Effects of predator density and duration of predator occupancy on crustacean abundance and diversity in experimental pools

Avi Eitam · Leon Blaustein

Abstract Keystone predators, by reducing the abundance of competitively superior prey, may have indirect positive effects on weak competitors, possibly increasing their abundance or preventing local competitive exclusion. By analogy to the Intermediate Disturbance Hypothesis, we would expect species diversity to peak at intermediate predator densities. In a replicated artificial pool experiment, we examined the relationships between density of the backswimmer *Notonecta maculata* (0, 1, 2, and 4 per 30 l pool) and invertebrate taxon diversity over an 11-week period of predator occupancy. Diversity reached high levels at high predator density sooner than at intermediate density. At the end of the experiment, taxon diversity was greatest at densities of 2 and 4 *Notonecta* per pool. While the overall predator density–diversity curve was in line with the intermediate disturbance hypothesis, the reduction in diversity from intermediate to high predator density was not statistically significant. Density of the preferred prey *Daphnia magna* decreased with *Notonecta* density, while densities of the smaller cladocerans *Moina brachiata* and *Ceriodaphnia* spp. increased. Suppression of *Daphnia* at high *Notonecta* densities may partially explain the increase in *Moina* and *Ceriodaphnia* densities. However, most of the relationship between *Notonecta* and the smaller cladocerans appears to be independent of *Daphnia*, suggesting complex interactions within the community. Our results suggest that keystone predation plays a strong role in structuring this community. Although diversity did not decrease significantly at the highest predator density as predicted, such a decrease may be more likely for pools with longer durations of predator occupancy or with higher predator densities.

Keywords Keystone predation · Intermediate disturbance hypothesis · Notonectidae · Predator-mediated coexistence · Species diversity

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Introduction

Predators often have strong effects on prey community structure (Sih et al., 1985). Direct consumption can lead to reduced densities or even elimination of prey. In addition, predators can alter the prey community composition through their indirect effects (Paine, 1966; Morin, 1999). Indirect consequences can occur within a trophic level, such as predator-mediated

coexistence (e.g., Shurin & Allen, 2001), or across trophic levels (trophic cascade; Maezono & Miyashita, 2003).

The role of predation in structuring prey communities should depend largely on the duration of predation pressure, the density of predators, and their prey preference. Duration of predation may be brief because the habitat is temporary or seasonal, or because the timing of colonization by a predator of a particular site is stochastic (e.g., Wilcox, 2001).

Consumptive effects may lead to complex relationships between predator density and prey species diversity. At low to intermediate predator densities, if predators prey at random or preferred prey species are competitive dominants, consumption may lead to an increase in the density of competitively inferior species (Arner et al., 1998), causing an increase in species diversity (keystone predation; Paine, 1966). At high predator densities, preferred prey could be largely eliminated, and then consumption would shift to less-preferred prey. The resulting decrease in density of such species, with consumption outweighing predator-mediated coexistence, would be expressed as a decrease in species diversity. Random predation at high predator densities may reduce scarce prey to extinction, similarly leading to decreased diversity. Thus, as predicted by Leibold (1996) in his modeling of keystone predation, we would expect species diversity to peak at intermediate predator densities.

The intermediate disturbance hypothesis (IDH) predicts maximal diversity at intermediate levels of abiotic environmental disturbance (Connell, 1978). Thus, the predicted effect of predation on species diversity is similar to that predicted for abiotic disturbance as formulated by the IDH. Shea et al. (2004) argued that the IDH could be expanded to include biotic disturbances including predation (Thorp & Cothran, 1984) and herbivory (Lubchenco, 1978). However, despite this strong theoretical foundation and considerable empirical testing of keystone predation, empirical testing of the relationship between predator density and prey diversity is largely lacking (Kneitel & Miller, 2002).

