

Avoidance by *Daphnia magna* of Fish and Macrophytes: Chemical Cues and Predator-Mediated Use of Macrophyte Habitat



Torben L. Lauridsen; David M. Lodge

Limnology and Oceanography, Vol. 41, No. 4 (Jun., 1996), 794-798.

Stable URL:

<http://links.jstor.org/sici?sici=0024-3590%28199606%2941%3A4%3C794%3AABDMOF%3E2.0.CO%3B2-P>

Limnology and Oceanography is currently published by American Society of Limnology and Oceanography.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/limnoc.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

- cladoceran populations. *Int. Ver. Theor. Angew. Limnol. Verh.* **22**: 3083–3087.
- U.S. ENVIRONMENTAL PROTECTION AGENCY. 1985. Water quality criterion for ammonia. U.S. EPA 440/5-84-001. NTIS.
- VIJVERBERG, J. 1989. Culture techniques for studies on the growth, development and reproduction of copepods and

cladocerans under laboratory and in situ conditions: A review. *Freshwater Biol.* **21**: 317–373.

Submitted: 14 July 1994
Accepted: 13 November 1995
Amended: 12 February 1996

Limnol. Oceanogr., 41(4), 1996, 794–798
 © 1996, by the American Society of Limnology and Oceanography, Inc.

Avoidance by *Daphnia magna* of fish and macrophytes: Chemical cues and predator-mediated use of macrophyte habitat

Abstract—Recent biomanipulation studies suggest that macrophytes are an important refuge from fish predation for large pelagic zooplankton. We conducted two laboratory experiments that tested the behavioral responses of *Daphnia magna* to a macrophyte (*Myriophyllum exalbescens* L.) and a sunfish (*Lepomis cyanellus* Rafinesque) and whether responses were chemically (for fish) or structurally (for macrophytes) mediated. In the first experiment, we measured *Daphnia* response to four treatments in separate 38-liter tanks. In controls without macrophytes and fish, ~15% of the daphnids were found in the central zone (~50% of the tank area); the others were found around the tank perimeter (especially in the corners). With macrophytes present, 80% of the daphnids were found in the central zone (unvegetated in all treatments). When fish or fish odor alone were present ~35% and ~45%, respectively, of the *Daphnia* occupied the central zone. Thus, chemically mediated avoidance of *Lepomis* caused *Daphnia* to increase its occupation of macrophytes. In the second experiment, we tested whether the repellent effect of *Myriophyllum* resulted from structural characteristics of the macrophyte; the results suggest that both chemical and structural cues contributed to *Daphnia* avoidance of the macrophyte. Overall, our results are consistent with the suggestion that large pelagic zooplankton may use macrophytes as a refuge in shallow lakes where vertical migration is restricted.

Macrophytes fill multiple roles in ecosystem function (Carpenter and Lodge 1986) and in the mediation of predator-prey interactions involving fish and macroinvertebrates (Crowder and Cooper 1982; Savino and Stein 1982). Investigators have suggested that macrophytes provide a refuge to *Daphnia* from fish predation and thus contribute to biomanipulation efforts to reduce phytoplankton standing stock (Timms and Moss 1984; Jeppesen et al. 1991). Scheffer et al. (1993) suggested that macrophyte refuges for *Daphnia* contribute significantly to the stability of the high *Daphnia*-low phytoplankton-high macrophyte state in shallow lakes.

Recent documentation of diel horizontal migration of zooplankton in shallow lakes, in which large zooplankton congregate in or near macrophytes and other littoral zone structure during the day, are consistent with this hypoth-

esis (e.g. Davies 1985; Paterson 1993). The assumption is that macrophytes in shallow lakes, as in the metalimnion and hypolimnion in deeper lakes (e.g. Gliwicz 1986; Ringelberg 1991; Lampert 1993), offer large zooplankton a refuge from fish predation. (Timms and Moss 1984; Jeppesen et al. 1991). However, we know of no direct test of the hypothesis that zooplankton movement into macrophytes is a response to fish. The use of macrophyte habitats by pelagic zooplankton seemingly contradicts earlier field (Hasler and Jones 1949; Pennak 1966) and laboratory (Pennak 1973) results that suggest that daphnids are repelled by macrophytes. We hypothesized that when faced with a choice of remaining in the presence of fish or moving into macrophytes, predation-vulnerable zooplankton seek refuge in macrophytes despite their repellency. We conducted laboratory experiments to test whether macrophytes repel *Daphnia* in the absence of fish, whether *Daphnia* avoids fish, and whether behavioral avoidance of fish overrides avoidance of macrophytes. We also tested whether the stimuli for avoidance behavior were structural for macrophytes and chemical for fish.

