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Ecology, Vol. 74, No. 2 (Mar., 1993), 320-331.

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LINKING PREDATION RISK MODELS WITH BEHAVIORAL MECHANISMS: IDENTIFYING POPULATION BOTTLENECKS¹

CRAIG E. WILLIAMSON

Department of Earth and Environmental Sciences, Lehigh University,
Bethlehem, Pennsylvania 18015 USA

Abstract. A comprehensive understanding of the factors controlling predation risk in natural communities is dependent upon knowledge of both the patchiness of predator and prey populations in nature, and on the outcome of behavioral interactions between predator and prey individuals. While both of these areas of predation ecology are rich in theory and data, there are no models that permit these two fundamental components of predation risk to be combined in a quantitative way. Here a model is developed to combine these density risk and prey vulnerability components of predation. The model is used to estimate the contribution of predator and prey population overlap to predation risk, and to quantify both density risk and prey vulnerability components of predation risk for two planktonic invertebrate predators and five rotifer prey. Behavioral data from the literature are used to interpret the prey vulnerability values and demonstrate the utility of the model. The predation risk values obtained for each prey species also are compared to the intrinsic population growth rates (r_{\max}), taken from previous studies. In addition, I test the a priori hypothesis that prey population growth will be negative when predation risk exceeds r_{\max} . The results reveal the presence of severe bottleneck periods where predation risk exceeds the r_{\max} of four of the five prey species, thus supporting the a priori prediction of negative population growth or extremely low prey populations during these periods.

Key words: behavioral mechanism; community structure; invertebrate predation; population overlap; predation risk model; zooplankton.

INTRODUCTION

Our understanding of the dynamics of predator–prey and other consumer–resource interactions has been advanced considerably in recent years through the application of behavioral models of the type pioneered by Holling (1966). This approach involves breaking down predation into a series of discrete events. Although the exact sequence varies with the predator, it generally involves some combination of encounter, attack, capture, and ingestion. In practice, direct observations of predator–prey interactions are made, the frequency of individual behavioral events is scored, and conditional probabilities (e.g., probability of capture after attack) are computed and used to interpret the behavioral mechanisms that regulate predation rates.

Use of these behavioral models has generated a great deal of insight into the ecology and evolution of predator–prey interactions in plankton communities. Two recent reviews have demonstrated the importance of behavioral mechanisms in our understanding of particle selection in suspension-feeding zooplankton (Price 1988) and in the role of individual behavior in regulating predator–prey population dynamics (Ohman 1988). Holling's behavioral approach has been instru-

mental in our understanding of the mechanisms that underlie selective predation by a wide variety of predatory zooplankton (Kerfoot 1977, Gilbert and Williamson 1978, O'Brien 1979, 1987, Pastorok 1980, Williamson 1980, 1983, 1984, 1987, Williamson and Gilbert 1980, Greene 1983, Riessen et al. 1984, Roche 1987, 1990a). Behavioral approaches have also contributed to our understanding of the role of unsuccessful predation in the evolution of predator–prey interactions (Vermeij 1982). Hypotheses concerning the effectiveness of different morphological and behavioral adaptations (sensu Gould and Vrba 1982) to specific phases of predation can be directly examined with behavior experiments.

A current challenge is placing these mechanistic behavioral studies in the context of the natural environment where predator and prey distributions are often extremely patchy. In plankton communities population densities in patches are commonly several orders of magnitude greater than average densities (Malone and McQueen 1983). Variation in the spatial and temporal overlap of invertebrate predators and their prey may play a major role in determining which prey are consumed by a variety of predators ranging from the dipteran larvae of *Chaoborus* spp. (Fedorenko 1975, Hairston 1980, Melville and Maly 1981), and the mysid shrimp *Mysis relicta* (Bowers and Vanderploeg 1982, Folt et al. 1982, Schulze and Brooks 1987), to the

¹ Manuscript received 16 March 1992; revised 15 May 1992; accepted 22 May 1992.

calanoid copepod *Diaptomus nevadensis* (Hairston 1980), and the cyclopoid copepods *Mesocyclops edax* (Williamson and Magnien 1982) and *Acanthocyclops robustus* (Roche 1990b). Quantitative estimates of the effect of spatial overlap of predator and prey populations on predation risk suggest that prey mortality rates due to predation may be under or overestimated by a factor of two or more if the patchiness of predator and prey populations in nature is not taken into consideration (Williamson and Stoeckel 1990). Zooplankton that migrate down to deeper, darker strata of the water column during daylight may reduce predation risk by visual predators to an even greater extent.

Data on behavioral mechanisms and population overlap need to be translated into a common theoretical framework if we are to interpret the relative importance of these two components of predation in nature. The need to link these two important components of predation has become increasingly apparent in recent years with the discovery that the vertical distribution of prey, and hence their overlap with predators in nature, may be influenced by short-term behavioral responses of prey to the presence of predators (Levy 1990, Neill 1990, Tjossem 1990), or to the availability of food resources (Johnsen and Jakobsen 1987).

Here I present a model that integrates Holling's behavioral components approach with a measure of overlap of predator and prey populations in nature. The model is developed from an exponential population growth rate equation, and incorporates the encounter rate model of Gerritsen and Strickler (1977). The result is a quantitative technique that can be used to estimate predation risk and all of its subsidiary components. The structure of the model permits it to be interpreted and applied at both the individual and the population level for use in evolutionary as well as ecological studies. While no direct behavioral observations are made in this study, field data on two invertebrate predators and five rotifer prey are presented to illustrate the model and a graphical method of expressing predation risk that facilitates the evaluation of predation risk values and their primary components. The predation risk model is also used to explore changes in the overlap between predator and prey during their observed diel vertical migrations, and the presence of population bottlenecks during which mortality rates due to predation exceed the maximum potential reproductive rates of each species. These field data are then discussed in light of past behavioral data on the same species in an attempt to understand the observed predation risk values obtained in the field.

THE MODEL

Predation risk (PR) can be most simply expressed as the instantaneous mortality rate (d) in the standard equation for exponential population growth:

$$N_t = N_0 e^{rt}$$

where

$$r = b - d$$

and

$$d = PR. \tag{1}$$

Here r is the exponential growth rate of the population (day^{-1}), b is the instantaneous birth rate (day^{-1}), N_0 is the initial population size, N_t the population size at time t , and e is the base of the natural logarithms.

