

Evaluation of alternative prey-, predator-, and ratio-dependent functional response models in a zooplankton microcosm

Christina M. Prokopenko, Katrine Turgeon, and John M. Fryxell

Abstract: There is strenuous debate among ecologists regarding the inclusion of predator density into the originally prey-dependent functional response. We provided comprehensive empirical comparisons of alternative functional response models for the predatory ostracod *Heterocypris incongruens* (Ramdohr, 1808) and the rotifer *Brachionus calyciflorus* (Pallas, 1766) as its prey in small freshwater microcosms. Prey killed was measured at factorial combinations of four predator densities and five prey densities, and was recorded at 3 min intervals over 60 min experiments. To support the potential effect of predator interference on per capita kill rate, we recorded ostracod activity and aggression. Kill rate increased following a saturating function with increasing prey density and decreased with increasing predator density. Model evaluation using an information-theoretic approach indicated that the Arditi–Ginzburg type II ratio-dependent model performed best, followed by the Arditi–Akçakaya and Beddington–DeAngelis type II predator-dependent models, suggesting that predator interference was important in predicting kill rates. Interference among predators increased and their activity decreased with increasing predator density, providing confirmation that interference was responsible for the predator-dependent effect. By combining a microcosm experiment and behavioral observations, our results suggest that predator interference at realistic population densities influences ostracod kill rates and this form of interference was best accommodated by predator-dependent models.

Key words: *Brachionus calyciflorus*, freshwater zooplankton, *Heterocypris incongruens*, predator interference, ostracod, predation, rotifer.

Résumé : Un débat houleux existe chez les écologistes concernant l'inclusion de la densité des prédateurs dans la réponse fonctionnelle initialement dépendante des proies. Nous présentons des comparaisons empiriques exhaustives de différents modèles de réponse fonctionnelle pour l'ostracode prédateur *Heterocypris incongruens* (Ramdohr, 1808) et le rotifère *Brachionus calyciflorus* Pallas, 1766, sa proie, dans de petits microcosmes d'eau douce. Le nombre de proies tuées a été mesuré pour des combinaisons factorielles de quatre densités de prédateurs et cinq densités de proies, et a été enregistré toutes les 3 min durant des expériences de 60 min. Pour appuyer un éventuel effet de l'interférence entre prédateurs sur le taux d'élimination par individu, nous avons enregistré l'activité et l'agressivité des ostracodes. Le taux d'élimination augmentait avec la densité de proies selon une courbe de saturation et diminuait quand la densité de prédateurs augmentait. L'évaluation des modèles par une approche de théorie de l'information indique que le modèle dépendant du rapport Arditi–Ginzburg de type II donne les meilleurs résultats, suivi par les modèles dépendants des prédateurs Arditi–Akçakaya et Beddington–DeAngelis de type II, donnant à penser que l'interférence entre prédateurs est importante pour la prédiction des taux d'élimination. L'interférence entre prédateurs augmente et leur activité diminue parallèlement à l'augmentation de la densité de prédateurs, ce qui confirme que l'interférence est responsable de l'effet dépendant des prédateurs. En combinant une expérience en microcosme et des observations comportementales, nos résultats semblent indiquer que l'interférence entre prédateurs à des densités réalistes influence les taux d'élimination des ostracodes, et des modèles dépendants des prédateurs représentent le mieux cette forme d'interférence. [Traduit par la Rédaction]

Mots-clés : *Brachionus calyciflorus*; zooplancton d'eau douce, *Heterocypris incongruens*, interférence entre prédateurs, ostracodes, prédation, rotifère.

Introduction

Predator–prey dynamics underlie population patterns and behavioral processes; thus, predation theory has dominated ecology from its inception to the most contemporary research. The functional response is used to predict how the per capita kill rate of an individual predator varies in relation to changes in prey density (Holling 1959). There has been much debate over the years about the frequency and magnitude of predator influence in the functional response, recently reviewed by Arditi and Ginzburg (2012),

Barraquand (2014), and Abrams (2015). The inclusion of predator- or ratio-dependent effects can profoundly alter model predictions of predator–prey interactions (Abrams 1994; Fussmann and Blasius 2005; Arditi and Ginzburg 2012; Barraquand 2014). This is of primordial importance because the functional response is a cornerstone of much ecological theory, underpinning topics as diverse as optimal foraging, niche theory, interspecific competition, and food-web dynamics (Fussmann 2008; Van Moorter et al. 2013; Wasserman et al. 2016).

Received 10 May 2016. Accepted 3 December 2016.

C.M. Prokopenko. Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada; Department of Biology, Memorial University of Newfoundland, St. John's, NL A1B 3X9, Canada.

K. Turgeon. Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada; Department of Biology, Stewart Biology Building, McGill University, Montreal, QC H3A 1B1, Canada.

J.M. Fryxell. Department of Integrative Biology, University of Guelph, Guelph, ON N1G 2W1, Canada.

