DISCRIMINATION BETWEEN EXPLOITATIVE AND INTERFERENCE COMPETITION BETWEEN CLADOCERA AND *KERATELLA COCHLEARIS*[1]

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Abstract. Rotifers and cladocerans are important components of most freshwater plankton communities. Large cladocerans can suppress rotifers through both mechanical interference competition (IC) and exploitative competition (EC) for shared food resources. We assessed the relative extent by which small- and large-bodied cladocerans suppressed the rotifer *Keratella cochlearis* by these mechanisms, using circulating algal suspensions in dual-chamber laboratory cultures and natural animal densities. The small-bodied cladoceran *Ceriodaphnia dubia* suppressed *Keratella* exclusively through EC, while a slightly larger species (*Daphnia ambigua*) did it primarily by this mechanism. Adults (*Daphnia galeata mendotae* and *Daphnia pulex*) and subadults (*Daphnia pulex*) of two much larger bodied cladocerans suppressed *Keratella* primarily through IC. The ratio of initial *Keratella* to adult *Daphnia pulex* density had little effect on the relative importance of the mechanisms—IC always greatly exceeded EC. Suppression by EC occurred in all treatments only after food was depleted below the concentration necessary to support maximal rotifer population growth, while suppression by IC occurred at both high and low food concentrations.

These two mechanisms by which cladocerans interact with rotifers should affect the composition of natural rotifer communities in markedly different ways; IC should favor invulnerable rotifer species, many of which are large bodied, while EC should favor rotifer species with low food requirements, which tend to be small bodied.

Key words: Ceriodaphnia; Cladocera; community structure; Daphnia; exploitative competition; food concentration; interference competition; Keratella; Rotifera; zooplankton.

INTRODUCTION

Interspecific competition is often viewed as a potent force molding the species composition and size structure of natural communities. Exploitative competition (EC) involves the utilization by conspecific or heterospecific individuals of common resources, the supply of which is limited (Tilman 1982). Interference competition (IC) encompasses a broad array of interactions including overgrowth, allelopathy, territoriality, and encounter competition (see review: Schoener 1983). Descriptions of interference among invertebrates have been limited primarily to insects and sessile inhabitants of intertidal and subtidal coral-reef environments (Schoener 1983); only recently have chemical (Folt and Goldman 1981) and encounter (Gilbert and Stemberger 1985) interference been demonstrated among taxa of freshwater zooplankton.

Daphnia can impose appreciable mortality on rotifer populations through encounter IC (Gilbert and Stemberger 1985, Burns and Gilbert 1986a, b, Gilbert 1988a). Susceptible rotifers are swept into the branchial chamber of *Daphnia* after becoming entrained in

its inhalant feeding current. Many rotifers are rapidly rejected unharmed from the branchial chamber; however, some are retained and rejected damaged or dead, and some are ingested (Gilbert and Stemberger 1985, Burns and Gilbert 1986b, Gilbert 1988a, 1989). This rotifer–cladoceran interaction is considered a form of encounter IC and not predation for a number of reasons. First, these taxa eat largely the same array of resources, while the diets of true predators often differ radically from those of their prey (Burns and Gilbert 1986a). Second, although large cladocerans can injure or kill rotifers, only very large ones can ingest them (Burns and Gilbert 1986a). Third, cladocerans may reap little nutritional benefit from the ingestion of rotifers; they probably rarely ingest them and may have difficulty digesting species with loricae. Finally, this rotifer–cladoceran interaction corresponds closely with that of "encounter interference" as defined and reviewed by Schoener (1983). IC likely occurs frequently between these large cladocerans and rotifers because both are important components of many lentic, freshwater communities.

Cladocerans and rotifers also compete indirectly for shared food resources. Rotifer food niches are often more specialized than, but generally included within, those of cladocerans (Bogdan and Gilbert 1987). Zooplankton feeding may significantly reduce the concen-

tration of edible phytoplankton, possibly causing "clear water phases" (reviewed in Lampert 1988) and increasing the potential for EC among the grazers (Kerfoot et al. 1985, Lampert et al. 1986, Sommer et al. 1986, Lair and Ayadi 1989). Rotifers and cladocerans would compete intensively during such phases (Neill 1984).

The results we present here are unusual in that quantitative discrimination between EC and IC has rarely been achieved (see Table 1). Yet the relative importance of these mechanisms may have important implications for rotifer community size structure and species composition. IC may select for rotifer species relatively immune to interference, i.e., large species or those protected by spines, mucus, coloniality, or escape responses (Gilbert 1988a), while EC between these groups may favor rotifer species with low food requirements (threshold food levels) (Stemberger and Gilbert 1985, Gilbert 1988a). Stemberger and Gilbert (1985) found that threshold food levels varied seventeen-fold among tested rotifer species and reasoned that small species with low thresholds should be favored over larger forms in habitats with consistently low food concentrations.

Quantification of EC and IC in the suppression of rotifers by cladocerans has remained inscrutable because the mechanisms are not easily separated when they operate concomitantly. Separation of the mechanisms is achieved most easily using laboratory experiments. In this study we employed press-style experimental methods to assess the importance of EC and IC in the suppression of the ubiquitous rotifer *Keratella cochlearis* f. *tecta* by adult cladocerans of different body sizes (*Daphnia pulex, Daphnia galeata mendotae, Daphnia ambigua,* and *Ceriodaphnia dubia*). *D. pulex,* the largest cladoceran, has been demonstrated to interfere strongly with this rotifer (Burns and Gilbert 1986a), while *D. ambigua* and *C. dubia* should be too small to interfere with all but newborn individuals (Gilbert and MacIsaac 1989). *D. galeata mendotae* is intermediate in size and should have intermediate interference effects. We also examined the importance of the initial abundance ratio of *D. pulex* to *K. cochlearis* by varying separately the densities of each species. Finally, we investigated the effect of intraspecific body size variation on the relative importance of EC and IC by using two size classes (adult and subadult) of *D. pulex*.

MATERIALS AND METHODS

Clonal cultures of each cladoceran species and *Keratella cochlearis* f. *tecta* were maintained on *Cryptomonas* sp. (5 × 10³ cells/mL, dry mass: 0.45 μg/mL) for >2 months in glass-fiber-filtered pond water supplemented (9:1, volume : volume) with MBL algal growth medium, at 20°C under a photoperiod (15:9, L:D) (MacIsaac and Gilbert 1989). Experiments were conducted under the same conditions in 250-mL glass
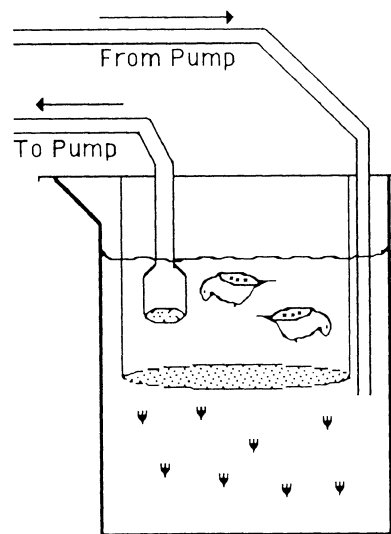

FIG. 1. Depiction of experimental vessels used to separate the effects of exploitative and interference competition in the suppression of *Keratella* by cladocerans. Rotifer populations were limited to the outer cup, while cladocerans were present in the inner cup (exploitative competition, as shown) or the outer cup (exploitative + interference competition), or were absent (rotifer control populations). The 60-μm mesh bottom on the inner cup permitted food but not animals to flow between chambers. Food was circulated with a peristaltic pump.

beakers into which were suspended 100-mL plastic beakers with 60 μm Nitex-mesh bottoms (Fig. 1). A total of 215 mL *Cryptomonas* suspension (5 × 10³ cells/mL) was added to each glass beaker, apportioned as ≈80 and 135 mL in the inner and outer cups, respectively. The end of 2.38-mm (inside diameter) silicone tubing (Manosil) was fitted with a plastic funnel covered with 316 μm Nitex mesh and placed in the inner cup. The tubing was directed through a peristaltic pump (Manostat) into the lower section of the outer cup of the same experimental vessel (Fig. 1). The pump operated continuously at a flow rate of ≈120 mL/h to minimize the possibility of an inequitable distribution of phytoplankton resulting from differential depletion of food in inner and outer cups. This flow rate circulated the suspension ≈13.4 times per day. Preliminary trials at this flow rate revealed that *Cryptomonas* did not accumulate in any region of the test containers (inner and outer cup densities = 4820 ± 2237 cells/mL, 4448 ± 1655 cells/mL [mean ± SD], $n = 3$, paired t test, $t = 0.86$, $P = .48$). Cultures were checked every 12 h to ensure that air bubbles did not form in the silicone tubing. Tubing was cleaned every 2 d.

