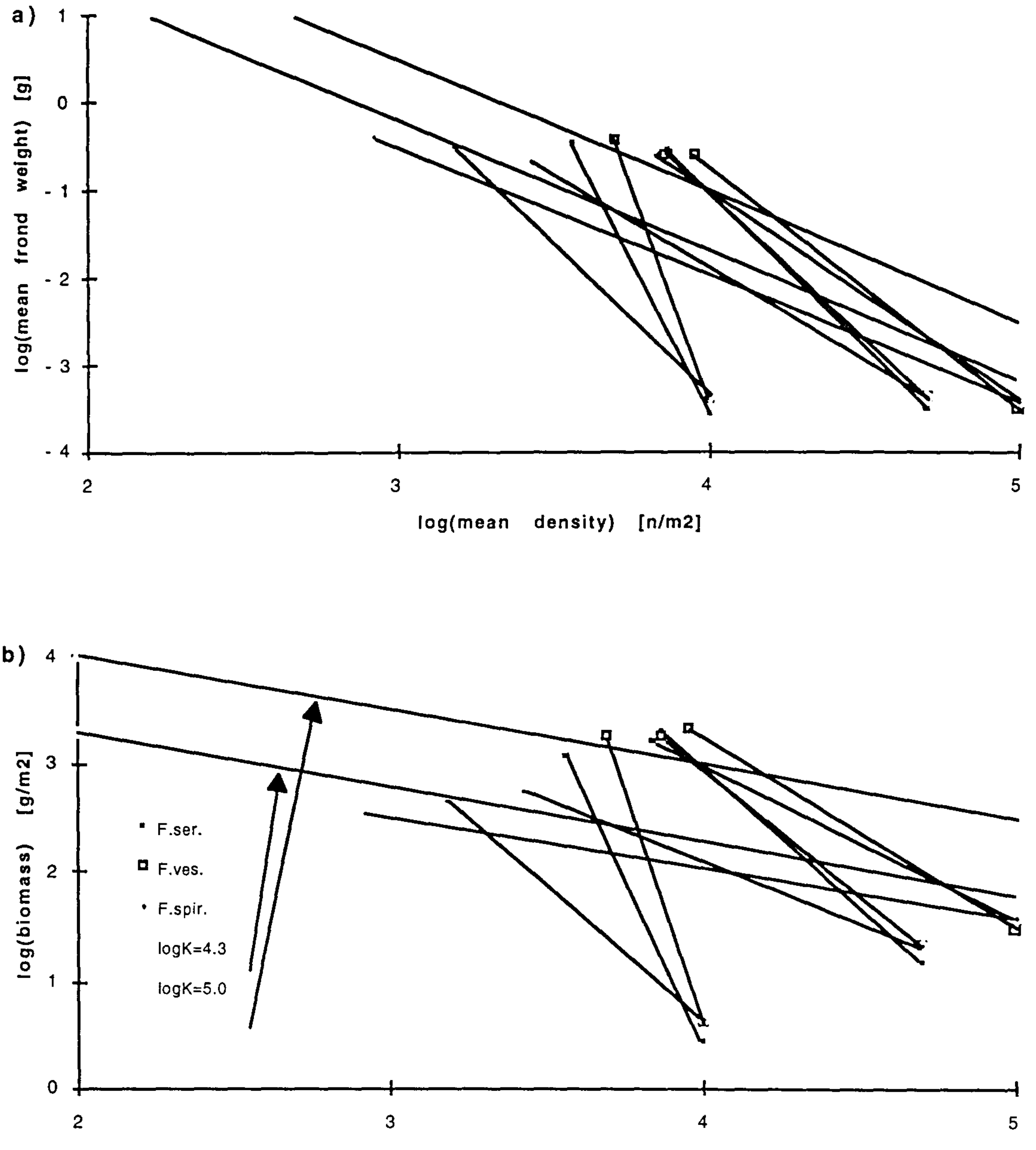


Figure 18: "Trajectories" of log mass *versus* log density of monocultures from replacement series. a) log weighed means of frond weights, b) log total final biomass. Two commonly used self-thinning lines with ordinate intersections at 4.3 and 5.0 are given for comparison. Data points are mean values of 5 replicates.

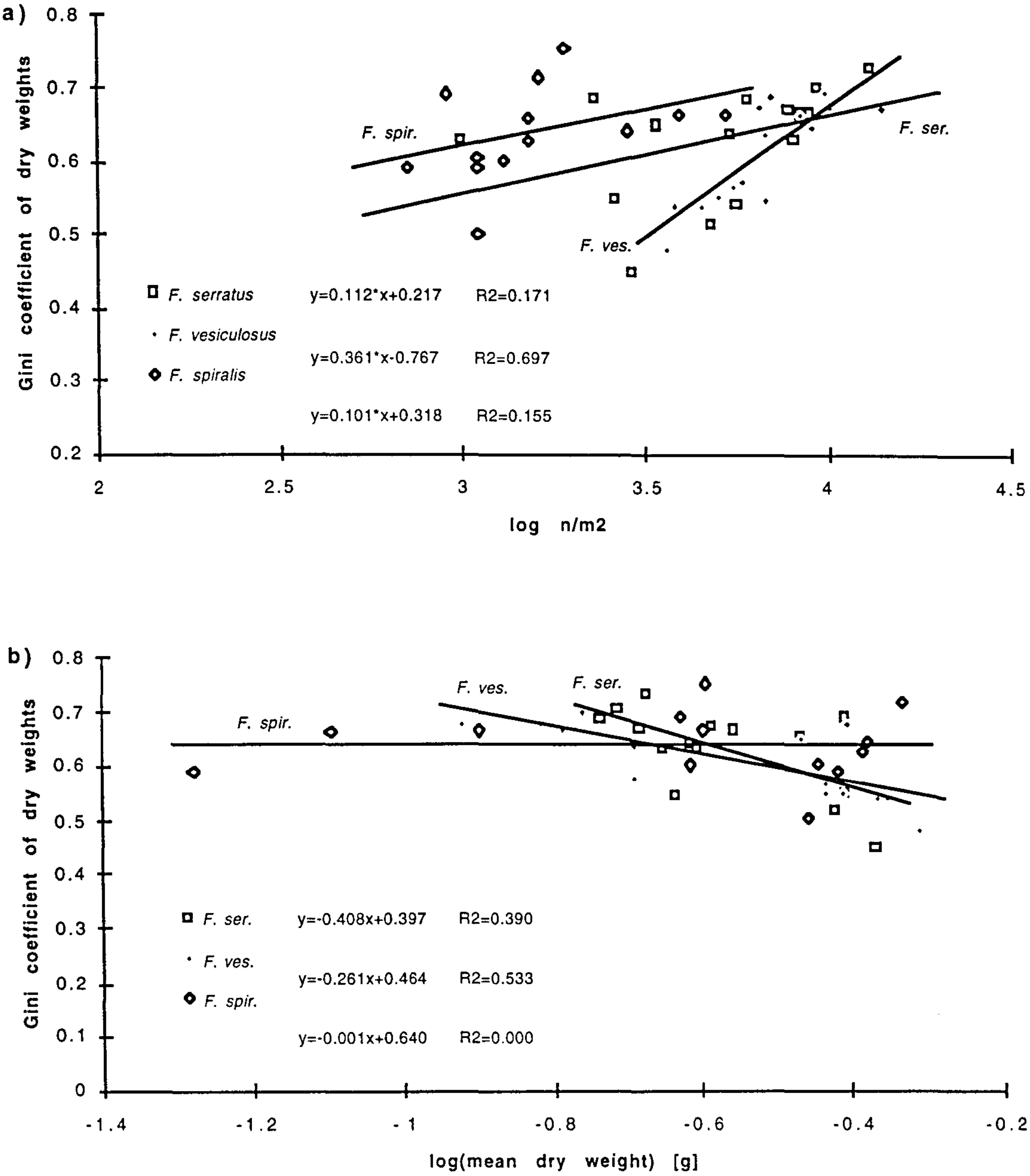


Figure 19: Gini coefficients of final individual dry masses from monospecific *Fucus* stands included in replacement series experiments installed in the lower intertidal zone of Helgoland. Gini coefficients a) plotted against log density, b) plotted against log individual dry weight. Per *Fucus* species, monocultures started from three different initial densities. Lines derived from linear regression are shown for each *Fucus* spp.

2.3.2 Replacement series experiment in the laboratory

Replacement series graphs

Replacement series graphs of laboratory cultures in replacement series design are shown in Figure 20 (left) for *F. serratus-F. vesiculosus* mixtures (mean values of 4 replicates). Yields of *F. serratus* were lower than expected yields in all mixtures at all three densities, while yields of *F. vesiculosus* were higher than expected yields. This is indicative of competitive dominance of *F. vesiculosus* over *F. serratus.*

In experimental combinations from *F. vesiculosus-F. spiralis* replacement series (Figure 20, right), yields revealed a frequency-dependent pattern (Khan *et al.* 1975). At low input frequencies of *F. vesiculosus,* the yields of this species are higher than expected, while yields of *F. spiralis* were lower than expected. At high input frequencies of *F. vesiculosus*, this species yielded less than expected, while *F. spiralis* yielded more. Though not very pronounced, this pattern is consistent for all three experimental densities.

Most obvious is the pattern of the total yield in all 6 replacement series experiments in laboratory cultures (Figures 20a,b). Total yield is a straight horizontal line in all densities, i.e. all mixed and monospecific treatments had about the same total yield (means of 4 replicates). Mean yields from *F. serratus* and *F. vesiculosus* mixtures were between 14 and 16 g per beaker, those for *F. vesiculosus-F spiralis* mixtures between 15 and 18 g. This is in contrast to the total yields of field experiments which had a more or less convex shape. Additionally, in most cases, yield from laboratory experiments was clearly lower than corresponding yield from field experiment (Table 13). It seems obvious that the environment in the laboratory experiment (2 l seawater) 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. Of course, these conditions are constraints of the chosen design (beaker), as is the mortality, that was high in the field but nil in the laboratory. Additionally, in the field, small algae were crowded by taller individuals, and died eventually, while in the laboratory, small algae were favoured in their light reception.

In all mixtures from laboratory replacement series experiments, a gain in yield of one species (compared to 'expected yields') must have been compen-

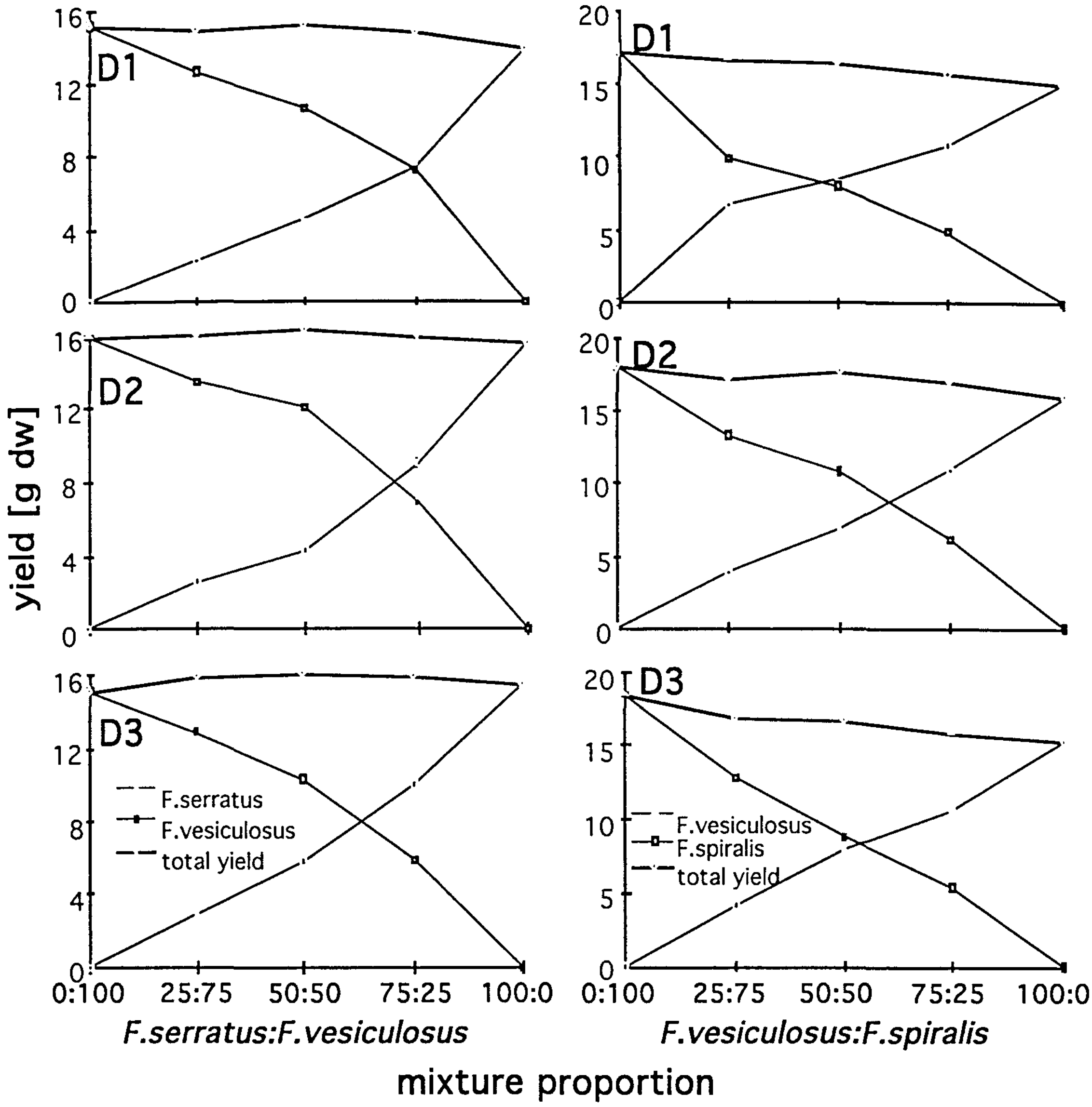


Figure 20: Replacement series graphs from laboratory replacement series experiments with *Fucus serratus* and *F. vesiculosus* (left) or with *F. vesiculosus* and *F. spiralis* (right) at three total densities (D1=130, D2=650, D3=1300 initial shoots per beaker). Mean values of 4 replicates.

sated for by a loss in the other's yield. For *F. serratus-F. vesiculosus* mixtures, *F. vesiculosus* is clearly able to use the restricted resource better at the cost of *F. serratus.*

The interpretation of replacement series with *F. vesiculosus* and *F. spiralis* is not so straightforward. Deviations from expected yields are not very pronounced. Under laboratory conditions, the competitive dominance of *F. vesiculosus* revealed in the field experiment, seems to be altered. In contrast to the

Table 13: Total yields [g dry weight] from replacement series experiments in the Helgoland intertidal and in the laboratory. Yields per experimental unit (ceramic tile or 3 l mason jar, respectively) and yields of laboratory experiment reduced to the same surface area as in field experiment (100 cm^2). Mean values of 5 or 4 replicates, respectively.

F.ser.:F.ves.	**density**	**total yield lab. yield/jar**	**corr. yield lab. yield/100 cm^2**	**total yield field yield/100 cm^2**
0:100	1	15.10	11.62	17.87
25:75	1	14.90	11.47	16.61
50:50	1	15.06	11.58	15.19
75:25	1	14.72	11.32	15.56
100:0	1	13.82	10.63	11.47
0:100	2	15.84	12.18	17.90
25:75	2	15.93	12.26	24.16
50:50	2	16.25	12.50	21.31
75:25	2	15.78	12.14	19.46
100:0	2	15.38	11.83	19.37
0:100	3	15.15	11.65	20.89
25:75	3	15.89	12.23	19.53
50:50	3	16.03	12.33	22.66
75:25	3	15.88	12.21	13.92
100:0	3	15.51	11.93	15.56
F.ves.:F.spir.				
0:100	1	17.21	13.24	4.58
25:75	1	16.73	12.87	12.59
50:50	1	16.46	12.66	11.14
75:25	1	15.71	12.09	16.32
100:0	1	15.10	11.62	17.87
0:100	2	17.97	13.82	5.43
25:75	2	17.14	13.19	17.77
50:50	2	17.70	13.61	22.05
75:25	2	16.87	12.98	26.31
100:0	2	15.84	12.18	17.90
0:100	3	18.49	14.22	3.06
25:75	3	16.86	12.97	7.54
50:50	3	16.76	12.89	22.44
75:25	3	15.95	12.27	21.15
100:0	3	15.15	11.65	20.89

field experiment, and despite the permanent submergence in the laboratory of this high eulittoral seaweed, *F. spiralis* yielded more than its congeners in most treatments.

Crowding coefficients

For the calculation of crowding coefficients the number of surviving plants is needed, since individual weights are used. In this experiment the final number of fucoids was estimated only for the experimental units from two replicates at lowest density D1. Here, the number of shoots increased but the number of genets remained constant, each genet consisting of several shoots with different lengths (pattern depending on species). Genets are used here for calculation instead of shoots, and final number was assumed to be the same as initial number, since small plants remained in the beakers and stayed alive, because they still had a certain amount of light due to the mixing effect of the aeration. At the termination of the experiment in high density beakers (D3), there were many plants of 1 cm length that had only a minor contribution to total final biomass.

Individual crowding coefficients from *F. serratus-F. vesiculosus* replacement series are shown in Table 14 and indicate that *F. vesiculosus* performed better in mixtures than in monocultures whereas *F. serratus* yielded more in monocultures. Relative crowding coefficients K_{vs} are all >1 (all but one >1.6), which is indicative of competitive dominance of *F. vesiculosus* over *F. serratus*.

For *F. vesiculosus-F. spiralis* mixed laboratory cultures, individual crowding coefficients for *F. vesiculosus* are >1 only at the lowest density (Table 15). In mixtures with highest frequency of *F. spiralis*, values of K_v are <1. Individual crowding coefficients for *F. spiralis* are all near 1.

Relative crowding coefficients (K_{vp}) are >1 only at the two lowest absolute frequencies of *F. vesiculosus* (D1: V:P 1:3 and 2:2). At the highest frequencies of *F. vesiculosus*, values of K_{vp} are lowest.

Deviations from 1 are not very pronounced for values of crowding coefficients for *F. vesiculosus-F. spiralis* mixed cultures and show the same frequency-dependent pattern as replacement series graphs (see above).

Table 14: Individual and relative crowding coefficients from replacement series experiments with *Fucus serratus* and *F. vesiculosus* at three densities (D1-D3). Data from laboratory cultures in aerated 3 l jars. Mean values of 4 replicates. $K_{serratus}$ and $K_{vesiculosus}$ are individual crowding coefficients. K_{sv}= relative crowding coefficient *F. serratus* on *F. vesiculosus*. K_{vs}= relative crowding coefficient *F. vesiculosus* on *F. serratus*.

		F. serratus : F. vesiculosus		
	density	**25:75**	**50:50**	**75:25**
$K_{serratus}$	D1	0.78	0.80	0.75
	D2	0.84	0.60	0.82
	D3	0.59	0.68	0.76
$K_{vesiculosus}$	D1	1.60	1.42	2.10
	D2	0.89	1.19	1.89
	D3	1.00	1.56	1.47
K_{sv}	D1	0.49	0.56	0.36
	D2	0.95	0.50	0.43
	D3	0.60	0.43	0.52
K_{vs}	D1	2.06	1.79	2.78
	D2	1.06	2.00	2.31
	D3	1.68	2.30	1.94

Table 15: Individual and relative crowding coefficients from replacement series experiments with *Fucus vesiculosus* and *F. spiralis* at three densities (D1-D3). Data from laboratory cultures in aerated 3 l jars. Mean values of 4 replicates. $K_{vesiculosus}$ and $K_{spiralis}$ are individual crowding coefficients. K_{vp}= relative crowding coefficient *F. vesiculosus* on *F. spiralis*. K_{pv}= relative crowding coefficient *F. spiralis* on *F. vesiculosus*.

		F. vesiculosus : F. spiralis		
	density	**25:75**	**50:50**	**75:25**
$K_{vesiculosus}$	D1	1.93	1.36	1.15
	D2	0.93	1.00	0.81
	D3	1.06	0.74	0.75
$K_{spiralis}$	D1	0.93	0.96	1.39
	D2	1.01	1.06	1.07
	D3	1.05	0.92	1.02
K_{vp}	D1	2.08	1.42	0.86
	D2	0.92	0.94	0.76
	D3	1.00	0.80	0.74
K_{pv}	D1	0.48	0.70	1.16
	D2	1.09	1.06	1.32
	D3	1.00	1.26	1.36

Input-output ratio diagrams

At each of three densities, the *F. serratus*:*F. vesiculosus* ratio diagram line falls below and parallel to the slope of 1.0 (Figure 21a). Hence, all output ratios are less than input ratios. This configuration is indicative of unstable mixtures, and predicts that *Fucus serratus* would go to extinction (Khan *et al.* 1975). The distance from the line of unit slope is smaller compared to ratio diagrams from the field experiment.

Ratio diagrams for *F. vesiculosus-F. spiralis* mixtures, like replacement series graphs and crowding coefficients, show a competitive dominance of *F. vesiculosus* at its lowest input frequencies (at D1; Figure 21b). Deviations from the slope of 1.0 are not very pronounced. All other data points lie more or less on the slope 1.0 and indicate stable mixtures through time.

Comparison of intraspecific and interspecific interactions in additive designs

The field experiment designs for comparisons among mean yields from selected experimental units were used for laboratory cultures (EAD and MASD, see Figures 9 and 10). Mean values for yields from the laboratory were derived from 4 replicates. Yield of 650 (for EAD, instead of 500 in the field experiment) or 325 (for MASD, instead of 250) from different treatments were compared.

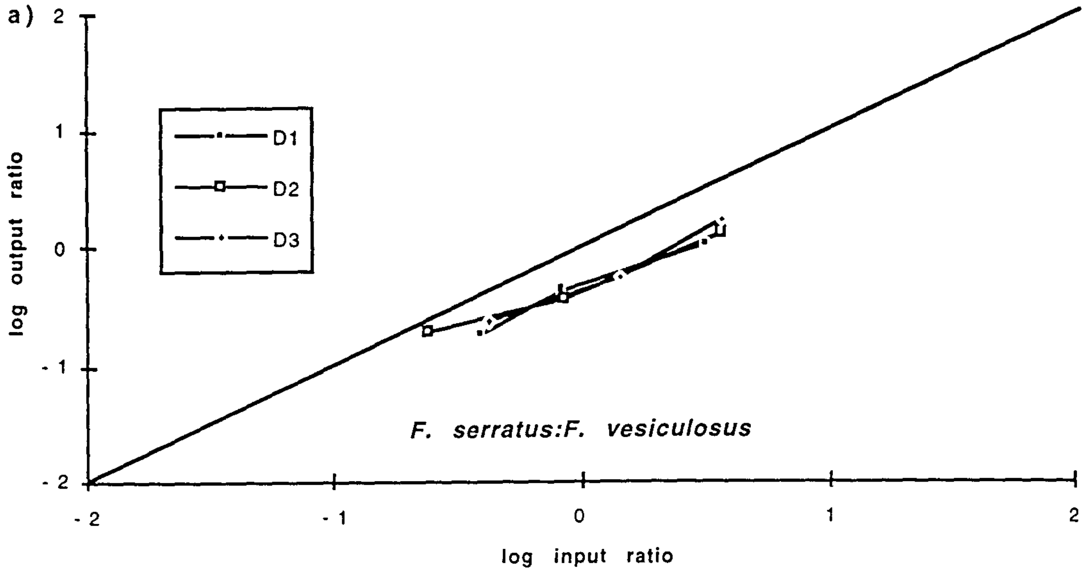
Results from EAD-comparison are shown in Table 16 (one-way ANOVA) and in Figure 22 (Tukey-Kramer *post hoc* multiple comparisons).

In all 4 EAD-comparisons the pattern of significant differences is the same: both high density plots are significant different from the control plot (TK, α=0.05) due to reduction of yield from intra- and interspecific competition, respectively. Differences between the high density plots were insignificant.

For *F. serratus*, yield reduction due to interspecific competition from *F. vesiculosus* was greater than reduction due to intraspecific competition (Figure 22a).

F. vesiculosus suffered more yield reduction from intraspecific competition compared to reduction from interspecific competition from *F. serratus* (Figure 22b) or *F. spiralis* (Figure 22c).

Interspecific effects from *F. vesiculosus* led to greater yield reduction for *F. spiralis* than intraspecific effects (Figure 22d).



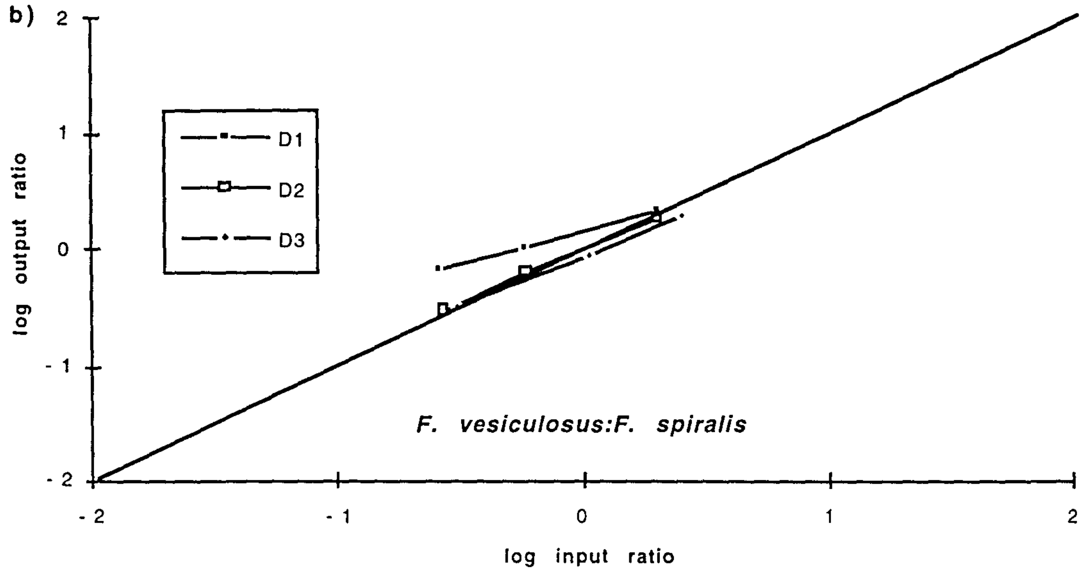


Figure 21: Ratio diagrams from replacement series experiments with laboratory cultures of a) *Fucus serratus* and *F. vesiculosus* or b) *Fucus vesiculosus* and *F. spiralis* at three total densities (D1=130, D2=650, D3=1300 shoots per beaker). The logarithm of the output ratio [a): *F. serratus*:*F. vesiculosus*, b): *F. vesiculosus*:*F. spiralis*] is plotted against the log input ratio. Mean values of 4 replicates.

Results for MASD-comparisons of plots from laboratory replacement series with *F. serratus* and *F. vesiculosus* are shown in Table 17 and Figure 23a,b.

Table 16: EAD-comparisons (ANOVA): Mean yields of 4 replicates.

Comparison of intraspecific effects of *F. serratus* (S) and interspecific effects of *F. vesiculosus* on *F. serratus*. One row has been excluded from calculations because of a missing value.

source of variation	df	MS	F	p	conclusion
650S in diff. treatm.	2	85.1	39.87	0.0001	***
error	8	2.1			

Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. serratus* on *F. vesiculosus.*

source of variation	df	MS	F	p	conclusion
650V in diff. treatm.	2	71.1	38.09	0.0001	***
error	9	1.9			

Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. spiralis* on *F. vesiculosus.*

source of variation	df	MS	F	p	conclusion
650V in diff. treatm.	2	87.5	13.76	0.0018	**
error	9	6.4			

Comparison of intraspecific effects of *F. spiralis* (P) and interspecific effects of *F. vesiculosus* on *F. spiralis.*

source of variation	df	MS	F	p	conclusion
650P in diff. treatm.	2	106.4	14.87	0.0014	**
error	9	7.2			

The pattern of competitive effects on *F. serratus* (Figure 23a) is similar to the results of the field experiment (compare Figure 14a). Yield of *F. serratus* was depressed significantly more by interspecific competition from *F. vesiculosus* than from intraspecific competition (4.26 vs. 7.69 g, respectively) at lower density (D2). At high density plots (D3), *F. serratus* also showed modest yields under intra- and interspecific influence.

Yield reduction due to intraspecific effects was significant (7.69 to 3.88 g; α=0.05, TK). Reduction of yield from interspecific competition of 975 compared to 325 *F. vesiculosus* plants was greater (3.50 and 4.26 g yield, respectively), although this difference was not very pronounced and insignificant.

Patterns of yield reduction of 325 *F. vesiculosus* plants were also similar for field and laboratory experiments (Figure 23b, compare with Figure 14b). *F.*

vesiculosus yielded most when grown together with the same initial number of *F. serratus* (12.00 g) at the lower denstity (D2). Yield was significantly reduced from additional interspecific competition (to 5.86 g) from *F. serratus*. Intraspecific effects also significantly reduced the yield of *F. vesiculosus* (7.92 to 3.79 g). Substitutive comparisons of intra- and interspecific competition showed a prominent greater reduction of yield due to intraspecific at both, D2 and D3, with only the former being significant.

In summary, *F. serratus* suffered more from interspecific competition from *F. vesiculosus* than from intraspecific competition, whereas intraspecific competition had the most severe effect on *F. vesiculosus*. Differences between intra- and interspecific competition were most pronounced at lower density (D2) plots. At the highest density (D3), the total density seems to have a great negative effect on single plant yield, no matter which of the species contributed to the high density. Yield reduction patterns were similar to the results of the field experiments, although absolute values differed, and differences were more likely to be significant under more homogeneous laboratory conditions.

MASD-comparisons for *F. vesiculosus-F. spiralis* replacement series are shown in Table 17 (ANOVA) and Figure 23c,d (Tukey-Kramer test). In contrast to the field experiment and to EAD-comparisons, *F. vesiculosus* suffered more from interspecific competition from *F. spiralis* than from intraspecific competition at D2 (6.73 g and 7.92 g yield, respectively), although this difference was not significant. At D3, intraspecific effects led to the greatest yield reduction (3.79 vs. 4.11 g yield). Additive comparisons revealed an interspecific and an intraspecific negative effect on yield, only the latter being significant.

Unlike the field experiment, the presence of *F. vesiculosus* seemed to have a positive effect on yield of 325 *F. spiralis* plants (substitutive comparisons, inter- vs. intraspecific competition), although these differences were not significant. Intraspecific and interspecific effects both led to a significant reduction of yield (additive comparisons).

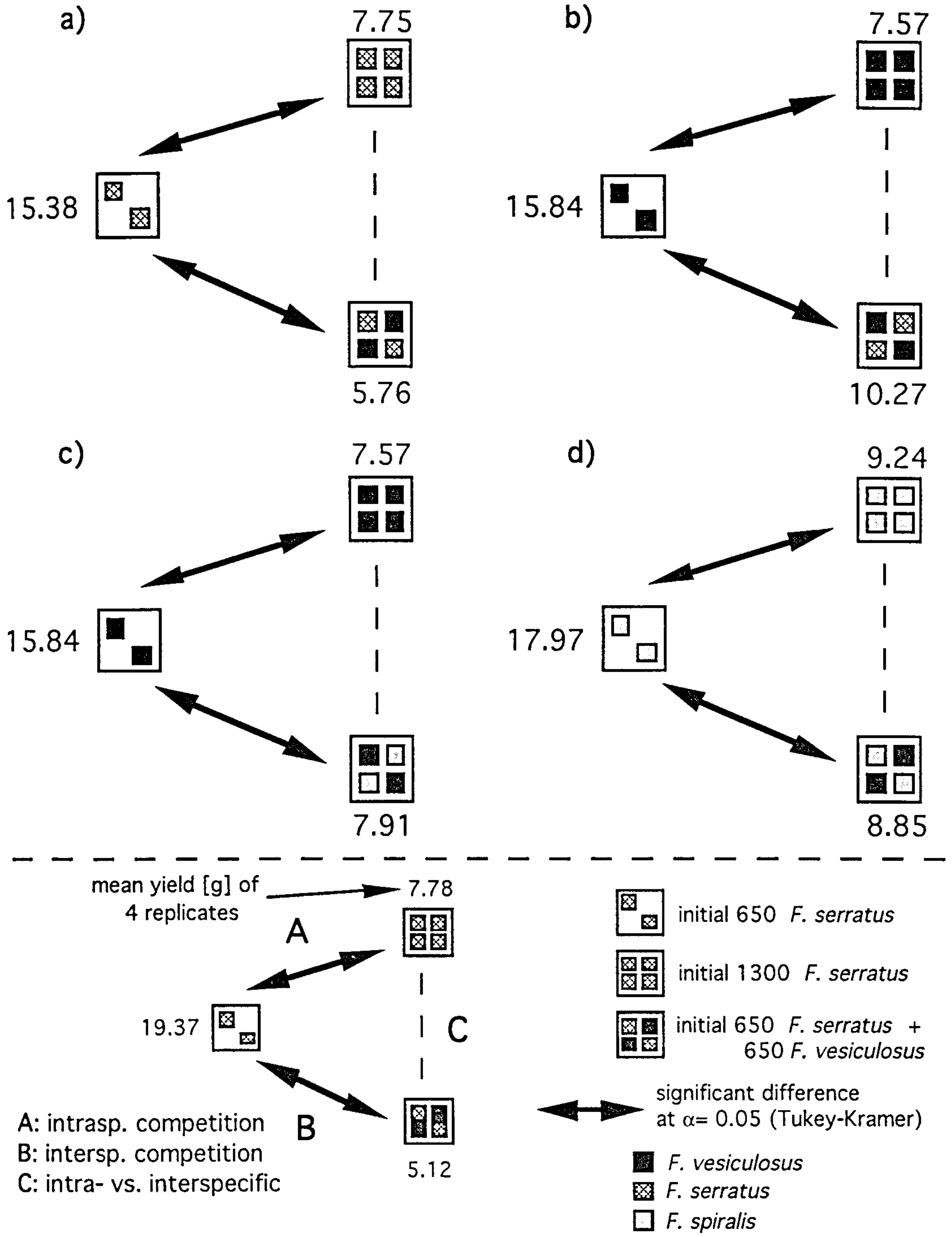


Figure 22: Comparisons (ANOVA) of certain treatments from replacement series with laboratory cultures according to the 'extended additive design' (EAD, compare Figures 6 and 9). a)-d) Effects on (an initial) 650 germlings. a) Effects on *F. serratus*, b) on *F. vesiculosus* from *F. serratus-F. vesiculosus* replacement series. c) Effects on *F. vesiculosus*, d) on *F. spiralis* from *F. vesiculosus-F. spiralis* replacement series. Mean values of 4 replicates. Arrows indicate significant differences with Tukey-Kramer *post hoc* tests at α=0.05.

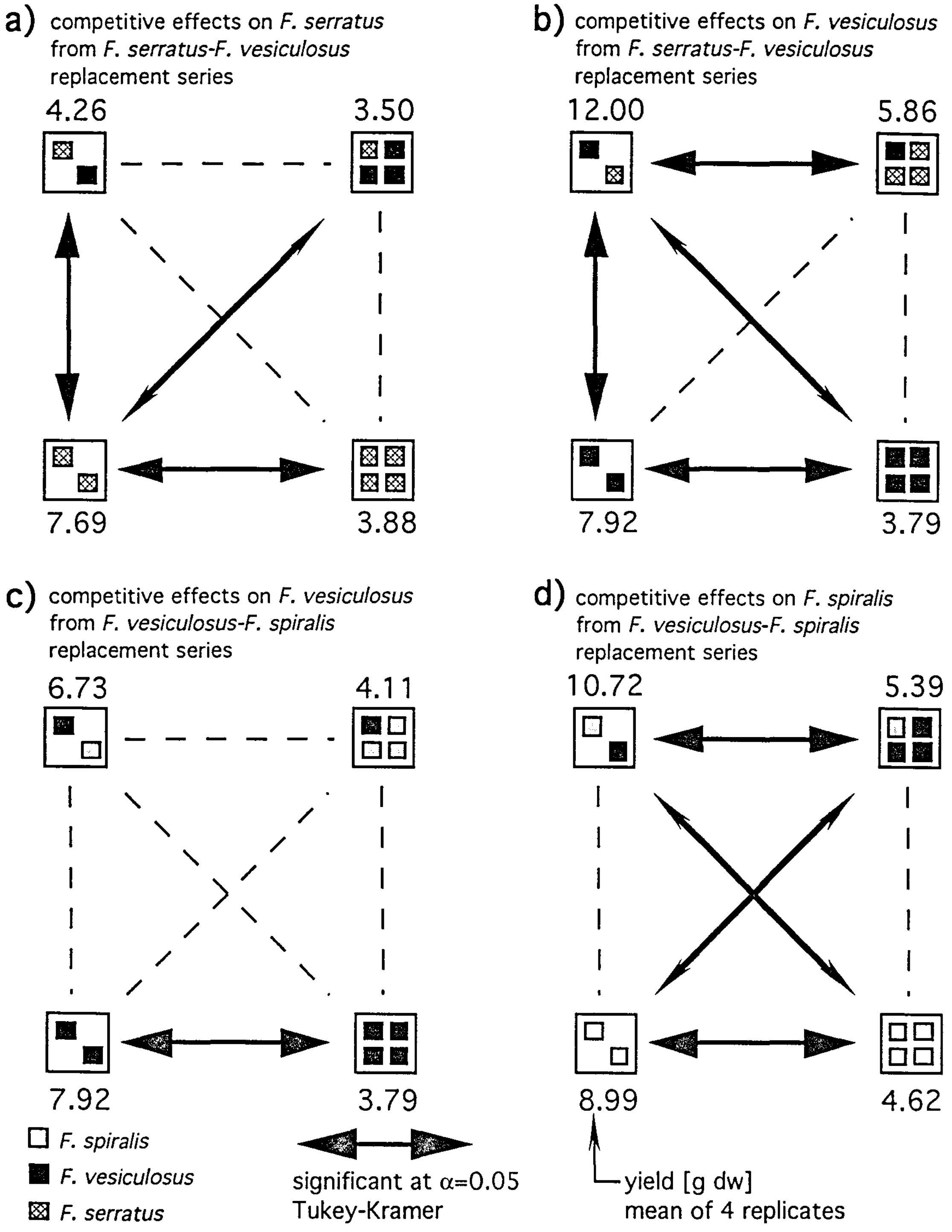


Figure 23: Results of 'mixed additive substitutive design'-comparisons (MASD) from certain treatments of laboratory replacement series experiments performed with *Fucus serratus* and *F. vesiculosus* (a+b) or with *F. vesiculosus* and *F. spiralis* (c+d). Data are yields of 325 *F. serratus* (a), 325 *F. vesiculosus* (b+c) or 325 *F. spiralis* (d) under different intra- or interspecific conditions (mean values of 4 replicates). Arrows indicate significant differences in Tukey-Kramer *post hoc* tests at α=0.05 done subsequently to ANOVA. For further explanations see Figure 10 and text.

