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Journal of the North American Benthological Society, Vol. 20, No. 4 (Dec., 2001),
615-628.

Stable URL:

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Pelagic prey and benthic predators: impact of odonate predation on *Daphnia*

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Abstract. Interactions between benthic predators and pelagic prey, such as larval odonates and *Daphnia*, are often used to describe classic predator–prey relationships in laboratory studies. However, few field studies explore the potential impact of benthic predators on pelagic prey. Recent studies of cladocerans document diel horizontal migration (DHM), where large-bodied zooplankton (i.e., *Daphnia*) decrease their exposure to pelagic predators by seeking refuge among macrophytes. However, daphnids undergoing DHM may simultaneously increase their likelihood of encountering benthic predators that commonly occur in littoral zones. In laboratory experiments, we showed that dragonfly nymphs (*Epiheca cynosura*) effectively eliminated all *Daphnia* within 24 h, regardless of macrophyte presence or architecture. We also tested whether additions of larval damselflies (*Ischnura elegans*, *Coenagrion puella*, *C. pulchellum*) and dragonflies (*Somatochlora flavomaculata*) (total odonate density of 35–55/m²) significantly reduced total zooplankton or benthic invertebrate abundance in field enclosures with different macrophyte densities (20, 40, 80% volume infested [PVI]). Odonates significantly reduced *Daphnia* abundance at 20 PVI. However, the magnitude of the influence of odonates on daphnids, as well as *Ceriodaphnia* and *Polyphemus*, decreased with increasing macrophyte density. Odonate predation did not significantly affect benthic taxa abundance. Thus, daphnids undergoing DHM may lower predation from pelagic predators, but our results suggest that mortality from littoral predators may be significant. The net benefit of DHM may, therefore, differ among lakes as a function of the relative threats posed by pelagic and littoral predators.

Key words: littoral, macrophytes, zooplankton, diel horizontal migration, shallow lakes, refuge.

Predation is recognized as a key, but also complex, structuring force in lake food webs (Kerfoot and Sih 1987). In pelagic zones, planktivorous fishes forage for zooplankton prey and can produce cascading effects down to lower trophic levels (Carpenter and Kitchell 1993). In deep lakes, large-bodied zooplankton, such as *Daphnia*, minimize the impacts of pelagic fishes and pelagic invertebrates (e.g., *Chaoborus*) by migrating vertically and hiding in deeper, darker, colder water during the day (Lampert 1993). However, in unstratified shallow lakes, i.e., in the absence of a hypolimnetic refuge, swarms of daphnids migrate horizontally and seek refuge among littoral-zone macrophytes to avoid pe-

lagic fishes and invertebrates (Kvam and Kleiven 1995, Lauridsen and Buenk 1996). This behavior is termed diel horizontal migration (DHM) and is considered a predator-avoidance strategy, although other mechanisms may play a role (RLB, unpublished data).

The structural complexity of littoral zones may afford daphnids refuge from fish predation (Winfield 1986, Diehl 1992), but macrophytes are also habitat for epiphytic and benthic invertebrates that readily prey on zooplankton (Kornijów and Kairesalo 1994, Lombardo 1997). Relative to deep lakes, increased benthic resources in shallow lakes (because of greater light penetration) sustain more fishes that, in turn, increase predation pressure on daphnids (Jeppesen et al. 1997). Therefore, the need to escape open-water predators may increase the likelihood that pelagic daphnids will encounter ben-

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thic predators. Larval odonates commonly occur at densities of 10 to 50/m² (Crowley and Johnson 1992, Johnson et al. 1996) and have been observed at densities >1000/m² (Benke 1976, Wissinger 1988). Furthermore, odonates occupy an important intermediate position as both predator and prey in benthic food webs (Johnson et al. 1987, 1995). *Daphnia* are also important grazers in shallow lake ecosystems (Jeppesen 1998) and help maintain clear water conditions. Thus, potential loss of *Daphnia* as a result of odonate predation could influence whether shallow lakes maintain a clear water state or shift to a turbid state (Scheffer 1998).

Daphnid-odonate interactions in the laboratory are often used as a model system to illustrate predation. For example, consumption of *Daphnia magna* by the damselfly *Ischnura elegans* is a textbook example of a Holling's Type II functional response (Thompson and Pickup 1984). Furthermore, the availability of alternative prey (*D. magna*) for dragonflies (*Aeshna juncea*) illustrates an indirect effect by decreasing intraguild predation and cannibalism on smaller dragonflies and damselflies (*Coenagrion hastulatum* and *Leucorrhinia dubia*) (Johansson 1993). In addition, studies of odonate larvae and daphnids are commonly used to illustrate shifts in foraging strategies. For example, search activity of the damselfly *Lestes sponsa* increased when exposed to low versus intermediate densities (2 and 40/L, respectively) of *D. magna*, and then subsequently declined at high densities (Hirvonen 1999). In contrast, the frequency of ambush attacks by *L. sponsa* continued to increase with increasing prey density (Hirvonen 1999). Thus, laboratory studies using daphnids as prey and odonates as predators help illustrate mechanisms behind the complex interactions associated with predation. However, few studies consider the potential effects of odonate predation on daphnid populations in natural systems.

The lack of field studies examining daphnid-odonate interactions is understandable. Traditional limnology categorizes *Daphnia* as pelagic prey and odonates as benthic predators, implying that this prey is unlikely to encounter that predator. However, in shallow lakes, daphnids undergoing DHM create a link between pelagic and littoral zones (Lodge et al. 1988). Most field studies document the impact of odonates on zooplankton by analyzing gut content or fecal pellet composition. Multiple studies show that

larval odonates feed extensively on littoral-associated cladocerans (Pritchard 1964, Mahato and Johnson 1991, Koperski 1998a), and in some cases odonate diets include a substantial portion of typically pelagic zooplankton (Blois 1985). Even with this corroborative evidence, however, few field studies have directly tested the impact of odonate predation on pelagic zooplankton.