Experimental design

Zooplankton.—Three experiments designed to determine the effect of cladoceran body size on the relative importance of EC and IC in the suppression of *Keratella* were initiated by placing 120 *K. cochlearis*

TABLE 1. Review of studies examining the simultaneous influence of exploitative competition (EC) and interference competition (IC) on inter- and intraspecific population dynamics. The review is based on a 10-yr (1978–1988) computer search of Biological Abstracts (using as key words: interference, exploit-, and competition), field studies reviewed in Schoener (1983: Table 1) in which a combination of EC and IC mechanisms are listed as operating, and other studies of which we are aware. We have followed the original authors' views of the existence and nature of competition.*

Taxa	Exploitation competition demonstrated?	Interference competition demonstrated?	Relative importance of mechanisms quantified?	Test environment	Comments	Investigator(s)
		1) Interspecific Competition				
A) Invertebrata						
Platyhelminthes	I	I	N	L		Young and Reynoldson 1988
Rotifera	Y	Y	N	L		Gilbert and Confer 1986
Rotifera vs. Arthropoda	Y	N	NA	F	PE	Neill 1984
Rotifera vs. Arthropoda	Y	N	NA	F	PE	Neill 1985
Rotifera vs. Arthropoda	Y	N	N	F	PE	Vanni 1986
Rotifera vs. Arthropoda	I	I	I	F	PE	May and Jones 1989
Rotifera vs. Arthropoda	I	Y	N	L	PI	Gilbert 1989
Rotifera vs. Arthropoda	I	I	I	L		MacIsaac and Gilbert 1989
Rotifera vs. Arthropoda	Y	Y	Y	L	PI	Schneider 1990
Rotifera vs. Arthropoda	?	I	N	F	PI	MacIsaac and Gilbert 1990
Rotifera vs. Arthropoda	Y	Y	Y	L	PI, PE, B	This study
Mollusca	I	?	N	F	PE, B	Brown 1982
Mollusca	?	I	N	F	PI	Fletcher and Underwood 1987
Mollusca	?	I	Y	F	PI	Peterson and Andre 1980
Mollusca vs. Arthropoda	?	I	N	F	?	Peterson 1979
Mollusca vs. Arthropoda	I	I	N	F	B	Creese 1982
Arthropoda						
Crustacea						
Malacostraca	Y	Y	I	L	R, B, X	Bertness 1981a
Malacostraca	I	Y	N	F	R, B	Bertness 1981b
Malacostraca	I	Y	N	F, L	B	Bovbjerg 1970
Copepoda	I	I	N	L		Bergmans and Janssens 1988
Arachnida	Y	Y	I	F	B, S	Spiller 1984
Insecta						
Diptera	I	I	N	L	PE	Budnik and Brncic 1974
Plecoptera	I	Y	N	F	PI, B, X	Peckarsky and Penton 1985
Trichoptera vs. Ephemeroptera	Y	N	Y	F	PE, B	McAuliffe 1984
Hemiptera	I	Y	N	F	PE	Pajunen 1982
Odonata	N	Y	NA	F	PI, S, B	Johnson et al. 1985
Mecoptera	N	Y	NA	F	PI, B	Thornhill 1987
Hymenoptera	I	I	N	F		Davidson 1980
Hymenoptera	I	Y	N	F	R	Fellers 1987
Hymenoptera	I	Y	N	F	PE, B	Pontin 1969
Bryozoa	I	Y	N	F	R	Rubin 1985
Echinodermata	I	?	N	F, L		Menge 1972
Echinodermata	I	Y	N	F, L	R, S	Menge and Menge 1974
B) Vertebrata						
Osteichthyes	I	I	N	F	S	Tonn 1985
Osteichthyes	I	Y	N	F, L	PI	Ebersole 1985
Osteichthyes	N	Y	N	F, L	PI, B	Larson 1980
Osteichthyes	N	Y	NA	F		Roberts 1987
Osteichthyes	I	I	N	F		Werner and Hall 1977
Osteichthyes	N	Y	NA	F, L	B	Nilsson 1963
Amphibia	I	Y	NA	L	B	Wrobel et al. 1980
Amphibia	N	Y	NA	F		Hariston 1983
Amphibia	I	N	N	F, L	S	Jaeger 1972
Amphibia	I	Y	N	L	R, B	Walls and Jaeger 1987
Aves	Y	Y	N	F		Pimm 1978
Aves	I	Y	N	F	R, S, B	Ford 1979
Aves	I	Y	N	F, L	S, B	Dhont and Eyckerman 1980
Aves	I	I	N	F	PI	Alatalo 1981
Aves	Y	Y	N	F	R, S, B	Minot and Perrins 1986
Aves	I	Y	N	L	R	Alatalo and Moreno 1987
Aves vs. Insecta (Hymenoptera)	I	Y	N	F		Gill et al. 1982
Mammalia						
Carnivora	I	I	N	F	R, B	King and Moors 1979

TABLE 1. Continued.

Taxa	Exploitation competition demonstrated ?	Interference competition demonstrated ?	Relative importance of mechanisms quantified?	Test environment	Comments	Investigator(s)
		2) Intraspecific competition				
A) Invertebrata						
Ciliophora	I	I	Y	F, L	Z	Gill 1972
Arthropoda						
Arachnida	N	Y	NA	F		Wise 1983
Insecta						
Diptera	Y	I	NA	L		Moore and Whitacre 1972
Diptera	I	I	N	L		Gilpin 1974
Diptera	I	I	N	L		Hughes 1980
Diptera	Y	N	NA	L	PE	Dye 1982
Diptera	Y	Y	Y	L, F	C	Quiring and McNeil 1984
Trichoptera	Y	I	Y	L, F	PE	Hart 1987
Odonata	?	I	N	F	PI	Van Buskirk 1987
Odonata	Y	Y	Y	F	PI	Anholt 1990
Heteroptera	I	I	I	F	PI	Heliövaara and Väisänen 1986
B) Vertebrata						
Amphibia	Y	Y	I	L	X	Steinwascher 1978
Amphibia	Y	I	?	L		Steinwascher 1981

* Key: Y = yes; N = no; I = inferred; NA = not applicable; ? = inconclusive or contradictory; L = laboratory; F = field; PE = primarily or exclusively exploitation; PI = primarily or exclusively interference; R = mechanism-dependent competitive outcome, with superior exploitative competitor inferred as inferior interference competitor; X = interference effects inferred to be relatively stronger under low food (resource) conditions, exploitation under high food conditions; S = competition intensity varies seasonally; B = intraspecific competition also involved; C = competition mechanisms operate on different larval instars; Z = interference operates among field populations, exploitation with laboratory populations.

of mixed reproductive status into the outer beaker either alone (controls), with cladocerans in the inner cup to quantify EC (Fig. 1), or with cladocerans in the outer cup to quantify the combined effects of EC and IC. Cladoceran biomasses were similar across species treatments, ≈ 40 μg dry mass. Experiments were initiated with 10 gravid *C. dubia* (adult body length [ABL, $\bar{X} \pm$ SD] = 885 $\pm$ 66 μm, $n = 26$), 2 gravid *D. pulex* (ABL = 2095 $\pm$ 137 μm, $n = 10$) or 6 gravid *D. ambigua* (ABL = 1063 $\pm$ 72 μm, $n = 33$) per container (experiments 1, 2, and 5, respectively). These cladoceran and *K. cochlearis* densities are well within the ranges reported in nature (see Gilbert 1988*b*, May and Jones 1989). A similar experiment with *D. galeata mendotae* (ABL = 1612 $\pm$ 118 μm, $n = 18$) was conducted using 6 gravid individuals (experiment 1). *Keratella* was always placed in the lower chamber to simplify their subsequent enumeration and transfer to fresh media; this arrangement was also desirable because it minimized the possibility of chemical interference against *Keratella* by drawing any labile cladoceran factor away from rather than toward the rotifers in EC treatments (see Fig. 1).

The influence of initial conditions on the importance of EC and IC was assessed directly by conducting simultaneous experiments with either 1 or 4 gravid *D. pulex* adults per container with 120 *K. cochlearis* (experiment 3), and indirectly by comparing *K. cochlearis*

performance in experiments initiated with 1 gravid *D. pulex* adult and either 120 or 200 rotifers (experiments 3 and 4). The importance of intraspecific variation in cladoceran body size was examined in treatments with either 4 gravid or 8 subadult *D. pulex* (body length [$\bar{X} \pm$ SD] = 1581 $\pm$ 111 μm, $n = 67$) and 200 *K. cochlearis* (experiment 4).