We conducted two experiments in August–September 1994. The first experiment tested the behavioral response of *Daphnia magna* Straus to combinations of the presence of a macrophyte (*Myriophyllum exalbescens* L.), green sunfish (*Lepomis cyanellus* Rafinesque) and associated odor, and sunfish odor alone. The second experiment tested whether the stimulus for avoidance of *Myriophyllum* was structural (visual, tactile, etc.). *Daphnia* was purchased from Ward's Natural Science Establishment and kept in fish-free laboratory aquaria. In experiments, we only used *Daphnia* > 2 mm long so that the animals were easily observable and could not enter fish enclosures (*see below*). We collected aboveground portions of apparently vigorous *Myriophyllum* from Stone Lake (Cass County, southern lower Michigan) and held them in fish-free laboratory aquaria for no more than 2 d before experiments. We used dipnets to collect *Lepomis* (4–5-cm total length) from St. Joseph Lake (campus of the University of Notre Dame, Indiana) and kept them in laboratory aquaria. Young green sunfish eat zooplankton, such as large cla-

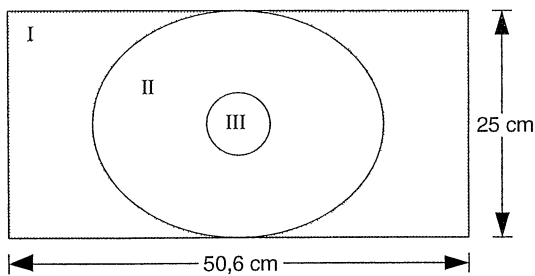


Fig. 1. Setup of 38-liter tanks (from above): I—peripheral zone (50% of the total area) either covered with macrophytes or without macrophytes; II—central zone always without macrophytes; III—cage for fish. Zones I and II are separated by netting (see text).

docerans (Carlander 1977), and green sunfish are common in ponds, lakes, and streams throughout central North America (Robinson and Buchanan 1988). *D. magna* can survive in the parts of habitats in which green sunfish live, at least in the absence of fish. If fish are present, *D. magna* needs an effective refuge to survive (Lauridsen and Buenk in prep.). Consequently, the interaction we simulated in the laboratory could occur in the field.

Both experiments were conducted in half-filled 38-liter glass aquaria in a controlled climate room (20°C) with a 15 : 9 L/D cycle. Each aquarium was separated by vertical plastic netting (mesh openings, 20 × 20 mm) into two zones of equal area (Fig. 1). The oval central zone of the tanks (50% of the tank) was without macrophytes in all treatments. In all treatments, the center of this open area contained a cylindrical fish enclosure cage (7-cm diam = 3% of the tank area) of standard fiber-glass window screening (mesh size, 1 × 1.5 mm), which was too small for *Daphnia* to pass through.

In treatments with natural macrophytes (in both experiments), the peripheral part of each tank contained 36 shoots of *Myriophyllum*, each 10–15 cm long, producing a biomass of 128 ± 13 g dry wt m^{-2} . For the treatment with plastic macrophytes (second experiment), we purchased artificial *Myriophyllum verticillatum* (Second Nature Plantastics). To control for differences between plastic and real macrophytes in shoot diameter [2.92 ± 0.49 and 3.64 ± 0.75 cm (mean \pm SD, $n = 50$), respectively] and internode distance [1.13 ± 0.12 and 1.59 ± 0.35 cm ($n = 50$), respectively], we equalized the plant-filled water volume (PV) by regulating the number of plastic macrophyte stems according to

$$PV_{\text{real}} = PV_{\text{plastic}}$$

$$= \frac{[(\pi r^2_{\text{plastic}})L_{\text{plastic}}]N_{\text{plastic}}(I_{\text{plastic}}/I_{\text{real}})}{V} \times 100.$$

r is shoot radius; N is number of stems; L is mean macrophyte length; I is internode macrophyte distance; and V is total water volume, PV is similar to the term “percent volume infested” introduced by Canfield et al. (1984). For both real and plastic macrophytes, PV was 28% of the total water volume in the tanks, comparable to mac-