Dense macrophytes could serve as poor refuges for daphnids because macroinvertebrate density, including odonates, often increases with increasing macrophyte density (Kornijów and Kairesalo 1994, Cattaneo et al. 1998). In contrast, dense macrophytes might reduce the effectiveness of odonate foraging, and thus constitute a stabilizing force on odonate-cladoceran interactions. The objective of our field and laboratory studies was to investigate the ability of larval odonates to prey on *Daphnia* and other taxa among different types and densities of macrophytes. We expected that odonates would effectively prey on *Daphnia* among different types of vegetation (floating submerged versus anchored) in the laboratory. In our field experiments, we expected odonates to target the largest prey available, and anticipated that increased macrophyte density would modify the ability of odonates to significantly impact taxa.

Methods

Laboratory predation experiments

We conducted a laboratory predation study at the University of Notre Dame to test the potential of odonates as predators on *Daphnia* among macrophytes. We examined daphnid mortality in the presence and absence of submerged macrophytes and odonate nymphs. Experiments took place in sixteen 75-L buckets (48 cm diameter) that were located in a greenhouse, which provided natural light. Each bucket contained 27 cm of water and 2 cm of sand. We used plastic macrophytes (imitation *Myriophyllum*) or live *Ceratophyllum demersum* (95 g wet mass) to evaluate the ability of larval odonates to prey on *Daphnia* among different architectural types of macrophytes. Plastic macrophytes were gathered into 4 bundles composed of five 21-cm shoots (~70% volume infested [PVI], Canfield et al. 1984) that were anchored in the sand, whereas *C. demersum* floated freely in the tank and covered nearly 100% of the surface area in

the buckets. PVI is a metric used to describe macrophyte coverage (originally applied to nuisance macrophytes in Florida), and is calculated as the area of macrophyte coverage multiplied by the plant height divided by the water depth (Canfield et al. 1984). We chose to test real and plastic macrophytes because daphnids may react differently to structure, depending on the presence of chemical cues (Burks et al. 2001).

With both plastic and real macrophytes, we examined daphnid mortality in the presence or absence of 4 dragonfly nymphs, *Epiptera cynosura* (Corduliidae) (23 nymphs/m²), collected with dip nets from Stone Lake, Michigan, USA. We conducted this experiment at 2 different durations to adequately assess the ability of odonates to prey on *Daphnia*. First, we allowed dragonflies (penultimate instars, head capsule width = 5–7 mm) to prey on 25, large-bodied (>2 mm) *D. magna* (original culture purchased from Ward's Biological Co., Rochester, New York) over 48 h ($n = 4$). In a subsequent experiment, we used 50 daphnids, and shortened the duration to 24 h ($n = 4$). In both experiments, *D. magna* were added 1 h before the predators. After the conclusion of each experiment, we drained each tank to recover remaining *Daphnia*. Our reported mortality included all daphnids not recovered. Daphnids that were recovered were alive and swimming. Individual daphnids were not used more than once in these experiments. We tested how plants and odonates impacted daphnid mortality using a 1-way analysis of variance (ANOVA), followed by Tukey's multiple comparison tests (MCTs) to resolve significant differences between treatments.

Field study on odonate predation

We conducted a 4-wk field study (2–23 July 1999) using large enclosures in Lake Torup, Denmark, to test whether predation by odonate nymphs (both dragonflies and damselflies) reduced zooplankton or benthic taxa abundance in a more realistic field setting. Enclosures were established in April 1999 with natural zooplankton communities. All fish were removed during enclosure establishment. Each of 5 enclosures (5 m diameter) was divided into 3 pie-shaped sections that each held a different density of plastic macrophytes (ivy imitation) (20, 40, or 80 PVI). Strands of plastic macrophytes were suspended with small strings and occupied the entire water

column (i.e., from the water surface to within 10 cm of the bottom sediments). Each section (1/3 of enclosure) occupied 6.5 m². Zooplankton (from Lake Torup) colonized different macrophyte densities in the enclosures until the curtains separating these macrophyte sections were installed in June. Therefore, at the time of the experiment, a curtain separated sections from each other so that animals could not move between the different macrophyte densities. Variation between plant densities occurred because of a tendency of daphnids to avoid vegetation (Lauridsen and Lodge 1996, Burks et al. 2001). We kept all enclosures fishless by trapping and gill netting throughout the experiment.

Odonate addition.—We added odonates to 2 enclosures, leaving 3 as controls. To simulate a natural set of odonate predators, we used 1 species of larval dragonfly (*Somatochlora flavomaculata*, family Corduliidae) and pooled 3 species of damselflies (~70% *Ischnura elegans*, ~30% *Coenagrion puella* + *C. pulchellum*, family Coenagrionidae). We collected *S. flavomaculata* from sediments in a small pond in Silkeborg, Denmark, whereas damselflies came from submerged vegetation (*Elodea canadensis* and *Potamogeton pectinatus*) in Lake Karl (Karlsø). All 4 odonate species are commonly found in Denmark (Nordic Odonatological Society 1996). *Somatochlora flavomaculata* co-occurs with the damselflies and *Daphnia* in Karlsø, but was more easily collected in the small pond. All species of odonates utilized macrophyte habitat and readily consumed *D. magna* in the laboratory. In addition, dragonflies did not consume damselflies when both types of odonates were kept together in an aerated tank in the laboratory; however, damselflies decreased their foraging relative to their foraging in the absence of dragonflies (RLB, unpublished data). We collected odonates within a week of their release into mesocosms (9 July 1999).