Predation risk has two major components, density risk (DR), which accounts for all of the direct density terms of the prey and predator, and prey vulnerability (PV), which is a per capita predation rate coefficient commonly referred to as the feeding rate coefficient, clearance rate, or grazing rate (Williamson et al. 1989):

$$PR = DR \cdot PV. \tag{2}$$

If PV is expressed in units of litres per predator per day, and DR in units of predators per litre, then PR is a mortality rate coefficient with units of day^{-1} .

Holling's behavioral components can be incorporated into this model through the prey vulnerability component. Prey vulnerability is a function of the predator-specific volume (or area in a two-dimensional model) encountered per unit time by the prey (V_e), and the probability that the prey will be ingested following an encounter ($P_{v/e}$):

$$PV = V_e \cdot P_{v/e}. \tag{3}$$

$P_{v/e}$ is a function of the series of conditional probabilities (probabilities of attack after encounter, capture after attack, and ingestion after capture, $P_{a/e}$, $P_{c/a}$, and $P_{i/c}$, respectively):

$$P_{v/e} = P_{a/e} \cdot P_{c/a} \cdot P_{i/c}, \tag{4}$$

while the volume encountered per unit time by a prey (V_e) is a function of prey (u) and predator (v) swimming speeds as well as the encounter radius (R) of the predator (Gerritsen and Strickler 1977). PV and its sub-components are specific to a given predator-prey pair, and may be interpreted from the perspective of either predator or prey. The corresponding units of V_e will be litres per predator per day or litres per prey per day depending upon which perspective is adopted.

Data on predator and prey distributions in nature (overlap) can be incorporated into the second major component of predation risk, density risk (Eq. 2). When prey or predator populations are uniformly distributed, density risk is equal to the predator density. When both predator and prey are patchily distributed in space or time, density risk is a function of predator density (N) and the overlap of the predator and prey populations (O_{ij} ; Williamson et al. 1989):

$$DR = N_j O_{ij}, \tag{5}$$

where

$$O_{ij} = \frac{\sum_{z=1}^m (N_{jz} n_{iz}) m}{\sum_{z=1}^m (N_{jz}) \cdot \sum_{z=1}^m (n_{iz})}, \quad (6)$$

z is an individual patch sample, m is the number of patches sampled, and N_j and n_i are population densities for the predator type j and prey type i , respectively. When either prey or predator populations (or both) are uniformly distributed, O_{ij} is equal to one. Values of less than one represent lower overlap, with a theoretical lower limit of zero. Values greater than one represent greater overlap than would be expected with uniform prey and predator distributions, where the upper limit is determined by the number of patches sampled. DR is mathematically equivalent to Lloyd's (1967) mean crowding.

APPLICATION OF THE MODEL

This predation risk model can be applied at several different levels. Three levels of application are examined here. First, the predation risk model is used to examine changes in the overlap of predator and prey populations for two invertebrate predators and five rotifer prey during their diel vertical migrations over a 16-wk period. Second, Eq. 2 and a new graphical technique are used to examine the relationship between prey vulnerability, density risk, and predation risk for these two predators and their prey. Third, weekly predation risk values are compared with maximum potential reproductive rates of each prey species to identify population bottlenecks during which mortality rates due to predation exceed the reproductive potential of each species.

METHODS

Predation risk was examined in a natural zooplankton community during a 16-wk period from 15 May to 26 August 1986 for two predators and five prey species that were consumed by both predators. The predators were the rotifer *Asplanchna girodi*, and the cyclopoid copepod *Mesocyclops edax* (subadult CIV and CV and adult females). Replicate zooplankton samples were collected weekly at odd-metered depths during the middle of the day and the middle of the night at a central station with an 8.2-L Van Dorn bottle and a 48- μ m mesh rotifer cone. The study was carried out in Hellertown Reservoir, a small (surface area < 1 ha, maximum depth 10 m), mesotrophic system in Northampton County, Pennsylvania, USA.

Density risk values were estimated for each predator-prey pair from prey and predator densities using Eqs. 5 and 6, and overlap values calculated from Eq. 6. Prey vulnerability values were estimated from enclosure experiments in which whole-water samples with natural prey assemblages were incubated in 1-L glass bottles on a rotating plankton wheel for 24 h with and

without the addition of predators. The *Mesocyclops* experiments were performed on 9 July and 5 August 1986, and 20 predators were added to each experimental bottle. Mean PV values for these two dates are used here. Details of field sampling and *Mesocyclops* enclosure experiments are given in Williamson et al. (1989). The enclosure experiments with *Asplanchna* as predator were similar in design to those for *Mesocyclops*, except that they were run on 26 May 1987 for 24 h using additions of 200 or 300 *Asplanchna* per experimental bottle. Although *Mesocyclops* shows no consistent change in predation rates at different temperatures (Williamson 1986), all enclosure experiments were run at the mean water column temperature at the time of the experiment (20°C for *Mesocyclops*, 13°C for *Asplanchna*) in order to minimize any possible temperature effects.

Predation risk values were calculated for the entire 16-wk period, and individually for each week. The primary difference here is in how Eq. 6 is applied. For the 16-wk PR values, O_{ij} is estimated from vertical profiles of prey and predator densities during the day and during the night over the entire 16-wk period. For the weekly PR values, vertical profiles of prey and predator densities from day and night samples for each week are used. Simple averaging of weekly PR values would not give accurate PR values for the 16-wk period because temporal and spatial overlap would not be treated equally.

Hairston (1987) has suggested that the "catastrophic" mortality rate of a prey population should be equal to its observed reproductive rate during a given period. Very simply, when the death rate of the population exceeds the birth rate, the population growth rate falls below zero. Hairston (1987) predicted catastrophic mortality rates of between 0.04 and 0.06 for populations of the calanoid copepod *Diaptomus sanguineus*.

This concept can be extended to estimate an intrinsic catastrophic predation risk value (ICPR) from the intrinsic rate of population increase (r_{\max}) known for the prey species under consideration. The ICPR can be defined as the threshold value above which predation risk alone can account for negative prey population growth. It is essentially a predation-induced bottleneck for prey population growth. The prediction that arises is that in the absence of immigration, the population growth rate of a prey population will be negative during periods when the estimated predation risk is greater than the ICPR.