Table 17: MASD-comparisons (ANOVA): Mean yields of 4 replicates.

Comparison of intraspecific effects of *F. serratus* (S) and interspecific effects of *F. vesiculosus* on *F. serratus*. One row has been excluded from calculations becauses of a missing value.

source of variation	df	MS	F	p	conclusion
325S in diff. treatm.	3	12.1	6.33	0.0094	**
error	11	1.9			

Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. serratus* on *F. vesiculosus*.

source of variation	df	MS	F	p	conclusion
325V in diff. treatm.	3	49.1	14.62	0.0003	***
error	12	3.4			

Comparison of intraspecific effects of *F. vesiculosus* (V) and interspecific effects of *F. spiralis* on *F. vesiculosus*.

source of variation	df	MS	F	p	conclusion
325V in diff. treatm.	3	16.2	4.46	0.0253	*
error	12	3.6			

Comparison of intraspecific effects of *F. spiralis* (P) and interspecific effects of *F. vesiculosus* on *F. spiralis*.

source of variation	df	MS	F	p	conclusion
325P in diff. treatm.	3	33.7	13.59	0.0004	***
error	12	2.5			

In summary, in MASD-comparisons of data from the laboratory experiment, *F. spiralis* revealed the yield pattern that seems to be typical for the competitive dominant: better performance when grown with the opponent species, *F. vesiculosus*, and greatest yield reduction due to intraspecific effects. *F. vesiculosus* showed the pattern of the inferior species: Greater yield reduction from interspecific than from intraspecific competition (at D2). In EAD-comparisons, in contrast, *F. vesiculosus* had the greater negative effect (not significant) on yield, intraspecifically and interspecifically on *F. spiralis*.

2.4 Summary of results

In the field experiment the ranks of competitive dominance were clearly:

F. serratus < *F. vesiculosus* and *F. vesiculosus* > *F. spiralis.*

Replacement series graphs, crowding coefficients, ratio diagrams and EAD- and MASD-comparisons unequivocally gave this result. *F. spiralis* performed poorly in replacement series experiments at all three initial densities.

In contrast the ranks of competitive dominance from the laboratory experiment were:

F. serratus < *F. vesiculosus* and *F. vesiculosus* ≤ *F. spiralis*

Laboratory experiments, as done here, seem not to be suitable for detecting competitive relations that lead to dominance and zonation in the field. Competitive ability does not seem to be a species inherent characteristic for *Fucus* (one of the assumptions of Keddy's competitive hierarchy model) under different environmental conditions.

Neither competitive ranks from the field experiment nor those from the laboratory cultures are concordant with the prediction from the competitive hierarchy model (*F. serratus* > F. *vesiculosus* > *F. spiralis*).

NICHES 3

3.1 Introduction

The 'niche' of a species was defined by Hutchinson (1957) as subset of the n-dimensional hyperspace of environmental conditions and resources the species needs to survive and to reproduce. Every resource (e.g. nutrients) or condition (e.g. temperature) forms one of the axes of which this hypothetical space is composed.

Without biotic interactions (competition, predation), the space inside the n-dimensional hyperspace that might be occupied by a species is the species' 'fundamental niche'. Its 'realized niche' is the range of distribution met under natural field conditions with biotic influences acting. Hence, the realized niche of a species is only a subset of the fundamental niche. Taking into account all axes at once is impossible and the usefulness of Hutchinson's model is theoretical rather than practical. However, single axes might be surveyed experimentally. Realized niches would be determined by descriptive studies of field patterns. For estimating fundamental niches, two major experimental designs have been developed: 'release experiments' and 'transplants'. In release experiments, biotic influences are removed experimentally and the expansion of the species' distribution from realized to fundamental niche is recorded. Depending on the species' growth rate, reproductive output and dispersal capability, such an experiment might last several years. In contrast, in transplantation experiments, individuals are transplanted to other parts of the resource or condition axis. The survival and/or performance is recorded and compared to control transplants, i.e. individuals treated in the same way but replaced in the section of the gradient from which they had come. Experimental time may be reduced with the transplantation approach which was used here.

For the purposes of this study, it was only necessary to estimate the fundamental niches of the three *Fucus* species on that section of the gradient of tidal emergence on which the realized niches of *Fucus* spp. were located. There were clear predictions from the model to be tested experimentally for this section of the gradient. In addition to adult plants, juveniles were transplanted in another experiment to all three *Fucus* zones, since different life stages may respond differentially to environmental conditions.

The competitive hierarchy model predicts that fundamental niche breadths are ranked *F. serratus* < *F. vesiculosus* < *F. spiralis*. In other words, *F. spiralis* and *F. vesiculosus* should perform equally well or better, when transplanted below their natural zones, *F. serratus* and *F. vesiculosus* should not survive transplantation above the zones of their natural occurrence.

The exclosure of littorinid grazers was not possible in the transplantation experiments performed in this study. Densities of *Littorina* spp. were obviously lower at both experimental sites compared to the rocky intertidal zone, where the competition experiment was installed. Grazing damage was never observed on experimental transplant units. However, a perfect experimental design to determine fundamental niches should exclude grazing as a biotic effect.

3.2 Material & methods

3.2.1 Transplants of laboratory germlings

Installation and maintenance of the experiment

Germlings of *Fucus serratus*, *F. vesiculosus* and *F. spiralis* were obtained and cultivated on the unglazed sides of ceramic tiles (15x15 cm^2) as described in 2.2. When fucoids had grown to an average length of 1.0-1.5 cm, ceramic tiles bearing germlings were fixed to the side of the Helgoland "N-Mole" facing NE. The mole is a seawall protecting the rocky intertidal (as described in chapter 1) from western storms (Figure 3).

Three ceramic tiles with central holes were screwed to sheets of PVC, each tile bearing a different *Fucus* species (Figure 24). These PVC carriers were fixed to the seawall in each of the three *Fucus* zones and supported experimental ceramic tiles. This was done with seven replicates along the seawall.

The ceramic tiles had 8 elevated areas (Figure 24). Prior to installation of tiles on the seawall, algae were scraped from randomly located small areas (ca. 1

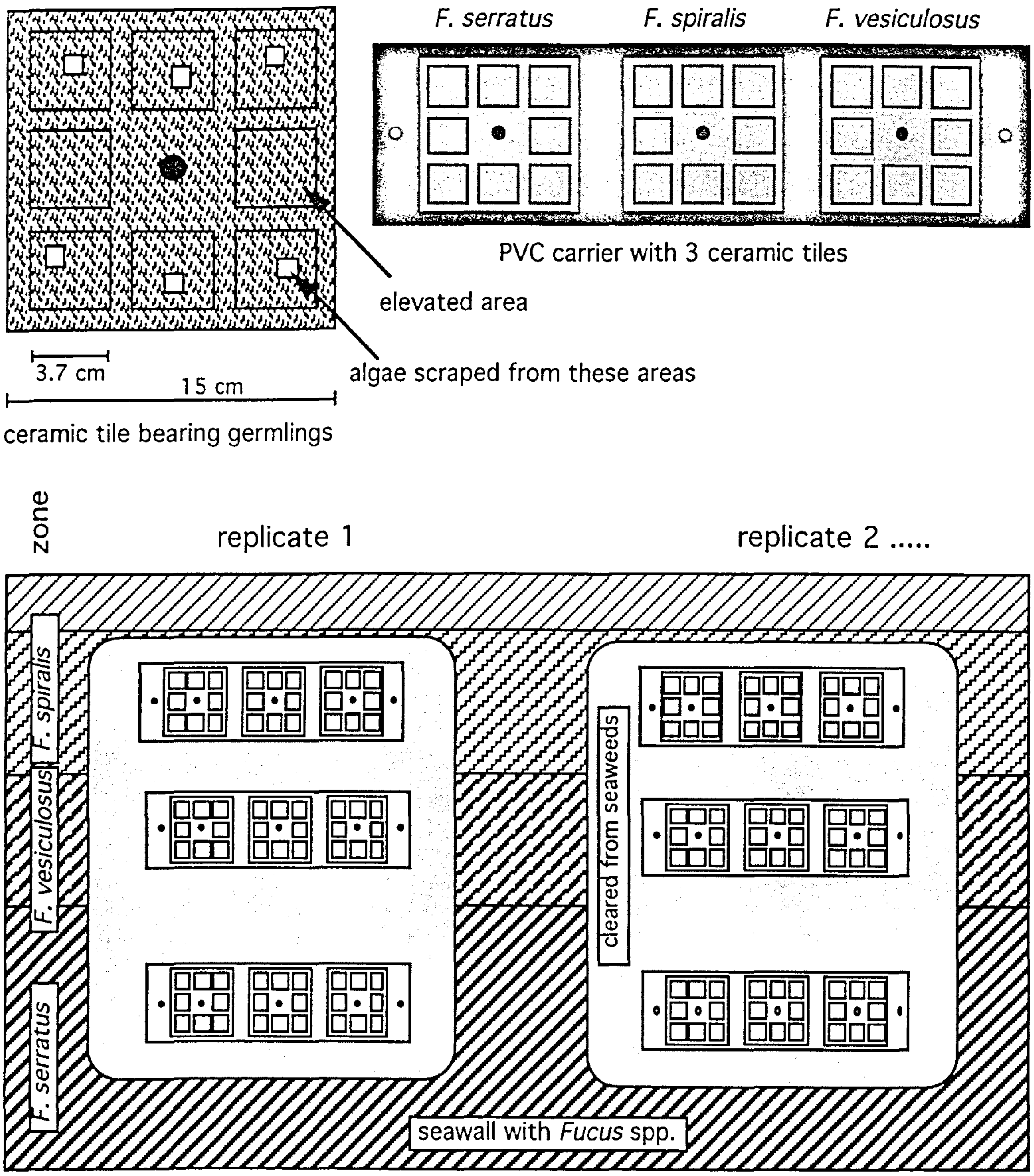


Figure 24: Experimental design of transplants of laboratory *Fucus* germlings fixed to the Helgoland northern seawall ('N-Mole'). Ceramic tiles (upper left) had 8 elevated areas. Three tiles, each bearing another *Fucus* species (upper right), were fixed to each *Fucus* zone on the seawall (bottom). Natural vegetation around experimental units was removed (i.e. there were no interspecific competitive effects). For further explanations see text.

cm^2) on each tile located at the three upper and lower elevations (Figure 24). The algae were counted and weighed (dry weight, see 2.2) to obtain an estimate of the starting density and biomass for each experimental tile.

When algae were cultivated in the laboratory for the experiments (see 2.2) there was no control of the sowing density. Hence, densities varied, but were similar among tiles within single plastic trays. Accordingly, within single trays, 3 tiles bearing germlings of one of the *Fucus* species were removed and distributed among the 3 zones on the seawall (one per zone = total of 3; repeated for each of 3 *Fucus* species). Otherwise, tiles were distributed randomly.

In September 1993, experimental units were installed on the seawall and maintained there until August 1994. During the time of exposure, wild fucoids were regularly removed from the seawall in a circle of ca. 2 m around each replicated set of nine tiles (Figure 24, bottom) to prevent whiplash effects and unwanted recruitment on the experimental tiles.

In August 1994, tiles were returned to the laboratory. Remaining algae were scraped from the tiles, censused and dry weights determined.

3.2.2 Transplants of adult field plants

Installation and maintenance of the experiment

For the transplantation of field material of seaweeds, it is necessary to obtain individuals attached to their substratum. The natural substratum in the rocky intertidal of Helgoland, red sandstone, is very soft and brittle. Gluing tests with fragments of red sandstone showed that they would likely be lost. Hence, a field of concrete bunker rubble seawards from the eastern seawalls of Helgoland (Figure 3) was used as the source of experimental material and site for transplantation. Here all three *Fucus* species occurred on concrete blocks in the usual zonation pattern (see above).

Adult plants of various lengths of all three *Fucus* species still attached to lumps of concrete were chipped off of concrete blocks by means of hammer and chisel. These were taken to the laboratory and glued to PVC tiles (15x15 cm^2) with 'sea goin' poxy putty' (Permalite, Newport Beach, USA). Lengths of fucoids varied between 2-30 cm. Taller plants were omitted (*F. serratus* and *F. vesiculosus*) to avoid excessive load on the cement. Four to 10 concrete lumps bearing algae (of a single *Fucus* species) were glued to one PVC tile. Such tiles were screwed to PVC carriers, similar to those fixed to the seawall in 3.2.1, but with more space (8 cm) between tiles, and scattered at the site, fixed to single concrete blocks. Six tiles bearing one *Fucus* species were fixed to each of the three *Fucus* zones. Tiles were taken randomly from the pool of tiles, only the last tile for each zone was selected to compensate deviations from equal distribution to the three zones. For the different *Fucus* species, the number of inital shoots varied due to different average numbers of shoots per holdfast (see Table 19 in 3.3.2).

Tiles were taken to the field on 1995/03/03 and returned to the laboratory on 1995/08/15. During that time, neighbouring naturally grown algae long enough to interfere with experimental tiles were removed regularly.

Prior to installation, the number of shoots on each concrete lump for each tile was recorded. At the termination of the experiment, final numbers per lump were determined and compared to starting numbers.

An equivalent experiment was installed in September 1994, but a southerly storm destroyed most of the experimental units (ceramic tiles instead of PVC tiles) in October 1994.

The remains of this experiment were returned to the laboratory and analysed at the beginning of March 1995. The results give supplementary information on survival of fucoids during winter.

3.3 Results

3.3.1 Transplants of laboratory germlings

Mean values of final density, survival, total and individual dry weight and yield per experimental tile for each *Fucus* species-zone combination are shown in Table 18. Mean values were tested with one-way-ANOVA and Tukey-Kramer test ($\alpha=0.05$, Table 18) for differences between the three zones. Prior to analyses, data were checked for homoscedasticity with Cochran's test and, if necessary, log-transformed (indicated in Table 18).

At the onset of the experiment, densities of fucoid germlings on experimental tiles were high (17-43/cm^2). The highest survivorship was 4.73% for a single tile of *F. vesiculosus* in the *F. spiralis* zone and, for means calculated for replicates, 2.58% for the same alga-zone combination. Hence, all mean survivals lay between 0 and 2.58% and differences were not significant (Table 18). Probably, self-thinning mortality is the reason for such low survival rates in experimental fucoid stands that produced high standing crops at the termination of the experiment and, therefore, must have been transplanted to sections of the desiccation gradient within the species' fundamental niches. For that reason, final density was a better parameter for detecting differences between performances in the three zones statistically. Since density decreases when plants grow (= attain more mass) and individual plants remain smaller due to density-competition effects, density and individual plant mass should be considered together. Total final mass or final yield is the product of density and individual mass.

Although variation in the data is high, the total biomass parameters (total final biomass and yield) unequivocally show the highest mass of each *Fucus* species developed on tiles transplanted to the zone of natural occurrence (Table 18 and Figure 25).

Final biomass of *F. spiralis* was significantly lower in the zone of *F. serratus* compared to biomass in both upper zones that had approximately the same high biomass. Density-related parameters, individual mass, survival and final density, were also lower in the *F. serratus* zone (Table 18). Relative yield of *F. spiralis*, i.e. yield in relation to the zone of natural occurrence, was highest (100%, of course) in the native zone, slightly less than 100% in the zone of *F. vesiculosus* and <14% in the lowermost zone (Figure 25).

Data for final density of transplanted *F. vesiculosus* had variances too heterogeneous (even when transformed) for an analysis of variance. Survival and final density were highest in the zone of *F. spiralis*, slightly less in the zone of natural occurrence and lowest in the *F. serratus* zone. Biomass data (final biomass and yield) clearly show highest values in the own zone of *F. vesiculosus* and approximately equal lower masses in the zone below and above. Data of individual biomass indicate that the surviving plants in the uppermost zone remained comparably small (significant in ANOVA, Table 18). Relative yield was only ca. 50% in the upper and lower zone (Figure 25).

Table 18: Performance parameters of laboratory-raised germlings from three Helgoland *Fucus* species cultivated on ceramic tiles and transplanted to the three *Fucus* zones on a Helgoland seawall (September 1993 - August 1994). Mean values and standard deviations of 7 replicates except % survival for *F. spiralis* (4 replicates). A and B refer to Tukey-Kramer test that was performed when ANOVA indicated significant differences. Prior to analyses of variance, data were checked for homoscedasticity with Cochran's test and transformed as indicated when necessary.

final density [n/cm²]		***Fucus* species**	
zone	*F. spiralis*	*F. vesiculosus*	*F. serratus*
F. spiralis	0.601 ± 0.239 **A**	0.935 ± 0.546	0.329 ± 0.438
F. vesiculosus	0.530 ± 0.134 **A**	0.801 ± 0.155	0.397 ± 0.276
F. serratus	0.199 ± 0.156 **B**	0.556 ± 0.119	0.444 ± 0.159
ANOVA	$F_{2,18}=9.757$ p=0.0013	data heteroscedastic	$F_{2,18}=0.241$ p=0.7881

survival [%]		***Fucus* species**	
zone	*F. spiralis*	*F. vesiculosus*	*F. serratus*
F. spiralis	2.16 ± 0.62	2.58 ± 1.26	1.34 ± 1.75
F. vesiculosus	1.52 ± 0.28	2.50 ± 0.73	1.69 ± 1.30
F. serratus	0.75 ± 1.06	1.93 ± 0.61	1.66 ± 0.62
ANOVA	data heteroscedastic	$F_{2,18}=1.001$ p=0.3871	data heteroscedastic
transformation	angular	angular	angular

final total dry weight [g]		***Fucus* species**	
zone	*F. spiralis*	*F. vesiculosus*	*F. serratus*
F. spiralis	26.68 ± 6.40 **A**	13.22 ± 6.43	2.67 ± 3.54
F. vesiculosus	26.55 ± 8.97 **A**	19.05 ± 7.56	5.71 ± 6.98
F. serratus	7.49 ± 9.08 **B**	12.51 ± 3.83	10.75 ± 10.71
ANOVA	$F_{2,18}=12.552$ p=0.0004	$F_{2,18}=2.392$ p=0.1199	$F_{2,18}=1.986$ p=0.1662

final individual dry weight [g]		***Fucus* species**	
zone	*F. spiralis*	*F. vesiculosus*	*F. serratus*
F. spiralis	0.221 ± 0.085 ns	0.068 ± 0.025 ns	0.028 ± 0.014 **A**
F. vesiculosus	0.229 ± 0.073 ns	0.112 ± 0.060 ns	0.052 ± 0.023**AB**
F. serratus	0.122 ± 0.088 ns	0.102 ± 0.027 ns	0.093 ± 0.065 **B**
ANOVA	$F_{2,18}=3.714$ p=0.0446	$F_{2,18}=3.701$ p=0.0451	$F_{2,18}=6.870$ p=0.0061
transformation		log	log

yield [g]		***Fucus* species**	
zone	*F. spiralis*	*F. vesiculosus*	*F. serratus*
F. spiralis	22.80 ± 6.96 **A**	7.87 ± 6.56	-1.45 ± 3.33
F. vesiculosus	22.30 ± 9.40 **A**	13.94 ± 7.43	1.19 ± 6.12
F. serratus	3.08 ± 9.59 **B**	7.22 ± 3.80	6.35 ± 10.62
ANOVA	$F_{2,18}=11.60$ p=0.0006	$F_{2,18}=2.60$ p=0.1021	$F_{2,18}=3.39$ p=0.0561
transformation			log

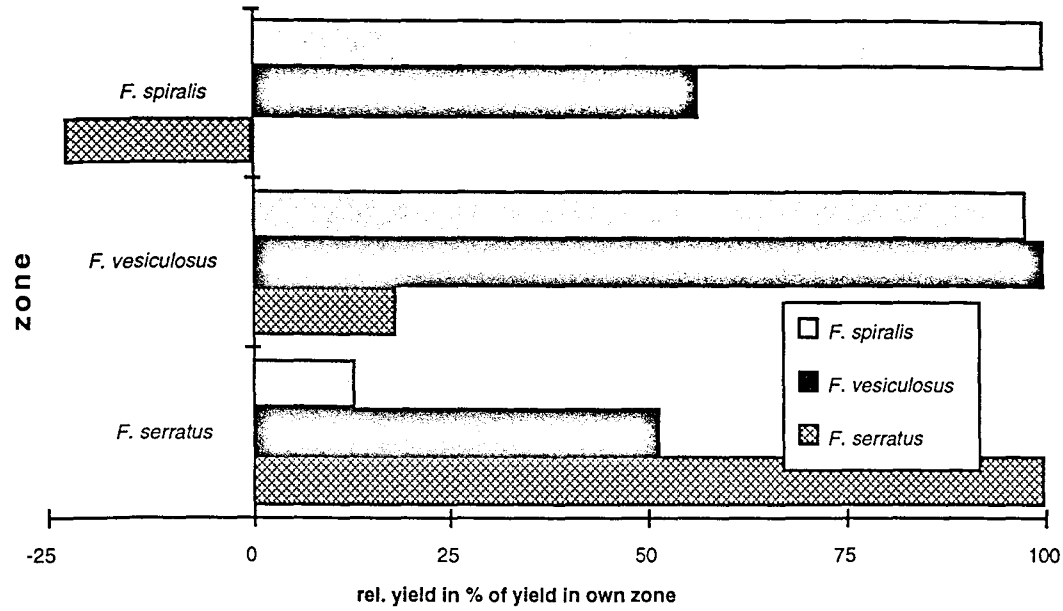


Figure 25: Yields of transplanted *Fucus* germlings as percentages of yield in the zone of natural occurrence. Weight loss during the course of the experiment led to negative yield of *F. serratus* in the *F. spiralis* zone. Mean values of 7 replicates.

Density and survival of *F. serratus* were lowest in the uppermost zone of *F. spiralis*, but differences from the lower zones were insignificant (Table 18). Individual plant mass was significantly lower in the *F. spiralis* zone compared to the *F. serratus* zone. All mass related parameters (final biomass, individual biomass and yield) had the highest values in the zones of natural occurrence and decreased in the progressively higher zones. Yield was negative in the zone of *F. spiralis*, i.e. here final biomass was less than starting biomass. Relative yield (Figure 25) was only 19% in the *F. vesiculosus* and negative in the *F. spiralis* zone.

In summary, all three species performed best when transplanted to their zones of natural occurrence. *Fucus* spp. clearly did not grow better when transplanted to a presumably more benign section of the desiccation gradient. For all parameters considered here, *F. spiralis* and *F. vesiculosus* clearly performed worst in the lowermost zone, contrary to the predictions of the competitive hierarchy model. Transplantations upwards reduced mass related parameters but the decline in survival for those transplants was not so severe as might have been expected from the competitive hierarchy model. Even germlings of *F. serratus* survived in the uppermost zone, although these plants remained very small. I assume, that the orientation of the seawall lessened the effect of desiccation. The side of the N-Mole to which tiles were fixed got direct sunlight only in early morning.

Both of the furthest transplantations had the lowest relative yields: transplants from high eulittoral *F. spiralis* to the lowermost intertidal zone of *F. serratus* and vice versa (Figure 25), and performance was best in the zones of natural occurrence for each *Fucus* species. These findings support the model of niche differentiation rather than Keddy's model of competitive hierarchies.

It is conspicuous that *F. serratus* yielded only 6.35 g per tile, while *F. spiralis* achieved values of 22.80 g (max. mean individual biomass 0.22 and 0.09 g, respectively). In the field, *F. serratus* normally has highest growth rates and individual plants might have lengths >1 m while adult plants of *F. spiralis* remain rather small with far less biomass.

3.3.2 Transplants of adult field plants

Initial and final numbers of transplants of all three *Fucus* species are shown in Table 19. Differences in percentage survival were tested with ANOVA after arcsin transformation as suggested by Sokal & Rohlf (1995).

All three *Fucus* species showed the greatest percentage survival in the zone of *F. serratus* and successively fewer surviving plants in the zones above this tidal level. None of the *F. serratus* plants survived tranplantation to the zone

Table 19: Initial and final numbers of transplants of *Fucus* spp. plants derived from concrete blocks in the Helgoland intertidal and transplanted to the three *Fucus* zones. In brackets percentage survival. ANOVA performed with survivals of transplanted fucoids per experimental tile. n=6 for *F. serratus* and *F. spiralis*, n=5 for *F. vesiculosus*. A and B refer to Tukey-Kramer test at $\alpha=0.05$. Data were angular transformed prior to analyses (Sokal & Rohlf 1995).

		***Fucus* species**	
zone	*F. spiralis*	*F. vesiculosus*	*F. serratus*
F. spiralis	373→ 64 (17.2%) **A**	244→ 78 (32.0%)	113→ 0 (0.0%) **A**
F. vesiculosus	374→166 (44.4%) **B**	268→133 (49.6%)	114→ 5 (4.4%) **A**
F. serratus	374→198 (52.9%) **B**	240→121 (50.4%)	114→ 26 (22.8%) **B**
ANOVA	$F_{2,15}=8.193$ p=0.0039	$F_{2,12}=2.375$ p=0.1352	$F_{2,15}=16.460$ p=0.0002

of *F. spiralis*. Survival of *F. serratus* transplanted above its zone was significantly less than survival in the *F. serratus* zone (Table 19).

Transplanting itself might have had a great influence on mortality, since at least 47% of individuals died even in the *F. serratus* zone. Mortality was highest for *F. serratus*; only 23% survived in the *F. serratus* zone.

All three species of *Fucus* had the highest mean individual dry mass in the zone of *F. serratus* (Figure 26). Here, *F. serratus* had the highest individual mass (nearly 8 g/plant), higher than *F. vesiculosus* (ca. 3 g) and *F. spiralis* (ca. 1 g). Individual mass was strongly reduced in transplants to higher shore levels. In the *F. spiralis* zone even *F. spiralis* plants had on average a mass of only 0.3 g dry weight. Survival of *F. spiralis* was significantly higher when transplanted below its own zone (Table 19).

Numbers of concrete fragments bearing *Fucus* from the winter transplantation experiment that survived the storm were too few for statistical analysis (Table 20). However, the most complete data for *F. serratus* show the same trend of survival as summer transplants, but presumably lower desiccation stress led to survival of a few plants in the *F. spiralis* zone. This may also have led to the high survival, compared to summer transplants, of *F. vesiculosus* and *F. spiralis* in the highest zone.

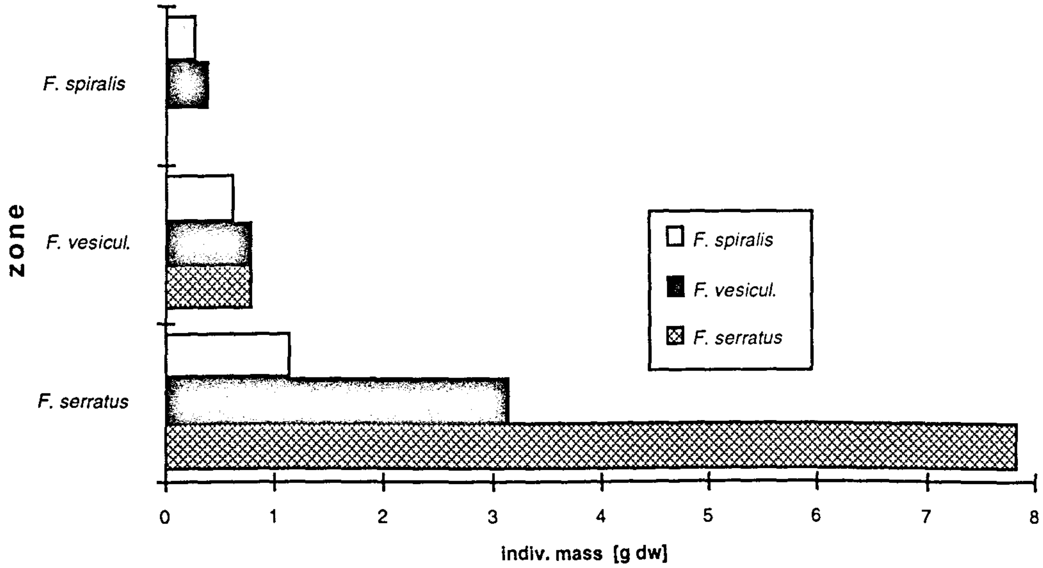


Figure 26: Mean individual dry masses of adult thalli of all three *Fucus* species transplanted to all three *Fucus* zones in an intertidal field of concrete bunker rubble seawards from the eastern seawalls of Helgoland.

Table 20: Winter transplants of fucoids from an experiment mostly destroyed by a storm. Initial and final numbers of shoots from concrete fragments that withstood the storm. In brackets percentage survival.

		***Fucus* species**	
zone	*F. spiralis*	*F. vesiculosus*	*F. serratus*
F. spiralis	69→ 69 (100.0%)	28→ 24 (85.7%)	64→ 8 (12.5%)
F. vesiculosus	---no-data---	---no-data---	24→ 8 (33.3%)
F. serratus	---no-data---	24→ 13 (54.2%)	68→ 56 (82.4%)

3.4 Summary of results

The two transplantation experiments differed in their results. Transplants of laboratory germlings performed best in their native zones. Survivorship (% survival, final density) and biomass production (yield, final biomass, individual biomass) were highest in zones of natural occurrence. These are features of the model of niche differentiation. Transplants of adult wild *Fucus*, in contrast, performed best in the lowermost zone of *F. serratus*, where they suffered least from desiccation, while survival rates on higher shore levels were lower and individual plant mass decreased sharply. These findings are concordant with the competitive hierarchy hypothesis.

A common feature of both experiments was the reduced performance of *F. serratus* and *F. vesiculosus* when transplanted above their native zones, with no survival at all for *F. serratus* in the uppermost *F. spiralis* zone (at least in summer when desiccation stress is greatest). It seems clear that here, for both *Fucus* species, a physiological limit of desiccation tolerance was approached or exceeded. This is in concordance with both the competitive hierarchy and the niche differentiation models.

With only the information from transplantation experiments performed in this study, it is not possible to interpret the different outcomes of the two experiments as result of the different origin of the experimental algae (laboratory or field) or of usage of different life stages (germlings or adolescent/adult plants).

GRAZING 4

4.1 Introduction

Along with physical factors and interspecific competition, herbivory is another important factor potentially controlling the distribution of intertidal algae (reviewed e.g. in Chapman 1995). Causes of zonation may be differential grazing pressure along the tidal gradient (e.g. Janke 1990; Worm & Chapman in prep.) and selective grazing among macroalgae (e.g. Watson & Norton 1985, 1987; Barker & Chapman 1990; Denton & Chapman 1991). As is the case for competition, grazing frequently influences upper (Cubit 1975 cited by Lubchenco 1980; Underwood 1980) or lower boundaries of intertidal macroalgae (Lubchenco 1980; Moreno & Jaramillo 1983). In some cases, competition in combination with grazing seemed to prevent the establishment of *Fucus* (Lubchenco 1982, 1986; Worm & Chapman in prep.).

The most conspicuous grazers in the NE intertidal zone of Helgoland are littorinids. Here, *Littorina littorea* and *L. mariae* play the most important role, while its congeners *L. obtusata* and *L. saxatilis* are only of minor abundance and importance (Janke 1986, 1990).

L. littorea feeds epilithically (Hawkins & Hartnoll 1983) and is a generalist, consuming a range of algae, but showing clear preferences when given a choice (Lubchenco 1978, 1982; Watson & Norton 1985). *L. mariae* may feed epilithically and epiphytically and is normally associated with *Fucus* (Watson & Norton 1987). Despite the apparent similarity between both species of flat periwikle, *L. obtusata* and *L. mariae*, these snails differ in various important respects (Gallardo & Götting 1985; Reid 1990; Tatarenkov 1995), notably feeding mode and food preferences (Watson & Norton 1987; Norton *et al.* 1990). It is therefore impossible, to extrapolate from the larger amount of published data for *L. obtusata* to *L. mariae*.

Preferecences for certain macroalgal species may not be the only critical factor. Certain algal life stages may be preferred by herbivores, and life stages may differ in their susceptibility to grazing. "Preferential grazing of the juvenile stages has the potential to influence community structure and algal distribution in a way that selectivity at the adult phase cannot do, unless grazing is abnormally intensive" (from Watson & Norton 1985). If grazing on juveniles leads to the death of the algae whereas adults are scarcely harmed by it, the early life stages, which often suffer high mortalities from other causes (Dean *et al.* 1989; Brawley & Johnson 1991; Kendrick 1994; Kendrick & Walker 1995), can be regarded as "bottlenecks" stage also in this respect (Lubchenco 1983). This is especially true for species such as *Fucus* that do not have a crust that may survive grazing or a heteromorphic life cycle where one morph represents an escape from grazing (Lubchenco & Cubit 1980).

Lubchenco (1983) found that germlings of *F. vesiculosus* were grazed by L. *Littorina* but, depending on littorinid density, by chance could grow to sizes relatively safe from grazing damage by *L. littorea* ("size escape").

In one of her experiments, Lubchenco offered small *F vesiculosus* germlings of 1-3 cm lengths and "medium *Fucus*" plants of 5-7 cm together to *L. littorea.* The snails completely consumed the former leaving the latter.

The objective of the following experiments was to examine whether escape in size may also exist for Helgoland *F. vesiculosus.* Escape in size could also play a role in the lower intertidal zone where *L. littorea* still has mean densities of ca. 100/m^2 (140/m^2 at mid tidal levels; Dahms 1993). Hence, the experiment was repeated with germlings of *F. serratus.* I chose three germling size classes. The biggest was at the upper limit of the range of Lubchenco's small germlings (3 cm). In this way, I could test if an escape in size occurs already at an earlier stage and if there is some threshold or successively decreasing consumption with increasing germling size. The experiments were repeated with *L. mariae* as the grazer.

In another set of experiments, preferences among *Fucus* species were examined. As mentioned above, preferential grazing may be another cause of *Fucus* zonation patterns.

Work from the NW Atlantic has dealt with littorinid grazing on *F. vesiculosus* only (New England: Lubchenco 1978, 1982, 1983; Petraitis 1987), on *F. vesiculosus* and *F. spiralis* (Nova Scotia: Chapman 1989; Barker & Chapman, 1990; Denton & Chapman 1991; Worm & Chapman in prep.), and on other species not found on Helgoland (*F. distichus*, *F. evanescens*). From European coasts there are data for all three Helgoland *Fucus* species from Watson & Norton (1985, 1987), but not all (Helgoland) *Fucus-Littorina* combinations were included. While many data exist from grazing experiments with *L.*

littorea and *L. obtusata* (Hunter 1981; Lubchenco 1982; Barker & Chapman 1990; Chapman 1990b) data on *L. mariae* grazing are scarce.

For all the experiments I chose to use attached germlings instead of tissue fragments or algal extracts in agar. Attached germlings more closely represent natural situations, but pure tissue characteristics (nutrition value, content of herbivore deterrents) may be confounded with species specific characteristics of growth form. Exeriments with adults and juveniles and surveys of the phenolic contents of both life stages indicate that data from juveniles should not be extrapolated to adults (Denton *et al.* 1990).

The design and analysis of preference experiments has undergone dramatic changes in the last few years. Roa (1992) and Manly (1993, 1995) proposed methods of analysis that have overcome the problem of lack of independence in data from simultaneously offered food items. In this study all tests proposed in Roa's and Manly's papers were applied to genuine and complete data sets from feeding preference experiments - to my knowledge for the first time. The utility of analyses from differently designed experiments are discussed. Differences among the methods in detection of preferences are reported. For better clarity in the main text body, the detailed descriptions, results and comparisons of the different methods are presented as an appendix. The present chapter is concerned with the experimental design and the ecological relevance of the results only. To keep both parts understandable, the quintessence of statistical analyses in the appendix is repeated in this chapter. The descriptions in the appendix have been deliberately written as recipes for the user rather than from the viewpoint of a statistician, since preference experiments are well established in the training of students. A comparison of the statistical methods showed that the method based on Yao (1965) and recommended by Manly (1993) should be used for experiments when there are differences in the initial masses of foods types offered. When equal masses can be offered, selection indices from Manly (1995) should be calculated. A detailed discussion of the methods is given in the appendix.

4.2 Material & methods

Cultivation of *Fucus*, preparation and weighing of food items

Zygotes of all three Helgoland *Fucus* species were sown and cultivated on the unglazed side of ceramic tiles as described in 2.2.

The unglazed sides of the tiles had 8 sections elevated ca. 0.5 mm and with an area of 3.7x3.7 cm^2 each (see Figure 24 in 3.2.1). When the fucoids had grown to experimental size, tiles were cut with a diamond saw to fragments of ca. 5x5 cm^2, each including one elevation in the centre.

With a scalpel, fucoid shoots were scraped from the rim of the tile fragments around the elevations. In this way experimental units with a well defined area were obtained. With the rim, tile fragments could be handled easily without damaging the algae.

These experimental units were weighed before and after exposure to grazers subsequent to an empirically determined "best procedure" for removing adhering water: Before weighing, tile fragments were rinsed with running tap water for 5 sec, held vertically for another 5 sec, shaken vigorously 3 times and placed on dry paper tissue with the glazed side down for 10 sec. Then tiles with algae were weighed to 4 decimal places on a balance (Feinwaage 1602 MP, Sartorius).

At the end of the experiment, subsequent to weighing, algae were scraped from the tile fragment. These were weighed immediately in preweighed aluminium hulls. Tile framents without fucoids were weighed immediately thereafter. After drying at 60° C for 3 days, algae were weighed again for calculation of dry weight.

The reliability of the weighing procedure was tested prior to experiments. The same tile fragments bearing algae were weighed 10 times subsequent to the procedure described above. Between measurements, algae were allowed to recover for 10 min in sterile seawater. Coefficient of variation was ca. 0.2% for tile fragments plus algae or ca. 3% for algal fresh weight alone. This test was done with several tile fragments with different *Fucus* species, algal size classes and densities.

After removing adhering water, weight loss due to evaporation during weighing was estimated to be ca. 5 mg/min per tile fragment bearing algae. Since all tile fragments were handled equally and weighed within ca. 15 sec after the 'drying' procedure this error contributed just to the general weighing error which was low compared to grazing effects of up to 1.2 g algal fresh weight per tile fragment.

Fresh weights of all algae per tile fragment ranged from ca. 1-3 g depending on *Fucus* species, size and density. Weights of tile fragments without algae ranged from 26-33 g.

Sampling and preparation of littorinid grazers

Individuals of rough (*Littorina littorea*) and flat (*L. mariae*) periwinkles were collected in the Helgoland NE-Intertidal at low tide. Gallardo & Götting (1985) and Wilhelmsen (pers. communication, unpublished data from 1994) found that, in the Helgoland intertidal, 99% of all flat periwinkles were *Littorina mariae*. The remainder were *L. obtusata*. Periwinkles were starved for one week in an aerated seawater tank covered with an opaque sheet of plastic to prevent escape of snails and growth of microalgae. A moderate flow of filtered seawater continually exchanged the medium. Faeces were removed every day.