All treatments in each experiment were run in triplicate. Zooplankton populations were transferred to fresh media every 2 d and counted every 2 or 4 d. Rotifers were counted in total when populations consisted of $< \approx 600$ individuals, or estimated by three subsamples with replacement when population sizes were larger. Additional subsamples were counted if one of the initial three population estimates appeared to be outlying; suspected subsample outliers were subsequently examined with Dixon's test and removed (6 of 505) when appropriate ($\alpha = .05$; Dunn and Clark 1974). The ratio of eggs to females (egg ratio) was recorded for the first 50 rotifers encountered during sample enumeration. Cladoceran populations were censused for adult survivorship and neonate production when rotifers were transferred to fresh media. Cladoceran biomass was re-equilibrated with new individuals to initial conditions when rotifer cultures were transferred. Cladoceran survivorship (not shown) was high in all experiments ($\sim 87\%$, H. J. MacIsaac, *personal observation*). Cladocerans replaced during culture

TABLE 2. Experimental design and results of analyses of variance with repeated measures describing cladoceran effects on the population dynamics of *Keratella cochlearis*. *Keratella* densities were log-transformed prior to statistical analysis. F values (degrees of freedom) and associated probabilities from partial sums-of-squares (Type III) models are shown.

| | Cladoceran | | | Kera-tella den-sity (initial) | Effects | | | | | |
| | | | | | Cladoceran | | Replicate | | | |
Experi-ment	Species	Stage†	Den-sity		F	df	F	df	Time	Cladoceran × Time
1	*Ceriodaphnia dubia*	A	10	120	4ᴺˢ	2,6	2ᴺˢ	6,42	310 (7,42)**	6 (14, 42)**
1	*Daphnia galeata mendotae*	A	6	120	44**	2,6	3*	6,42	7 (7,42)**	33 (14,42)**
2	*D. pulex*	A	2	120	76**	2,6	2ᴺˢ	6,30	1 (5,30)ᴺˢ	46 (10,30)**
3	*D. pulex*	A	1	120	11*	2,6	13**	6,30	32 (5,30)**	39 (10,30)**
3	*D. pulex*	A	4	120	1463**	2,6	2ᴺˢ	6,30	76 (5,30)**	496 (10,30)**
4	*D. pulex*	A	4	200	84**	2,6	4**	6,30	7 (5,30)**	61 (10,30)**
4	*D. pulex*	S	8	200	29**	2,6	10**	6,30	4 (5,30)*	86 (10,30)**
5	*D. ambigua*	A	6	120	4ᴺˢ	2,6	3*	6,30	840 (5,30)**	7 (10,30)**

$* P < .05, ** P < .005, $ NS $ = P > .05.$
† Cladoceran developmental stages: A = gravid adult, S = subadult.

transfer were preserved in Lugol's iodine and measured to the nearest 38 μm with a dissecting microscope.

Relative to control populations, suppression of *Keratella* by EC and IC was calculated as:

$$\text{Exploitative competition} = 100(A-B)/(A), \quad (1)$$

and

$$\text{Interference competition} = 100(B-C)/(A), \quad (2)$$

where A, B, and C are *Keratella* population densities in control, EC, and EC + IC treatments, respectively, averaged over replicates. Because IC and EC occurred in 135 mL and 215 (80 ± 135) mL, respectively, the values for IC suppression were mildly exaggerated. These values were volume-corrected (IC^1 = IC × [135/215]) prior to calculating the relative importance of interference (RIC) to modified total suppression (RIC = 100[IC^1/(IC^1 + EC)]). Calculations aimed at differentiating between the mechanisms assumed that no EC × IC interactions existed (i.e., exploitative effects were similar in both EC and EC + IC treatments). At least one interaction is possible, however. IC could intensify as food is depleted; Burns and Gilbert (1986*b*) observed that interference was greater at low than at high algal food levels.

Algae. — *Cryptomonas* in inner cups (Fig. 1) was usually sampled and enumerated when zooplankton was enumerated by removing 10 mL of suspension from throughout the inner chamber with a Pasteur micropipet. Samples were settled in Utermöhl chambers (Hasle 1978) after fixation with acid Lugol's solution. After 24 h, 8 to 10 fields were enumerated at 100 magnifications with a Zeiss inverted microscope.

Statistical analyses

The dependency of rotifer egg-ratio on food concentration was analyzed as a hyperbolic function (NLIN procedure, SAS Institute 1985) using single-species *Keratella* populations from experiment 1.

Keratella population growth and egg-ratios in control cultures were compared to those in EC and EC + IC treatments, for each cladoceran species, using univariate analysis of variance with repeated measures and the Ryan-Einot-Gabriel-Welsch (REGWQ) multiple comparisons means test (SAS Institute 1985). Population data were transformed to base-10 logarithms as log(x + 1) prior to analysis to stabilize variance, while egg-ratio data were arcsin(x)$^{0.5}$-transformed.

Comparisons of the extent to which *Keratella* populations were suppressed by EC or IC were limited to treatments that were run concurrently (see Table 2), because the growth of single-species populations differed significantly ($P < .05$, repeated-measures ANOVA) among experiments. The analysis of *D. pulex* density effects was not hampered by this problem, nor was the analysis of *D. pulex* body-size effects.

RESULTS

Comparisons among cladoceran species

The relative importance of EC and IC in the suppression of *Keratella* varied dramatically among cladoceran species and was strongly related to body size. The small cladoceran *C. dubia* suppressed *Keratella* exclusively through EC (Fig. 2a, b; Table 2), while larger cladocerans did it by both mechanisms (a and b in Figs. 3–9). The mechanisms also varied temporally in absolute and relative importance. In general, EC increased with time in both absolute and relative importance, while IC declined (b in Figs. 3–9).

Control *Keratella* populations diverged significantly from those in the EC (≈day 4) and EC + IC (≈day 8) treatments with *Ceriodaphnia* (Fig. 2a, b; Table 2: cladoceran × time effect). While *Ceriodaphnia* was unable to exclude *Keratella* in any treatment, overall mean *Keratella* densities were significantly lower in both EC and EC + IC treatments than in the control treatment
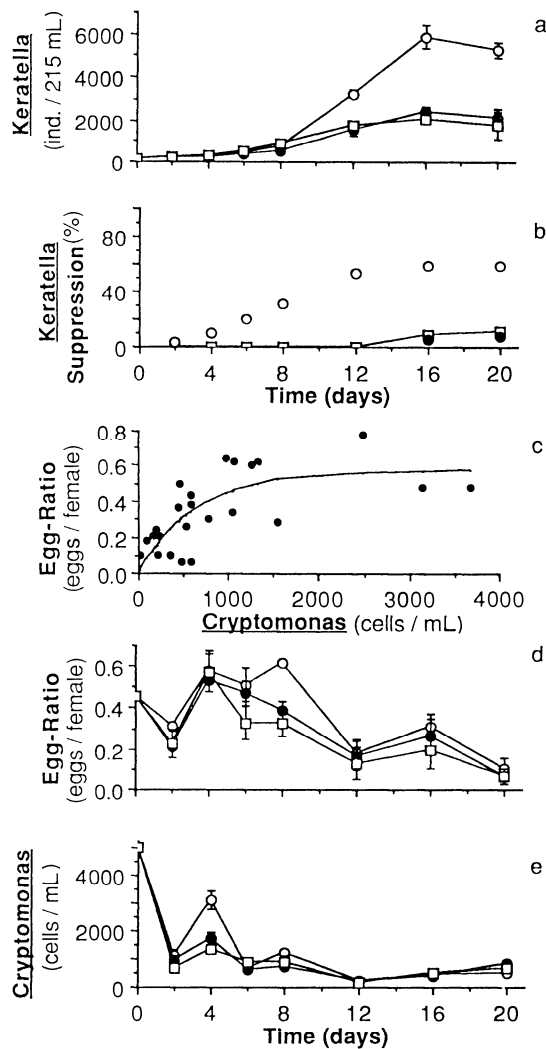
FIG. 2. (a) Density of *Keratella cochlearis* in single-species (O), exploitation only (●), and exploitative + interference (□) *Ceriodaphnia dubia* competition treatments (mean ± 1 SE, n = 3). Initial conditions: 120 K. *cochlearis*, 10 adult C. *dubia*. (b) Suppression of *Keratella* expressed as the percentage reduction from control populations, due to exploitative competition (O) and interference competition (●). The line with open boxes depicts the relative contribution of interference competition to total suppression. It is solid except when its determination was affected greatly by population densities in control and exploitation-only treatments (see *Discussion: Interference, exploitation, and food availability*). Interference effects are shown only when suppression by interference and exploitative competition combined exceeded exploitative competition alone. (c) Observed (●) and predicted (——) *Keratella* fecundity in relation to residual food concentration for control rotifer population cultures. (d) Mean *Keratella* egg-ratio and (e) residual food concentration in C. *dubia* treatments; symbols and values as per (a).

(REGWQ test, $P < .05$). However, mean rotifer density in EC and EC + IC treatments did not differ significantly (REGWQ test, $\alpha = .05$). Decreased *Keratella* densities in treatments with *Ceriodaphnia* were associated with significant declines in *Keratella* egg-ratio

(ANOVA, $P < .05$; Fig. 2d) and, concomitantly, with declines in food concentration (Fig. 2e). Food in all treatments was virtually always depressed below 10^3 cells/mL at the end of each 2-d interval after day 6. At these food levels *Keratella*'s fecundity was impaired for at least a portion of each 2-d interval between food replenishment pulses (Fig. 2c, d).