This a priori prediction was tested in the current study by calculating the total predation risk values (sum of PR values for both predators) for each prey on a weekly basis and obtaining the r_{\max} (=ICPR) values for as many of the prey species as possible from the literature. The total predation risk due to both predators was then plotted with the ICPR over time, and the change in population size during periods when predation risk exceeded the ICPR was calculated as:

$$r = \frac{\ln(n_{t+1}/n_t)}{t} \tag{7}$$

A search of the literature revealed estimates of r_{max} for only two of the five prey species (*Keratella cochlearis*, $r_{max} = 0.28$, and *Keratella crassa*, $r_{max} = 0.24$; Stemberger and Gilbert 1985). Although r_{max} values were not available for the other three species, the analysis was carried out using the lowest r_{max} value (0.24) reported for eight rotifers in a recent study by two investigators with extensive experience culturing rotifers (Stemberger and Gilbert 1985). Use of this lowest r_{max} for the ICPR provides a conservative test of the hypothesis that populations will decline during periods when predation risk exceeds the ICPR.

RESULTS

The timing and magnitude of the population peaks of the two predators differed greatly. Peak mean water column densities of the rotifer *Asplanchna* (296 individuals/L) were almost 40 times as high as water column densities of *Mesocyclops* (7.76 individuals/L; Table 1) and occurred 7 wk earlier in the year (Fig. 1). Interestingly, peaks in prey population density never coincided with peaks in predator density (Fig. 1).

Prey and predator populations varied with depth as well as over time. A simple index was developed to estimate vertical patchiness by dividing the maximum density of a given species observed at a single depth by the maximum density of that same species observed on a single date (water column average; Table 1). This index revealed that maximum species densities at a given depth were generally 3.5–5.7 times the water column means. The one exception to this was *Keratella cochlearis*, which had a vertical patchiness index of about one-half those of the other species (1.86; Table 1).

Fig. 2 presents contour plots of prey and predator densities over depth and time for both day and night distributions so that the influence of diel vertical migrations on overlap of populations can be examined. Both predators exhibited normal vertical migrations (up at night, down during the day), while three of the five prey species (*Ascomorpha ovalis*, *Polyarthra vulgaris*, and *Keratella cochlearis*) exhibited the opposite migration pattern (down at night, up during the day) (Fig. 2). Not only did the *Asplanchna* populations peak earlier in the year than the *Mesocyclops* populations, but they also remained at a greater depth. The result is a minimal overlap of these two predators in space and time (Fig. 2).

The overlap (O_{ij}) between the two predators and their prey was highly variable. Values for the five prey species differed by over two orders of magnitude for *Mesocyclops* (from 0.02 for *Kellicottia bostoniensis* to 2.75 for *Ascomorpha*), and by over an order of magnitude for *Asplanchna* (from 0.06 for *Keratella cochlearis* to 1.75 for *Kellicottia*; Table 2). The overlap of particular

TABLE 1. Maximum densities of predator and prey species by date (maximum water column mean on a single date) and by depth (maximum density observed at single point in space and time). A vertical patchiness index is estimated as depth values divided by date values.

Species	Maximum density (no./L)		Vertical patchiness
	Date	Depth	
<i>Asplanchna girodi</i>	296	1055	3.56
<i>Mesocyclops edax</i>	7.76	43.9	5.66
<i>Ascomorpha ovalis</i>	24.2	112	4.63
<i>Polyarthra vulgaris</i>	180	961	5.34
<i>Kellicottia bostoniensis</i>	12 719	71 493	5.62
<i>Keratella cochlearis</i>	278	517	1.86
<i>Keratella crassa</i>	759	3377	4.45

prey species with the two predators differed by 1–2 orders of magnitude for some prey (*Kellicottia*, *Keratella cochlearis*) but were quite similar for others (*Polyarthra*; Table 2).

The impact of diel vertical migration on overlap between predator and prey populations was estimated by calculating and comparing overlap values with Eq. 6 for each predator–prey pair under two conditions: (1) with the actual, observed prey and predator distributions unchanged, and (2) with the day and night distributions of the prey reversed so that predator day distributions were paired with prey night distributions and predator night distributions were paired with prey day distributions (“Day” and “Night,” respectively, in Table 2). If diel vertical migration was an effective predator avoidance strategy that reduced the overlap of the predator and the prey, then the “reversed” overlap values should be greater than the “actual” overlap values (Table 2).

This analysis indicated that diel vertical migration did not substantially reduce the overlap or predation risk of any of the five prey with *Asplanchna*. The maximum increase in the overlap values for reversed vs. actual prey distributions was 0.04 (Table 2). Vertical migration seemed to be a more effective strategy for reducing overlap with *Mesocyclops*. The overlap values for reversed prey distributions increased by 0.21 for *Keratella crassa*, by 1.36 for *Ascomorpha*, and by 1.44 (more than doubled) for *Polyarthra* (Table 2), suggesting that the reverse vertical migration of these prey species substantially reduces their density risk and hence predation risk with *Mesocyclops*.

The most fundamental question being asked here is how can we quantify predation risk in a way that will tie together its two primary components: density risk, which includes overlap, and prey vulnerability? In particular, how can we express these two components in a way that will give us insight into the relative importance of density risk and prey vulnerability in determining predation risk in natural communities? To answer these questions, density risk, prey vulnerability, and predation risk values were calculated for each pred-