Very small individuals were not used in the experiments. The biggest individuals were chosen randomly (without reference to size) from a pool of starved snails. The pool contained ca. double the number of animals required in the experiment. To make feeding rates comparable, approximately the same ash-free dry mass of both *Littorina* species was used in the experiments. Prior tests showed that the ash-free dry weight of 10 *Littorina mariae* was approximately the same as that of 1 *L. littorea.*

To obtain the organic dry weights of littorinids, they were rinsed with tap water and killed in a freezer. Afterwards they were dried in an annealed (6 h), preweighed crucible at 60° C for 5 days, weighed and combusted in a muffle furnace at 450° C for 24 h.

Implementation of feeding preference experiments

Three tile fragments bearing fucoids were submerged in 600 ml of filtered, sterile seawater in a 1 l glass dish (154 cm^2 bottom surface area) (Figure 27). Dishes were aerated with an airstone and covered with a glass lid. Dishes were kept in a temperature constant room at 13° C and 16:8 h L:D (60 µmol photons/m^2/s).

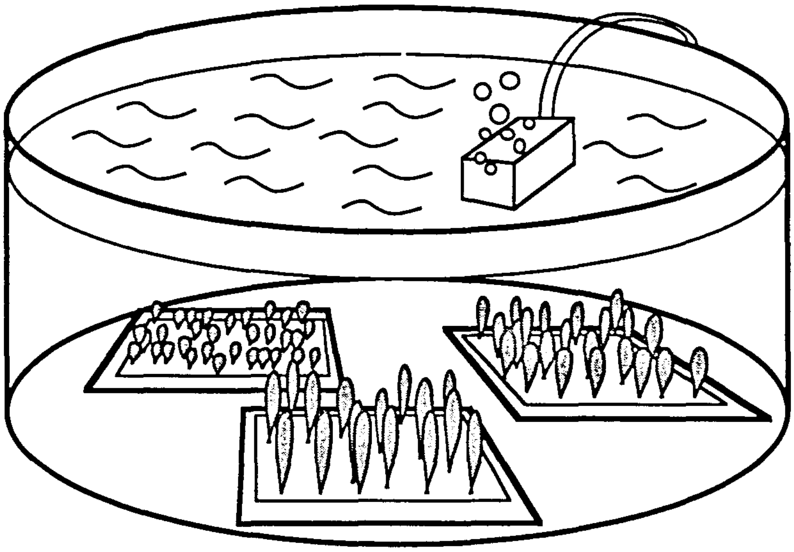


Figure 27: Experimental container (glass dish) with 3 fragments of ceramic tiles, each bearing another *Fucus* germling size class. For further explanations see text.

5 *Littorina littorea* or 50 *L. mariae* were put to the center of each dish. Additionally there were controls for autogenic changes of algae without grazers but treated in the same way in all other respects.

Algae were exposed to periwinkles for 60 h. In this period of time grazing was detectable but none of the tile fragments was grazed completely. Seawater was exchanged carefully after ca. 30 h. Snails were checked daily and occasional dead replaced by living (starved) specimens. In all experiments, only 6 individuals of *Littorina mariae* died.

At the end of the experiment, periwinkles were removed and deep frozen. Later they were weighed and combusted as described above. Tile fragments were weighed as described above and remaining algae were scraped from the fragments, weighed and dried immediately afterwards.

4.2.1 Feeding preference among *Fucus* germling size classes

Three different size classes of *Fucus serratus* or *F. vesiculosus* were offered in a multiple choice design to 5 *Littorina littorea* or 50 *L. mariae* or were used as controls (Figure 28). Lengths of size classes were ca. 3 mm (I), 10 mm (II) or 30 mm (III). The experiment was done twice in February 1994. Both experiments were done in the same way and with 5 replicates each. The data from the two experiments were pooled. Experimental dishes (each with 3 tile fragments) were arranged randomly per replicate.

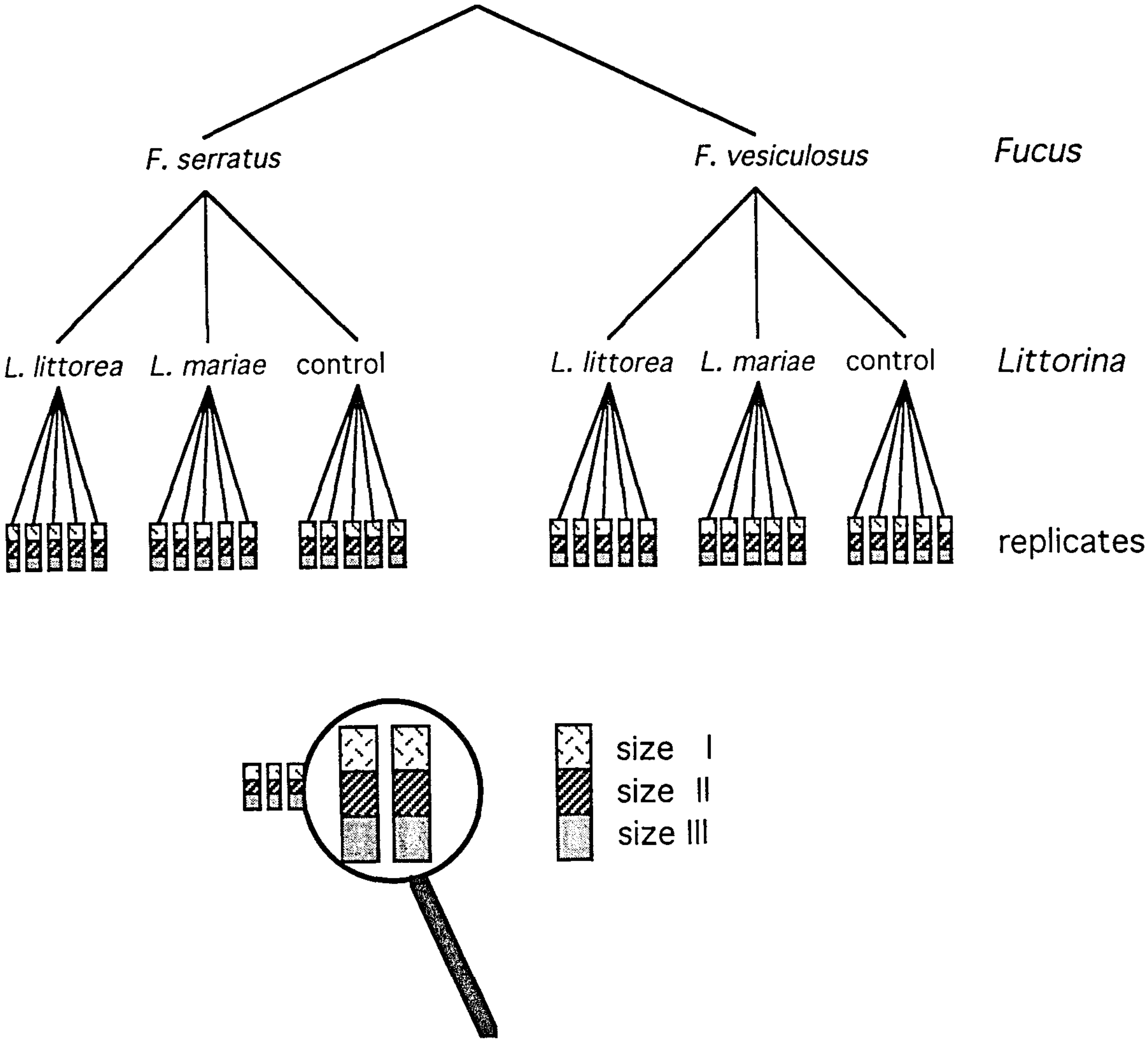


Figure 28: Design of a multiple choice experiment performed to detect preferences of *Littorina littorea* and *L. mariae* for germling size classes of *Fucus serratus* or *F. vesiculosus*. Three size classes were used: I: ca. 3 mm, II: ca. 10 mm, III: ca. 30 mm.

4.2.2 Feeding preference among *Fucus* species

Multiple choice and no choice feeding preference experiments were performed simultaneously. In the choice experiments, each experimental dish contained three tile fragments, each bearing germlings of a separate *Fucus* species. Five individuals of *Littorina littorea*, 50 of *L. mariae*, or no grazers as control were added to each dish (Figure 29a).

In no choice experiments, the same numbers of grazers were placed in dishes containing three tile fragments bearing either *F. serratus*, *F. vesiculosus* or *F. spiralis* (Figure 29b). Additionally adequate controls were established.

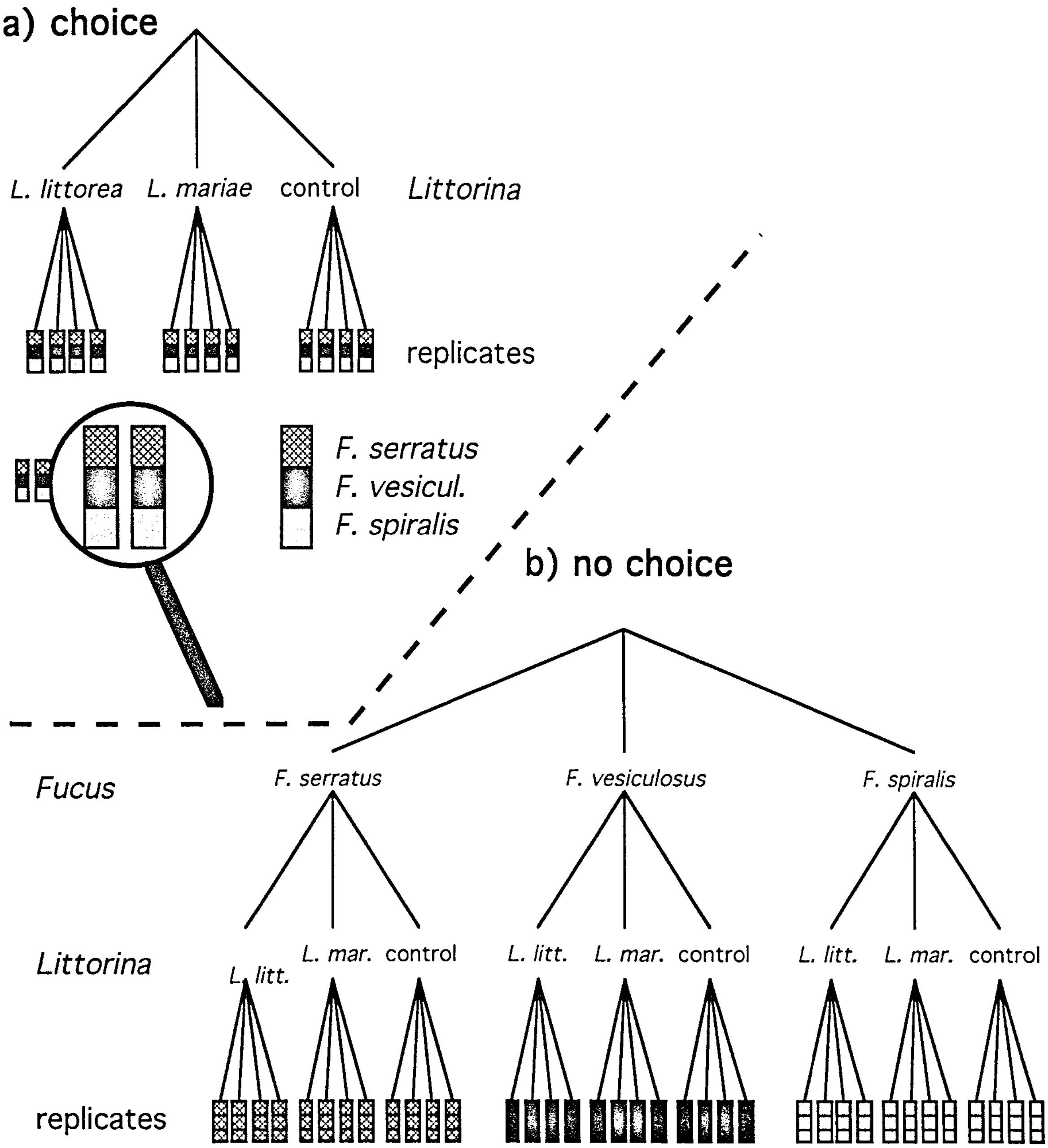


Figure 29: Design of an experiment performed to detect preferences of *Littorina littorea* and *L. mariae* for *Fucus* spp. Multiple choice (a) and no choice experiments (b) were done simultaneously.

This experiment was done in December 1994. All treatments were replicated 4fold. Even-aged germlings of different *Fucus* species differed in length, density and morphology (Table 21). Normally, one shoot of *F. serratus* grew from one zygote, but several shoots grew from zygotes of *F. vesiculosus*, and still more from those of *F. spiralis*.

Table 21: Frequency distribution of even-aged, monospecific stands of *Fucus* spp. germlings used in feeding preference experiments.

length (cm)	*F. serratus*	*F. vesiculosus*	*F. spiralis*
[0-1)	44	91	302
[1-2)	31	52	36
[2-3)	18	18	16
[3-4)	9	8	3
[4-5)	3	4	1
[5-6)	1	1	0
[6-7)	2	1	0
[7-8)	0	1	0
[8-9)	0	0	0
density (N/cm^2)	108	176	358
median (cm)	1.5	0.5	0.5

4.2.3 Littorinid densities in the Helgoland intertidal

Data on mean grazer densities in the Helgoland rocky intertidal already exist in the works of Janke (1986, 1990), Bock (1992) and Dahms (1993). To obtain data more explicitly related to *Fucus* cover, and to assess the maximum impact of herbivory, maximum *Littorina* densities were estimated in 0.25 m^2 quadrats in July 1995. Along the gradient of tidal level, locations with apparently high grazer densities and varying algal cover were chosen. Per type of algal cover, at ≥5 locations littorinids were censused. In the *F. serratus* zone, where locations were chosen randomly, data from 10 quadrats were obtained.

most. All confidence limits unequivocally indicated that rejection of smallest germlings was significant (see appendix, Figure A5).

Fucus vesiculosus grazed by *Littorina littorea*

The grazing on 3 size classes of *F. vesiculosus* by *L. littorea* followed the pattern for *F. serratus* (Figure 30). The total amount eaten was less with *F. vesiculosus*. Snails consumed most from size class I (3 mm). The least consumed was size class II (10 mm). Confidence limits show that rejection of the null hypothesis of equal consumption was due to preference for the smallest size class (see appendix, Figure A6).

Fucus vesiculosus grazed by *Littorina mariae*

The total amount of grazing was similar to that on *F. serratus*, but in this trial size class I and III (3 and 30 mm, respectively) were consumed to a similar extent, while size class II (10 mm) was barely grazed (Figure 30).

4.3.2 Feeding preference among *Fucus* species

Multiple choice experiment and biotic interactions

Analyses of fresh weight data

The amounts of mass (fresh weight) change, corrected for the controls, are given in Figure 31. For both littorinids, *F. spiralis* was consumed most, while only small amounts of *F. serratus* were eaten (destroyed). Fresh weight of *F. vesiculosus* was diminished by the snails to an intermediate level, that was nearly four times higher for *L. littorea* compared to *L. mariae*.

Yao's test, which is independent of random pairing, revealed significant differences among *Fucus* species for both experiments, with *L. littorea* they were highly significant ($p<0.001$, Table 23).

Manly's (1995) preference indices revealed significant rejection of *F. serratus* by both periwinkle species (Figure A11 and A12, left in the appendix). *F. spiralis* was significantly preferred by both littorinids, but for *L. littorea* only when normal t-distribution limits were used. The intermediate consumption of *F. vesiculosus* was not significantly different from 1/no. of food items = 0.33.

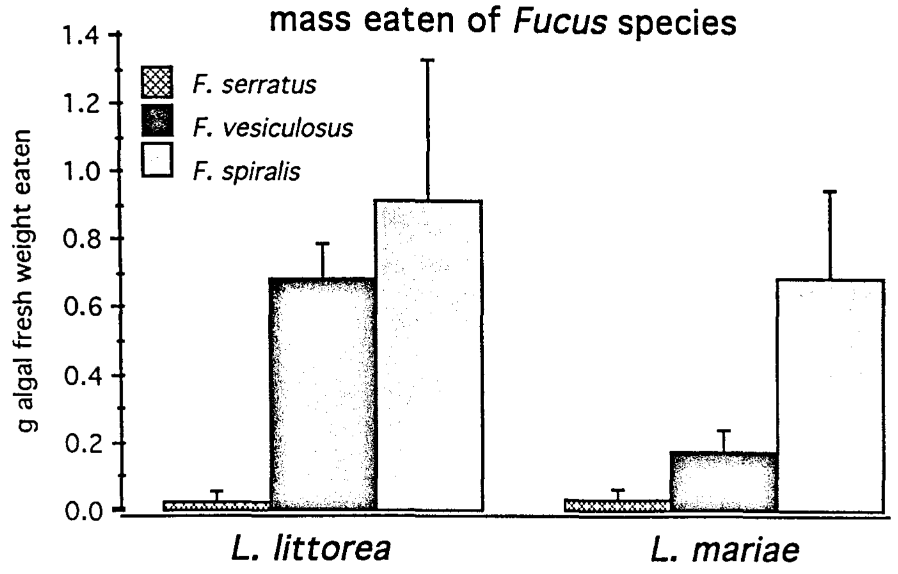


Figure 31: *Fucus* spp. fresh weight consumed by *Littorina* spp. in a multiple choice feeding preference experiment. Mean values of 4 replicates and SD corresponding to random pairing of treatments and controls yielding minimal F-values.

Table 23: Results of Yao's test as proposed by Manly (1993) (which is independent of random pairing) for feeding preference experiments with *Littorina littorea* or *L. mariae* grazing on 3 *Fucus* spp.

grazer	**F**	**df**	**p**
L.littorea	936.21	2, 3.79	<0.001
L.mariae	21.87	2, 2.23	<0.05

Analyses with g algal dw * (g organic dw snail * d)$^{-1}$ data

Data of algal dry weight per organic dry weight of snails were calculated as indicated in the appendix. The mean relation of fresh weight to dry weight differed for *F. spiralis* compared to *F. serratus* and *F. vesiculosus*:

	F. serratus	*F. vesiculosus*	*F. spiralis*
fw:dw (±SD)	5.87 ± 0.18	5.94 ± 0.24	8.50 ± 1.46

This led to a shift in the patterns of consumption (compare Figure 31 with Figure 32). With dry weight data, *F. vesiculosus* was the most consumed algae by *L. littorea*. As with fresh weight data, *F. serratus* was clearly avoided by both littorinids and *F. vesiculosus* was eaten by *L. mariae* only to an intermediate extent. It is not possible to apply Yao's test to dry weight per snail dry weight data, because controls have to be offset with treatments in a way that would require the same algal dw per snail dry weight data also for controls (see appendix). Since there is no logical relation between controls (without grazers) and grazers, this calculation was not sensible. When the flaws of Manly's (1995) selection index for unbalanced initital weights are taken into account, confidence limits failed to show significant preference/avoidance for any food (Figure A14 in the appendix).

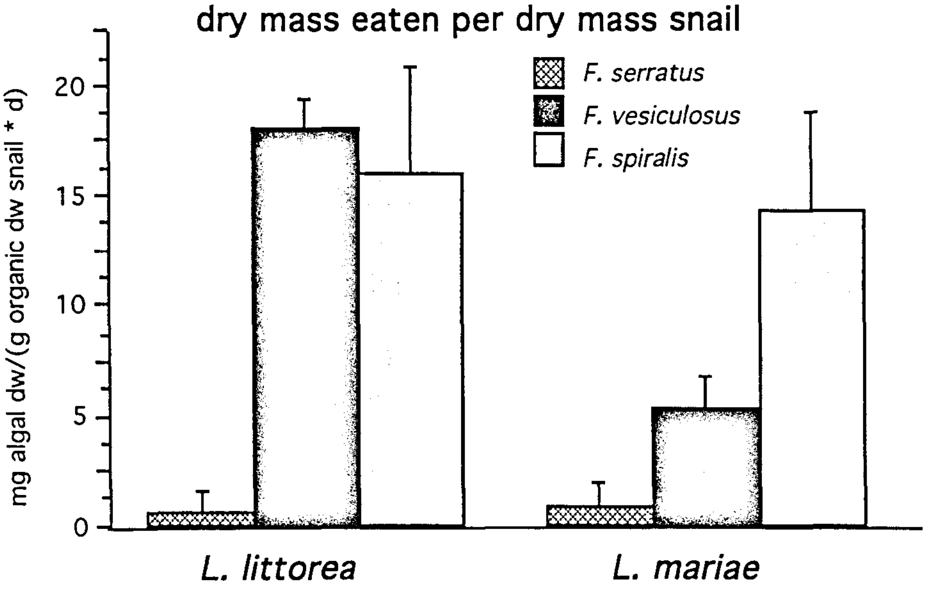


Figure 32: *Fucus* spp. dry weight consumed per organic dry weight of *Littorina* spp. in a multiple choice feeding preference experiment. Mean values of 4 replicates and SD corresponding to random pairing of treatments and controls yielding minimal F-values. Compare with Figure 31 for fresh weight consumption patterns.

No choice experiment

For the analysis of no choice experiments, the data from three tile fragments bearing the same *Fucus* species in one experimental container were pooled (summed). Fresh weight data (g fw eaten per container) and dw/dw snail data (mg algal dw * g organic dw snail $^{-1}$ * d^{-1}) were used for analyses. Initial fresh weight is shown in Figure 33. The initial amount of *F. serratus* was slightly less than that of *F. vesiculosus* and *F. spiralis*. The changes in fresh weight during the course of the experiment indicate only small average growth rates for control trials (Figure 34). Figure 35 shows the corrected amounts of fresh weight eaten (destroyed) by littorinids.

As in the multiple choice experiment, *F. spiralis* had less dry mass per unit fresh weight compared to its congeners:

	F. serratus	*F. vesiculosus*	*F. spiralis*
fw:dw (±SD)	5.84 ± 0.07	5.87 ± 0.14	8.15 ± 0.36

Hence, ratios of dry weight consumption between *Fucus* species (Figure 36) are slightly different when compared to fresh weight data (in Figure 35), but *F. spiralis* is still the most consumed *Fucus* species and *F. serratus* the conspicuously least consumed.

One-way ANOVAs were performed with *Fucus* species as factor for experiments with *L. littorea* or *L. mariae*. This was done with both g fresh weight and dw/dw snail data. Tukey-Kramer test was done to determine which *Fucus* species comparisons yielded significant differences ($\alpha = 0.01$). Results were similar for fresh weight and dry weight data (summarized in Table 24).

With *L. littorea* as grazer, consumption on *F. serratus* differed significantly from that on *F.vesiculosus* and *F. spiralis*. In experiments with *L. mariae*, all pairwise *post hoc* comparisons revealed significant differences between consumption of *Fucus* species.

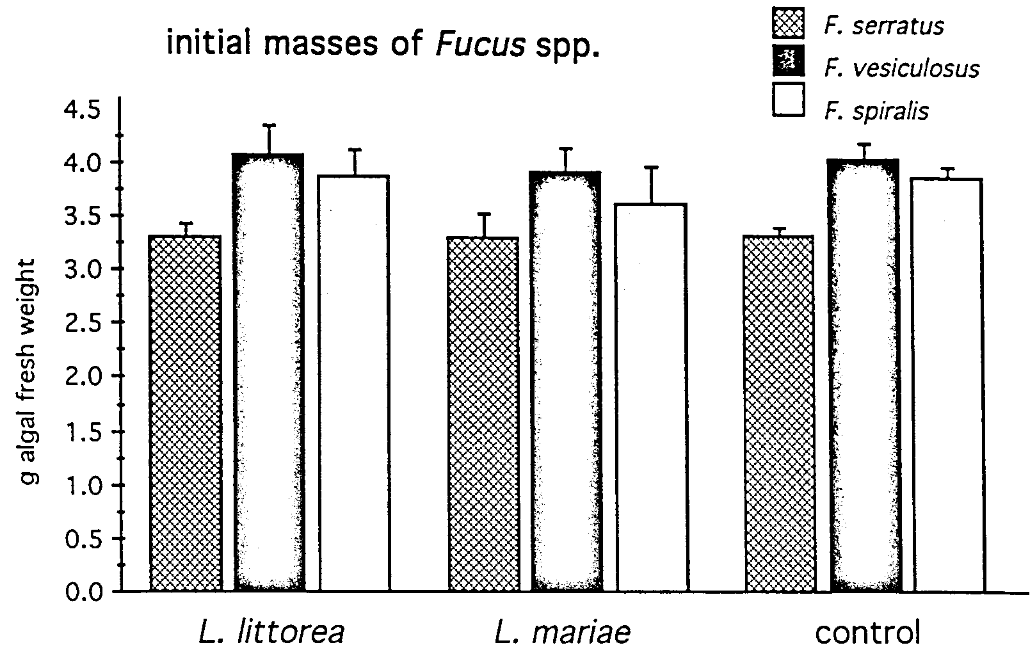


Figure 33: Inital masses of *Fucus* spp. offered to *Littorina* spp. in a no choice feeding experiment (plus control).

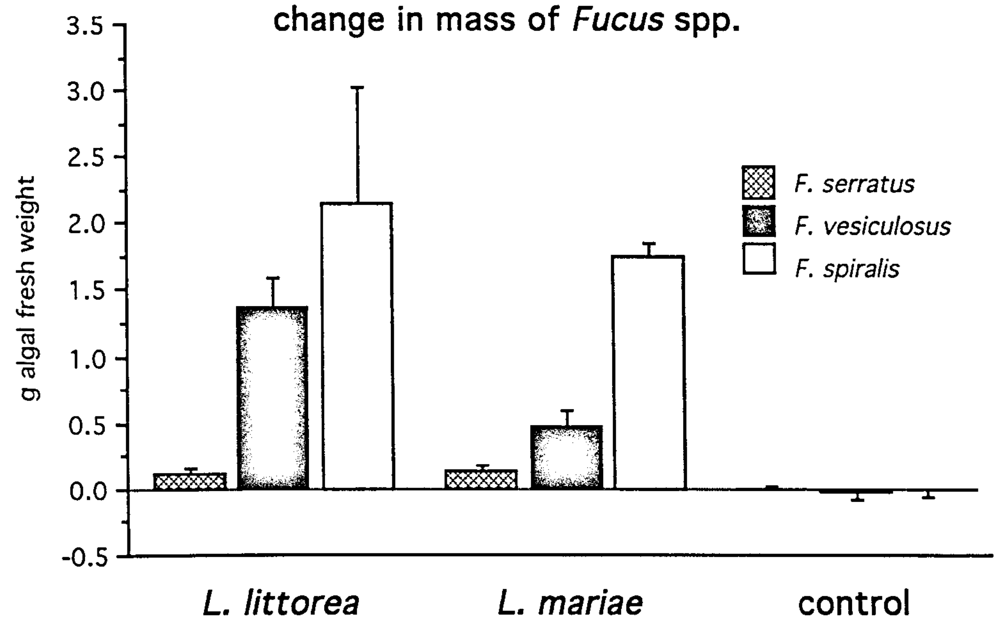


Figure 34: Change in masses of *Fucus* spp. offered to *Littorina* spp in a no choice feeding experiment (plus control).

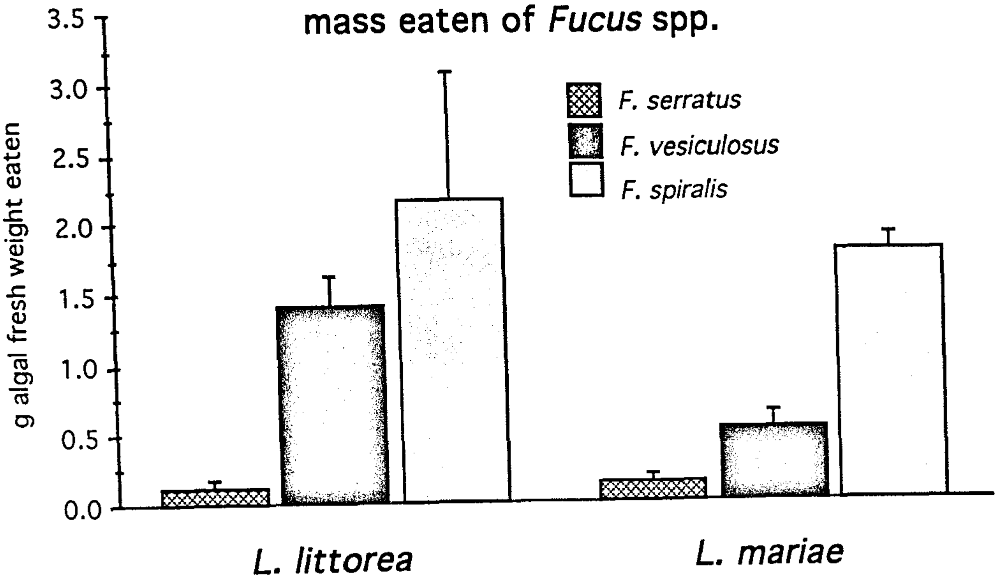


Figure 35: Fresh masses of *Fucus* spp. consumed by *Littorina* spp. in a no choice feeding experiment.

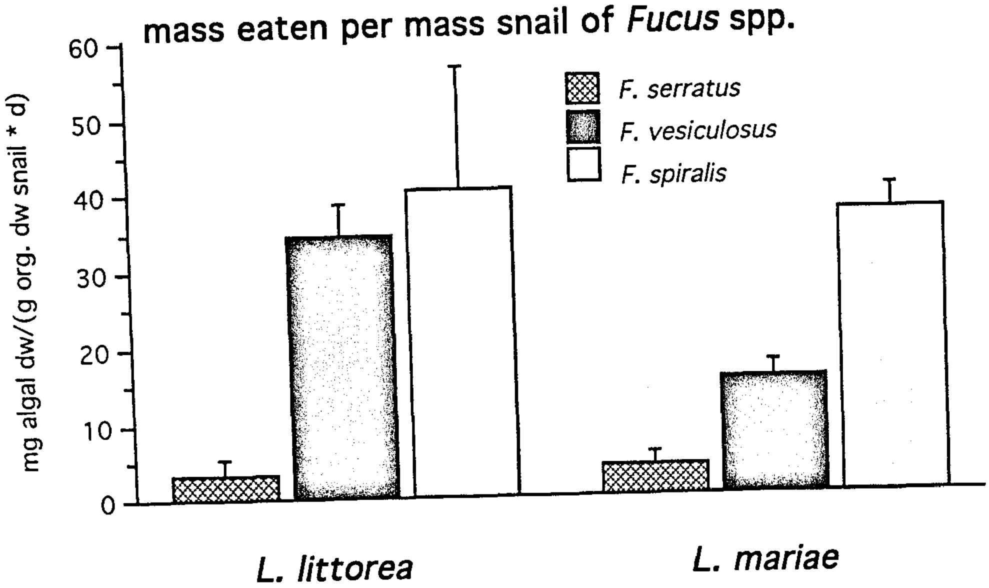


Figure 36: *Fucus* spp. dry weight consumed per organic dry weight of *Littorina* spp. in a no choice feeding experiment.

Table 24: Comparison of amounts eaten in no choice experiments to measure edibility of *Fucus* species for *Littorina* spp. Results of ANOVAs performed with no choice data. A, B, C refer to Tukey-Kramer test at $\alpha=0.01$.

	Littorina littorea		*Littorina mariae*	
	choice	**no choice**	**choice**	**no choice**
g fresh weight				
F. serratus	0.02	0.12 **A**	0.03	0.14 **A**
F. vesiculosus	0.68	1.41 **B**	0.18	0.51 **B**
F. spiralis	0.91	2.17 **B**	0.69	1.78 **C**
sum	**1.61**		**0.90**	
ANOVA		$F_{2,9}=56.41$ $p=0.0001$		$F_{2,9}=321.97$ $p=0.0001$
transformation		log		
mg dw/g dw snail and day				
F. serratus	0.59	3.36 **A**	0.92	3.92 **A**
F. vesiculosus	18.00	34.57 **B**	5.16	15.40 **B**
F. spiralis	16.05	40.40 **B**	14.30	37.38 **C**
sum	**34.64**		**20.38**	
ANOVA		$F_{2,9}=26.04$ $p=0.0002$		$F_{2,9}=196.51$ $p=0.0001$
transformation		log		

Comparison of choice and no choice results

Comparisons of choice and no choice experiments must be done very carefully, since conditions are fundamentally different. When fresh weight data are considered, amounts of *F. spiralis* consumed when offered alone exceeded the total amount consumed in multiple choice trials (sum of three *Fucus* spp., Table 24). With fresh weight data, lower masses of *F. vesiculosus* were consumed in no choice trials compared to the total amount eaten in multiple choice experiments. With dw/dw snail data, total mass in choice and mass of *F. vesiculosus* in no choice experiments were equal with *L. littorea* as consumer. *F. serratus* clearly was rejected by both littorinid grazers in choice and no choice trials.

With dw/dw snail data the ratio between *F. spiralis* and *F. vesiculosus* is shifted to higher consumed amounts of the latter, but patterns of preferences and edibility are similar to those with fresh weight data.

4.3.3 Littorinid densities in the Helgoland intertidal

Maximum values of densities of *Littorina littorea* and *L. mariae* are given in Table 25. For censuses in the *F. serratus* zone, where a dense canopy prevented selection of high littorinid density locations, mean values of 10 quadrats are given together with maximum densities.

Table 25: Littorinid grazer densities in the Helgoland rocky intertidal. Haphazardly measured in 0.25 m^2 quadrats at locations with different covers. In the table, locations are arranged according to their level on the shore gradient. Locations were selected for maximum rather than for average densities, except mid and lower *F. serratus* zone, where dense fucoid cover prevented selection for high grazer densities (here additional MV±SD from 10 quadrats). LAI: leaf area index. Data per m^2. Survey was done in July 1995.

cover	*L. littorina*	*L. mariae*	
	>10 mm	>5 mm	<5mm
F. spiralis	0	8 in total	
F. vesiculosus+*F. spiralis*	0	8 in total	
F.ser.+*F.ves.* on elevated rocks in *Enteromorpha* zone	0	56	12
Enteromorpha	8	8	0
lower border of *Enterom.*[1]	368	4	0
F.ser., LAI≈1, *Myt.* underneath	96	44	8
Mytilus+ca.5%*Fucus*[2]	80	0	0
mid *F.ser.* zone, LAI>>1	196	80	20
mean	(71.3±61.0)	(44.7±18.6)	(7.0± 6.2)
low *F.ser.* zone, LAI>>1	120	76	48
mean	(60.0±37.1)	(38.7±20.3)	(25.3±10.6)
groove[3]	124	0	0

1: probably feeding on drift algae
2: >60% of littorinids spatially associated with *Fucus* cover
3: 50-80% cover of *Corallina officinalis*, *Ulva* sp., *Cladophora rupestris*, *Chondrus crispus*, *Laminaria* juveniles

4.4 Summary of results

The preferences for size classes of *Fucus* germlings differed between *Littorina littorea* and *L. mariae*. Preference was detected in each experiment with one of four *Littorina-Fucus* combinations. *L. littorea* clearly preferred the smallest size of both *Fucus serratus* and *F. vesiculosus*. This is not surprising, since *L. littorea* is known to graze epilithically (Hawkins & Hartnoll 1983). However, the preferences show no trend with increasing length of germlings. For unknown reasons, the intermediate size class of 10 mm was the least consumed. When the intermediate consumption of the biggest size class (30 mm) is compared with that of the smallest size class (3 mm), it must be remembered that consumption of equal masses would mean a few somewhat damaged large thalli *versus* hundreds of killed smaller individuals. Germlings of size class II and III (10 and 30 mm, respectively) were frequently found uneaten but detached from tile fragments at the termination of the experiment, indicating that the devastating effect on fucoids (consumption plus 'bulldozing') was higher than would be measured in ingestion rate experiments. The pattern of preferences was similar with both fucoids, but *F. vesiculosus* was consumed to a lower extent.

L. mariae showed preferences for increasingly large size classes of *F. serratus*. With *F. vesiculosus*, the intermediate size class was avoided, but preferences were less significant (summarized over all statistical methods applied) than for the other *Littorina-Fucus* combinations. Individuals of *L. mariae* regularly were observed to crawl on bigger size class algae of both *Fucus* spp. Numbers of uneaten but detached fucoids seemed to be smaller. Unfortunately these observations were not measured in the experiments (but should be in future), therefore it remains speculative that broader *F. serratus* germling thalli provided a better substrate for crawling and grazing (leading to greater mass loss of *F. serratus*) and that bulldozing was less with *L. mariae* as grazer, leading to smaller changes in algal mass in the experiments with this snail.

Dahms (1993) found on average 140/m^2 *L. littorea* in the zone of *F. vesiculosus*, 100/m^2 in the *F. serratus* zone and <20/m^2 in the *F. spiralis* zone in the Helgoland intertidal. A rapid survey of littorinid numbers showed that the snails reached a density of ca. 325/m^2 (as used in this experiment) only locally. From other studies even higher desities are known (e.g. Watson & Norton 1985 found locally up to 10,000/m^2). The experiment was terminated after 2.5 days, before periwinkles were able to completely consume the fucoids of any tile fragment. If grazing rates and densities are the same in the field, *L. littorea* should be capable of destroying all young germlings on smooth surfaces. Survival may then depend on crevices, as proposed by Lubchenco (1980, 1983), where germlings grow ('escape') to bigger sizes. These are less susceptible to littorinid induced mortality, as shown in the present study.

Experimental densities by far exceeded natural densities for *L. mariae*. The density of ca. 3250/m^2 was chosed to have comparable organic dry weights of both littorinids. *L. mariae* feeds mostly epiphytically and will therefore harm bigger germlings and adult thalli but not necessarily kill them. Despite the high consumer density, very young germlings were only moderately consumed. These findings suggest, that *L. mariae* should play only in minor role in controlling the abundance of *Fucus*.

Although *F. serratus* and *F. vesiculosus* germling size classes were not offered together and, therefore, there was no real choice, the data suggest, that *F. serratus* should be the preferred species. At least, a higher mass was consumed compared to *F. vesiculosus*. This is in striking contrast to the findings of the experiment where even-aged germlings of all three *Fucus* species were offered together to detect preferences for *Fucus* species. Here, *F. serratus* was conspicuously avoided by both littorinids in multiple choice experiments and consumed to only minor amounts when offered alone to grazers. The explanation for this discrepancy may lie in the differing sizes and densities of fucoids in the experiments. In the 'preference for size class' experiment, density and length of germlings were negatively correlated. This was not thought to be an incorrect design, since it is the situation met in the field due to self-thinning of algal stands. Further, it would have been impossible to offer the same density and mass together of different size classes, unless very low densities of larger size classes were used and this would have flawed the experiment in another way. In the 'preference for *Fucus* spp.' experiment, size and density differed and this may have had a confounding effect. Again, this was an inherent characteristic rather than incorrect experimental design, since germlings of similar age differred in number of ramets and, consequently, in density and length between species. Since *L. littorea* clearly showed a preference for very small germlings, in the 'preference for *Fucus* spp.' experiment some avoidance may be explained by the on average bigger size of germlings. But this cannot be the only explanation, because bigger size classes were also consumed (or destroyed) to some extent. Although the reasons for the discrepancy are not fully understood the second experiment should correctly answer, which *Fucus* species is preferred/avoided in even-aged stands. Edibility, tested with no choice experiments, was highest for *F. spiralis*, intermediate for *F. vesiculosus* and conspicuously low for *F. serratus* for both littorinids.