Macroinvertebrate density often increases with macrophyte density (Kornijów and Kairesalo 1994, Cattaneo et al. 1998), so we added more odonates to high macrophyte densities (Table 1). Our range of total predator densities (35–55/m²) reflects common field densities found in the literature (Crowley and Johnson 1992, Johnson et al. 1996). The increase of odonates was not proportional to increasing macrophyte density in our experiment because we could not collect our target number of nymphs.

TABLE 1. Densities of odonates (no./m²) and absolute numbers (in parentheses) added to 6.5/m² sections of enclosures in the field experiment. No odonates were added to control enclosures ($n = 3$). Dragonfly = *Somatochlora flavomaculata*; Damselflies = *Ischnura elegans*, *Coenagrion puella*, and *C. pulchellum*. PVI = % volume infested.

Macrophyte density (PVI)	Odonates added ($n = 2$)		
	Dragonflies	Damselflies	Total
20	13 (85)	22 (143)	35 (228)
40	19 (124)	26 (169)	45 (293)
80	25 (163)	30 (195)	55 (358)

In addition, the treatment effects of predator density and macrophyte density are combined in our experimental design. However, using an alternative approach (i.e., adding the same number of predators at each plant density) would have likely produced unnatural confounding effects because surface area dramatically increases at high plant densities. Therefore, we purposefully chose a design that mimicked what naturally occurs in the field: increasing odonates with increasing macrophytes.

We used calipers to measure the head capsule width (HCW) of 60 haphazardly selected dragonflies and 30 damselflies in each genus to provide an estimate of odonate size. HCW of *S. flavomaculata* measured $0.33 \text{ cm} + 0.006$ (mean + 1 SE), whereas average HCW of the 3 damselfly species was $0.17 \text{ cm} + 0.006$. We added odonates to 2 randomly chosen enclosures on 9 July 1999. We did not observe any significant odonate emergence from the enclosures during the study period. Although we made no attempt to recover odonates at the end of the experiment, we did not find exuviae or dead individuals in our samples.

Sampling zooplankton and benthos.—To sample zooplankton, we collected 6 L of water with a cylindrical tube sampler (10 cm diameter, 1.5 m length) from the water column of each section (20, 40, 80 PVI) of each mesocosm ($n = 15$ samples). We then filtered the water through a 50- μm mesh. The tube sampler integrated the entire water column apart from the lower 3 cm. We sampled a week prior (2 July 1999) to odonate addition and 2 wk after (23 July 1999). We preserved zooplankton samples in 100 mL of water with Lugol's solution for later enumera-

tion. Under a stereomicroscope (40 \times), we counted at least two 5-mL subsamples from the 100-mL sample to determine zooplankton abundance. We took sediment cores (10 cm diameter) before and after odonate addition to assess the impact of odonates on benthic invertebrates (including sediment-associated zooplankton and chironomids). We kept the upper 5 cm of the sediment core (393 cm³). Sediment samples were preserved with Lugol's. We then picked out the invertebrates, identified, and counted them under a stereomicroscope.

The Torup enclosures were relatively species-poor systems. We tested whether odonates significantly reduced the abundance of the most commonly occurring taxa. These taxa included: *D. magna* and *D. galeata* (pooled into *Daphnia* spp.), *Ceriodaphnia dubia*, *Polyphemus pediculus*, cyclopoid copepods (consisting of *Macrocyclus viridis*, *Mesocyclops leuckarti*, and *Megacyclus* sp.), *Eurycerus lamellatus*, and Chironomidae. Other common pelagic invertebrate predators, such as *Chaoborus* spp. and *Leptodora kindtii*, were not found in the enclosures. We then combined our results from pelagic and benthic habitats to examine total abundance (no./L) in each mesocosm section. We did not sample invertebrates occurring on macrophytes. However, most of these taxa, including cyclopoid copepods and *Eurycerus*, also occurred in the sediment (RLB, personal observation).

We used initial density as a covariate in our ANOVA to account for potential statistical differences in the initial population sizes of taxa among macrophyte densities and between control and predator treatments. Using a 2-way ANOVA for each taxon, we examined the impacts of odonates and macrophyte density on the difference in abundance (final minus initial) of taxa between the beginning (2 July 1999) and end (23 July 1999) of the experiment. We performed post-hoc, pair-wise, difference comparisons between control and odonate treatments using least squared means to identify significant differences at single macrophyte densities.

Abiotic conditions.—We collected water from the enclosures to examine initial total N (TN = NO₃-N + NO₂-N after persulphate digestion, Solórzano and Sharp 1980) and total P (TP) concentrations (as orthophosphate after persulphate digestion, APHA 1998) to exclude alternative explanations for treatment effects based on differences in abiotic conditions. When we sam-

