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ORIGINAL ARTICLE

Biological Control Through Intraguild Predation: Case Studies in Pest Control, Invasive Species and Range Expansion

C. J. Bampfylde[a,*], M. A. Lewis[a,b]

[a] *Centre for Mathematical Biology, Department of Mathematical and Statistical Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2G1*
[b] *Department of Biological Sciences, University of Alberta, Edmonton, Alberta, Canada T6G 2E9*

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Abstract Intraguild predation (IGP), the interaction between species that eat each other and compete for shared resources, is ubiquitous in nature. We document its occurrence across a wide range of taxonomic groups and ecosystems with particular reference to non-indigenous species and agricultural pests. The consequences of IGP are complex and difficult to interpret. The purpose of this paper is to provide a modelling framework for the analysis of IGP in a spatial context. We start by considering a spatially homogeneous system and find the conditions for predator and prey to exclude each other, to coexist and for alternative stable states. Management alternatives for the control of invasive or pest species through IGP are presented for the spatially homogeneous system. We extend the model to include movement of predator and prey. In this spatial context, it is possible to switch between alternative stable steady states through local perturbations that give rise to travelling waves of extinction or control. The direction of the travelling wave depends on the details of the nonlinear intraguild interactions, but can be calculated explicitly. This spatial phenomenon suggests means by which invasions succeed or fail, and yields new methods for spatial biological control. Freshwater case studies are used to illustrate the outcomes.

Keywords Competition · Intraguild predation · Mathematical model · Biological control · Travelling waves · Reaction–diffusion · Differential equations · Range expansion · Non-indigenous species

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*Corresponding author.
E-mail addresses: cbampfylde@math.ualberta.ca (C.J. Bampfylde); mlewis@math.ualberta.ca (M.A. Lewis).

1. Introduction and biological background

Interspecific interactions include competition and predation. The combination of these two is intraguild predation (IGP), defined as the killing or eating of species that use similar, often limiting, resources and are thus potential competitors (Polis et al., 1989). The importance and occurrence of IGP has been documented across taxonomic groups and is prevalent in nature (reviewed by Polis et al., 1989). Theoretical treatments of IGP suggest alternative stable states occur, such as two alternative stable equilibria (Polis et al., 1989; Holt and Polis, 1997; Mylius et al., 2001; Diehl, 2003), while experimental studies have confirmed theoretical predictions (Holyoak and Sachdev, 1998; Morin, 1999; Diehl and Feißel, 2000; Schroder et al., 2005). IGP is likely to occur in populations structured by size or stage (Ebenman and Persson, 1988) and where organisms undergo ontogenetic niche shifts, that is to say the patterns in resource use that develop as an organism increases in size from juvenile to adult (Werner and Gilliam, 1984).

Natural enemies are often employed as biological control predators for pest species, however IGP is common in biological control species interactions (for a review in arthropod and nematode communities, see Rosenheim et al., 1995). There are many examples in agricultural environments (see Table 1).

The alternative food source allows the biological control predators to persist even at times of low prey abundance, but the competition for resources weakens the predatory effect on the pest species. From the perspective of the prey species, IGP adds an additional detrimental effect, not only does the prey suffer mortality due to predation, but it also has less resource available due to competition. What are the consequences of IGP for biological control?

IGP can be observed in many interactions between exotic and native species (see Table 1). Examples can be seen across a wide range of ecosystems, such as brown tree snake and mangrove monitor, and rusty crayfish and smallmouth bass. A more detailed treatment of the interaction between rusty crayfish and smallmouth bass can be found elsewhere (Drury et al., manuscript in preparation). In both these examples, mutual IGP (Polis et al., 1989) is observed.

Given the prevalence of IGP in the interactions between pest species (native and non-indigenous species) and their competitors and natural enemies, how can the theory be employed to help inform the management and biological control of pest species? In order to address this question, we build a general model for IGP with an intraguild predator and an intraguild prey who compete for shared resources. We develop a mathematical model for the population density of the predator and prey as they change over time. Initially, we consider a spatially independent formulation of the problem and determine all possible outcomes of the dynamical system. We find the parameter regimes under which biological control of the exotic is possible (under manipulation of predator or prey or both) and deduce where perturbations are unlikely to change the steady state of the system.

Previous theoretical treatment of IGP in the literature has included different predation functional responses (linear and nonlinear) at different productivity levels. For example, a Type I functional response (Holling, 1959) has been used to model the predation interaction (Polis et al., 1989) and the possible dynamical outcomes described: exclusion of intraguild prey by the intraguild predator;

Table 1 Examples of intraguild predation in nature

Predator (P)	Consumer (C)	Resource (R)	Locations	References
Agricultural pests and their biological control agents				
Mullein plant bug (*Campylomma verbasci*)	Apple rust mites (*Aculus schlechtendali*), pear psylla (*Cacopsylla pyricola*)	Apples, pears	Fruit growing regions of northern U.S. and southern Canada	McMullen and Jong (1970); Thistlewood (1990)
Bigeyed bugs (*Geocoris punctipes*, *G. pallens*, *G. bullatus*, *G. uligosus*)	Lepidopteran pests of cotton: whiteflies, mites and aphids, bollworm, tobacco budworm	Cotton	Southern U.S. (especially cotton belt)	Tamaki and Weeks (1972); Hagler and Cohen (1991); Hagler and Naranjo (1994); Hagler et al. (2004)
Minute pirate bug (*Orius tristicolor*), insidious flower bug (*O. insidiosus*)	Thrips, spider mites, aphids, small caterpillars	Agricultural crops, cotton, orchard crops, greenhouse crops		Askari and Stern (1972)
Green lacewings (*Chrysoperla carnea*, *C. rufilabris*)	Aphids, spider mites, thrips, whiteflies, leafhoppers, moths, leafminers, small caterpillars	Cotton, sugar beets and vineyards	North America, Russia, Germany, Europe	Limburg and Rosenheim (2001); Pree et al. (1989); Albuquerque et al. (1994); Tauber and Tauber (1983)
Zetzellia mali (predaceous mites)	Apple rust mite, European red mite, two-spotted spider mite	Apples	Apple orchards	Walter (1987); Kain and Nyrop (1995)
Euseius tularensis (predaceous mites)	Citrus red mite, citrus thrips, two-spotted spider mite, scale insects, whiteflies	Citrus fruit	Citrus plantations	Ouyang et al. (1992); Congdon and McMurtry (1988); Grafton-Cardwell and Ouyang (1993); Grafton-Cardwell et al. (1999)
Neoseiulus californicus, *Phytoseiulus persimilis* (predaceous mites)	Red spider mites (*Tetranychus* spp.)	Vegetable and greenhouse crops	Spain	Escudero and Ferragut (2005)
Decollate snail (*Rumina decollata*)	Brown garden snail (*Helix aspersa*)	Citrus crop and seedlings	California	Cowie (2001)
Epistrophe balteata, *Paragus qudrifasciatus*, *Syrphus corollae* (hoverflies, syrphid family)	Cotton aphid (*Aphis gossypii*)	Cotton, alfalfa	China	Zhang et al. (2004)