Corresponding author: Christina M. Prokopenko (email: cmprokopenko@mun.ca).

Copyright remains with the author(s) or their institution(s). Permission for reuse (free in most cases) can be obtained from RightsLink.

The Holling type I formulation is independent of density, describing a linear increase in kill rate with prey density. The linear form of the type I functional response derives from a constant search efficiency or attack rate (a), which dictates the frequency with which predators encounter and kill their prey (Holling 1959). The Holling type II functional response includes handling time (h), which provides a physical limit on the maximum kill rate of the predator, producing a decelerating hyperbolic relationship between kill rate and prey density. The Holling type III functional response curve displays a sigmoid-shaped relationship between prey abundance and feeding rates. It often stems from prey switching or reduced predator motivation to hunt at low prey densities. Hence, kill rate increases slowly until a threshold of prey density is surpassed.

By adding predator density (P) and an interference coefficient (c) to the Holling type II functional response, we arrive at the Beddington–DeAngelis model (Beddington 1975; DeAngelis et al. 1975). The Arditi–Ginzburg model (Arditi and Ginzburg 1989) is another modification of the purely prey-dependent Holling framework, which incorporates the ratio of prey density to predator density (N/P) and not these densities separately as in the Beddington–DeAngelis model. From these variations, it is possible to picture a spectrum along which predator interference is thought to influence kill rate. The purely prey-dependent Holling models lie at one extreme and the ratio-dependent Arditi–Ginzburg model at the other, with various predator-dependent models in between. Some model formulations are dynamic in describing the role of predator density and interference on kill rates. Both Arditi–Akçakaya (Arditi and Akçakaya 1990) and Hassell–Varley (Hassell and Varley 1969) formulations include an interference coefficient (c , which can vary between 1 and -1) that becomes more negative as competition increases, thus reaching ratio dependence at extreme values. Similarly, the Tyutyunov model (Tyutyunov et al. 2008) resembles a prey-dependent Holling model at low predator densities, whereas at high predator densities it bears resemblance to a ratio-dependent Arditi–Ginzburg model.

Considering the importance of the issue and the strength with which alternate points of view have been debated, surprisingly little experimental work to date has used formal model evaluation to compare prey-, predator-, and ratio-dependent models and none to our knowledge has simultaneously measured the frequency of agonistic interactions among predators that could explain predator- or ratio-dependent effects (Schenk et al. 2004; Kratina et al. 2009; Hossie and Murray 2016). Here we offer a synthetic series of laboratory functional response trials to address both issues of model fit and behavioral mechanism, using a rotifer as prey and ostracods as predators in microcosms.

Materials and methods

Data collection

The rotifer *Brachionus calyciflorus* (Pallas, 1766) is a well-studied species often used in consumer–resource and food-web experiments, whereas ostracods (identified as *Heterocypris incongruens* (Ramdohr, 1808) using DNA barcoding at the Biodiversity Institute of Ontario at the University of Guelph) were used opportunistically as their predator. Ostracods were originally isolated from a natural population collected in Guelph (Ontario) well water. The populations were maintained at 20 °C in 24 000 L tanks containing an algal solution in the Limnotron facility at the University of Guelph. The alga *Chlorella vulgaris* Beijerinck, 1890 (obtained from G. Fussmann at McGill University, originally from Culture Collection of Algae, University of Göttingen, Göttingen, Germany) was cultured using COMBO medium (Kilham et al. 1998). Rotifer cultures consisting solely of females (encysted rotifers from Aquatic

Eco-Systems, Inc., Apopka, Florida, USA) were kept in an incubator at a temperature of 20 °C in 250 mL flasks filled with *C. vulgaris* and COMBO culture medium.

A subset of ostracods was removed from the Limnotron tanks 24 h prior to functional response trials to standardize motivational state of the predator. Ostracods were first filtered from the algal solution using 20 µm Nitex material and then placed in 16.8 mL wells of a 6-well cell culture tray filled with 10 mL COMBO culture medium (7–10 ostracods·well⁻¹). Trays were kept in an incubator at 20 °C for 24 h.

On the day of trials, rotifers were filtered from the algal solution into COMBO culture medium. The rotifers were transferred using a pipette into wells of a 24-well cell culture tray (working volume of 2.75 mL·well⁻¹ was used for this experiment) at varying densities. The target densities for prey were 1.45, 4.36, 7.27, 12.72, and 18.18 rotifers·mL⁻¹ (4, 12, 20, 35, and 50 rotifers·well⁻¹, respectively), with sampling variation around these targets resulting in a more continuous data set. The densities of predators were 0.36, 0.72, 1.09, and 1.45 ostracods·mL⁻¹ (1, 2, 3, and 4 ostracods·well⁻¹, respectively). A minimum of four replicates were completed at each density combination.