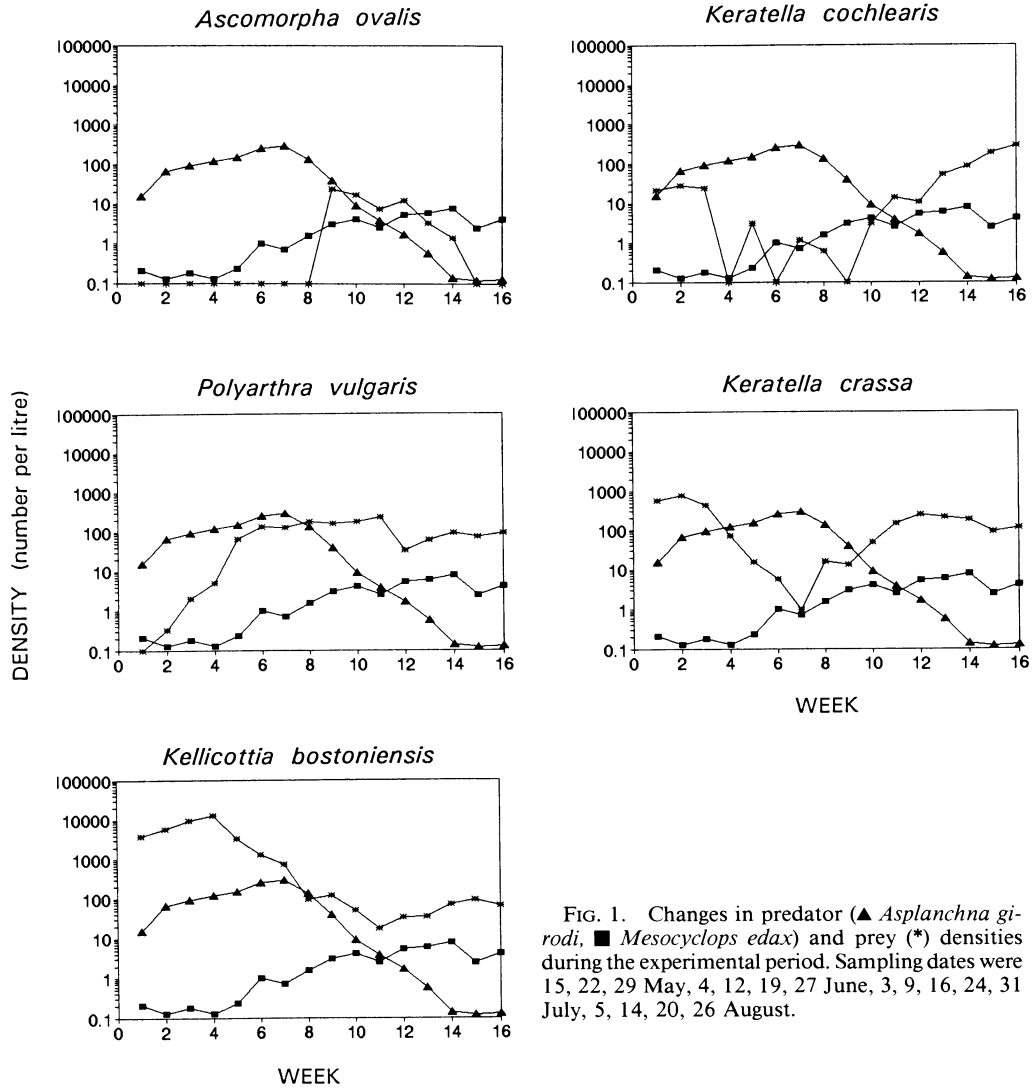


FIG. 1. Changes in predator (\blacktriangle *Asplanchna girodi*, \blacksquare *Mesocyclops edax*) and prey ($*$) densities during the experimental period. Sampling dates were 15, 22, 29 May, 4, 12, 19, 27 June, 3, 9, 16, 24, 31 July, 5, 14, 20, 26 August.

TABLE 2. Overlap and predation risk (PR) values of five prey species with the two predators estimated from actual observed prey and predator distributions (Act), and when day and night densities of the prey are reversed (Rev) to nullify the effects of diel vertical migration on overlap.*

Prey species		<i>Asplanchna</i> predator overlap			PR (d ⁻¹)	<i>Mesocyclops</i> predator overlap			PR (d ⁻¹)
		Day	Night	Total		Day	Night	Total	
<i>Ascomorpha ovalis</i>	Act	0.08	0.27	0.19	0.0314	2.14	2.97	2.75	0.0104
	Rev	0.23	0.09	0.16	0.0270	4.00	4.26	4.11	0.0156
<i>Polyarthra vulgaris</i>	Act	0.43	1.49	0.92	0.0716	0.92	1.54	1.24	0.0627
	Rev	1.15	0.77	0.93	0.0724	1.89	2.83	2.68	0.1360
<i>Kellicottia bostoniensis</i>	Act	1.81	1.70	1.75	0.1245	0.03	0.02	0.02	0.0005
	Rev	2.24	1.06	1.58	0.1124	0.04	0.02	0.03	0.0006
<i>Keratella cochlearis</i>	Act	0.07	0.06	0.06	0.0303	1.88	2.68	2.38	0.0287
	Rev	0.08	0.08	0.08	0.0379	1.50	2.76	2.38	0.0288
<i>Keratella crassa</i>	Act	0.52	0.32	0.41	0.1957	0.84	0.75	0.79	0.0321
	Rev	0.50	0.40	0.45	0.2121	0.90	1.08	1.00	0.0405

* Overlap values are calculated for day distributions alone (Day), night distributions alone (Night), and for day and night distributions of predator and prey (Total).