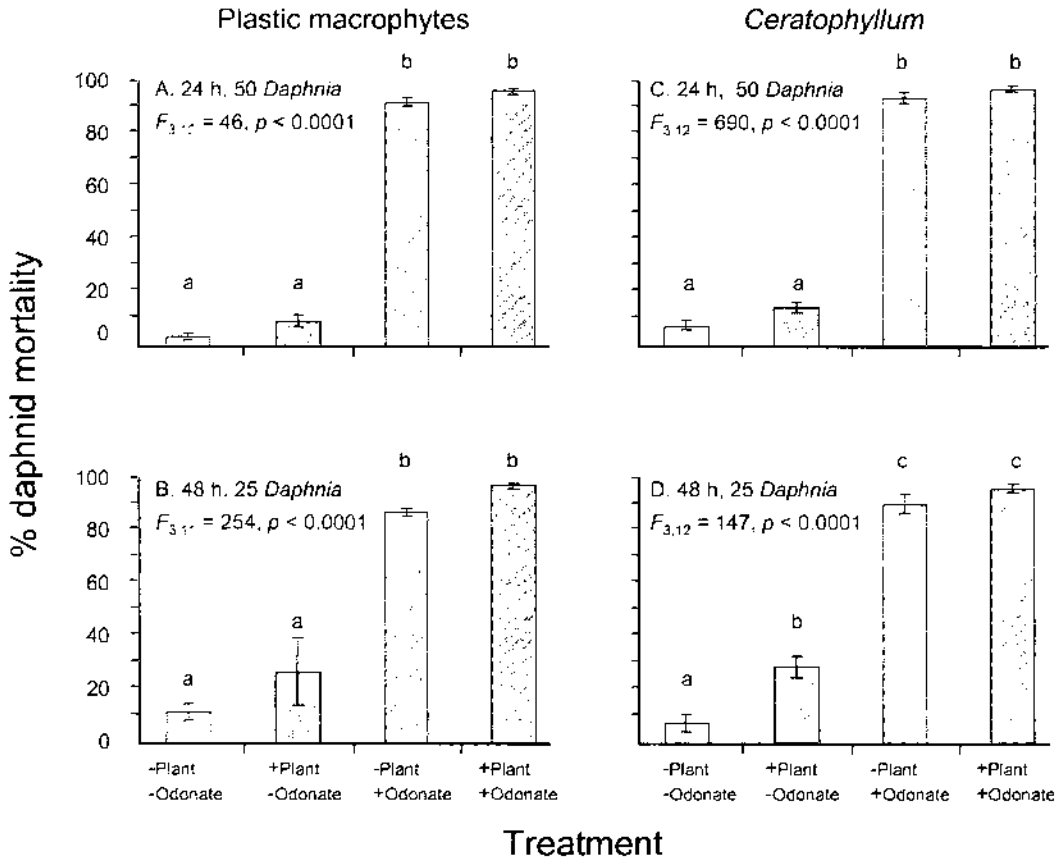


FIG. 1. Relationship between daphnid % mortality (± 1 SE) and the presence and absence of structure and odonates. A and B.—Daphnid mortality when plastic macrophytes (imitation *Myriophyllum*) were used. C and D.—Daphnid mortality in experiments with *Ceratophyllum demersum*. A and C.—Experiments using a 24-h predation time with 50 daphnids as prey. B and D.—The same experiment conducted over 48 h with 25 daphnids. On the x-axis, + and - symbols represent the presence or absence, respectively, of either plants (shaded bars) or odonates (striped bars). Open bars are controls. F-statistics and p-values are from 1-way analyses of variance. Small letters above bars indicate statistical differences between treatments (Tukey's multiple comparison test).

pled zooplankton, we also measured temperature, dissolved oxygen (DO) and pH (YSI-Model 58 probe), and collected water to analyze for chlorophyll *a* (using ethanol extraction, Jespersen and Christoffersen 1987).

Results

Laboratory predation experiments

We found low daphnid mortality (mean ± 1 SD, 5.0% \pm 3.0%, 6.0% \pm 3.7%, for plastic and real macrophytes, respectively) in the absence of predators and macrophytes (controls) (Fig. 1).

Daphnid mortality tended to be slightly higher (18.0% \pm 18.0%, 23.25% \pm 9.6%, for plastic and real macrophytes, respectively) when macrophytes were present than when macrophytes were absent. However, daphnid % mortality in the presence and absence of macrophytes did not differ significantly, except that the presence of *Ceratophyllum* increased the mortality of 25 daphnids relative to controls after 48 h (Fig. 1D; a versus b, $p = 0.008$).

We found strong predation by dragonfly nymphs on daphnids in all 4 experiments (i.e., plastic plants, *Ceratophyllum*, 24 h and 48 h, Fig. 1). Furthermore, the trends among treatments

remained consistent between experiments. For experiments using plastic macrophytes, the presence of plastic macrophytes did not significantly influence daphnid mortality (Fig. 1A, B; MCT, p -values all > 0.05), but the presence of odonates increased mortality by a factor of 3 to 9 (a's versus b's, p -values < 0.001). In experiments using *Ceratophyllum*, dragonflies also ate almost all of the available daphnids, regardless of predation time or the number of daphnids available (Fig. 1C, D).

Field study on odonate predation

Initial densities of *Daphnia* (Table 2) did not significantly differ between treatments with and without odonates (2-way ANOVA; $F_{1,9} = 0.023$, $p = 0.882$), but decreased with increasing macrophyte density ($F_{2,9} = 5.825$, $p = 0.024$). For initial daphnid densities, no significant interaction occurred between predator treatments and macrophyte densities ($F_{1,9} = 1.258$, $p = 0.330$). Initial densities of all other taxa (e.g., *C. dubia*, *P. pediculus*, cyclopoid copepods, *E. lamellatus*, and chironomids) did not differ significantly between macrophyte densities or between treatments (2-way ANOVAs; all p 's > 0.05) and significant interactions did not occur for these taxa.

The presence of odonates significantly influenced the dynamics of daphnids in our field enclosures (Fig. 2, top row; $F_{1,8} = 31.36$, $p = 0.0005$). Overall, macrophyte density did not have a significant effect on the change in daphnid abundance ($F_{2,8} = 2.43$, $p = 0.1500$). However, at low macrophyte density (20 PVI), the number of daphnids in control enclosures increased, whereas the numbers of daphnids in odonate enclosures significantly declined ($p = 0.0004$). Variation in initial density of *Daphnia* did not contribute significantly to these results (Table 2; $p = 0.6911$). The magnitude of the predation impact by odonates on *Daphnia* declined with increasing macrophyte density (Fig. 2) as evidenced by a significant interaction between odonate presence and macrophyte density (Ode*PVI, $F_{2,8} = 6.72$, $p = 0.0194$).

