

Mechanisms and consequences of intra- and interspecific interference competition in *Idotea baltica* (Pallas) and *Idotea emarginata* (Fabricius) (Crustacea: Isopoda): A laboratory study of possible proximate causes of habitat segregation

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Abstract

The ecologically very similar sympatric congeners *Idotea baltica* and *I. emarginata* are associated with macroalgal debris which provides the animals with both food and shelter. Habitat segregation seems to be the major factor contributing to the coexistence of these two species: *I. baltica* is the dominant species among surface drift weed, whereas *I. emarginata* occurs mainly on the sea bed among accumulations of broken decaying algae. In laboratory cultures with food in excess, there is intense intra- and interspecific competition through direct interference. Single-species cultures of both species thrive and rapidly attain an equilibrium population size which is about four times greater in *I. emarginata* than in *I. baltica*. In mixed-species cultures, *I. baltica* lacks a ‘realized niche’; independent of starting densities, *I. baltica* is competitively excluded by *I. emarginata* within a short period of time. The crucial behavioural mechanism of interference is cannibalism (intraspecific competition) and mutual predation (interspecific competition). Both intra- and interspecific interference occur mainly through density-dependent control of juvenile mortality by cannibalistic/predatory adults. Experiments on the relative strengths of intra- and interspecific interference revealed strong asymmetries in competitive relationships: Intraspecific inhibitory effects in *I. baltica* are much greater than in *I. emarginata*; *I. emarginata* exerts much more inhibition on *I. baltica* than on itself, whereas *I. baltica* exerts much more inhibition on itself than on its congener *I. emarginata*. These asymmetries account for a complete competitive dominance of *I. emarginata* over *I. baltica*, and (according to the Lotka–Volterra model of interspecific competition) inevitably result in competitive exclusion of *I. baltica* by *I. emarginata*. All types of asymmetry are due to the fact that juveniles of *I. emarginata* are much better protected from being cannibalized and preyed upon by conspecifics and heterospecifics, respectively, than juveniles of *I. baltica*. This protection is probably based on an active chemical defense mechanism that becomes ineffective immediately after death. The possibility is discussed that current interference competition is an important factor in maintaining habitat segregation in *I.*

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baltica and *I. emarginata* in the field. Extrapolation of the laboratory results to the field suggests an essentially unidirectional effect, with *I. emarginata* itself being largely unaffected by *I. baltica* but competitively excluding the latter from zones of potential overlap. © 1998 Elsevier Science B.V.

Keywords: Behavioural interactions; Experimental populations; Habitat segregation; *Idotea*; Interference competition; Marine isopods

1. Introduction

Idotea baltica (Pallas) and *I. emarginata* (Fabricius) are among the eight species of the genus *Idotea* (Isopoda) which occur sympatrically around the rocky island of Helgoland, German Bight (unpublished). Congeneric species often have very similar ecologies and thus may be expected to show intense interspecific competition when living in the same area. The distributions of the species of *Idotea* at Helgoland, however, overlap little on a finer spatial scale, each species being preferentially associated with a specific microhabitat. Both *I. baltica* and *I. emarginata*, for instance, live amongst macroalgal debris which provides the animals with both food and shelter; *I. baltica*, however, is the dominant species among surface drift weed, whereas *I. emarginata* is mainly associated with accumulations of broken decaying algae at the sea bottom (Naylor, 1955a,b; personal observations at Helgoland). Like in many other sympatric congeners (Schoener, 1986), differences in habitat rather than those in diet and/or time seem to be the most important factor by which available resources are divided among sympatric *Idotea* species, allowing them to coexist on a larger spatial scale.

Avoidance of interspecific competition may be regarded as the ‘ultimate cause’ of habitat segregation. However, ignoring whether or not habitat segregation (as other kinds of ecological diversification among species) is an evolutionary response to intense interspecific competition in the past (Connell, 1980), we may focus on the ‘proximate causes’, i.e. the factors which maintain current distribution patterns. Potential actual causes of habitat segregation include: (1) Innate differences in physiological and/or other characteristics, resulting in differential survivorship and/or reproductive success with respect to habitat (e.g., Connell, 1972; Grant, 1981). In the extreme case, each species might be able to exist only within the physico-chemical environment of its specific microhabitat. For instance, *I. baltica* might not be adapted to tolerate conditions of reduced oxygen supply which occur at times in the habitat of *I. emarginata* (but not in that of *I. baltica*). This would exclude *I. baltica* at least temporarily from habitats specific to *I. emarginata*. (2) Divergent microhabitat preferences of the species; i.e. non-overlapping microgeographical distributions, might be a direct consequence of habitat selection (e.g., Douglass, 1976). (3) Differential predation: A species may be excluded from a certain habitat because of being a preferred prey of a local predator that shows differential predation on a number of potential prey species (Fairweather, 1987). (4) Current interspecific competition by which a species excludes other species from habitats where it is competitively superior to them. Whereas competition is widely

accepted as a significant force in moulding the ecologies of species and natural communities over evolutionary time, actual interspecific competition is difficult to detect in nature and, therefore, much controversy exists over its importance in explaining current events (Connell, 1983; Schoener, 1983; Simberloff, 1982; Underwood, 1986; Keddy, 1989).

In our laboratory we have been culturing populations of various *Idotea* species continuously since 1989 in large tanks from which large numbers of individuals of all stages are available for experiments throughout the year. This offers an excellent opportunity for comparative laboratory and field studies on niche differences, resource partitioning and the factors controlling distribution and abundance in *Idotea* species.

The present paper is part of an experimental analysis of habitat segregation in *Idotea* species at Helgoland. It deals with laboratory experiments on interactions within and between two ecologically very similar sublittoral species, *I. baltica* and *I. emarginata*. The study was inspired by the following observation: In laboratory tanks with identical constant conditions, both *I. baltica* and *I. emarginata* develop thriving populations as long as the species are kept separately. However, to maintain laboratory populations of *I. baltica* over some period of time, it proved to be essential strictly to avoid ‘contamination’ by even a small number of *I. emarginata*, otherwise *I. baltica* will be driven to extinction, within only a few months, by a rapidly growing population of *I. emarginata*. A population of *I. emarginata*, in contrast, is not affected by an occasional import of individuals of *I. baltica*, the latter apparently being unable to establish a growing population in the presence of the former.

Based on these findings, controlled laboratory experiments were carried out on the effects and underlying mechanisms of intra- and interspecific competition in *I. baltica* and *I. emarginata*. A complete understanding of the consequences of interspecific competition requires intra- and interspecific competitive processes to be studied simultaneously in order to determine their relative strengths (Connell, 1983; Underwood, 1986). As *I. baltica* had been found to be eliminated very rapidly by *I. emarginata* from cultures, even though the resources (particularly food) for which the populations might compete were not in limiting supply, the mechanism of competition could be expected to be drastic direct interference between individuals of the two populations, with *I. emarginata* being the dominant competitor.

Competition is, by definition, a kind of interaction between organismic units which is detrimental to all concerned. However, the situation is usually more or less asymmetrical; i.e. if two populations (species 1 and species 2) compete interspecifically, the fitness-reducing influence of species 1 on species 2 will usually be found not equal to that which species 2 exerts on species 1 (Schoener, 1983; Connell, 1983; Lawton and Hassell, 1981). At the most, one member of a pair of species is highly affected by the second, while any effect of the first on the second species is nearly undetectable.