With a dissecting microscope, we counted the number of rotifers before the ostracods were introduced to determine the exact initial density. Rotifer density was recorded at roughly 3 min intervals over the duration of each 60 min feeding trial (mean = 2.95 min, SD = 1.48 min), although challenges in accurate counting and recording data occasionally led to intervals that were slightly shorter or longer than the norm.

At each time interval, observations on predator behavior were also recorded, including whether any predators were inactive (i.e., they were not moving, had a closed shell, and were floating near the surface) or aggressive acts among predators were observed (i.e., direct and prolonged contact between ostracods, attacks, injury of one ostracod by another). The activity and aggression of ostracods was scored as the mean proportion of inactive predators or number of attacks on other ostracods for each trial, respectively.

Model fitting and data analysis

Functional response models were compared to explain observed kill rates by ostracods (Table 1). There has been growing appreciation in recent years that depletion over the course of functional response experiments can lead to biased parameter estimation, potentially affecting inference with respect to model evaluation (Rogers 1972; Arditi et al. 1991; Bolker 2008). One way to deal with this bias is to integrate the functional response over each time interval. Although analytical solutions are possible for a couple of the functional response variants (Bolker 2012), closed form solutions are not currently known for the majority of the functional response formulas in the published literature, including several of the equations considered here. We accordingly used the included R code (Supplementary material)¹ to numerically simulate prey depletion as a continuous process over each observed sampling interval to estimate the best-fit parameter estimates for a (area searched per unit time), h (handling time), and c (the interference coefficient among predators) for each model variant. Based on these parameters, we then calculated negative log-likelihoods for each best-fit formula to calculate values of Akaike's information criterion (AIC) scores (Akaike 1973).

The effect of predator density on activity level and predator interference was tested using a generalized linear model (glm function from R version 2.13.1; R Development Core Team 2011) with a binomial error distribution. For activity level, if at least one ostracod was inactive during a trial, then that trial was assigned a score of 0, whereas a score of 1 was assigned if all predators were

¹Supplementary material is available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjz-2016-0106>.

Table 1. Equations for the null, prey-dependent (Holling type I, type II, type III), predator-dependent (Beddington–DeAngelis type I, type II; Arditi–Akçakaya type I (Hassell–Varley), type II; Tyutyunov type II), and ratio-dependent (Arditi–Ginzburg type I, type II) models tested, where N is prey density, P is predator density, a is the searching efficiency or attack rate, h is the handling time, and c is the interference coefficient.

Model name	Equation	References
Null model	$f(N) = a$	
Prey-dependent model		
Holling type I	$f(N) = aN$	Holling 1959
Holling type II	$f(N) = \frac{aN}{1 + ahN}$	Holling 1959
Holling type III	$f(N) = \frac{aN^2}{1 + ahN^2}$	Holling 1959
Predator-dependent model		
Beddington–DeAngelis type I	$f(N, P) = \frac{aN}{1 + cP}$	
Hassell–Varley (Arditi–Akçakaya type I)	$f(N, P) = \frac{aN}{P^c}$	Hassell and Varley 1969
Beddington–DeAngelis type II	$f(N, P) = \frac{aN}{1 + ahN + cP}$	Beddington 1975; DeAngelis et al. 1975
Arditi–Akçakaya type II	$f(N, P) = \frac{aN P^c}{1 + ahNP^c}$	Arditi and Akçakaya 1990
Tyutyunov type II	$f(N, P) = \frac{aN}{\frac{P}{c} + \exp\left(\frac{-P}{c}\right) + ahN}$	Tyutyunov et al. 2008
Ratio-dependent model		
Arditi–Ginzburg type I	$f\left(\frac{N}{P}\right) = aN$	Arditi and Ginzburg 1989
Arditi–Ginzburg type II	$f\left(\frac{N}{P}\right) = \frac{a\frac{N}{P}}{1 + ah\frac{N}{P}}$	Arditi and Ginzburg 1989

active for all observations during a trial. For trials in which at least one ostracod was inactive, we also tested the effect of predator density on the proportion of active predators using a glm with a Gaussian error distribution. For predator interference, if any instances of predator interference were observed during a trial, then the trial was given a score of 1, conversely trials with a score of 0 had no observed predator interference. The effect of predator density on the number of predator interference events (i.e., when at least one attack was observed during the trial) were tested using a glm with a Gaussian error distribution.

Results

Mean rates of prey killed by ostracods were positively related to rotifer density, but the degree of prey dependence was less pronounced at high predator densities (Fig. 1). The Arditi–Ginzburg type II predator-dependent model (AIC weight = 0.83) provided the most parsimonious fit to the data, followed by Arditi–Akçakaya type II (AIC weight = 0.15) and Beddington–DeAngelis type II (AIC weight = 0.02), relative to other predator-dependent models and purely prey-dependent models (Table 2). All the best-fit models predict that ostracod kill rates increase with rotifer density, but the magnitude of prey-dependent increase in killing is depressed as predators become more abundant (Fig. 2). This effect becomes gradually more muted, however, with increasing numbers of predators.

