

Trophic interactions of the freshwater jellyfish *Craspedacusta sowerbii*

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The predatory impact and the trophic role of the freshwater jellyfish, Craspedacusta sowerbii, was studied using microcosm and enclosure experiments as well as a 3-year pond survey. The results showed a significant decrease of small herbivorous crustaceans, i.e. Bosmina longirostris and juvenile cyclopoid copepods, in the medusa treatments of the microcosms and the enclosure experiments. Chlorophyll concentrations in the enclosure experiment were significantly increased in the medusa treatment, suggesting that C. sowerbii may cause cascading effects in the food chain. A comparison of daily zooplankton losses during the pond survey caused by medusae and fish (roach, Rutilus rutilus), and their food selectivities suggest food separation of these two predators and reveal a strong negative impact of medusae on the copepod pond community. In the case of a jellyfish bloom, our results show that both food chains can co-occur in lakes because of a weak interaction between these top predators, fish and jellyfish, with simultaneous impacts on the zooplankton structure.

INTRODUCTION

Changes at the top of food webs can have cascading effects (Carpenter and Kitchell, 1996). However, although evidence is accumulating that shows the importance of invertebrates in freshwater habitats (MacKay *et al.*, 1990; Barry, 1997; Yan and Pawson, 1997; Caramujo and Boavida, 2000; Dumitru *et al.*, 2001; Hoffman *et al.*, 2001), there is a lack of information from marine sites and, in particular, for gelatinous predators in both habitats (Purcell, 1997). This study focuses on the impact of freshwater jellyfishes on aquatic food webs, their relevance for trophic cascade and the comparison with fish.

Gelatinous predators are found throughout the world's oceans, from the poles to the equator and from the ocean surface to the ocean floor (Heeger, 1998). They have received increased attention over the past few decades because of massive occurrences ('blooms') of some species in coastal waters (Purcell *et al.*, 2001). The ecology of gelatinous predators is generally poorly known because of a variety of difficulties in studying them: damage, gut evacuation or net feeding rates by specimens collected in nets, e.g. make estimates of feeding suspect (Purcell, 1997). Further difficulties exist when conducting experimental laboratory work

because of the large size of many species: in most enclosures, for instance, their feeding rate tends to become decreased (de Lafontaine and Leggett, 1987). Despite these difficulties, development of new techniques has increased our knowledge of these predators (Purcell, 1997). For example, some species are known to feed selectively on other jellyfish or ichthyoplankton, but some are zooplanktivorous and feed mostly on copepods, the generally predominant metazoan zooplankton in marine systems (Costello and Colin, 2002). Generally, predation by individual species on copepods is believed to be too small to affect trophic interactions at marine sites (Purcell, 1997). However, some correlative field observations suggest that jellyfish can have an impact on trophic structure (Feigenbaum and Kelly, 1984; Schneider and Behrends, 1998; Schneider, 1999). Furthermore, there is some evidence from enclosure experiments that marine gelatinous predators may decrease herbivorous zooplankton biomass to such an extent that algal biomass is significantly enhanced (Verity and Smetacek, 1996; Uye and Shimauchi, 2005).

We used the zooplanktivorous freshwater jellyfish *Craspedacusta sowerbii* (Hydrozoa: Olindiidae) to explore

the importance of medusae in freshwater food webs. Freshwater jellyfish are suitable organisms to study the impact of gelatinous predators on food webs, because they are small in size (<20 mm), which reduces artifacts in container experiments (de Lafontaine and Leggett, 1987), and they are distributed worldwide in many different habitats, ranging from small ponds to large reservoirs (Dumont, 1994; Jankowski, 2001). Most studies on *C. sowerbii* revealed predation rates too small to cause population declines (Dodson and Cooper, 1983; Spadinger and Maier, 1999). However, there is evidence from experimental studies (Jankowski and Ratte, 2001) and observational studies (Davis, 1955; Green, 1998) that suggests much higher predation rates, possibly leading to a decrease in zooplankton standing stocks. Furthermore, blooms of freshwater jellyfish have been regularly observed and are often followed by a decline in crustacean zooplankton (Dumont, 1994), suggesting strong predation pressure. Additionally, there is some evidence for morphological changes in bosminid populations in the presence of *C. sowerbii* (Jankowski, 2004).

Compared with other freshwater invertebrate predators, *Craspedacusta* has some special features. In contrast with *Chaoborus* and *Leptodora*, e.g. *Craspedacusta* regularly co-occurs with highly abundant fish. Furthermore, *Craspedacusta* is not eaten by fish, but there is some evidence that *Craspedacusta* may feed on fish eggs and kill fish larvae (Kramp, 1951; DeVries, 1992). The feeding behavior of *Craspedacusta* also differs remarkably from that of the other freshwater invertebrate predators. While feeding, *Craspedacusta* sinks from the surface to deeper regions. During this time, the tentacles are exposed like a filter; thus water flow brings prey towards the tentacles (Spadinger and Maier, 1999). It is known from marine medusae that the vulnerability of prey species varies with nematocyst type (Purcell and Mills, 1988) and with the number and spacing of the tentacles (Purcell, 1997). Another phenomenon, uncommon in other invertebrate predators, is the irregular occurrence of freshwater jellyfish—they can occur at high abundance during several consecutive years, but may then be absent for several years subsequently (Acker and Muscat, 1976). Although this phenomenon is poorly understood, there is some evidence that it is caused by the dependence of the budding of medusae from the polyp stage on temperature (DeVries, 1992) and food (Lytle, 1961). However, this irregular occurrence is at least partly responsible for our poor knowledge of the food-web interactions of *C. sowerbii*, because the unpredictable occurrence of medusae makes experiments difficult to plan.

In order to investigate the importance of jellyfish to aquatic food webs and to assess potential indirect effects, we conducted short-term microcosm experiments to

examine their size-dependent predation rate on different prey taxa and a long-term field enclosure experiment (Jankowski and Ratte, 2001) to examine community and ecosystem effects. We compared these results with the results of a 3-year field survey. Finally, the results were used to compare the predatory impact of jellyfish on zooplankton with that of fish (*Rutilus rutilus*), using selectivity indices and estimates of the zooplankton losses caused by each of these predators.