Table 1 Continued

Predator (P)	Consumer (C)	Resource (R)	Locations	References
Syrphid fly larvae (hoverfly larvae)	Russian wheat aphid (*Diuraphis noxia*)	Spring barley (*Hordem vulgare*)	Ethiopia	Adisu and Freier (2003)
Episyrphus balteatus (hoverflies, syrphid family)	Winter wheat aphids (*Metopolophium dirhodium*)	Winter wheat	Germany	Tenhumberg and Poehling (1995)
Pseudodorus clavatus (hoverflies, syrphid family)	Brown citrus aphid (*Toxoptera citridia*)	Citrus fruit	North America	Michaud (1999); Michaud and Belliure (2001)
Pipiza festiva, *Heringia heringii* (hoverflies, syrphid family)	Gall forming aphids	Fruit trees	Southeastern Spain	Rojo and MarcosGarcia (1997)
Heringia calcarata (hoverflies, syrphid family)	Woolly apple aphid (*Eriosoma lanigerum*)	Apple orchards	Virginia, U.S.	Brown and Schmitt (1994); Short and Bergh (2004)
Invasive species and their interactions with native species (invader denoted†*, mutual IGP* §*)*				
Lake trout (*Salvelinus namaycush*)†	Cutthroat trout (*Oncorhynchus clarki bouvieri*)	Zooplankton, amphipods, chironomidae, invertebrates and leeches and shelter	Yellowstone Lake	Crossman (1995); Munro et al. (2005); Ruzycki et al. (2003); Behnke (1992)
Smallmouth bass (*Micropterus dolomieu*)§	Rusty crayfish (*Orconectes rusticus*)†§	Macroinvertebrates, macrophytes	Northeastern U.S. and Ontario, Canada	Momot et al. (1988); Momot (1992); Capelli (1982); Capelli and Magnuson (1983); Lodge et al. (1986); Olsen et al. (1991); Lodge et al. (1994); Stein (1977); Didonato and Lodge (1993); Garvey et al. (2003); Hamr (2001); Lodge et al. (1985); Momot (1992); Dorn and Wojdak (2004)
Rainbow trout (*Oncorhynchus mykiss*)†	Other salmonids, humpback chub (*Gila cypha*), suckers, squawfish	Amphibians, invertebrates	New Zealand, North America	Boustead (1993); Fuller (2000); Robinson et al. (2003); Martinez et al. (1994); Gadomski et al. (2004)

Table 1 Continued

Predator (*P*)	Consumer (*C*)	Resource (*R*)	Locations	References
Brown tree snake (*Boiga irregularis*)†§	Mangrove monitor lizard (*Varanus indicus*)§	Small vertebrates, invertebrates, bird and reptile eggs	Guam	Fritts and Rodda (1998)
Ctenophore (*Beroe ovata*)†§	Comb jelly (*Mnemiopsis leidyi*)†§	Zooplankton, fish eggs and larvae	Azov, Marmara, Aegean, Mediterranean and Caspian Seas	Kideys (1994); Kideys et al. (2000); Secord (2003); Kideys and Moghim (2003)
European green crab (*Carcinus maenas*)†	Shore crabs (*Hemigrapsus sanguineus*†, *H. oregonensis*)	Mussels, clams, snails, isopods, barnacles, algae, space, shelter	East coast and West coast North America	Grosholz and Ruiz (1995); Grosholz et al. (2000); Jensen et al. (2002)
27 species of endemic predatory mites	Prickly pear mites (*Tetranychus desertorum*)†, passionvine mites (*Brevipalpus phoenicis*)† and privet mites (*B. obovatus*)†	Lantana (*Lantana camara*)†	Australia	Walter (1999)
Birds	Brown anole (*Norops sagrei*)†	Terrestrial invertebrates	North America, Hawaii, Jamaica and Granada	Waide and Reagan (1983); Wright (1981)
Eurasian perch (*Perca fluvitilis*)†	Freshwater fish, e.g. common bully (*Gobiomorphus cotidianus*)	Zooplankton, macroinvertebrates	Australia, China, Cyprus, Italy, Morocco, New Zealand, Spain, South Africa	Kristensen and Closs (2004)

Table 1 Continued

Predator (P)	Consumer (C)	Resource (R)	Locations	References
Species undergoing range expansion and their interspecific interactions (invader denoted †*, mutual IGP* §*)*				
Piscivorous fish§, e.g. lake trout (*Salvelinus namaycush*), lake sturgeon (*Acipenser fulvescens*), smallmouth bass (*Micropterus dolomieu*)	Round goby (*Neogobius melanostomus*)†§	Native invertebrates, dreissenids, refugia	Great Lakes	Jude et al. (1992); Schaeffer et al. (2005); Vanderploeg et al. (2002)
Coyotes (*Canis latrans*), bobcats (*Lynx rufus*)	Raccoon (*Procyon lotor*)†	Small mice, juvenile birds, eggs, frogs, crayfish, crabs	Northern prairies of Canada, U.S.	Greenwood (1981); Kamler et al. (2003); Lariviere (2004)
Salamanders (*Desmognathus quadramaculatus*, *D. monticola*)§	Salamanders (*D. fuscus*, *D. ochrophaeus*)§	Earthworms, insects, arthropods	Appalachian mountains	Hairston (1980); Hairston (1986); Rissler et al. (2004)
Amphipods (*Gammarus pulex*)†§	*G. duebeni celticus*§	Zooplankton	Irish streams and lochs	MacNeil et al. (2004a); MacNeil et al. (2001, 2004b)
Daphnia lumholtzi†§	Competing *Daphnia* spp.§	Zooplankton	Southern U.S.	Lennon et al. (2001)

See model food web in Fig. 1 for clarification of column entries.
Invader denoted †, mutual IGP §, both invader and mutual IGP denoted †§.

coexistence; or a priority effect (single species equilibria dependent on initial conditions). When the resource is also explicitly modelled and included in the Type I predator–prey system (Holt and Polis, 1997; Diehl and Feißel, 2000; Diehl, 2003), the outcome is dependent on the productivity of the system (for example, the resource carrying capacity). At low productivity, the intraguild prey excludes the intraguild predator, while at high productivity, the predator excludes the prey. At intermediate productivities, both species are able to coexist (Holt and Polis, 1997; Diehl and Feißel, 2000; Diehl, 2003). Nonlinear predation responses have also been used, for example, a Type II functional response (Mylius et al., 2001) and an adaptation of the Schoener model (Schoener, 1974, 1976; Polis et al., 1989; Holt and Polis, 1997). The results for these models are qualitatively similar. Under low and high productivities the outcomes are as for the Type I functional response, while at intermediate productivity the system is bistable, such that both predator and prey coexist or the predator excludes prey (dependent on initial conditions). In order for the possibility of coexistence to occur, the prey is assumed to be a superior exploitative competitor of the shared resource (Polis et al., 1989; Polis and Holt, 1992; Holt and Polis, 1997), but see Diehl (2003).

We choose not to model the resource explicitly, to gain analytical tractability and improved intuition regarding the interactions between the intraguild predator and prey. See Mylius et al. (2001) for an example model with an explicit resource.

The inclusion of space into ecological models has often shown to produce very different outcomes to non-spatial models (Kareiva, 1990; Lewis and van den Driessche, 1993). We therefore later consider a spatially explicit model allowing individuals to diffuse throughout their domain. We consider a particular regime where the spatially homogeneous model is bistable (alternative stable states with one or the other species dominating). The bistability suggests the possibility of travelling waves, and we are able to find critical conditions where a small-scale perturbation gives rise to control of invasive species, where the wave advances, or if the condition is not met a wave of the native species extinction spreads throughout the landscape.

In this paper, we first state the assumptions that underly our models (Section 2). We employ two complementary modelling approaches, a spatially independent one (Section 3) and a spatially explicit one (Section 4). For each modelling approach, we give biological interpretations of the mathematical results as well as analytical insights and numerical simulations. Finally, we discuss the biological implications of the model results and give limitations of our models, suggesting future avenues for research (Section 5).

2. Modelling assumptions

The assumptions are divided into three groups: those underlying the modelling philosophy and approach used here (M); those concerning the uniformity of the population and the environment (U); and those governing species interactions (I).

We adopt a process-based model to obtain insight into the mechanisms that govern species coexistence. This leads to a nonlinear system of equations and hence a nonlinear model (M1). We choose a deterministic approach, rather than a

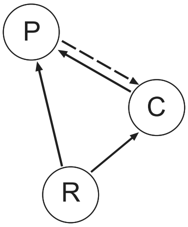

Fig. 1 Model food web for intraguild predation. *P* represents the intraguild predator, *C* represents the intraguild prey or consumer, *R* represents the shared resource. *Arrows* indicate direction of energy flow. *Solid lines* comprise the basic intraguild-predation model. The *dashed line* indicates predation by the consumer on the predator and is only present in cases of mutual intraguild predation (§ in Table 1). See Table 1, for example food webs.

stochastic approach (M2) and the dependent variables of our system are densities of individuals of each species, not total numbers of individuals within the arena of interaction (M3).