GENERAL DISCUSSION 5

Test of the validity of the competitive hierarchy hypothesis

In the present study, I tested whether the Helgoland *Fucus* species follow the predictions of the 'competitive hierarchy hypothesis' (Keddy 1989a). I determined the competitive ranks of Helgoland *Fucus* species and their fundamental niches in the section of the intertidal zone naturally populated by members of the genus.

Competitive abilities of Helgoland *Fucus* species

In replacement series experiments set up in the Helgoland intertidal zone, *Fucus vesiculosus* clearly was the dominant competitor in mixtures with both *F. spiralis* or *F. serratus.*

Although, in the present study, the experiments were installed in the lower intertidal zone, the results for *F. vesiculosus-F. spiralis* experiments at all three densities were very similiar to those of Chapman (1990a), who installed his replacement series cultures (triplicated, with the same mixture proportions, at my lowest density) in the mid intertidal zone in Nova Scotia. The competitive exclusion of *F. spiralis* from the mid intertidal zone occupied by *F. vesiculosus* was also shown by Schonbeck & Norton (1980).

The competitive dominance of *F. vesiculosus* over *F. serratus* was less pronounced than over *F. spiralis*. Additional analysis of the data in an additive design showed that competitive ability was asymmetric (*sensu* Shipley & Keddy 1994): the intraspecific yield reduction of *F. vesiculosus* was more severe than the reduction in mixtures with *F. serratus* or *F. spiralis*, respectively. In both *F. serratus* and *F. spiralis*, interspecific competition had a stronger effect on yield reduction than intraspecific competition. The terms 'symmetric/asymmetric competition' have different meanings in ecology (as variously discussed by Underwood 1986 and Shipley & Keddy 1994) and were applied here in the sense of Shipley and Keddy (1994) who evaluated the predominance of asymmetric interactions from terrestrial plant literature data (Keddy & Shipley 1989; Shipley 1993) and concluded that competitive interactions are primarily asymmetric and transitive, leading to competitive hierarchies in herbaceous plant communities.

F. vesiculosus was also the dominant competitor when Goldberg's definition of competitive ability was used: the 'competitive effect' of *F. vesiculosus* on either *F. spiralis* or *F. serratus* was stronger than the effect of congeners on *F. vesiculosus* ('competitive response', Goldberg 1990; Goldberg & Landa 1991).

In this study, competitive interactions between *F. serratus* and *F. spiralis* were not tested, because these species normally have no common border on strictly zoned seawalls on Helgoland and because of limited facilities and manpower. However, on boulders scattered in the mid intertidal zone of the NE-rocky intertidal all three *Fucus* species may be found together in proximate vicinity (pers. observation; Janke 1986; for British coasts: Hawkins & Hartnoll 1985). From my experiments, the competitive relationships

F. vesiculosus > *F. serratus* and *F. vesiculosus* > *F. spiralis*

could be easily shown. There is evidence that the complete rank would be

F. vesiculosus > *F. serratus* > *F. spiralis*

when the strength of yield reduction effects from *F. vesiculosus* on *F. serratus* and *F. spiralis* are compared in the 'extended additive design' (reduction to 26.4% and 18.4%, respectively, compare Figure 13). In the same design, yield of *Fucus vesiculosus* was reduced by 2% in the presence of *F. serratus*, but even elevated by 20% when grown with the same amount of *F. spiralis*. Hence, *F. spiralis*, compared to *F. serratus*, is more affected by *F. vesiculosus*, but affects *F. vesiculosus* less negatively in return. Ranks of competitive effect and response are not necessarily positively correlated (Goldberg & Landa 1991; Keddy *et al.* 1994), but they are in this case.

The order of rank predicted from the competitive hierarchy model (Keddy 1989a) was only partially met by Helgoland *Fucus* spp. Only one of the two experimentally tested competitive relations (*F. vesiculosus* > *F. spiralis*) matched Keddy's hypothesis. With the inferred transitive ranks, two competitive relations (*F. vesiculosus* > *F. spiralis* and *F. serratus* > *F. spiralis*) met the predictions, one did not (*F. vesiculosus* > *F. serratus*). Although the competitive dominance of *F. vesiculosus* over *F. serratus* was less pronounced, this deviation from the predicted order of rank should be be judged as serious, since at the benign end of the model gradient the prevalence of competition as structuring force is predicted to be greatest, whereas "species at the periphery [i.e. the less benign end of the gradient] tend toward distinct niche structure" (Keddy 1990). The proportion of correct predictions of 1/2 or 2/3 is not different from a null model assigning competitive dominance by chance. Hence, the hypothesis ($H_{0\text{-}1}$) that competitive ranks of Helgoland *Fucus* species can be explained with the predictions from the competitive hierarchy model must be rejected.

Assessment of replacement series as experimental design

The use of replacement series has been criticized by several authors for being a substitutive design (e.g. Connolly 1986; Underwood 1986), for the density dependence of its findings (e.g. Inouye & Schaffer 1981; Taylor & Aarssen 1989; Silvertown & Dale 1991), for its special conditions seldom found in nature (Herben & Krahulec 1990; Silvertown & Dale 1991) or for the prerequisite of similar sizes of the plants used (Harper 1977; Keddy 1989a, 1990; Silvertown & Dale 1991). Only few went as far as Connolly (1986) who stated "that it [the replacement series] is usually a misleading tool for research on mixtures", but most concluded that it may be a valuable method, when the flaws are taken into account (Firbank & Watkinson 1990; Cousens 1991). Cousens & O'Neill (1993) felt a necessity to defend this experimental design because they were afraid that the popularity of criticizing replacement series would lead to rejection of findings of well performed experiments, too.

However, as mentioned in 2.1, replacement series have their difficulties, as have other designs to detect competition, and several total densities should be used along with similar sized plants to keep the flaws in check. In the present study the findings from replacement series with different densities (D1-D3) were similar, supporting the evidence found by others that dominance seldom changed with density (Fowler 1982; Cousens & O'Neill 1993). For this to be true, both species must achieve constant final yield, when grown alone at the density of their mixture proportion (Taylor & Aarssen 1989; Cousens & O'Neill 1993). In the present study, no tests of this kind were done explicitly. However, for each *Fucus* species, final densities of monospecific treatments, although from three different starting densities (D1-D3), achieved the same order of magnitude (Figure 17). Initial density D1 was 1/5 x D2. In 25:75%-

two species mixture treatments at D2, the species with the density 25% of D2 still had a higher ("monospecific") density (1/4 x D2) than in D1 monocultures. Hence, at least at initial desities D2 and D3, all *Fucus* spp. in all treatments should have met the prerequisite demanded by Taylor & Aarssen (1989) and others. Since findings of all three experimental densities were similar (Figures 11+12), all *Fucus* spp. in all proportions and all densities (D1-D3) may have achieved constant final yield, i.e. even at the lowest density, but this must remain speculative.

The assumption of similar sizes was probably met with congeneric *Fucus* species in this study. Despite differences in maximum length and growth rates (see below) these species should be more similar than many pairs used in terrestrial studies of grasses and herbs (e.g. Fowler 1982).

However, from the findings of the competition experiments, only germling dominances may be assessed safely. When competing (macroalgal) species differ in life stage, different outcomes are possible, e.g. due to shading or preemptive effects (Herben & Krahulec 1990; Silvertown & Dale 1991; Benedetti-Cecchi & Cinelli 1996).

Density effects in monospecific *Fucus* stands

The monocultures of the replacement series represent monospecific even-aged stands and may be examined in the light of self-thinning and the competition-density effect. All of the values for log mean frond weight vs. log final density of *F. vesiculosus*, most of *F. serratus* and some of *F. spiralis* transgressed the line of boundary conditions of the '-3/2 power law' with log K = 4.3 as proposed by Cousens & Hutchings (1983) for seaweeds (Figure 17). However, when geometric instead of arithmetic means (Cousens & Hutchings 1983) and log K = 5 (proposed by Firbank & Watkinson 1990 as "overall boundary line" for terrestrial plants; see also Westoby & Howell 1986) were used, virtually all data points fell below the line. However, although convincingly criticized by Weller (1987), most authors have used regression analysis (e.g. Martínez & Santelices 1992) to obtain their boundary lines. Such lines are normally derived from data points that lie below and above the line.

Despite the existence of data beyond the self-thinning line, the validity of the '-3/2 power law', that often has been praised for its broad generality (e.g. White & Harper 1970; Norberg 1988), does not seem to be contradicted by the data of the present study. For a final acceptance or rejection of the often debated (e.g. Westoby 1984; Westoby & Howell 1986; Weller 1987, 1991;

Lonsdale 1990) general validity of the '-3/2 power law' (and well-defined deviations under special conditions) special, carefully controlled experimentation is needed as emphasized by Lonsdale (1990) and Weller (1991).

Westoby (1984) and others (Weller 1987; but see Petraitis 1995) proposed using log biomass - log density graphs rather than log mean weight - log density, because, along with other problems, higher mortality of small plants may strongly decrease density, and consequently mean plant mass, while total stand mass decreases only insignificantly in log mean weight plots. However, in the present examination, the pattern was conspicuously similar for both forms of expression (Figure 18).

With only two points in time (start and termination of experiment), trajectories tell little about the approach to and the falling in with the self-thinning line (Figure 17). Apparently, higher densities have less steep trajectories more parallel to the thinning line. Hence, they must have fallen in with the line earlier, as shown in the plots of Lonsdale & Watkinson (1982) and many others.

Compared to the vast number of publications from terrestrial plant stands undergoing self-thinning, there is only little contribution to the subject from marine scientists. For some macroalgae, a negative effect of density on survival (Black 1974; Chapman & Goudey 1983; Chapman 1984; Creed 1995) or on growth rate (Reed 1990) was recorded, for others a high density of conspecific neighbours had a positive effect (Schiel & Choat 1980; Hay 1981) or had a positive effect only for young life stages (for *Fucus* distichus: Ang & DeWreede 1992). In the present study, survival clearly was negatively correlated with density, but experiments were not designed to detect a possible shift from positive to negative correlation. From laboratory cultures of *Fucus* at different densities on ceramic tiles, there is only anecdotal evidence for an initial positive effect, since dense stands of small germlings (<5mm) seemed to be less susceptible to invasion of contaminants of green ephemeral algae or diatoms. Other positive effects of dense stands were reported by Schonbeck & Norton (1978: clumps of transplanted *Fucus* suffered less from desiccation), Hruby & Norton (1979: young intertidal macroalgae survived better in high density settlement) and Hay (1981: turf-forming algae suffered less from desiccation and herbivory). However, in contrast to competition, positive interactions (inter- and intraspecific) have rarely been looked for and, thus, found less frequently (Bertness & Callaway 1994).

Only few of the authors have explicitly tested the applicability of the '-3/2 power' law to marine benthic algae (Schiel & Choat 1980; Cousens &

Hutchings 1983; Martínez & Santelices 1992) or animals (Hughes & Griffiths 1988; Fréchette & Lefaivre 1990). As indicated above, data from Cousens & Hutchings (1983) fell below the line only, when geometric mean was used instead of arithmetic mean. Data for coalescent *Iridaea laminarioides* stands from Martínez & Santelices (1992) clearly transgressed the thinning line. Schiel & Choat (1980) found negative correlations between density and mortality for *Sargassum sinclairii* and *Ecklonia radiata* and concluded that the thinning law is unlikely to apply to these algae. Later, however, Cousens & Hutchings (1983) showed that these data fell well below their boundary line and do not violate the law.

Despite limited information on the general validity of the '-3/2 power law' for terrestrial plant stands after more than 30 years research since Yoda *et al.*'s (1963) paper, still less seems clear for marine macroalgae. Here, special designs are needed that take into account general deviations from terrestrial conditions (e.g. no roots in algae, light regime changes with submergence). In addition, certain conditions have to be considered that already proved to have an influence on the behaviour of the self-thinning line in terrestrial research (e.g. light saturation: Lonsdale & Watkinson 1982; clonal growth: Hutchings 1979; de Kroon & Kwant 1991).

Before and while mortality due to self-thinning starts reducing density of monospecific stands, there is a plastic response of crowded plants leading to reduced individual weights (competition-density effect). Normally it is assumed that small inequalities in environmental homogeneity, age distribution, seed dispersal mechanism (see citations in Creed *et al.* 1996b), spatial distribution (Bonan 1988) or growth rate (Hutchings & Budd 1981) lead to small initial size inequalities. Taller plants are believed to asymmetrically reduce light supply of smaller plants and gain more and more advantage over them (Weiner 1986). Small initial size inequalities lead to marked size hierarchies and consequently to mortality of the smaller plants (Creed 1995). Size distribution of monocultures may become first positively skewed (few large and more smaller plants; Creed *et al.* 1996a) and subsequent less skewed, due to mortality of smaller plants (Hutchings & Budd 1981; Dean *et al.* 1989). At this stage, Gini coefficients should decrease, indicating increased size equality. In the present study, although, except for *F. vesiculosus*, linear regression lines fitted the data poorly, there was a general trend for monocultures of all three *Fucus* species to show a decrease of Gini coefficients with decreasing density (Figure 19a). Such a trend is consistent with 'one-sided' competition of the 'asymmetric competition hypothesis', where large plants suppress small plants more than the converse, and more than would be expected by relative size alone (Weiner & Thomas 1986). Weiner & Thomas suggested that such asymmetries are primarily due to competition for light and contrasted the asymmetric view with a 'resource depletion' or 'two sided' model. The decreasing inequality with decreasing density also suggests that competition was a main source for mortality (see above) and that monocultures entered a stage where smaller plants died more than expected from proportion alone.

Very recently, Creed *et al.* (1996a,b) found that under adult stands of *Fucus vesiculosus* and *F. serratus* thousands of small but "old" germlings ('microrecruits' as found by Ang 1991, for *F. distichus*) survived and functioned as "seed" bank, growing to 'macrorecruits', when adults were thinned experimentally. These findings deviate from the normal pattern of self-thinning, but, since microrecruits are very small and hard to detect, they may occur rather frequently in macroalgal stands and should be sought for in future.

Plant traits for competitive dominance

Many plant ecologists believe that size is a trait positively correlated with competitive dominance (Grime 1974, 1977; Gaudet & Keddy 1988; Keddy 1989b; but see Olson & Lubchenco 1990, for other traits in macroalgae) due to a greater depletion zone for resources, especially light. For Helgoland *Fucus* species, such an assumption would be in concordance with the predictions from the competitive hierarchy hypothesis: *F. serratus* achieves the greatest biomass of the three *Fucus* species in the Helgoland intertidal as an often bushy thallus up to 1 m length, most *F. spiralis* remain only a few cm long. *F. spiralis* achieves lengths of 40-50 cm only at its lowermost limit of natural occurrence (Kornmann & Sahling 1977). *F. vesiculosus* grows to intermediate lengths and biomasses. Hence, the tallest species is the predicted competitive dominant, the smallest the subordinate species, partially in contrast to my findings.

Growth rates of *F. spiralis* were lower compared to *F. vesiculosus* in a study of Wright & Reed (1990). Hurd & Dring (1990) summarized mean weekly growth rates found by Knight & Parke (1950) and rates found by Schonbeck & Norton (1980) on a monthly scale: *F. serratus*: 1.9-3.7, *F. vesiculosus* 1.0-2.8 and *F. spiralis* 1.5-2.3 cm/mo. Schonbeck & Norton (1980) interpreted the same data in months needed to reach 1 cm: *F. spiralis* required about 6 months, while its congeners both reached 1 cm within 2 months. Hence, their growth rates are conspicuously lower but lead to the same ranks. Niemeck & Mathieson (1976) found rates comparable to Hurd & Dring's (1990) for *F. spiralis* of 1.9-2.8 (average 1.2) cm/mo for summer months.

For Helgoland *Fucus* species, maximum length and growth rate are concordant with Keddy's predictions, however, competitive relationship between *F. serratus* and *F. vesiculosus* is not.

A problem of published growth rates and maximum lengths in the context of the competitive hierarchy model is that they are normally measured inside the realized niche of the species or under laboratory conditions which are difficult to extrapolate to the field. Lubchenco (1980) reported higher growth rates of *F. distichus* (=*F. evanescens*) on the low shore. Schonbeck & Norton (1980) found *F. spiralis* growing "vigorously" when transplanted to midshore (1.5 cm/mo compared to 0.5 cm/mo in its own zone). In their laboratory cultures, the first 30 d of growth for embryos revealed growth rates ranked in concordance with competitve dominances from the competitive hierarchy model (*F. serratus* > *F. vesiculosus* > *F. spiralis*), but when the five biggest germlings of each species were cultured further to an age of 140 d, growth rates were in concordance with the findings of the field experiment of the present study: *F. vesiculosus* (1.48) > *F. serratus* (0.92) > *F. spiralis* (0.84 cm/mo).

Hence, under equal conditions for all species (in the laboratory or the same intertidal zone), growth rates and maximum height may differ from patterns observed in realized niches in the field.

Competitive ranks from laboratory experiments

In the replacement series set up as aerated laboratory cultures of floating thalli the competitive dominances were:

F. vesiculosus > *F. serratus* and *F. vesiculosus* ≤ *F. spiralis*

Again a rank may be inferred taking into account strengths of asymmetries:

F. spiralis ≥ *F. vesiculosus* > *F. serratus*.

In analyses of additive data (Figure 22), yield of *F. serratus* was reduced more by interspecific competition from *F. vesiculosus* than by intraspecific effects, whereas for *F. vesiculosus*, intraspecific effects were more severe. For mixtures of *F. vesiculosus* with *F. spiralis*, for both species intra- and interspecific effects led to similar yield suppression. Although competitive abilities were not tested experimentally, the dominance of *F. spiralis* in culture over *F. serratus* may cautiously be inferred from the greater suppression of yield of *F. vesiculosus* by *F. spiralis* compared to suppression by *F. serratus*.

This finding clearly does not support the competitive hierarchy hypothesis, since the ranks of competitive dominance are exactly inverse to its predictions. However, data should be evaluated very cautiously because experimental conditions were very different from nature. In laboratory cultures mortality due to self-thinning was suppressed in that small thalli had a greater chance of being whisked in air bubbles to the upper layers of the beaker and consequently to a better light supply. Hence, density (genets) did not decrease, shoot density (ramets) even increased in *F. vesiculosus* and *F. spiralis*. In the field, small plants eventually died and were washed away, leading to pronounced decreases in density. Laboratory plants were submerged permanently in contrast to field plants in the lower intertidal zone. Light and temperature regimes were different and nutrient supply pulses very different, as were concentrations of nutrients. Limitation of resources (space, light, nutrients?) seemed to be more severe in the laboratory culture. Cultures had reached the capacity of their artificial environment in some way, leading to similar final total biomasses for all treatments (Table 13).

However, all three *Fucus* species grew well under these laboratory conditions, hence, the conditions seem to have met their fundamental niches. But this may be true only for thalli with lengths of ca. 2-30 cm. In the present experiment, temporally limited to several months, no single plant became fertile. Preceding attempts to cultivate *Fucus* under these conditions from zygotes instead of germlings, totally failed. Hence, it must be doubted that *Fucus* would be able to persist over whole life cycles under these laboratory conditions.

The two different competition experimens led to two different competitive hierarchies. In the following paragraph, the predictions of Keddy's model regarding consistent hierarchies are examined more thoroughly.

Theoretical problems with Keddy's hypothesis

Keddy's hypothesis seems quite coherent as long as only one resource gradient is considered. In an extension in combination with Rosenzweig & Abramsky's (1986) model, Keddy (1989a, 1990) proposed a centrifugal model, where a central habitat is occupied by a top competitor (*Typha*) from where several axes of combinations of fertility and disturbance lead to periphere habitats occupied by subordinate species, specialized to tolerate certain levels of low fertility (= high stress) and high disturbance. While the unidimensional model implies a defined resource axis (an axis of nutrients or light or space, which can be limited; but see below), axes in the centrifugal model are poorly defined mixtures of resources (fertility may be derived by a mixture of several resources) and disturbance. While the original hypothesis modelled a static equilibrium situation, the centrifugal extension quite unconvincingly tries to incorporate disturbance as a non-equilibrium force. It seems rather difficult and confusing to add one or several additional axes to the centrifugal model shown by Keddy (1989a, p. 76; 1990, p. 284).

One of Keddy's assumptions for the competitive hierarchy model is that "competitive ability is an inherent characteristic of a species" and that "competitive ability is an inherent trait of a species rather than a trait which is strongly dependent upon the environment" (Keddy 1989a, p. 73). 'Environment' are all the factors and resources that build the axes of Hutchinson's (1957) n-dimensional niche hypervolume. Hence, it follows that a top competitor for one resource gradient must be the competitive dominant species in all combinations with levels of other resource gradients and environmental factors, as long as it does not leave its fundamental niche. This view is consistent with Grime's (1974, 1977) opinion. It is depicted in the centrifugal extension of the competitive hierarchy model (Keddy 1989a; and see Figure 2), where the central benign habitat is occupied by *Typha*, the competitive dominant species for all axes of the model.

A problem with the inclusion of disturbance as a parameter of axis quality is that it eliminates the need for competitive hierarchies and thus destroys the original model. In the peripheral habitats of the centrifugal model's axes, different levels of stress and disturbance prevail. If the peripheral ends of axes with low levels of stress but with high levels of disturbance are considered (axis "H" in Figure 2a,b), competitive ability is no longer a trait for dominance (in sense of abundance). Although a high growth rate is a trait for competitive dominance <u>and</u> for successful performance in disturbed habitats (Grime 1974, 1977), in the second case it is exclusively or mainly important for fast successful reproduction. Other traits may be equally important to withstand or tolerate disturbance or to complete reproduction in less disturbed intervals (e.g. Grime 1974, 1977; ruderal "strategy"). In accordance with Keddy's views, the importance and intensity of competition decreases towards the more disturbed periphery (Wilson & Keddy 1986a,b). Hence, the gradient is a transition from undisturbed more central habitats, where species are ranked according to their competitive ability, to more peripheral habitats, where species are ranked according to their ability of fast seed establishment and growth to maturity. Thus, the parameter of ranking changes along the gradient. The original assumption of competitive abilities ranked inversely to fundamental niche breadths is no longer valid. Thus, the centrifugal model is another model rather than an extension of the competitive hierarchy model.

Competitive abilities of *Fucus* spp. under different environmental condititions

Despite the poor performance of *F. spiralis* in competition experiments in the Helgoland lower intertidal zone, all three *Fucus* species should have been inside their fundamental niches under these (special due to possible special cage conditions) environmental conditions. At the termination of the experiment some of the bigger thalli of *F. vesiculosus* and *F. spiralis* had developed conceptacles, indicating that reproduction may be successful here. It is a prediction from the model, that all *Fucus* species are at or near the benign end of their fundamental niches in the lower intertidal zone. Time of submergence should give the gradient its quality as fertility gave quality to the spatial gradient of Keddy's (and co-workers) lake shores (Keddy 1984; Wilson & Keddy 1985, 1986a,b).

In the laboratory experiment, none of the species became fertile, but with a duration of only 4 months this is no surprise. All species survived without severe damage and should also have been within their fundamental niches in the laboratory. Hence, in both experiments, the *Fucus* spp. were somewhere inside the limits of their fundamental niches and ranks of competitive dominance should be the same. The differences of resulting ranks of competitive dominance from the experiments contradict the model's assumption of competitive ability being a characteristic independent of environmental conditions (rejection of H_{0-2}).

Niches and adaptation to the intertidal environment of *Fucus*

Transplants of adult *F. spiralis* survived significantly better when transplanted below their zone, those of *F. serratus* survived significantly worse when transplanted above their natural zone, whereas transplants of adult *F. vesiculosus* showed no significant differences between transplants to all zones, but survival rates were lower when transplanted to the upper eulitoral zone (Table 19). Mean individual dry weights were greatest in the lowermost zone and progressively decreased in upper zones for all three species (Figure 26). Patterns of transplants of laboratory germlings were similar in that *F. vesiculosus* clearly was able to survive in the uppermost zone and *F. serratus* performed poorly when transplanted above its natural zone. However, in this experiment, each *Fucus* species showed best performance in the zone of its natural occurrence and there was no general trend for better performance in lower zones. This pattern is in accordance with the model of niche differentiation, but not with the competitive hierarchy hypothesis. Even in the uppermost zone, a few thalli of *F. serratus* survived on some ceramic tiles, contradicting both models. However, the seawall, chosen for its nearness to the enclosure cages and good accessibility, had a location and orientation allowing direct sunlight to shine on the treatments only in early morning (Figure 3). Later they were shaded by the rocks of the island and finally by the wall itself. Effects of high temperature and desiccation should be ameliorated on this NE-facing side of the seawall and, probably, facilitated the survival of *F. serratus* and *F. vesiculosus* in higher zones. However, less stressful conditions do not explain the poor performance of *F. spiralis* and the inferior performance of *F. vesiculosus* in the lowermost zone (in comparison with performance in its natural zone). Both species grew well in permanent submergence in the laboratory experiment.

While the upper border of the distribution of *F. serratus* along the intertidal gradient can obviously be set by physical constraints, *F. vesiculosus* seems to be able to survive in the higher *F. spiralis* zone. The survival of *F. vesiculosus* above the zone of its natural occurrence has been observed repeatedly before (Schonbeck & Norton 1978; Hawkins & Hartnoll 1985; Chapman & Johnson 1990). This would be still consistent with Keddy's relaxation of the formerly strict assumptions of his model, where at a species' upper border the competitive dominance is successively weakened by environmental conditions and the (originally subordinate) species with the adjacent realized niche becomes more and more dominant until physical constraints finally prevent further occurrence of the lower, originally dominant species (Keddy 1989a, p. 75). This variant seems more realistic compared to the originally strict assumptions of sharp borders of occurrence inevitably linked with invariable competitive ability and permits dominant/subordinate pairs to change under different environmental conditions and, hence, weakens the assumption of competitive ablity as in inherent character independent of conditions. Examples for competitive reversals have been repeatedly reported for plants (Russell & Fielding 1974; Fowler 1982; Rice & Menke 1985). Arrontes (1993) suggested that competitive exclusion of *F. serratus* from some localities in northern Spain was due to certain environmental conditions.

With the relaxed model, the upward shift of occurrence of *F. serratus* into the *F. vesiculosus* zone in release experiments performed by Hawkins & Hartnoll (1985) might also be explained. Schonbeck & Norton (1978) also proposed, that upper limits of *F. serratus* and *F. vesiculosus* are not set by physical conditions alone.

The better performance of intertidal algae near the lower boundaries of natural occurrence has often been observed (Niemeck & Mathieson 1976; Kornmann & Sahling 1977; pers. observation with all Helgoland *Fucus* spp.). Physiological response in realized niches of intertidal macroalgae indeed seems to increase in direction of the benign end of gradients as drawn by Keddy (1989a, p. 71). If competitive ability is related to growth rate and length of plants in some way, it should be related to 'physiological response', too. Zero competition ability (Figure 37) should then coincide with the limit of fundamental niches (see Keddy 1989a, p. 71, and General Introduction), but curves of competitive ability should be staggered at the gradient's benign end. Borders between macroalgae belts in the intertidal zones would reflect neither a limit of competitive dominance *per se* nor real physiological limitations, but the point where competitive ability curves of neighbouring species intersect (Figure 37). However, Figure 37 depicts only what Keddy (1989a) described and 'competitive ability' must remain obscure as long the precise nature of competed-for resources and their gradients remains so.

Competition for nutrients and for space have been thought frequently as fundamentally different (Yodzis 1986; Begon *et al.* 1990). Except in dense packings of, e.g., mussels, and especially for plants, space often is "a 'portmanteau' term to describe the resources that may be captured within it rather than regarding space as a resource itself" (Begon *et al.* 1990, p. 117). A resource gradient is necessarily implemented spatially. However, Keddy's (1989a) original introduction of the competitive hierarchy hypothesis, although it is

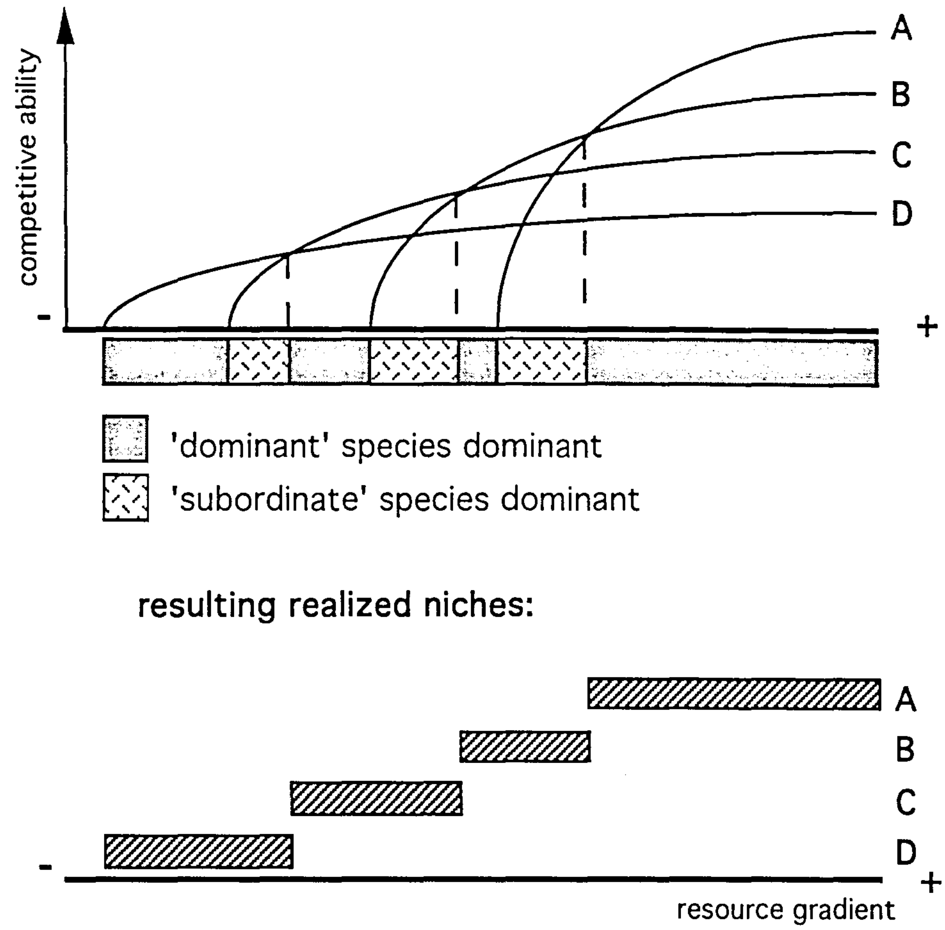


Figure 37: Curves of competitive ability along a resource gradient as predicted from the relaxed variant of the competitive hierarchy model (Keddy 1989a). At the bottom, realized niches are shown that result from the competitive pattern of the relaxed variant. Two kinds of competitive dominance are distinguished: dominance in the ranking of the narrow competitive hierarchy model ('CHM-dominance') and actual dominance ('ACT-dominance') under field conditions (in the sense of the more relaxed variant of the competitive hierarchy hypothesis). The border of each species' realized distribution derives from the intersection point of competitive ability curves of two neighbouring species. Thus, the border is set by neither the final exhaustion of tolerance of low resource levels (that would coincide with zero competitive ability) nor by competitive exclusion from a CHM-dominant species from its whole fundamental niche. Shaded areas indicate sections of the gradient where the species occupying that section is the CHM-dominant. Hatched areas indicate sections where the CHM-dominant species is ACT-subordinate and, therefore, its occurrence is prevented by the CHM-subordinate, being the ACT-dominant under the conditions prevailing at this section. For further explanations see text.

meant "to account for observed patterns of resource partitioning and the differential distribution of species along environmental gradients", suggests a resource gradient, defined as "a gradient of resource quantity", to be the spatial arrangement of one single resource. Keddy (1989a) was aware of the problem and distinguished gradients of resource quantity from gradients of resource quality ("kind of food and ratios of nutrients") and communities with strong gradients with such with more homogeneous conditions. However, he still owes the reader a precise definition of 'resource' in this context. The overall impression is that 'environmental gradient' would have been a term more appropriate, not suggesting a commonly used definition of 'resource' (emphasizing the possibility of consumption).

On the intertidal gradient tested in the present study, there are the same problems. Space, the resource that is apparently competed for, is such a portmanteau resource, being a combination of desiccation and temperature stress with light, nutrient and CO_2 availability. All these factors together define the quality of space on a certain sector of the gradient of emergence. The gradients which Keddy developed and introduced with his model, were the same space-combined-with-a-quality gradients. Hence, in the present study, his model has been checked on his own terms. As stated above, a more precise definition of the nature of gradients (what is a resource gradient in the model's sense, and what is not!) is urgently needed for the competitive hierarchy hypothesis. Unlike the approaches of Tilman (1981, 1987b) and Grime (1974, 1977), Keddy's proposal does not claim universal validity in all communities (Keddy 1989a). Therefore, empirical testing is necessary to unravel in which communities the competitive hierarchy model can explain species distribution and in which it can not. However, proper testing would need properly defined resource axes.

For the intertidal zone of rocky shores, there are several experimental results suggesting an adaption of fucoid (and others, e.g. Thomas *et al.* 1987) species to their zone of occurrence on the intertidal gradient of emergence:

Schonbeck & Norton (1979a) found drought avoidance to be of minor importance in fucoids and assumed that desiccation tolerance should allow survival of these intertidal macroalgae along the desiccation gradient. Dring & Brown (1982; and see Beer & Kautsky 1992) confirmed their supposition experimentally: *F. spiralis* was able to recover fully from more severe drought (80-90% water loss) than *F. vesiculosus* (70%); *F. serratus* only recovered fully after up to 60% water loss. Schonbeck & Norton (1978) also demonstrated that the ability to tolerate desiccation and then, when re-submerged, to resume growth and photosynthesis was highest in fucoids from the upper shore and progressively less in species inhabiting lower levels. Summer plants of *F. spiralis* grew equally well when submerged only for one out of every twelve hours as they did when submerged for 11 hours, while *F. serratus* performed best when submerged 11 hours (Schonbeck & Norton 1979b). Initial phosphate uptake rate is greatest in *F. spiralis*, the species with least time for nutrient uptake per tidal cycle (Hurd & Dring 1990), rate and extent of recovery of phosphate uptake after re-submersion following desiccation increased with the height on the shore fucoid species are typically found (Hurd & Dring 1991).

However, these obviously increasing adaptations with increasing time of emergence cannot help to distinguish between a model of niche differentiation (competition acting in the past) and the model of competitive hierarchies with a contemporary trade-off between competitive ability and adaptation to low resource levels. Only controlled experiments as performed it this study can tell us about the validity of Keddy's model.

For the intertidal macroalgal community on Helgoland it does not seem to be valid. The original, strict variant is contradicted by all experiments performed: Competitive abilities were not as predicted by the model (rejection of H_{0-1}), they differed under different conditions (rejection of H_{0-2}), transplants of adults behaved mostly according to the predictions, but *F. vesiculosus* survived above its zone and transplants of germlings showed patterns of survival more in accordance with a model of niche differentiation (rejection of H_{0-3} and H_{0-4}).

With the extension and relaxation of the competitive hierarchy, the difference of competitive ranks found in laboratory and field experiments may be explained as transition condition where a dominant species approaches the limit of its fundamental niche (see above) in one or the other experiment, but this must remain speculative.

With the relaxed competitive hierarchy model, the deviations are less, but still the clear competitive dominance of *F. vesiculosus* over *F. serratus* is in striking constrast to model predictions.

The present study would be a genuine test of the competitive hierarchy model only if the underlying assumption is correct, i.e. that the tidal gradient forms an environmental gradient in the sense of the model. It can be argued that the mid intertidal zone occupied by *F. vesiculosus* is the central benign habitat, where desiccation is still not severe and light extinction by the water column during high tide is insufficient to limit growth rates. The former or the latter factor may make conditions less favourable in the upper and lower intertidal zones, respectively. Due to the turbid nature of the water around Helgoland, with a Jerlov water type rated as Coastal 7 (Lüning & Dring 1979; Lüning 1985), light limitation of photosynthesis may occur in the lower intertidal zone. However, this assumption is contradicted by two facts: firstly, the same three *Fucus* species occur in the same order on the shore on other European coasts (e.g. west coast of Scotland, Lewis 1964), where more transparent water types prevail (Jerlov type 1-3 for coastal waters, according to Lüning 1985) and the gradient of light is much less steep. Secondly, the survival and individual growth rates of all three Helgoland *Fucus* species were highest in the lowermost intertidal zone, and were successively reduced in the upper zones (Table 19 and Figure 26). Therefore, I believe that the tidal gradient of Helgoland did represent a true gradient in the sense of the competitive hierarchy model, with the lowermost zone of *F. serratus* as the benign end of the gradient.

Grazing by *Littorina* spp.

Besides physical constraints and biotic competition, grazing is often a structuring force in intertidal macroalgae communities (e.g. Lubchenco 1978, 1980, 1982; Underwood & Jernakoff 1981; Hawkins & Hartnoll 1983; Petraitis 1987). Limpets, important in these respects on many coasts (e.g. Black 1976; Southward & Southward 1978; Jernakoff 1985; Beovich & Quinn 1992), are absent from the Helgoland intertidal. Here, the most conspicuous grazers are periwinkles, especially *Littorina littorea* and *L. mariae*. Studies by many workers have shown that feeding preferences, behaviour and impact on the community are by no means uniform among the species of the genus *Littorina* (reviewed e.g. by Norton *et al.* 1990; Chapman 1995).

Feeding preferences among *Fucus* germling size classes

In the present study, laboratory feeding experiments revealed dissimilar preferences between *Littorina littorea* and *L. mariae* for germling size classes of *Fucus serratus* or *F. vesiculosus*. *L. littorea* significantly preferred 3 mm over bigger germlings of both *Fucus* species, whereas *L. mariae* preferred the biggest size class (30mm) of *F. serratus* and showed no clear preferences for *F. vesiculosus* germling size classes.

Littorina littorea is known to graze epilithically (Hawkins & Hartnoll 1983; Watson & Norton 1985) but it can be found crawling on *Fucus serratus* quite regularly (pers. observations). It is therefore not surprising that *L. littorea* preferred to graze upon small algae by crawling directly upon the experimental ceramic tiles. However, 30 mm fucoid germlings were also harmed (ca. 60% or 50% of fresh weight change of smallest germling size class for *F. serratus* and *F. vesiculosus*, respectively). With the experimental design used it is not possible to discriminate between true consumption and a pure damaging effect due to 'bulldozing'. The latter was observed to occur in all experimental containers but the amount was not measured. Watson & Norton (1985) observed dislodgement of *Ascophyllum* germlings by bulldozing only and without any active feeding. Obviously, in the present study, masses of bulldozed uneaten germlings were greater for the bigger size classes than for 3 mm germlings, but numbers might not have been. Norton *et al.* (1990) recorded bulldozing by *L. littorea* and subsequent consumption of *Fucus* germlings. Unfortunately the algal lengths were not given. However, the present study was directed at assessing the impact on *Fucus* by periwinkles and not the nutrition of the latter.