Predator activity levels decreased as predator density increased in terms of the overall occurrence of inactivity in trials (glm with binomial error structure, $z = -2.91$, $p = 0.004$). However, the proportion of inactive individuals in trials, where inactive predators were observed, did not change with increasing predator density (glm with Gaussian error structure, $t = 1.17$, $p = 0.249$). The interference among predators increased in incidence, i.e., if interference occurred during a trial (glm with binomial error structure,

$z = 2.37$, $p = 0.018$) but not intensity, i.e., how many aggressive interactions occurred (glm with Gaussian error structure, $t = 0.80$, $p = 0.441$) as predator density increased.

Discussion

By using alternative kill rate models, factorial combinations of predator and prey densities in small freshwater microcosms, and direct measurements of interference rates at realistic predator densities, we completed a comprehensive empirical comparison among prey-, predator-, and ratio-dependent functional response models. Our study provides clear evidence that the kill rate of ostracods was influenced by both prey and predator density, with strong support for ratio- or predator-dependent functional response. Overall, the kill rate of ostracods was a positive decelerating functional response reaching a plateau of maximal ingestion and decreased with increasing predator density. The support for ratio dependence and predator dependence with a large interference coefficient combined with purely prey-dependent models being less consistent with the data suggest that predators play an important role in shaping the functional response for this predator. Furthermore, our study extended beyond model evaluation by demonstrating that direct aggressive interference was the causal mechanism underlying the observed functional response.

Functional responses in other invertebrate predator–prey laboratory experiments have been shown to be consistent with predator-dependent models (Skalski and Gilliam 2001) or ratio-dependent models (Hansson et al. 2001; Spataro et al. 2012; Médoc et al. 2013). This suggests that some degree of predator interference occurs in a variety of systems, although the degree of interference differs among systems and species (Delong and Vasseur 2011). Previous work with ostracods found that the intake rate of ostracods feeding on alga was well depicted by a type II functional

Fig. 1. Observed ostracod *Heterocypris incongruens* kill rates (grey circles) and binned means (black circles with vertical error bars) in relation to variation in the rotifer *Brachionus calyciflorus* prey, with the three best-fit functional response curve Arditi–Ginzburg type II (solid line; Akaike’s information criterion (AIC) weight = 0.83), Arditi–Akçakaya type II (broken line; AIC weight = 0.15), Beddington–DeAngelis type II (dotted line; AIC weight = 0.02).