We assume there is no age or size-structure in both the predator and the prey populations. That is, the individuals of one species are identical (i.e. same age and size) and we ignore any differences between individuals of the same species (U1). Although size-structure may be an important factor in IGP population dynamics (Werner and Gilliam, 1984) and has been considered elsewhere (de Roos and Persson, 2003), we do not include it and instead focus on the competition and predation dynamics. The environment is assumed to be constant in space and time and thus there is no extrinsic spatial heterogeneity, thus the intrinsic vital rates (birth and death) and the carrying capacity (maximum density) of the environment remain constant (U2). The predator and prey populations are assumed to be sufficiently high, to allow the populations to exist as a continuum and reproduce continuously over time, leading to an ordinary differential equation structure (U3). We assume, initially (Section 3), there is population mixing and thus use a spatially independent system (U4). This assumption is relaxed later (Section 4) where individuals diffuse spatially throughout the domain.

The last set of assumptions describe the model interactions between the predator and prey. Intraspecific competition occurs between individual conspecifics (I1). Cannibalism can occur in either population (I2). Interspecific competition occurs between individuals of different species (I3). Mutual predation (between the intraguild predator and the intraguild prey) can occur (I4). The growth of each population in the absense of the other is logistic (I5). The intraguild prey is assumed to be the superior competitor for the shared resource (as assumed elsewhere, Polis et al., 1989; Polis and Holt, 1992; Holt and Polis, 1997; Diehl and Feißel, 2000) (I6). This is observed in the examples of European green crab and shore crabs (Jensen et al., 2002), cutthroat trout and lake trout (Behnke, 1992), rusty crayfish and smallmouth bass (Hamr, 2001) and piscivorous and non-piscivorous fish where the specialist feeding morphology affects the resource consumption (Werner and Gilliam, 1984).

3. Non-spatial intraguild predation model

We use a system of ordinary differential equations to describe the population dynamics of the interacting species: intraguild prey (which we define here as the consumer) and intraguild predator (which we will refer to as the predator). A general model to describe these interactions (assumptions I1–I6 above) follows mathematically and in words:

$$\underbrace{\frac{\mathrm{d}C}{\mathrm{d}t}}_{\substack{\text{rate of change}\\\text{of consumer}}} = \underbrace{r_c\left(1-\frac{C}{\kappa_c}\right)C}_{\substack{\text{growth, intraspecific}\\\text{competition}\\\text{and cannibalism}}} \underbrace{-r_c\alpha_{PC}\frac{P}{\kappa_c}C}_{\substack{\text{interspecific}\\\text{competition}}} \underbrace{-Pp_{pc}(C)}_{\substack{\text{predation}\\\text{by predator}}} \underbrace{+\beta_{pc}Cp_{cp}(P)}_{\substack{\text{ingestion}\\\text{of predator}}} \tag{1}$$

$$\underbrace{\frac{\mathrm{d}P}{\mathrm{d}t}}_{\substack{\text{rate of change}\\\text{of predator}}} = \underbrace{r_p\left(1-\frac{P}{\kappa_p}\right)P}_{\substack{\text{growth, intraspecific}\\\text{competition}\\\text{and cannibalism}}} \underbrace{-r_p\alpha_{CP}\frac{C}{\kappa_p}P}_{\substack{\text{interspecific}\\\text{competition}}} \underbrace{-Cp_{cp}(P)}_{\substack{\text{predation}\\\text{by consumer}}} \underbrace{+\beta_{cp}Pp_{pc}(C)}_{\substack{\text{ingestion}\\\text{of consumer}}} \tag{2}$$

where $C(t)$ denotes the consumer population density, $P(t)$ denotes the predator population density, r_c is the consumer intrinsic growth rate, r_p is the predator intrinsic growth rate, κ_c is the consumer carrying capacity, κ_p is the predator carrying capacity, α_{PC} is the competition coefficient measuring the effect of predator on consumer, α_{CP} is the competition coefficient measuring the effect of consumer on predator, $p_{pc}(C)$ is the predation function of predator on consumer, $p_{cp}(P)$ is the predation function of consumer on predator, β_{pc} is the conversion efficiency from predator to consumer biomass, and β_{cp} is the conversion efficiency from consumer to predator biomass. The parameters for all the models in this study are summarised in Table 2.

The general structure of our model allows for flexibility and there is some choice over how to incorporate cannibalism and predation on both species. We discuss some alternatives here. Cannibalism (if it occurs) is included in the intraspecific competition terms. The functional form of the predation functions $p_{pc}(P)$ and $p_{cp}(C)$ as we discussed in Section 1 needs to be appropriately chosen.

We assume that the intraguild predator is the main predator in the interaction and that any predation by the consumer on the predator is limited (e.g. predation on eggs and recruitment interference by rusty crayfish on smallmouth bass, Dorn and Wojdak, 2004; cutthroat trout consumption of juvenile lake trout, Behnke, 1992; Ruzycki et al., 2003). Thus, we allow consumer predation on predator to be negligible at this point (i.e. $p_{pc}(P) \equiv 0$). This assumption can be relaxed in future. Mutual predation could also be incorporated, instead of explicitly including another function, by changing the competition coefficients (α_{PC} and α_{CP}) or the predator intrinsic growth rate (r_p). If we assumed Lotka–Volterra type predation by consumer on predator, then the modification would be to decrease α_{PC} and increase α_{CP}. Alternatively, recruitment interference (observed in many systems,

Table 2 Parameter definitions in Eqs. (1)–(6) and their units, where [predator] indicates predator density and [consumer] indicates consumer density

Symbol	Parameter definition	Units
r_c	Consumer intrinsic growth rate	$[\text{Consumers}][\text{consumer}]^{-1}[\text{time}]^{-1}$
r_p	Predator intrinsic growth rate	$[\text{Predators}][\text{predator}]^{-1}[\text{time}]^{-1}$
κ_c	Consumer carrying capacity	[Consumer density]
κ_p	Predator carrying capacity	[Predator density]
α_{PC}	Competition coefficient of predator on consumer	$[\text{Unit density}]^{-1}$
α_{CP}	Competition coefficient of consumer on predator	$[\text{Unit density}]^{-1}$
$p_{pc}(C)$	Predation function of predator on consumer	$[\text{Consumers}][\text{predator}]^{-1}[\text{time}]^{-1}$
$p_{cp}(P)$	Predation function of consumer on predator	$[\text{Predators}][\text{consumer}]^{-1}[\text{time}]^{-1}$
a_{pc}	Encounter rate or capture efficiency	$[\text{Consumers}][\text{consumer}]^{-1}[\text{time}]^{-1}[\text{predator}]^{-1}$
β_{pc}	Conversion efficiency from predator to consumer biomass	$[\text{Consumers}][\text{predator}]^{-1}$
β_{cp}	Conversion efficiency from consumer to predator biomass	$[\text{Predators}][\text{consumer}]^{-1}$
h_c	Prey handling time	$[\text{Time}][\text{consumer}]^{-1}[\text{predator}]$
$a_{pc}h_c$	$(\text{Half saturation constant})^{-1}$	$[\text{Consumer}]^{-1}$

Fritts and Rodda, 1998; Secord, 2003; Grosholz et al., 2000) could be modelled by decreasing r_p. The qualitative dynamics of the model will remain the same while the signs of the parameters α_{PC} and α_{CP} remain the same, because the structural form of the equations will not be changed.