D. ambigua significantly (ANOVA, $P < .05$; Table 2: cladoceran × time effect) suppressed *Keratella* in both EC and EC + IC treatments (Fig. 3a, b). The evidence for IC by *D. ambigua* is equivocal because rotifer populations in the EC + IC treatment were larger than those in the EC treatment on the final days despite being smaller earlier in the experiment (Fig. 3a). Weak or non-existent IC by *D. ambigua* (and C. *dubia*) is also suggested by the lack of a significant main term (cladoceran) effect (Table 2). The EC + IC treatment experienced a slightly but insignificantly (REGWQ test, $\alpha = .05$) higher mean egg ratio than the control and EC treatments after day 8 (Fig. 3c). Food levels declined rapidly (in < 4 d) and remained low in each treatment for the duration of the experiment (Fig. 3d).
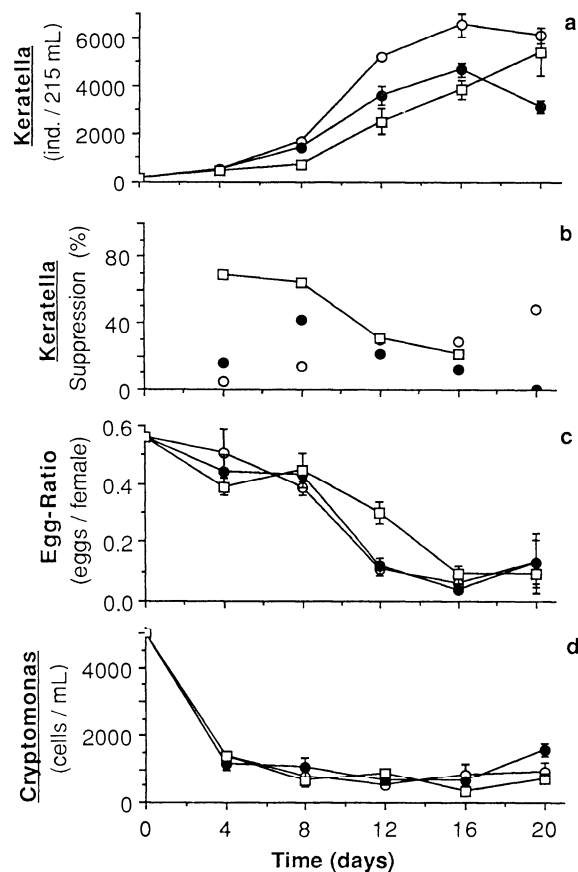

FIG. 3. *Keratella cochlearis* (a) density, (b) suppression, and (c) fecundity, and (d) residual food concentration, in *Daphnia ambigua* treatments (mean ± 1 SE; n = 3). Initial conditions: 120 K. *cochlearis*, 6 adult *D. ambigua*. Symbols and values as per Fig. 2a, b.
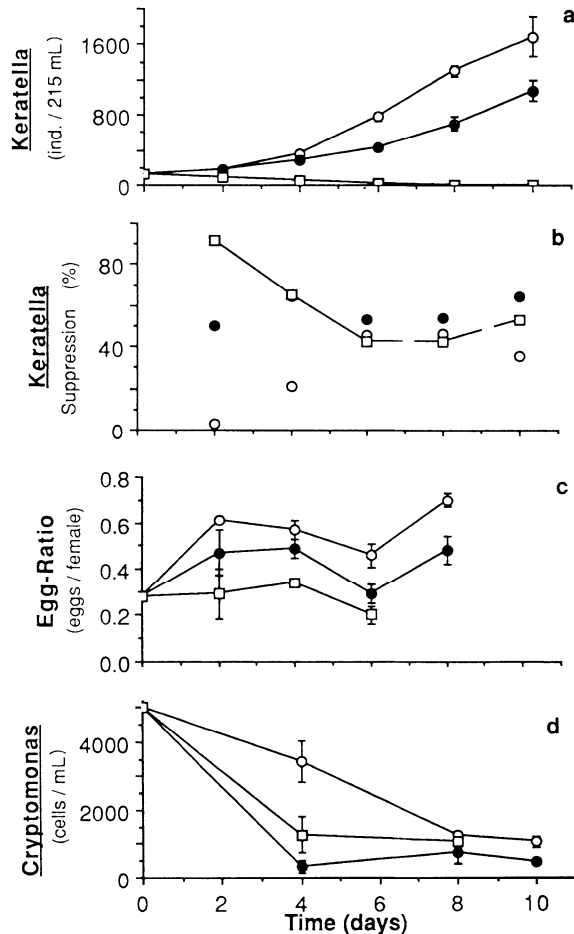
FIG. 4. *Keratella cochlearis* (a) density, (b) suppression, and (c) fecundity, and (d) residual food concentration, in *Daphnia pulex* treatments (mean ± 1 SE; n = 3). Initial conditions: 120 *K. cochlearis*, 2 adult *D. pulex*. Symbols and values as per Fig. 2a, b. All replicate *K. cochlearis* populations in the exploitative + interference treatment went extinct after day 8.

In trials with a similar biomass of the large cladoceran *D. pulex, Keratella* went extinct in all EC + IC treatment replicates within 10 d (Fig. 4a). The severity of EC with *D. pulex* increased more rapidly, between days 2 and 4, than with the small-bodied cladocerans (graph b in Figs. 2–4). Mean *Keratella* population densities differed significantly (REGWQ test, P < .05) between all *D. pulex* treatments. While the maximal degree of suppression due to EC (≈46%) was lower than that observed with the smaller cladoceran species, IC was clearly the dominant mechanism by which *D. pulex* suppressed *Keratella* (Fig. 4b). *Keratella* fecundity was significantly higher in the control treatment than in both competition treatments (REGWQ test, P < .05; Fig. 4c). Despite higher food levels, rotifer fecundity was significantly (REGWQ test, P < .05) lower in the EC + IC treatment than in the EC treatment (Fig. 4c, d).

Keratella was excluded or suppressed to near ex-

tinction in each replicate of the EC + IC treatment with *D. galeata mendotae*, but persisted at suppressed levels in the EC treatment with this cladoceran (Fig. 5a, b, Table 2). Evidence of EC did not become marked until after day 8, unlike the onset of IC, which began soon after the experiment was initiated (Fig. 5a, b). Relative to rotifer populations in the control treatment, egg-ratios were significantly lower in the EC treatment but not in the EC + IC treatment (REGWQ test, P < .05; Fig. 5c). The egg-ratio in the latter treatment actually increased as *Keratella* became increasingly suppressed (Fig. 5c). This pattern was complemented, and possibly initiated, by higher food levels and smaller rotifer populations in the EC + IC treatment (Figs. 5c, d, 2c).

Differences in the abilities of *C. dubia, D. ambigua, D. galeata mendotae* and *D. pulex* to suppress *Keratella* related primarily to their abilities to interfere with *Keratella*, as each species suppressed *Keratella* populations by ≈46–60% through EC (graph b in Figs. 2–5). Only
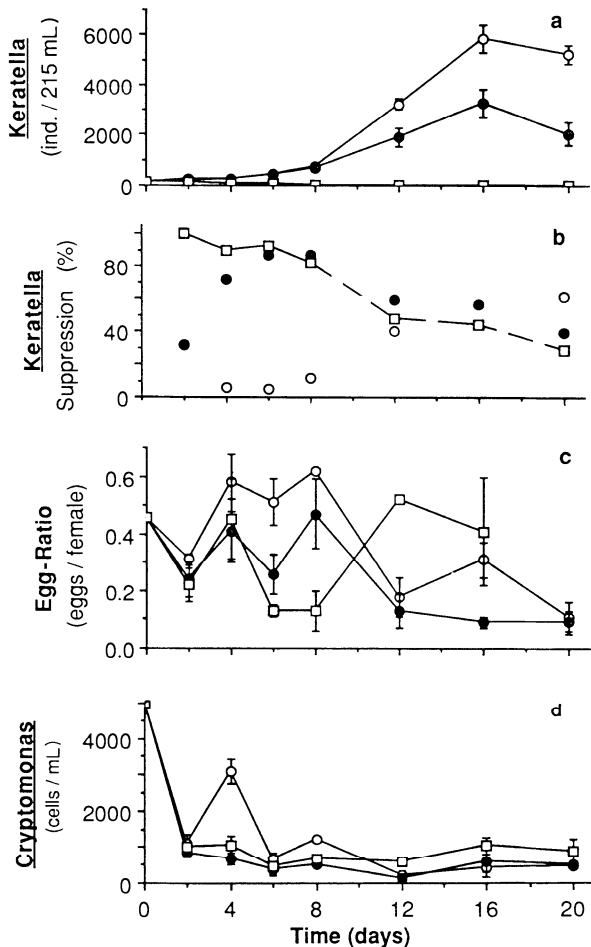

FIG. 5. *Keratella cochlearis* (a) density, (b) suppression, (c) fecundity, and (d) residual food concentration, in *Daphnia galeata mendotae* treatments (mean ± 1 SE; n = 3). Initial conditions: 120 *K. cochlearis*, 6 adult *D. galeata mendotae*. Symbols and values as per Fig. 2a, b.
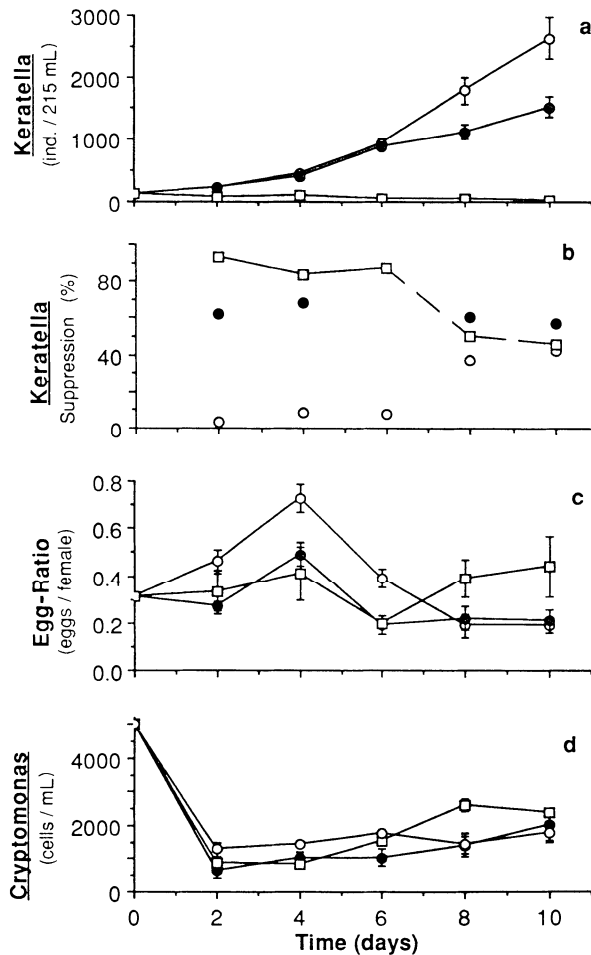
FIG. 6. *Keratella cochlearis* (a) density, (b) suppression, (c) fecundity, and (d) residual food concentration, in *Daphnia pulex* treatments (mean ± 1 SE; n = 3). Initial conditions: 120 *K. cochlearis*, 1 adult *D. pulex*. Symbols and values as per Fig. 2a, b.

the larger species, *D. galeata mendotae* and *D. pulex*, demonstrated unequivocal evidence of IC against *Keratella*.