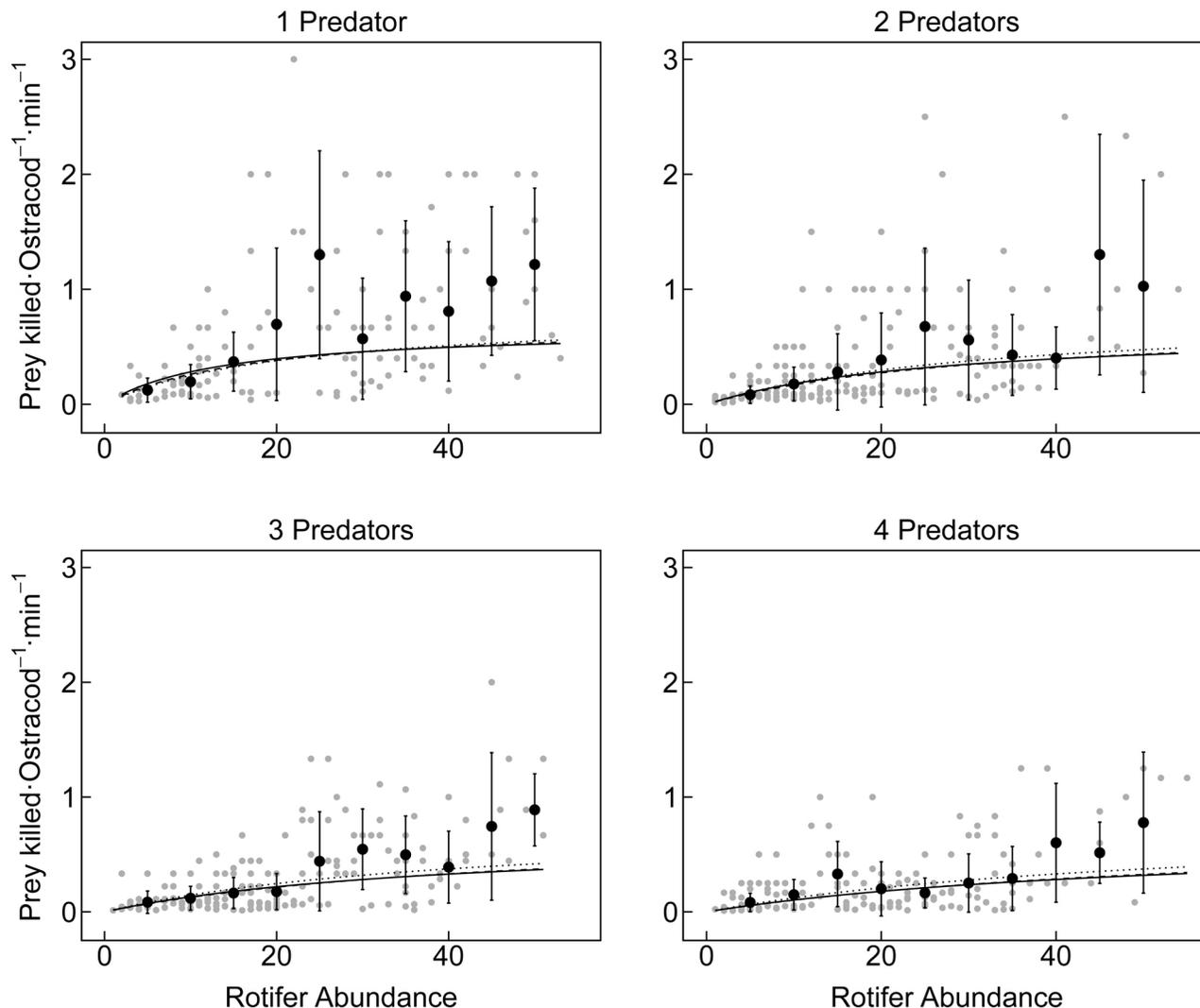
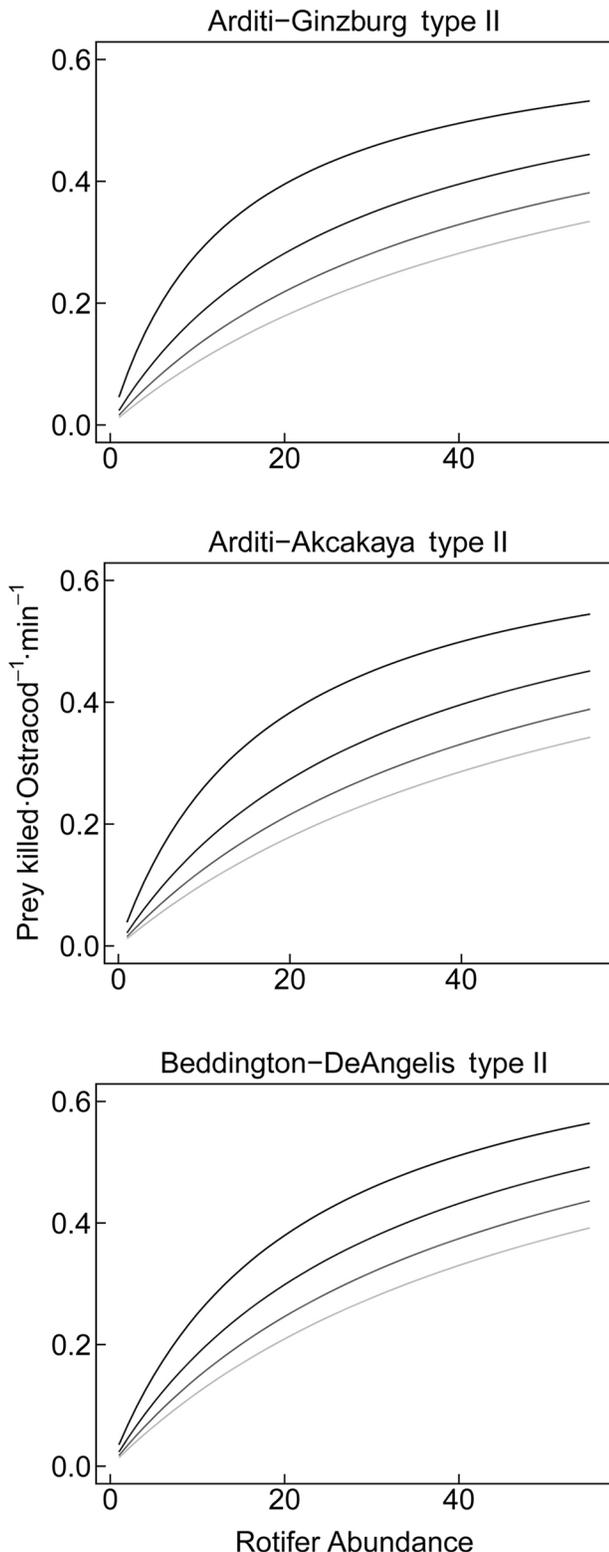


Table 2. Best-fit parameter values, Δ AIC scores, and Akaike’s information criterion (AIC) weight for the functional response models tested using the per capita kill rate (i.e., prey killed per minute per individual predator) over a short time interval (1–5 min) for starved ostracod *Heterocypris incongruens* predators feeding on rotifer *Brachionus calyciflorus* prey (values in boldface type indicate models with noteworthy support).