The presence of odonates did not significantly impact *Ceriodaphnia* (Fig. 2, middle row; $F_{1,8} = 1.55$, $p = 0.2481$). *Ceriodaphnia* appeared to increase in control enclosures, but declined in enclosures with odonates at 20 PVI. *Ceriodaphnia* abundance also appeared to increase with increasing macrophyte density ($F_{2,8} = 4.00$, $p =$

0.0626). This pattern was more pronounced in enclosures with odonates (Fig. 2), although these results were not statistically significant. Variation in initial density of *Ceriodaphnia* did not contribute significantly to these results (Table 2; $p = 0.5268$), and no significant interactions occurred between predator treatments and macrophyte densities (Fig. 1; $F_{2,8} = 2.58$, $p = 0.1368$).

Our covariate analysis indicated that high initial densities of *Polyphemus* at 80 PVI (in enclosures without odonates) significantly influenced the overall change in *Polyphemus* abundance during the experiment (Table 2, Fig. 2, bottom right panel; $p = 0.005$). However, no other clear trends were present across predator treatments or macrophyte densities (Fig. 2, bottom row). No other statistical analyses indicated that odonate presence ($F_{1,8} = 1.06$, $p = 0.3343$), macrophyte density ($F_{2,8} = 0.91$, $p = 0.4406$), or interactions between the 2 factors ($F_{2,8} = 0.31$, $p = 0.7395$) significantly impacted *Polyphemus* abundance (Fig. 2, bottom row).

Cyclopoid copepods appeared to increase overall in the enclosures with odonates and tended to decline where odonates were absent (Fig. 3, top row). Both *Eurycerus* and chironomids decreased over the course of the experiment, regardless of the presence of odonates or macrophyte density (Fig. 3, middle and bottom rows, respectively). In contrast to *Daphnia*, the change in abundance of each predominately benthic taxon was not significantly different in enclosures with odonate nymphs relative to controls (Fig. 3; all p -values > 0.05). Macrophyte density also had no significant effect on benthic taxa and no significant interactions between predator treatments and macrophyte densities occurred (all p -values > 0.05). Initial densities of cyclopoid copepods and chironomids did not significantly influence the change in abundance (Table 2; $p = 0.3515$, and 0.0585 , respectively), although variation in initial *Eurycerus* densities was significant (Table 2; $p = 0.0173$).

Abiotic conditions for field study.—Abiotic conditions (TN, TP, temperature, DO, and pH) did not differ appreciably between enclosures with and without odonate nymphs. DO at the bottom of the enclosures was the only parameter that varied by $>5\%$ between treatments, but concentrations were at least 9.4 mg/L ($\sim 95\%$ saturation) at that depth during the entire study duration. All abiotic conditions fell well within the range of tolerance for zooplankton, odonates,

TABLE 2. Mean (± 1 SD, no./L) initial densities of most common taxa occurring in Lake Torup enclosures for each predator treatment (control, odonate) and macrophyte density (20, 40, 80% volume infested [PVI]). *F*-statistics and *p*-values are for 2-way analyses of variance (ANOVAs) with initial density as a covariate. Degrees of freedom (df) represent covariate and error, respectively. Significant *p*-values (i.e., ≤ 0.05) appear in bold.

Taxa	Treatment	Replicates	Macrophyte density (PVI)				ANOVA results (covariate)		
			20	40	80	<i>F</i> -statistic	df	<i>p</i> -value	
<i>Daphnia</i>	Control	3	128 (62)	86 (34)	24 (4.7)	0.17	1,8	0.6911	
	Odonates	2	217 (129)	29 (12)	10 (6.7)				
<i>Ceriodaphnia</i>	Control	3	105 (31)	209 (111)	167 (79)	0.44	1,8	0.5268	
	Odonates	2	132 (9)	358 (178)	116 (28)				
<i>Polyphemus</i>	Control	3	25 (8.7)	26 (18)	62 (43)	14.67	1,8	0.0050	
	Odonates	2	22 (17)	28 (23)	21 (2.9)				
Cyclopoid copepods	Control	3	33 (18)	48 (22)	41.43 (5.9)	0.98	1,8	0.3515	
	Odonates	2	29 (4.1)	47 (0.7)	43 (6.4)				
<i>Eurycecus</i>	Control	3	16 (15)	20 (13)	15 (9.6)	8.94	1,8	0.0173	
	Odonates	2	15 (7.6)	20 (1.2)	23 (1.2)				
Chironomids	Control	3	67 (30)	29 (13)	17 (19)	5.40	1,8	0.0585	
	Odonates	2	46 (0)	33 (13)	25 (2.5)				