For the predator predation on consumer, we use a Type II functional response (Holling, 1959) which is more realistic than Type I (e.g. Polis et al., 1989) as it incorporates predator satiation through the assumption that predators have a prey handling time. As we will show, the results with Type II differ from those with Type I, and the results are qualitatively different from previous work with the resource modelled explicitly (Mylius et al., 2001). Thus, the predation function for predator on consumer is given by

$$p_{pc}(C) = \frac{a_{pc}C}{1 + a_{pc}h_c C}, \tag{3}$$

where a_{pc} is the encounter rate (or capture efficiency), h_c is the handling time and $a_{pc}h_c$ is the reciprocal of the half-saturation constant.

Thus, the system of equations is

$$\frac{\mathrm{d}C}{\mathrm{d}t} = r_c\left(1 - \frac{C}{\kappa_c} - \alpha_{PC}\frac{P}{\kappa_c}\right)C - a_{pc}\frac{PC}{1 + a_{pc}h_c C}, \tag{4}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = r_p\left(1 - \frac{P}{\kappa_p} - \alpha_{CP}\frac{C}{\kappa_p}\right)P + \beta_{cp}a_{pc}\frac{PC}{1 + a_{pc}h_c C}, \tag{5}$$

noting that if we set $h_c = 0$ we return to a Type I predation functional response, which has been investigated in detail by Polis et al. (1989).

Harvesting or other predation on both consumer and predator (e.g. rainbow trout angling) is not included in this model, but modelling these approaches have been well documented elsewhere (e.g. Clark, 1985, 1990). Instead, we analyse the simplest form of the model, Eqs. (4) and (5).

To simplify the problem and find significant parameter combinations, we start by non-dimensionalising, taking

$$\begin{gathered} c = \frac{C}{\kappa_c}, \qquad p = \frac{P}{\kappa_p}, \qquad \tau = r_c t, \quad \alpha_{pc} = \alpha_{PC}\frac{\kappa_p}{\kappa_c}, \qquad a = a_{pc}\frac{\kappa_p}{r_c}, \\ h = a_{pc}h_c\kappa_c, \qquad r = \frac{r_p}{r_c}, \qquad \alpha_{cp} = \alpha_{CP}\frac{\kappa_c}{\kappa_p}, \qquad \beta = \beta_{cp}a_{pc}\frac{\kappa_c}{r_c}. \end{gathered} \tag{6}$$

The non-dimensional forms of Eqs. (4) and (5) become

$$\frac{\mathrm{d}c}{\mathrm{d}\tau} = f(c, p), \tag{7}$$

$$\frac{\mathrm{d}p}{\mathrm{d}\tau} = g(c, p), \tag{8}$$

where

$$f(c,p) = \left(1 - c - \left(\alpha_{pc} + \frac{a}{1+hc}\right)p\right)c, \tag{9}$$

$$g(c,p) = r\left(1 - p - \left(\alpha_{cp} - \frac{\beta/r}{1+hc}\right)c\right)p, \tag{10}$$

with the initial conditions

$$c(0) = c_0 \quad \text{and} \quad p(0) = p_0. \tag{11}$$

3.1. *Analysis*

In order to investigate the long-term behaviour of the system (7)–(8), we look for the (spatially homogeneous) steady states where neither, one or both species coexist. These are found by setting both (7) and (8) equal to zero. The nullclines of the system are given when $f = 0$ and $g = 0$ in (9) and (10). The c nullclines are:

$$c = 0, \tag{12}$$

$$p = \frac{1-c}{\alpha_{pc} + \frac{a}{1+hc}}, \tag{13}$$

and the p nullclines are:

$$p = 0, \tag{14}$$

$$p = 1 - c\left(\alpha_{cp} - \frac{\beta/r}{1+hc}\right). \tag{15}$$

From the intersections of the nullclines, we find the following trivial steady states: $(c,p) = (0,0), (1,0), (0,1)$. Linear stability analysis is carried out in the usual way (e.g. Jordan and Smith, 1988), and shows $(c,p) = (0,0)$ is always an unstable node (eigenvalues $\lambda = 1, r$), $(c,p) = (1,0)$ is a stable node if $\alpha_{cp} - \frac{\beta/r}{1+h} > 1$ or otherwise a saddle point (eigenvalues $\lambda = -1, r(1 - \alpha_{cp} + \frac{\beta/r}{1+h})$), and $(c,p) = (0,1)$ is a stable node if $\alpha_{pc} + a > 1$ or otherwise a saddle point (eigenvalues $\lambda = -r, 1 - \alpha_{pc} - a$).

The interior non-trivial steady states are found by setting (13) equal to (15), from which we obtain a cubic equation in c:

$$l(c) = 0,$$

$$l(c) \equiv l_3c^3 + l_2c^2 + l_1c + l_0, \tag{16}$$

where the polynomial coefficients are given in (A.1)–(A.4). We find there are at most two positive roots to (16), and these translate to either two, one or no interior

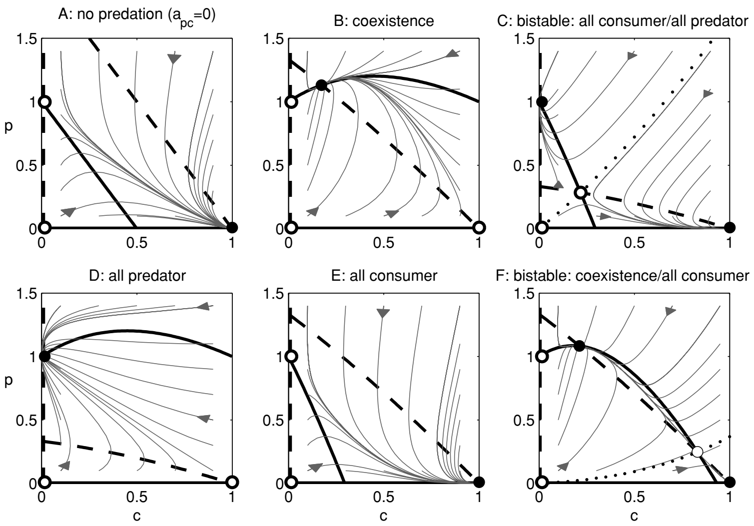

Fig. 2 Phase plane behaviour of system (7)–(10). Stable steady states are shown by *solid black dots*. Unstable steady states are shown by *open circles*. c nullclines are shown by *dashed lines* and p nullclines are shown by *solid lines*. Sample trajectories are shown by *thin grey lines*, with *arrows* indicating direction of flow. For panels C and F, there is a separatrix in the system which is denoted by a *dotted line* in each case. Different parameter values are used in each panel A–F (Table 3). Panel A shows example dynamics when predation is absent and the only interaction between consumer and predator is competition, with panels B–F presenting results for both competition and predation. The system of equations is solved using Matlab ode 45 (MathWorks Inc., 2004).

steady states depending on the intersections of the nullclines and the axes. The dynamics of the system can be grouped into five general structures (coexistence; all predator; all consumer; bistable: all consumer/all predator; and bistable: all consumer/coexistence). Example parameter sets with steady states, nullclines and trajectories are shown in Fig. 2.