Effects of initial conditions

Keratella was significantly suppressed (Table 2) in EC + IC treatments regardless of whether experiments were conducted with 1 or 4 adult *D. pulex* (experiment 3, Figs. 6a and 7a, respectively). Mean *Keratella* densities differed significantly between control and competition treatments in the experiments with both 1 and 4 *Daphnia* (REGWQ tests, P < .05). IC greatly exceeded EC in treatments with both one and four *Daphnia* (Figs. 6b and 7b), but some differences between *Daphnia* density treatments were evident. Suppression by EC began earlier (≈day 2 vs. ≈day 4), egg-ratios were consistently lower (Figs. 6c and 7c), and food depletion was more extensive (Figs. 6d and 7d) in treatments with four *D. pulex* than with one *D. pulex*. Maximal suppression of *Keratella* through EC was also

greater in treatments with four *Daphnia* (Figs. 6b and 7b). Overall mean *Keratella* density was significantly higher in the one-*Daphnia* EC treatment than in the corresponding four-*Daphnia* treatment (REGWQ test, P < .05). Treatments with different *Daphnia* densities differed most with respect to the intensity of IC; *Keratella* went extinct in all EC + IC replicates with four *Daphnia* by day 4, but persisted in all of the corresponding one-*Daphnia* replicates. Overall mean *Keratella* density was significantly greater in the EC + IC treatment with only one *Daphnia* (REGWQ test, P < .05). These results correspond closely with those described for two adult *D. pulex* (experiment 2), in which *Keratella* was excluded in the EC + IC treatment by day 10 (Fig. 4a).

The effect of varying initial *Keratella* density can be assessed qualitatively from treatments with four adult *D. pulex* (experiments 3 and 4, Figs. 7a and 8a). The main difference between treatments initiated with 120
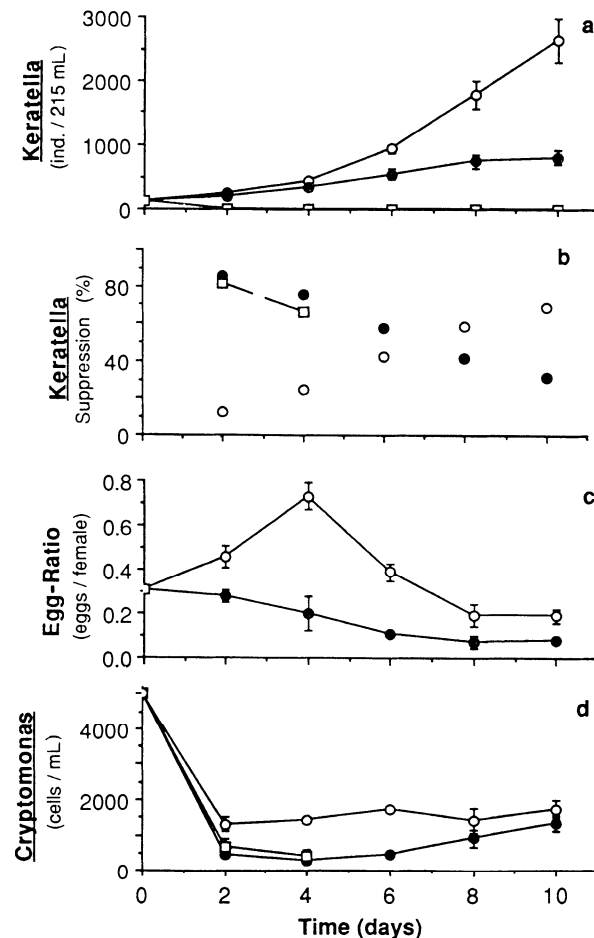

FIG. 7. *Keratella cochlearis* (a) density, (b) suppression, (c) fecundity, and (d) residual food concentration, in *Daphnia pulex* treatments (mean ± 1 SE; n = 3). Initial conditions: 120 *K. cochlearis*, 4 adult *D. pulex*. Symbols and values as per Fig. 2a, b. All replicate *K. cochlearis* populations in the exploitative + interference treatment were extinct by day 4.
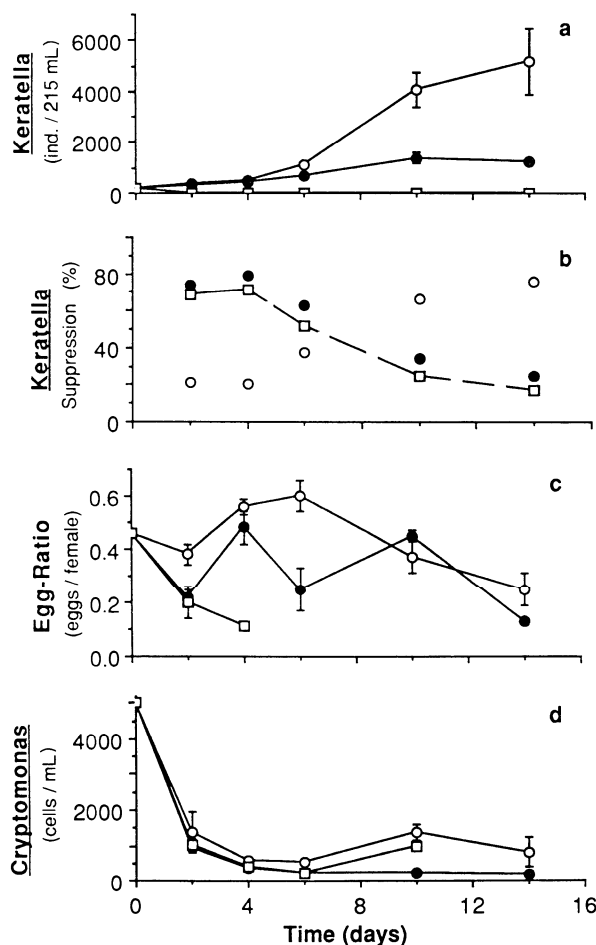
FIG. 8. *Keratella cochlearis* (a) density, (b) suppression, (c) fecundity, and (d) residual food concentration, in *Daphnia pulex* treatments (mean ± 1 SE; *n* = 3). Initial conditions: 200 *K. cochlearis*, 4 adult *D. pulex*. Symbols and values as per Fig. 2a, b. All replicate *K. cochlearis* populations in the exploitative + interference treatment went extinct by day 10.

and 200 individuals was the mean size of the control populations at day 10 (2634 and 4045, respectively). The effect of EC, and the time to exclusion of *Keratella* in EC + IC treatments, did not differ markedly between experiments with different initial rotifer densities.

Daphnia *developmental stage*

Adult and subadult *D. pulex* had similar overall effects on the population dynamics of *Keratella*, though the effects exerted by the former were generally stronger and occurred more rapidly than those of the latter. *Keratella* population growth was suppressed significantly in EC treatments in both four-adult (Fig. 8a; Table 2) and eight-subadult *D. pulex* treatments (Fig. 9a, Table 2) relative to control populations. The extent of the suppression of *Keratella* populations by EC was very similar between *Daphnia* developmental stages (Figs. 8b and 9b; REGWQ test, *P* > .05). *Keratella* egg-ratios were significantly (REGWQ tests, *P* < .05)

lower in both adult (Fig. 8c) and subadult (Fig. 9c) *D. pulex* EC and EC + IC treatments relative to control populations. The pattern of egg-ratio decline was coincident with a rapid decline in food availability in all mixed-species cultures and, to a lesser extent, in control *Keratella* cultures (Figs. 8d and 9d).

IC was a potent suppressive agent of *Keratella* for both *Daphnia* size classes (Figs. 8b and 9b). *Keratella* population dynamics (Table 2) and mean population sizes (REGWQ tests, *P* < .05) were significantly different in the EC + IC treatment compared to the EC and control treatments for both adult and subadult *Daphnia*. Combined effects of EC + IC competition were significantly greater (REGWQ test, *P* < .05) with adult *Daphnia* than with subadult *Daphnia*, though *Keratella* densities were strongly reduced by both size classes.