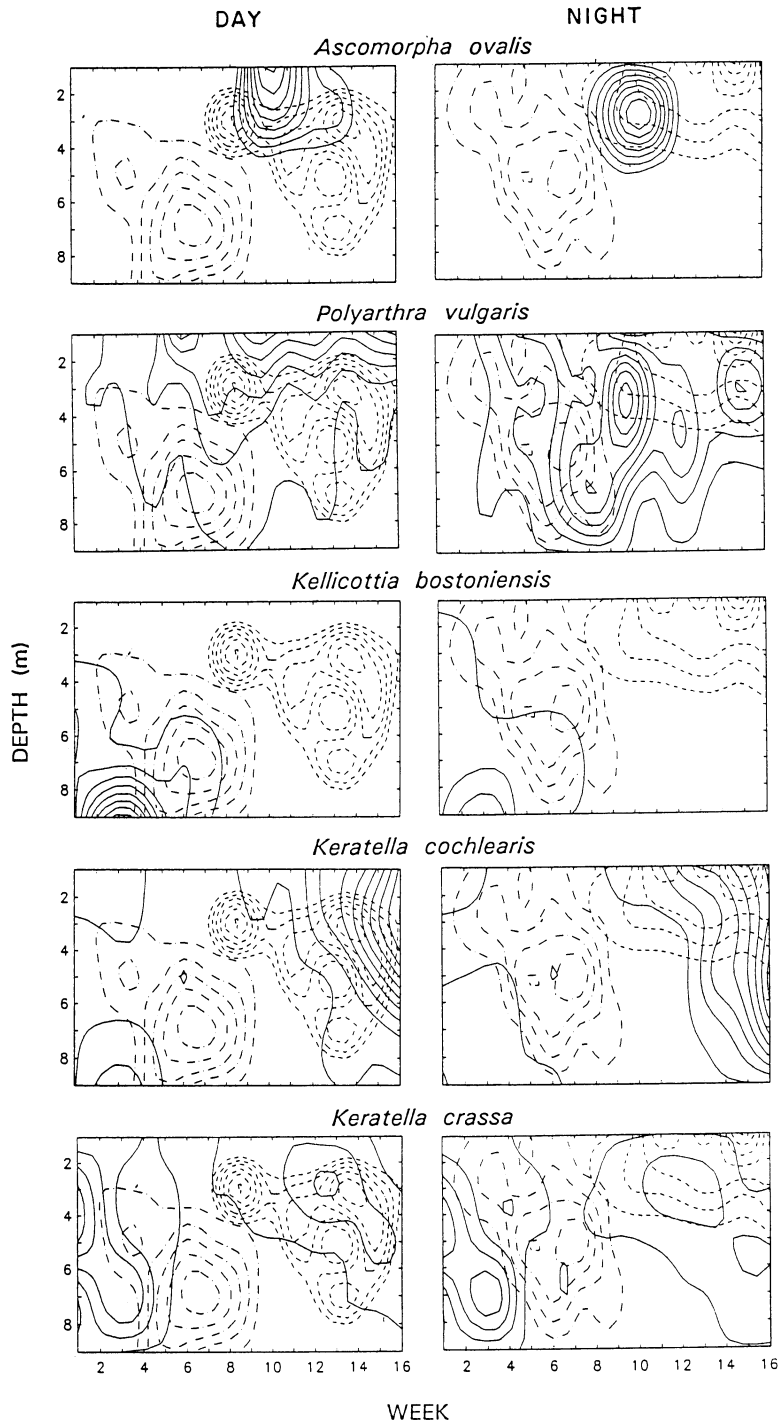


FIG. 2. Depth-time contour plots of predator (*Asplanchna girodi* ---, *Mesocyclops edax* -----) and prey (—) distributions during the day (left column) and the night (right column). The contour lines represent population densities over depth and time where innermost contour is peak density and outermost contour is 10% of maximum population density; maximum densities are given in Table 1. See Fig. 1 for sampling dates.

ator-prey pair for the total 16-wk study period (Table 3).

Examination of the predation components for the two predators reveals that density risk values were gen-

erally much higher when *Asplanchna* was the predator (range 4.67–128.32) than when *Mesocyclops* was the predator (range 0.05–6.50, Table 3). In some cases these differences in density risk were due to differences in

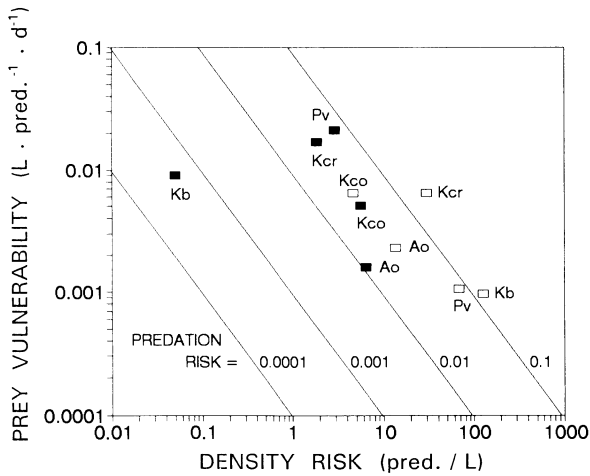


FIG. 3. Predation risk isocline plots for five rotifer prey of the predatory cyclopoid copepod *Mesocyclops edax* (■) and the predatory rotifer *Asplanchna girodi* (□). Each point represents a single predator-prey pair, and predation risk isoclines appear as diagonal lines. Predation risk and component values are estimated from the entire 16-wk day and night data set.

both predator density and the overlap between predator and prey populations (*Kellicottia*, see total actual overlap values for two predators in Table 2), while in other cases the overlap was very similar for the two predators, and differences in density risk are attributable primarily to differences in predator density (*Polyarthra*, and *Keratella crassa*; Table 2).

The relative contribution of density risk and prey vulnerability components to predation risk can be analyzed by plotting prey vulnerability vs. density risk to provide predation risk isoclines (Fig. 3). Predator-prey pairs can then be represented as individual points and predation risk isoclines can be drawn as diagonal lines. This plot can then be used to compare the predation risk values of all of the predator-prey pairs in a given community, as well as the relative importance of density risk and prey vulnerability values in determining predation risk.

For example, the predation risk isocline plot for the community of five prey and two predators examined here reveals that *Kellicottia* had one of the highest (with the predator *Asplanchna*) and the lowest (with the pred-

ator *Mesocyclops*) predation risk values observed (Fig. 3). This suggests that *Asplanchna* is an important predator of this rotifer, while *Mesocyclops* is not. The predation risk values for *Kellicottia* with these two predators differ by >2 orders of magnitude. The primarily horizontal separation of the two points for this prey indicates that density risk is primarily responsible for these sizable differences in predation risk to the two predators (Fig. 3). The vertical separation of these two points by ≈ 1 order of magnitude suggests that prey vulnerability also contributes to these differences, but is less important.

Polyarthra on the other hand has very similar predation risk values for the two predators (the points for the two predators fall in a similar position with respect to the predation risk isoclines), but differs substantially in its density risk and prey vulnerability values with respect to the two predators (Fig. 3). A third type of relationship is seen in *Keratella cochlearis*, which has very similar predation risk, density risk, and prey vulnerability values with respect to both predators (Fig. 3).

Although density risk varies by 2–3 orders of magnitude for the predator-prey pairs in this community, most of the predation risk values differ by only ≈ 1 order of magnitude, which raises the interesting question of whether there could be some maximum predation risk value that can be sustained by rotifer prey in this community.

In order to assess the potential impacts of predation on prey populations, some knowledge of the reproductive rates of the prey is necessary. Here the maximum potential intrinsic reproductive rate for a given prey species was defined as the intrinsic catastrophic predation risk value (ICPR, see *Methods*). The a priori hypothesis tested was that the growth rate of a prey population would not be positive during weeks when predation risk exceeds the ICPR.