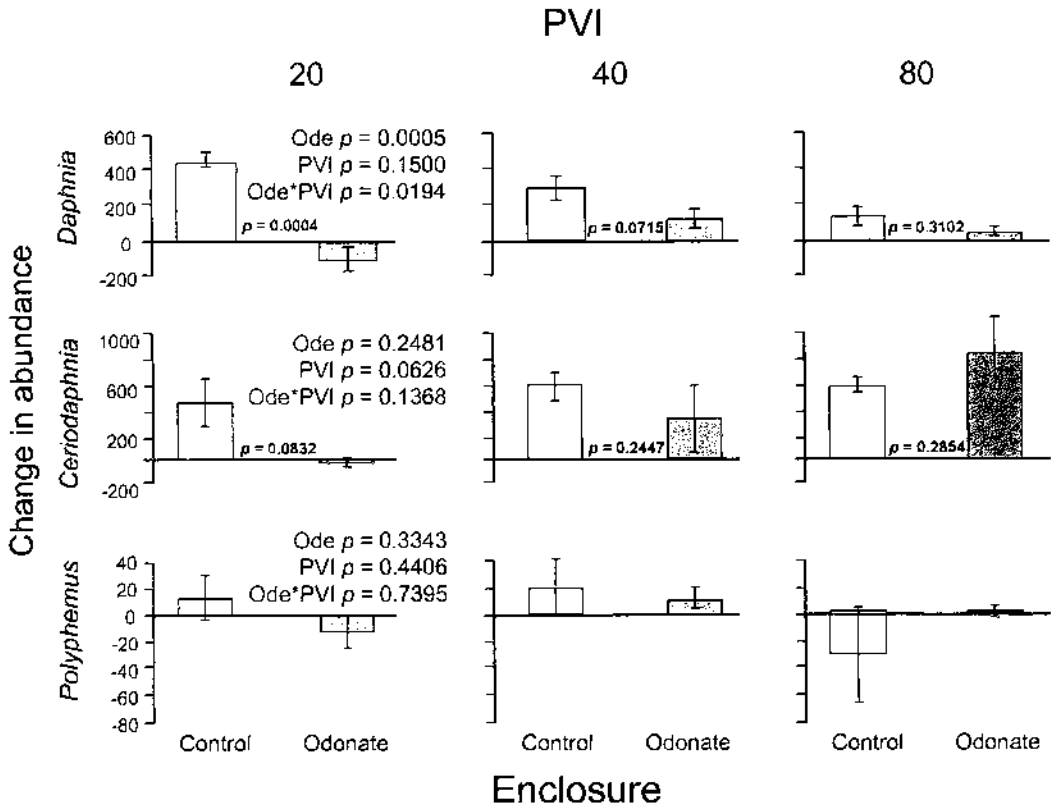


FIG. 2. Change in abundance (no./L \pm 1 SE) for predominately pelagic taxa: *Daphnia* (top row), *Ceriodaphnia* (middle row), and *Polyphemus* (bottom row) at 3 macrophyte densities in enclosures with (shaded bars) or without (open bars) odonate nymphs. Data combine both pelagic and benthic samples. Note the different y-axis scales between taxa. Statistics are from 2-way analyses of variance. Ode = odonate impact, PVI = % volume infested impact, Ode*PVI = odonate-PVI interaction. Pair-wise difference comparisons of enclosures with and without odonates are shown at the bottom center of each panel if a factor approached or reached statistical significance ($p = 0.05$).

and other benthic organisms (17.9–18.6°C surface temperature; 16.9–18.6°C bottom temperature; 1.0–2.2 mg/L TN; 0.053–0.143 mg/L TP; 9.5–12.2 mg/L surface DO; 9.4–11.7 mg/L bottom DO; and 7.8–8.1 pH).

Discussion

Daphnia abundance declined in our laboratory and field experiments where odonate nymphs occurred in the absence of fish and pelagic invertebrate predators. Dragonflies consumed nearly every available daphnid in our laboratory experiments, despite high densities of vegetation. Daphnids increased in enclosures without odonates in the field experiment with low macrophyte densities, but declined in enclosures

where we added damselflies and dragonflies. Our studies, therefore, provide direct evidence that littoral predators may strongly impact pelagic prey.

Predation by littoral invertebrates may be a substantial cost for daphnids undergoing DHM

Ecologists commonly characterize *Daphnia* as pelagic zooplankters, but recent studies suggest that daphnids also occur in littoral habitats (Lauridsen and Buenk 1996). Littoral-pelagic links may be important structural forces in aquatic food webs in shallow lakes. Daphnids are keystone grazers (*sensu* Power et al. 1996) in shallow lakes because they control algal populations (Scheffer 1998). However, because of