Temporary pools provide an ideal model for studying the relationships between predation and community structure, where predation occurs in short pulses. These habitats contain relatively simple communities (Wilbur, 1997; Blaustein & Schwartz, 2001; De Meester et al., 2005), with predators being mostly invertebrates. Notonectids are widely studied predators that can have profound effects on the structure of these communities (Murdoch et al., 1984; Blaustein et al., 1995; Arner et al., 1998; Blaustein, 1998; Shurin, 2001; Eitam et al., 2002). Furthermore, assessing whether predator-mediated coexistence or a hump-shaped predator density–species diversity relationship can occur over short durations is ecologically relevant in temporary pools; predation duration is short, both because the habitat is ephemeral and because predators tend to colonize after their prey (e.g., Service, 1977; Ward & Blaustein, 1994).

Here, we examine whether, and to what degree, predatory effects on prey abundances and species diversity are dependent on predator density over short, but ecologically relevant, durations. In experimental pools, we examined the relationships between density of *Notonecta maculata* Fabricius and crustacean taxon diversity, with particular emphasis on the effects of predator density on the abundance of the cladocerans most common in our study—*Daphnia magna* Straus, *Moina brachiata* (Jurine), and *Ceriodaphnia* spp. *Notonecta* are size-selective predators, preferring large *Daphnia* over smaller cladocerans (Cooper, 1983; Murdoch & Scott, 1984; Blaustein, 1998). We hypothesized that *Daphnia* populations would decrease with increased predator density, while populations of the smaller *Moina* and *Ceriodaphnia*, released from competition by *Daphnia*, would increase (Arner et al., 1998). We further expected that at high predator density, with *Daphnia* largely exhausted (Murdoch et al., 1984), a shift to predation on the smaller cladocerans would reduce their numbers.

Methods

We conducted an artificial pool experiment using 20 plastic tubs (volume ~ 30 l, 48×27 cm at the base, 55×33 cm at the top, height 19 cm) in a 10×2 array under a canopy of *Pinus halepensis* Mill. (providing shade to avoid lethal temperatures) at the University of Haifa campus. These artificial pools are similar in size to many natural rock pools, and we have found similar results when comparing similarly sized artificial pools and natural pools (Blaustein, 1998; Blaustein et al., 2004).

On 15 April 2002, we filled the pools with tap water. On 18 April, we added to each pool 250 cm³ of

Quercus leaf litter and 10 cm³ of soil from several previously used experimental tubs (pooled before added to tubs), which provided an inoculum of algae, crustaceans and other microfauna. *Pinus* litter was removed throughout the experiment to maintain low heterogeneity in litter accumulation among pools. To assure a relatively diverse community of crustaceans, we added the following to each pool: on 18 April, ∼50 *D. magna*, randomly assigned from an existing population; on 21 April, the contents of a single S-shaped sweep with a 12 × 10 cm net (mesh size: 250 µm) through a previously used experimental pool, containing *Arctodiaptomus similis* (Baird) and some ostracods; and on 22 April, half of the contents of a similar sweep through a different experimental pool, containing *Ceriodaphnia* spp., *M. brachiata*, several species of ostracods, and some chydorids.

On 12 May, we added fourth- and fifth-instar *N. maculata* nymphs to the pools (these instars have similar prey size class preferences: Gergs & Ratte, 2009). Thus, we added the predator after prey communities had some time to establish, just as predator colonization lags behind prey colonization in nature (Blaustein et al., 1995). We established densities of 0, 1, 2, or 4 *Notonecta* nymphs per pool, with five replicates per density. Densities established are within the range observed in most natural pools (Ward & Blaustein, 1994; Blaustein, 1998); higher densities can be found in shrinking pools. Density levels and nymphal instars were assigned randomly among the pools. We replaced dead or missing *Notonecta* with new nymphs, collected from a natural pool, every 2–3 days to maintain constant densities (beginning 11 June, only fifth-instar nymphs were added). In addition, *Notonecta* that had molted to adults were replaced with nymphs until 23 June, when nymphs were no longer found in natural pools. From this date, pools contained an increasing number of adults, all of which remained in the pools. The molting rates were similar for all treatments. Water volume was maintained at between 25–30 l throughout the experiment by adding either distilled or aged tap water. Pools were not covered, allowing colonization/oviposition and emigration of insects (Eitam & Blaustein, 2004). However, no colonization by predators, including additional *Notonecta*, was observed by either visual observation or sampling. This is likely because no natural pools were near this experimental site. Therefore, we assume uncontrolled effects of other predators to be negligible.