In my experiments, equal areas bearing fucoids were offered to periwinkles rather than equal initial algal masses (see 4.2). The same mass consumed may represent totally cleared areas on tiles with 3 mm germlings, or a few consumed (bulldozed) 30 mm germlings, respectively. Five *L. littorea* would have been capable of completely clearing 3 mm germlings from the 3.7x3.7 cm^2 area of a tile fragment in a few days (compare Barker & Chapman 1990, for same devastating effect on a few days old germlings of *F. spiralis* and *F. vesiculosus*), but not from the bigger size classes. Hence, locally, *L. littorea* should be able to prevent the establishment of recently settled *Fucus* germlings. Such prevention by *L. littorea* has been reported by other workers (Lubchenco 1983; Petraitis 1987; Janke 1990), but depends on grazer densities (Lubchenco 1978). If a choice among several germling sizes is given to the periwinkles in the field as in my multiple choice experiment, bigger germlings should be able to survive and finally 'escape in size' from lethal *L. littorea* grazing (Hawkins 1981; Lubchenco & Gaines 1981; Lubchenco 1983). This should again depend on the grazer density, since bigger germlings are harmed to some extent and even a one year old canopy of *F. vesiculosus* was demolished in Petraitis' (1987) study. The experimental density of 325/m^2 may be achieved locally in the Helgoland intertidal zone. *L. littorea* enclosures of Janke (1990) indicated that establishment of *Fucus* is not prevented at mean natural grazer densities in the mid and lower zone (100-120/m^2), however, double density did prevent establishment of *Fucus* on experimentally cleared areas. It is approximately the same density (ca. 200/m^2) that Lubchenco (1983) had in her low density enclosure treatments. On smooth surfaces, without barnacles or crevices, this density was sufficient to prevent establishment of New England *F. vesiculosus* totally. Lubchenco's experiments suggested that even the survival of germlings between barnacles depends on grazer densities. At another, 3-4 fold higher, experimental density, establishment of *Fucus* was prevented even with crevices. However, in the Helgoland intertidal zone mean densities are visibly lower than her low density. Barnacles are conspicuously absent, probably because of the brittle substratum (they readily settled on PVC frames of exclosure cages). Personal observations did not indicate that all *Fucus* germlings in the Helgoland intertidal were limited to microhabitats in crevices. I believe that, at the prevailing comparable low densities of *L. littorea*, spatial escapes of *Fucus* germlings should be quite frequently possible. However, dense stands (up to 70,000/m^2) of 1-2 cm germlings may be found frequently, but only in the upper intertidal zone where littorinid density is low. In the lower zones, densities of germlings of that size are clearly lower; in the mid eulittoral zone, extended patches without any visible fucoid cover occur.

The experiments of the present study extend the hypothesis of (grazer density dependent) escapes in size from *F. vesiculosus* (Lubchenco 1983) to *F. serratus*. Patterns of preference were similar for germling size classes of both *Fucus* species.

In another set of enclosure experiments, Lubchenco (1983) found that *L. littorea* (or *L. obtusata*) at a density of 400/m^2 (1600/m^2) grazed *Fucus vesiculosus* cover of, on average, 8 mm germlings to zero in 6 months, while germlings of 39 mm initial length achieved 100% cover in the otherwise identical treatment. The experimental design was a no choice offer of germlings. In my study, the medium size class of 10 mm, most similar to Lubchenco's 8 mm plants, was grazed only to a minor extent, whereas 3 mm germlings were severely consumed. It does not seem possible to estimate an overall threshold for a safe escape in size of *Fucus* germlings from *L. littorea* grazing. This limit is a function of circumstances (no choice vs. other *Fucus* size classes or more preferred green ephemerals available) and littorinid density. Petraitis (1987) challenged the findings of Lubchenco (1983) with those of his enclosure experiments. *L. littorea* were enclosed at a density of ca. 220/m^2 (when enclosed surface is used as base for calculation). This is a slightly higher density than Lubchenco's (1983) "natural" density used in experiments. At this density, *L. littorea* was not only capable of preventing any *Fucus* establishment in Petraitis' experiments, but totally removed 1-year-old *F. vesiculosus* cover.

Littorina mariae, like its visually similar and more thoroughly examined congener *L. obtusata*, feeds predominantly epiphytically but is additionally known to graze epilithically (Watson & Norton 1987; Norton *et al.* 1990). In the Helgoland intertidal, most specimens found are associated with *Fucus* (see Watson & Norton 1987; Janke 1990 for the same observation), but *L. mariae* quite frequently may also be found crawling on the red sandstone. Unlike *L. obtusata*, it mainly feeds on epiphytic microalgae growing on *Fucus* thalli rather than on the fucoid itself (Norton *et al.* 1990). Hence, it is possible that *L. mariae*, by removing epiphytic microalgae, benefits growth of adult *Fucus* rather than curtailing it (Norton *et al.* 1990; Williams 1990; see Brawley & Adey 1981 for similar suggestion with amphipods grazing on *Hypnea*; Brönmark 1985 for freshwater case).

In the present study, *L. mariae* revealed an increasing preference for the bigger size classes of *Fucus serratus* germlings. For *F. vesiculosus* there was no clearcut preference. I hypothesize that the somewhat broader thalli of *F. serratus* are better suited as a crawling substratum and only in this case (biggest size class = 30 mm of *F. serratus*) germlings started to become a suitable substratum. Hence, food preference may be confounded with habitat preference in this case.

The experimental density of 3250/m^2 was used for a better comparison with *L. littorea* on a 'per organic dw of snail' base. It exceeded natural maximum densities for the Helgoland NE-Intertidal by more than the 20-fold. Despite this fact, the total mass consumed per experimental container was lower than that of *L. littorea* in all experiments performed. In no case there was an indication that a prolongation of the experimental time would have led to complete extinctions of 3 mm *Fucus* germlings, as with *L. littorea*. As mentioned above, *L. mariae* is also known to graze epilithically on microalgae. The smallest *Fucus* size class used in the experiment may already have been too big for this grazing mode of *L. mariae*. I attempted to keep *Fucus* cultures as unialgal as possible. Diatom growth was suppressed by means of germanium dioxide. Hence, the original food sources of *L. mariae*, microalgae, may have been scarce in the experiment and consumption of *Fucus* tissue only an unwelcome compromise. Williams (1990) speculated that *L. mariae* could play an important role in structuring intertidal algal communities, mainly by removing epiphytes from *F. serratus* fronds. In my experiments, *L. mariae* at an unnaturally high density consumed *Fucus* tissue, but only to a minimal extent. Despite the absence of littorinids, *Fucus* plants in the competition experiment had no increased load of epiphytes. I therefore doubt the importance of *L. mariae* as a structuring factor in the Helgoland intertidal zone, either by diminishing ephipytes (positive effect on *Fucus*) or by feeding on *Fucus* itself. However, *Fucus vesiculosus* and *F. spiralis*, from higher tidal levels with lower densities of *L. mariae*, had a conspicuously higher load of epiphytic algae than *F. serratus*, when sampled and prepared for gamete release (2.2, pers. observation)

There are two different phenomena described by the term 'size escape' (Lubchenco & Gaines 1981). Algae can grow to a size where they are no longer a feasible prey (e.g. Underwood & Jernakoff 1981) or where they are still consumed, but consumption no longer has a lethal effect. My experiment suggests that very small *Fucus serratus* germlings would escape from *L. mariae* with epilithic grazing mode at a size of 3 mm. Later, at a germling size of ca. 3 cm or more, *F. serratus* should again become a prey of *L. mariae*, now feeding epiphytically. But this may be true only without the availability of epiphytic microalgae. In their review, grouping herbivorous molluscs and their prey into functional groups, Steneck & Watling (1982) suggested that erect algae of intermediate size (1-10 cm) are eaten to a lesser extent, because they are too large to be rasped from the substratum and too small for herbivores to climb upon.

Fucus germlings of >10 mm should have escaped epilithic direct grazing by *L. littorea*, but may still be killed by bulldozing. Adult *Fucus* seems to escape in size in both senses at the prevailing grazer densities.

Feeding preference among *Fucus* species

As shown in several studies, *L. littorea* prefers green ephemeral algae to fucoids, although small germlings of the latter will be readily consumed (Lubchenco 1978; Watson & Norton 1985). The data on preferences among different *Fucus* species are not unequivocal and several aspects have to be considered when data of different workers are compared:

- Test of attractiveness vs. test of edibility (Nicotri 1980; Imrie *et al.* 1989)
- Preferences among germlings may be different from those among adult fucoids (Watson & Norton 1985, 1987; Chapman 1989: grazers had significant effect on adult *F. spiralis*, but not on juveniles).
- Contents of anti-herbivore repellants differ between different *Fucus* species (Denton *et al.* 1990; Denton & Chapman 1991).
- Per species contents may vary seasonally (Ragan & Jensen 1977; Steinberg 1995 for laminarian *Ecklonia radiata*).
- Amounts of repellants may be increased by preceding grazing (Van Alstyne 1988).
- Amounts of repellants may be different in thalli of different sizes (Denton *et al.* 1990).
- Amounts may be different in different parts of thalli.
- Grazer densities may vary seasonally.
- Grazer sizes (and thus effects) may vary seasonally.
- Grazing rate varies seasonally (less activity in winter) and affects algae differentially among seasons (Watson & Norton 1987).
- Effects on fucoids may be more severe when reproductive tissue is preferentially consumed (Watson & Norton 1985, 1987).
- Habitat preferences may be confounded with food preferences for epiphytically grazing species (*L. mariae* on *Fucus serratus*: Watson & Norton 1987).
- Designs of experiments of various workers are different in many respects:
  - laboratory trials vs. field enclosures
  - preceding starvation vs. feeding [habituation] (e.g. Watson & Norton 1985; Imrie *et al.* 1989)
  - usage of a fixed algal species as a probe (Watson & Norton 1985) vs. multiple choice vs. no choice (e.g. Barker & Chapman 1990; Schaffelke *et al.* 1995)
  - recording of grazers' preferential crawling to certain foods offered vs. feeding rates (Watson & Norton 1985)
  - offer of punched out tissue vs. attached erect thalli vs. offer of homogenized algae in agar (Hunter 1981; Imrie *et al.* 1989)
  - "natural densities of grazers" (as used in some experiments) may be very different (Norton *et al.* 1990); additionally the density calculation may be

  very different and lead to differing apparent experimental densities. For example, Petraitis (1987) gave a range of two densities, one based on the surface of offered algae bearing granite blocks (→ high experimental density), the other based on the total inner surface of his enclosure baskets where *L. littorea* could crawl and graze on (→ low density). Normally, as in the present study, density is based on the surface area of cage or container bottom, leading to an intermediate experimental density.
  - cage size may influence grazers (Quinn & Keough 1993).
- Statistical analyses may differ considerably between workers as discussed in the appendix.

In the present study, only preferences among the three Helgoland *Fucus* species were tested in no choice and multiple choice experiments. Patterns of edibility (no choice) and attractiveness (choice) *sensu* Nicotri (1980) were conspicuously similar. *F. serratus* was clearly rejected by both littorinid species. *F. spiralis* was the most consumed fucoid by *L. mariae* and also by *L. littorea* when algal fresh weight is considered. Consumption of *F. vesiculosus* was at an intermediate low level for *L. mariae* and intermediate but comparable (difference insignificant) to that of *F. spiralis* for *L. littorea*. Consumption (bulldozing?) rates were lower with *L. mariae* foraging.

On a dw/organic snail dw basis, Barker & Chapman (1990) found consumption rates in no choice experiments with ***L. littorea*** grazing on tissue of adult *F. vesiculosus* and *F. spiralis* to be not significantly different and of similar magnitude (per day) as those of the present study: ca. 15 mg/g at 5° C and ca. 40 mg/g at 15° C. In my no choice experiment the mean rate was 34 and 40 mg/g at 13° C for *F. vesiculosus* and *F. spiralis*, respectively. In most of their experiments (multiple and no choice), there was no significant difference in the consumption of *F. spiralis* and *F. vesiculosus*. Only in a multiple choice experiment with adult *Fucus* tissue was *F. vesiculosus* consumed to a greater extent than *F. spiralis*. Watson & Norton (1985) and Norton *et al.* (1990) compared only *Fucus serratus* with species of other seaweed genera. The ranking of attractiveness, included in findings from tests with seaweed extracts done by Imrie *et al.* (1989) was the same as the grazing ranks published by Norton *et al.* (1990): *F. serratus* > *F. spiralis* ≥ *F. vesiculosus*. It is contradicted by my findings for the rank of *F. serratus*. However, this must be considered cautiously because, on average, germlings of *F. serratus* were bigger than those of *F. vesiculosus* and *F. spiralis*. Since smaller germlings were preferred over bigger by *L. littorea* in the other grazing experiment (see above), this may have been a confounding factor.

When Norton *et al.* (1990) surveyed the feeding preferences of ***L. mariae*** in laboratory experiments including several macroalgae, they found highest ranks of attractiveness for all three *Fucus* species (occurring on Helgoland). Palatability indices (amount consumed in relation to *Ulva* consumed in pairwise offer) were ranked as in the present study (*F. spiralis* > *F. vesiculosus* > *F. serratus*).

In studies of Williams (1990) and Watson & Norton (1987), *L. mariae* was associated more or less exclusively with *F. serratus*. The feeding rejection of *F. serratus* in the present study suggests that this bond could be exclusively a result of habitat selection or possible availabilty of preferred microalgae growing on *Fucus* fronds.

Although, as discussed above and in 4.4, average experimental lengths of germlings varied with *Fucus* species and both littorinid species responded very differently to germling size classes in the other grazing experiment, the two *Littorina* species revealed similar patterns of preference for *Fucus* species. This may be indicative of some strong alga inherent factors (nutrition value, repellants) that influenced choice in a similar way in both *Littorina* species. Brown algae produce 'phlorotannins' (Hay & Fenical 1988), which seem to deter herbivores generally (Steinberg 1988), while other secondary metabolites vary in their negative effect on different grazers (Hay *et al.* 1988). Data on polyphenolic contents in *Fucus* spp. differ and lead to different ranks among the three *Fucus* species (Ragan & Jensen 1977; Ragan & Glombitza 1986; Watson & Norton 1987; Ilvessalo & Tuomi 1989; Denton *et al.* 1990; Norton *et al.* 1990; Denton & Chapman 1991). However, in my experiments phenolic contents were not measured. Van Alstyne (1988) found that higher phenol levels were induced by natural and artificial grazing. This should not have been a confounding factor in the present study, since *Fucus* species were treated in the same way during cultivation and preparation for the experiments.

Can *Littorina* affect *Fucus* establishment and zonation?

The distribution of periwinkles along the shore gradient determines the probability of encountering the different *Fucus* species and, in combination with preferences, the impact on fucoid vegetation (Lubchenco & Gaines 1981). My experiments suggest that *F. spiralis* has the lowest resistance to grazing among the *Fucus* species examined. In the zone of its natural occurrence, it encounters only very low grazer densities in the Helgoland NE-intertidal zone. In addition, the time per tidal cycle where grazing is physiologically possible for littorinids may be restricted and may further reduce grazing pressure, although higher grazing rates of upper intertidal specimens may compensate for this reduction (Newell *et al.* 1971; but see discussion of the subject in Underwood 1979). A density of 40/m^2 *L. littorea* (+ 60/m^2 *L. saxatilis*) in the upper intertidal zone was sufficient to prevent establishment of *Fucus* in Janke's (1990) enclosures. Grazing pressure from littorinids should be highest at mid tidal levels and may, therefore, explain the restriction of *F. spiralis* to the upper eulittoral despite a broader fundamental niche. However, the similarly preferred congener, *F. vesiculosus*, populates the zone of highest mean densities of *L. littorea*. Higher growth rates should enable *F. vesiculosus* to a faster escape in size compared to *F. spiralis*. However, in the mid littoral zone (NE of Helgoland) *F. vesiculosus* does not form a dense canopy as *F. serratus* does in the lower zone but is distributed rather patchily. Great parts of the rock surface are bare, covered by neither *Fucus* nor *Mytilus* or green ephemeral algae. *L. littorea* densities of 100/m^2 could not totally prevent establishment of *Fucus* or destroy established *Fucus* canopy in Janke's (1990) herbivore enclosures, but totally prevented otherwise dominant *Ulva*. Without further field experimentation it must therefore remain uncertain whether patchy distribution of grazers or other factors prevent a total coverage of the mid shore zone with *Fucus vesiculosus*.

In my experiments, *F. serratus* germlings were significantly avoided when offered alone or together with *F. vesiculosus* and *F. spiralis* germlings. With a lower density of *L. littorea*, compared to the mid intertidal zone, establishment and renewal of the *F. serratus* canopy should therefore easily be possible. Only unnaturally high densities (200/m^2) of *L. littorea* prevented establishment of *F. serratus* in Janke's (1990) experiments. However, there is no explanation as to why competitively superior *F. vesiculosus* does not invade into this zone, and thus escapes the higher *L. littorea* grazing pressure in the zone of its natural occurrence.

In summary, at NE Helgoland mid intertidal levels only *L. littorea* (but not *L. mariae*) is assumed to occur at sufficient densities to significantly influence the community structure through grazing germlings of *F. vesiculosus*.

Other factors potentially influencing *Fucus* zonation

Recently, smaller grazer guilds have achieved increasing attention (Denton & Chapman 1991; Viejo & Arrontes 1992; Parker & Chapman 1994). These may, sometimes interactively (Viejo & Arrontes 1992: isopod+amphipod; Parker & Chapman 1994: periwinkles+amphipods), significantly reduce algal cover. In the Helgoland intertidal, grazers other than the two *Littorina* species examined may be quite abundant. There is some information on their effect on macroalgae from other sites (*Hyale nilssoni*: Viejo & Arrontes 1992; *Lacuna divaricata* [= *L. vincta*]: Fralick *et al.* 1974, Thomas & Page 1983). Other prosobranch gastropods (*Littorina obtusata*, *L. saxatilis*, *Gibbula cineraria*) may be found regularly but seem unimportant as structuring forces in the NE intertidal zone of Helgoland. However, since preferences and feeding rates of the above (and others) grazers were not examined in this study, the importance of their effects remains speculative.

Interactions among green ephemeral algae (*Ulva*, *Enteromorpha*) and *Fucus*, and the potential important role of herbivory by *L. littorea* feeding preferentially on ephemeral green algae (Lubchenco 1978; Lein 1980; Watson & Norton 1985; Janke 1990) were not examined in the present study. However, *Enteromorpha* sp. plays an important role in the Helgoland NE-Intertidal, forming seasonally vast zones in the upper intertidal (see Janke 1986, 1990 for a comprehensive description). In exclosure cages of the competition experiments, without littorinid grazers, *Ulva* sp. settled heavily in spring and summer on the ceramic tiles, easily overgrowing young *Fucus* plants, and had to be removed regularly.

It would have been desirable to include *Enteromorpha* into the competition experiments as another zone-forming species in the Helgoland intertidal, but it would have been impossible to control experimental densities of this green algae in replacement series or additive experimental designs.

Final conclusions

From the findings of the present study it seems clear that the competitive hierarchy hypothesis cannot explain the distribution of *Fucus* species along the tidal gradient of Helgoland. More specifically, the existence of *F. serratus* in the lower intertidal zone must remain unclear, with *F. vesiculosus* as a competitive dominant species that seems physiological capable of persisting and reproducing in this zone, where it, additionally, may escape higher grazer densities of its own zone. Further experimentation should examine whether *F. vesiculosus* really is able to persist over more than one generation in the lowermost intertidal zone. For this, transplanted or experimentally sown stands of *F. vesiculosus* in the *F. serratus* zone should be monitored. Additionally, the densities of littorinids and/or smaller grazers and of new *F. serratus* recruits may be manipulated in a factorial design.

The second open question is: why does *F. vesiculosus* not extend its distribution to higher shore levels? Denton & Chapman (1991) tested the prediction that *F. spiralis* should be better defended against grazing as trade-off with competitive ability. On their Nova Scotian coast periwinkle density may be higher in the zone occupied by *F. spiralis* compared to the zone of *F. vesiculosus* (Chapman & Johnson 1990). However, their prediction was only partly confirmed by feeding experiments and not by measurements of phlorotannin contents. My feeding experiments indicate that *F. spiralis* is not better defended. Grazing pressure by Helgoland periwinkles is highest in the zone of *F. vesiculosus*. My laboratory competition experiment showed a situation where the competitive dominance of *F. vesiculosus* over *F. spiralis* was leveled out or slightly inversed. I therefore suggest that, in the sense of the relaxed variant of the competitive hierarchy hypothesis, the competitive dominance of *F. vesiculosus* is weakened in the upper intertidal and it may persist there only without competiton from *F. spiralis*. Future competition experiments set up in the upper and in the mid intertidal zone may shed light on this question.

Trade-offs between the resource demands of different vital functions of seaweeds have frequently been discussed, but, in most single studies, only 2 vital functions have been taken into consideration (competitive ability vs. physiological tolerance of low resource levels in Lubchenco 1980 and Keddy's 1989a 'competitive hierarchy hypothesis'; grazer resistance vs. competitive ability: Denton & Chapman 1991; but see Grime 1974 for three vital functions).

From my studies, I am able to show how 3 *Fucus* species on Helgoland differ in their abilities to tolerate: a) competitive stress, b) physiological stress and c) grazing stress. Presumably these differences reflect underlying patterns of resource allocation, though this was not measured:

	competitor	stress tolerator	grazing resistance
F. spiralis	-	++	-
F. vesiculosus	++	+	-
F. serratus	+	-	++

ACKNOWLEDGEMENTS

I would like to thank Prof. Dr. U. Sommer who kindly supervised and supported me when he inherited me with his Chair. I am extremely grateful for the excellent, committed and patient supervision of Prof. Dr. A.R.O. ("Tony") Chapman who taught me the basics of modern experimental design and never refused to answer even the simplest of questions.

I am deeply grateful for the hospitality and support of the Biologische Anstalt Helgoland (BAH) and the whole staff on Helgoland, especially Ute Alexander, Olaf Goemann, Franz & Traudel Hennemann, Werner Lorenzen, Brigitte Rauch, Walter Reck, Hans Reichenberger, Martin Schelp (†), Günter Tadday (†), Andreas Wagner and Anne Wüpping. Without the technical support, high skills and hours of overtime of Rolf Haack none of the experiments could have been implemented. Not only for this help, I owe him the greatest thanks.

Several colleagues helped me with practical work, above all Volker Jacobs to whom I owe special thanks. Experiments and writing of this thesis were only possible with the kind help of Gesche Bock, Hilke Döpke, Karin Finsterle, Gunnar Gerdts, Andrea Häberlein, Christian Kabatnik, Hinnerk Karez, Maike Lorenz, Andreas Rings, Annette Tempelmann, Andreas Wagner, Catharina Wagner, Astrid Werner, Antje Wichels and others. I am very grateful for their help and I thank Thomas Wiedemann for teaching me so impressively that even my patience has its limits.

Many thanks for scientific help with my experiments to Dr. P. Kornmann (†), H. Reichenberger, P.-H. Sahling and Dr. B. Schaffelke.

For help with statistics, for reviewing parts of this dissertation and/or for fruitful scientific dispute, I thank Dr. R.M. Forster, Dr. G. Gerdts, Dr. J. Harms, M. Hoffman-Wecker, Dr. T. Reusch, Dr. B. Schaffelke, A. Tempelmann and U. Wilhelmsen.

For help and advice during the years on Helgoland I would like to thank my "ground control" in Kiel, especially Heike Lotze, Thomas Meyer, Akira Peters, Thorsten Reusch, Britta Schaffelke, Cordula Stielau and Mary Strasdas.

I would like to thank my parents for additional help and support from the mainland.

Very special thanks to Annette for her kind support and patience during the months in which I wrote this thesis.

This study was funded by a grant of the Deutsche Forschungsgemeinschaft (DFG).

REFERENCES

Aarssen, L. W., 1983. Ecological combining ability and competitive combining ability in plants: toward a general evolutionary theory of coexistence in systems of competition. Am. Nat. 122, 707-731.

Aarssen, L. W., 1985. Interpretation of the evolutionary consequences of competition in plants: an experimental approach. Oikos 45, 99-109.

Abramsky, Z., Bowers, M. A. & Rosenzweig, M. L., 1986. Detecting interspecific competition in the field: testing the regression method. Oikos 47, 199-204.

Ang, P. O., 1991. Natural dynamics of a *Fucus distichus* (Phaeophyceae, Fucales) population: reproduction and recruitment. Mar. Ecol. Prog. Ser. 78, 71-85.

Ang, P. O. & De Wreede, R. E., 1992. Density-dependence in a population of *Fucus distichus*. Mar. Ecol. Prog. Ser. 90, 169-181.

Arrontes, J., 1993. Nature of the distributional boundary of *Fucus serratus* on the north shore of Spain. Mar. Ecol. Prog. Ser. 93, 183-193.

Austin, M. P., 1990. Community theory and competition in vegetation. In "Perspectives on Plant Competition". J. B. Grace & D. Tilman (eds.). Academic Press, San Diego, pp. 215-238.

Austin, M. P. & Austin, B. O., 1980. Behaviour of experimental plant communities along a nutrient gradient. J. Ecol. 68, 891-918.

Barker, K. M. & Chapman, A. R. O., 1990. Feeding preferences of periwinkles among four species of *Fucus*. Mar. Biol. 106, 113-118.

Beer, S. & Kautsky, L., 1992. The recovery of net photosynthesis during rehydration of three *Fucus* species from the Swedish west coast following exposure to air. Bot. Mar. 35, 487-491.

Begon, M., Harper, J. L. & Townsend, C. R., 1990. "Ecology. Individuals, Populations and Communities". 2nd ed. Blackwell Scientific Publications, Boston, USA.

Bendel, R. B., Higgins, S. S., Teberg, J. E. & Pyke, D. A., 1989. Comparison of skewness coefficient, coefficient of variation, and Gini coefficient as inequality measures within populations. Oecologia 78, 394-400.

Benedetti-Cecchi, L. & Cinelli, F., 1996. Patterns of disturbance and recovery in littoral rock pools: nonhierarchical competition and spatial variability in secondary succession. Mar. Ecol. Prog. Ser. 135, 145-161.

Beovich, E. K. & Quinn, G. P., 1992. The grazing effect of limpets on the macroalgal community of a rocky intertidal shore. Austr. J. Ecol. 17, 75-82.

Bertness, M. D., 1991a. Interspecific interactions among high marsh perennials in a New England salt marsh. Ecology 72(1), 125-137.

Bertness, M. D., 1991b. Zonation of *Spartina patens* and *Spartina alterniflora* in a New England salt marsh. Ecology 72(1), 138-148.

Bertness, M. D. & Callaway, R., 1994. Positive interactions in communities. Trends Ecol. Evol. 9, 191-193.

Bertness, M. D. & Hacker, S. D., 1994. Physical stress and positive associations among marsh plants. Am. Nat. 144, 363-372.

Black, R., 1974. Some biological interactions affecting intertidal populations of the kelp *Egregia laevigata*. Mar. Biol. 28, 189-198.

Black, R., 1976. The effects of grazing by the limpet, *Acmaea insessa*, on the kelp, *Egregia laevigata*, in the intertidal zone. Ecology 57, 265-277.

Bock, G. M., 1992. Die Besiedlung der Uferschutz- und Hafenmolen in der Gezeitenzone von Helgoland. Diploma thesis, University of Marburg, Marburg, Germany.

Bonan, G. B., 1988. The size structure of theoretical plant populations: spatial patterns and neighborhood effects. Ecology 69(6), 1721-1730.

Brawley, S. H. & Adey, W. H., 1981. Micrograzers may affect macroalgal density. Nature 292, 177.

Brawley, S. H. & Johnson, L. E., 1991. Survival of fucoid embryos in the intertidal zone depends upon developmental stage and microhabitat. J. Phycol. 27, 179-186.

Brönmark, C., 1985. Interactions between macrophytes, epiphytes and herbivores: an experimental approach. Oikos 45, 26-30.

Buss, L. W. & Jackson, J. B. C., 1979. Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. Am. Nat. 113, 223-234.

Campbell, B. D., Grime, J. P., Mackey, J. M. L. & Jalili, A., 1991. The quest for a mechanistic understanding of resource competition in plant communities: the role of experiments. Functional Ecology 5, 241-253.

Carpenter, R. C., 1990. Competition among marine macroalgae: a physiological perspective. J. Phycol. 26, 6-12.

Chapman, A. R. O., 1973. A critique of prevaling attitudes towards the control of seaweed zonation on the sea shore. Bot. Mar. 16, 80-82.

Chapman, A. R. O., 1974. The ecology of macroscopic marine algae. Ann. Rev. Ecol. Syst. 5, 65-80.

Chapman, A. R. O., 1979. "Biology of Seaweeds. Levels of Organization". Edward Arnold, London.

Chapman, A. R. O., 1984. Reproduction, recruitment and mortality in two species of *Laminaria* in southwest Nova Scotia. J. Exp. Mar. Biol. Ecol. 78, 99-109.

Chapman, A. R. O., 1986. Population and community ecology of seaweeds. Adv. Mar. Biol. 23, 1-161.

Chapman, A. R. O., 1989. Abundance of *Fucus spiralis* and ephemeral seaweeds in a high eulittoral zone: effects of grazers, canopy and substratum type. Mar. Biol. 102, 565-572.

Chapman, A. R. O., 1990a. Competitive interactions between *Fucus spiralis* L. and *F. vesiculosus* L. (Fucales, Phaeophyta). Hydrobiologia 204/205, 205-209.

Chapman, A. R. O., 1990b. Effects of grazing, canopy cover and substratum type on the abundances of common species of seaweeds inhabiting littoral fringe tide pools. Bot. Mar. 33, 319-326.

Chapman, A. R. O., 1995. Functional ecology of fucoid algae: twenty-three years progress. Phycologia 34, 1-32.

Chapman, A. R. O. & Goudey, C. L., 1983. Demographic study of the macrothallus of *Leathesia difformis* (Phaeophyta) in Nova Scotia. Can. J. Bot. 61, 319-323.

Chapman, A. R. O. & Johnson, C. R., 1990. Disturbance and organization of macroalgal assemblages in the northwest Atlantic. Hydrobiologia 192, 77-121.

Colman, J., 1933. The nature of the intertidal zonation of plants and animals. J. mar. biol. Ass. U.K. 18, 435-476.

Colwell, R. K & Fuentes, E. R., 1975. Experimental studies of the niche. Ann. Rev. Ecol. Syst. 6, 281-310.

Connell, J. H., 1961a. Effects of competition, predation by *Thais lapillus*, and other factors on natural populations of the barnacle *Balanus balanoides*. Ecol. Monogr. 31, 61-104.

Connell, J. H., 1961b. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology 42(4), 710-723.

Connell, J. H., 1978. Diversity in tropical rain forests and coral reefs. Science 199, 1302-1310.

Connell, J. H., 1980. Diversity and the coevolution of competitors, or the ghost of competition past. Oikos 35, 131-138.

Connell, J. H., 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. Am. Nat. 122, 661-696.

Connolly, J., 1986. On difficulties with replacement-series methodology in mixture experiments. J. Appl. Ecol. 23, 125-137.

Connor, E. F. & Simberloff, D., 1986. Competition, scientific method, and null models in ecology. Am. Sci. 74, 155-162.

Cousens, R., 1985. A simple model relating yield loss to weed density. Ann. appl. Biol. 107, 239-252.

Cousens, R., 1991. Aspects of the design and interpretation of competition (interference) experiments. Weed Technol. 5, 664-673.

Cousens, R., Firbank, L. G., Mortimer, A. M. & Smith, R. G. R., 1988. Variability in the relationship between crop yield and weed density for winter wheat and *Bromus sterilis*. J. Appl. Ecol. 25, 1033-1044.

Cousens, R. & Hutchings, M. J., 1983. The relationship between density and mean frond weight in monospecific seaweed stands. Nature 301, 240-241.

Cousens, R. & O'Neill, M., 1993. Density dependence of replacement series experiments. Oikos 66, 347-352.

Creed, J. C., 1995. Spatial dynamics of a *Himanthalia elongata* (Fucales, Phaeophyta) population. J. Phycol. 31, 851-859.

Creed, J. C., Norton, T. A. & Harding, S. P., 1996a. The development of size structure in a young *Fucus serratus* population. Eur. J. Phycol. 31, 203-209.

Creed, J. C., Norton, T. A. & Kain (Jones), J. M., 1996b. Are neighbours harmful or helpful in *Fucus vesiculosus* populations? Mar. Ecol. Prog. Ser. 133, 191-201.

Creese, R. G. & Underwood, A. J., 1982. Analysis of inter- and intra-specific competition amongst intertidal limpets with different methods of feeding. Oecologia (Berl.) 53, 337-346.

Cubit, J., 1975. Interactions of seasonally changing physical factors and grazing affecting high intertidal communities on a rocky shore. Dissertation. University of Oregon, Eugene, Oregon, USA.

Dahms, S., 1993. Die Besiedlung verschiedener Helgoländer Standorte durch die Strandschnecke *Littorina littorea* (Linnaeus, 1758). Diploma thesis, University of Marburg, Marburg, Germany.

Day, R. W. & Quinn, G. P., 1989. Comparisons of treatments after an analysis of variance in ecology. Ecol. Monogr. 59(4), 433-463.

Dayton, P. K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecol. Monogr. 41, 351-389.

Dayton, P. K., 1975. Experimental evaluation of ecological dominance in a rocky intertidal algal community. Ecol. Monogr. 45, 137-159.

Dean, T. A., Thies, K. & Lagos, S. L., 1989. Survival of juvenile giant kelp: the effects of demographic factors, competitors, and grazers. Ecology 70(2), 483-495.

Denton, A. B. & Chapman, A. R. O., 1991. Feeding preferences of gammarid amphipods among four species of *Fucus*. Mar. Biol. 109, 503-506.

Denton, A., Chapman, A. R. O. & Markham, J., 1990. Size-specific concentrations of phlorotannins (anti-herbivore compounds) in three species of *Fucus*. Mar. Ecol. Prog. Ser. 65, 103-104.

Doty, M. S., 1946. Critical tide factors that are correlated with the vertical distribution of marine algae and other organisms along the Pacific coast. Ecology 27, 315-328.

Dring, M. J. & Brown, F. A., 1982. Photosynthesis of intertidal brown algae during and after periods of emersion: a renewed search for physiological causes of zonation. Mar. Ecol. Prog. Ser. 8, 301-308.

Firbank, L. G. & Watkinson, A. R., 1985. On the analysis of competition within two-species mixtures of plants. J. Appl. Ecol. 22, 503-517.

Firbank, L. G. & Watkinson, A. R., 1990. On the effects of competition: from monocultures to mixtures. In "Perspectives on Plant Competition". J. B. Grace & D. Tilman (eds.). Academic Press, San Diego, pp. 165-192.

Fowler, N., 1981. Competition and coexistence in a North Carolina grassland. II. The effects of the experimental removal of species. J. Ecol. 69, 843-854.

Fowler, N., 1982. Competition and coexistence in a North Carolina grassland. III. Mixtures of component species. J. Ecol. 70, 77-92.

Fralick, R. A., Turgeon, K. W. & Mathieson, A. C., 1974. Destruction of kelp populations by *Lacuna vincta* (Montagu). Nautilus 88, 112-114.

Fréchette, M. & Lefaivre, D., 1990. Discriminating between food and space limitation in benthic suspension feeders using self-thinning relationships. Mar. Ecol. Prog. Ser. 65, 15-23.

Gallardo, C. S. & Götting, K.-J., 1985. Reproduktionsbiologische Untersuchungen an drei *Littorina*-Arten der südlichen Nordsee. Helgoländer Meeresunters. 39, 165-186.

Gaudet, C. L. & Keddy, P. A., 1988. A comparative approach to predicting competitive ability from plant traits. Nature 334, 242-243.

Gause, G. F., 1932. Experimental studies on the struggle for existence. I. Mixed populations of two species of yeast. J. Exp. Biol. 9, 389-402.

Gause, G. F., 1934. "The Struggle for Existence". Hafner, New York.

Gause, G. F., 1935. Experimental demonstration of Volterra's periodic oscillation in the numbers of animals. J. Exp. Biol. 12, 44-48.

Goldberg, D. E., 1990. Components of resource competition in plant communities. In: "Perspectives on Plant Competition". J. B. Grace & D. Tilman (eds.). Academic Press, San Diego, pp. 27-49.

Goldberg, D. E. & Landa, K., 1991. Competitive effect and response: hierarchies and correlated traits in the early stages of competition. J. Ecol. 79, 1013-1030.

Grace, J. B., 1990. On the relationship between plant traits and competitive ability. In "Perspectives on Plant Competition". J. B. Grace & D. Tilman (eds.). Academic Press, San Diego, pp. 51-65.

Grace, J. B., 1991. A clarification of the debate between Grime and Tilman. Functional Ecology 5, 583-587.

Grace, J. B. & Wetzel, R. G., 1981. Habitat partitioning and competitive displacemant in cattails (*Typha*): experimental field studies. Am. Nat. 118, 463-474.

Grime, J. P., 1974. Vegetation classification by reference to strategies. Nature 250, 26-31.

Grime, J. P., 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. Am. Nat. 111, 1169-1194.

Grime, J. P., 1988. Limiting factors for modellers. Nature 336, 630.

Grime, J. P., 1995. Functional types: a comment on Steneck and Dethier (1994). Oikos 73, 120-121.

Hardin, G., 1960. The competitive exclusion principle. Science 131, 1292-1297.

Harms, J., 1993. Check list of species (algae, invertebrates and vertebrates) found in the vicinity of the island of Helgoland (North Sea, German Bight) - a review of recent records. Helgoländer Meeresunters. 47, 1-34.

Harper, J. L., 1977. "The Population Biology of Plants". Academic Press, London.

Hartnoll, R. G. & Hawkins, S. J., 1985. Patchiness and fluctuations on moderately exposed rocky shores. Ophelia 24, 53-63.

Hawkins, S. J., 1981. The influence of season and barnacles on the algal colonization of *Patella vulgata* exclusion areas. J. mar. biol. Ass. U.K. 61, 1-15.

Hawkins, S. J. & Hartnoll, R. G., 1983. Grazing of intertidal algae by marine invertebrates. Oceanogr. Mar. Biol. Ann. Rev. 21, 195-282.

Hawkins, S. J. & Hartnoll, R. G., 1985. Factors determining the upper limits of intertidal canopy-forming algae. Mar. Ecol. Prog. Ser. 20, 265-271.

Hay, M. E., 1981. The functional morphology of turf-forming seaweeds: persistence in stressful marine habitats. Ecology 62(3), 739-750.

Hay, M. E. & Fenical, W., 1988. Marine plant-herbivore interactions: the ecology of chemical defense. Ann. Rev. Syst. 19, 111-145.