Model	a	h	c	Δ AIC	AIC weight
Null	0.196			237.00	0.00
Holling type I	0.009			68.10	0.00
Holling type II	0.014	1.102		59.80	0.00
Holling type III	0.00027	0.049		225.00	0.00
Beddington–DeAngelis type I	0.019		0.049	27.40	0.00
Beddington–DeAngelis type II	0.078	1.280	1.114	4.00	0.02
Hassell–Varley type I	0.015		0.440	25.50	0.00
Arditi–Akçakaya type II	0.041	1.392	-0.892	1.70	0.15
Tyutyunov type II	0.032	0.069	-2.7	44.70	0.00
Arditi–Ginzburg type I	0.023			124.90	0.00
Arditi–Ginzburg type II	0.049	1.509		0.00	0.83

Note: a is the searching efficiency or attack rate, h is the handling time, and c is the interference coefficient.

Fig. 2. The three best-fit functional response curve Arditi–Ginzburg type II ($y = 0.049 \times (N/P)/1 + 0.049 \times 1.509 \times (N/P)$; AIC weight = 0.83), Arditi–Akçakaya type II ($y = 0.041 \times (N \times P^{-0.892})/1 + 0.041 \times 1.392 \times (N \times P^{-0.892})$; AIC weight = 0.15), Beddington–DeAngelis type II ($y = 0.078 \times N/1 + 0.078 \times 1.280 \times N + 1.114 \times P$; AIC weight = 0.02) for ostracod *Heterocypris incongruens* predators in relation to variation in the rotifer *Brachionus calyciflorus* prey (N) and predator (P) densities. Lines from top to bottom correspond to 1, 2, 3, and 4 predators (black to light grey).



response curve, but in this case, predator density did not have a statistically significant influence on intake rates (Grant et al. 1983). Furthermore, type III sigmoidal functional responses have been demonstrated in some microcosm studies with carnivores (Kratina et al. 2009) and natural herbivorous systems (Morozov 2010).

The wide range of rotifer densities that we used in our trials were realistic with those found in both laboratory and natural populations. The population density of ostracods in our trials ranged between 1 and 4 individuals·mL⁻¹, well within the observed range of ostracod densities (1–6 individuals·mL⁻¹) recorded during 180 day predator–prey trials with the same rotifer prey species in large experimental mesocosms (J.M. Fryxell, unpublished data). In natural settings, the ostracod *Cyprinotus carolinensis* Ferguson, 1967 has been recorded at densities of 4 individuals·mL⁻¹ (Grant et al. 1983). Rotifers usually occur at densities <1 individual·mL⁻¹ (Yoshida et al. 2000), but have been observed in the field to fluctuate across a wide range of densities (over 5 rotifers·mL⁻¹ in Jurgens et al. 1999) to 47 rotifers·mL⁻¹ (Lampert and Rothhaupt 1991). Thus, the levels of predator interference found in our experimental trials is consistent with densities found under some natural conditions.

We found evidence that ostracod activity and interference patterns changed with predator density, supporting the interference hypothesis. Agonistic interactions between predators, such as interference, can increase the time between attacks on prey. This offers some insight into the causal mechanism behind the observed predator-dependent effects on ostracod functional responses. The mechanisms resulting in predator dependence can be behavioral (Abrams and Ginzburg 2000) or spatial (Cosner et al. 1999) in nature and can occur over short or long time scales (Fussmann 2008). Predator dependence can arise as a statistical artifact of resource depletion (Abrams 1994), direct interference due to aggressive interactions among predators (Beddington 1975; DeAngelis et al. 1975), from spacing behavior among predators to avoid agonistic interactions (Abrams and Ginzburg 2000), or as a by-product of antipredator behavior (Preston et al. 1999). Our behavioral results support the latter predator aggression hypothesis and our observations support the avoidance between predators (C.M. Prokopenko, personal observation). We found that activity among ostracods decreased with predator density. In addition to behavior of predators, we observed that the spatial distribution of rotifers in the arena was rarely purely homogenous, either due to predator consumption or prey behavior (C.M. Prokopenko, personal observation). Rotifers have previously been shown to exhibit antipredator behavior by decreasing swimming speed as predators approach (Preston et al. 1999). As predator dependence was detected even over short time intervals, depletion itself cannot explain this effect.

Previous studies have often used variable time scales of observations to estimate the predator functional response (Fussmann et al. 2005; Kratina et al. 2009). Fussmann et al. (2005) found a prey-dependent Holling type III functional response (a sigmoid relationship) in herbivorous zooplankton using short-term rates. Our findings, recorded over short time intervals, were consistent with those from a similar microcosm experiment by Kratina et al. (2009), who found that predator dependence described the functional response of invertebrate predators. This suggests that predator-dependent effects are not a simple artifact of extended time intervals of observations, an artifact that is enhanced when there is appreciable prey depletion over the course of each observation interval (Bolker 2012).