DISCUSSION

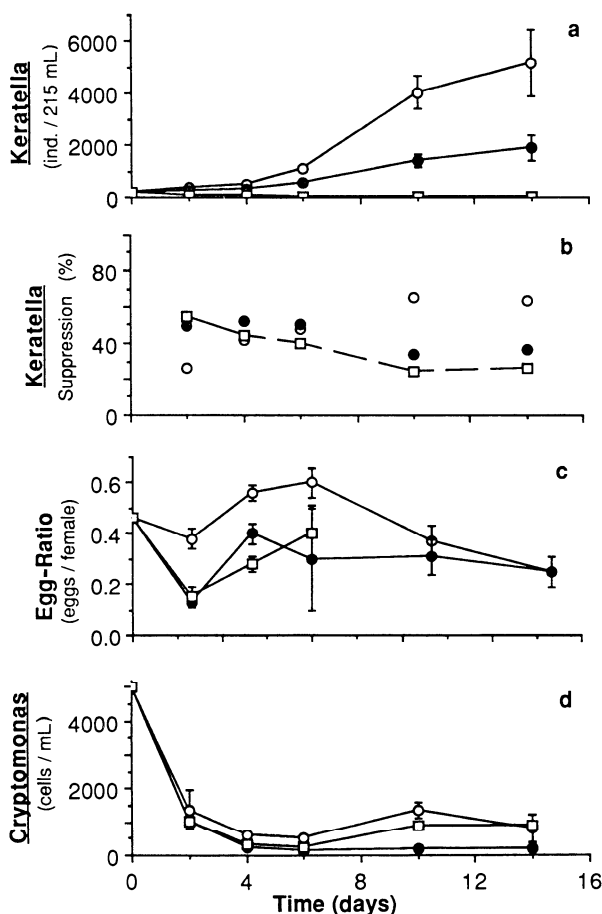Interference and exploitative competition have been demonstrated separately with many taxa in the field

FIG. 9. *Keratella cochlearis* (a) density, (b) suppression, (c) fecundity, and (d) residual food concentration, in *Daphnia pulex* treatments (mean ± 1 SE; *n* = 3). Initial conditions: 200 *K. cochlearis*, 8 subadult *D. pulex*. Symbols and values as per Fig. 2a, b.

(see Connell 1983, Schoener 1983). However, investigators have encountered great difficulty in attempting to quantitatively separate their relative importance (Table 1; but see Groves and Williams 1975, Hart 1987, Anholt 1990, Schneider 1990). In this study we have demonstrated that the mechanisms can operate simultaneously and, further, that their relative importance is contingent upon the size (species and developmental stage) of cladoceran involved.

Interference, exploitation, and food availability

Differences among cladoceran species in their ability to suppress rotifers through IC and EC are related to cladoceran body length and density. Burns and Gilbert (1986a) found direct correspondence between cladoceran body length and interference potential, while Burns and Rigler (1967) observed a similar pattern between body length and filtering rate. Suppression of *Keratella* by IC requires a minimum *Daphnia* body length of ≈ 1.2 mm (Burns and Gilbert 1986a), but may occur at any food concentration (Figs. 4–9; Gilbert 1988a). The efficacy of IC also varies according to the species and age (size) of rotifer involved (Gilbert and Stemberger 1985, Gilbert 1988a, Gilbert and MacIsaac 1989).

Suppression of *Keratella* through EC by small- and large-bodied cladocerans can occur only after food resources have been depleted below the level necessary to support maximal rotifer population growth (r_{max}), a level determined by Kirk and Gilbert (1990) to be $\approx 1.1 \times 10^3$ cells/mL for *K. cochlearis* fed *Cryptomonas* sp. Our experiments indicate that the small-bodied cladoceran *Ceriodaphnia dubia* suppressed *Keratella* by EC only, and only after food became limited in supply (Fig. 2a, b, and e). The results for *D. ambigua* are more difficult to interpret, as it appeared to suppress *Keratella* by IC early in the experiment (Fig. 3a and b). Because the IC effect was not sustained, however, interference was not likely responsible for the differences in *Keratella* population sizes between EC and EC + IC treatments. This argument is supported by Burns and Gilbert's (1986b) determination that *D. ambigua* has a very low ability to kill *K. cochlearis*, and by Gilbert and MacIsaac's (1989) finding that very high densities of *D. ambigua* are required to significantly interfere with this species.

The larger-bodied cladocerans *D. galeata mendotae* and *D. pulex* suppressed *Keratella* abundance by both mechanisms when food was scant, and by IC only when food was abundant. This result contradicts Steinwascher's (1978) contention that IC mechanisms supplant EC at low food density. Steinwascher based his hypothesis on studies of intraspecific competition among tadpoles of the Southern Leopard frog *Rana utricularia* and found support for it with other vertebrate and invertebrate taxa (see Steinwascher 1978). It should be recalled, however, that EC can occur only when common resources are in short supply. This condition necessarily precludes the possibility of EC at high food levels, even though one species may achieve numerical dominance over another under these conditions. Such a pattern appears to occur commonly in zooplankton competition studies (see MacIsaac and Gilbert 1989).

The importance of EC relative to IC increased through time in many of the cladoceran treatments (b in Figs. 3–9) for at least two reasons. First, EC did not occur until food became limiting, after which time it increased in both absolute and relative terms (d in Figs. 2–9). Second, the absolute amount of suppression by IC was calculated using information from the control and EC treatments (in addition to the EC + IC treatment); when rotifer populations in the IC treatment were nearly extinct, absolute suppression by IC was determined almost entirely by the relationship between the control and EC treatments. It should be noted, however, that cladocerans capable of inflicting high rates of interference-induced mortality on rotifers minimize EC with rotifers by reducing the number of potential competitors.

While this study was designed to discriminate only between EC and encounter IC, it also suggests that cladocerans are unlikely to chemically interfere with *Keratella*. Chemical interference should cause populations in both EC and EC + IC treatments to diverge from corresponding control populations even in the absence of food limitation or encounter IC. This was not evident in our experiments; control rotifer populations were tracked for 6–8 d by both EC and EC + IC populations in *Ceriodaphnia* experiments (Fig. 2a), 8 d in the *D. ambigua* and *D. galeata mendotae* EC treatments (Figs. 3a, 5a), and 6 d in a *D. pulex* EC treatment (Fig. 6a).

Interference costs and interference–exploitation tradeoffs

Competition theorists have speculated that IC is likely to evolve when the potential for intense EC between species is high (Case and Gilpin 1974). Much of this vertebrate-oriented theory has assumed that interference is directed or intentional, and that it involves an energy cost to the interfering species. Of the four primary IC mechanisms described by Schoener (1983)—overgrowth, encounter, chemical, and territorial—at least the latter two presumably entail an energy cost to the interfering species. For example, nectar-feeding stingless bees prevent hummingbirds from exploiting nectar in *Passiflora* flowers by aggressively pursuing individuals approaching flowers exploited by the bees (Gill et al. 1982). While chasing off approaching birds, the bees expend rather than acquire energy. IC by cladocerans against rotifers provides a contrasting variant on this generality; it is unlikely that interference involves a direct energy cost to *Daphnia* because the expulsion of rotifers entrained in the branchial chamber or food groove requires only a momentary cessa-

tion of feeding by the cladoceran (Burns and Gilbert 1986b). The *Daphnia*–rotifer interaction can thus be categorized as "gratuitous competition" (Case and Gilpin 1974) in addition to encounter competition (Schoener 1983).

Literature reports of a tradeoff between abilities for EC and IC are common (see Table 1: Comments). Many species appear to counteract inferior interference ability with superior exploitative ability. As examples, Rubin (1985) reported that bryozoans were able to coexist with superior interference-competing polychaetes by preempting space, while Fellers (1987) determined that inferior interference-competing woodland ant species located and exploited new food sources significantly faster than coexisting superior interference-competing species.

Our studies have revealed that the dynamics of competition between rotifers and cladocerans should be affected by at least four factors—cladoceran density and body size distribution, susceptibility of rotifer species to interference, and the concentration of food—and that tradeoffs may exist between abilities for EC and IC between the groups. Laboratory studies have demonstrated that large cladocerans exclude some rotifers through a combination of EC and IC (a in each of Figs. 4–5, 7–9; see also Gilbert 1985, 1989, Gilbert and Stemberger 1985, MacIsaac and Gilbert 1989). Gilbert (1988a) reasoned that, in the presence of populations of large *Daphnia*, rotifer communities would be dominated by large or small, interference-invulnerable species when food is abundant, but only by small interference-invulnerable species under conditions of food limitation. These postulated patterns are based on the general invulnerability of large rotifer species to interference (Gilbert 1988a), the greater reproductive potentials of large rotifers when food is abundant, and the lower threshold food levels of small species (Stemberger and Gilbert 1985). The predictions are supported by some field evidence (see review, Gilbert 1988a).

Other factors affect competition between small-bodied (≤1.2 mm) cladocerans and rotifers. Competition between these taxa appears to be primarily or exclusively exploitative in nature (a and b in Figs. 2–3; see also Gilbert and MacIsaac 1989, MacIsaac and Gilbert 1989), and rotifers appear to be superior competitors under some conditions. For example, Kirk and Gilbert (1990) determined that *K. cochlearis* f. *tecta* has a lower threshold food level than *D. ambigua*, and, according to resource-based competition theory (see Tilman 1982), should be favored when competing with it. Competitive exclusion of *D. ambigua* by *K. cochlearis* has been observed under low but not high food concentrations in laboratory studies (MacIsaac and Gilbert 1989). Thus, while large cladocerans are superior competitors to many rotifer species through a combination of EC and, especially, IC mechanisms, at least one common rotifer species appears to be an effective ex-

ploitative competitor against at least one cladoceran by virtue of its low threshold food requirements. Moreover, the numerical responses of many rotifer species are greater than those of cladocerans, thereby allowing them to exploit resources before interference increases. Fellers (1987) has also described such a pattern for ants. Rapid numerical responses may permit even interference-vulnerable rotifer species to persist in systems with large cladocerans through temporal separation of the taxa. Such a sequence has been described by Neill (1984).