Hay, M. E., Renaud, P. E. & Fenical, W., 1988. Large mobile versus small sedentary herbivores and their resistance to seaweed chemical defenses. Oecologia (Berlin) 75, 246-252.

Herben, T. & Krahulec, F., 1990. Competitive hierarchies, reversals of rank order and the de Wit approach: are they compatible? Oikos 58, 254-256.

Hruby, T. & Norton, T. A., 1979. Algal colonization on rocky shores in the Firth of Clyde. J. Ecol. 67, 65-77.

Hughes, R. N. & Griffiths, C. L., 1988. Self-thinning in barnacles and mussels: the geometry of packing. Am. Nat. 132, 484-491.

Hunter, J., 1981. Feeding preferences and competitive herbivory studies on two species of periwinkles, *Littorina obtusata* and *Littorina littorea*. (Abstract). Biol. Bull. mar. biol. Lab., Woods Hole 161, 328.

Hurd, C. L. & Dring, M. J., 1990. Phosphate uptake by intertidal algae in relation to zonation and season. Mar. Biol. 107, 281-289.

Hurd, C. L. & Dring, M. J., 1991. Desiccation and phosphate uptake by intertidal fucoid algae in relation to zonation. Br. phycol. J. 26, 327-333.

Hurlbert, S. H., 1981. A gentle depilation of the niche: Dicean resource sets in resource hyperspace. Evol. Theory 5, 177-184.

Huston, M., 1979. A general hypothesis of species diversity. Am. Nat. 113, 81-101.

Hutchings, M. J., 1979. Weight-density relationships in ramet populations of clonal perennial herbs, with special reference to the -3/2 power law. J. Ecol. 67, 21-33.

Hutchings, M. J., 1983. Ecology's law in search of a theory. New Sci. 98, 765-767.

Hutchings, M. J. & Budd, C. S. J., 1981. Plant competition and its course through time. BioScience 31, 640-645.

Hutchinson, G. E., 1957. Concluding remarks. Cold Spring Harbor Symp. Quant. Biol. 22, 415-427.

Ilvessalo, H. & Tuomi, J., 1989. Nutrient availability and accumulation of phenolic compounds in the brown alga *Fucus vesiculosus*. Mar. Biol. 101, 115-119.

Imrie, D. W., Hawkins, S. J. & McCrohan, C. R., 1989. The olfactory-gustatory basis of food preference in the herbivorous prosobranch, *Littorina littorea* (Linnaeus). J. Moll. Stud. 55, 217-255.

Inouye, R. S. & Schaffer, W. M., 1981. On the ecological meaning of ratio (de Wit) diagrams in plant ecology. Ecology 62(6), 1679-1681.

Ives, A. R., 1995. Measuring competition in a spatially heterogeneous environment. Am. Nat. 146, 911-936.

Jacobs, V., 1993. Vorkommen und Substratwahl von *Spirorbis spirorbis* im Helgoländer Felswatt. Diploma thesis, University of Marburg, Marburg, Germany.

Janke, K., 1986. Die Makrofauna und ihre Verteilung im Nordost-Felswatt von Helgoland. Helgoländer Meeresunters. 40, 1-55.

Janke, K., 1989. Lebensgemeinschaften und ihre Besiedlungsstrukturen in der Gezeitenzone felsiger Meeresküsten. Dissertation. University of Kiel, Kiel, Germany.

Janke, K., 1990. Biological interactions and their role in community structure in the rocky intertidal of Helgoland (German Bight, North Sea). Helgoländer Meeresunters. 44, 219-263.

Jernakoff, P., 1985. An experimental evaluation of the influence of barnacles, crevices and seasonal patterns of grazing on algal diversity and cover in an intertidal barnacle zone. J. Exp. Mar. Biol. Ecol. 88, 287-302.

Johnson, C. R. & Field C. A., 1993. Using fixed-effects model multivariate analysis of variance in marine biology and ecology. Oceanogr. Mar. Biol. Annu. Rev. 31, 177-221.

Jolliffe, P. A., Minjas, A. N. & Runeckles, V. C., 1984. A reinterpretation of yield relationships in replacement series experiments. J. Appl. Ecol. 21, 227-243.

Karez, R., 1991. Die Besiedlung sublitoraler Rotalgen am Felssockel von Helgoland. Diploma thesis, University of Marburg, Marburg, Germany.

Karlson, R. H. & Jackson, J. B. C., 1981. Competitive networks and community structure: a simulation study. Ecology 62(3), 670-678.

Keddy, P. A., 1984. Plant zonation on lakeshores in Nova Scotia: a test of the resource specialization hypothesis. J. Ecol. 72, 797-808.

Keddy, P. A., 1989a. "Competition." Chapman and Hall, London.

Keddy, P. A., 1989b. Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. Can. J. Bot. 67, 708-716.

Keddy, P. A., 1990. Competitive hierarchies and centrifugal organization in plant communities. In "Perspectives on Plant Competition". J. B. Grace & D. Tilman (eds.). Academic Press, San Diego, pp. 265-290.

Keddy, P. A., 1992. A pragmatic approach to functional ecology. Functional Ecology 6, 621-626.

Keddy, P. A. & Shipley, B., 1989. Competitive hierarchies in herbaceous plant communities. Oikos 54, 234-241.

Keddy, P. A., Twolan-Strutt, L. & Wisheu, I. C., 1994. Competitive effect and response rankings in 20 wetland plants: are they consistent across three environments? J. Ecol. 82, 635-643.

Kendrick, G. A., 1994. Effects of propagule settlement density and adult canopy on survival of recruits of *Sargassum* spp. (Sargassaceae: Phaeophyta). Mar. Ecol. Prog. Ser. 103, 129-140.

Kendrick, G. A. & Walker, D. I., 1995. Dispersal of propagules of *Sargassum* spp. (Sargassaceae: Phaeophyta): observations of local patterns of dispersal and consequences for recruitment and population structure. J. Exp. Mar. Biol. Ecol. 192, 273-288.

Khan, M. A., Putwain, P. D. & Bradshaw, A. D., 1975. Population interrelationships. 2. Frequency-dependent fitness in *Linum*. Heredity 34(2), 145-163.

Kiirikki, M., 1996. Mechanisms affecting macroalgal zonation in the northern Baltic Sea. Eur. J. Phycol. 31, 225-232.

Knight, M. & Parke, M., 1950. A biological study of *Fucus vesiculosus* L. and *F. serratus* L. J. Mar. Biol. Ass. U.K. 29. 439-515.

Kornmann, P. & Sahling, P.-H., 1977. Meeresalgen von Helgoland. Helgoländer wiss. Meeresunters. 29, 1-289.

Kremer, B. P., 1981. Gametenfreisetzung und Befruchtung bei *Fucus*. Biologie in unserer Zeit 11(2), 58-61.

Kroon, H. de & Kwant, R., 1991. Density-dependent growth responses in two clonal herbs: regulation of shoot density. Oecologia 86, 298-304.

Law, R. & Watkinson, A. R., 1987. Response-surfaces analysis of two-species competition: an experiment on *Phleum arenarium* and *Vulpia fasciculata*. J. Ecol. 75, 871-886.

Lein, T. E., 1980. The effects of *Littorina littorea* L. (Gastropoda) grazing on littoral green algae in the inner Oslofjord, Norway. Sarsia 65, 87-92.

Levin, S. A. & Paine, R. T., 1974. Disturbance, patch formation, and community structure. Proc. Nat. Acad. Sci. USA 71, 2744-2747.

Lewin, R., 1983. Santa Rosalia was a goat. Science 221, 636-639.

Lewis, J. R., 1961. The littoral zone on rocky shores - a biological or physical entity? Oikos 12, 280-301.

Lewis, J. R., 1964. "The Ecology of Rocky Shores". English University Press.

Lobban, C. S. & Harrison, P. J., 1994. "Seaweed Ecology and Physiology". Cambridge University Press, Cambridge, USA.

Loehle, C., 1987. Hypothesis testing in ecology: psychological aspects and the importance of theory maturation. Quart. Rev. Biol. 62, 397-409.

Loehle, C., 1988. Problems with the triangular model for representing plant strategies. Ecology 69(1), 284-286.

Lonsdale, W. M., 1990. The self-thinning rule: dead or alive? Ecology 71(4), 1373-1388.

Lonsdale, W. M. & Watkinson, A. R., 1982. Light and self-thinning. New Phytol. 90, 431-445.

Lubchenco, J., 1978. Plant species diversity in a marine intertidal community: importance of herbivore food preference and algal competitive abilities. Am. Nat. 112, 23-39.

Lubchenco, J., 1980. Algal zonation in the New England rocky intertidal community: an experimental analysis. Ecology 61(2), 333-344.

Lubchenco, J., 1982. Effects of grazers and algal competitors on fucoid colonization in tide pools. J. Phycol. 18, 544-550.

Lubchenco, J., 1983. *Littorina* and *Fucus*: effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64(5), 1116-1123.

Lubchenco, J., 1986. Relative importance of competition and predation: early colonization by seaweeds in New England. In "Community Ecology". J. Diamond & T. J. Case (eds.). Harper & Row, New York, pp. 537-555.

Lubchenco, J. & Cubit, J., 1980. Heteromorphic life histories of certain marine algae as adaptations to variations in herbivory. Ecology 61(3), 676-687.

Lubchenco, J. & Gaines, S. D., 1981. A unified approach to marine plant-herbivore interactions. I. Populations and communities. Ann. Rev. Ecol. Syst. 12, 405-437.

Lüning, K., 1970. Tauchuntersuchungen zur Vertikalverteilung der sublitoralen Helgoländer Algenvegetation. Helgoländer wiss. Meeresunters. 21, 271-291.

Lüning, K., 1985. "Meeresbotanik". G. Thieme Verlag, Stuttgart, Germany.

Lüning, K.& Dring, M. J., 1979. Continuous underwater light measurement near Helgoland (North Sea) and its significance for characteristic light limits in the sublittoral region. Helgoländer wiss. Meeresunters. 32, 403-424.

Manly, B. F. J., 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. Oecologia 93, 149-152.

Manly, B. F. J., 1995. Measuring selectivity from multiple choice feeding-preference experiments. Biometrics 51, 709-715.

Markham, J. W. & Hagmeier, E., 1982. Observations on the effects of germanium dioxide on the growth of macro-algae and diatoms. Phycologia 21, 125-130.

Markham, J. W. & Munda, I. M., 1980. Algal recolonization in the rocky eulittoral at Helgoland, Germany. Aquat. Bot. 9, 33-71.

Martínez, E. & Santelices, B., 1992. Size hierarchy and the -3/2 "power law" relationship in a coalescent seaweed. J. Phycol. 28, 259-264.

McCook, L. J. & Chapman, A. R. O., 1992. Vegetative regeneration of *Fucus* rockweed canopy as a mechanism of secondary succession on an exposed rocky shore. Bot. Mar. 35, 35-46.

McCook, L. J. & Chapman, A. R. O., 1993. Community succession following massive ice-scour on a rocky intertidal shore: recruitment, competition and predation during early, primary succession. Mar. Biol. 115, 565-575.

McLachlan, J., Chen, L. C.-M. & Edelstein, T., 1971. The culture of four species of *Fucus* under laboratory conditions. Can. J. Bot. 49, 1463-1469.

Menge, B. A. & Sutherland, J. P., 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. Am. Nat. 110, 351-369.

Metaxas, A., Hunt, H. L. & Scheibling, R. E., 1994. Spatial and temporal variability of macrobenthic communities in tidepools on a rocky shore in Nova Scotia, Canada. Mar. Ecol. Prog. Ser. 105, 89-103.

Mitchley, J. & Grubb, P. J., 1986. Control of relative abundance of perennials in chalk grassland in southern England. I. Constancy of rank order and results of pot- and field-experiments on the role of interference. J. Ecol. 74, 1139-1166.

Moreno, C. A. & Jaramillo, E., 1983. The role of grazers in the zonation of intertidal macroalgae of the Chilean coast. Oikos 41, 73-76.

Newell, R. C., Pye, V. I. & Ahsanullah, M., 1971. Factors affecting the feeding rate of the winkle *Littorina littorea*. Mar. Biol. 9, 138-144.

Nicotri, M. E., 1980. Factors involved in herbivore food preference. J. Exp. Mar. Biol. Ecol. 42, 13-26.

Niemeck, R. A. & Mathieson, A. C., 1976. An ecological study of *Fucus spiralis* L. J. Exp. Mar. Biol. Ecol. 24, 33-48.

Norberg, R. Å., 1988. Theory of growth geometry of plants and self-thinnig of plant populations: geometric similarity, elastic similarity, and different growth modes of plant parts. Am. Nat. 131, 220-256.

Norton, T. A., Hawkins, S. J., Manley, N. L., Williams, G. A. & Watson, D. C., 1990. Scraping a living: a review of littorinid grazing. Hydrobiologia 193, 117-138.

Olson, A. M. & Lubchenco, J., 1990. Competition in seaweeds: linking plant traits to competitive outcomes. J. Phycol. 26, 1-6.

Paine, R. T., 1966. Food web complexity and species diversity. Am. Nat. 100, 65-75.

Paine, R. T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia (Berl.) 15, 93-120.

Paine, R. T., 1977. Controlled manipulations in the marine intertidal zone, and their contributions to ecological theory. Academy of Natural Sciences, Philadelphia, Special Publication 12, 245-270.

Paine, R. T. & Levin, S. A., 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecol. Monogr. 51(2), 145-178.

Parker, T. & Chapman, A. R. O., 1994. Separating the grazing effects of periwinkles and amphipods on a seaweed community dominated by *Fucus distichus*. Ophelia 39, 75-91.

Pennings, S. C. & Callaway, R. M., 1992. Salt marsh plant zonation: the relative importance of competition and physical factors. Ecology 73(2), 681-690.

Peterson, C. H. & Renaud, P. E., 1989. Analysis of feeding preference experiments. Oecologia 80, 82-86.

Petraitis, P. S., 1987. Factors organizing rocky intertidal communities of New England: herbivory and predation in sheltered bays. J. Exp. Mar. Biol. Ecol. 109, 117-136.

Petraitis, P. S., 1995. Use of average vs. total biomass in self-thinning relationships. Ecology 76(2), 656-658.

Pfister, C. A., 1995. Estimating competition coefficients from census data: a test with field manipulations of tidepool fishes. Am. Nat. 146, 271-291.

Quatrano, R. S., 1980. Gamete release, fertilization and embryogenesis in the Fucales. In "Handbook of Phycological Methods (Developmental and Cytological Methods)." E. Gantt (ed.). Cambridge Univ. Press, Cambridge, pp. 59-68.

Quinn, G. P. & Keough, M. J., 1993. Potential effect of enclosure size on field experiments with herbivorous intertidal gastropods. Mar. Ecol. Prog. Ser. 98, 199-201.

Ragan, M. A. & Glombitza, K.-W., 1986. Phlorotannins, brown algal polyphenols. Prog. Phyc. Res. 4, 130-241.

Ragan, M. A. & Jensen, A., 1977. Quantitative studies on brown algal phenols. I. Estimation of absolute polyphenol contents of *Ascophyllum nodosum* (L.) Le Jol. and *Fucus vesiculosus* (L.). J. Exp. Mar. Biol. Ecol. 30, 209-221.

Reader, R. J., Wilson, S. D., Belcher, J. W., Wisheu, I., Keddy, P. A., Tilman, D., Morris, E. C., Grace, J. B., McGraw, J. B., Olff, H., Turkington, R., Klein, E., Leung, Y., Shipley, B., van Hulst, R., Johansson, M. E., Nilsson, C., Gurevitch, J., Grigulis, K. & Beisner, B. E., 1994. Plant competition in relation to neighbor biomass: an intercontinental study with *Poa pratensis*. Ecology 75(6), 1753-1760.

Reed, D. C., 1990. An experimental evaluation of density dependence in a subtidal algal population. Ecology 71(6), 2286-2296.

Reid, D. G., 1990. Note on the discrimination of females of *Littorina mariae* Sacchi & Rastelli and *L. obtusata* (Linnaeus). J. Moll. Stud. 56, 113-114.

Rice, K. J. & Menke, J. W., 1985. Competitive reversals and environment-dependent resource partitioning in *Erodium*. Oecologia (Berlin) 67, 430-434.

Roa, R., 1992. Design and analysis of multiple-choice feeding-preference experiments. Oecologia 89, 509-515.

Rosenzweig, M. L. & Abramsky, Z., 1986. Centrifugal community organization. Oikos 46, 339-348.

Roughgarden, J., 1983. Competition and theory in community ecology. Am. Nat. 122, 583-601.

Russ, G. R., 1982. Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. Oecologia (Berl.) 53, 12-19.

Russell, G. & Fielding, A. H., 1974. The competitive properties of marine algae in culture. J. Ecol. 62, 689-698.

Sachs, L., 1984. Angewandte Statistik. 6th ed. Springer, Berlin, Germany.

Schaffelke, B., Evers, D. & Walhorn, A., 1995. Selective grazing of the isopod *Idotea baltica* between *Fucus evanescens* and *F. vesiculosus* from Kiel Fjord (western Baltic). Mar. Biol. 124, 215-218.

Schiel, D. R. & Choat, J. H., 1980. Effects of density on monospecific stands of marine algae. Nature 285, 324-326.

Schoener, T. W., 1974. Resource partitioning in ecological communities. Science 185, 27-39.

Schoener, T. W., 1983. Field experiments on interspecific competition. Am. Nat. 122, 240-285.

Schonbeck, M. & Norton, T. A., 1978. Factors controlling the upper limits of fucoid algae on the shore. J. Exp. Mar. Biol. Ecol. 31, 303-313.

Schonbeck, M. & Norton, T. A., 1979a. An investigation of drougth avoidance in intertidal fucoid algae. Bot. Mar. 22, 133-144.

Schonbeck, M. & Norton, T. A., 1979b. The effects of brief periodic submergence on intertidal fucoid algae. Estuar. Coast. Mar. Sci. 8, 205-211.

Schonbeck, M. & Norton, T. A., 1980. Factors controlling the lower limits of fucoid algae on the shore. J. Exp. Mar. Biol. Ecol. 43, 131-150.

Shipley, B., 1993. A null model for competitive hierarchies in competition matrices. Ecology 74(6), 1693-1699.

Shipley, B. & Keddy, P. A., 1994. Evaluating the evidence for competitive hierarchies in plant communities. Oikos 69, 340-345.

Shmida, A. & Ellner, S., 1984. Coexistence of plant species with similar niches. Vegetatio 58, 29-55.

Silander, J. A. & Antonovics, J., 1982. Analysis of interspecific interactions in a coastal plant community - a perturbation approach. Nature 298, 557-560.

Silvertown, J. & Dale, P., 1991. Competitive hierarchies and the structure of herbaceous plant communities. Oikos 61, 441-444.

Snow, A. A. & Vince, S. W., 1984. Plant zonation in an Alaskan salt marsh. II. An experimental study of the role of edaphic conditions. J. Ecol. 72, 669-684.

Sokal, R. R. & Rohlf, F. J., 1995. Biometry. 3rd ed. W. H. Freeman and Company, New York.

Sommer, U., 1983. Nutrient competition between phytoplankton species in multispecies chemostat experiments. Arch. Hydrobiol. 96, 399-416.

Sommer, U., 1996. Nutrient competition experiments with periphyton from the Baltic Sea. Mar. Ecol. Prog. Ser. 140, 161-167.

Southward A. J. & Southward, E. C., 1978. Recolonization of rocky shores in Cornwall after use of toxic dispersants to clean up the Torrey Canyon spill. J. Fish. Res. Board Can. 35, 682-706.

Spitters, C. J. T., 1983a. An alternative approach to the analysis of mixed cropping experiments. 1. Estimation of competition effects. Neth. J. agric. Sci. 31, 1-11.

Spitters, C. J. T., 1983b. An alternative approach to the analysis of mixed cropping experiments. 2. Marketable yield. Neth. J. agric. Sci. 31, 143-155.

Starr, R. C. & Zeikus, J. A., 1987. Utex - the culture collection of algae at the University of Texas at Austin. J. Phycol. 23, Suppl., 1-47.

Steinberg, P. D., 1988. Effects of quantitative and qualitative variation in phenolic compounds on feeding in three species of marine invertebrate herbivores. J. Exp. Mar. Biol. Ecol. 120, 221-237.

Steinberg, P., 1995. Seasonal variation in the relationship between growth rate and phlorotannin production in the kelp *Ecklonia radiata.* Oecologia 102, 169-173.

Steneck, R. S., 1995. Are functional classifications different for marine vs terrestrial plants? A reply to Grime. Oikos 73, 122-124.

Steneck, R. S. & Dethier, M. N., 1994. A functional group approach to the structure of algal-dominated communities. Oikos 69, 476-498.

Steneck, R. S. & Watling, L., 1982. Feeding capabilities and limitation of herbivorous molluscs: a functional group approach. Mar. Biol. 68, 299-319.

Stephenson, T. A. & Stephenson, A., 1972. Life between Tidemarks on Rocky Shores. W. H. Freeman & Co., San Francisco.

Tamelen, P. G. van, 1996. Algal zonation in tidepools: experimental evaluation of the roles of physical disturbance, herbivory and competition. J. Exp. Mar. Biol. Ecol. 210, 197-231.

Tatarenkov, A. N., 1995. Genetic divergence between sibling species *Littorina mariae* Sacchi & Rastelli and *L. obtusata* (L.) (Mollusca: Gastropoda) from the White Sea. Ophelia 40, 207-218.

Taylor, D. R. & Aarssen, L. W., 1989. On the density dependence of replacement-series competition experiments. J. Ecol. 77, 975-988.

Thomas, M. L. H. & Page, F. H., 1983. Grazing by the gastropod, *Lacuna vincta*, in the lower intertidal area at Musquash Head, New Brunswick, Canada. J. mar. biol. Ass. U.K. 63, 725-736.

Thomas, T. E., Turpin, D. B. & Harrison, P. J., 1987. Desiccation enhanced nitrogen uptake rates in intertidal seaweeds. Mar. Biol. 94, 293-298.

Tilman, D. 1981. Tests of resource competition theory using four species of Lake Michigan algae. Ecology 62(3), 802-815.

Tilman, D., 1982. "Resource Competition and Community Structure". Princeton University Press, Princeton.

Tilman, D., 1985. The resource-ratio hypothesis of plant succession. Am. Nat. 125, 827-852.

Tilman, D., 1987a. On the meaning of competition and the mechanisms of competitive superiority. Functional Ecology 1, 304-315.

Tilman, D., 1987b. The importance of the mechanisms of interspecific competition. Am. Nat. 129, 769-774.

Tilman, D., 1989. Competition, nutrient reduction and the competitive neighbourhood of a bunchgrass. Functional Ecology 3, 215-219.

Tilman, D. & Wedin, D., 1991. Dynamics of nitrogen competition between successional grasses. Ecology 72(3), 1038-1049.

Underwood, A. J., 1979. The ecology of intertidal gastropods. Adv. Mar. Biol. 16, 111-210.

Underwood, A. J., 1980. The effects of grazing by gastropods and physical factors on the upper limits of distribution of intertidal macroalgae. Oecologia (Berl.) 46, 201-213.

Underwood, A. J., 1986. The analysis of competition by field experiments. In "Community Ecology: Pattern and Process". J. Kikkawa & D. J. Anderson (eds.). Blackwell Scientific Publications, Melbourne, pp. 240-268.

Underwood, A. J., 1990. Experiments in ecology and management: their logics, functions and interpretations. Aust. J. Ecol. 15, 365-389.

Underwood, A. J. & Jernakoff, P., 1981. Effects of interactions between algae and grazing gastropods on the structure of a low-shore intertidal algal community. Oecologia (Berl.) 48, 221-233.

Van Alstyne, K. L., 1988. Herbivore grazing increases polyphenolic defenses in the intertidal brown alga *Fucus distichus*. Ecology 69(3), 655-663.

Vandermeer, J. H., 1972. Niche theory. Ann. Rev. Ecol. Syst. 3, 107-132.

Viejo, R. M. & Arrontes, J., 1992. Interactions between mesograzers inhabiting *Fucus vesiculosus* in northern Spain. J. Exp. Mar. Biol. Ecol. 162, 97-111.

Watson, D. C. & Norton, T. A., 1985. Dietary preferences of the common periwinkle, *Littorina littorea* (L.). J. Exp. Mar. Biol. Ecol. 88, 193-211.

Watson, D. C. & Norton, T. A., 1987. The habitat and feeding preferences of *Littorina obtusata* (L.) and *L. mariae* Sacchi et Rastelli. J. Exp. Mar. Biol. Ecol. 112, 61-72.

Weiner, J., 1985. Size hierarchies in experimental populations of annual plants. Ecology 66(3), 743-752.

Weiner, J., 1986. How competition for light and nutrients affects size variability in *Ipomoea tricolor* populations. Ecology 67(5), 1425-1427.

Weiner, J. & Solbrig, O. T., 1984. The meaning and measurement of size hierarchies in plant populations. Oecologia (Berl.) 61, 334-336.

Weiner, J. & Thomas, S. C., 1986. Size variability and competition in plant monocultures. Oikos 47, 211-222.

Welden, C. W. & Slauson, W. L., 1986. The intensity of competition versus its importance: an overlooked distinction and some implications. Quart. Rew. Biol. 61, 23-44.

Weller, D. E., 1987. A reevaluation of the -3/2 power rule of plant self-thinning. Ecol. Monogr. 57(1), 23-43.

Weller, D. E., 1991. The self-thinning rule: dead or unsupported? - A reply to Lonsdale. Ecology 72(2), 747-750.

Werner, P. A., 1979. Competition and coexistence of similar species. In "Topics in Plant Population Biology". O. T. Solbrig, S. Jain, G. B. Johnson & P. H. Raven (eds.). Columbia University Press, New York, pp. 287-310.

Westoby, M., 1984. The self-thinning rule. Adv. Ecol. Res. 14, 167-225.

Westoby, M. & Howell, J., 1986. Influence of population structure on self-thinning of plant populations. J. Ecol. 74, 343-359.

White, J., 1980. Demographic factors in populations of plants. In "Demography and Evolution in Plant Populations." O. T. Solbrig (ed.). University of California Press, Berkeley, California, USA, pp. 21-48.

White, J. & Harper, J. L., 1970. Correlated changes in plant size and number in plant populations. J. Ecol. 58, 467-485.

Whittington, R., 1984. Laying down the -3/2 power law. Nature 311, 217.

Willey, R. W. & Rao, M. R., 1980. A competitive ratio for quantifying competition between intercrops. Expl. Agric. 16, 117-125.

Williams, G. A., 1990. *Littorina mariae* - a factor structuring low shore communities? Hydrobiologia 193, 139-146.

Wilson, J. B., 1988. Shoot competition and root competition. J. Appl. Ecol. 25, 279-296.

Wilson, S. D. & Keddy, P. A., 1985. Plant zonation on a shoreline gradient: physiological response curves of component species. J. Ecol. 73, 851-860.

Wilson, S. D. & Keddy, P. A., 1986a. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. Am. Nat. 127, 862-869.

Wilson, S. D. & Keddy, P. A., 1986b. Species competitive ability and posititon along a natural stress/disturbance gradient. Ecology 67(5), 1236-1242.

Wilson, S. D. & Tilman, D., 1991. Components of plant competition along an experimental gradient of nitrogen availability. Ecology 72(3), 1050-1065.

Wit, C. T. de, 1960. On competition. Versl. Landbouwkd. Onderz. 66, 1-82.

Wolken, K., 1994. Grazing in Seegraswiesen. Diploma thesis, University of Kiel, Kiel, Germany.

Wright, P. J. & Reed, R. H., 1990. Effects of osmotic stress on gamete size, rhizoid initiation and germling growth in fucoid algae. Br. phycol. J. 25, 149-155.

Yang, W. X., 1993. Morphological study on the inhibitory effect of germanium dioxide on growth and development of brown algae. Scientific Papers of the Institute of Algological Research, Hokkaido Univ. 9(1), 33-64.

Yao, Y., 1965. An approximate degrees of freedom solution to the multivariate Behrens-Fisher problem. Biometrika 52, 139-147.

Yoda, K., Kira, T., Ogawa, H. & Hozumi, K., 1963. Self-thinning in overcrowded pure stands under cultivated and natural conditions. J. Biol., Osaka City University 14, 107-129.

Yodzis, P., 1986. Competition, mortality, and community structure. In "Community Ecology". J. Diamond & T. J. Case (eds.). Harper & Row, N.Y, pp. 480-491.

APPENDIX

ANALYSIS OF FEEDING PREFERENCE

Detection of preference: recent revolutions of statistical analysis

The design and analysis of preference experiments has undergone dramatic changes in the last few years. The objectives of such experiments comprise not only the detection of feeding preferences of consumers, but also analysis of habitat selection and many components of consumer-prey relations structuring communities (reviewed by Roa 1992). Here, I will review recent changes of statistical approaches for preference experiments from a practical viewpoint. Only preference for food is considered.

As pointed out by Nicotri (1980), there are two distinct components of food preference: attractiveness, relating to the selection of a potential prey, and edibility, relating to the rate of prey ingestion.

To test for attractiveness, prey items are offered simultaneously to the consumer (hereafter referred to as '(multiple) choice experiments') whereas edibility is tested in 'no choice experiments' with separate single offers of different food types. Both experimental designs may reflect the same attractiveness or palatability, but multiple choice experiments alone allow detection of a genuine choice by the consumer (Peterson & Renaud 1989). To draw predictions about food preferences from only no choice experiments can produce confusing results when large quantities of less preferred foods are consumed to compensate for low nutritional quality (Hay *et al.* 1988).

A comprehensive study should encompass both choice and no choice experiments (Watson & Norton 1985), especially in cases were food types also represent habitats for the consumers, as e.g. in the case of small crustaceans feeding on macroalgae (Schaffelke *et al.* 1995).

The analysis of no choice feeding experiments is rather straightforward. Analysis of variance could be used to detect differences in consumption of different food types. Nevertheless, there are some problems with controls that will be considered separately below. If not stated otherwise explicitly, the following discussion refers to multiple choice experiments.

means of uncentered data for each food type against the vector whose components consist of the overall mean k only:

$$H_0: \begin{bmatrix} \mu_1 \\ \mu_2 \\ \vdots \\ \mu_{p-1} \\ \mu_p \end{bmatrix} = \begin{bmatrix} k \\ k \\ \vdots \\ k \\ k \end{bmatrix}$$

Columns of corrected and centered data may now be used in statistical software packages such as Systat (Systat Inc.), but if no such package is available, spreadsheet calculation is easy with some basic skills in vector and matrix calculation. Hotelling's T^2 is then calculated as

$$T^2 = n(\mu - k)' S^{-1} (\mu - k)$$

where (μ-k) is the vector of differences of the means of the food types ("μ" is an estimate of x_i, x_i is used in the calculation) and the overall mean k

$$(\mu - k) = \begin{bmatrix} x_1 - k \\ x_2 - k \\ \vdots \\ x_{p-1} - k \\ x_p - k \end{bmatrix}$$

and S^{-1} is the inverse of the covariance matrix S

$$S = \begin{bmatrix} \mathrm{var}(x_1) & \mathrm{cov}(x_1,x_2) & .. & \mathrm{cov}(x_1,x_{p-1}) & \mathrm{cov}(x_1,x_p) \\ \mathrm{cov}(x_2,x_1) & \mathrm{var}(x_2) & .. & \mathrm{cov}(x_2,x_{p-1}) & \mathrm{cov}(x_2,x_p) \\ \vdots & \vdots & \vdots & \vdots & \vdots \\ \mathrm{cov}(x_{p-1},x_1) & \mathrm{cov}(x_{p-1},x_2) & .. & \mathrm{var}(x_{p-1}) & \mathrm{cov}(x_{p-1},x_p) \\ \mathrm{cov}(x_p,x_1) & \mathrm{cov}(x_p,x_2) & .. & \mathrm{cov}(x_p,x_{p-1}) & \mathrm{var}(x_p) \end{bmatrix}$$

From T^2, F is calculated as

$$F = \frac{n-p}{p(n-1)} T^2$$ with p and n-p degrees of freedom, n must be > p.

F then can be compared with tabulated $F_{\alpha;p;n-p}$. If H_0 is rejected, different food types are not consumed evenly.

Simultaneous confidence intervals may be calculated for each food type:

$$x_i \pm \left[\frac{1}{n} s_i^2 \frac{(n-1)p}{n-p} F_{\alpha;p;n-p} \right]^{\frac{1}{2}},$$

where s_i^2 is the corresponding variance of the mean of food type i. When the overall mean k is not included in the interval, food type i contributed to the rejection of H_0.

Manly (1993)

In a critique of Roa's proposal, Manly (1993) pointed out three problems with the design:

1. The resulting F, and consequently the level of significance, very much depend on the special random pairing used to offset controls with treatments.

2. The reason for using multivariate statistics is that there is a correlation between the foods in experimental units. Some correlation may also exist between changes in control foods because they experience very similar experimental conditions. In the way that Roa subtracts controls from treatments to obtain corrected data for further calculation, this correlation is lost for treatment and control containers. To overcome this loss of correlation, the changes in mass of food types from **one** random control container must be subtracted from the changes of the corresponding foods in **one** treatment container exposed to a consumer. For example, the random pairing j - m is chosen for the correction of the j-th treatment with the m-th control:

$$x_{1j} = t_{1j} - c_{1m},\ x_{2j} = t_{2j} - c_{2m},\ x_{3j} = t_{3j} - c_{3m},\ \ldots\ x_{pj} = t_{pj} - c_{pm} \qquad j,m = 1,2,\ldots n$$

With this procedure the underestimation of the experimental error is avoided and the correlation between food types maintained.

3. There must be some sampling error of the overall mean, k, that is ignored by Roa (1992) but assumed to be known for the use of Hotelling's T^2. This problem is overcome by Manly by omitting the overall mean k and calculating differences between changes in different food types instead:

$$y_{1j} = x_{1j} - x_{2j},\ y_{2j} = x_{2j} - x_{3j},\ y_{3j} = x_{3j} - x_{4j},\ \ldots\ y_{p-1j} = x_{p-1j} - x_{pj} \qquad j = 1,2,\ldots n$$

With this approach, the null hypothesis that mean amounts of consumption are equal for all p food types

$$H_0: \mu_1 = \mu_2 = \mu_3 = \ldots = \mu_p$$

is changed to

$$H_0: \mu_1 - \mu_2 = \mu_2 - \mu_3 = \mu_3 - \mu_4 = \ldots = \mu_{p-1} - \mu_p = 0$$

From p data columns, p-1 columns of differences are derived and analysed with the Hotelling's T^2 test as shown above. The degrees of freedom change from p and n-p to p-1 and n-(p-1) (i.e. from 3 and 7 to 2 and 8 in the example above).

The problem of dependence of significance on the control-treatment random pairing is not overcome by Manly's modifications of Roa's analytical design. Manly compared frequency distribution histograms of F-values from Roa's design and his modified design. He found a narrower range of F-values for the modification but pointed out that the range is still unsatisfactory (15% of randomizations gave significant results at α=5% in Manly's recalculation of Roa's data).

Yao's test in Manly (1993)

To overcome the problem of differing F-values depending on random pairing, Manly proposed a new test based on Yao (1965). Here, first the differences between food types are calculated for treatments and controls (note, that in Manly's modification of Roa, first the controls were offset with treatments and then differences were calculated):

$$u_{1j} = t_{1j} - t_{2j},\ u_{2j} = t_{2j} - t_{3j},\ u_{3j} = t_{3j} - t_{4j},\ \ldots\ u_{p-1j} = t_{p-1j} - t_{pj} \quad \text{with} \quad j = 1,2,\ldots n_t$$

for treatments and

$$v_{1j} = c_{1j} - c_{2j},\ v_{2j} = c_{2j} - c_{3j},\ v_{3j} = c_{3j} - c_{4j},\ \ldots\ v_{p-1j} = c_{p-1j} - c_{pj} \quad \text{with} \quad j = 1,2,\ldots n_c$$

for controls.

In this way, from a table for treatments with p columns for food types and n_t rows for replicates, a table with p-1 columns and n_t rows is derived. Likewise, from a table for controls with p columns and n_c rows, a table with p-1 columns and n_c rows is derived.

Mean values are then calculated for each column:

$$\bar{u}_i = \frac{1}{n_t}\sum_{j=1}^{n_t} u_{ij}$$

for differences between treatments and

$$\bar{v}_i = \frac{1}{n_c}\sum_{j=1}^{n_c} v_{ij}$$

for differences between controls.
The number of treatments (n_t) and of controls (n_c) does not have to be the same.

Significant preference is now tested by rejecting the null hypothesis that the vectors $u = (u_1, u_2, u_3, ..., u_{p-1})$ and $v = (v_1, v_2, v_3, ..., v_{p-1})$ are equal. Different covariance structures for treatments and controls indicate that the samples of u_{ij} and v_{ij} may be from populations with different covariance matrices.

R is calculated by

$$R = (\bar{u} - \bar{v})' S_T^{-1} (\bar{u} - \bar{v}),$$

where $(\bar{u} - \bar{v})$ is the vector of differences between $\bar{u}_j$ and $\bar{v}_j$ values

$$(\bar{u} - \bar{v}) = \begin{bmatrix} \bar{u}_1 - \bar{v}_1 \\ \bar{u}_2 - \bar{v}_2 \\ \vdots \\ \bar{u}_{p-2} - \bar{v}_{p-2} \\ \bar{u}_{p-1} - \bar{v}_{p-1} \end{bmatrix}$$

$$S_T = \frac{S_u}{n_t} + \frac{S_v}{n_c}$$

is the estimated covariance matrix for the difference $\bar{u} - \bar{v}$ with S_u as covariance matrix of u_{ij} values and S_v as covariance matrix of v_{ij} values.

For the calculation of F and degrees of freedom, first f has to be calculated from:

$$\frac{1}{f}=\frac{1}{(n_t-1)}\left[\frac{(\bar{u}-\bar{v})'S_T^{-1}S_uS_T^{-1}(\bar{u}-\bar{v})}{Rn_t}\right]^2+\frac{1}{(n_c-1)}\left[\frac{(\bar{u}-\bar{v})'S_T^{-1}S_vS_T^{-1}(\bar{u}-\bar{v})}{Rn_c}\right]^2$$

F may then be calculated as:

$$F=\frac{(f+2-p)R}{f(p-1)}$$

with and p-1 and f+2-p degrees of freedom. F then is compared with tabulated

$$F_{\alpha;p-1;f+2-p}.$$

Manly (1995)

In this paper, Manly introduces a quite different method for the analysis of preference experiments. Not significant differences are uncovered, but a selection index is calculated for each different food type, indicating whether a food type is preferred or rejected, together with confidence intervals for each index. With Manly's method the number of controls (n_c) does not have to be the same as the number of treatments (n_t) and there are no changes in significance due to random pairing.