METHOD

Study site

Lake Alsdorf is a small eutrophic shallow pond near Aachen, Germany (50°51'46" N, 6°9'13" E). It has a maximum depth of 4.1 m, a mean depth of around 2.6 m and a surface area of ~3.1 ha. A stable thermal stratification with an anoxic hypolimnion begins in late spring and persists throughout the entire summer (Strauss and Ratte, 2002). The mean total phosphorus concentration (P_{tot}) in 1997 was 4.0 μM , and the maximum P_{tot} was 7.0 μM (Strauss and Ratte, 2002). The zooplankton community is characterized by small species. This is a result of the high abundance of fish (~350 kg ha⁻¹, dominated by roach, *R. rutilus*; Strauss and Ratte, 2002). The abundance of fish did not differ significantly between 1995 and 1997.

Microcosm experiments

Predation by *C. sowerbii* on natural crustacean plankton was investigated in laboratory experiments. Four experiments were carried out between 9 June and 17 June 1996. Each experiment included four replicates to record zooplankton initial densities, four replicates with medusae (M) and four replicates without medusae (C, details in Table I). The experiments were carried out as follows. A container was first filled with 20 L of natural pond water and mixed well. From this container, 12 glass jars were each filled with 1 L of water. Every third jar (=4 replicates) was randomly chosen for the determination of initial zooplankton densities (N_0) by filtering the water through a 55- μm net and fixing the zooplankton in a 70% ethanol–30% water (vol : vol; plus 40 g sucrose L⁻¹ and 40 g Glycin L⁻¹) solution. Five medusae were added to each of another four jars. At the end of the experiment, these jars provided information on zooplankton densities under the impact of jellyfish predation (N_M). The remaining four jars were employed to assess the net growth rate of the zooplankton; i.e. at the end of the experiment, they provided information on zooplankton densities without predation (N_C). The bell diameter of each of the medusae used in the experiment

Table I: Experimental conditions of the microcosm experiments

Experiment	Start	Duration (h)	Medusae			
			Number of medusae	Mean bell diameter (mm)	Mean dry weight (mg medusa ⁻¹) ^a	Mean carbon content (mgC medusa ⁻¹) ^b
1	9 June 1996	42	5	2.36 (0.48)	0.026	0.034
2	14 June 1996	48	5	5.54 (0.20)	0.166	0.073
3	24 June 1996	48	5	11.10 (0.21)	0.759	0.234
4	17 July 1996	24	5	14.53 (0.26)	1.368	0.608

Number of *Craspedacusta sowerbii* medusa, mean bell diameter (±SD) and mean biomass (as dry weight and carbon) at the beginning of each experiment.

^aCalculated from Jankowski (2000).

^bmgC = 0.0272 + 0.273 × mg (dry weight), adopted from Jankowski (2000).

was measured and converted to dry weight (Jankowski, 2000). The jars were kept at 20 ± 1°C in a constant temperature room with a photoperiod L:D = 16:8 (about 12 μmol m⁻² s⁻¹), and the experiments were run for 24–48 h. At the end of each experiment, the medusae were removed from the jars, and their bell diameters were measured. The water from each jar was then filtered through a 55-μm net, and the material retained on the net preserved in 70% ethanol–sucrose solution. The crustaceans were counted from the whole sample with an inverted microscope at magnifications of 40× and 100×.

The instantaneous predation rates of *C. sowerbii* (PR, in predator⁻¹ day⁻¹) were calculated as the difference between the mean population size of the crustaceans in the controls (C) and in the medusa treatments (M) at the end of the experiments (de Lafontaine and Leggett, 1987) as follows:

$$PR = \frac{(\ln N_C - \ln N_M)}{(N_{\text{predators}} \times t)} \quad (1)$$

where N_C is the number of prey organisms in the control, N_M is the number of prey organisms in the medusa treatments at the end of the experiment, $N_{\text{predators}}$ is the density of medusae used and t is the duration of the experiment. PR computed from equation (1) provides a conservative estimate of the predation rate, because the number of zooplankton killed but not ingested by predators could not be assessed. This is the reason why we chose the term ‘predation’ rather than ‘ingestion’. Daily predation (DP , in individuals predator⁻¹day⁻¹) was obtained, according to de Lafontaine and Leggett (1987):

$$DP = N_0 \times (1 - \exp^{-PR}) \quad (2)$$

where N_0 represents the initial prey density in the microcosms.

For the statistical analysis, we used the Community Analysis software of Hommen *et al.* (1994). The data were analyzed using a t test, if the variances were homogeneous, and an U test, if they were not ($\alpha < 0.05$).

The selectivity of *C. sowerbii* in natural assemblages of plankton prey was evaluated using Pearre’s selectivity index (Pearre, 1982), C , calculated as follows:

$$C = \pm \left[\frac{(|a_d b_c - b_d a_c| - \frac{d}{2})^2}{abde} \right]^{1/2} \quad (3)$$

with terms defined as in Table II. Here, the prey abundance in the environment is the final zooplankton abundance in the medusa treatment (N_M), whereas DP [equation (2)] refers to the prey ingested. The selectivity data are based on the number of prey items. Index values range from -1 to +1. Positive and negative values indicate selection for and against a given prey category, respectively, while a value of zero indicates no selection in either direction. Calculated selectivity indices were tested for significance using the χ^2 statistic.