One possible outcome of the ICPR analysis was that none of the observed predation risk values of the prey ever exceeded the prey's ICPR. In fact, *Ascomorpha* consistently had predation risk values well below the minimum ICPR of 0.24 (Fig. 4), so testing the relationship between ICPR and population declines was not possible for this species. *Polyarthra* only had one PR value >0.24, during which period the population

TABLE 3. Prey vulnerability (PV), density risk (DR), and predation risk (PR) values for five rotifer prey ingested by both the predatory rotifer *Asplanchna girodi* and the predatory cyclopoid copepod *Mesocyclops edax*.

Prey species	<i>Asplanchna</i> predator			<i>Mesocyclops</i> predator		
	DR (pred./L)	PV (L · pred. ⁻¹ · d ⁻¹)	PR (d ⁻¹)	DR (pred./L)	PV (L · pred. ⁻¹ · d ⁻¹)	PR (d ⁻¹)
<i>Ascomorpha ovalis</i>	13.72	0.00229	0.0314	6.50	0.0016	0.0104
<i>Polyarthra vulgaris</i>	67.59	0.00106	0.0716	2.93	0.0214	0.0627
<i>Kellicottia bostoniensis</i>	128.32	0.00097	0.1245	0.05	0.0091	0.0005
<i>Keratella cochlearis</i>	4.67	0.00648	0.0303	5.64	0.0051	0.0287
<i>Keratella crassa</i>	30.15	0.00649	0.1957	1.88	0.0171	0.0321

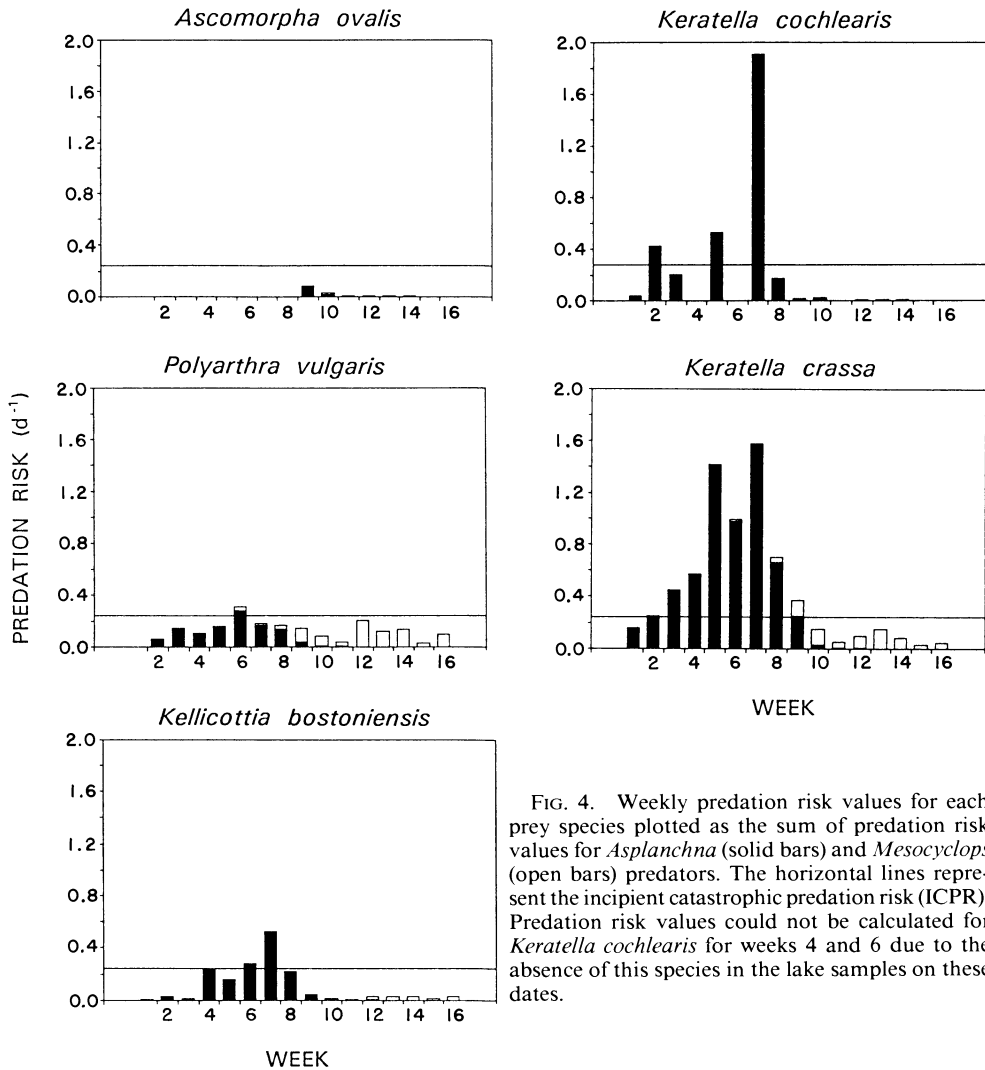


FIG. 4. Weekly predation risk values for each prey species plotted as the sum of predation risk values for *Asplanchna* (solid bars) and *Mesocyclops* (open bars) predators. The horizontal lines represent the incipient catastrophic predation risk (ICPR). Predation risk values could not be calculated for *Keratella cochlearis* for weeks 4 and 6 due to the absence of this species in the lake samples on these dates.

declined (Fig. 4, Table 4). *Kellicottia* had three PR values that exceeded the ICPR during weeks 4, 6, and 7, and population growth was negative during all three of these periods (Fig. 4, Table 4).

For *K. cochlearis*, predation risk exceeded the ICPR in weeks 2, 5, and 7. The *K. cochlearis* populations showed declines following weeks 2 and 7 (Table 4), while the absence of any *K. cochlearis* in the samples during weeks 4 and 6 prevented estimation of rates of population change during week 5. Predation risk values could not be estimated for weeks 4 and 6 for the same reason (Table 4).

For *K. crassa*, predation risk exceeded the ICPR in weeks 2–9 (Table 4), and populations of this rotifer declined during 6 out of 8 of these weeks (Table 4). The two exceptions were week 7 where population densities increased from their lowest point of 0.87 individuals/L to 16 individuals/L between weeks 7–8, and at the very end of this high predation risk period (week 10) during which *K. crassa* started a population in-

crease which persisted for 3 wk (Fig. 1). *Asplanchna* was a much more important predator than *Mesocyclops* for both *Keratella* species (Fig. 4).