While in earlier approaches the dependent variable is normally the absolute change in mass (area) of food items expressed as difference between the initial and the final amount, Manly calculates the proportion of change of the initial amount for each food type for treatments (t) and controls (c).

$$t_{ij}=\ln\left(\frac{t_{ij,final}}{t_{ij,initial}}\right) \quad \text{and} \quad c_{ij}=\ln\left(\frac{c_{ij,final}}{c_{ij,initial}}\right) \quad \text{with } i=1,2,\dots p \text{ and } j=1,2,\dots n.$$

Since Manly derived his formulas from differential calculus leading to exponential functions, the natural logarithm must be calculated from the proportions to obtain the exponents.

The mean consumption corrected for autogenic changes may now be estimated for food type i as

$$\hat{\alpha}_i=\bar{c}_i-\bar{t}_i$$

where $\bar{t}_i$ is the mean of all t_{ij} with $j=1,2,\dots n_t$

$$\bar{t}_i = \frac{1}{n_t}\sum_{j=1}^{n_t} t_{ij}$$

and $\bar{c}_i$ is the mean of all c_{ij} with $j = 1,2,\ldots n_c$

$$\bar{c}_i = \frac{1}{n_c}\sum_{j=1}^{n_c} c_{ij}$$

The selection index β for each food type i then can be estimated by

$$\hat{\beta}_i = \frac{\hat{\alpha}_i}{\sum_{h=1}^{p} \alpha_h}$$

When there is no preference, the $\hat{\beta}_i$-values for all food types should equal 1/p. Values of $\hat{\beta}_i$ greater than 1/p indicate preference, values less than 1/p rejection.

Confidence intervals are proposed by Manly that assume a t-distribution of $\hat{\beta}_i$. From several he tested with simulated data, Manly recommended two confidence intervals: 'simple t-distribution limits' and 'corrected t-distribution limits'.

For the calculation of these intervals, estimates for several parameters have to be calculated:

The covariances between $\hat{\alpha}_i$ and $\hat{\alpha}_h$

$$v_{ih} = \operatorname{cov}(\hat{\alpha}_i, \hat{\alpha}_h) = \frac{\operatorname{cov}(c_i, c_h)}{n_t} + \frac{\operatorname{cov}(t_i, t_h)}{n_c} \quad \text{with} \quad i,h = 1,2,\ldots p$$

for the special case i=h:

$$v_{ii} = \frac{\operatorname{var}(c_i)}{n_t} + \frac{\operatorname{var}(t_i)}{n_c}$$

Here, for further calculations, the covariance matrix of all v_{ih} should be calculated.

From this the following two estimates are derived:

$$S_{vi} = \sum_{h=1}^{p} v_{ih} \quad \text{with} \quad i = 1,2,\dots p$$

as sums of rows (or columns) from the covariance matrix of v_{ih} and

$$S_v = \sum_{i=1}^{p} S_{vi}$$

as sum of all values from the covariance matrix of v_{ih}. T is calculated as sum of α values for all food types:

$$T = \sum_{j=1}^{p} \alpha_j$$

Later T^2 will be needed and should be calculated.
An approximation for the covariances of $\hat{\beta}_i$ and $\hat{\beta}_h$ is

$$\operatorname{cov}(\hat{\beta}_i, \hat{\beta}_h) \approx \frac{v_{ij} + \hat{\beta}_i \hat{\beta}_h S_v - \hat{\beta}_h S_{vi} - \hat{\beta}_i S_{vh}}{T^2}.$$

For the special cases i=h:

$$\operatorname{var}(\hat{\beta}_i) \approx \frac{v_{ii} + \hat{\beta}_i^2 S_v - 2\hat{\beta}_i S_{vi}}{T^2}$$

For the calculation of simple t-distribution limits, all $\operatorname{var}(\hat{\beta}_i)$ should be calculated.

Simple t-distribution limits are calculated as:

$$\hat{\beta}_i \pm t_{v,0.025} \hat{S}E(\hat{\beta}_i),$$

where the v degrees of freedom are calculated by an approximation on Yao's (1965) method as: $v = 2(n-1)$, and $\hat{S}E(\hat{\beta}_i)$ is estimated as squareroot of $\operatorname{var}(\hat{\beta}_i)$.

Corrected t-distribution limits are calculated as:

$$\frac{\hat{\beta}_i T^2 - t^2_{v,0.025} S_{vi}}{T^2 - t^2_{v,0.025} S_v} \pm \frac{\sqrt{(\hat{\beta}_i T^2 - t^2_{v,0.025} S_{vi})^2 - (t^2_{v,0.025} S_v - T^2)(t^2_{v,0.025} v_{ii} - \hat{\beta}_i^2 T^2)}}{T^2 - t^2_{v,0.025} S_v}$$

When 1/p is not included in the limits for a food type this food type is significantly preferred ($\beta_i > 1/p$) or rejected ($\beta_i < 1/p$) at $\alpha = 5\%$.

Values of limits may exceed 1 or be lower than 0. For these cases, Manly recommended that limits should be given as 1 or 0, respectively.

No choice experiments

In no choice experiments the separately offered food types are independent. Hence, multivariate analysis is not necessary and, if the assumption of homoscedasticity is met, analysis of variance may be used.

Peterson & Renaud (1989) proposed the interaction significance in a two factor ANOVA as test of such experiments in which food type and consumer presence/absence are crossed. However, most workers that have used ANOVA subtracted controls from treatments in some or other way prior to analysis (e.g. Denton & Chapman 1991), very recently in the way proposed by Roa (1992) (Wolken 1994; Schaffelke *et al.* 1995). Hereafter, simple one-way ANOVA is used.

APPLICATION TO THE DATA OF THIS STUDY

Roa (1992) used data of a feeding experiment in which the sea urchin *Tetrapygus niger* fed on six algal species. To achieve the adequate structure of data to demonstrate his proposed method he had to omit the data of 3 algal foods from the data set and to pool data from different experiments. Manly in his following papers (1993, 1995) used Roa's mutilated data for the demonstration of his analyses. To produce his selection index, Manly (1995) did not use the true initial amounts of foods in his calculations of the proportion consumed, but used the mean values from a range given by Roa. Roa only gave a range of 8-11 g for initial amounts of foods in his experiment and Manly simply used the mean, 9.5 g, as initial amount for all treatments.

In the present study, probably for the first time, the three methods are compared with complete data sets from 4 experiments run simultaneously testing preferences among germling size classes with 4 combinations of littorinid grazers and *Fucus* spp. This design with p=3 foods and n=10 replicates readily demonstrated significant effects, and may be compared with a second series of experiments, where littorinids were offered a choice of p=3 different *Fucus* species but with only n=4 replicates.

With the data of these experiments, described in detail in 4.2 of the the main part of this thesis, the pure method of Roa (1992) is compared with (1) Manly's modification that keeps the correlation by correct usage of controls, and (2) with all modifications proposed by Manly (1993), including the calculation of differences between food types. For both of Manly's modifications, all n! F-values are calculated, for the pure method of Roa, 3 millions random pairs. Ranges, frequency distributions and means of F-values will be shown.

The recommended alternative method derived from Yao's test (Manly 1993) will be used to test for significant differences between consumption of food types without the disadvantages of random pairing.

Finally, the results of calculations of Manly's (1995) selection indices will be given (with 'simple' and 'corrected' t-distribution limits).

The outcomes of these applications of the methods described above will be shown in the results of this chapter.

RESULTS

Feeding preference among *Fucus* germling size classes

Grazing by snail species among *Fucus* size classes

In Figure A1 the initial fresh weights of offered algae are shown. Mean mass of the biggest size class exceeded the mass of the smaller size classes, but ratios of masses were consistent for each *Fucus* species between trials with *Littorina littorea* and *L. mariae* and controls. In a perfect design the masses of all food types should be equal. But when the choice is between items of different masses (sizes), this is difficult to accomplish. However, areas bearing the different size classes were equal, differences in mass in controls were the same as in treatments and algae on a tile fragment were never consumed completely. Therefore I believe that this experiment produced appropriate data.

The average changes in fresh weight are shown in Figure A2. Change in controls is less pronounced than in treatments, in most cases control algae gained mass during the course of the experiment. For unknown reasons control algae of size class II of both *Fucus* spp. slightly lost weight. Figure A3 shows the average change of the four choice experiments with subtracted controls. The standard deviations correspond to the random pairing with the minimal F-value found for each experiment by modified calculations after Roa (1992) (MR, see below).

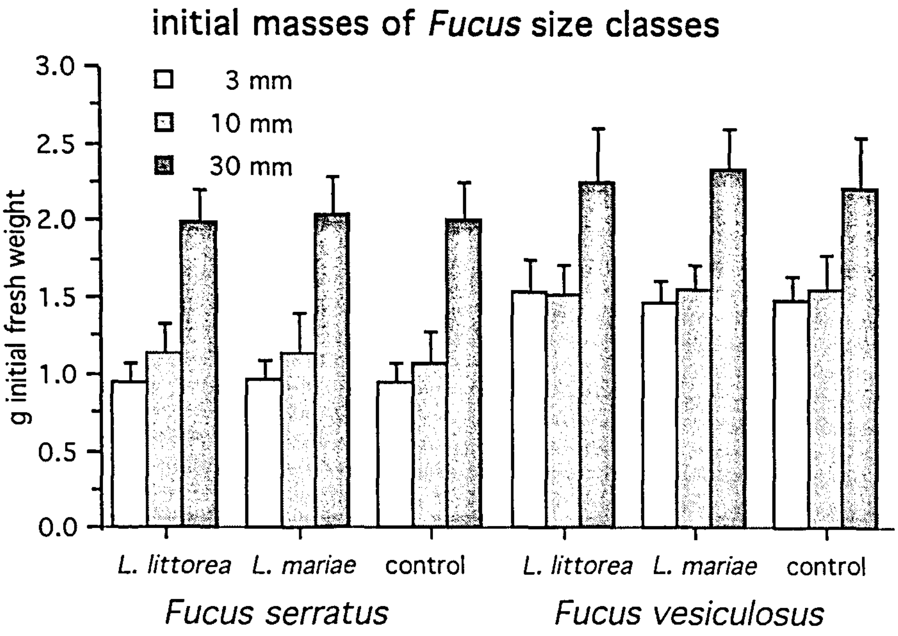


Figure A1: Initial masses of *Fucus* germling size classes offered to *Littorina* spp. in multiple choice feeding experiments. Means of 10 replicates and SD.

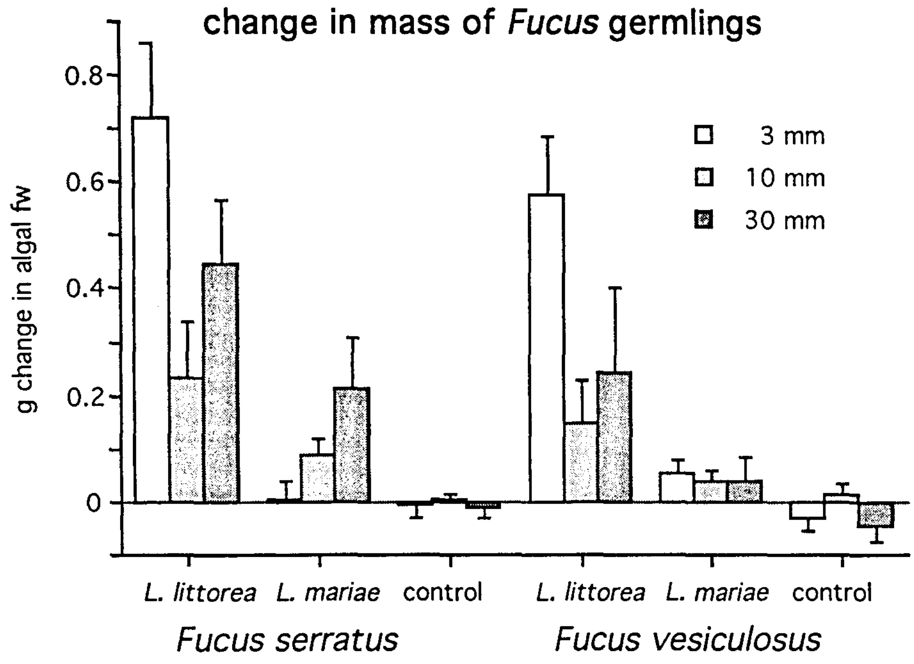


Figure A2: Change in masses of *Fucus* germling size classes offered to *Littorina* spp. in multiple choice feeding experiments. Means of 10 replicates and SD. Negative values indicate growth, positive values loss of weight.

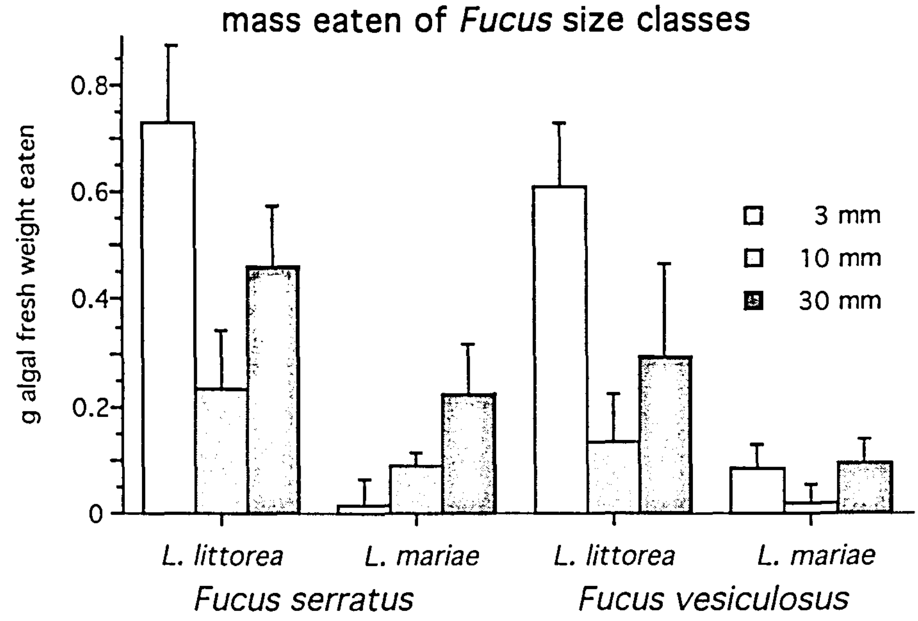


Figure A3: Masses of three *Fucus* germling size classes consumed by *Littorina* spp. in multiple choice feeding experiments. Treatments were offset with controls in pairings yielding minimal F-values. Means of 10 replicates and SD. For further explanations see text.

Fucus serratus grazed by *Littorina littorea*

Although initially the least mass of the smallest size class of *F. serratus* was offered (Figure A1), it was the most grazed by *L. littorea* (Figure A3). Size class II was the least eaten, while size class III was consumed at an intermediate level.

Fucus serratus grazed by *Littorina mariae*

The amount of *F. serratus* eaten by 50 *L. mariae* was smaller than the amount eaten by 5 *L. littorea* (Figure A3). Size class I was barely consumed, size class II intermediately and size class III was consumed most.

Fucus vesiculosus grazed by *Littorina littorea*

The grazing on 3 size classes of *F. vesiculosus* by *L. littorea* followed the pattern for *F. serratus* (Figure A3). The total amount eaten was less with *F. vesiculosus*. Snails consumed most from size class I. The least consumed was size class II.

Fucus vesiculosus grazed by *Littorina mariae*

The total amount eaten was similar to that of *F. serratus*, but in this trial size class I and III were consumed to a similar extent, while size class II was barely grazed (Figure A3).

These obvious findings were tested with statistical analyses recommended by Roa (1992) and Manly (1993, 1995):

1. With a custom computer program, Hotelling's T^2 and subsequently F-values were calculated for 3 million random pairings *sensu* Roa (1992) of control and treatment food items. Minimum (F_{min}) and maximum F (F_{max}) were obtained with this program along with the mean F (F_{mean}±SD) and a frequency distribution of F. Percentages were calculated for F-values that fell below the tabulated $F_{0.05;3,7} = 4.35$ (Sachs 1984). Results obtained by this random pairing will be referred to as 'pure Roa' (PR).

2. With a similar program, F_{min}, F_{max}, F_{mean} (±SD), minimal and maximal random pairings and the frequency distribution of F were obtained for all possible 10! = 3,628,800 random pairings when the modified random pairing, recommended by Manly (1993), was used to preserve the correlation between food types in treatments and controls. For pairings yielding F_{max} and F_{min}, respectively, the confidence intervals proposed by Roa (1992) were calculated. Percentages were calculated for F-values that fell below the tabulated $F_{0.05;3,7} = 4.35$ (Sachs 1984). Results obtained by this random pairing will be referred to as 'modified Roa' (MR).

3. With another modification of the computer program, for all 10! random pairings as in 2., the Hotelling's T^2 statistic was calculated for the differences between changes in food types as proposed by Manly (1993) to avoid the error-prone overall mean k (see above). Again F_{min}, F_{max}, F_{mean} (±SD), minimal and maximal random pairings and the frequency distribution of F were obtained along with percentages of F-values that fell below tabulated $F_{0.05;2,8} = 4.46$ (Sachs 1984). Results obtained by this random pairing will be referred to as 'Manly's differences' (MD).

Correctness of calculations of Hotelling's T^2 test was checked with recalculation of assorted random pairings with Systat 5.1 (SYSTAT Inc.). F-values were normally the same to the fourth decimal, but deviated for very high F-values, presumably due to differences in rounding off.

Data used in Hotelling's T^2 tests were checked for multivariate normality with Hawkins test (Johnson & Field 1993). All data fulfilled the recommendations of Johnson & Field for balanced designs (i.e. range of medians of all groups < 0.85)

4. The test for significant differences between consumption of food types proposed by Manly (1993) and based on Yao (1965) was calculated. From this test, there is only one resulting F-value, since the test is not dependent on random pairing.

5. Selection indices (β_i) and corresponding simple and corrected t-distribution limits were calculated according to Manly (1995).

The F_{min}, F_{max}, F_{mean} (±SD) and the percentages of insignificant F-values (at α=0.05) are shown in Table A1. For all 4 *Fucus-Littorina* combinations, the analyses based on different random pairings of treatments and controls unequivocally indicated significant differences (at $\alpha = 0.05$) between the consumption of different size classes of *Fucus* spp. Only 0.05% of F-values for the feeding experiment with *F. vesiculosus* and *L. mariae* fell below the tabulated F and indicated insignificance when PR was used.

The application of Yao's test as recommended by Manly (1993) revealed highly significant differences in consumption of the three size classes ($p < 0.001$) for all *Fucus-Littorina* combinations (Table A2).

Table A1: Range of F-values for different methods of treatment-control random pairing. Data from preference experiments (*Littorina* spp. grazing on *Fucus* spp. size class). S = *F. serratus*, V = *F. vesiculosus*, L = *L. littorea*, M = *L. mariae*. PR = pure Roa, MR = modified Roa, MD = Manly's differences. $F_{0.05;p,n-p} = 4.35$ for PR and MR, =4.46 for MD. Level of significance of F_{min}: ***: $p \leq 0.001$, **: $p \leq 0.01$, *: $p \leq 0.05$. For further explanations see text.

alga-grazer	rand. pair.	F_{min}	F_{max}	F_{mean}	SD	median	95% above	$< F_{0.05;p,n-p}$ [%]	p
S-L	PR	11.81	1248.83	31.33	17.58	26.5	15.5	0.000	***
	MR	19.20	33.08	25.05	2.50	25.5	21.5	0.000	***
	MD	30.60	47.47	39.03	3.54	39.5	32.5	0.000	***
S-M	PR	8.72	6290.07	33.14	24.84	26.5	14.5	0.000	**
	MR	18.16	680.23	47.72	27.67	39.5	23.5	0.000	**
	MD	14.27	100.40	26.94	10.46	23.5	17.5	0.000	**
V-L	PR	13.72	4801.78	47.13	31.77	38.5	22.5	0.000	**
	MR	27.46	74.99	42.45	8.13	41.5	31.5	0.000	***
	MD	44.83	128.39	69.74	13.66	67.5	51.5	0.000	***
V-M	PR	3.88	1233.46	14.14	10.73	11.5	6.5	0.051	n.s.
	MR	7.05	262.83	15.05	6.72	13.5	8.5	0.000	*
	MD	9.71	128.11	18.16	6.20	16.5	11.5	0.000	**

Table A2: Results of Yao's test as proposed by Manly (1993) (which is independent of random pairing) for feeding preference experiments with *Littorina littorea* or *L. mariae* grazing on 3 size classes of *Fucus serratus* or *F. vesiculosus.*

alga	*grazer*	*F*	*df*	*p*
F. serratus	*L. littorina*	*38.65*	*2, 8.39*	*<0.001*
F. serratus	*L. mariae*	*24.57*	*2, 12.06*	*<0.001*
F. vesiculosus	*L. littorea*	*67.72*	*2, 9.59*	*<0.001*
F. vesiculosus	*L. mariae*	*16.41*	*2, 11.12*	*<0.001*

Fucus serratus grazed by *Littorina littorea*

In Figure A4a the selection indices after Manly (1995) are shown together with corresponding simple and corrected t-distribution limits for *L. littorea* feeding on three size classes of *F. serratus*. Confidence limits of selection indices for all three size classes do not include $1/p = 0.33$.

The smallest size class was clearly preferred with a β of >0.8, size classes II and III were avoided. Certain problems that arise from differences in initial amounts of food types will be discussed below. The extent of avoidance of size class III here should be overestimated due to unequal starting conditions. This can be seen when Roa's confidence intervals are considered (Figure A4b).

With Roa's confidence intervals, only size class I and III contributed to the rejection of the null hypothesis of equal consumption, while the overall mean k was included in the limits of size class II.

In summary, it seems clear that 3 mm small germlings of *F. serratus* are preferred and 30 mm germlings avoided by *L. littorea.*

Fucus serratus grazed by *Littorina mariae*

For the experiment on feeding preferences of *L. mariae* among germling size classes of *F. serratus*, selection indices indicated avoidance of 3 mm germlings and preference for the biggest algal size class (Figure A5a). With Roa's confidence limits (Figure A5b), preference for 30 mm germlings was significant only for some random pairings of treatments and controls. With the pairing yielding F_{min}, the overall mean k is included in the confidence limits.

In summary, *L. mariae* preferred the biggest size class of *F. serratus* and significantly avoided the smallest size class.

Fucus vesiculosus grazed by *Littorina littorea*

When a choice of *F. vesiculosus* germling size classes was offered to *L. littorea*, the smallest size class was preferred significantly (Figure A6) while the bigger size classes were avoided. However, the avoidance of size class III was only significant with Manly's selection index intervals, and again it must be assumed that β of size class III would have been higher (its limits including 1/p?) with equal inital amounts of foods.

In summary, *L. littorea* preferred the smallest size class of *F. vesiculosus* germlings over bigger size classes.

Fucus vesiculosus grazed by *Littorina mariae*

For *L. mariae* feeding on *F. vesiculosus* germlings, preferences were inconspicuous (Figure A7). There seems to be a preference for 3 mm germlings from Manly's

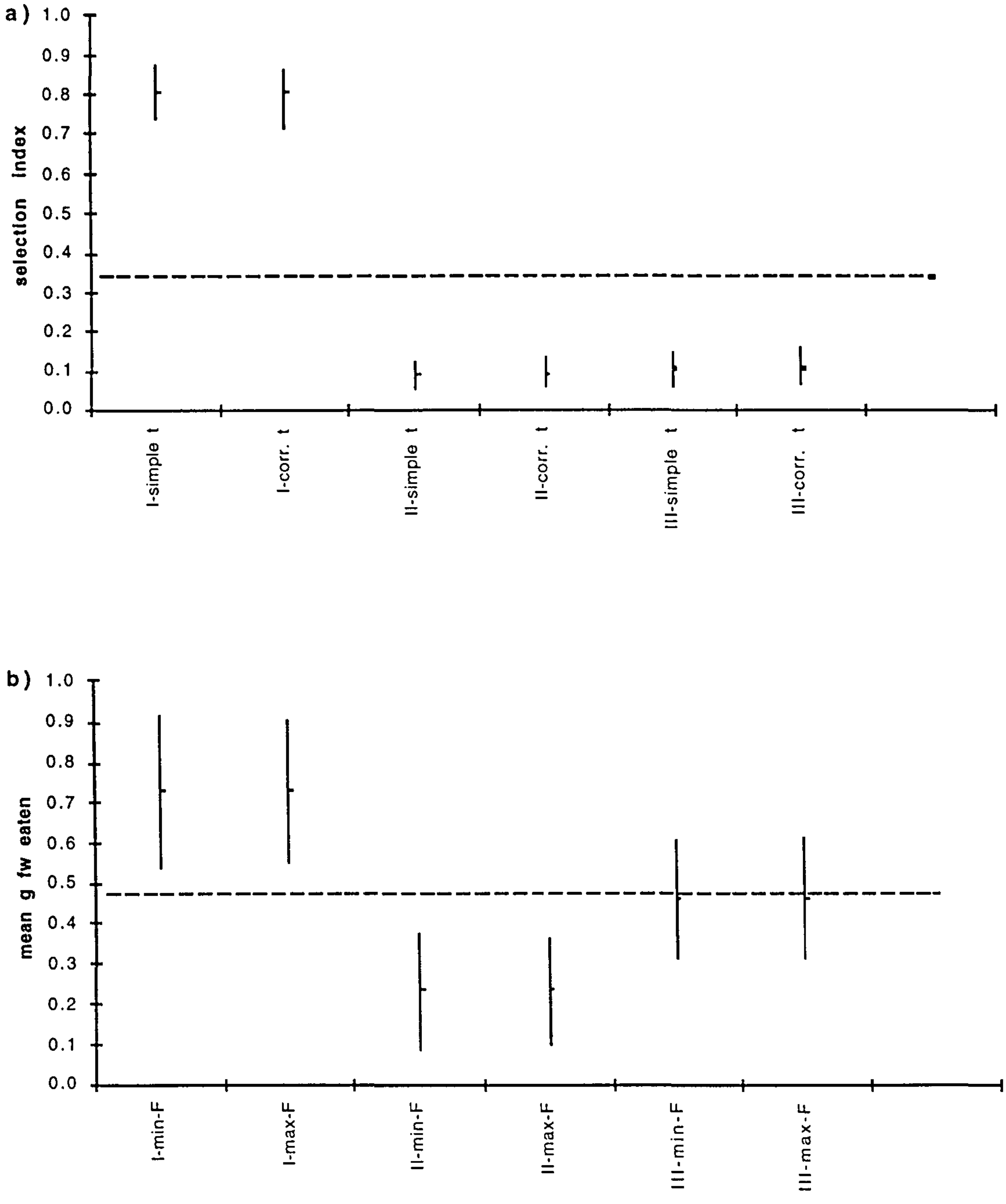


Figure A4: Estimates of preferences/rejections for single *Fucus serratus* germling size classes (I-III) offered to *Littorina littorea* in a multiple choice feeding experiment. a) Manly's selection index (simple and corrected t-distribution confidence limits). Confidence limits that do no intersect the dashed line indicate significant preference (above the line) or rejection (below) at α=0.05. b) Roa's simultaneous confidence intervals. Confidence limits that do not intersect the dashed line contributed significantly to rejection of the null hypothesis of equal consumption.

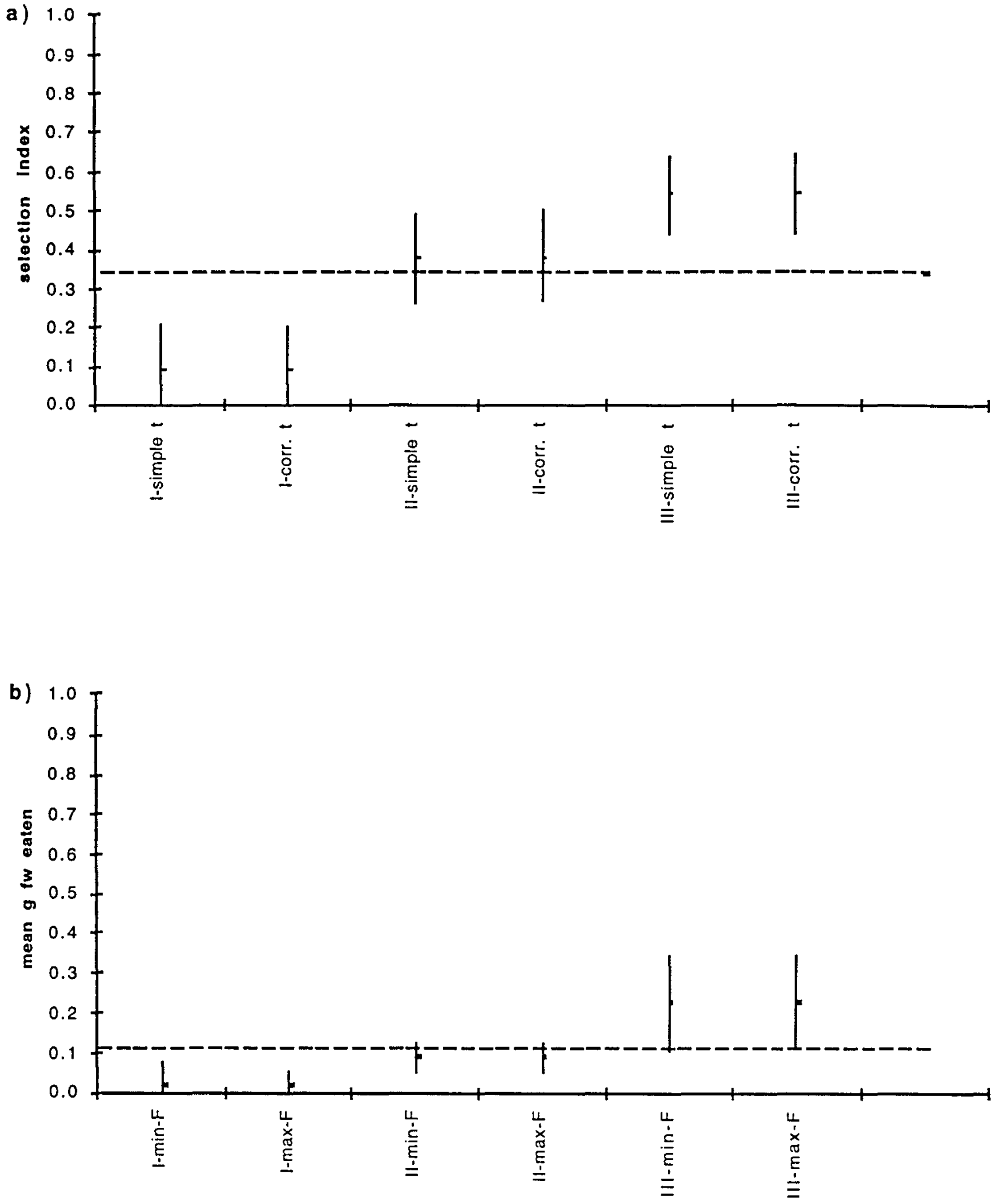
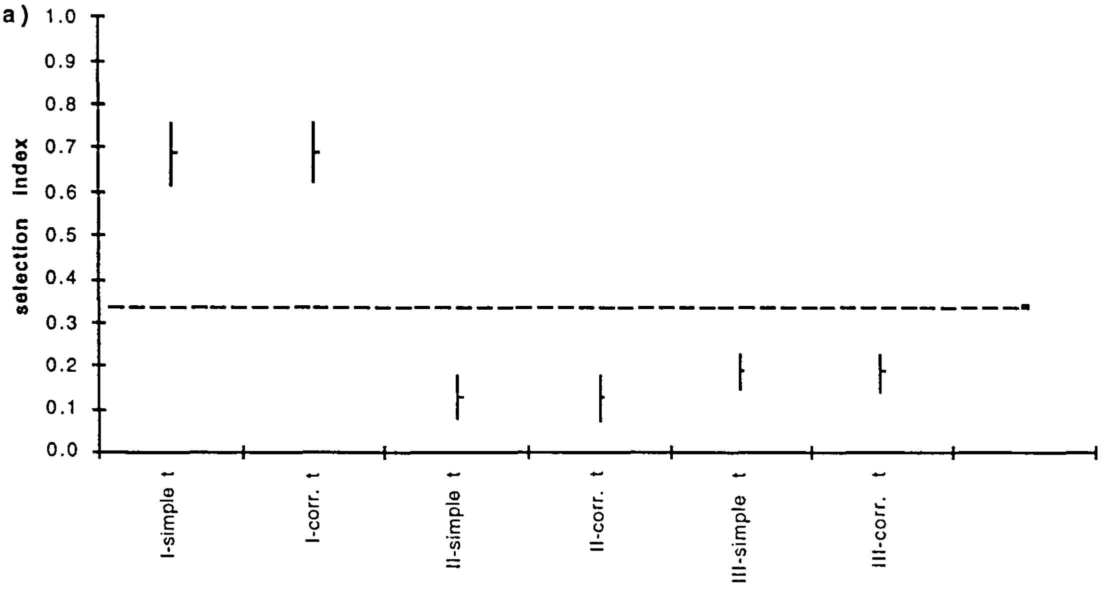


Figure A5: Estimates of preferences/rejections for single *Fucus serratus* germling size classes (I-III) offered to *Littorina mariae* in a multiple choice feeding experiment. For further explanations see Figure A4.



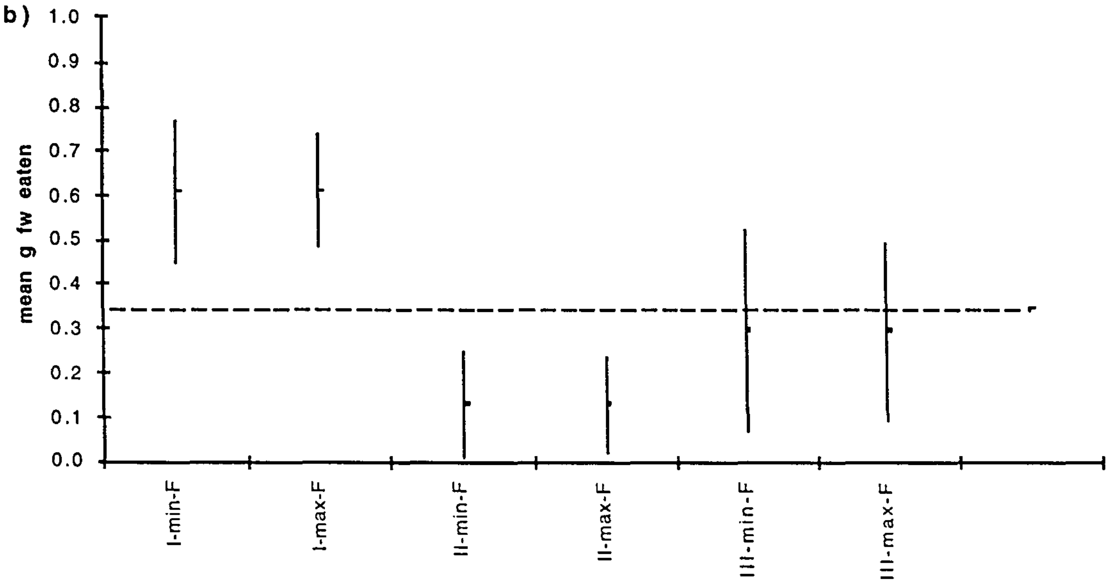


Figure A6: Estimates of preferences/rejections for single *Fucus vesiculosus* germling size classes (I-III) offered to *Littorina littorea* in a multiple choice feeding experiment. For further explanations see Figure A4.

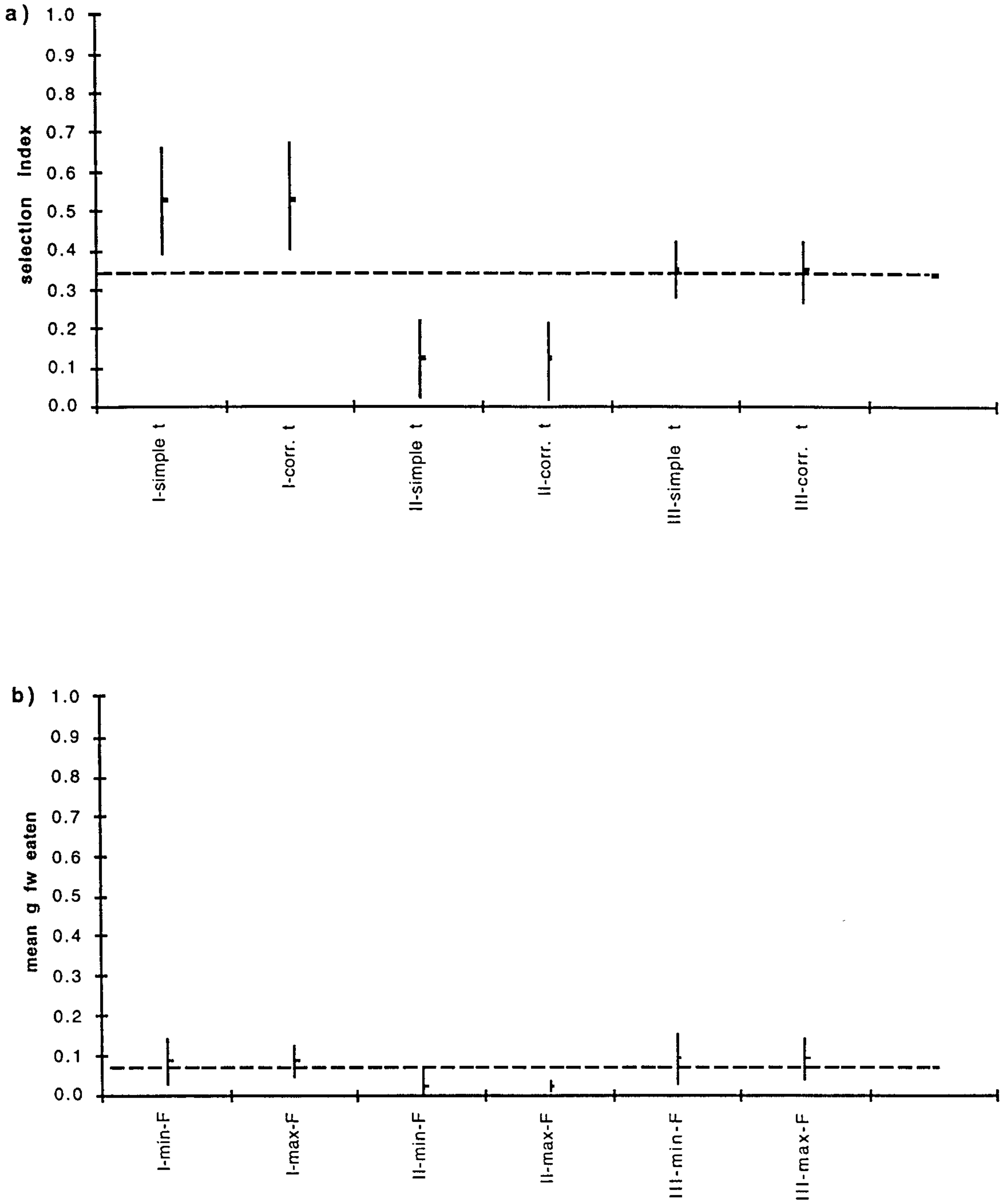


Figure A7: Estimates of preferences/rejections for single *Fucus vesiculosus* germling size classes (I-III) offered to *Littorina mariae* in a multiple choice feeding experiment. For further explanations see Figure A4.

selection index. But again the value of β_I probably would have been smaller, and that of β_{III} higher, if initial masses of size classes had been equal. With Roa's confidence intervals, only avoidance of size class II contributed to rejection of the null hypothesis of balanced consumption (Figure A7b).