Table II: Definitions of terms for the calculation of C , Pearre’s selectivity index (Pearre, 1982)

	Prey category		
	A	Others	Total
Ingested	a_d	b_d	$d = a_d + b_d$
Environment	a_e	b_e	$e = a_e + b_e$
Total	$a = a_d + a_e$	$b = b_d + b_e$	$n = a_d + a_e + b_d + b_e$

Enclosure experiment

During summer 1996, a 23-day (19 June–12 July) enclosure experiment was carried out to determine the relative importance of predation by *C. sowerbii* on the food-web structure (Jankowski and Ratte, 2001). Six enclosures (2 m depth, 1 m diameter) were filled with pond water filtered through a plankton net with a mesh size of 800 µm to exclude medusae and fishes. We employed two treatments in this experiment: three enclosures with natural plankton densities without the addition of jellyfish (controls, C), and three enclosures enriched with 800 jellyfish per enclosure (nearly 450 individuals m⁻³; medusa treatments, M). The abundance in the enclosures represented the maximum abundance of medusae observed in the lake in 1995. The medusae had a mean diameter of about 10 mm. Samples from the enclosures were taken at three sampling depths (surface, 1 m and 2 m) using a Ruttner water sampler. Zooplankton was sampled on six sampling dates and was counted and measured using an inverted microscope (magnification: 100×). Zooplankton abundances were converted into biomass (µg dry weight L⁻¹; Dumont *et al.*, 1975; Bottrell *et al.*, 1976; Ruttner-Kolisko, 1977; percentage of carbon content to dry weight is around 48 for *Bosmina* to 47 for cyclopoid copepods, Strauss, unpublished). In this article, we focus on the main effects occurring in the enclosures to link the microcosm experiments to the 3-year pond survey (for details of the experiment, see Jankowski and Ratte, 2001). We used (i) repeated-measurement ANOVA to determine differences between treatments and (ii) a one-way ANOVA of the data, pooled over the last two sampling days of the experiment (07 July and 12 July). All data were log₁₀ transformed prior to analysis. Predation rates (PR) were calculated according to equation (1) using the mean zooplankton abundance on the last two sampling dates of the enclosure experiment (07 July and 12 July).

Pond survey

Lake Alsdorf was sampled every 4–17 days from April to September in 1995, 1996 and 1997. Samples of zooplankton and physico-chemical variables were taken with a Ruttner water sampler at the surface and at 1, 2 and 3.5 m water depth. *Craspedacusta sowerbii* abundance was determined by vertical net hauls (250-µm and 800-µm nets). Measurements of zooplankton abundance and biomass were carried out as in the enclosure experiment. For the analysis, whole-pond volume-weighted samples (obtained by combining plankton density from each stratum in proportion to its volume) on each sampling date were used. Total fish abundance was estimated by echosounding in November 1995 and April 1997.

Estimating the predatory impact of jellyfish and fish

To estimate the relative importance of the predatory impact of jellyfish and fish on zooplankton in the pond, we calculated the percentage of the daily loss of the dominant crustacean zooplankton taxa attributable to each of these predators.

Predation rates of *C. sowerbii* in the pond were estimated from the enclosure experiment according to equation (1). The daily mortality of prey taxa (expressed as % individuals lost) caused by the *C. sowerbii* population was calculated using equation (2) (de Lafontaine and Leggett, 1987), where N_0 represents the abundance of zooplankton species in the pond. As predation rates differ with the size of the medusae, the pond survey data used were confined to those sampled on dates on which the mean size of the medusae was at least as large as that of the medusae in the enclosure experiment (≥ 10 mm). Because of this and because of irregularities in the sampling scheme, only three pond surveys could be used (those on 27 June 1996, 7 July 1996 and 22 July 1996).

To estimate the predatory impact of fish on zooplankton, we analyzed the gut content of fish (according to Persson, 1982) caught by electrofishing and angling. From June 1996 to July 1997, we analyzed the gut contents of small roach (*R.utilus*, mean length \pm SD = 10.4 \pm 1.6 cm) using 8–11 fish each time. Using the following expression of Persson (1982) for the gut evacuation rate (R) of roach per hour:

$$R = 0.032 \times \exp^{0.115 \times T} \quad (4)$$

the daily intake (DI) of a single zooplankton taxon by an individual roach (in mg dry weight fish⁻¹ day⁻¹) can be calculated as:

$$DI = R \times S \times W \times \zeta \times F \times 24 \text{ h} \quad (5)$$

where S is the average weight of food items in the intestine (mean value: 1.51 mg dry weight g⁻¹ fish, Strauss and Ratte, 2002), W is the mean fresh weight per fish (g fish⁻¹), ζ is the biovolume fraction of zooplankton in the fishes' guts and F is the fraction of the zooplankton community in the gut, in terms of dry weight, accounted for by a single zooplankton taxon. Subsequently, the DI calculated in terms of biomass was converted into ingested individuals fish⁻¹ day⁻¹. For further calculations, we assumed the mean wet weight of roach to be 8.8 g, which corresponds to a body length of 10 cm. The percentage daily loss of a single zooplankton taxon owing to predation by roach in the lake (% individuals day⁻¹) was calculated as

$$\% \text{ daily loss} = \frac{DI \times \text{fish abundance}}{\text{prey density}} \times 100 \quad (6)$$

with a fish density of 0.001 fish L⁻¹ for Lake Alsdorf. To compare the impact of roach and jellyfish on the zooplankton community, the daily loss caused by fish was calculated during the jellyfish bloom from June to August 1996.

To evaluate the selectivity of roach, we used the same selectivity index (Pearre's *C*, Pearre, 1982) as for the jellyfish [equation (3)]. For prey ingested by roach, the total number of counted individuals of a prey item in the gut was used (Table III). To obtain more robust data on the selectivity of roach with respect to copepods, additional analyses of data sampled on other dates in 1997 on which copepod densities in the pond were higher were conducted.

RESULTS

Microcosm estimates of predation rates

The microcosm experiments indicate a strong predatory impact of *C. sowerbii* on the crustaceans. The strongest effects by number were observed for naupliar larvae and *Bosmina longirostris*. *Craspedacusta sowerbii* decreased the abundance of these two taxa significantly in all experiments, except in the first one, in which the medusae were very small (Table IV). A significant predatory impact on copepodids was observed only for medusae >10 mm in diameter. No significant effects on adult cyclopoids were observed. The predation rates on nauplii, bosminids and copepodids increased with medusa size but were relatively similar for medusae >10 mm. Predation rates (Table IV) of medusae >10 mm (experiments 3 and 4) were highest for nauplii (0.36–0.41 predator⁻¹ day⁻¹) but were also high for copepodids (0.12–0.2 predator⁻¹ day⁻¹) and bosminids (0.12–0.15 predator⁻¹ day⁻¹). These correspond to carbon-specific daily predation ranging from 14 to 52 mgC_{prey} mgC_{predator}⁻¹ day⁻¹ for bosminids and 0.5–22 mgC_{prey} mgC_{predator}⁻¹ day⁻¹ for nauplii (Table IV).