To estimate the effect of *Notonecta* density on community structure, we sampled the pools on 12 May, 3 June, 23 June, 15 July and 28 July, corresponding to 0, 3, 6, 9 and 11 weeks after addition of the predator. We performed a single S-shaped sweep through each pool (allowing for sampling of different parts of the pool including edges and middle) with a 10 × 7 cm net (mesh size: 250 µm), sampling through approximately 9 l of water. We preserved the samples in 95% ethyl alcohol and identified and counted all invertebrates under a stereomicroscope. In this article, we consider only "passively dispersing" macroinvertebrates, excluding "actively dispersing" species (typically insects) which can select pools for colonization. All passively dispersing species in this study were crustaceans.

For an estimate of taxon diversity, we calculated exp(Shannon entropy) (Jost, 2006) for each pool on each date. An analysis of variance showed no significant differences among predator densities for this variable on the date of addition of the predator (week 0) ($F = 0.56$, df = 3, 16, $P = 0.64$). Indices for weeks 3–11 were analysed by repeated measures ANOVA, followed by univariate analyses for each sampling time. Diversity at different densities of *Notonecta* was compared with the Tukey–Kramer HSD test.

Repeated measures ANOVAs were also performed for each of the taxa. Numbers per sample were square-root transformed ($\sqrt{x + 0.5}$) prior to analysis. We report results for three cladocerans, *D. magna*, *M. brachiata*, and *Ceriodaphnia* spp.; these were the most abundant taxa throughout the study. Analyses for all other taxa were not statistically significant. Analyses of variance showed no significant differences among predator levels at week 0. *Notonecta* density was treated as an ordinal variable. We also explored whether the suspected dominant competitor, *Daphnia*, may have released other cladocerans from resource competition using multiple regression (see "Results" section for details). All analyses were performed with JMP software (SAS Institute, 2007).

Results

Over the course of the study, 13 crustacean taxa were observed: the cladocerans *Alona* spp., *Ceriodaphnia* spp., *D. magna*, *M. brachiata*, and *Pleuroxis leto-urneuxi* (Richard); the copepods *Arctodiaptomus*

Table 1 Repeated measures ANOVAs for effects of *Noto-necta* density on taxon diversity [exp(Shannon entropy)] and densities of common cladocerans

Response variable	Source	df	F	P
Taxon diversity	Density	3, 16	10.95	0.0004
	Time	3, 48	0.05	0.99
	Time × density	9, 48	3.75	0.0013
Daphnia	Density	3, 16	5.27	0.0101
	Time	3, 48	11.12	<0.0001
	Time × density	9, 48	2.86	0.0088
Moina	Density	3, 16	13.49	<0.0001
	Time	3, 48	0.05	0.99
	Time × density	9, 48	4.05	0.0007
Ceriodaphnia	Density	3, 16	3.24	0.0501
	Time	3, 48	0.09	0.96
	Time × density	9, 48	1.91	0.0731

Analyses begin with week 3

similis and an unidentified cyclopoid; and the ostracods *Cypris* sp., *Eucyprinotus rostratus* (Sywula), *Heterocypris* sp., *Ilyocypris* sp., *Potamocypris arcuata* (Sars), and *Tonnacypris lutaria* (Koch). The majority of genera were represented by a single species, but a few (e.g., *Ceriodaphnia*) probably included more than one species; we therefore conservatively describe diversity using the term 'taxon diversity'. The number of taxa observed in any one pool at one time ranged from 4–10.

Taxon diversity, as estimated by exp(Shannon entropy), was significantly affected by *Notonecta* density and time × density (Table 1; Fig. 1), with statistically significant differences among densities at all sampling periods after predator introduction. In pools without *Notonecta*, diversity remained stable over 6 weeks, followed by a decline in weeks 9 and 11. In pools with one *Notonecta*, diversity increased until week 6, and declined slightly in week 11. In pools with two *Notonecta*, there was a general increase in diversity throughout the study, including a sharp rise between 3 and 6 weeks. In pools with four *Notonecta*, diversity was high in week 3, and remained at that level for the remainder of the experiment.