A chi-square test was run to test the null hypothesis that obtaining 12 negative and 2 positive population growth values out of a total of 23 negative and 30 positive population growth weeks for the four prey species was due to chance alone. The null hypothesis was rejected ($P < .005$), supporting the alternative hypothesis that positive population growth will not be observed during periods when predation risk is greater than the ICPR. This leads to the conclusion that these two invertebrate predators, and *Asplanchna* in particular, can cause serious bottlenecks in the population growth rates of their prey.

DISCUSSION

Prior studies on the behavioral components of some of the prey represented here give some insight into the mechanisms that underlie the observed prey vulnera-

TABLE 4. Data for testing the hypothesis that population growth rate (r) of a prey species will be negative during periods when predation risk (PR) values exceed the incipient catastrophic predation risk (ICPR).

Prey species	Week (n)	ICPR* (d^{-1})	PR† (d^{-1})	r (d^{-1})
<i>Ascomorpha ovalis</i>	all	(0.24)	≤ 0.084	N.A.‡
<i>Polyarthra vulgaris</i>	6	(0.24)	0.316	-0.0003
<i>Kellicottia bostoniensis</i>	4	(0.24)	0.241	-0.167
	6	(0.24)	0.280	-0.071
	7	(0.24)	0.526	-0.341
<i>Keratella cochlearis</i>	2	0.28	0.431	-0.018
	5	0.28	N.A.	N.A.
	7	0.28	1.910	-0.122
<i>Keratella crassa</i>	2	0.24	0.251	-0.074
	3	0.24	0.447	-0.312
	4	0.24	0.570	-0.194
	5	0.24	1.420	-0.138
	6	0.24	0.994	-0.233
	7	0.24	1.580	+0.485
	8	0.24	0.705	-0.034
	9	0.24	0.376	+0.188

* ICPR values in parentheses represent minimum estimates of ICPR based on prior studies where actual ICPR values are not available for a given species.

† Weekly predation risk values are given as the sum of PR values for both predators on each prey during weeks when $PR > ICPR$.

‡ not applicable.

bility patterns shown in Fig. 3. In particular, the greater vulnerability of *Polyarthra* to *Mesocyclops* vs. *Asplanchna* predation can be attributed to the effectiveness of *Polyarthra*'s jumping escape response, which reduces the probability of capture after encounter with *Asplanchna* ($P_{ce} \leq 0.05$). This escape response is less effective against *Mesocyclops* ($P_{ca} = 0.49$) due to the rapid pouncing attack of this predator (Gilbert and Williamson 1978, Williamson and Gilbert 1980).

These same behavioral studies can explain the somewhat greater prey vulnerability of *K. cochlearis* to *Asplanchna* vs. *Mesocyclops* (Table 3, Fig. 3). *Asplanchna* is able to ingest this small rotifer whole, while *Mesocyclops* must first tear it apart. The hard lorica of this rotifer thus results in a lower probability of ingestion after capture with *Mesocyclops* (0.23) than with *Asplanchna* (≥ 0.43) (Gilbert and Williamson 1978, Williamson and Gilbert 1980). Although no behavioral data are available for the other prey species, these examples show how the predation risk model presented here can be used to link behavioral mechanisms from laboratory observations with prey vulnerability, density risk, and predation risk values observed in nature.

Several authors have developed definitions of prey vulnerability and linked them to Holling's behavioral approaches. The definition of prey vulnerability presented here is consistent with these prior definitions, and is a logical extension that adds a field overlap component to prey vulnerability to provide a more comprehensive estimate of predation risk in nature.

Gerritsen and Strickler (1977) were among the first to recognize the strength of the behavioral approach to understanding predator-prey dynamics in plankton communities. They broke the predator-prey sequence down into four events: encounter, attack, capture, and ingestion. They then proceeded to develop a three-dimensional encounter rate model that they used to estimate encounter rates between predator and prey. In this model, Gerritsen and Strickler made the assumption that prey and predator populations were randomly distributed.

Pastorok (1981) used Gerritsen and Strickler's encounter model and Holling's concept of behavioral components and developed a concise definition of prey vulnerability as the product of encounter rate and strike efficiency (essentially equivalent to my Eq. 3). Pastorok found that when the abundance of different-sized *Daphnia* prey in nature was weighted by this prey vulnerability, he could account for the prey size composition in the diet of *Chaoborus*. The uniform depth distribution of the different sizes of *Daphnia* in nature permitted Pastorok to ignore predator and prey overlap in nature.

Riessen et al. (1988) combined Pastorok's definition of prey vulnerability with an encounter rate model developed specifically for *Chaoborus* (Giguere et al. 1982) and came up with a behaviorally based model that permitted them to accurately predict differential predation by *Chaoborus* on several prey species in nature. By performing their work in a shallow (<1 m deep) well-mixed pond, these authors were also able to ignore overlap of predator and prey populations.

Williamson et al. (1989) developed a model to quantify overlap of predator and prey populations in nature, but did not integrate the behavioral components into this model. The current study is the first to link Holling's behavioral components and these prior definitions of prey vulnerability to overlap of predator and prey populations in nature.

Other definitions of prey vulnerability have similarly been based on either relativized clearance rates (Greene and Landry 1985), or encounter volumes (Leucke and O'Brien 1981). In addition to being used as estimates of prey vulnerability, relativized or normalized clearance rates provide a convenient index of selectivity in a variety of consumer-resource interactions (Vanderploeg and Scavia 1979, Bogdan and Gilbert 1984, 1987, Sterner 1989).

In the current study predation risk exceeded the r_{max} (=ICPR) for 4 out of 5 of the prey species a total of 14 times, and negative population growth rates were observed during 12 of these high predation risk periods. The two exceptions occurred during weeks 7 and 9 for *Keratella crassa*, a period during which the extremely low population densities of this prey may have enabled recruitment from resting eggs to influence population growth rates (De Stasio 1989). Very low population densities also increase the chance of sampling errors in estimates of population densities and growth

rates. The prey species that suffered the most prolonged period during which predation risk exceeded the ICPR was *Keratella crassa*. Most of this predation risk was attributable to *Asplanchna*. This is consistent with previous studies of the population dynamics of *Keratella crassa* and *Asplanchna girodi* that have demonstrated that *A. girodi* can play a major role in regulating the seasonal abundance of *K. crassa* (Magnien 1983).