Since in the absense of IGP, the consumer is the superior exploitative competitor we take $\alpha_{pc} < 1$ and $\alpha_{cp} > 1$ which describes this competitive hierarchy. Thus, in Fig. 2A, at equilibrium the consumer excludes the predator in the absense of predation ($a_{pc} = 0$). When predation is included in the system ($a_{pc} > 0$) there are five different scenarios depending on the parameter regime (see Table 3). In panel B, both species are able to coexist at equilibrium because the predation confers a benefit to the predator population ($\beta > 0$) but is not too detrimental to the consumer population (a small). In panel C, there are two alternative stable states, either predator exclusion of the consumer or consumer exclusion of the predator. In this scenario, the initial conditions determine which steady state the system will tend towards. The separatrix (dotted line) indicates the edges of the basin of attraction for each steady state. Biologically, this means predation considerably hinders the consumer population growth but does not confer much benefit on the predator population growth. In panel D, the predation allows the predator to increase in density, but the negative impact on the consumer is very high (a high). Thus, consumer is excluded by predator. If the predation has little effect on either

Table 3 Parameter values used in Fig. 2

	Panel					
	A	B	C	D	E	F
Parameter	(no predation) *c*	(coexistence) *cp*	(bistable) *cp* or *p*	(predator only) *p*	(consumer only) *c*	(bistable) *c* or *cp*
α_{pc}	0.50	0.50	0.50	0.50	0.50	0.50
a	0.00	0.25	2.50	2.50	0.25	0.25
h	0.00	0.50	0.50	0.50	0.50	0.45
r	1.00	1.00	1.00	1.00	1.00	1.00
α_{cp}	2.00	2.00	6.00	2.00	6.00	6.00
β	0.00	3.00	3.00	3.00	3.00	7.00

Each parameter set leads to qualitatively different outcomes.

species, then the consumer still excludes the predator (panel E). When the predation confers a benefit to the predator and the detrimental effect on the consumer is not too high, alternative stable states arise with either coexistence or the consumer excluding the predator (panel F). These alternative stable states are qualitatively different to patterns observed previously for IGP models (Polis et al., 1989; Holt and Polis, 1997; Mylius et al., 2001). We see bistability between coexistence and consumer excluding predator rather than bistability between coexistence and predator excluding consumer. The boundaries between these different scenarios can be determined analytically (as a function of the parameters). We discuss this further in Section 3.2.

The nonlinearity of the nullclines, due to the Type II functional response (i.e. when $h > 0$), allows for the possibility of multiple interior fixed points. Changes in the system behaviour can be determined by the intersections of the nullclines with the axes. However, the saddle-node that occurs when the dynamics change from the type shown in Fig. 2E and F can be determined as a function of parameters by using the method of resultants (Bôcher and Duval, 1938; Allgower and Georg, 1990). The bifurcation occurs when the nullclines (13) and (15) intersect and their gradients are equal. This leads to two polynomials in c, (16) and,

$$k(c) \equiv k_2c^2 + k_1c + k_0, \tag{17}$$

where coefficients of the polynomial are given in (A.5)–(A.7). A method for finding simultaneous zeros of two polynomials (16) and (17) is finding the resultant of k and l (that is to find the determinant of the Sylvester Matrix, $M(l, k)$), and setting this to zero (Allgower and Georg, 1990),

$$\det(M) = \operatorname{res}(l, k). \tag{18}$$

We highlight the use of this method here since it has received little attention in population dynamics (but see Hadeler and Lewis, 2002). The matrix M is given in (A.8). As an example, we can pick h as a bifurcation parameter and determine the value at which the bifurcation occurs, keeping all other parameters fixed (Fig. 3). Zeros of (18) are found numerically using Matlab fzero (MathWorks Inc., 2004).

3.2. *Invasibility criteria*

Since the problem we are studying is one of invasion, coexistence and exclusion, we can analytically determine the invasibility criteria for each species, that is whether a species can increase from low density in the presense of other species (*sensu* Chesson, 2000). Biologically, this gives us the conditions of the interaction parameters that allow each species to persist. We should note this is different to other measures of invasibility such as habitat characteristics (see, for example, Jules et al., 2002). Analytically, the invasibility criteria can be determined by finding the criteria for the population to increase at low density while the other species is at the carrying capacity, i.e. (for the dimensionless system) $\frac{\mathrm{d}c}{\mathrm{d}\tau}|_{p=1} > 0$ and $\frac{\mathrm{d}p}{\mathrm{d}\tau}|_{c=1} > 0$

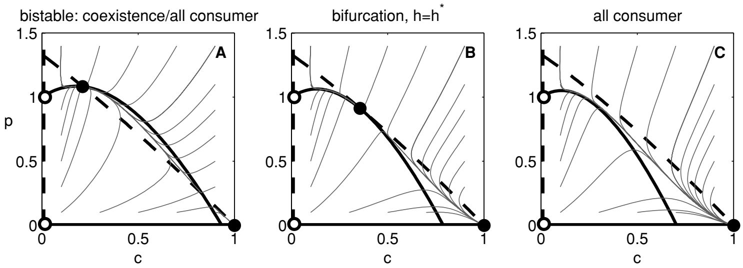

Fig. 3 Phase plane behaviour of system (7)–(10). Stable steady states are shown by *solid black markers*. Unstable steady states are shown by *open circles*. c nullclines are shown by *dashed lines* and p nullclines are shown by *solid lines*. Example trajectories are shown by *thin grey lines*. In each panel, all parameters are fixed apart from h. $(\alpha_{pc}, a, r, \alpha_{cp}, \beta) = (0.50, 0.25, 1.00, 6.00, 7.00)$. $h = 0.45, 0.6077, 0.75$ in panels A, B, and C, respectively. As h increases from zero, the dynamics change from a bistable case to consumer excluding predator. The bifurcation occurs when $h = h^* = 0.6077$.

in (7)–(10). The conditions for persistence of the consumer are

$$\alpha_{pc} + a < 1, \tag{19}$$

and for the predator,

$$\alpha_{cp} - \frac{\beta/r}{1+h} < 1, \tag{20}$$

which are exactly the reverse of the conditions for the stability of the single species steady states $(c, p) = (0, 1)$ and $(c, p) = (1, 0)$, respectively, found above. These invasibility criteria can be interpreted as being comprised of two components, one related to the competitive interaction (α_{pc} and α_{cp} terms) and another to the predation interaction (a and $-\frac{\beta/r}{1+h}$ terms). The predation contribution in the predator criterion is negative due to the benefit the predator gains from predation, while other components in both equations are positive indicating a loss due to predation (by the predator) or competition (by the other species).

Based on these criteria, coexistence is possible if both (19) and (20) hold (Fig. 2B); the predator excludes the consumer if only (20) holds (Fig. 2D); the system is bistable if neither (19) nor (20) holds (Fig. 2C), then the dominant species depends on initial conditions (founder control, Keddy and Shipley, 1989). There are two alternatives when only (19) holds (Fig. 2E and F). If

$$\frac{\beta}{r} < \alpha_{cp} \tag{21}$$

also holds, then the gradient of the p nullcline (15) at $c = 0$ is negative and there can be no interior fixed points. Again, there is a contribution from competition and predation in the inequality. Ecologically, the inequality states that the impact of consumer competition on the predator is greater than the benefit the predator receives from predation on the consumer. In this circumstance, the only steady state is the consumer excluding the predator (Fig. 2E). If only (19) holds, but neither (21) nor (20) holds then the method of resultants (18) can be used to determine if the dynamics are of the type in Fig. 2E or F. In F, the system is bistable with the coexistence steady state and consumer exclusion of the predator both being stable.

3.3. Biological interpretation of the spatially homogeneous model

The system of two ordinary differential Eqs. (4) and (5) can lead to a variety of different dynamics which depend on the particular parameter regime of the system of interest (Fig. 2). Due to data limitations, it may be difficult to determine many of these parameter values, but by rescaling the system (6), we reduced the number of parameters from 9 (Eqs. (4) and (5)) to 6 (Eqs. (7)–(10)), which simplifies the analysis.

Pest management options can be divided into two mathematical classes: altering the parameter values of the system (for example, reducing the intrinsic growth rate of one species); or perturbing the system, by adding or removing individuals, to move the system to a new initial condition from where it may follow a different trajectory. The former approach may be difficult in practice, since to shift the system from one type of dynamics to another may require considerable effort to manipulate a parameter value, and perhaps only be possible temporarily. For example, decreasing α_{cp} could change the dynamics from Type E to Type B in Fig. 2, that is from the consumer-only state being stable to the coexistence state being stable, thus allowing both predator and consumer to persist. However, the temporary nature of the parameter change may allow the coexistence state to lose stability and the dynamics to return to the original undesirable state.