The functional response of predators has important implications for both theoretical and applied ecology. The type of functional response included in models can strongly influence population and food-web dynamics (Fussmann and Blasius 2005). Although it is always possible that such patterns are a simple artifact of bench-top laboratory conditions, our results nonetheless suggest that predator interference can be strong even at realistic predator densities and

when functional responses are measured over short time intervals, and therefore worthy of consideration in predator–prey systems of a similar nature.

Acknowledgements

We thank K. McCann, T. Avgar, L. Vander Vennen and G. Street for helpful discussion during data collection and model fitting. We acknowledge G. Fiorino for valuable help in the laboratory and C. Hart and K. Wagner for comments on an early version of this manuscript. Our work was supported by a Natural Sciences and Engineering Research Council of Canada (NSERC) Discovery Grant to J.M.F. and a Fonds de recherche du Québec – Nature et technologies (FQRNT) postdoctoral scholarship to K.T.

References

- Abrams, P.A. 1994. The fallacies of “ratio-dependent” predation. *Ecology*, **75**: 1842–1850. doi:10.2307/1939644.
- Abrams, P.A. 2015. Why ratio dependence is (still) a bad model of predation. *Biol. Rev. Camb. Philos. Soc.* **90**: 794–814. doi:10.1111/brv.12134. PMID:25099654.
- Abrams, P.A., and Ginzburg, L.R. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends Ecol. Evol.* **15**: 337–341. doi:10.1016/S0169-5347(00)01908-X. PMID:10884706.
- Akaike, H. 1973. Information theory as an extension of maximum likelihood principle. In *Second International Symposium of Information Theory*, Tsahkadsor, Armenia, U.S.S.R., 2–8 September 1971. Edited by B.N. Petrov and F. Csaki. Akadémiai Kiadó, Budapest, Hungary. pp. 267–281.
- Arditi, R., and Akcakaya, H.R. 1990. Underestimation of mutual interference of predators. *Oecologia*, **83**: 358–361. doi:10.1007/BF00317560.
- Arditi, R., and Ginzburg, L.R. 1989. Coupling in predator–prey dynamics: ratio-dependence. *J. Theor. Biol.* **139**: 311–326. doi:10.1016/S0022-5193(89)80211-5.
- Arditi, R., and Ginzburg, L.R. 2012. *How species interact: altering the standard view on trophic ecology*. Oxford University Press, New York.
- Arditi, R., Ginzburg, L.R., and Akcakaya, H.R. 1991. Variation in plankton densities among lakes: a case for ratio-dependent predation models. *Am. Nat.* **138**: 1287–1296. doi:10.1086/285286.
- Barraquand, F. 2014. Functional responses and predator–prey models: a critique of ratio dependence. *Theor. Ecol.* **7**: 3–20. doi:10.1007/s12080-013-0201-9.
- Beddington, J. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.* **44**: 331–340. doi:10.2307/3866.
- Bolker, B.M. 2008. *Ecological models and data in R*. Princeton University Press, Princeton, N.J.
- Bolker, B. 2012. Maximum likelihood estimation and analysis with the bbmle package. pp. 1–19. Available from <https://cran.r-project.org/web/packages/bbmle/vignettes/mle2.pdf>.
- Cosner, C., DeAngelis, D.L., Ault, J.S., and Olson, D.B. 1999. Effects of spatial grouping on the functional response of predators. *Theor. Popul. Biol.* **56**: 65–75. doi:10.1006/tpbi.1999.1414. PMID:10438669.
- DeAngelis, D.L., Goldstein, R.A., and O'Neill, R.V. 1975. A model for trophic interaction. *Ecology*, **56**: 881–892. doi:10.2307/1936298.
- DeLong, J.P., and Vasseur, D.A. 2011. Mutual interference is common and mostly intermediate in magnitude. *BMC Ecol.* **11**: 1. doi:10.1186/1472-6785-11-1. PMID:21211032.
- Fussmann, G.F. 2008. Experimental measurements of functional response: what is the relevance for food web theory? *Verh. Int. Verein. Limnol.* **30**: 255–258.
- Fussmann, G.F., and Blasius, B. 2005. Community response to enrichment is highly sensitive to model structure. *Biol. Lett.* **1**: 9–12. doi:10.1098/rsbl.2004.0246. PMID:17148115.
- Fussmann, G.F., Weithoff, G., and Yoshida, T. 2005. A direct, experimental test of resource vs. consumer dependence. *Ecology*, **86**: 2924–2930. doi:10.1890/04-1107.