Rotifer abundance and community structure

The impact of EC and IC by cladocerans on rotifers should vary according to the form and intensity of predation exerted on the plankton community. EC may assume a relatively greater role in communities with size-selective planktivorous fish and small-bodied cladocerans (Lynch 1979). By contrast, IC should become increasingly important in systems without vertebrate planktivores and with large-bodied cladocerans.

Two field studies provide data suitable for an examination of the relative roles of cladoceran EC and IC in affecting rotifer abundance and community structure. Rotifers are abundant in oligotrophic Gwendoline Lake, British Columbia, only during spring before *Daphnia rosea* increases in body size (≈2 mm adult body length) and adult density (Neill 1984). Based on experimental enclosures with varying *Daphnia* densities, Neill argued that EC rather than IC (predation) was responsible for the suppression of the rotifers *Conochilus hippocrepis, Polyarthra vulgaris, Kellicottia longispina,* and *K. cochlearis* by *D. rosea* in Gwendoline Lake. Two lines of evidence provide some support for Neill's view. First, Gilbert (1988a) determined that congeneric members of the three former taxa were quite invulnerable to interference by *D. pulex; Conochilus* colonies are too large to enter the branchial chamber of *Daphnia, Polyarthra* has an effective escape response when entrained in *Daphnia* inhalant currents, and the elongate, spined lorica of *Kellicottia* provides effective protection against interference. Second, the egg-ratios of the *Kellicottia* and *Keratella* populations increased when food supplies were indirectly increased (Neill 1984). *K. cochlearis* was the only rotifer in Neill's study potentially affected by *Daphnia* interference. Juvenile *Daphnia* overlapped spatially and temporally more extensively than adults with *K. cochlearis* in a control enclosure, but small cladocerans have limited interference abilities against this rotifer (a and b in Figs. 2 and 3). *K. cochlearis* was absent from the enclosure when adult *D. rosea* density (≈5 individuals/L) and interference potential (*Daphnia*-induced *Keratella* death rate: ≈0.17/day) (derived from formula in Gilbert 1989) where maximal. Our results with *Daphnia* of a similar size and density (Fig. 6a, b and d) indicate that the concentration of food would have to be chronically low in order for EC suppression to approach the intensity

of IC suppression. This condition appears to be satisfied, generally, in Gwendoline Lake as phytoplankton is abundant only sporadically (Neill 1984).

May and Jones (1989) analyzed the dynamics of *Keratella cochlearis* and *Daphnia hyalina* var. *lacustris* in Loch Leven, Scotland, over a 5-yr time span. During each year the densities of the species were always inversely related. May and Jones argued that EC was the primary mechanism by which *Daphnia* suppressed *Keratella*. They suggested that rotifer birth rates and chlorophyll *a* concentrations appeared to decrease during periods when *Daphnia* filtering rates were high. However, correlations between rotifer birth rate, a measure of rotifer fitness, and chlorophyll *a* concentration, a measure of food concentration, indicated that *Keratella* was not food limited for four of the five study years (MacIsaac and Gilbert 1990). Therefore, it seems unlikely that EC was responsible for the suppression of *Keratella*. However, comparisons between predicted *Daphnia*-induced *Keratella* death-rate values and corresponding *Keratella* abundance patterns indicate that *Keratella* was rare whenever the interference potential was high, and abundant only when the interference potential was low (MacIsaac and Gilbert 1990). These relationships provide circumstantial support for the regulation of *Keratella* density in Loch Leven by IC rather than EC from *Daphnia*.

In conclusion, our laboratory study has demonstrated that both EC and IC contribute to the suppression of *Keratella cochlearis* by cladocerans. The intensity of both mechanisms increases with increasing cladoceran body length and density, as does the primacy of IC over EC. The mechanisms can operate simultaneously at low food concentrations, but only IC can occur when food is not limiting. Field studies indicate that both mechanisms likely affect *Keratella* densities in the field, though their relative importance is very difficult to assess. The relative importance of the mechanisms may strongly influence rotifer community size structure and species composition.

LITERATURE CITED

Alatalo, R. V. 1981. Interspecific competition in tits *Parus* spp. and the goldcrest *Regulus regulus*: foraging shifts in multispecific flocks. Oikos 37:335–344.

Alatalo, R. V., and J. Moreno. 1987. Body size, interspecific interactions, and use of foraging sites in tits (Paridae). Ecology 68:1773–1777.

Anholt, B. R. 1990. An experimental separation of interference and exploitative competition in a larval damselfly. Ecology 71:1483–1493.

Bergmans, M., and P. P. M. Janssens. 1988. Competition between the sibling species *Tisbe holothuriae* and *T. battagliai* (Harpacticoida). Hydrobiologia 167:455–462.

Bertness, M. D. 1981*a*. Interference, exploitation, and sexual components of competition in a tropical hermit crab assemblage. Journal of Experimental Marine Biology and Ecology 49:189–202.

———. 1981*b*. Competitive dynamics of a tropical hermit crab assemblage. Ecology 62:751–761.

Bogdan, K. G., and J. J. Gilbert. 1987. Quantitative comparison of food niches in some freshwater zooplankton: a multi-tracer cell approach. Oecologia (Berlin) 72:331–340.

Bovbjerg, R. V. 1970. Ecological isolation and competitive exclusion in two crayfish (*Oronectes virilis* and *Oronectes immunis*). Ecology 51:225–236.

Brown, K. M. 1982. Resource overlap and competition in pond snails: an experimental analysis. Ecology 63:412–422.

Budnik, M., and D. Brncic. 1974. Preadult competition between *Drosophila pavani* and *Drosophila melanogaster*, *Drosophila simulans*, and *Drosophila willistoni*. Ecology 55:657–661.

Burns, C. W., and J. J. Gilbert. 1986*a*. Effect of daphnid size and density on interference between *Daphnia* and *Keratella cochlearis*. Limnology and Oceanography 31:848–858.

Burns, C. W., and J. J. Gilbert. 1986*b*. Direct observations of the mechanisms of interference between *Daphnia* and *Keratella cochlearis*. Limnology and Oceanography 31:859–866.

Burns, C. W., and F. H. Rigler. 1967. Comparison of filtering rates of *Daphnia rosea* in lake water and in suspensions of yeast. Limnology and Oceanography 12:492–502.

Case, T. J., and M. E. Gilpin. 1974. Interference competition and niche theory. Proceedings of the National Academy of Sciences (USA) 71:3073–3077.

Connell, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. American Naturalist 122:661–696.

Creese, R. G. 1982. Distribution and abundance of the Acmaeid limpet, *Patelloida latistrigata*, and its interactions with barnacles. Oecologia (Berlin) 52:85–96.

Davidson, D. W. 1980. Some consequences of diffuse competition in a desert ant community. American Naturalist 116:92–105.

Dhont, A. A., and R. Eyckerman. 1980. Competition between the Great Tit and the Blue Tit outside the breeding season in field experiments. Ecology 61:1291–1296.

Dunn, O. J., and V. A. Clark. 1974. Applied statistics: analysis of variance and regression. John Wiley & Sons, Toronto, Canada.

Dye, C. 1982. Intraspecific competition amongst larval *Aedes aegypti*: food exploitation or chemical interference? Ecological Entomology 7:39–46.

Ebersole, J. P. 1985. Niche separation of two damselfish species by aggregation and differential microhabitat utilization. Ecology 66:14–20.

Fellers, J. H. 1987. Interference and exploitation in a guild of woodland ants. Ecology 68:1466–1478.

Fletcher, W. J., and A. J. Underwood. 1987. Interspecific competition among subtidal limpets: effect of substratum heterogeneity. Ecology 68:387–400.

Folt, C. L., and C. R. Goldman. 1981. Alleopathy in zooplankton: a mechanism for interference competition. Science 213:1133–1135.

Ford, H. A. 1979. Interspecific competition in Australian honeycreepers—depletion of common resources. Australian Journal of Ecology 4:145–164.

Gilbert, J. J. 1985. Competition between rotifers and *Daphnia*. Ecology 66:1943–1950.

———. 1988*a*. Susceptibilities of ten rotifer species to interference from *Daphnia pulex*. Ecology 69:1826–1838.

———. 1988*b*. Suppression of rotifer populations by *Daphnia*: a review of the evidence, the mechanisms, and the effects on zooplankton community structure. Limnology and Oceanography 33:1286–1303.

———. 1989. The effect of *Daphnia* interference on a natural rotifer and ciliate community: short-term bottle experiments. Limnology and Oceanography 34:606–617.

Gilbert, J. J., and J. L. Confer. 1986. Gigantism and the potential for interference competition in the rotifer genus *Asplanchna*. Oecologia (Berlin) 70:549–554.

Gilbert, J. J., and H. J. MacIsaac. 1989. The susceptibility of *Keratella cochlearis* to interference from small cladocerans. Freshwater Biology 22:333–339.