The latter approach, to apply a perturbation to the population densities, may allow the system to follow a trajectory to a different steady state. This would only occur in a bistable case (Fig. 2C and F), where a perturbation would be required to move the system to the other side of the separatrix and into the basin of attraction of a different fixed point. For example, if the system were in parameter regime C, approaching consumer dominance, say $(c, p) = (0.5, 0.2)$, then increasing the non-dimensional density of predator to $p = 0.6$ would move the system across the separatrix and towards the predator monoculture state. Ecologically, the perturbation is a fixed, one-time change to the ecosystem, which may produce long-term desirable dynamics. This would not be possible in Types B, D and E (Fig. 2).

We need to consider desirable outcomes of a control effort depending on identity of the interacting consumer and predator. In the examples of pest control in Section 1, all predators are beneficial species, while the prey are pest species. This is also the case in the invasive species interactions of smallmouth bass (predator) and rusty crayfish (prey), *Beroe ovata* (predator) and *Mnemiopsis leidyi* (prey), predaceaous mites (predator) and herbivorous mites (prey) on lantana and birds (predator) and brown anole. In these scenarios, the objective of a control operation would be to reduce consumer density while increasing predator density. Possible perturbations for an aquatic invader include trapping (Hein, 2004; Hein et al., 2006) and trawling (D. Lodge et al., personal communication), trapping for a terrestrial invader (Engeman et al., 2003) and also for intertidal invaders (Miller and Addison, 1995; Grosholz et al., 2000).

Alternative examples where the predator is an invasive species and the consumer is native have been given in Section 1 and Table 1, such as lake trout and cutthroat trout, rainbow trout and native fish, brown tree snake and mangrove monitor, and European green crab and shore crabs. In these scenarios, the objective of a management initiative would be to reduce the predator density. Possible perturbations for sporting fish invaders include changing fishing regulations, and including catch-and-release, length limits and daily harvest limits (Noble and Jones, 1999; Noble, 2002).

The analytical and numerical results in this section have relied on the assumption that the consumer and predator are ubiquitous throughout the landscape. The length scale of movements for each species might in practice be very different. For example, predaceous mites move much faster and turn more quickly than herbivorous mites and only stop to feed (Hoffmann and Frodsham, 1993). Lake trout are much more aggressive and territorial than cutthroat trout (Behnke, 1992; Crossman, 1995) and are only found in one bay in Yellowstone Lake, while cutthroat trout are found throughout (Ruzycki et al., 2003). Crayfish are observed to move large distances daily (Momot and Gowing, 1972; Kershner and Lodge, 1995), while bass are territorial (Carlander, 1977; Suski and Philipp, 2004).

In the next section, we will consider two case studies of aquatic invaders: lake trout invasion in Yellowstone Lake and rusty crayfish in Sparkling Lake (Hein et al., 2006; Roth et al., 2006). We relax the assumption that there is a uniform density of individuals, in other words, we consider the biologically realistic scenario of mobile predators and consumers and develop a spatially explicit model.

4. Spatial intraguild predation model

We use a reaction–diffusion type model to describe the spatio-temporal dynamics of the populations of predator and consumer. Each species has both population dynamics and diffusion throughout the domain. We use one spatial dimension to model the narrow littoral zone around a large lake. The littoral zone is the region where cutthroat trout and lake trout (Behnke, 1992) and crayfish and bass (Momot, 1992) are likely to interact. The spatial extension of Eqs. (4) and (5) is the following system of partial differential equations:

$$\underbrace{\frac{\partial C}{\partial t}}_{\substack{\text{rate of change}\\ \text{of consumer}}} = \underbrace{r_c\left(1 - \frac{C}{\kappa_c} - \alpha_{PC}\frac{P}{\kappa_c}\right)C}_{\substack{\text{growth, competition}\\ \text{and cannibalism}}} \underbrace{-a_{pc}\frac{PC}{1 + a_{pc}h_c C}}_{\text{predation}} \underbrace{+D_c\frac{\partial^2 C}{\partial x^2}}_{\substack{\text{diffusion}\\ \text{of consumer}}} \tag{22}$$

$$\underbrace{\frac{\partial P}{\partial t}}_{\substack{\text{rate of change}\\ \text{of predator}}} = \underbrace{r_p\left(1-\frac{P}{\kappa_p}-\alpha_{CP}\frac{C}{\kappa_p}\right)P}_{\substack{\text{growth, competition}\\ \text{and cannibalism}}} \underbrace{+\beta_{cp}a_{pc}\frac{PC}{1+a_{pc}h_cC}}_{\substack{\text{ingestion}\\ \text{of consumer}}} \underbrace{+D_p\frac{\partial^2 C}{\partial x^2}}_{\substack{\text{diffusion}\\ \text{of predator}}} \tag{23}$$

where D_c is the diffusion coefficient of the consumer and D_p is the diffusion coefficient of the predator. We non-dimensionalise using (6) and

$$\xi = \sqrt{\frac{r_c}{D_c}}x, \qquad \epsilon = \frac{D_p}{D_c}, \tag{24}$$

leading us to the non-dimensional system,

$$\frac{\partial c}{\partial \tau} = \left(1-c-\left(\alpha_{pc}+\frac{a}{1+hc}\right)b\right)c+\frac{\partial^2 c}{\partial \xi^2}, \tag{25}$$

$$\frac{\partial p}{\partial \tau} = r\left(1-b-\left(\alpha_{cp}-\frac{\beta/r}{1+hc}\right)c\right)b+\epsilon\frac{\partial^2 p}{\partial \xi^2}. \tag{26}$$

The analysis of the system of ordinary differential equations in Section 3 gives us the spatially uniform behaviour of the system including spatially uniform steady-state solutions. In the parameter regime where we observe dynamics of the type shown in Fig. 2F, there are two spatially homogeneous stable steady states, one with the consumer excluding the predator, and one where both species coexist with the predator at a high density and the consumer at a low density. As we discussed in the non-spatial model (Section 3.3) in a bistable system, perturbing the population densities may move the system across a separatrix and into the basin of attraction of an alternative stable steady state. Once space is included explicitly, an alternative management method for control is to perturb the system in a local, bounded region (practically this is a small, contained area) and cause the dynamics to switch from one steady state to another by the population reproducing and spreading out across the domain. Since we have a bistable system, we look for travelling wave solutions joining the two spatially homogeneous steady states, consumer only and coexistence.

4.1. Analysis

Travelling wave solutions to Eqs. (25) and (26) can be expressed in terms of the travelling wave coordinate, $z = \xi - v\tau$, where $c(\xi, \tau) = c(z)$ and $p(\xi, \tau) = p(z)$. We consider solutions that join the consumer-only steady state $[(c, p) = (1, 0)$ as $z \to -\infty]$ with the coexistence steady state $[(c, p) = (c_1, p_1)$ as $z \to \infty]$. When the wave velocity is positive ($v > 0$), the wave moves to the right and there is an outbreak of consumer excluding the predator. While when the wave velocity is negative ($v < 0$), the wave moves to the left and coexistence is observed.