Competitive inhibition covers both indirect effects arising from reduced availability of a common resource in short supply (exploitation competition), and direct effects (interference competition) by which competitors are prevented from gaining access to a resource. The latter may occur even if resources are not (or not yet) limiting. Particularly in marine organisms, interference competition (rather than competition through exploitation) seems to be the dominant form of interspecific competition, often resulting in

localised exclusion of a weaker competitor from habitats occupied by a superior one (Branch, 1984; Branch and Barkai, 1988). An extreme form of interspecific interference competition between closely related species is mutual predation (Sokoloff and Lerner, 1967; Fox, 1975). By demonstrating a behavioural mechanism of highly asymmetric interference, this paper indicates that present-day interspecific competition may play an important role in habitat segregation of *I. baltica* and *I. emarginata*.

2. Materials and methods

Idotea species play an important ecological role at Helgoland as they are the main primary consumers of the large brown algae such as *Fucus* and *Ascophyllum*. Damaged or eroding parts of algal thalli are the animals' principal food, but they also feed as scavengers and may even prey upon various kinds of small live animals (Naylor, 1955c and personal observations). On the other hand, *Idotea* species are subject to severe predation, particularly by fish (Wallerstein and Brusca, 1982).

Since 1989 we have been maintaining laboratory mass cultures of *I. baltica* and *I. emarginata* (original material collected at Helgoland). The two species are very similar with respect to food demands, body size, growth rate, and fecundity. In our cultures, individuals of both species attain sexual maturity 10–12 weeks after hatching from the marsupium. Mature females are able to produce several successive broods at intervals of about 4 weeks. The number of offspring per brood varies, depending on female body size, between 50 and more than 300 (details will be reported elsewhere). Short generation time and high reproductive potential render both species suitable for laboratory studies on intra- and interspecific competition.

The experimental animals (*I. baltica*, henceforth referred to as BA; and *I. emarginata*, referred to as EM) were obtained from our laboratory mass cultures. All experiments were performed at a constant temperature (16°C) and under an artificial LD 16:8 light–dark cycle.

2.1. Development of single- versus mixed-species cultures

Round plastic tanks (0.5 m diameter; about 40 l of sea water) were stocked with experimental populations of adult *Idotea* (males and females always at equal rates). All nine types of experiment (Table 1) were replicated three times. The tanks were run as flow-through systems (complete renewal of the water body within every 24 h; draining off through a 40 µm gauze). Food was available in excess throughout the experimental period of 9 months. Thalli of the brown alga *Ascophyllum nodosum* (L.) Le Jol were provided, serving the experimental animals both as substratum to cling on and food. *A. nodosum* was preferred to *Fucus* sp. because the former, in contrast to the latter, does not undergo rapid decay once detached from its natural substratum. The algal mass (250 g wet weight) was kept constant by being supplemented whenever necessary. *Artemia* nauplii were supplied to the experimental animals as an additional (animal) source of food. Both BA and EM have been found preying intensively on living *Artemia* nauplii, the concentrated valuable nutrients of which support growth and female

Table 1

Development of BA and EM populations in single-species and mixed-species cultures. N_i = number of individuals at the outset. Each type of experiment (1–9) was replicated three times

Type of experiment	N_i			
	BA males	BA females	EM males	EM females
BA single-species culture				
1	5	5		
2	100	100		
3	200	200		
EM single-species cultures				
4			5	5
5			100	100
6			200	200
BA/EM mixed-species cultures				
7	100	100	100	100
8	100	100	5	5
9	5	5	100	100

fecundity (unpublished). The nauplii are captured from the water body on random contact with the aid of the first pereopods. Newly-hatched nauplii were added daily to the tanks so that an excess average density of 2 nauplii/ml was kept constant throughout the experiment. At regular intervals (3, 5, 7, and 9 months after the start of the experiments), population development in the cultures was ascertained by counting those individuals which were retained by a 1.5 mm sieve (i.e. individuals > 7 mm body length). In the case of mixed-species cultures, these animals were first sorted to species and then counted separately. After census, the animals were replaced in the tanks. Individuals which had passed through the sieve (i.e. animals < 7 mm body length) were replaced directly without having been counted.

2.2. The mechanism of interference: Experimental Set 1

The cannibalistic/predatory behaviour of adults towards conspecific/heterospecific juveniles was studied in small groups of animals representing the experimental unit. 20 × 20 × 6 cm plastic boxes (supplied with 1 l of aerated sea water and a fragment of *Ascophyllum*) were each stocked with 10 adults (male BA, female BA, male EM, female EM, respectively) and 100 freshly-hatched juveniles (manca I stage) of BA and EM, respectively. After 20 h the numbers of surviving juveniles were determined. Controls were performed with 100 juveniles each (BA and EM juveniles, respectively) in the absence of adults. The experiments were run under two different food conditions: in the absence and presence, respectively, of *Artemia* nauplii (about 10 nauplii/ml). All 16 types of experiment (eight different combinations of juveniles and adults, at two different food conditions each) as well as the respective controls (four) were replicated 12 times (20 treatments × 12 replicates = 240 experimental units). Because of the amount of work, the experiments were conducted in complete blocks on 12 successive days, each block (20 experimental units) including a single treatment of each type.

From the results of this set of experiments, competition coefficients (see Discussion)

were estimated in the following way. First, the average percent mortality of BA juveniles in the presence of conspecific and heterospecific adults (males and females together), respectively, was calculated (x_1 , x_2); the same was done for EM juveniles (y_1 , y_2). The values of x_1 and y_1 can be thought of as measures of the intensity of intraspecific competition, and the values of x_2 and y_2 as measures of the intensity of interspecific competition. By convention, intraspecific competition coefficients (α_{BA-BA} and α_{EM-EM}) are set to 1.00. Interspecific competition coefficients then can be calculated as $\alpha_{BA-EM} = x_2/x_1$ (effect of EM on BA, relative to the effect of BA on itself) and $\alpha_{EM-BA} = y_2/y_1$ (effect of BA on EM relative to the effect of EM on itself).

2.3. The mechanism of interference: Experimental Set 2 (choice tests)

In this set we studied the responses of *single* adults (BA and EM, respectively) which were given a choice between a conspecific and a heterospecific juvenile (choice tests). Only female adults were used in this second set of experiments. The females were taken at random from laboratory mass cultures and were placed singly in small glass bowls (40 ml of sea water). After 24 h of isolation and starvation, two juveniles each (a conspecific and a heterospecific) were added simultaneously. The age of the juveniles was 2–4 d after hatching from the brood pouch. In this developmental stage (manca I), however, juvenile BA and EM cannot be distinguished morphologically. To discriminate juvenile BA and EM once mixed and added to the experimental females, we made use of the fact that both EM and BA are polymorphic species. Either occur in a number of colour pattern varieties, the extremes of which are represented by uniformly coloured individuals on the one hand (phenotype *uniformis*), and laterally white-spotted individuals (phenotype *albufusca*) on the other (Tinturier-Hamelin, 1963). Differences in colour patterns can be recognized with the naked eye even in freshly hatched juveniles.