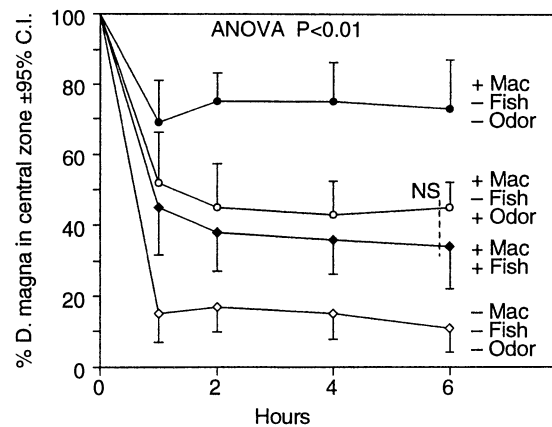


Fig. 2. Percentage of *Daphnia magna* in the central zone in the four treatments of the first experiment. ANOVA P -value is for the treatment effect (conducted for hour 6). Tukey's test results are indicated by vertical broken line that connects treatments that do not differ significantly (NS).

rophyte-dominated mesotrophic-eutrophic shallow lakes (Canfield et al. 1984; Schriver et al. 1995).

At the start of each experiment, we added 10 *Daphnia* to the central zone of each aquarium. In both experiments, the response variable was the visually determined number of *Daphnia* in the central zone monitored at 1–2-h intervals for 6 h. Experiments were stopped after 6 h because preliminary experiments lasting 24–30 h showed that the daytime response did not change after 4–6 h.

In the first experiment, we measured *Daphnia* response to four treatments: control (i.e. without macrophytes, fish, or fish odor); with macrophytes, but without fish or fish odor; with macrophytes and fish and fish odor; and with macrophytes and fish odor, but without fish. In treatments with fish or fish odor, two fish were added to the fish cage in the center of the central zone 24 h before the experiment started. In treatments with fish odor, the fish were removed immediately before the experiment started. This experiment was blocked for time because conducting all 10 replicates on the same date was not logistically possible: $N = 5$ on 23 August; $N = 5$ on 26 August.

In the second experiment, aquaria were set up as for the first experiment except that no fish cages were included (because no fish or fish odor treatments were included). To test whether the repellent effect of macrophytes (see below) resulted from structural stimuli, we measured *Daphnia* response to three treatments: control (i.e. without macrophytes); with natural *Myriophyllum*; and with plastic macrophytes. This experiment was blocked for time: $N = 5$ on 31 August; $N = 5$ on 2 September; $N = 5$ on 5 September.

Both experiments were analyzed with a two-way ANOVA (block and treatment main effects). Responses reached a near-asymptote after <1 h; the datum in the ANOVA for each aquarium was the number of *Daphnia* in the central zone at hour 6. When the block effect was not significant (first experiment), Tukey's test was applied to data pooled across blocks to test differences between treat-