Gilbert, J. J., and R. S. Stemberger. 1985. Control of *Keratella* populations by interference competition from *Daphnia*. Limnology and Oceanography 30:180–188.

Gill, D. E. 1972. Intrinsic rates of increase, saturation densities, and competitive ability. 1. An experiment with *Paramecium*. American Naturalist 106:461–471.

Gill, F. B., A. L. Mack, and R. T. Ray. 1982. Competition between hermit hummingbirds Phaethorninae and insects for nectar in a Costa Rican rain forest. Ibis 124:44–49.

Gilpin, M. E. 1974. Intraspecific competition between *Drosophila* larvae in serial transfer systems. Ecology 55:1154–1159.

Groves, R. H., and J. D. Williams. 1975. Growth of skeleton weed (*Chondrilla juncea* L.) as affected by growth of subterranean clover (*Trifolium subterraneum* L.) and infection by *Puccinia chondrillina* Bubak & Syd. Australian Journal of Agricultural Research 26:975–983.

Hairston, N. G. 1983. Alpha selection in competing salamanders: experimental verification of an *a priori* hypothesis. American Naturalist 122:105–113.

Hart, D. D. 1987. Experimental studies of exploitative competition in a grazing stream insect. Oecologia (Berlin) 73:41–47.

Hasle, G. R. 1978. The inverted microscope method. Pages 88–96 *in* P. A. Sournia, editor. Phytoplankton manual. UNESCO. Page Brothers, Paris, France.

Heliövaara, K., and R. Väisänen. 1986. Bugs in bags: intraspecific competition affects the biogeography of the alternate-year populations of *Aradus cinnamomues* (Heteroptera). Oikos 47:327–334.

Hughes, G. 1980. Larval competition in serially transferred populations of *Drosophila melanogaster*. Oecologia (Berlin) 45:396–403.

Jaeger, R. G. 1972. Food as a limited resource in competition between two species of terrestrial salamanders. Ecology 53:535–546.

Johnson, D. M., P. H. Crowley, R. E. Bohanan, C. N. Watson, and T. H. Martin. 1985. Competition among larval dragonflies: a field enclosure experiment. Ecology 66:119–128.

Kerfoot, W. C., W. R. DeMott, and D. L. DeAngelis. 1985. Interactions among cladocerans: food limitation and exploitative competition. Ergebnisse der Limnologie, Archiv für Hydrobiologie Beiheft 21:431–451.

King, C. M., and P. J. Moors. 1979. On co-existence, foraging strategy and the biogeography of weasels and stoats (*Mustela nivalis* and *M. erminea*) in Britain. Oecologia (Berlin) 39:131–150.

Kirk, K. L., and J. J. Gilbert. 1990. Suspended clay and the population dynamics of planktonic rotifers and cladocerans. Ecology 71:1741–1755.

Lair, N., and H. Ayadi. 1989. The seasonal succession of planktonic events in Lake Aydat, France. A comparison to the PEG model. Archiv für Hydrobiologie 115:589–602.

Lampert, W. 1988. The relationship between biomass and grazing: a review. Limnologica 19:11–20.

Lampert, W., W. Fleckner, H. Rai, and B. V. Taylor. 1986. Phytoplankton control by grazing zooplankton: a study on the spring clear-water phase. Limnology and Oceanography 31:478–490.

Larson, R. J. 1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecological Monographs 50:221–239.

Lynch, M. 1979. Predation, competition, and zooplankton community structure: an experimental study. Limnology and Oceanography 59:552–564.

MacIsaac, H. J., and J. J. Gilbert. 1989. Competition between rotifers and cladocerans of different body sizes. Oecologia (Berlin) 81:295–301.

MacIsaac, H. J., and J. J. Gilbert. 1990. Does exploitative or interference competition limit the abundance of *Keratella* in Loch Leven? A reassessment of May and Jones (1989). Journal of Plankton Research 12:1315–1322.

May, L., and D. H. Jones. 1989. Does interference competition from *Daphnia* affect populations of *Keratella cochlearis* in Loch Leven, Scotland? Journal of Plankton Research 11:445–461.

McAuliffe, J. R. 1984. Resource depression by a stream herbivore: effects on distributions and abundances of other grazers. Oikos 42:327–333.

Menge, B. A. 1972. Competition for food between two intertidal starfish species and its effect on body size and feeding. Ecology 53:635–644.

Menge, J. L., and B. A. Menge. 1974. Role of resource allocation, aggression and spatial heterogeneity in coexistence of two competing intertidal starfish. Ecological Monographs 44:189–209.

Minot, E. O., and C. M. Perrins. 1986. Interspecific interference competition—nest sites for Blue and Great Tits. Journal of Animal Ecology 55:331–350.

Moore, C. G., and D. M. Whitacre. 1972. Competition in mosquitoes. 2. Production of *Aedes aegypti* larval growth retardant at various densities and nutrition levels. Annals of the Entomological Society of America 65:915–918.

Neill, W. E. 1984. Regulation of rotifer densities by crustacean zooplankton in an oligotrophic montane lake in British Columbia. Oecologia (Berlin) 61:175–181.

———. 1985. The effects of herbivore competition upon the dynamics of *Chaoborus* predation. Archiv für Hydrobiologie Beiheft 21:483–491.

Nilsson, N. A. 1963. Interaction between trout and char in Scandinavia. Transactions of the American Fisheries Society 92:276–285.

Pajunen, V. I. 1982. Replacement analysis of non-equilibrium competition between rock pool corixids (Hemiptera, Corixidae). Oecologia (Berlin) 52:153–155.

Peckarsky, B. L., and M. A. Penton. 1985. Is predaceous stonefly behavior affected by competition? Ecology 66:1718–1728.

Peterson, C. H. 1979. The importance of predation and competition in organizing the intertidal epifaunal communities of Barnegat Inlet, New Jersey. Oecologia (Berlin) 39:1–24.

Peterson, C. H., and S. V. Andre. 1980. An experimental analysis of interspecific competition among filter feeders in a soft-sediment environment. Ecological Monographs 61:129–139.

Pimm, S. L. 1978. An experimental approach to the effects of predictability on community structure. American Zoologist 18:797–808.

Pontin, A. J. 1969. Population stabilization and competition between the ants *Lasius flavus* (F.) and *L. niger* (L.). Journal of Animal Ecology 30:47–54.

Quiring, D. T., and J. N. McNeil. 1984. Exploitation and

interference intraspecific larval competition in the dipteran leaf miner, *Agromyza frontella* (Rondani). Canadian Journal of Zoology 62:421–427.

Roberts, C. M. 1987. Experimental analysis of resource sharing between herbivorous damselfish and blennies on the Great Barrier reef. Journal of Experimental Marine Biology and Ecology 111:61–75.

Rubin, J. A. 1985. Mortality and avoidance of competitive overgrowth in encrusting Bryozoa. Marine Ecology, Progress Series 23:291–299.

SAS Institute. 1985. General user's guide: statistics. Fifth edition. Cary, North Carolina, USA.

Schneider, D. W. 1990. Direct assessment of the independent effects of exploitative and interference competition between *Daphnia* and rotifers. Limnology and Oceanography 35:916–922.

Schoener, T. W. 1983. Field experiments on interspecific competition. American Naturalist 122:240–285.

Sommer, U., Z. M. Gliwicz, W. Lampert, and A. Duncan. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. Archiv für Hydrobiologie 106: 433–471.

Spiller, D. A. 1984. Competition between two spider species: experimental field study. Ecology 65:909–919.

Steinwascher, K. 1978. Interference and exploitative competition among tadpoles of *Rana utricularia*. Ecology 59: 1039–1046.

———. 1981. Competition for two resources. Oecologia (Berlin) 49:415–418.

Stemberger, R. S., and J. J. Gilbert. 1985. Body size, food concentration, and population growth in planktonic rotifers. Ecology 66:1151–1159.

Thornhill, R. 1987. The relative importance of intra- and interspecific competition in scorpionfly mating systems. American Naturalist 130:711–729.

Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, New Jersey, USA.

Tonn, W. M. 1985. Density compensation in *Umbra–Perca* fish assemblages of northern Wisconsin lakes. Ecology 66: 415–429.

Van Buskirk, J. 1987. Density-dependent population dynamics in larvae of the dragonfly *Pachydiplax longipennis*: a field experiment. Oecologia (Berlin) 72:221–225.

Vanni, M. J. 1986. Competition in zooplankton communities: suppression of small species by *Daphnia pulex*. Limnology and Oceanography 31:1039–1056.

Walls, S. C., and R. G. Jaeger. 1987. Aggression and exploitation as mechanisms of competition in larval salamanders. Canadian Journal of Zoology 65:2938–2944.

Werner, E. E., and D. J. Hall. 1977. Competition and habitat shift in two sunfishes (Centrarchidae). Ecology 58:869–876.

Wise, D. H. 1983. Competitive mechanisms in a food-limited species: relative importance of interference and exploitative interactions among labyrinth spiders (Araneae: Araneidae). Oecologia (Berlin) 58:1–9.

Wrobel, D. J., W. F. Gergits, and R. G. Jaeger. 1980. An experimental study of interference competition among terrestrial salamanders. Ecology 61:1034–1039.

Young, J. O., and T. B. Reynoldson. 1988. Allopatric and sympatric populations of *Polycelis nigra* in competition with *P. tenuis* (Turbellaria:Tricladida). Journal of Zoology (London) 216:177–185.