2.3.1. Experiment 1

This experiment was designed to test whether the colour pattern of juveniles itself exerts any significant influence on the responses of adult females. The females were confronted with uniformly coloured EM juveniles and spotted BA juveniles on the one hand, and with a reciprocal arrangement (i.e. spotted EM juveniles and uniform BA juveniles) on the other. The experimental animals were monitored continuously until one of the two juveniles had been killed and eaten by the adult female. Each test was replicated 50 times.

2.3.2. Experiment 2

In this series of choice tests we studied the responses of adult females (BA and EM, respectively) to live versus dead BA and EM juveniles. Since (in Experiment 1) responses of adult females had proven to be independent of colour patterns of juveniles, we regularly used BA juveniles of the spotted type, and EM juveniles of the uniform type. Considering the large numbers of individual tests, these were not monitored continuously but were checked at intervals of 7.5, 15, 30, 60, and 150 min after the juveniles had been added. Dead juveniles had been killed immediately before the tests by placing them for 1 h in CO₂-saturated sea water.

It should be noted that, in all experiments of Set 2, the adult females were taken at random from mass cultures where animals were unsynchronized with respect to molting. This means that among tested females there was probably always a number of individuals which were unable to feed as they were preparing for a near molt or had undergone molting shortly before.

2.4. Data analyses

Final population densities in single- versus mixed-species cultures were compared by Student's *t*-test.

Experimental Set 1 (mechanism of interference) was designed as a $2 \times 2 \times 2 \times 2$ factorial. Survival in the experimental units of 100 juveniles each was studied with respect to four factors (feeding regime, species of adults, sex of adults, species of juveniles), each expressed at two levels. A four-way factorial ANOVA (model I, all four effects are fixed treatments) was carried out to determine significant main effects as well as first-, second- and third-order interaction effects. Controls were not incorporated into the statistical analysis. Following the ANOVA, pairs of single means were tested for significant differences using the multiple-range test of Tukey (T-method; Sokal and Rohlf, 1995).

Experimental Set 2 (mechanism of interference) involved single adults as the experimental unit. For statistical evaluation of the data, the *G*-statistic was applied. (*G*-test of independence, and *G*-test of goodness of fit). If necessary ($N < 200$), *G*-values were adjusted (G_{adj}) using Yates' correction for continuity (Sokal and Rohlf, 1995). *G*-values > 10.83 ($df=1$) indicate statistically significant differences at the 0.1% level. If even at the 10% level no statistical significance could be found ($G < 2.71$), differences were regarded as random.

3. Results

3.1. Development of single- versus mixed-species cultures

3.1.1. Single-species cultures (Fig. 1)

At the end of a 9-month period all experimental populations had obviously attained an equilibrium size with respect to the number of individuals with more than 7 mm body length. Cultures of BA showed about 200 individuals > 7 mm body length (pooled data of all three types of BA single-species culture: $\text{mean} \pm \text{SD} = 206 \pm 34$; $N=9$; range 111), largely independent of the initial number of individuals (N_i): 201 ± 34 ($N_i=10$), 194 ± 37 ($N_i=200$), and 224 ± 38 ($N_i=400$). Single-species cultures of EM also showed a clear tendency for the final density to be relatively constant despite the large range of starting densities: 787 ± 47 ($N_i=10$), 892 ± 44 ($N_i=200$), and 813 ± 73 ($N_i=400$). Thus, the number of EM individuals > 7 mm in population equilibrium (pooled data: $\text{mean} \pm \text{SD} = 831 \pm 68$; $N=9$; range 209) was about four times as large as that of BA.

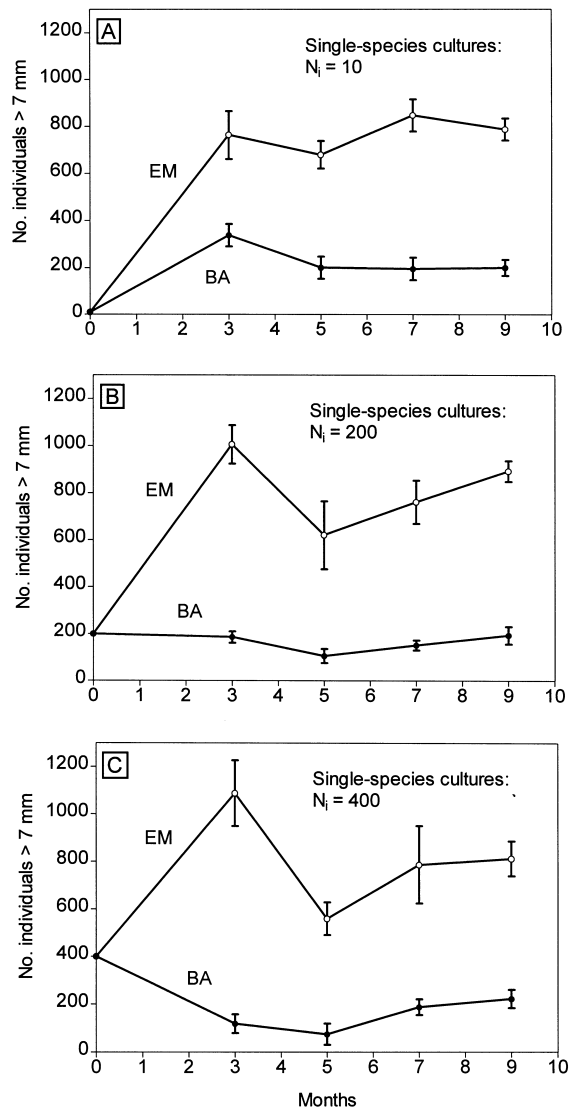


Fig. 1. Development of BA and EM populations in single-species cultures over a 9-month experimental period. The cultures were started at varying densities: N_i = initial number of individuals. Population development is represented by the numbers of individuals > 7 mm in body length. Mean \pm standard deviation of the three replicates are shown for each point.

3.1.2. Mixed-species cultures (Fig. 2)

In mixed-species cultures, BA was driven to extinction by EM within a relatively short period of time. This occurred independently of the initial composition of the cultures. In cultures started with BA and EM in equal numbers (200/200; Fig. 2A), BA was virtually absent after 3 months. Even in cultures started with a greatly excessive

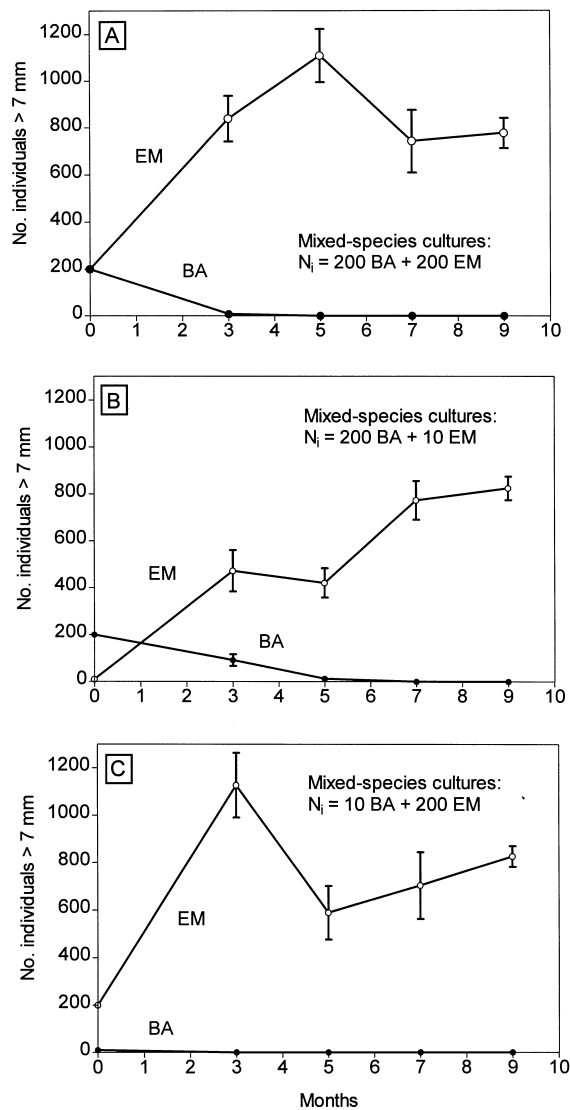


Fig. 2. Development of BA and EM populations in mixed-species cultures. Other details as for Fig. 1.