- Grant, I., Egan, E., and Alexander, M. 1983. Measurement of rates of grazing of the ostracod *Cyprinotus carolinensis* on blue-green algae. *Hydrobiologia*, **106**: 199–208. doi:10.1007/BF00008117.
- Hansson, S., De Stasio, B., Gorokhova, E., and Mohammadian, M. 2001. Ratio-dependent functional responses — tests with the zooplanktivore *Mysis mixta*. *Mar. Ecol. Prog. Ser.* **216**: 181–189. doi:10.3354/meps216181.
- Hassell, M.P., and Varley, G.C. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature*, **223**: 1133–1137. doi:10.1038/2231133a0. PMID:5810684.
- Holling, C.S. 1959. The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Can. Entomol.* **91**: 293–320. doi:10.4039/Ent91293-5.
- Hossie, T.J., and Murray, D.L. 2016. Spatial arrangement of prey affects the shape of ratio-dependent functional response in strongly antagonistic predators. *Ecology*, **97**: 834–841. doi:10.1890/15-1535.1. PMID:27220200.
- Jurgens, K., Skibbe, O., and Jeppesen, E. 1999. Impact of metazooplankton on the composition and population dynamics of planktonic ciliates in a shallow, hypertrophic lake. *Aquat. Microb. Ecol.* **17**: 61–75. doi:10.3354/ame017061.
- Killham, S.S., Kreeger, D.A., Lynn, S.G., Goulden, C.E., and Herrera, L. 1998. COMBO: a defined freshwater culture medium for algae and zooplankton. *Hydrobiologia*, **377**: 147–159. doi:10.1023/A:1003231628456.
- Kratina, P., Vos, M., Bateman, A., and Anholt, B.R. 2009. Functional responses modified by predator density. *Oecologia*, **159**: 425–33. doi:10.1007/s00442-008-1225-5.
- Lampert, W., and Rothhaupt, K.O. 1991. Alternating dynamics of rotifers and *Daphnia magna* in a shallow lake. *Arch. Hydrobiol.* **120**: 447–456.
- Médoc, V., Spataro, T., and Arditi, R. 2013. Prey:predator ratio dependence in the functional response of a freshwater amphipod. *Freshw. Biol.* **58**: 858–865. doi:10.1111/fwb.12091.
- Morozov, A.Y. 2010. Emergence of Holling type III zooplankton functional response: bringing together field evidence and mathematical modelling. *J. Theor. Biol.* **265**: 45–54. doi:10.1016/j.jtbi.2010.04.016. PMID:20406647.
- Preston, B.L., Cecchine, G., and Snell, T.W. 1999. Effects of pentachlorophenol on predator avoidance behavior of the rotifer. *Aquat. Toxicol.* **44**: 201–212.
- R Development Core Team. 2011. *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna, Australia. Available from <https://www.r-project.org>.
- Rogers, D. 1972. Random search and insect population models. *J. Anim. Ecol.* **41**: 369–383. doi:10.2307/3474.
- Schenk, D., Bersier, L.-F., and Bacher, S. 2004. An experimental test of the nature of predation: neither prey- nor ratio-dependent. *J. Anim. Ecol.* **74**: 86–91. doi:10.1111/j.1365-2656.2004.00900.x.
- Skalski, G., and Gilliam, J. 2001. Functional responses with predator interference: viable alternatives to the Holling type II model. *Ecology*, **82**: 3083–3092. doi:10.1890/0012-9658(2001)082[3083:FRWPIV]2.0.CO;2.
- Spataro, T., Bacher, S., Bersier, L., Arditi, R., and Ersier, L.I.X.B. 2012. Ratio-dependent predation in a field experiment with wasps. *Ecosphere*, **3**: 1–12. doi:10.1890/ES12-00133.1.
- Tyutyunov, Y., Titova, L., and Arditi, R. 2008. Predator interference emerging from trophotaxis in predator–prey systems: an individual-based approach. *Ecol. Complex.* **5**: 48–58. doi:10.1016/j.ecocom.2007.09.001.
- Van Moorter, B., Visscher, D., Herfindal, I., Basille, M., and Mysterud, A. 2013. Inferring behavioural mechanisms in habitat selection studies — getting the null-hypothesis right for functional and familiarity responses. *Ecography*, **36**: 323–330. doi:10.1111/j.1600-0587.2012.07291.x.
- Wasserman, R.J., Alexander, M.E., Dalu, T., Ellender, B.R., Kaiser, H., and Weyl, O.L.F. 2016. Using functional responses to quantify interaction effects among predators. *Funct. Ecol.* **30**: 1988–1998. doi:10.1111/1365-2435.12682.
- Yoshida, T., Ban, S., Takenouchi, T., Aono, T., Ishikawa, Y., Mikami, H., Takano, K., Imada, K., Yasutomi, R., and Takeuchi, K. 2000. Top-down control of population dynamics of the dominant rotifers in two mesotrophic lakes in Hokkaido, Japan. *Arch. Hydrobiol.* **148**: 481–498. doi:10.1127/archiv-hydrobiol/148/2000/481.