Craspedacusta sowerbii exhibited both positive and negative selection for specific crustacean prey items (Table V). In all experiments, except experiment 1, *C. sowerbii* showed significant selection against *Bosmina longirostris*; this negative selection increased with the size of the medusae ($r^2 = 0.88$). In contrast, *C. sowerbii* exhibited a significant preference for nauplii in all experiments (except experiment 1). Selectivity for nauplii is also a function of the size of the medusae ($r^2 = 0.89$).

Results on trophic structure from the enclosure experiment

Craspedacusta sowerbii had a noticeable influence on the composition of the zooplankton community. Cladoceran biomass showed significant differences between medusae treatments and controls during the experiment (RM-ANOVA: $F_{1,20} = 10.57$, $P = 0.03$). At the start of the enclosure experiment, *Bosmina longirostris* was the dominant cladoceran species in the enclosures (>95% by numbers as well as by biomass). At the end of the experiment, we found a significant decrease in *B. longirostris* abundance in the enclosures containing medusae in comparison with the control enclosures (ANOVA, $F_{1,5} = 9.95$, $P = 0.03$; Fig. 1). The copepods developed differently through time between treatments, as indicated by day-treatment interaction (RM-ANOVA: $F_{5,20} = 10.49$, $P = 0.0001$). Copepod abundance at the end of the experiment was 65 times higher in the control enclosures than in the enclosures containing medusae (ANOVA, $F_{1,5} = 17.19$, $P = 0.01$; Fig. 1). More than the half (54%) of the copepod dry-weight biomass in the control enclosures consisted of naupliar stages. The copepod communities in the control enclosures were dominated by small cyclopoid copepod species, i.e. *Mesocyclops* sp. and *Thermocyclops* sp., known as rotifer predators (Williamson, 1980, 1984; Hopp *et al.*, 1997). High abundance of herbivorous cladocerans, nauplii and rotifer predators in the control enclosures caused indirect effects on rotifers and phytoplankton. We found significant day-treatment interaction in rotifer biomass (RM-ANOVA: $F_{5,20} = 5.50$, $P = 0.002$), and at the end of the experiment, the rotifer abundance was significantly decreased in the control enclosures (ANOVA, $F_{1,5} = 22.22$, $P = 0.009$; Fig. 1). The rotifer community was composed of soft-bodied species, like *Asplanchna* sp., *Synchaeta* sp. and *Pompholyx* sp. The differences in herbivore biomass between the control enclosures and those containing medusae were reflected in the phytoplankton content, measured as chlorophyll *a* (Chl *a*) concentration. The mean chlorophyll concentration at the end of the experiment was 30 µg Chl *a* L⁻¹ in the control enclosures, whereas in the enclosures containing medusae, chlorophyll concentrations reached 114 µg Chl *a* L⁻¹ (ANOVA, $F_{1,5} = 5.73$, $P = 0.07$; Fig. 1). Although the differences at the end of the experiment were only slightly significant (because variances were high), the Chl *a* concentrations developed differently during the experiment (day-treatment interaction of RM-ANOVA: $F_{7,28} = 5.01$, $P = 0.0009$), indicating that zooplankton grazing was higher in the control enclosures than in the enclosures containing medusae.

The *C. sowerbii* predation rates calculated from the enclosure experiment (PR, Table VI) were highest for nauplii (0.42 predator⁻¹ day⁻¹) but were also high for

Table III: Percentage daily loss of zooplankton in the pond caused by roach (*Rutilus rutilus*)

Date	Temperature (°C)	Ambient prey concentration in Lake Alsdorf						Zooplankton biomass in the guts (%)	Counted numbers (% dry weight of total zooplankton biomass) in the guts	Daily loss (% individual day ⁻¹)			
		Abundance (individual L ⁻¹)			Biomass (µg dry weight L ⁻¹)					<i>Bosmina longirostris</i>	Cyclopoid copepods	<i>Bosmina longirostris</i>	Cyclopoid copepods
		<i>Bosmina longirostris</i>	Cyclopoid copepods	Nauplii	<i>Bosmina longirostris</i>	Cyclopoid copepods	Nauplii						
18 June 1996	22.2	416	14	53	98	34	7	6.0	87 (92.9)	1 (3.5)	7.4	0.8	
22 July 1996	21.0	457	2	4	98	5	0.5	19.8	384 (72.3)	1 (0.7)	16.8	3.5	
05 August 1996	21.2	1032	3	8	314	6	1	30.2	576 (99.2)	0 (0.0)	11.1	0.0	
31 August 1996	16.3	334	78	175	126	73	28	8.6	226 (80.9)	10 (18.6)	3.7	1.4	
17 July 1997	21.6	1133	624	959	410	846	87	28.6	394 (59.9)	65 (24.8)	5.1	1.0	

Shown are the mean water temperature in 0–2 m water depth and the ambient prey concentrations in Lake Alsdorf, the total zooplankton biomass in the guts of roach (as % dry weight of total content), the total number of prey items counted (and % of total zooplankton biomass) in the guts of the roach examined and the daily loss of dominant zooplankton taxa in summer 1996 and July 1997. Cyclopoid copepods represents copepodid adult stages.