number of BA (200 BA/10 EM; Fig. 2B), BA was eliminated by a rapidly growing EM population within 5 months. Finally, when BA started at a density smaller than that of EM (10 BA/200 EM; Fig. 2C), BA disappeared rapidly from the cultures. The development of EM populations in mixed-species cultures was quite similar to that in corresponding single-species cultures. Only when EM started at the same or a smaller density than BA was growth of the EM population temporarily slowed (EM in Fig. 2B compared to Fig. 1A, and in Fig. 2A compared to Fig. 2B). However, once BA had been

eliminated, EM populations attained an equilibrium size which was independent of starting density (778 ± 64 for $N_i = 200$ BA + 200 EM; 825 ± 50 for $N_i = 200$ BA + 10 EM; and 827 ± 44 for $N_i = 10$ BA + 200 EM). The mean (\pm SD) of the pooled data (809 ± 52 ; $N=9$; range 173) is not different statistically (t -test, $P < 0.05$) from that calculated for EM single-species cultures (831 ± 68 , $N=9$; range 209).

3.2. The mechanism of interference: Experimental Set 1 (Table 2A,B)

In the absence of adults, nearly all juveniles (controls) survived the 20-h experimental period (mean survival rate of EM juveniles: 98.8 and 99.3% in the absence and presence of *Artemia* larvae, respectively; mean survival rate of BA juveniles: 99.2 and 99.1%, respectively). In the presence of adults, however, the numbers of juveniles were always found to be reduced to a lesser or greater extent. Disappearance of juveniles was caused by adults attacking, killing and devouring both conspecific and heterospecific juveniles. The extreme values were: reduction of BA juveniles by BA females in the absence of *Artemia* larvae by as much as 98.3% on average, and reduction of EM juveniles by EM females in the presence of *Artemia* larvae by only 5% on average).

The four-way factorial ANOVA (Table 3) shows the following main effects. The overall survival rate of juveniles in the presence of adults was strongly influenced by the feeding regime (Factor 1) as well as by what species the juveniles belonged to (Factor 4), but was independent of the species (Factor 2) and sex (Factor 3) of the adults. The significance/non-significance of first-, second- and third-order interactions of the four main factors is also given in Table 3. Any pair of the 16 single means of Table 2A,B is significantly different (at $\alpha = 0.05$) if the difference between the sample means equals or exceeds 19.1 (critical difference, calculated by the T-method after Tukey). The results of the statistical analyses can be interpreted as follows.

3.2.1. Interference in the absence of *Artemia* nauplii (Table 2A)

The mean juvenile survival rate for all treatments in the absence of *Artemia* nauplii was 45.2%. Adult BA and adult EM did not differ significantly with respect to their overall disposition to prey on *Idotea* juveniles (mean juvenile survival in the presence of BA and EM adults, respectively: 44.5% and 45.9%). Survival of juveniles in the presence of females (pooled data of BA and EM females) was 38.7%, on average, and 51.6% in the presence of males. Juveniles were thus reduced to a significantly greater extent by females than by males. This difference is also evident when adult BA and EM are considered separately (mean juvenile survival in the presence of BA females and BA males, respectively: 35.9% and 53.1%; in the presence of EM females and EM males, respectively: 41.5% and 50.3%). The most important findings relate to the quantitatively different responses of adults to BA and EM juveniles. BA juveniles (mean survival rate: 12.4%) were eliminated to a much greater extent than EM juveniles (mean survival rate: 78.0%). The survival rate of EM juveniles in the absence of *Artemia* nauplii was thus 6.3 times greater than that of BA juveniles. Quantitatively different responses to BA and EM juveniles (i.e. preference of BA juveniles as prey over EM juveniles) were highly significant in each type of adult tested (EM females, EM males, BA females, BA males).

Table 2

Numbers of BA and EM juveniles, respectively, out of 100 each, surviving a 20-h period of exposure to 10 adults each (BA males, BA females, EM males, and EM females, respectively); controls: numbers of surviving juveniles in the absence of adults. Each test was replicated 12 times. Food conditions: (A) No *Artemia* nauplii; (B) *Artemia* nauplii as an additional source of food

Replicated tests	Type of combination: adults/juveniles								Controls	
	BA males/ EM juv	BA males/ BA juv	BA females/ EM juv	BA females/ BA juv	EM males/ EM juv	EM males/ BA juv	EM females/ EM juv	EM females/ BA juv	None/ EM juv	None/ BA juv
(A) No <i>Artemia</i> nauplii										
1	62	11	47	0	91	11	57	0	95	100
2	71	40	78	4	93	24	94	0	99	98
3	92	56	75	2	87	19	96	3	97	98
4	81	16	31	1	89	29	80	1	100	100
5	53	8	75	0	81	8	88	3	100	99
6	89	53	93	4	96	12	87	10	100	100
7	75	15	86	2	53	27	73	8	99	100
8	95	33	78	0	62	6	59	0	100	100
9	82	47	56	0	89	15	96	0	97	98
10	77	39	65	4	95	10	81	0	100	100
11	80	19	90	0	90	23	81	5	98	100
12	69	10	77	1	87	9	72	4	100	97
Σ survivors (out of 1200 each)	926	347	841	20	1013	193	964	34	1185	1190
Mean survival rate (%)	77.2	28.9	70.1	1.7	84.4	16.1	80.3	2.8	98.8	99.2
(B) <i>Artemia</i> nauplii as an additional source of food										
1	90	51	99	71	95	23	99	43	100	100
2	41	75	98	58	98	31	97	85	96	94
3	65	35	96	72	96	32	90	51	98	99
4	87	17	78	32	94	23	90	84	100	99
5	79	19	95	51	80	17	98	66	100	100
6	74	6	69	11	90	32	100	57	100	99
7	68	23	82	44	81	12	93	80	100	100
8	95	21	71	61	93	13	95	25	99	100
9	82	45	91	39	87	9	95	58	100	100
10	67	50	80	57	99	30	100	19	100	98
11	71	22	78	45	89	26	87	72	98	100
12	80	34	94	60	84	15	96	44	100	100
Σ survivors (out of 1200 each)	899	398	1031	601	1086	273	1140	684	1191	1189
Mean survival rate (%)	74.9	33.2	85.9	50.1	90.5	22.8	95.0	57.0	99.3	99.1

In other words, adult BA (both males and females) eliminated conspecific juveniles to a much greater extent than heterospecific ones, whereas the situation was reversed in EM (both males and females).