Rewriting the system (25) and (26) in travelling wave coordinates (by substituting $z = \xi - v\tau$) and applying boundary conditions (shown in Fig. 4A), the travelling wave solutions satisfy

$$c_{zz} + vc_z + f(c, p) = 0, \tag{27}$$

$$\epsilon p_{zz} + vp_z + g(c, p) = 0, \tag{28}$$

$$\lim_{z\to-\infty}(c(z), p(z)) = (1, 0), \qquad \lim_{z\to\infty}(c(z), p(z)) = (c_1, p_1). \tag{29}$$

The scalar case ($p =$ constant) is well understood (Fife and McLeod, 1975, 1977). In this case, we conjecture there exists a solution to (27)–(29) with corresponding wave velocity v. This is supplemented by a numerical investigation. The direction of the travelling wave, or the sign of v, can be determined as a function of the parameter values of the system (in a similar fashion to determining the bifurcation using the method of resultants above, Section 3.1). We use the approach of Lewis and van den Driessche (1993) to determine the point at which the wave changes direction (when v changes sign) as a function of the system parameters. Bass are territorial (Suski and Philipp, 2004) as are lake trout (Carlander, 1977) and move much shorter distances than do their intraguild prey crayfish (Momot and Gowing, 1972; Kershner and Lodge, 1995) and cutthroat trout (Behnke, 1992), respectively. Hence, the ratio of the diffusion coefficients, ϵ is small. We set $v = 0$ and in the limit $\epsilon \to 0$, Eqs. (27) and (28) become

$$c_{zz} + f(c, p) = 0, \tag{30}$$

$$g(c, p) = 0. \tag{31}$$

From (31), p can be expressed as an algebraic function of c which we substitute into (30). This leads to an ordinary differential equation in c only:

$$c_{zz} + f(c, p(c)) = 0. \tag{32}$$

Using standard travelling wave techniques (e.g Kot, 2001; Murray, 2003), multiplying (32) by c_z, integrating over the range $-\infty < z < \infty$, and applying boundary conditions (29), we obtain

$$\int_1^{c_1} f(c, p(c))\,\mathrm{d}c = 0. \tag{33}$$

From (31) we find that

$$p = \begin{cases} 0, & \text{for } c > c_3, \\ 1 - \left(\alpha_{cp} - \frac{(\beta/r)}{1+hc}\right) \equiv g_1(c), & \text{for } c \le c_3, \end{cases} \tag{34}$$

which is analogous to the p nullclines (14)–(15) obtained in the spatially independent model above. Substituting the expressions for p into (33), we obtain

$$\int_1^{c_3} f(c,0)\,\mathrm{d}c + \int_{c_3}^{c_1} f(c,g_1(c))\,\mathrm{d}c = 0, \tag{35}$$

where the integral endpoints are defined graphically in Fig. 4A. Evaluating (35), we obtain

$$\int_1^{c_3} c(1-c)\,\mathrm{d}c + \int_{c_3}^{c_1} c\left[1-c-\left(\alpha_{pc}+\frac{a}{1+hc}\right)\left(1-\left(\alpha_{cp}-\frac{\beta/r}{1+hc}\right)c\right)\right]\mathrm{d}c = 0, \tag{36}$$

for which we can find an explicit expression in terms of the integral endpoints, c_1 and c_3,

$$\begin{aligned} 0 = {} & \left[-\frac{c^3}{3}+\frac{c^2}{2}\right]_1^{c_3} + \left[(\alpha_{pc}\alpha_{cp}-1)\frac{c^3}{3}+\left(\frac{a\alpha_{cp}}{h}-\frac{\alpha_{pc}\beta}{rh}+1-\alpha_{pc}\right)\frac{c^2}{2}\right]_{c_3}^{c_1} \\ & + \left[\left(\frac{\alpha_{pc}\beta}{r}-a\alpha_{cp}-\frac{a\beta}{r}-ah\right)\frac{c}{h^2}+\frac{a\beta}{rh^3(1+hc)}\right]_{c_3}^{c_1} \\ & + \left[\left(\frac{a}{h^2}-\frac{\alpha_{pc}\beta}{rh^3}+\frac{a\alpha_{cp}}{h^3}+\frac{2a\beta}{rh^3}\right)\log(1+hc)\right]_{c_3}^{c_1}, \end{aligned} \tag{37}$$

where c_1 is the smallest positive root of (16) and c_3 is found by setting (15) to 0:

$$0 = h\alpha_{cp}c^2 + c\left(\alpha_{cp}-h-\frac{\beta}{r}\right)-1, \tag{38}$$

and taking the positive root as c_3. Equation (37) must be satisfied by the parameters α_{pc}, a, h, r, α_{cp} and β.

4.2. Numerical solutions

If all but one of the system parameters are fixed, say h, then we can find a critical value of $h = h_0$ which leads to a stationary wave ($v = 0$), in the absense of predator diffusion. We compute numerical solutions of (37) with (38) and (16), using Matlab fzero to iteratively define an estimate for h to find h_0. There is also a critical value for $h = h^{\mathrm{c}}$ determined from (20) for which the consumer monoculture state disappears and the coexistence state is the only stable steady state. For the parameter set $(\alpha_{pc}, a, r, \alpha_{cp}, \beta) = (0.50, 0.25, 1.00, 6.00, 7.00)$, then $h_0 = 0.4845$ and $h^{\mathrm{c}} = 0.4$.

Numerical solutions of the full PDE system (25)–(26) result in a stationary wave profile for $h_0 = 0.4845$ as predicted by the travelling wave and stationary wave

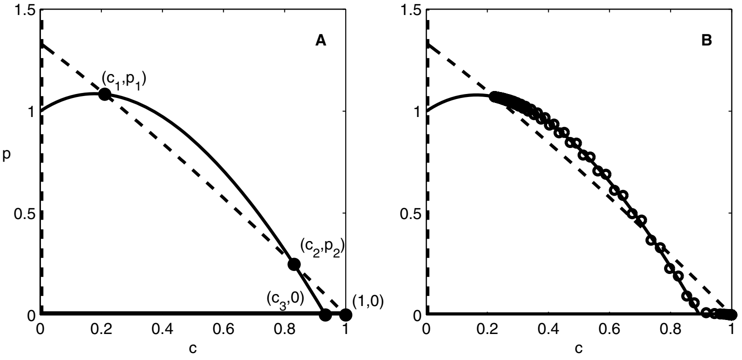

Fig. 4 In both panels c nullclines are shown by *dashed lines* and p nullclines are shown by *solid lines*. (A) The spatially homogeneous steady states and integral endpoints (c_i, p_i) are defined for Eqs. (29) and (34)–(37). The intersections of the nullclines are labelled. Parameter values used for the sketch are as follows: $(\alpha_{pc}, a, h, r, \alpha_{cp}, \beta) = (0.50, 0.25, 0.45, 1.00, 6.00, 7.00)$. (B) Numerical solutions of the system of PDEs (25)–(26) using Matlab pdepe. Stationary wave profile ($v = 0$) after 1000 time intervals plotted in the phase plane (*circles*). Travelling wave solutions join (c_1, p_1) to $(1, 0)$, see panel A for definitions. Initial conditions are as for Fig. 5. Parameter values used are $(\alpha_{pc}, a, h, r, \alpha_{cp}, \beta) = (0.50, 0.25, 0.4845, 1.00, 6.00, 7.00)$ and $\epsilon = 1 \times 10^{-8}$. We can see that the travelling wave profile closely follows the p nullclines.

analysis. Numerical results are presented in Fig. 5. In each case, the distribution of each species is shown across the domain for every 100 time intervals. In Fig. 5A and B, the numerical solutions for the stationary wave are shown. In this case, the wave profile remains the same and in the same ξ location for each time point, since solutions at subsequent time points are exactly overlain. In Fig. 5C and D, where $h > h_0$, a rightward moving wave is observed. The wave profile is fixed and moving at constant speed. As the wave moves, areas of low consumer density are replaced by areas of high consumer density, while areas of high predator density are replaced by areas of low predator density. In panels E and F, $h < h_0$, a leftward moving wave is observed. In this case, as the wave moves, the predator is able to control the consumer population and the predator excluded area is replaced by a coexistence zone.

If these results were applied to Yellowstone Lake, a rightward moving wave would be helpful in displacing lake trout by cutthroat trout. One possible method for implementation would be trapping for lake trout (Ruzycki et al., 2003). For Sparkling Lake, a leftward moving wave would be beneficial, allowing bass to control the crayfish. A potential implementation method could be trawling for crayfish in a local area (D. Lodge et al., personal communication). In each of these scenarios careful parameterisation would need to be carried out to determine the relative magnitude of the wave speed in relation to the lifespan of individuals from both populations. The wave of control would need to spread throughout the arena within a small number of generations to be of use from a management perspective.