Table IV: *Craspedacusta sowerbii* predation rates (PR) estimated in microcosm experiments

Prey	Exp.	N_0 (individual L ⁻¹)	N_C (individual L ⁻¹)	N_M (individual L ⁻¹)	PR (day ⁻¹)	DP (individual predator ⁻¹ day ⁻¹)	Carbon-specific DP (mgC mgC ⁻¹ day ⁻¹)	s.l.
<i>Bosmina longirostris</i>	1	695.8 (299.3)	1018.75 (229.9)	915.25 (354.0)	0.01	8.5	27.35	–
<i>Bosmina longirostris</i>	2	947.0 (344.3)	1681.3 (241.2)	1127.3 (101.9)	0.04	37.1	51.92	*
<i>Bosmina longirostris</i>	3	227.8 (18.3)	140.3 (22.1)	33.0 (6.2)	0.15	30.7	13.65	*
<i>Bosmina longirostris</i>	4	1089.0 (394.9)	1212.0 (377.6)	653.5 (124.0)	0.12	126.6	26.03	*
Other cladocerans	4	19.5 (9.5)	13 (5.8)	9.75 (2.3)	0.06	1.09	0.30	–
Nauplii	1	79.5 (12.0)	52.00 (7.6)	45.00 (17.3)	0.02	1.3	1.22	–
Nauplii	2	85.5 (11.2)	68.5 (17.9)	32.0 (12.9)	0.08	6.3	2.21	*
Nauplii	3	16.3 (3.5)	15.3 (3.4)	0.3 (0.4)	0.41	5.5	0.54	+
Nauplii	4	1236.0 (85.5)	1124.0 (176.1)	188.0 (49.5)	0.36	371.6	21.98	*
Copepodids	1	34.3 (9.3)	48.0 (1.9)	63.8 (5.7)	–	–	–	*
Copepodids	2	50.3 (7.3)	49.3 (14.9)	32.8 (8.6)	0.04	2.0	4.66	–
Copepodids	3	1.5 (1.1)	5.5 (2.3)	0.8 (0.8)	0.20	0.3	0.19	*
Copepodids	4	254.0 (39.8)	174.5 (6.5)	94.5 (16.0)	0.12	29.3	10.07	*
Cyclopoids (adult)	1	0.8 (1.3)	3.5 (1.5)	3.0 (1.0)	0.02	0.01	0.39	–
Cyclopoids (adult)	2	12.0 (4.0)	2.8 (0.4)	2.8 (1.5)	0	0	0	–
Cyclopoids (adult)	4	57.5 (6.9)	14.5 (5.1)	14.5 (9.4)	0	0	0	–

Exp., number of experiment (Table I); N_0 , number of prey at the beginning; N_C , number of prey in controls treatments at the end of the experiment; N_M , number of prey in medusa treatments at the end of the experiment; s.l., significance level. The mean (\pm SD) of four replicates are listed. The PR was calculated from equation (1) and daily predation (DP) from equation (2). Carbon-specific DP is roughly approximated from prey carbon measurements of pond samples in 2003 (Strauss, unpublished) and medusae carbon content (Table I). The symbols * (t test) or + (U test) indicate significant differences ($\alpha < 0.05$) between N_C and N_M and – indicates not significant. No adult cyclopoids were found in experiment 3.

Table V: Prey selectivity coefficient (C, Pearre, 1982) of *Craspedacusta sowerbii* calculated from the microcosm experiment

Experiment	Prey category				
	<i>Bosmina longirostris</i>	Other cladocerans	Nauplii	Copepodids	Adult cyclopoids
1	0.01	NP	0.02	–0.05	–0.1
2	–0.1 ^d	NP	0.11 ^e	0.01	–0.04
3	–0.17 ^a	NP	0.21 ^b	–0.06	NP
4	–0.42 ^e	–0.04 ^a	0.50 ^e	–0.07	–0.07 ^c

NP, prey was not present in the assemblage.

^a χ^2 test ($\alpha = 0.05$) = <0.1.

^b χ^2 test ($\alpha = 0.05$) = <0.05.

^c χ^2 test ($\alpha = 0.05$) = <0.01.

^d χ^2 test ($\alpha = 0.05$) = <0.001.

^e χ^2 test ($\alpha = 0.05$) = <0.0001.

copepodids (0.34 predator⁻¹ day⁻¹) and *B. longirostris* (0.13 predator⁻¹ day⁻¹). The rates of predation of *C. sowerbii* on nauplii and *B. longirostris* in the enclosure experiment were almost on the same order of magnitude as in microcosm experiments 3 and 4 with medusae >10 mm (Table IV). However, the estimate of the predation rate on copepodids obtained from the enclosure experi-

ment (0.34 predator⁻¹ day⁻¹) was clearly higher than that obtained from the microcosm experiment (0.12–0.2 predator⁻¹ day⁻¹; Table IV).

Pond survey

We found mass developments of freshwater medusae to have occurred in two of the three years studied; viz. in

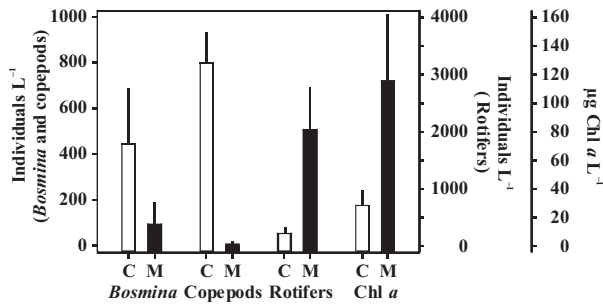


Fig. 1. Results of the enclosure experiment. Mean (\pm SE) abundance (individuals L⁻¹) of *Bosmina longirostris*, cyclopoid copepods and rotifers and mean (\pm SE) chlorophyll concentration [μ g chlorophyll a (Chl a) L⁻¹] on the last two sampling dates in the control (C) and medusae (M) enclosures. Note the different axes for *B. longirostris* and copepods on the left-hand side and for rotifers on the right-hand side.