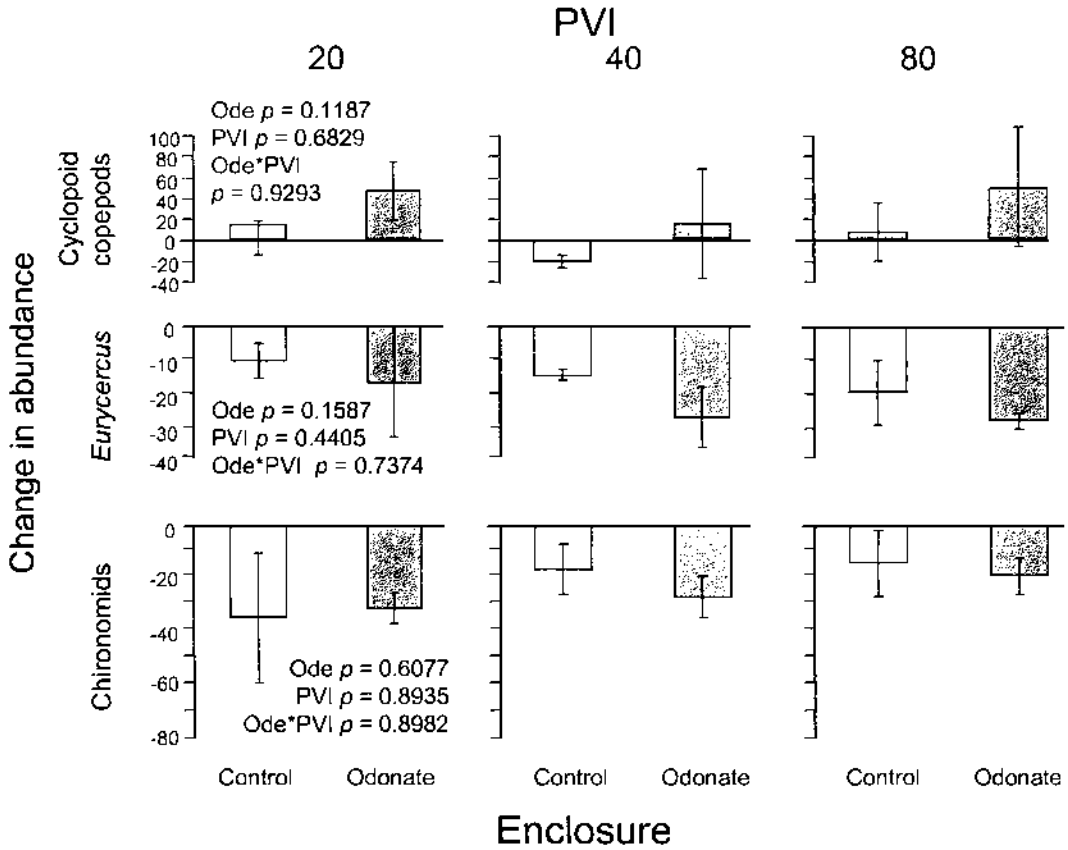


FIG. 3. Change in abundance (no./L \pm 1 SE) for predominately benthic taxa: cyclopoid copepods (top row), *Eurycerus* (middle row), and chironomids (bottom row) at 3 macrophyte densities in enclosures with (shaded bars) or without (open bars) odonate nymphs. Note the different y-axis scales between taxa. Statistics are from 2-way analyses of variance. Ode = odonate impact, PVI = % volume infested impact, Ode*PVI = odonate-PVI interaction. Pair-wise difference comparisons are not included because no significant differences existed between enclosures with and without odonates or between macrophyte densities for benthic taxa.

their size, daphnids are also the preferred food of planktivorous fishes in the pelagic zone. Current research suggests that daphnids adaptively seek refuge in macrophytes when they perceive a predation threat from pelagic planktivorous fishes (Lauridsen and Lodge 1996, Burks et al. 2001), although the degree of migration depends on plant density and distribution and abundance of the fish (Jeppesen et al. 1998). Horizontal migration to escape pelagic fishes or pelagic predacious invertebrates (Kvam and Kleiven 1995), however, forces daphnids into the domain of other predators associated with littoral vegetation and sediment.

Only one previous field study strongly linked pelagic zooplankton as prey to predacious odonates (Blois 1985). Three different species of

dragonflies (*Anax imperator*, *Aeshna cyanea*, and *Libellula depressa*) all readily consumed *Daphnia* (based on availability) in a small, vegetated pond in France (Blois 1985). Our results also suggest that, in some situations, daphnids occupying the littoral zone can suffer high mortality from odonate predation. Body size of prey in our field experiment may explain why odonate predation significantly reduced daphnids, but not ceriodaphnids, at low macrophyte densities. Size-selective foraging theory suggests that predators will preferentially consume the largest prey (Brooks and Dodson 1965). Odonates easily consume large (>2 mm) daphnids in laboratory studies (Thompson and Pickup 1984, Wissinger 1988). Both species of daphnids that occurred in the enclosures, *D. magna* and *D.*

galeata, are significantly larger than ceriodaphnids. In addition, jerky swimming movements of large *Daphnia* probably attracted the attention of sit-and-wait odonate nymphs.

Predation impacts on daphnids go beyond size-selective predation

Other mechanisms besides size-selective predation may partially explain why odonates significantly reduced the predominantly pelagic taxa in our experiment, and not those commonly associated with littoral vegetation or sediment. Large-bodied *E. lamellatus* and *M. viridis* composed the microcrustaceans in the sediments of our field experiment, whereas other common, smaller taxa including *Chydorus*, *Bosmina*, and large *Simocephalus* (a member of the Daphnidae family) were absent from the sediments and plants (RLB, personal observation). If size-selective predation adequately explained our results, then we would have expected a similar reduction in these benthic taxa as we found for *Daphnia*. Larval dragonflies and damselflies readily consumed littoral-associated cladocerans in other studies (Pritchard 1964, Benke 1976, Koperski 1998a). For example, small chydorids, including *Alona*, *Kurzia*, and *Simocephalus*, were the main prey of *E. cynosura* in the well-studied littoral zone of a Tennessee lake (Mahato and Johnson 1991).

Constantly faced with predation pressure, large plant-associated cladocerans or copepods, such as *E. lamellatus* or *M. viridis*, have likely developed antipredator behaviors that allow their coexistence with littoral predators (Pierce and Hinrichs 1997, Beklioglu and Jeppesen 1999). In contrast, pelagic cladocerans may encounter littoral predators sporadically in many lakes, and selective pressures may therefore be inconsistent. This irregular selective pressure may be particularly true for daphnid populations that lack previous exposure to littoral predators, which we presume is the case for our laboratory populations (from Ward's Biological). Documentation of predation impacts of littoral predators on pelagic prey appears less frequently in the literature than evidence regarding pelagic predators (Koperski 1998b). However, our results with the Lake Torup *Daphnia* suggest that even *Daphnia* co-occurring with littoral predators may suffer significant mortality.

Lack of predatory impact on benthos

We also did not detect a significant impact of odonate predation on other benthic taxa that predominately occurred within the sediments. Soft-bodied chironomids are often the preferred prey item of burrowing odonates (Pritchard 1964, Thorp and Cochran 1984), suggesting that they are the most vulnerable of sediment-associated prey. Chironomids composed the largest biomass in our sediment samples in the beginning of our study, and then declined in all enclosures, regardless of odonate presence. This decline may reflect predation by other invertebrate predators like leeches (although we did not find them in our samples) or emergence. Even at 80 PVI, where the number of odonates per benthic area was the highest (55/m²), no significant decreases in chironomids, or copepods and *Eurycerus*, occurred in enclosures with odonates relative to controls. Copepods actually tended to increase in enclosures with odonates, which may partially result from decreased competition with *Daphnia*. However, more studies are required to understand connections between pelagic and benthic prey dynamics.

Previous studies also have found either small or no impacts on benthic prey by odonates (Thorp and Cochran 1984, Blois-Heulin et al. 1990). This lack of impact on the benthos in previous studies and in our study may suggest that odonates are feeding on alternative, i.e., pelagic, food resources. Odonates are known to switch between available prey resources (Akre and Johnson 1979, Johnson and Crowley 1980). For example, when Bays Mountain Lake was invaded by the aggressive *Dromogomphus spinosus* (Gomphidae), the smaller *E. cynosura* switched its diet and ate more microcrustaceans (*Alona*, *Chydorus*, *Kurzia*, *Pleuroxus*, *Simocephalus*) associated with the vegetation (Mahato and Johnson 1991). Pritchard (1964) and Blois (1985) also demonstrated that odonate gut contents often mirror prey availability.