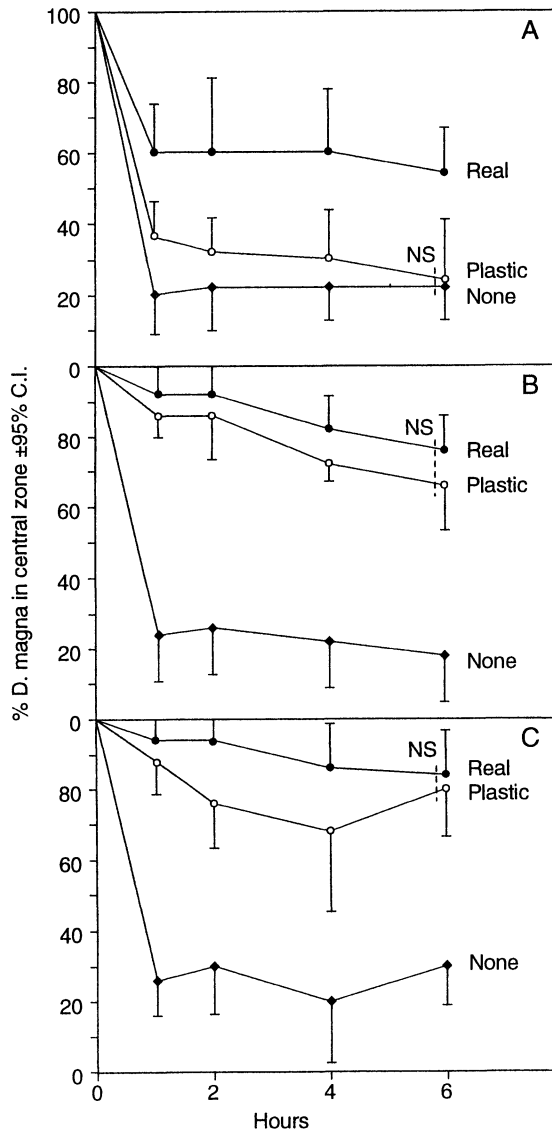


Fig. 3. Percentage of *Daphnia magna* in the central zone in the three different treatments in each of three experimental blocks (A,B,C) of the second experiment. ANOVA $P < 0.01$ for the block-specific treatment effect (conducted for hour 6) on all three experimental blocks. Block-specific Tukey's test results are indicated by vertical broken lines that connect treatments that do not differ significantly (NS).

ments. When the block effect was significant (second experiment), a one-way ANOVA and Tukey's test were applied within each block.

In the first experiment, there was a significant treatment (but no block) effect (treatment $MS = 6,629.17$, $F_{3,32} = 25.87$, $P < 0.01$; block $MS = 122.50$, $F_{1,32} = 0.47$, $P = NS$; $t \times b$ $MS = 89.17$, $F_{3,32} = 0.35$, $P = NS$). In the control treatment, 12% of the *Daphnia* occupied the central area at 6 h (Fig. 2); the remainder aggregated primarily in aquarium corners. Relative to this behavior in the control, *Daphnia* strongly avoided macrophytes: 73% of the *Daphnia* occupied the central zone when macrophytes

were in the peripheral zone (Fig. 2). Consistent with our hypothesis, however, macrophyte avoidance was partially overcome in the presence of *Lepomis* and in the presence of *Lepomis* odor only, with 34 and 46% of *Daphnia* in the central zone, respectively (Fig. 2). The latter two treatments were the only two that did not differ significantly (Tukey's test, $P > 0.05$; Fig. 2).

In the second experiment, treatment ($MS = 9,075.00$, $F_{2,36} = 75.00$, $P < 0.01$), block ($MS = 3,775.50$, $F_{2,36} = 31.20$, $P < 0.01$), and interaction ($MS = 932.2$, $F_{4,36} = P < 0.01$) effects were all significant. Because of the significant block and interaction effects, we conducted independent one-way ANOVAs and Tukey's tests to test for treatment effects within each block. In all three blocks, the rank order of treatments was the same, with the least number of *Daphnia* in the central zone in the control treatment (no macrophytes) and the greatest number in the central zone in the real *Myriophyllum* treatment (Fig. 3). The absolute magnitude of the *Daphnia* response in control treatments was similar in all blocks, with 20–28% in the central zone (Fig. 3). However, in the first block, there was no significant difference between plastic macrophytes and control treatments (Fig. 3A). Results of this block suggest that avoidance of macrophytes is chemically mediated. In contrast, in the second and third blocks, these treatments differed significantly, but no difference existed between the real and plastic macrophyte treatments (Fig. 3B, C). Results of the last two blocks therefore suggest that macrophyte avoidance is structurally mediated.