Table VI: Predation rates (PR) estimated from the final (mean of the last two sampling days) zooplankton abundance in medusa treatments (N_M) and controls (N_C) in the enclosure experiment

Prey category	N _C (individuals L ⁻¹)	N _M (individuals L ⁻¹)	PR (day ⁻¹)
<i>Bosmina longirostris</i>	589	235	0.13
Nauplii	1410	20	0.42
Copepodids	169	5	0.34

1995 and 1996. In both years, medusae first occurred in late spring (May/June) and were found until August. The abundance of the medusae was high in both years, with a maximum of about 1000 individuals m⁻² in 1995 and 400 individuals m⁻² in 1996 (Fig. 2). The zooplankton community reflected these interannual differences in the abundance of medusae. In all 3 years, cyclopoid copepods reached a spring biomass peak of about 100–400 μ g dry weight L⁻¹ (indicated with a ‘1’ in Fig. 2). These peaks were dominated by large *Cyclops* sp. (mainly *Cyclops vicinus*). Only in the year when medusae were absent (1997) was a peak observed in summer, when the cyclopoid copepod population attained a maximum biomass of over 1000 μ g dry weight L⁻¹. This peak (indicated with a ‘2’ in Fig. 2) was dominated by the smaller species *Mesocyclops* sp. and *Thermocyclops* sp., which were very rare or absent during the pond survey in 1995 and 1996 and were also only observed in the enclosures with no medusae (in 1996). Bosminids showed a two-peak succession with a strong summer depression in all 3 years (Fig. 2). The early summer biomass peak was lowest in 1995, the year with the highest abundance

of *C. sowerbii*, but was highest in the medusa-free year 1997 and intermediate in 1996. In contrast, the late summer biomass peak, which occurred after the jellyfish blooms in 1995 and 1996, showed no clear variation between years.

The abundance of fish did not differ significantly between 1995 (1.17 ± 0.24 fish m⁻³) and 1997 (0.87 ± 0.07 fish m⁻³), with a mean of 0.98 fish m⁻³. Roach (*R. rutilus*) dominated the fish community, accounting for 80% of fish by numbers.

In the summer months, only between 6 and 31% of the gut volume of the roach was filled with zooplankton (Table III); the rest contained other food items, such as detritus, sediment and macrophytes (Strauss and Ratte, 2002). On average, from June to August 1996, the ingested zooplankton consisted of about 86% of the cladoceran *B. longirostris* and 5.7% of copepods (calculated as % dry weight). Additional subdominant cladoceran taxa were *Daphnia cucullata*, *Ceriodaphnia* sp. and *Chydorus sphaericus*. No nauplii were found in the guts of the roach.

In 1996 and 1997, the roach showed a strong preference for bosminids (mean selectivity = 0.24) and other cladoceran species (0.16) but not for the sum of copepodids and adult cyclopoids (–0.11) and nauplii (–0.35) (Table VII).

Estimated zooplankton mortality in Lake Alsdorf caused by predation

Estimates of the daily mortality of zooplankton taxa (expressed as a % age of standing stock) attributable to *C. sowerbii* were calculated from the predation rates in the enclosures and the zooplankton abundance in the pond (Table VIII). Predation by *C. sowerbii* resulted in an average daily loss of about 2.4% of nauplii, 2.1% of copepodid and adult copepods and 0.9% of bosminids (Table VIII).

Zooplankton losses caused by predation differed noticeably between medusae and fish. On average, roach caused a daily mortality of 9.7% of the bosminid population from June to August 1996 but only 1.4% of the adult and copepodid copepod population (Table III). No impact of predation by roach was found on naupliar stages. We found the percentage daily loss to be consistent despite large variations in both the abundance of microcrustaceans and community composition (e.g. at high copepod densities in July 1997; Table III) and to be independent of the presence or absence of jellyfish.

DISCUSSION

Our experimental results reveal that the jellyfish exerted a substantial predation pressure on copepods (predation