Interspecific competition coefficients calculated (see Material and Methods) from the data of Table 2A are $\alpha_{BA-EM} = 1.07$ and $\alpha_{EM-BA} = 1.49$

3.2.2. Interference in the presence of *Artemia nauplii* (Table 2B)

In the presence of *Artemia nauplii* as an additional source of food, the experimental results differed in a number of respects from those recorded in the absence of nauplii:

(1) The overall juvenile survival rate was significantly increased (from 45.2% in the absence of *Artemia nauplii* to 63.7% in their presence).

(2) The overall juvenile survival rate (and its increase) proved to be independent of Factor 2 (species of adults): 61.0% and 66.3% in the presence of BA and EM adults, respectively.

(3) The overall juvenile survival, however, was dependent on Factor 3 (sex of adults). A significant increase in juvenile survival occurred only when adult females were involved. The increase in overall juvenile survival resulted from a highly significant decrease in predatory/cannibalistic attacks by adult females (for BA females: increase of juvenile survival by 89.5%; for EM females: 82.8%), whereas males did not show a significant change in behaviour (for BA males: increase in juvenile survival by 1.9%; for

Table 3

Analyses of variance ($2 \times 2 \times 2 \times 2$ factorial ANOVA) on the survival rate of *Idotea* juveniles (experimental Set 1; data of Table 2); NS refers to non-significance at $P > 0.05$

Source of variation	df	SS	MS	F	P value
(a) Main effects					
Factor 1 (feeding regime)	1	16 391.02	16 391.02	90.18	<0.001
Factor 2 (species of adults)	1	546.77	546.77	3.01	NS
Factor 3 (sex of adults)	1	168.77	168.77	0.93	NS
Factor 4 (species of juveniles)	1	149 075.54	149 075.54	820.18	<0.001
(b) First-order interactions					
Factors 1×2	1	176.36	176.36	0.97	NS
Factors 1×3	1	10 502.11	10 502.11	57.78	<0.001
Factors 1×4	1	4700.54	4700.54	25.86	<0.001
Factors 2×3	1	581.00	58.00	3.20	NS
Factors 2×4	1	2465.32	2465.32	13.56	<0.001
Factors 3×4	1	30.07	30.07	0.17	NS
(c) Second-order interactions					
Factors $1 \times 2 \times 3$	1	28.50	28.50	0.15	NS
Factors $1 \times 2 \times 4$	1	0.72	0.72	<0.01	NS
Factors $1 \times 3 \times 4$	1	3168.72	3168.72	17.43	<0.001
Factors $2 \times 3 \times 4$	1	892.03	892.03	4.91	<0.05
(d) Third-order interactions					
Factors $1 \times 2 \times 3 \times 4$	1	141.51	141.51	0.78	NS
Within subgroups (error)	176	31 990.00	181.76		
Total	191	85900	220		

EM males: 12.7%). As a consequence, males (both BA and EM males) eliminated more juveniles than did females (juvenile survival in the presence of males and females, respectively: 55.4% and 72.0%), which is quite the contrary to the animals' behaviour in the absence of *Artemia* nauplii. It was only by compensation of these opposite effects that the overall survival rate of juveniles for all treatments proved to be independent of the sex of the adults (see above).

(4) The survival rates of both EM and BA juveniles were increased compared with those recorded in the absence of *Artemia* nauplii. BA juveniles, however, benefitted, with respect to survival, to a much greater extent from the presence of *Artemia* nauplii than did EM juveniles (mean survival rate of BA juveniles: 40.8% compared with 12.4%; mean survival rate of EM juveniles: 86.6% compared with 78.0%). Nevertheless, in the presence of *Artemia* nauplii, as in their absence, each type of adult showed a significant preference for preying on BA juveniles rather than on EM juveniles. Therefore, the overall survival rate of EM juveniles was still greater (2.1 times, compared with 6.1 times in the absence of *Artemia* nauplii) than that of BA juveniles.

Interspecific competition coefficients calculated from the data of Table 2B are $\alpha_{\text{BA-EM}} = 1.03$ and $\alpha_{\text{EM-BA}} = 2.70$.

3.3. The mechanism of interference: Experimental Set 2 (choice tests)

3.3.1. Experiment 1 (Table 4)

When single adult females were offered a choice between a BA and a EM juvenile, their predatory/cannibalistic response (i.e. the question of whether the BA or the EM juvenile was eliminated first) clearly did not depend on the juveniles' colour patterns (G -test of independence with Yates' correction for continuity; $G_{\text{adj}} = 0.62 < \chi^2_{0.1(1)} = 2.71$ for EM, and $G_{\text{adj}} = 0.49 < \chi^2_{0.1(1)} = 2.71$ for BA). Both EM and BA females preferred, to a high degree, BA juveniles over EM juveniles: 91:9 (BA female), and 93:7 (EM female) (pooled data of the two reciprocal arrangements each). The divergence from a 1:1 value is statistically highly significant (G -test of goodness of fit, with Yates'

Table 4

Choice tests (Experiment 1): Responses of single females (BA and EM, respectively) in experimental arrangements with two juveniles each (one conspecific and one non-conspecific juvenile). For both BA and EM females, two series of tests were performed: In the first series (a), BA juveniles showed the spotted colour pattern (spo), whereas EM juveniles were uniform in colour (uni); in the second series (b), the situation was reversed

	Test series			
	a	b	a	b
Arrangement	1 BA female	1 BA female	1 EM female	1 EM female
(1 female + 2	+ 1 BA juv/spo	+ 1 BA juv/uni	+ 1 BA juv/spo	+ 1 BA juv/uni
juveniles):	+ 1 EM juv/uni	+ 1 EM juv/spo	+ 1 EM juv/uni	+ 1 EM juv/spo
No. tests:	50	50	50	50
No. (and %)				
BA eaten first	44 (88.0)	47 (94.0)	45 (90.0)	48 (96.0)
EM eaten first	6 (12.0)	3 (6.0)	5 (10.0)	2 (4.0)

Table 5

Choice tests (Experiment 2): Responses of single females (BA and EM, respectively) in experimental arrangements with two juveniles each (one conspecific and one non-conspecific juvenile). For both BA and EM females, two series of tests were performed: In the first series (a) juveniles were alive, whereas in the second series (b) juveniles had been killed just prior to the experiment

	Test series			
	a	b	a	b
Arrangement	1 BA female	1 BA female	1 EM female	1 EM female
(1 female + 2	+ 1 BA juv/live	+ 1 BA juv/dead	+ 1 BA juv/live	+ 1 BA juv/dead
juveniles):	+ 1 EM juv/live	+ 1 EM juv/dead	+ 1 EM juv/live	+ 1 EM juv/dead
No. tests:	133	132	133	133
No. (and %)				
BA eaten first	65 (48.9)	39 (29.3)	54 (40.9)	33 (24.8)
EM eaten first	1 (0.8)	35 (26.3)	3 (2.3)	35 (26.3)
Both eaten	8 (6.0)	53 (39.8)	4 (3.0)	62 (46.4)
None eaten	59 (44.4)	6 (4.5)	71 (53.8)	3 (2.3)

correction for continuity: $G_{\text{adj}} = 75.84 > \chi^2_{0.001(1)} = 10.83$ for BA females, and $G_{\text{adj}} = 85.35 > \chi^2_{0.001(1)} = 10.83$ for EM females). In other words, BA females preferred conspecific over heterospecific juveniles, whereas EM females did just the opposite.