After 11 weeks, diversity increased from low to intermediate predator density, and was significantly higher at densities of 2 or 4 *Notonecta*, than at densities of 0 or 1 (Fig. 1B). Diversity tended to be slightly less at four predators per pool than two
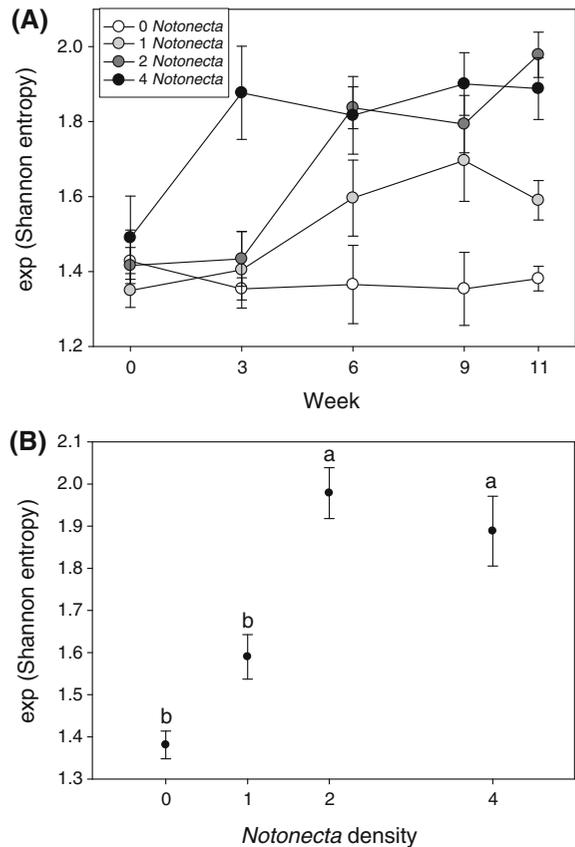

Fig. 1 A Dynamics of taxon diversity in pools containing various densities of *Notonecta maculata*. **B** Taxon diversity across predator densities 11 weeks after introduction of the predator. *Error bars* denote ±1 SE

predators per pool, but this difference was not statistically significant.

Populations of all large (*Daphnia*; length 2–5 mm) and intermediate-sized (*Moina* and *Ceriodaphnia*; 0.7–1.0 mm) cladocerans declined between 0 and 3 weeks at all predator densities. However, the taxa differed in the manner in which they recovered from this crash (Fig. 2). The density of *Daphnia* was significantly affected by that of *Notonecta*, time and time x density (Table 1). *Daphnia* density continued to decline for 6 weeks and began to recover at 9 weeks (Fig. 2). There were statistically significant differences among *Notonecta* densities at 9 and 11 weeks, but not at 3 or 6 weeks. At 11 weeks, *Daphnia* density was significantly higher in pools without *Notonecta* than in pools with 2 or 4 *Notonecta* (Fig. 2A).
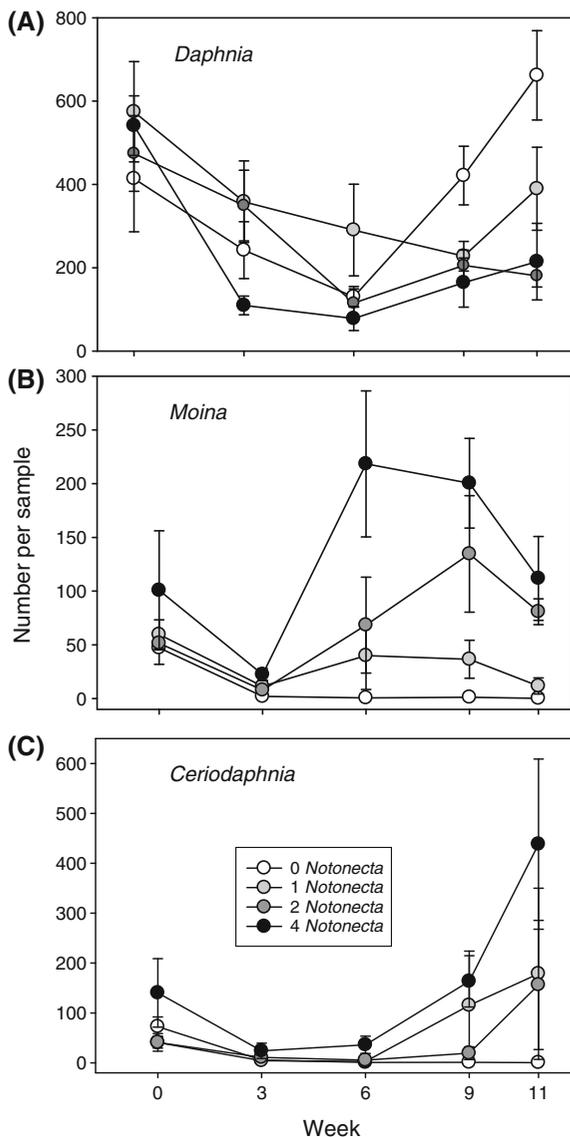
Fig. 2 Dynamics of the cladocerans **A** *Daphnia magna*, **B** *Moina branchiata*, and **C** *Ceriodaphnia* spp. in pools containing various densities of *Notonecta maculata*. *Error bars* denote ±1 SE