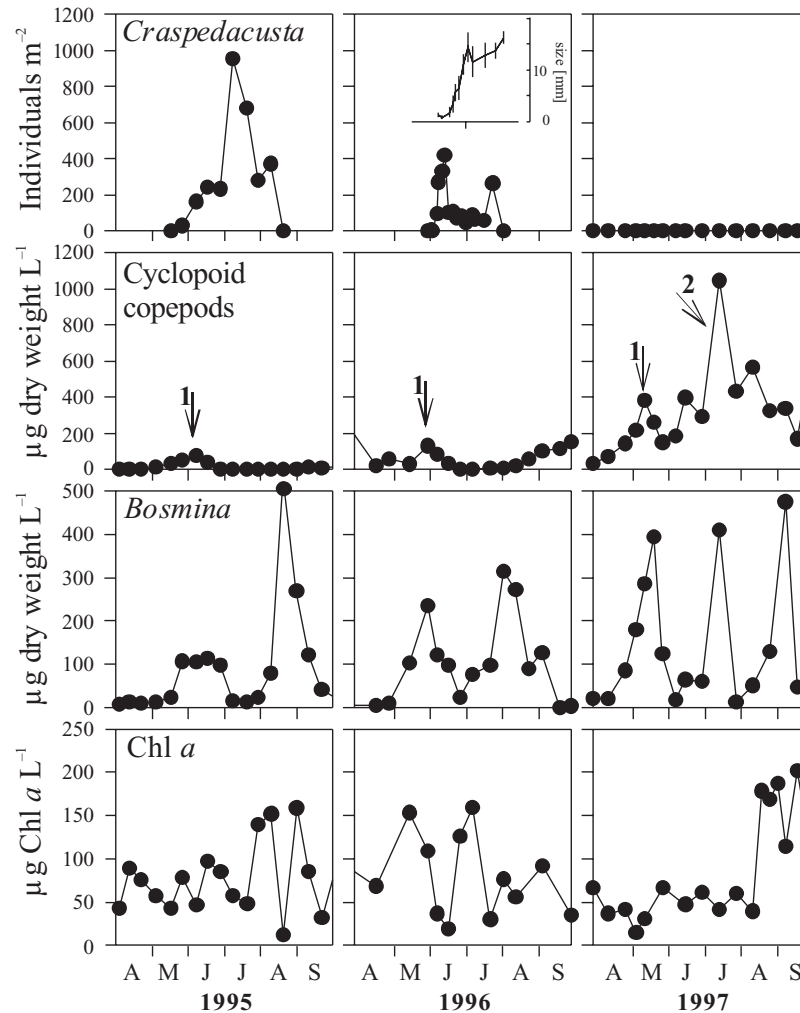


Fig. 2. Results of the 3-year field survey of Lake Alsdorf. Shown are the abundance (individuals m^{-2}) of *Craspedacusta sowerbii* (**upper panels**), the biomass ($\mu\text{g dry weight L}^{-1}$) of cyclopoid copepods (**upper middle panels**) and *Bosmina longirostris* (**lower middle panels**) and the mean chlorophyll *a* (Chl *a*) concentration in the uppermost 2 m of the lake (**lower panels**) during the period of occurrence of *C. sowerbii* in the three consecutive years 1995–1997 (**left to right**). The numbers indicate peak biomass of cyclopoid copepods dominated by different species: *Cyclops* sp., *Thermocyclops* sp. and *Mesocyclops* sp. The inset shows the mean (\pm SD) size (in mm) of *C. sowerbii* in 1996.

rates around 0.4 day^{-1} , Tables IV and VI) and a somewhat weaker predation pressure on bosminids (predation rates around 0.1 day^{-1} , Tables IV and VI). Additionally, there is some evidence that predation on herbivorous zooplankton was responsible for causing cascading effects in the enclosures. The comparison of jellyfish and fish with regard to their feeding selectivity and daily predation on the standing stock of the lake zooplankton populations suggests different main food resources, with *C. sowerbii* showing a preference for copepods (Tables V and VIII) and roach for bosminids (Tables III and VII).

In our experiments, *C. sowerbii*, like hydromedusae from marine and brackish sites, not only showed a preference for copepods (Purcell and Nemazie, 1992; Mills

and Sommer, 1995; Purcell *et al.*, 1999), but also showed an increasing predation rate and increasing selectivity for small copepod stages as its bell diameter increased (Purcell *et al.*, 1999). In our microcosm experiments, the impact of *C. sowerbii* on different copepod stages varied with the size of the medusae. In the case of the marine relatives of *C. sowerbii*, it is also known that small medusae prefer nauplii (Purcell *et al.*, 1999), whereas preference for copepodids increases with the size of the medusae (Purcell and Nemazie, 1992; Purcell, 1997; Purcell *et al.*, 1999). Not only was the food preference of *C. sowerbii* comparable with that of its marine relatives, but the zooplankton mortality caused by the medusae was also. Predation by *Phialidium hemisphericum*, for instance, has been estimated to be $2\% \text{ day}^{-1}$ of the

Table VII: Prey selectivity coefficient (C, Pearre, 1982) of roach (*Rutilus rutilus*) in 1996 and 1997

Date	Prey category			
	<i>Bosmina</i>	Other cladocerans	Cyclopoid copepods	Nauplii
18 June 1996	0.11 ^c	0.10 ^c	-0.03	-0.13 ^d
22 July 1996	-0.20 ^e	0.23 ^e	-0.003	-0.04 ^a
5 August 1996	0.13 ^e	NP	-0.05 ^b	-0.11 ^e
31 August 1996	0.34 ^e	NP	-0.13 ^c	-0.33 ^e
28 September 1996	0.04	0.35 ^e	0.04	-0.58 ^e
31 October 1996	0.36 ^e	0.17 ^e	-0.23 ^e	-0.56 ^e
16 April 1997	0.49 ^e	0.13 ^c	-0.30 ^e	-0.57 ^e
9 May 1997	0.60 ^e	0.01	-0.25 ^e	-0.57 ^e
17 July 1997	0.29 ^e	0.14 ^e	-0.08 ^e	-0.27 ^e

NP, prey was not present in the assemblage.

^a χ^2 test ($\alpha = 0.05$) = <0.1.

^b χ^2 test ($\alpha = 0.05$) = <0.05.

^c χ^2 test ($\alpha = 0.05$) = <0.01.

^d χ^2 test ($\alpha = 0.05$) = <0.001.

^e χ^2 test ($\alpha = 0.05$) = <0.0001.

copepod population (Daan, 1989), and in Saanich Inlet, Canada, predation by gelatinous zooplankton (primarily *Phialidium* sp.) was 5–10% day⁻¹ of the mesozooplankton (Larson, 1987). However, the importance of predation by gelatinous predators can be much greater, depending on prey and predator abundance (Matsakis and Conover, 1991; Purcell and Nemazie, 1992).

The results presented here on the predatory impact of *C. sowerbii* on small crustaceans, especially bosminids and nauplii, agree with the results of correlative studies of nematocyst type and diets of pelagic hydrozoa (Purcell and Mills, 1988). The specific combination of nematocysts possessed by *C. sowerbii* (microbasic euryteles,

Jankowski, 2001) enable it to penetrate through the exterior surfaces of prey organisms (Purcell and Mills, 1988), such as juvenile copepods and small cladocerans. In addition to preying on small crustaceans, *C. sowerbii* is also known to feed on rotifers and larger cladocerans, such as daphnids (Dodson and Cooper, 1983).

Predation rates on daphnids can exceed predation rates on bosminids and nauplii (Dodson and Cooper, 1983). Dodson and Cooper (1983) have therefore suggested that *C. sowerbii* has a similar diet spectrum as other, better-known, invertebrate predators in freshwater systems. Larvae of small and medium-sized *Chaoborus* species (e.g. *C. punctipennis*) and small instars of large *Chaoborus* species (e.g. *C. trivittatus*) feed more on rotifers and small crustaceans, like nauplii and bosminids, whereas third and fourth instars of *C. trivittatus* also feed on small and medium-sized daphnids (Soranno *et al.*, 1996). It has also been suggested that the predatory crustaceans *Bythotrephes* sp. and *Leptodora* sp. feed on small and medium-sized crustaceans (Lunte and Luecke, 1990; Yan and Pawson, 1997; Branstrator, 1998; Dumitru *et al.*, 2001).