Our direct observations on the interactions between adults and juveniles can be summarized as follows. Neither BA nor EM females seem to be capable of discriminating between BA and EM juveniles from a distance as juveniles were attacked and seized at random. EM juveniles were, however, usually released without having suffered any obvious harm, sometimes abruptly pushed away (fright reaction). In contrast, juvenile BA, once picked up, were generally treated as prey and devoured immediately. Neither BA nor EM juveniles showed any physical resistance or behavioural reaction when seized by an adult. This suggests that discrimination between BA and EM juveniles by adults is based on a chemical signal, specific to EM, exerting its effect when adults and juveniles come into direct contact.

3.3.2. Experiment 2 (Table 5 and Fig. 3)

These choice tests were evaluated from two different points of view. First, as in Experiment 1, emphasis was laid on which of the two juveniles was eaten first ('BA eaten first' and 'EM eaten first'), ignoring the fate of the remaining juvenile (Table 5). Since the tests were not monitored continuously, it could, however, happen that either juvenile was eaten between two successive checks so that a decision on which juvenile had been eaten first was impossible (cases classified as 'both eaten'). Finally, cases in which none of the two juveniles was eaten within the 150-min observation period were classified as 'none eaten'. As evident from Table 5, the responses of both BA and EM females clearly depended upon whether juveniles were live or dead. In the case of live juveniles, a preference of BA juveniles over EM juveniles was highly significant in both BA females (65:1; G -test of goodness of fit with Yates' correction for continuity: $G_{\text{adj}} = 77.18 > \chi^2_{0.001(1)} = 10.83$) and EM females (54:3; $G_{\text{adj}} = 52.71$), which is in line

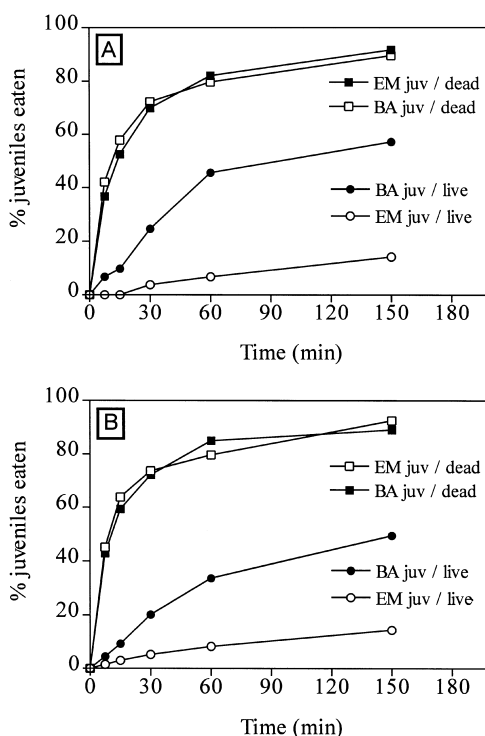


Fig. 3. Choice tests (Experiment 2). Percentage of juveniles (live BA juveniles, live EM juveniles, dead BA juveniles, and dead EM juveniles, respectively) eaten by adult females within 7.5, 10, 15, 30, 60, and 150 min after the start of the experiment, in experimental arrangements consisting of one adult female each (BA and EM, respectively) and two juveniles (one conspecific and one heterospecific juvenile). (A) Juveniles with BA females. (B) Juveniles with EM females.

with the results of Experiment 1. In both BA and EM females there was a large number of 'none eaten', whereas the numbers of 'both eaten' were small.

In the case of dead juveniles, the situation was completely different. As indicated by the large numbers of 'both eaten' and the small numbers of 'none eaten', a much greater proportion of dead juveniles than of live juveniles were devoured within the observation period by BA and EM females. Most remarkably, however, BA and EM females no longer exhibited any significant preference of BA to EM juveniles or vice versa (BA females: $G = 0.22 < \chi^2_{0.1(1)} = 2.71$; EM females: $G = 0.06$).

Fig. 3 shows an evaluation of Experiment 2 from a different point of view. After one of the two juveniles had been eaten, it could happen that some time later the other one was also devoured. Fig. 3 shows the overall numbers of the four types of juveniles (BA live, BA dead, EM live, EM dead) which had been eaten by the successive times of check. There was clearly no difference in the responses of BA females (Fig. 3A) and EM females (Fig. 3B). At any time within the observation period, (1) significantly more dead than live juveniles had been eaten, (2) the numbers of dead BA juveniles eaten was statistically not different from the number of dead EM juveniles eaten, and (3)

significantly more live BA juveniles had been eaten than live EM juveniles. In other words, BA and EM females could both discriminate between BA and EM juveniles as long as they were alive, but they did not discriminate dead BA juveniles from dead EM juveniles.

4. Discussion

The applied laboratory regime clearly provided a suitable habitat (fundamental niche) for both EM and BA which, when kept alone, developed stable populations. Independent of starting densities, single-species populations of both species rapidly reached an equilibrium population size at their respective carrying capacities (K_{EM} and K_{BA}), indicating strong intraspecific competition. Since equilibrium population size of EM was about four times that of BA, BA apparently encountered a much higher level of intraspecific competition than EM. In mixed-species populations highly asymmetric interspecific competition occurred, which invariably resulted in a rapid exclusion of BA by EM, even if cultures had begun with a marked numerical preponderance of BA. Under the applied experimental conditions, BA thus lacks a ‘realized niche’ when in competition with the superior competitor EM.

The ‘Lotka–Volterra’ model of interspecific competition specifies (for a number of simplifying preconditions) which circumstances lead to competitive exclusion of a species by a superior competitor (MacArthur, 1972; Wissel, 1989). According to the model, EM can be expected invariably to outcompete BA, if the following equations are met:

$$a_{BA-EM}/K_{BA} > 1/K_{EM} \quad (1)$$

and

$$a_{EM-BA}/K_{EM} < 1/K_{BA}. \quad (2)$$

K_{EM} and K_{BA} are the carrying capacities of the logistic growth of EM and BA in the absence of one another. The competition coefficient α_{1-2} is a conversion factor expressing the number of individuals of Species 2 which have the same ‘inhibitory effect’ on the growth of a Species 1 population as one individual of Species 1 has on its own population’s growth. ‘Inhibitory effects’ involve indirect effects through reduction of common resources as well as any kind of direct physical interference preventing competitors from gaining access to common resources. In the present experiments there was certainly exploitation of common resources by both species. Food (probably the most important resource potentially competed for) was, however, always available in excess, and so mechanisms of direct interference rather than a shortage of common resources must have been the dominant (or even single) factor controlling and limiting densities in single- and mixed-species populations. Furthermore, there is every reason to believe that intra- as well as interspecific interference occurred mainly through density-dependent control of juvenile survival by cannibalistic/predatory adults: Adults of each species cannibalized conspecific juveniles (intraspecific interference by cannibalism) and ate juveniles of the other species (interspecific interference by mutual predation), while

aggressive interactions among adults (whether conspecifics or heterospecifics) seem to be comparatively inconsequential. It may therefore be justified to estimate competition coefficients solely from the effects which adults exert upon mortality of conspecific and heterospecific juveniles, respectively. Then, the inhibitory effect of EM on BA is found to be relatively high but virtually identical to that which BA exerts on itself ($\alpha_{BA-EM} = 1.07$ and 1.03 , respectively, in the absence and presence of *Artemia* nauplii); and the effect of BA on EM turns out to be relatively low but of the same order of magnitude as that of EM on other EM ($\alpha_{EM-BA} = 1.49$ and 2.70 , respectively). Since, furthermore, K_{EM} is about four times as high as K_{BA} , Inequations (1) and (2) are clearly met.