Results of our first experiment demonstrate clearly that *D. magna* will occupy macrophytes to avoid fish. This result may explain the paradox between documented macrophyte avoidance by *Daphnia* and apparent use of macrophyte habitats as a refuge from fish predation in shallow lakes. To our knowledge, our results are the first experimental documentation that behavioral avoidance of fish at least partially overcomes behavioral avoidance of macrophytes by zooplankton. The similarity in response of *Daphnia* in the fish and fish-odor-only treatments further suggests that this behavior is predominantly chemically mediated, which is consistent with other chemically mediated fish-avoidance behaviors by *Daphnia* (De Meester 1993). The identity of the active compounds is unknown. The importance of chemical stimuli in the horizontal migration we observed is consistent with the importance of chemical stimuli in the better documented vertical migration of zooplankton (e.g. Dodson 1988; Ringelberg 1991; Loose and Dawidowicz 1994). Thus, it is plausible that the behaviors we documented in the laboratory account for the daytime concentrations of large pelagic zooplankton observed in macrophytes in shallow European lakes (Davies 1985; Lauridsen and Buenk in prep.).

Avoidance of the macrophyte *M. exalbescens* by the pelagic zooplankton *D. magna* in both our experiments confirmed earlier findings that macrophytes repel zooplankton (Pennak 1973). Furthermore, results of the first block of our second experiment (and the consistent rank

order of treatments in all three blocks) provide strong support for the suggestion by Pennak (1973) that the zooplankton response to macrophytes is in part chemically mediated. Chemical repellency might differ among macrophyte species (Pennak 1973; Quade 1969), but the identity of active compounds and differences in activity among macrophyte species are unknown.

The similarity in response by *Daphnia* to real and plastic plants in the second and third blocks of our second experiment suggests that the structure of macrophytes also contributes to their repellency. Because *Daphnia* clustered in relatively dark aquarium corners in control treatments (Lauridsen pers. obs.), avoidance of structures seems to entail a mechanism other than negative phototaxis (see De Meester 1993). It is plausible that macrophytes interfere with locomotion by daphnids. We do not understand why results differed among blocks of the second experiment.

We believe that we may have answered one question, but another remains. It is well documented that small fish (many of which are zooplanktivores) also use littoral habitats as daytime refuges from piscivores (e.g. He and Lodge 1990; Venugopal and Winfield 1993). Although macrophytes may reduce the per capita effectiveness of zooplanktivorous fish or, in dense macrophyte beds, even prevent fish from moving into the beds (Jensen 1994; Lene Jacobsen unpubl. data), moving into macrophytes may sometimes expose *Daphnia* to higher densities of zooplanktivores. Thus, direct comparisons of mortality rates in open vs. vegetative habitats are needed to more fully evaluate the macrophyte refuge hypothesis.

Nevertheless, the *Daphnia* behaviors we documented are consistent with the suggestion by Moss et al. (1994) that macrophytes are important refuges for large zooplankton in shallow lakes and allow zooplankton to suppress phytoplankton abundance even in the presence of zooplanktivorous fish.

Torben L. Lauridsen¹
David M. Lodge

Department of Biological Sciences
University of Notre Dame
Notre Dame, Indiana 46556

¹ Corresponding author, present address: National Environmental Research Institute, Department of Freshwater Ecology, Vejlsovej 25, POB 314, DK-8600 Silkeborg, Denmark.

Acknowledgments

We thank Bob Spence and Kay Stewart for help with the setup, Kathe Møgelvang for the drawings, Anne Mette Poulsen for manuscript preparation, and Greg Cronin for a helpful review of a previous version of the manuscript.

Financial support for this research came from the Danish Research Academy (T.L.L.), National Science Foundation grant DEB 91-07569 (D.M.L.), and the Graduate School of the University of Notre Dame.