The density of *Moina* was significantly related to *Notonecta* density and time x density (Table 1). *Moina* density increased at all *Notonecta* densities after their initial decline (except for pools without *Notonecta*, where density remained extremely low), peaking at 6 or 9 weeks (Fig. 2). There were statistically significant differences among *Notonecta* densities at 3, 6, 9, and 11 weeks. At 11 weeks, *Moina* density was significantly higher in pools with

2 or 4 *Notonecta* than in pools with 0 or 1 *Notonecta* (Fig. 2B).

After declining initially, density of *Ceriodaphnia* increased with time at all *Notonecta* densities (except for pools without *Notonecta*, where density remained extremely low) (Fig. 2C). *Ceriodaphnia* density increased with *Notonecta* density, bordering on statistical significance (Table 1, Fig. 2C).

There was a negative relationship between the densities of *Daphnia* and *Moina* at week 11 ($y = 13.4 - 0.44 * x$, $R^2 = 0.50$, $P = 0.0005$), suggesting that *Notonecta* predation on *Daphnia* may have released *Moina* from resource competition. To explore this possibility, we examined whether there was any interactive effect of *Notonecta* and *Daphnia* densities on *Moina*, testing the effects of both concurrent and prior *Daphnia* densities. First, we ran a multiple regression, with *Notonecta* density, *Daphnia* density at week 11 and *Notonecta* density × *Daphnia* density as independent variables, and *Moina* density at week 11 as the dependent variable (all variables were square-root transformed). The model was statistically significant ($F = 15.9$, df = 3, 16, $P < 0.0001$), explaining 75% of the variance. Of the parameters tested, only *Notonecta* density was significant ($P = 0.0012$), not *Daphnia* density ($P = 0.11$) or *Notonecta* density × *Daphnia* density ($P = 0.18$). Next, we ran a similar analysis, but with *Daphnia* density after 9 weeks (i.e., testing effects of *Daphnia* density 2 weeks prior). This model was also statistically significant ($F = 23.5$, df = 3, 16, $P < 0.0001$), explaining 82% of the variance. However, in contrast with the previous model, both *Notonecta* density ($P = 0.0004$) and *Daphnia* density ($P = 0.02$) were significant, and *Notonecta* density × *Daphnia* density was marginally insignificant ($P = 0.07$). Thus, prior *Daphnia* density had a greater effect on *Moina* than did concurrent *Daphnia* density, and the interactive effect with *Notonecta* was inconclusive.

Discussion

A keystone species is commonly defined as a species that has an inordinately large impact on its community (Power & Mills, 1995). In this study, *Notonecta* had large impacts on both species diversity and species assemblage; given this definition, it is clearly a keystone predator in our system. While studies on

keystone predation often consider only the presence and absence of a predator, we found that predator density, and the duration of its presence, strongly influenced its effect on the community.