However, there seem to be strong differences between food-web structures that include freshwater medusae and those that include other freshwater invertebrate predators. *Chaoborus* sp., *Leptodora* sp. and *Bythotrephes* sp. not only compete with planktivorous fish, they are also preyed upon by them. These invertebrates are therefore only abundant in lakes in which the abundance of planktivorous fish is low, or, in the case of larger *Chaoborus* larvae (such as *C. trivittatus* or *C. obscuripes*), in lakes in which such fish are very rare or even absent (Soranno *et al.*, 1996; Wissel and Benndorf, 1998). In contrast, *C. sowerbii* occurs in very high numbers even if fish abundance is high (Dumont, 1994). For example, in Lake Alsdorf *C. sowerbii* reached abundances of several hundred individuals per square meter although planktivorous fish biomass was around 350 kg ha⁻¹. In contrast to the other invertebrate

Table VIII: Percentage of daily loss of zooplankton in the pond caused by predation by *Craspedacusta sowerbii*

Date ^a	Abundance (individual L ⁻¹)			Medusae (individual m ⁻³)	Daily loss (% individual day ⁻¹)		
	<i>Bosmina</i>	Nauplii	Copepodids		<i>Bosmina</i>	Nauplii	Copepodids
27 June 1996	113	5	1	40	0.5	1.4	1.2
7 July 1996	270	1.3	0.4	43	0.5	1.5	1.2
22 July 1996	457	4	2	130	1.6	4.5	3.8
Mean	280	3	1	71	0.9	2.4	2.1

Calculations based on the *PR* estimated from the enclosure experiment (Table VI).

^aOnly dates where medusae were >10 mm.

predators, *C. sowerbii* seems not to be under predatory pressure from fish (Dumont, 1994). However, *C. sowerbii* occurs when planktivorous fish biomass is high, and our enclosure experiment showed some evidence that *C. sowerbii* may influence trophic cascade. If this is true, it would seem, at least partly, to contradict the trophic cascade hypothesis, which states that planktivory by invertebrates is inversely related to planktivory by fishes; if planktivorous fish are absent, invertebrate planktivores predominate (Carpenter *et al.*, 1985). In the case of a jellyfish bloom, our results show that both food chains can co-occur in lakes due to the lack of a strong interaction between these top predators, fish and jellyfish, with simultaneous impacts on the trophic cascade.

For other invertebrate predators, cascading effects are more pronounced for larger species (e.g. *C. trivittatus*) that feed efficiently on larger herbivores such as daphnids, which have a great ability to reduce phytoplankton biomass and therefore transmit top-down effects effectively (Gliwicz, 1990). However, as already mentioned, these larger species occur only in lakes where fish are rare or absent. The smaller invertebrate predator species, like *C. punctipennis* and *C. flavicans*, which are more likely to co-occur with fish, lack significant relationships with their prey (Wissel and Benndorf, 1998). This was found to be the case even at *Chaoborus* densities 20 times greater than those found in the field (Rodusky and Havens, 1996). In contrast, we found evidence for cascading effects during the enclosure experiment (Fig. 1) at densities of *C. sowerbii*, which, though high, are not uncommon in aquatic habitats (Dumont, 1994).

However, experiments in containers may bias the ecological interpretation, because (i) container size affects predation rates (de Lafontaine and Leggett, 1987; Martin, 2001), i.e. predation rates decrease with decreasing container size; and (ii) zooplankton abundance, particularly in small containers (like our microcosms), is finite, possibly resulting in depletion of the zooplankton before the end of the experiment. Both factors can result in the underestimation of the actual predation rate. In the enclosure experiment and in microcosm experiments 3 and 4, in which medusa sizes were comparable (>10 mm), calculated predation rates were in the same range, at least for bosminids and nauplii, suggesting that container effects were relatively low. However, for copepodids, the calculated PR in microcosm experiments 3 and 4 were one half to two thirds of the PR calculated for the enclosure experiment, suggesting that container size may have biased the predatory impact on copepodids more in the microcosms than in the enclosures.

Comparison of the estimated daily loss of zooplankton due to predation by *C. sowerbii* compared with that due to

predation by roach suggests that the predatory impact of roach on bosminids is higher than the predatory impact of *C. sowerbii*. Considering that the predatory impact of underyearling (0+) roach on *Bosmina* sp. can be much higher than our estimates for older individuals (Svensson, 1997), our calculation (Table III) probably underestimates the predation pressure of roach on bosminids in the pond. On the other hand, *C. sowerbii* seems to have caused a greater decrease in the copepod population than roach, as suggested by the percentage intake of standing stock (Tables III and VIII) and the selectivity indices (Tables V and VII). The impact of roach on nauplii seems to be zero in this study, confirming the results of other studies (Hammer, 1985), in which even roach larvae appeared not to ingest nauplii in any considerable quantity. Additionally, a negative selectivity for the older stages of cyclopid copepods by underyearling roach is consistent with other studies (e.g. Winfield *et al.*, 1983).

To summarize, roach showed a higher preference for bosminids and other cladocerans, but less for nauplii and copepodids. In contrast, *C. sowerbii* had a strong impact on nauplii and copepods but was also able to affect bosminid populations. Hence, both *C. sowerbii* and roach are effective predators but use different parts of the prey spectrum. However, in Lake Alsdorf, effects on bosminids are probably compensated for by bottom-up control. The rapid phosphorus turnover, as indicated by the high phosphorus loading from the external inflow, additional phosphorus excretion by sediment feeding fish and sediment release (Strauss and Ratte, 2002), probably stimulates phytoplankton growth, balancing out the expected top-down effects of *C. sowerbii* and roach. This could be the reason that the detectable effect of predation in the field is much smaller in the case of bosminids than in the case of copepodids. The rapid parthenogenetic reproduction of bosminids enables them to react quickly to changes in phytoplankton production, thus compensating for mortality by predation. In contrast, copepods have much longer generation times and cannot compensate for the heavy naupliar mortality that results from predation by *C. sowerbii* as rapidly as the bosminids can. This explains why the predatory effect of *C. sowerbii* and fish in the pond survey was only detectable on the copepod population.

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