References

- CANFIELD, D. E., JR., AND OTHERS. 1984. Prediction of chlorophyll in Florida Lakes: Importance of aquatic macrophytes. *Can. J. Fish. Aquat. Sci.* **41**: 497–501.
- CARLANDER, K. D. 1977. Handbook of freshwater fishery biology. V. 2. Iowa State.
- CARPENTER, S. R., AND D. M. LODGE. 1986. Effects of submersed macrophytes on ecosystem processes. *Aquat. Bot.* **26**: 341–370.
- CROWDER, L. B., AND W. E. COOPER. 1982. Habitat structural complexity and the interaction between bluegills and their prey. *Ecology* **63**: 1802–1813.
- DAVIES, J. 1985. Evidence for a diurnal horizontal migration in *Daphnia hyalina lacustris* Sars. *Hydrobiologia* **120**: 103–105.
- DE MEESTER, L. 1993. Genotype, fish-mediated chemicals, and planktonic behavior in *Daphnia magna*. *Ecology* **74**: 1467–1474.
- DODSON, S. 1988. The ecological role of chemical stimuli for the zooplankton: Predator avoidance behavior in *Daphnia*. *Limnol. Oceanogr.* **33**: 1431–1439.
- GLIWICZ, M. Z. 1986. Predation and evolution of vertical migration in zooplankton. *Nature* **320**: 746–748.
- HASLER, A. D., AND E. JONES. 1949. Demonstration of the antagonistic action of large aquatic plants on algae and rotifers. *Ecology* **30**: 359–364.
- HE, X., AND D. M. LODGE. 1990. Using minnow traps to estimate fish population size: The importance of spatial distribution and relative species abundance. *Hydrobiologia* **190**: 9–14.
- JENSEN, L. N. 1994. Macrophytes as a structuring factor for young of perch, *Perca fluviatilis*, and roach, *Rutilus rutilus* in Lake Stigsholm [in Danish]. M.S. thesis, Natl. Environ. Res. Inst. and Biol. Inst. Odense Univ.
- JEPPESEN, E., AND OTHERS. 1991. Recovery resilience following a reduction in external phosphorus loading of shallow, eutrophic Danish lakes: Duration, regulating factors and methods for overcoming resilience. *Mem. Ist. Ital. Idrobiol.* **48**: 127–148.
- LAMPERT, W. 1993. Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator-avoidance hypothesis. *Ergeb. Limnol.* **39**: 79–88.
- LOOSE, C., AND P. DAWIDOWICZ. 1994. Trade-offs in diel vertical migration by zooplankton: The costs of predator avoidance. *Ecology* **75**: 2255–2263.
- MOSS, B., S. MCGOWAN, AND L. CARVALHO. 1994. Determinations of phytoplankton crops by top-down and bottom-up mechanisms in a group of English lakes, the West Midland meres. *Limnol. Oceanogr.* **39**: 1020–1029.
- PATERSON, M. 1993. The distribution of microcrustacea in the littoral zone of a freshwater lake. *Hydrobiologia* **263**: 173–183.
- PENNAK, R. W. 1966. Structure of zooplankton populations in the littoral macrophyte zone of some Colorado lakes. *Trans. Am. Microsc. Soc.* **85**: 329–349.
- . 1973. Some evidence for aquatic macrophytes as repellents for a limnetic species of *Daphnia*. *Int. Rev. Gesamten Hydrobiol.* **58**: 569–576.
- QUADE, H. W. 1969. Cladoceran faunas associated with aquatic macrophytes in some lakes in northwestern Minnesota. *Ecology* **50**: 170–179.
- RINGELBERG, J. 1991. Enhancement of the phototactic reaction in *Daphnia hyalina* by a chemical mediated by juvenile perch (*Perca fluviatilis*). *J. Plankton Res.* **13**: 17–25.

- ROBINSON, H. W., AND T. M. BUCHANAN. 1988. Fishes of Arkansas. Univ. Arkansas.
- SAVINO, J. F., AND R. A. STEIN. 1982. Predator-prey interaction between largemouth bass and bluegills as influenced by simulated, submersed vegetation. *Trans. Am. Fish. Soc.* **111**: 255–266.
- SCHEFFER, M., S. H. HOSPER, M.-L. MEIJER, B. MOSS, AND E. JEPPESEN. 1993. Alternative equilibria in shallow lakes. *Trends Ecol. Evol.* **8**: 275–279.
- SCHRIVER, P., J. BØGESTRAND, E. JEPPESEN, AND M. SØNDERGAARD. 1995. Impact of submerged macrophytes on the interactions between fish, zooplankton and phytoplankton: Large-scale enclosure experiments in a shallow eutrophic lake. *Freshwater Biol.* **33**: 255–270.
- TIMMS, R. M., AND B. MOSS. 1984. Prevention of growth of potentially dense phytoplankton populations by zooplankton grazing, in the presence of zooplanktivorous fish, in a shallow wetland ecosystem. *Limnol. Oceanogr.* **29**: 472–486.
- VENUGOPAL, M. N., AND I. J. WINFIELD. 1993. The distribution of juvenile fishes in a hypereutrophic pond: Can macrophytes potentially offer a refuge for zooplankton? *J. Freshwater Ecol.* **8**: 389–396.