The terms of Inequations (1) and (2) can also be interpreted ecologically. The reciprocal value of K ($1/K$) measures the depressing effect which one individual of a species exerts upon its own population's growth (=intensity of intraspecific competition), while the quotient a_{1-2}/K_1 gives the inhibition which one individual of Species 2 exerts upon the population of Species 1 (=intensity of interspecific competition). Consequently, Inequations (1) and (2) read as follows: BA will be eliminated invariably by EM from mixed populations, if BA individuals exert less inhibition upon EM than upon their own species (Inequation (1)), and if EM individuals exert more inhibition upon BA than upon conspecifics (Inequation (2)), then BA would suffer more overall competition (intra- plus interspecific) than EM, and mixed populations would transform into monocultures where only EM survives. These conditions are clearly met: Aggressive attacks of BA adults are directed much more often towards conspecific juveniles than towards EM juveniles, while the attacks of EM adults clearly concentrate on BA juveniles rather than on conspecific ones. So the outcome of our competition experiments is just what is predicted by competition theory. This is not very surprising since the experimental design clearly met the simplifying preconditions (populations in equilibrium; constant and homogeneous environment) on which the theory is based.

Eating juveniles, of course, is predation (and cannibalism, respectively). *Mutual* predation (with each of two closely related species preying on early stages of the respective other species), however, has nothing in common with the typical predator–prey relationship (one species being the prey, the other the predator). In a functional sense, mutual predation (as well as cannibalism) is an extreme form of interference competition because it reduces the number of potential competitors yet does not (normally) contribute substantially to the animals' consumption.

Interference competition leading to localized exclusion of a species by a superior competitor (often even in the presence of superabundant food) has been demonstrated for a number of species in laboratory as well as in field experiments (see review on marine organisms by Branch, 1984). In sand-burrowing intertidal amphipods, for instance, behavioural interactions have been suggested to be important to space partitioning among species (Croker and Hatfield, 1980). The precise mechanisms of interference are, however, usually unknown. The key phenomenon for the understanding of both intraspecific and interspecific competitive processes in BA/EM ($K_{EM} > K_{BA}$; and superiority of EM over BA) is the fact that EM juveniles are rather well protected from being cannibalized by EM adults as well as from being preyed upon by BA adults. The experimental results suggest that this protection is based on a chemical repellent. Since protection is lost immediately on death, the repellent is probably secreted actively when

EM juveniles are attacked by BA or EM adults. BA juveniles, in contrast, lack a similarly effective mechanism of defense, thus being cannibalized and preyed upon by conspecific and heterospecific adults to a much greater extent than EM juveniles. This quantitative difference in inherent protection and thus in survivorship of BA and EM juveniles has a profound impact on the development of both single- and mixed-species cultures. It produces a number of marked asymmetries/symmetries in competitive effects (Table 2A,B), allowing a clear ranking of the species in competitive ability.

(1) *Comparison of intraspecific effects*: Intraspecific competition within BA is much stronger than within EM. From the Lotka–Volterra inequalities (1) and (2) it can easily be derived that the species (out of a pair of potential competitors) which suffers less from intraspecific competition is (all other things equal) more likely to be superior in interspecific competition.

(2) *Comparison of interspecific effects*: Interspecific competition of EM on BA is much stronger than interspecific competition of BA on EM. This is the type of asymmetry usually invoked.

(3) *Comparisons of intra- and interspecific effects*. Two different types of such comparisons can be distinguished: (3a) Intraspecific competition within EM (BA) is less strong (stronger) than interspecific competition of EM on BA (BA on EM). Comparisons of this type provide the crucial information for predicting what will happen to single- or mixed-species populations, if the density of either species changes. (3b) Intraspecific competition within EM (BA) is of the same order of magnitude as the interspecific effects of BA on EM (EM on BA). Comparisons of this type lead to the estimation of the Lotka–Volterra competition coefficients. (Note that high competitive asymmetry does not necessarily imply competition coefficients strongly deviating from one.

Asymmetry in competitive relations among species seems to be the rule rather than the exception (Schoener, 1983; Lawton and Hassell, 1981). Underwood (1986) drew attention to the fact that different forms of symmetry/asymmetry can be distinguished which all may be relevant in some way for evaluating, and predicting the outcome of, competitive interactions.

The clear difference in the relative strengths of intraspecific interference in BA and EM (asymmetry of Type 1) is likely to reflect different competitive situations which EM and BA are usually confronted with in their typical habitats. Floating algal debris, the typical microhabitat (and food) of BA, is both spatially *and* temporally patchy. Food is a non-renewable resource which inevitably will become limiting within a short time. Intense intraspecific interference may promote dispersal and allow competitively superior individuals to monopolize the dwindling food resources (and so avoid the hazardous active search for new microhabitats) for as long as possible. The typical habitat of EM (local accumulations of broken decaying algae on the sea bed in 2–8 m depth), however, is more stable or even permanent. Food is a renewable resource which is brought along continuously with tidal currents so for populations in equilibrium there is no permanent threat that resources may become exhausted.

In the case of BA/EM, the degree of asymmetry depends to some extent on feeding regime. Asymmetry was marked in the presence of an appropriate animal source of food (Table 2B), yet it was increased in the absence of such food (Table 2A). In the latter case, adult females (both BA and EM), but not males, significantly increased the number

of cannibalistic/predatory attacks on juveniles, which probably reflects the fact that female sexual maturation depends to a greater extent on appropriate animal food than male maturation does. An increased overall number of attacks, however, will inevitably increase the degree of competitive asymmetries because the survival rate of BA is more strongly affected than that of EM.

The mechanism of competition in BA/EM resembles in some respects that in the flour beetles, *Tribolium castaneum* and *T. confusum* (Park et al., 1965). In these species, adults and larvae prey upon eggs and pupae of their own species as well as those of the other species. In contrast to the situation in EM/BA, however, either species was more affected by inter- than by intraspecific predation, and so the outcome of competition experiments was, in accordance with theory, not invariable but strongly dependent on the relative abundances of the competing species. Cannibalism and mutual predation (large larvae feeding on both conspecific and heterospecific small ones) have also been suggested, by field experiments, to play an important role in the regulation of sympatric odonate populations (Benke, 1978).