In summary, 10 mm germlings of *F. vesiculosus* were avoided by *L. mariae* compared to 3 and 30 mm germlings that also were consumed only to a small extent.

Comparison of different statistical analyses

The F_{min}, F_{max}, F_{mean} (±SD), median and limiting class of the 5% percentile (95% of all F-values were $\geq$ this value) are compared in Table A1. When, incorrectly, as Manly (1993) pointed out, correlation between food types is destroyed by PR random pairing of treatments and controls, the range of F increases dramatically (e.g. 8.7 - >6200 for *L. mariae* feeding on *F. serratus*). Since the n! MR-random pairings are a genuine subset of all $(n!)^{2p-1}$ possible PR-pairings, it should be clear that F-values from MR-paired data are a subset of those derived from PR-paired data. In fact, in all four experiments the range of F_{MR}-values is included in the range of F_{PR} (Table A1).

There was no other consistent trend when F_{mean} and median were considered. Histograms of F frequency distribution for PR, MR and MD that clarify the greater range of F_{PR} are shown in Figure A8a-d.

For feeding preference experiments, it is important to determine which proportion of F-values leads to significant results. For 3 of the present experiments, all random pairings with PR, MR and MD led to significant rejection of H_0. With PR-random pairing, 0.05% of F-values were insignificant, only for *L. mariae* feeding on germlings of *F. vesiculosus*. The median of the frequency class in which the 5% percentile lay is given in Table A1. In all four experiments this limit was higher for MR and MD compared to PR. In 75% of the cases, MD yielded the highest 5% limit. It must be noted that for MD, the tabulated F that has to be exceeded for significance was higher. However, for data from the present experiments with 3 food types and 10 replicates this difference was small (4.35 for PR and MR, 4.46 for MD at $\alpha=0.05$; Sachs 1984).

The last column of Table A1 shows the level of significance the minimal F-value yields. When there was a difference in the level of significance between different methods of random pairing, MD yielded the highest and PR the lowest level.

With Yao's method, differences in all four experiments were significant at $p < 0.001$ (Table A2).

Hence MD detected significant differences more easily than PR, and Yao's test yielded still more significant results. The same was shown by Manly (1993) when he compared the power of PR, MD and Yao's test with simulated data.

While with Roa's method and with Manly's modification the calculations are independent from the initial amounts of foods (preferences may not be), selection indices

are a function of relative amounts of different
It may be assumed that approximately the sam
trial with equal initial amounts of all food type
amounts. A food type whose initial mass ex

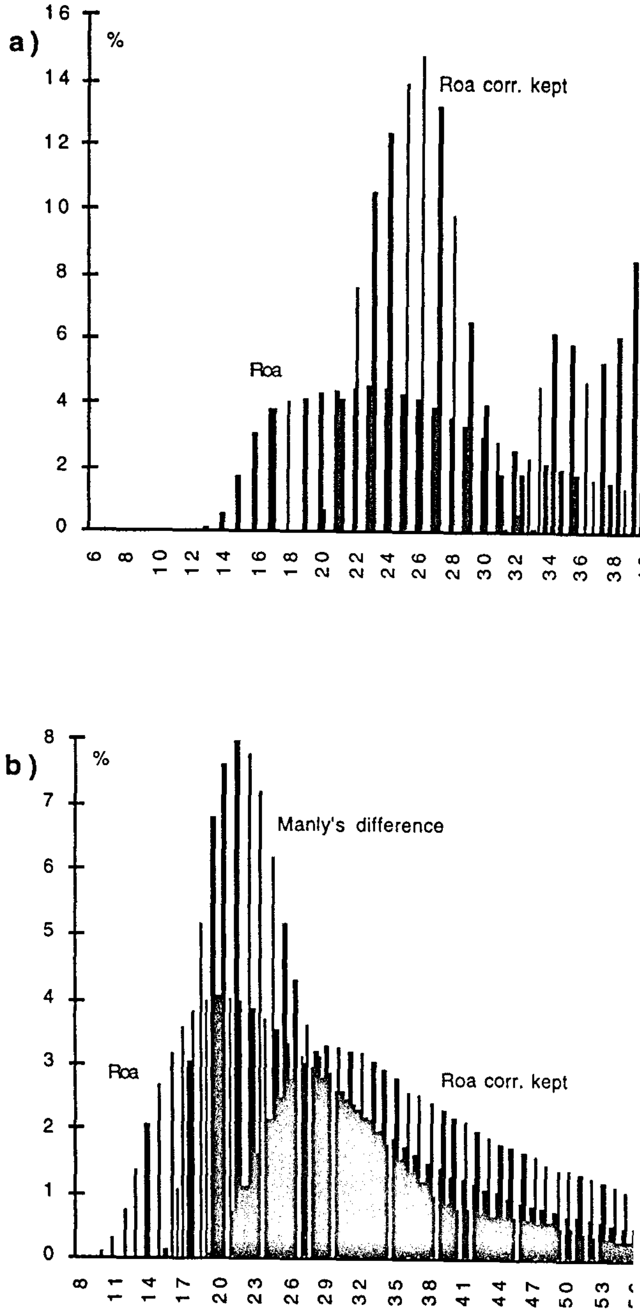


Figure A8a+b: Explanation for Figure 8a-d see nex

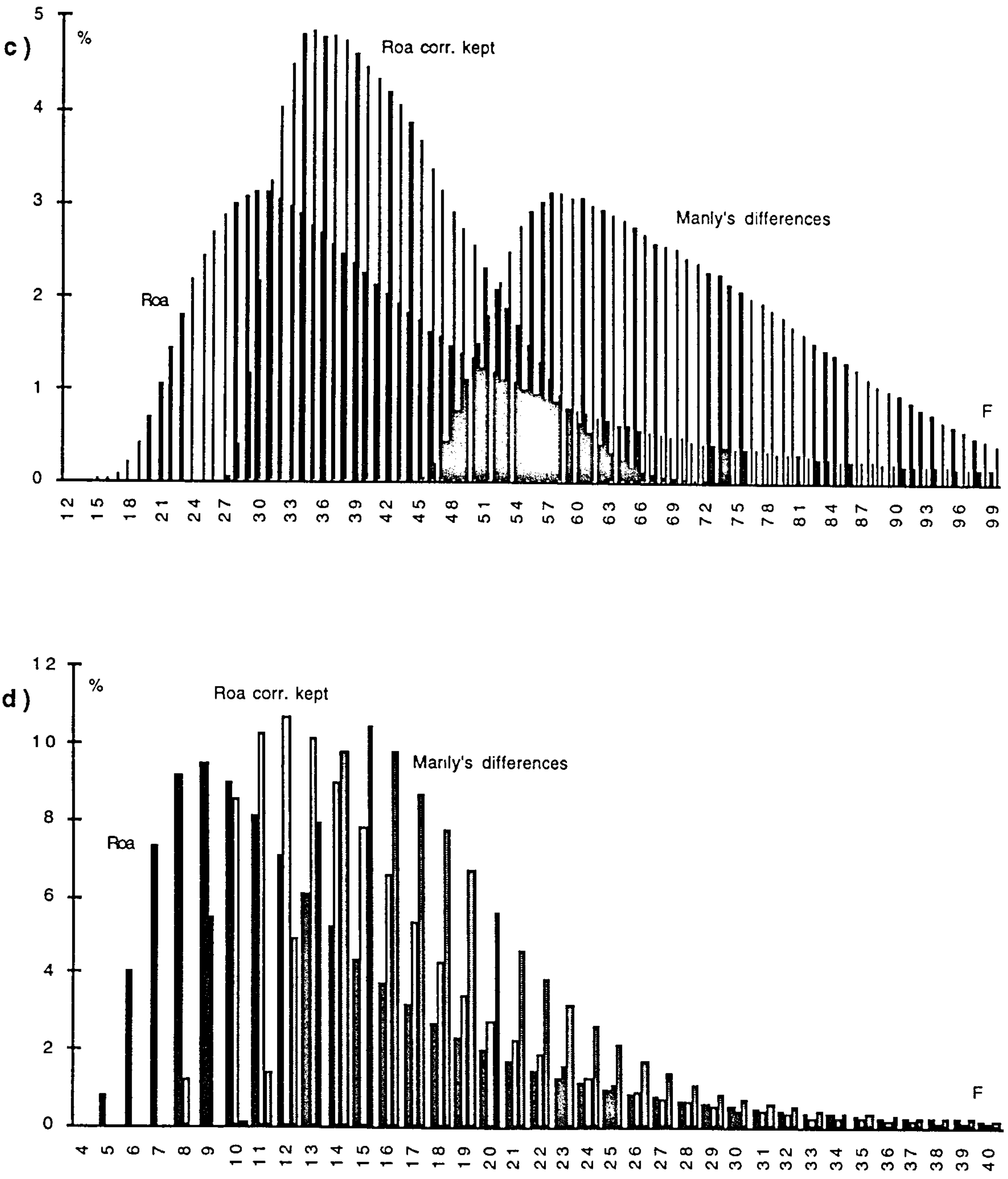


Figure A8: Relative frequency distributions of F-values from different methods of pairing to offset treatments with controls from *Fucus* germling size classes-*Littorina* multiple choice feeding experiments. 'Roa': F-values of three million random pairings (after Roa 1992, PR). 'Roa corr. kept': F-values of all 10! possible pairings modified after Manly (1993, MR). 'Manly's differences': F-values of all 10! possible pairings as proposed by Manly (1993, MD). For further explanations see text. a) *L. littorea* feeding on *F. serratus*. b) *L. mariae* feeding on *F. serratus*. c) *L. littorea* feeding on *F. vesiculosus*. d) *L. mariae* feeding on *F. vesiculosus*.

latter case (b) should then have a higher "true" selection index (i.e. in an experiment with equal initial amounts). Accordingly, the "true" selection index of a food type with less initial mass than mass of other food types should be lower than indicated by the flawed design. A prerequisite for this assumption is that in both cases during the experimental time there was enough of every food type to trigger off intrinsic preferences.

It is therefore very probable that, in the present study, indices show a distorted picture of true preferences due to the greater initial amount of the biggest size class, especially for experiments with *F. serratus* (compare Figure A1). When Manly's preference index is to be calculated, experimenters should make sure that variation in initial food masses is kept low. This would have been difficult here, since selection for different sizes (= different masses) of attached germlings was the concern of this experiment.

Feeding preference among *Fucus* species

Multiple choice experiment and biotic interactions

Analyses of fresh weight data

Fresh weights of fucoids offered initially to *L. littorea* or *L. mariae*, respectively, or that functioned as procedural controls are shown on the left of Figure A9. On average, the mass of *F. serratus* was slightly less than that of the other *Fucus* spp. It seems clear, that these differences cannot explain the differences in change of mass during the course of the experiment (Figure A9, right). The amounts of mass (fresh weight) change, corrected for the controls, are given in Figure A10. For both littorinids, *F. spiralis* was consumed most, while only small amounts of *F. serratus* were eaten. Fresh weight of *F. vesiculosus* was diminished by the snails to an intermediate level, that was nearly four times higher for *L. littorea* compared to *L. mariae*.

With modifications of the same computer program described above, the differences in consumption of *Fucus* spp. were checked for significance after several methods of random pairing (PR, MR, MD, see Table A3). Significance very much depended on random pairings of treatments and controls. For PR correction, F-values had a range over 9 decimals. The random pairing method preserving the correlation between food types and avoiding the error-prone overall mean k (MD) yielded the most significant results. With this method, differences between preferences for *Fucus* spp. by *L. littorea* were significant for all possible pairings ($\alpha = 0.05$). However, for *L. mariae* only 75% of all possible pairings were significant with MD.

Data used in Hotelling's T^2 tests were checked for multivariate normality with Hawkins test (Johnson & Field 1993). All data fulfilled the recommendations of Johnson & Field for balanced designs (i.e. range of medians of all groups < 0.85).

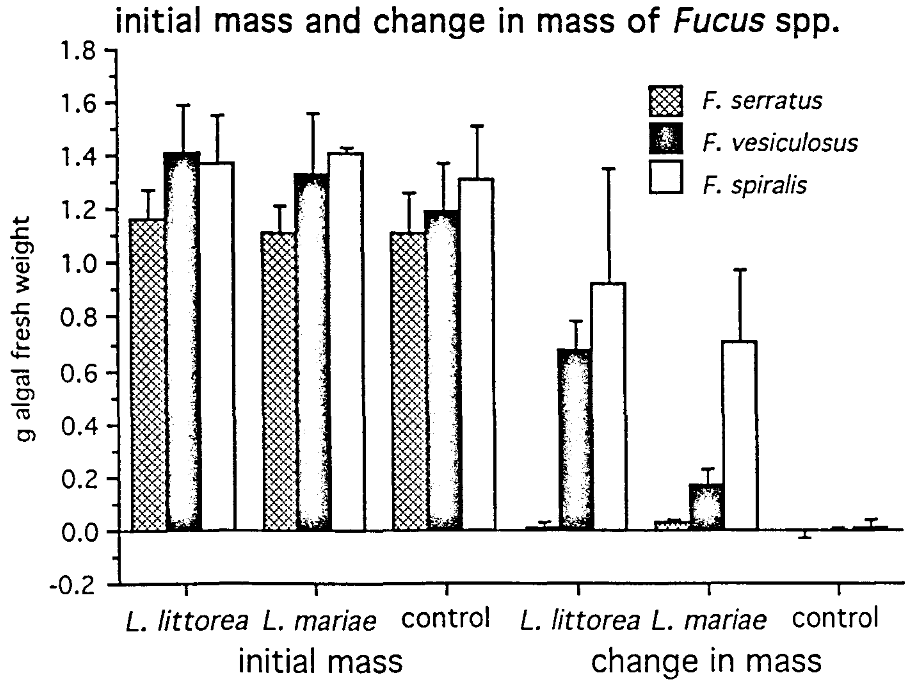


Figure A9: Initial mass (left) and change in mass (right) of *Fucus* spp. grazed by *Littorina* spp. in a multiple choice feeding preference experiment and of controls. Mean values from 4 replicates and SD.

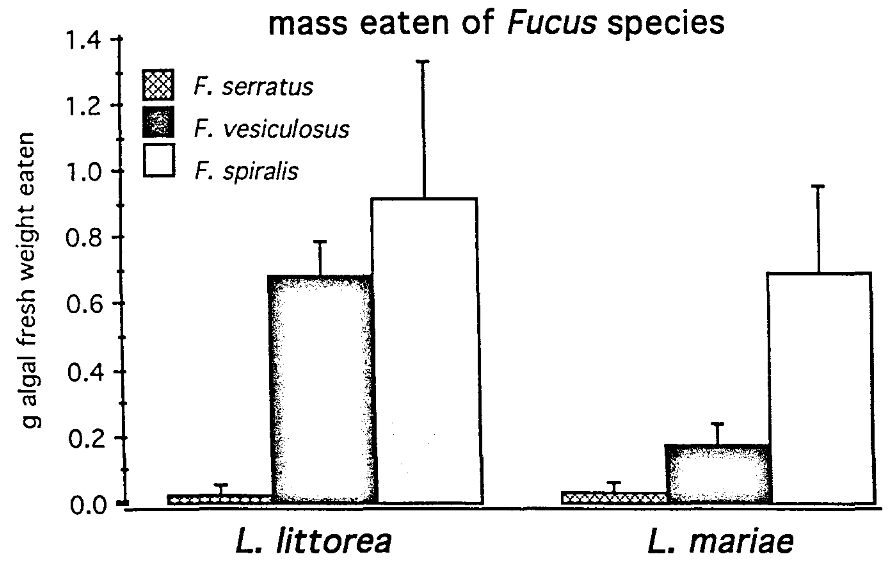


Figure A10: *Fucus* spp. fresh weight consumed by *Littorina* spp. in a multiple choice feeding preference experiment. Mean values of 4 replicates and SD corresponding to random pairing of treatments and controls yielding minimal F-values.

Yao's test, which is independent of random pairing, revealed significant differences for both experiments, with *L. littorea* they were highly significant ($p < 0.001$, Table A4).

Manly's (1995) preference indices revealed significant rejection of *F. serratus* by both periwinkle species (Figures A11a and A12a).

F. spiralis is significantly preferred by both littorinids, but for *L. littorea* only when simple t-distribution limits are used. The intermediate consumption of *F. vesiculosus* was not significantly different from $1/p = 0.33$. Asymmetry of corrected t-distribution limits probably reflects small number of replicates (B. Manly, pers. comm., compare Figures A4-A7 for higher numbers of replicates). Roa's confidence limits in most cases failed to show significant contribution to rejection of the null hypothesis that all *Fucus* species are consumed equally (Figures A11b and A12b). Only when the variance of corrected data that yielded $F_{max} = 22692$ was used for the calculation of limits, avoidance of *F. serratus* by *L. littorea* contributed significantly to the rejection of H_0 (Figure A11b).

Analyses with g algal dry weight/(g organic dry weight snail * d) data

A factor was calculated for each tile fragment to convert fresh weight (fw) data to dry weight (dw) data with algae that remained ungrazed:

factor = (dw of remaining algae)/(fw of remaining algae),

the fresh weight being the difference between the tile fragment with and without fucoids at the termination of the experiment.

The mean factor differed for *F. spiralis* compared to *F. serratus* and *F. vesiculosus* (here the inverse is given):

	F. serratus	*F. vesiculosus*	*F. spiralis*
fw:dw (±SD)	5.87 ± 0.18	5.94 ± 0.24	8.50 ± 1.46

For comparison with literature data,

dw/dw snail = mg algal dry weight eaten (g organic dry weight snail)$^{-1}$ d^{-1}

was calculated.

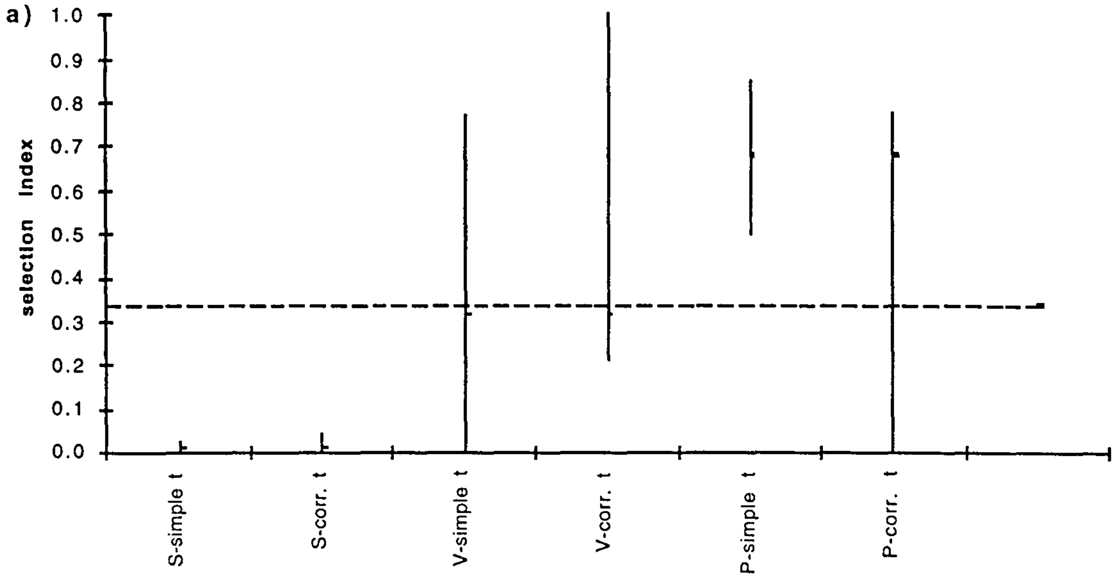
When 'fresh weight eaten' and 'dry weight per snail mass' are compared (Figures A10 and A13), the lower dry weight per unit fresh weight of *F. spiralis* led to a shift in the ratios between *Fucus* species. When dw per dw snail is considered, *F. vesiculosus* is the most preferred alga for *L. littorea* (instead of *F. spiralis* with fresh weights).

Table A3: Range of F-values for different methods of treatment-control random pairing. Data from preference experiments (*Littorina* spp. grazing on *Fucus* species). PR = pure Roa, MR = modified Roa, MD = Manly's differences. $F_{0.05;3,1} = 215.7$ for PR and MR, $F_{0.05;2,2} = 19.0$ for MD. PR: results from 3 million random pairings, MR and MD: results from all possible pairings (24). For further explanations see text.

grazer	random pairing	F_{min}	F_{max}	F_{mean}	SD	median	$<F_{\alpha;p,n-p}$ [%]	$p(F_{min})$
g freshweight data								
L.litt.	PR	102.6	$7.9\ 10^{11}$	$5.9\ 10^{7}$	$6.4\ 10^{9}$	ca. 1500	14.20	n.s.
	MR	144.7	22691.7	250.2	5306.4	416.3	16.67	n.s.
	MD	426.3	3631.9	1217.2	222.8	1127.1	0.00	<0.005
L.mar.	PR	20.1	$1.9\ 10^{10}$	$1.8\ 10^{6}$	$1.5\ 10^{8}$	ca. 350	49.37	n.s.
	MR	41.9	6408.8	715.6	1397.0	179.1	54.17	n.s.
	MD	14.8	31.5	22.8	5.9	22.5	25.00	n.s.
g algal dw/(g organic dw snail *d) data								
L.litt.	MR	75.8	22353.5	2736.4	5753.2	379.4	37.50	n.s.
	MD	182.1	516.6	295.1	105.3	260.3	0.00	<0.01
L.mar.	MR	23.7	155354.6	7061.8	31582.6	141.9	58.33	n.s.
	MD	15.0	38.9	24.6	7.6	24.2	29.17	n.s.

Table A4: Results of Yao's test as proposed by Manly (1993) (which is independent of random pairing) for feeding preference experiments with *Littorina littorea* or *L. mariae* grazing on 3 *Fucus* spp.

grazer	**F**	**df**	**p**
L. littorea	936.21	2, 3.79	<0.001
L. mariae	21.87	2, 2.23	<0.05



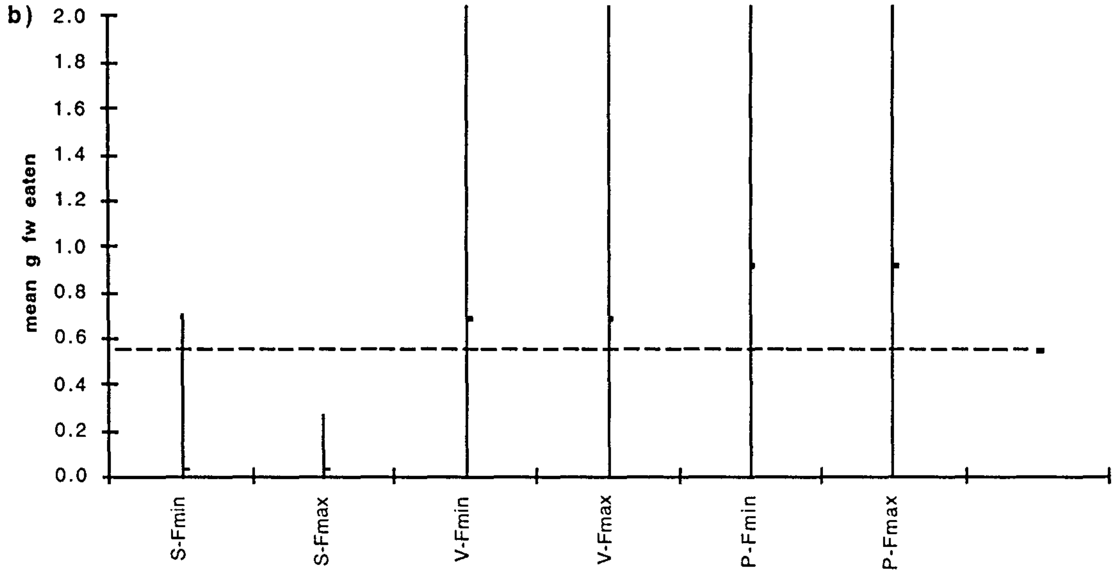
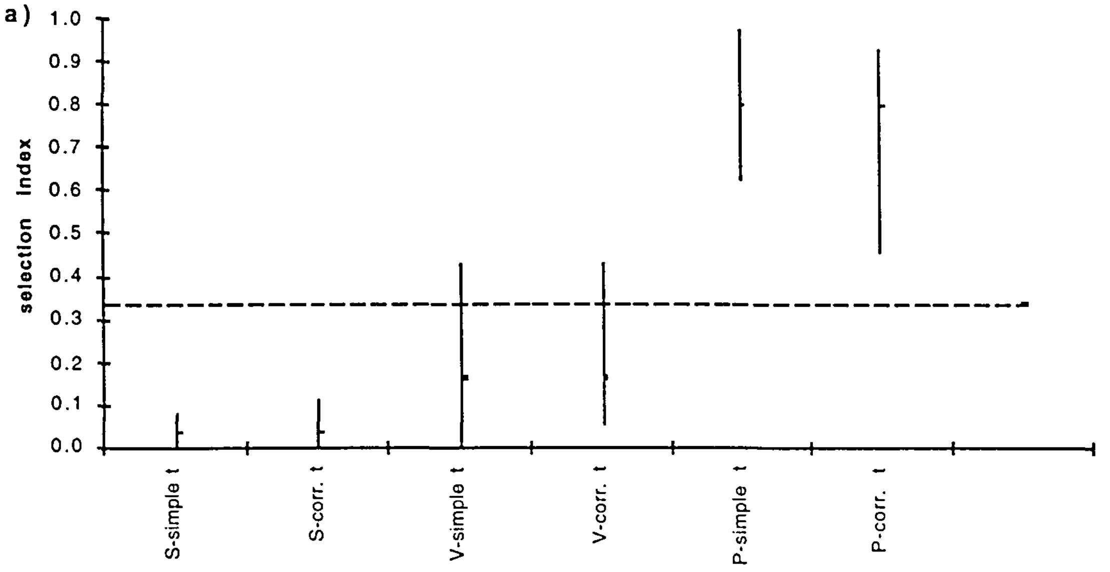


Figure A11: Estimates of preferences/rejections for single *Fucus* species offered to *Littorina littorea* in a multiple choice feeding preference experiment. S = *F. serratus*, V = *F. vesiculosus*, P = *F. spiralis*. a) Manly's selection index. b) Roa's confidence limits. For further explanations see Figure A4 and text.



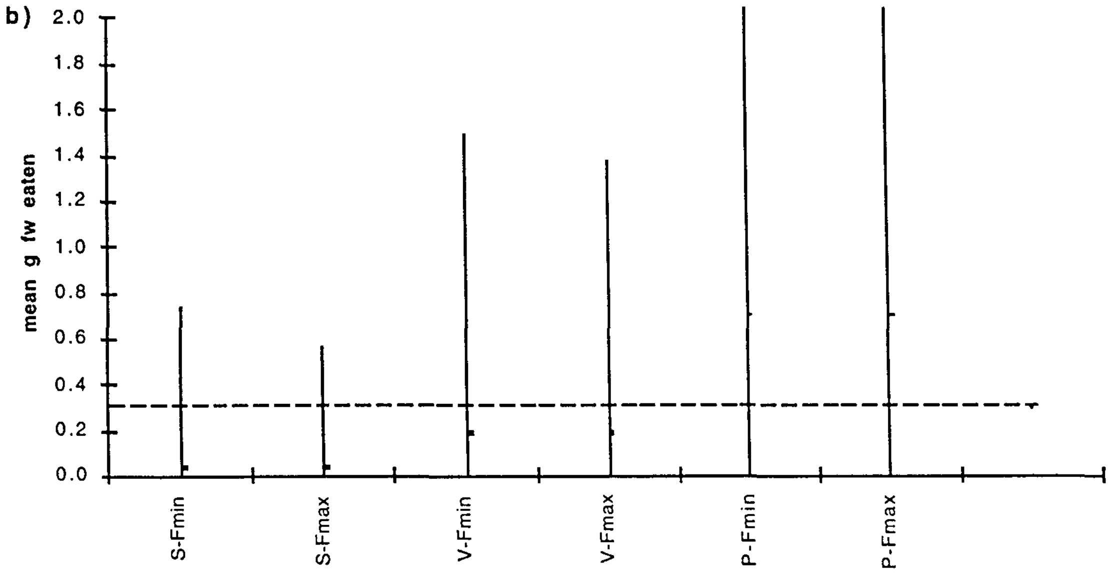


Figure A12: Estimates of preferences/rejections for single *Fucus* species offered to *Littorina mariae* in a multiple choice feeding preference experiment. S= *F. serratus*, V = *F. vesiculosus*, P = *F. spiralis*. a) Manly's selection index. b) Roa's confidence limits. For further explanations see Figure A4 and text.

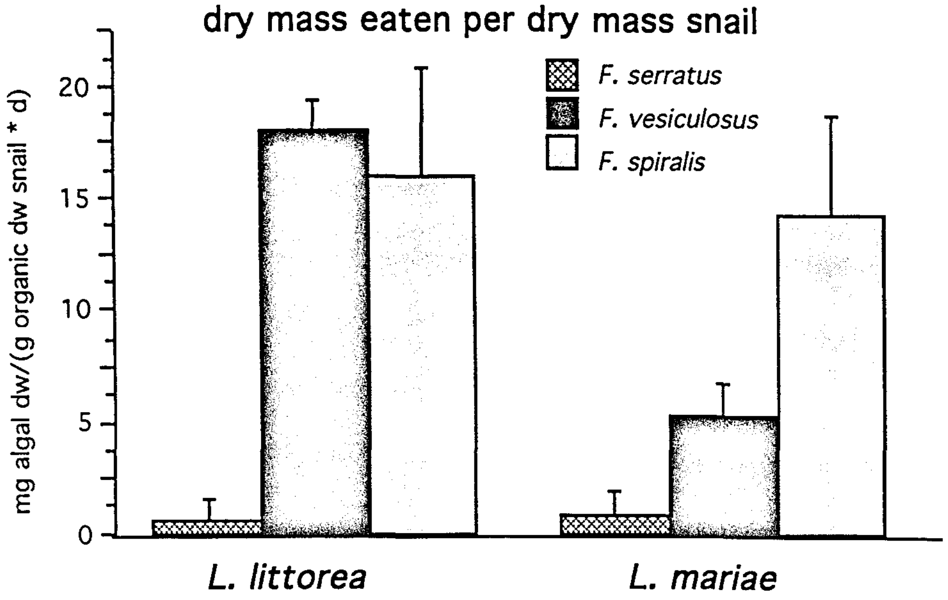


Figure A13: *Fucus* spp. dry weight consumed per organic dry weight of *Littorina* spp. in a multiple choice feeding preference experiment. Mean values of 4 replicates and SD corresponding to random pairing of treatments and controls yielding minimal F-values. Compare with Figure A10 for fresh weight consumption patterns.

Hotelling's T^2 test was calculated for MR and MD pairings of treatments and controls. For this, first by random pairing dw of change in treatments was corrected by dw of controls. Then data were divided by the ashfree dw of snails corresponding to treatment and by number of days (2.5).

Data used in Hotelling's T^2 tests were checked for multivariate normality with Hawkins test (Johnson & Field 1993). All data fulfilled the recommendations of Johnson & Field for balanced designs (i.e. range of medians of all groups < 0.85)

All 24 possible pairings were used to find F_{min}, F_{max} and percentages of pairings failing to yield significance (Table A3, bottom). More pairings yielded insignificant F-values compared with fresh weight data. Again, only data of *L. littorea* after MD pairing produced significant F-values (at α=0.05).

It was not possible to calculate Yao's test with dry weight data because controls have to be offset with treatments in a way that would require 'change of control dry mass per grazer dw per day'. Since controls are not logically related to grazers, the calculation seemed not reasonable.

In Manly (1995) f_i is calculated as (see above):

$$\begin{aligned} f_i &= \ln\{\text{final/initial}\} \\ &= \ln\{(\text{initial - eaten})/\text{initial}\} \\ &= \ln\{1 - \text{eaten/initial}\} \end{aligned}$$

with 'initial', 'final' and 'eaten' referring to algal mass.

This is true only for equal grazers in each experimental container. In personal communication, B. Manly recommended for the calculation of selection indices with dw/(dw snail *d) data to calculate f_i as:

$$\begin{aligned} f_i &= \ln\{1 - [(\text{eaten}/\text{initial}) * (\text{mscons}/\text{cons})/\text{days}]\} \\ &= \ln\{(\text{initial} - \text{eaten} * \text{mscons} * \text{cons}^{-1} * \text{days}^{-1})/\text{initial}\} \end{aligned}$$

where the amount eaten by a consumer of weight cons is normalized to the weight of a standard consumer (mscons with unit [g/d]), for which an estimate of per day consumption exists.

If the standard consumer (mscons) is set as K = 1 g/d, f_is will be calculated as

$$f_i = \ln\{1 - (\text{eaten}*K)/(\text{cons} * \text{days} * \text{initial})\}$$

and, in this way, practically dw/(dw * d) data are included in the calculation of f_i and consequently β_i.

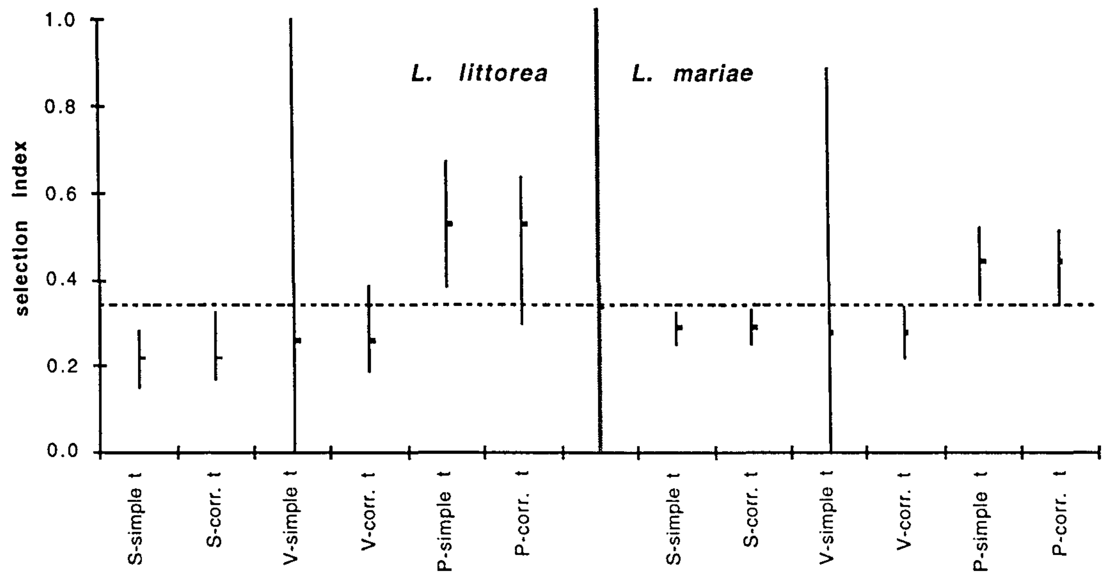


Figure A14: Manly's selection indices and t-distribution confidence intervals for dry weight per organic dry weight of snails per day data from a multiple choice feeding experiment. *Littorina* spp. were offered a choice of S = *Fucus serratus*, V = *F. vesiculosus* and P = *F. spiralis*. For further explanations see Figure A4a.

c_i was calculated in Manly (1995) as:

$$
\begin{aligned}
c_i &= \ln\{\text{final/ initial}\} \\
&= \ln\{(\text{initial-change})/\text{initial}\} \qquad \text{with growth 'change' is} < 0 \\
&= \ln\{1 - \text{change/initial}\}
\end{aligned}
$$

Consequently, corrected for number of days c_i should be calculated as:

$$c_i = \ln\{1 - \text{change/days/initial}\}$$

With these variables (calculated with algal dw data converted from fw data as shown above), Manly's selection indices were calculated again, along with simple and corrected t-distribution limits (Figure A14) The patterns of preferences/avoidances and significances are similar to those of fresh weight data (compare with Figures A11 and A12), but with dw/dw snail data β-values became more centered around 1/p=0.33.

Multiple choice experiment in relation to statistical analyses

With only 4 replicates, there was a strong dependence of significance on the random pairing with all methods. When Manly (1993) tested the power of Roa's Test (PR) and of his modification using differences between foods (MD) with simulated data, he found many more significant results with his modification. This real data set confirms Manly's assumption. Yao's test that had the greatest power in Manly's power analysis and was recommended by Manly (1993) yielded significance for the difference between consumption of *Fucus* species, without dependence on random pairing.

Ranges in F-values over 9 decimals (e.g. 20 to 1.9 10^{10} for *L. mariae*) very much suggest that Roa's original method should not be used anymore. Even when the correlation between foods is kept using MR random pairing, the range of F is still unsatisfactory.

For the usage of Roa's method with MR pairings, n should exceed p by more than just one as in the present experiment. Otherwise the "$(n-p)(p(n-1))^{-1}$" in Roa's formula to calculate F from T^2 and the inverse "$(n-1)^{-1}p(n-p)$" in his formula for calculation of confidence intervals produce low F-values with extensive intervals. 5 replicates would have reduced this factor from 9 to 6 (6 replicates to 5) for the confidence interval formula (from 1/9 to 1/6 or 1/5, respectively, for calculating F).

In contrast to Roa's confidence intervals, Manly's t-distribution limits revealed preferences/avoidances that seem reasonable at a visual evaluation of the data.

Presumably a higher experimetal error due to additional weighing errors in the conversion of fw to dw data and in weighing snails led to lower percentages of significant F-values when dw/dw snail data were used. Further, ratios of consumed amounts between *Fucus* spp. underwent a shift due to different dw:fw ratios of *Fucus* spp. (compare Figure A10 with A13), which suggests careful consideration of the special measured unit when results from various experiment(er)s should be compared.

SUMMARY

From the viewpoint of a user, Manly's (1993) test based on Yao should be the recommended, since it appeared to detect preferences most easily. Manly's (1995) selection index proved to reflect preferences and has the advantage of a selection value for each food item. For both methods from Manly, the experimental design does not have to be balanced for treatments and controls which may ease performances of certain experiments.

However, Manly's indices are distorted by differences in initial mass (area) and demand special care in this regard. In cases of strong differences, only Yao's test, as proposed by Manly (1993) should be used and preferences/rejections have to be judged graphically. To obtain intervals despite differences in initial mass, MR modification of Roa (1992) may be used, when F-values from all random pairings can be calculated to judge the safety of significances. But this still neglects the sampling error of k.

Roa's original design certainly should not be used anymore for the reasons pointed out by Manly (1993), especially not his correlation destroying method of random pairing between treatments and controls.