One mechanism of keystone predation is when a predator species, by depressing densities of a dominant competitor, promotes competitively inferior species that may not exist, or exist only in low numbers, in the absence of the predator's effect on the dominant competitor (Paine, 1966; Caswell, 1978). In our study, *Notonecta* had a negative effect on abundance of *Daphnia* and positive effects on *Moina* and *Ceriodaphnia*. We hypothesized that the suppression of *Daphnia* at high *Notonecta* densities may have enabled the increase in density of the smaller cladocerans. However, our analyses suggest that most of the relationship between *Notonecta* and the smaller cladocerans may be independent of *Daphnia*. Thus, this mechanism of keystone predation does not explain entirely the pattern observed.

Effects of predation on diversity should depend largely on whether the predator prefers common species, which are often competitive dominants, or rare species. In the former case, predators should cause an increase in diversity, while in the latter case, diversity should decrease (Almany & Webster, 2004). *Daphnia*, often the competitively dominant pelagic taxon in eutrophic, predator-free pools (Romanovsky & Feniova, 1985; Steiner, 2003, 2004; Stav et al., 2005), is a preferred prey of *Notonecta* when presented alongside smaller cladocerans, such as *Ceriodaphnia* or *Moina* (Cooper, 1983; Murdoch & Scott, 1984). We would therefore expect increased diversity with predation until *Daphnia* populations are largely exhausted (Murdoch et al., 1984; Arner et al., 1998).

Consistent with predator-mediated coexistence, taxon diversity reached its highest level at intermediate predator density at the end of the experiment. However, diversity did not drop significantly at the highest predator density. Populations of *Daphnia* were far from being exhausted at all predator densities (Fig. 2A). While some predation on less-preferred species (Blaustein, 1998) may have occurred, *Daphnia* likely remained the major prey item at all densities, thus explaining the lack of significant decrease in diversity at the highest predator density.

To get a more comprehensive understanding of the effects of predation, we considered the temporal dynamics, i.e., the duration of predation. In the absence of predation, there is a reduction in species diversity with time (Fig. 1), as may be expected from competitive interactions. As predicted by Shea et al. (2004), short-term exposure to high densities has a greater effect on species diversity than long-term exposure to low densities: even 11 weeks after introduction, one *Notonecta* per pool did not have the same effect on diversity that four *Notonecta* had after only 3 weeks (Fig. 1). Diversity reached high levels at both intermediate and high predator densities. However, while maximal diversity was reached at 3 weeks at high predator density, high diversity was observed at intermediate density only at 6 weeks (Fig. 1).

We expect that further increasing the duration of predation would suppress *Daphnia* to levels that would compel *Notonecta* to shift its consumption to less-preferred species (Murdoch et al., 1984), ultimately lowering diversity at high versus intermediate density. Thus, while our experiment does not conclusively support the hypothesis of maximal diversity at intermediate predator density in pools with relatively short hydroperiods or relatively short predator occupancies, it remains a viable hypothesis for longer duration/predator occupancy pools. Field observations suggest that under natural conditions, diversity in high-predator density pools is often lower late in the season than observed in our experimental pools. Pools with long hydroperiods often contain, late in the hydroperiod, high densities of notonectids and few other invertebrates besides notonectid and corixid bugs (Blaustein, 1998; Eitam, personal observations). While these field observations may be explained by other factors, such as increased competition by anuran larvae, they suggest that increasing both the intensity and duration of predation may cause a reduction in diversity. Long-term mesocosm studies should confirm or reject this hypothesis.

While we found strong effects of predation on species abundance and diversity, the mechanisms involved may be quite complex, and depend on the traits of each prey species and how they interact with each other as well as with the predator. Furthermore, the confounding effects of predator duration and predator instar (which also occurs naturally), as well as interactions between the predator and actively dispersing species, could have an important role in structuring the community. For example, in the current study, the mosquitoes *Culiseta longiareolata* Macquart and *Culex laticinctus* Edwards preferred to

oviposit in predator-free pools (Eitam and Blaustein, 2004).

This study is among the first to empirically demonstrate that the intensity and duration of predation can have a strong influence on the predator's ability to alter community composition. Future theoretical and empirical work should consider the effects of predator gradients and temporal dynamics on species abundance and diversity.

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