Odonates as model benthic invertebrate predators

Most odonate species are generalist feeders (Koperski 1998b), and will eat large cladocerans given the chance, although different odonate groups and ages may be more effective than others at consuming cladocerans (Westfall and

Tenessen 1996). Libellulidae and Corduliidae species may be better suited for catching cladocerans than other dragonfly families because of cage-like mouthparts (Pritchard 1964). Both species of dragonflies used in our laboratory and field experiments (*E. cynosura* and *S. flavomaculata*, respectively) belong to the family Corduliidae and commonly occur among littoral sediment and vegetation. These odonates are described as 'burrowers' or 'climbers' (Westfall and Tennessen 1996) and thus represent a potential littoral-zone predator of pelagic zooplankton. Dragonflies used in our laboratory and field experiments were at least penultimate instars and were stocked at realistic densities. We tried to isolate the impact of invertebrate predation and minimize intraguild predation by keeping our field enclosures fishless and using the largest damselflies possible, so that the dragonflies would have difficulty consuming them. However, by using dragonflies and damselflies known to prey on daphnids (Thompson and Pickup 1984, Koperski 1998a), our results could represent the upper end of the range of naturally occurring impacts.

On the other hand, elements of our experimental design also conferred a conservative interpretation to our results. Odonates must also avoid their own predators while capturing prey (Johnson and Crowley 1980) and damselflies may forage less in the presence of dragonflies because of a high perceived risk of intraguild predation (Pierce 1988, Koperski 1998a). We used a design for our field experiments where predator density increased with macrophyte density and the ratio of dragonflies to damselflies also increased. If we had not increased our predator densities, odonates would have been less likely to confront each other at high plant densities (which is not a good mimic of natural systems). Therefore, our approach tried to account for confounding effects of increased surface area, but naturally occurring behavioral interactions resulting from increased predator densities may have also influenced our results.

Potential behavior-mediated influences on daphnid predation

The magnitude of the predation impact on *Daphnia* by odonates declined with increasing macrophyte and predator density in our field experiment. Dense macrophytes may have pro-

vided a refuge for *Daphnia* and other taxa in the field, although our laboratory experiments indicated that dragonflies effectively foraged at high macrophyte densities. At high predator densities, odonates may have behavioral interference effects on each other, resulting in a smaller impact on zooplankton prey (Koperski 1998a). If applicable, reduced foraging rates of damselflies because of the presence of dragonflies would render our results (i.e., the reduction in *Daphnia*) more conservative. Using fewer dragonflies than damselflies (as opposed to equal numbers) may have minimized behavior-mediated interactions, but experiments that are specifically designed to test behavior-mediated predator effects are necessary in shallow systems.

Besides behavior-mediated effects, increased cannibalism and intraguild predation may have occurred at high odonate densities, thereby lowering the predation pressure on zooplankton. We tried to limit cannibalism by using similarly sized dragonflies (Wissinger 1988). We also did not observe dragonflies consuming damselflies when held together in the laboratory. Johansson (1993) also found that dragonflies reduced their predation on damselflies, and instead consumed zooplankton when available. However, if applicable, high intraguild predation of odonates would again make our impact on *Daphnia* more conservative, and perhaps suggest that odonates more strongly affect zooplankton populations in systems that lack larger prey. It is possible that in natural field situations odonates would forage less in the presence of fish (Pierce 1988, Blois-Heulin et al. 1990, Johnson et al. 1996), although some studies have shown no influence of fish on odonate foraging (Swisher et al. 1998). Therefore, although we suggest our results point to strong impacts of benthic predators on pelagic prey, interactions between littoral, benthic, and pelagic zones are inherently complex and require further investigation to understand their foodweb dynamics.

In conclusion, daphnids migrate vertically in deep lakes to avoid planktivorous fishes (Lampert 1993). It has also become increasingly clear that daphnids must also avoid pelagic predators in shallow lakes that lack a hypolimnetic refuge. Macrophytes decrease foraging efficiencies of some fishes (Winfield 1986, Diehl 1988) and may provide suitable refuge for daphnids against certain pelagic predators (Lauridsen and

Lodge 1996, Jeppesen 1998, Burks et al. 2001). However, migrating into the littoral zone introduces daphnids to an entirely different predator assemblage. Daphnids may undergo DHM to lower predation from pelagic predators, but our results suggest that mortality from littoral predators can be substantial. Therefore, the net benefit of DHM may differ among lakes as a function of the relative threat of pelagic and littoral predators.

Acknowledgements

We thank Tue Jacobsen for his many long hours in the field collecting enough odonates for this experiment. The Lake Group Technicians at the National Environmental Research Institute also provided technical assistance. At Notre Dame, Craig McAra and Áine Skow helped execute the laboratory experiments. RB thanks Dan Johnson and Sean Dunlap for discussions about the role of odonates in littoral zones. Comments from 2 anonymous reviewers substantially improved the manuscript. A Fulbright Fellowship for Study in Denmark (to RB) laid the groundwork for this study. During summer 1999, The American Scandinavian Foundation (grant to RB) provided research funds for travel and lodging. RB received financial support from a National Science Foundation Graduate Training Grant Traineeship (#9452655) to write this manuscript. US NOAA Sea Grant (DML #NA46RG0419-2, 643-1532-04) and NSF (DML #DEB 91-07569) provided additional support. We also acknowledge support from the Danish Natural Sciences Research Council (Grant # 960-1711) and the Research Program ('The Role of Fish in Aquatic Ecosystems' 1999-2001) from the Danish Ministry of Agriculture, Fisheries and Foods.

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Received: 14 November 2000

Accepted: 20 August 2001