Submitted: 16 June 1995
Accepted: 14 November 1995
Amended: 14 February 1996

Limnol. Oceanogr., 41(4), 1996, 798–801
© 1996, by the American Society of Limnology and Oceanography, Inc.

Feeding-deterrent properties of common oceanic holoplankton from Bermudian waters

Abstract—The feeding-deterrent properties of a suite of common holoplankton (nine species representing five phyla) collected from oceanic waters near Bermuda were investigated. The common planktivorous fish *Abudefduf saxatilis* (sergeant major) was used as a model predator. With the exception of the salp *Pegea bicaudata*, all plankton had significant ichthyodeterrent properties compared to squid tissue controls. These plankton generally lack structural defenses and are passive or sluggish swimmers; our observations suggest that they may derive protection by harboring defensive chemistry. Chemical defenses would have important implications for the regulation of material and energy flux in oceanic food webs, and such defenses may help explain the abundance of coexisting species, all competing for similar resources, in a seemingly homogeneous habitat (i.e. the paradox of the plankton).

Holoplanktonic marine algae and invertebrates are subject to intense predation pressure, primarily from crustaceans and fish. Cyanobacteria colonies, radiolarians, foraminiferans, and larvaceans move passively with the currents, while some gelatinous zooplankton such as salps, cnidarians, ctenophores, pteropods, and heteropods are generally sluggish swimmers. It is unlikely that they can avoid predatory crustaceans and fish by swimming. Some plankton may gain defense from their transparency, although many are colored or have conspicuously colored body parts (gonad and gut). Moreover, laboratory observations indicate that fish have little trouble visually detecting even minute zooplankton in aquaria (McClintock pers. obs.).

In gelatinous zooplankton there is no protection by skeletal components, although nematocysts may provide some protection to cnidarians. It is also unlikely that these organisms are protected due to a low nutritional content. Although some gelatinous zooplankton have been considered to have relatively low carbon contents (Curl 1962; Beers 1966), the low body C:N ratio in gelatinous zoo-

plankton such as salps (Madin et al. 1981) indicates they are potentially quite nutritious. Pelagic pteropods can be relatively rich in protein and lipid (Bryan et al. 1995). Moreover, the energetic value of their internal organs can be very high (Shenker 1985). Indeed, some predators of gelatinous zooplankton feed almost exclusively on these internal organs, avoiding the ingestion of gelatinous body parts (Harbison et al. 1977; Madin and Harbison 1977; Janssen and Harbison 1981). Some gelatinous zooplankton attain large body sizes or occur in swarms, making them an energetically attractive prey even if low in energy on an individual basis.

Diel vertical migration is often thought to be a response to grazing pressure, and between 20 and 50% of zooplankton populations are migratory (Longhurst and Harrison 1989). An alternate hypothesis for vertical migration is that zooplankton gain an energetic advantage by feeding in the evening on phytoplankton that have been fixing carbon during daylight hours (Enright 1977; Enright and Honegger 1977). Nonetheless, more evidence supports the predator avoidance hypothesis. Zooplankton biomass in the upper 160 m can nearly double at night near Bermuda (Roman et al. 1993). That these organisms invest such a considerable amount of energy in predator avoidance attests to the strong selective evolutionary pressure that can be imposed by predators. The investment of energy into defensive mechanisms such as chemical deterrents could also result from this strong selective pressure. In this study we examine the feeding-deterrent properties of a broad suite of oceanic holoplankton.

Holoplankton were collected in May–June 1995 at sites 5–20 km southeast of Bermuda by either deploying a 1-m-diameter plankton net (333- μ m mesh) or conducting blue-water dives and capturing individuals in hand-held jars. Following collection, holoplankton were returned to the laboratory and immediately subjected to feeding trials with the common planktivorous fish *Abudefduf saxatilis* (sergeant major) as a model predator. *A. saxatilis* was