Laboratory experiments involving extremely simplified competitive systems can reveal the intrinsic abilities of the involved species and tell us what could potentially happen in nature. Furthermore, only laboratory experiments can ascertain the precise mechanisms underlying competitive interactions. It is a truism that the results of such experiments cannot simply be applied to complex real communities. For instance, a natural habitat that offers juveniles a better chance to hide from adults might improve the relative competitive ability of BA, thus reducing the degree of asymmetry. Furthermore, interactions with other species (e.g., further competitors, predators) may modify the competitive situation in the real world. It is well known that predation on a superior competitor may prevent it from eliminating inferior competitors (e.g., Paine, 1974). Mortality suffered by a species because of predation may change significantly in the presence of alternative types of prey (Fairweather, 1985, 1987). Nevertheless, there may be little doubt that in the field also, interference mechanisms (cannibalism and mutual predation) are important for the distribution and abundance of EM and BA. Indirect competition through depletion of common food resources, however, may usually play a rather subordinate role in animals which are capable of utilizing a vast array of food types. However, algal debris provides EM and BA not only with food but also with shelter. By clinging strongly to their substratum, animals may reduce predation by fish. The high degree of both intra- and interspecific interference may have its ultimate cause in the context of competition for shelter (space) rather than for food.

In geographical areas where EM and BA co-occur each species has a fairly distinct microhabitat, although some mixing can occur (Naylor, 1955b and personal observations). This leads to the question of whether current interspecific competition might play a significant role in maintaining habitat segregation of BA and EM. Because of the clear ranking in competitive abilities (high dominance of EM over BA), we expect that any effect of BA on EM distribution is negligible, the distributional limits of EM being determined by factors other than competition with BA. In contrast, the range of habitats used by the inferior competitor BA might be restricted through interspecific competition. Whenever BA and EM come to overlap in distribution, interference competition through mutual predation may be expected to arise inevitably, with EM being more or less

dominant to BA. The typical habitat of EM (in contrast to that of BA) is a permanent one; here, interference might be sufficiently sustained to roughly produce an equilibrium. Under equilibrium conditions, however, EM should be able to competitively exclude its congener from zones of potential overlap, similar to the process in mixed laboratory cultures. BA, then, appears to be confined to a suboptimal (refuge) habitat where it can persist only by continual dispersal from one temporary patch (drifting sea weed) to another.

Any current influence of EM on the range of habitats used by BA presupposes that there is a real potential for distributional overlap; i.e. no inherent limitations exist which exclude BA per se from EM habitats, and, furthermore, BA does not principally avoid EM habitats as a result of specific habitat selection. In theory, a convincing way to demonstrate a role of present-day competition in habitat segregation is by means of well-designed manipulations of field populations (Underwood, 1986, 1988; Connell, 1983). However, there are a lot of inherent difficulties with the performance and evaluation of such experiments, and they are nearly impossible to realize in small, abundant and highly mobile marine organisms. So, in order to further elucidate the actual causes of habitat segregation in BA and EM, additional laboratory experiments have been carried out on inherent distributional limitations of the species, habitat selection, and possible habitat shifts in response to competition. In a subsequent paper (Franke and Janke, in preparation) we will show that BA and EM prefer the same microhabitat; in the presence of EM, however, BA has a clear tendency to avoid its preferred habitat and so to escape from detrimental effects of the dominant competitor.

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References

- Benke, A.C., 1978. Interactions among coexisting predators – a field experiment with dragonfly larvae. *J. Anim. Ecol.* 47, 335–350.
- Branch, G.M., 1984. Competition between marine organisms: Ecological and evolutionary implications. *Oceanogr. Mar. Biol. Annu. Rev.* 22, 429–593.
- Branch, G.M., Barkai, A., 1988. Interspecific behaviour and its reciprocal interaction with evolution, populations dynamics and community structure. In: Chelazzi, G., Vannini, M. (Eds.), *Behavioural Adaptations to Intertidal Life*. Plenum Press, New York, pp. 225–254.
- Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. *Annu. Rev. Ecol. Systemat.* 3, 169–192.
- 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.
- Crocker, R.A., Hatfield, E.B., 1980. Space partitioning and interactions in an intertidal sand-burrowing amphipod guild. *Mar. Biol.* 61, 79–88.

- Douglass, R.J., 1976. Spatial interactions and microhabitat selections of two locally sympatric voles. *Microtus montanus* and *Microtus pennsylvanicus*. Ecology 57, 346–352.
- Fairweather, P.G., 1985. Differential predation on alternative prey, and the survival of rocky intertidal organisms in New South Wales. J. Exp. Mar. Biol. Ecol. 89, 135–156.
- Fairweather, P.G., 1987. Experiments on the interaction between predation and the availability of different prey on rocky seashores. J. Exp. Mar. Biol. Ecol. 114, 261–273.
- Fox, L.R., 1975. Cannibalism in natural populations. Annu. Rev. Ecol. Systemat. 6, 87–106.
- Grant, J., 1981. Factors affecting the occurrence of intertidal amphipods in reducing sediments. J. Exp. Mar. Biol. Ecol. 49, 203–216.
- Keddy, P.A., 1989. Competition. Chapman and Hall, London.
- Lawton, J.M., Hassell, M.P., 1981. Asymmetrical competition in insects. Nature 289, 793–795.
- MacArthur, R.H., 1972. Geographical ecology. Harper and Row, New York.
- Naylor, E., 1955. The ecological distribution of British species of *Idotea* (Isopoda). J. Anim. Ecol. 24, 255–269.
- Naylor, E., 1955. The life cycle of the isopod *Idotea emarginata* (Fabricius). J. Anim. Ecol. 24, 270–281.
- Naylor, E., 1955. The diet and feeding mechanism of *Idotea*. J. Mar. Biol. Assoc. UK 34, 347–355.
- Paine, R.T., 1974. Intertidal community structure. Experimental studies on the relationship between a dominant competitor and its principal predator. Oecologia 15, 93–120.
- Park, T., Mertz, D.B., Grodzinski, W., Prus, T., 1965. Cannibalistic predation in populations of flour beetles. Physiol. Zool. 38, 289–321.
- Schoener, T.W., 1983. Field experiments on interspecific competition. Am. Nat. 122, 240–285.
- Schoener, T.W., 1986. Resource partitioning. In: Kikkawa, J., Anderson, D.J. (Eds.), Community Ecology: Pattern and Process. Blackwell, Oxford, pp. 91–126.
- Simberloff, D., 1982. The status of competition theory in ecology. Ann. Zool. Fenn. 19, 241–253.
- Sokal, R.R., Rohlf, F.J., 1995. Biometry, 3rd ed. W.H. Freeman, New York.
- Sokoloff, A., Lerner, I.M., 1967. Laboratory ecology and mutual predation in *Tribolium* species. Am. Nat. 101, 261–276.
- Tinturier-Hamelin, E., 1963. Polychromatisme et détermination génétique du sexe chez l'espèce polytypique *Idotea baltica* (Pallas) (Isopode Valvifère). Cah. Biol. Mar. 4, 473–591.
- Underwood, A.J., 1986. The analysis of competition by field experiments. In: Kikkawa, J., Anderson, D.J. (Eds.), Community Ecology: Pattern and Process. Blackwell, Oxford, pp. 240–268.
- Underwood, A.J., 1988. Design and analysis of field experiments on competitive interactions affecting behaviour of intertidal animals. In: Chelazzi, G., Vannini, M. (Eds.), Behavioural Adaptations to Intertidal Life. Plenum Press, New York, pp. 333–357.
- Wallerstein, B.R., Brusca, R.C., 1982. Fish predation: A preliminary study of its role in the zoogeography and evolution of shallow water idoteid isopods (Crustacea: Isopoda: Idoteidae). J. Biogeogr. 9, 135–150.
- Wissel, C., 1989. Theoretische Ökologie. Springer, Berlin.