One of the limitations with the ICPR concept is the difficulty of obtaining accurate estimates of r_{\max} . Laboratory estimates of r_{\max} are likely to be more useful than field estimates due to potential problems with egg age distributions (Threlkeld 1979), synchronous egg hatching (Gophen 1978, Magnien and Gilbert 1983, Tessier 1984), vertical migration (Magnien and Gilbert 1983), and resting egg hatching (De Stasio 1989) that bias field estimates.

In order to obtain good estimates of r_{\max} one must be able to culture a given species and know the optimal conditions for growth, including temperature and food type and quantity. Actual r_{\max} values are likely to be substantially lower in nature where temperature, food availability, and other environmental conditions are likely to be suboptimal. Thus, setting $\text{ICPR} = r_{\max}$ will usually overestimate the level of predation risk needed to cause negative population growth rates, making the estimate of the bottleneck periods with the ICPR a conservative approach. Predation can clearly cause negative population growth rates in prey populations even when predation risk values are substantially less than the ICPR.

It is not clear why the vertical patchiness index of *Keratella cochlearis* in this study is so much lower than those of the other four prey species (Table 1). This rotifer tends to be a generalist in its diet (Gilbert and Bogdan 1984, Bogdan and Gilbert 1987) and has an extremely low threshold food concentration for population growth (=food concentration at which $r = 0$). Stemberger and Gilbert (1985, 1987a) found *K. cochlearis* to have the lowest threshold food concentration of 10 rotifer species that they examined: 17 times lower than its congener *K. crassa*. This combination of a broad food niche and low threshold food concentration may permit *K. cochlearis* to persist over a broader range of depths than most other species.

Two of the most striking responses that zooplankton exhibit to predation are induced polymorphisms (Gilbert 1966, Havel 1987, Dodson 1989) and diel vertical migration (Haney 1988, Lampert 1989). These are two fundamentally different types of responses that can be quantitatively linked in the predation risk model because they correspond closely to the two major components of predation risk. Diel vertical migration effectively reduces the density risk of a prey with its predator by reducing the overlap of the prey and predator populations. The mechanism of reducing predation is density mediated. Induced polymorphisms on the other hand are prey vulnerability responses that reduce the ability of a predator to capture and ingest

its prey. The release of a chemical substance by the predator induces the growth of long spines, large helmets, or similar body protuberances that reduce the vulnerability of the prey to predation. The mechanism of reducing predation in this case is largely independent of predator and prey population densities, although predator density does play a roll in determining the presence or absence of the induction response in nature. Diel vertical migration may also be induced by chemicals released by the predator (Neill 1990).

In addition to density risk responses providing an escape in space, they may also provide an escape in time. For example, in planktonic copepods, the onset of diapause may be induced in response to the presence of either invertebrate (*Chaoborus*) or vertebrate (*Lepomis*) predators (Hairston 1987).

The predation risk model gives us a quantitative tool for exploring the relative importance of density risk and prey vulnerability for different predator-prey interactions. Prey may be more likely to respond to certain types of predators with density risk responses (density risk minimizers) and other types of predators with prey vulnerability responses (prey vulnerability minimizers). For example, in the current study none of the rotifer prey exhibited diel vertical migrations that reduced their density risk with *Asplanchna*, while three of the five prey exhibited reverse diel vertical migrations that reduced their density risk with *Mesocyclops*. Such reverse vertical migrations have been documented for other prey in response to invertebrate predators (Hairston 1980, Ohman et al. 1983), while the more common response to vertebrate predators is a nocturnal vertical migration upwards (Haney 1988, Lampert 1989). Research to date suggests that prey vulnerability responses involving induced polymorphisms are more commonly related to invertebrate rather than vertebrate predation (Havel 1987, Stemberger and Gilbert 1987b, Dodson 1989).

Density risk and prey vulnerability responses in turn have different implications for the ecology and evolution of prey species. Density risk responses may reduce the prey's access to critical resources or optimal environmental conditions, while prey vulnerability responses often have an associated cost that results in reduced reproductive rates for the prey (Riessen 1984, Havel and Dodson 1987, Black and Dodson 1990, Riessen and Sprules 1990, but see Stemberger 1988).

The predation risk model has several underlying assumptions that should be considered. First, it was developed for a relatively simple, unstructured, three-dimensional environment in which the consumers and resources are distributed. It can be equally applied to two-dimensional situations. The core of the model is a series of exponential equations that adopt the widespread assumption that grazing rates, prey mortality rates, and birth rates are constant across a wide range of population densities of both consumer and resource. In addition, it is assumed that the rates obtained through experiments at one or two points in time are good

estimates of rates over more extended time periods. These assumptions are clearly an oversimplification of systems where satiation, starvation, and a multiplicity of environmental factors may influence these rates. In this respect the predation risk model is at best a reasonable first approximation. Experiments can be performed more frequently and sampling can be carried out at closer intervals if more precision is desired. In this way PV and DR can be used as sensitive indicators of the response of consumers and resources to environmental changes.

Predation is clearly not the only factor influencing the distribution and abundance of zooplankton in nature. Abiotic factors such as oxygen, temperature, and light, as well as food resources may also be critical. Threshold food concentrations have been a particularly useful tool for examining consumer–resource interactions from the “bottom-up” perspective (Lampert and Schober 1980, Stemberger and Gilbert 1985, 1987a). Because these threshold food levels can be defined based on population growth rate coefficients (Lampert 1977, Stemberger and Gilbert 1985, DeMott 1989), there is the potential to quantitatively integrate the threshold food level concept with the current predation risk model. The ability to integrate the influence of both “top-down” and “bottom-up” factors in the analysis of population response and community structure is likely to provide a much more comprehensive understanding of factors regulating the structure of natural communities in the future.

ACKNOWLEDGMENTS

I thank Bill DeMott, Charles Greene, Peter Schulze, Robert Moeller, Horacio Zagarese, and an anonymous reviewer for their helpful comments on the manuscript. This project was supported in part by a grant from the Andrew W. Mellon Foundation and NSF grant BSR-9014414.

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