We noted above, under the conditions that we obtain a stationary wave ($v = 0$) and the predator moves much smaller distances than does the consumer, we could

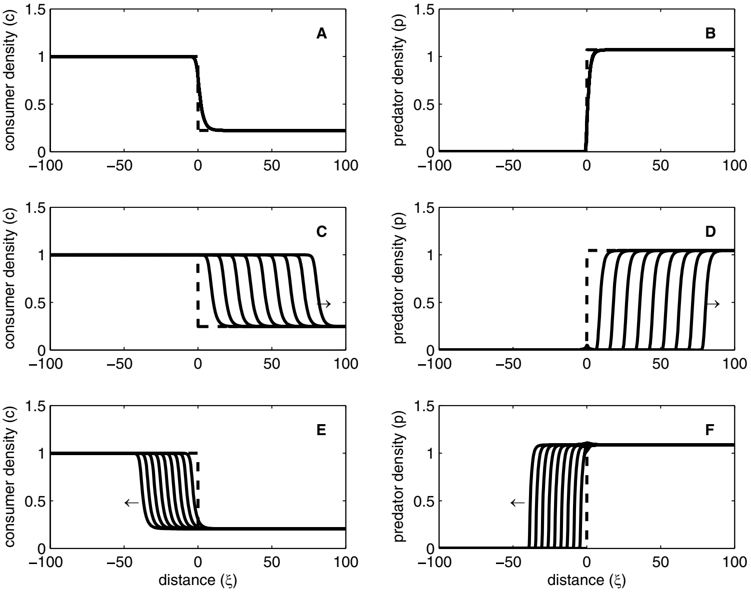

Fig. 5 Numerical solutions of the system of PDEs (25)–(26) using Matlab pdepe. *Left-hand* panels show the consumer population density, while *right-hand* panels show the predator population density over space. Travelling wave solutions join (c_1, p_1) to $(1, 0)$, see Fig. 4A. Initial conditions are indicated by the *dashed lines*, with solutions at time intervals of size 100. Parameter values used in all panels are $(\alpha_{pc}, a, r, \alpha_{cp}, \beta) = (0.50, 0.25, 1.00, 6.00, 7.00)$ and $\epsilon = 1 \times 10^{-8}$. (A and B) Stationary wave, $h = h_0 = 0.4845$. (C and D) Right moving wave, $v > 0$, there is a wave of extinction of predator, $h = h_0 + 0.05$. (E and F) Left moving wave, $v < 0$, there is a wave of control of consumer by predator, $h = h_0 - 0.05$.

find an algebraic expression for $p(c)$ (34) that matched the expressions for the p nullclines (14)–(15). We see that plotting the travelling wave front in the phase plane closely matches the nullclines (Fig. 4B).

We have already considered h as a bifurcation parameter in the non-spatial and the spatial frameworks. It is an important parameter. If $h = 0$ we return to a Type I predation functional response. As h increases from zero, the predation functional response changes from Type I to Type II and the possibility of bistability and interior steady states arises. Many of the parameters are likely to be fixed in a given system, but we may have some control over the intrinsic population growth rates (such as by stocking fish or trapping crayfish), and since $r = \frac{r_p}{r_c}$ is the ratio of growth rates, we choose this as a second bifurcation parameter (note that when $r = 1$ both population intrinsic growth rates are the same). Thus, we investigated the parameter space (h, r) keeping all other parameters fixed (Fig. 6). This figure shows the limits of the regions of existence of each stable steady state. The curve *SN* indicates the saddle–node bifurcation, found by solving Eq. (18). Above this line the consumer excludes the predator, while below this line, there are alternative stable states (coexistence or consumer only). The line *SW* indicates the parameter combination for the stationary wave, calculated from (37). Above this line, in the

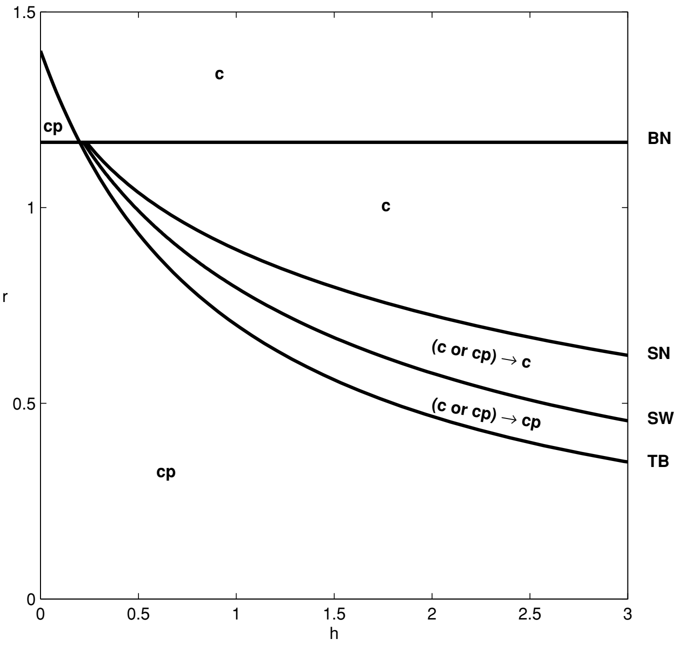

Fig. 6 Bifurcation diagram showing critical parameters values for the stationary wave (line *SW*), the line *TB* identifies the transcritical bifurcation where the consumer-only state loses stability and the system moves from dynamics of Type F (bistable: coexistence or consumer only) to Type B (coexistence) and the saddle–node bifurcation, depicted by the line *SN*, where the system dynamics move from Type F (bistable: coexistence or consumer only) to Type E (consumer only). The parameter space is divided into regions where different dynamics occur. Regions denoted by *cp* indicate dynamics of Type B (coexistence stable spatially homogeneous steady state), *c* indicates Type E (consumer only) and *c or cp* indicates Type F (bistable: coexistence or all consumer). In the spatial framework (*c or cp*) → *cp* indicates a travelling wave of coexistence, while (*c or cp*) → *c* indicates a travelling wave of consumer excluding predator. The line *BN* represents the neutrality of the condition (21), above which the interior steady states are no longer possible. Fixed parameter values used are $(\alpha_{pc}, a, \alpha_{cp}, \beta) = (0.50, 0.25, 6.00, 7.00)$.

spatial framework, a local perturbation will lead to consumer dominance, while below this line, a local perturbation will lead to coexistence. The line *TB* indicates the neutrality of Eq. (20). Above this the spatially homogeneous model gives rise to bistability (coexistence or consumer only), while below the line, coexistence is the only stable state. Finally, the neutrality of Eq. (21) is shown by the line *BN* above which bistability is not possible. From the results, we can see that considering the spatial framework has increased the area of parameter space where coexistence is likely (areas indicated by *cp* and (*c or cp*) → *cp*) over the area we would have determined from the non-spatial case alone (areas indicated by *cp*).

4.3. Biological interpretation of the spatially explicit model

There are different control strategies for removing aquatic invaders from problematic lakes. Methods often used are high effort trawling in a small area (D. Lodge, personal communication) or trapping over a large expanse (Ruzycki et al., 2003; Hein et al., 2006) resulting in the removal of a similar number of individuals in both cases. High impact trapping has also been used for lake trout (Ruzycki et al., 2003). We can include both types of removal in our spatial model framework. Mathematically, trawling removes a high density in a local area. Trapping, on the other hand, involves placing baited traps throughout the lake and collecting the catch at a later date. A local perturbation can be interpreted as trawling, while a lake-wide perturbation can be interpreted as trapping.

We present numerical simulations for different scenarios in a model lake with very low predator population density and high consumer density (a caricature of the situation in Sparkling Lake with crayfish and bass). Since the consumer is the pest here, the goal is to reverse the situation. Assuming we have a limited fixed quotum for invasive species removal, we can compare the trapping and trawling methods by keeping the volume of consumer removed equal in both cases. Results are shown in Fig. 7. In panels A and B, the consumer density is reduced over a small spatial range, while the density of the predator is assumed to be low but uniform throughout the lake. In the parameter regime $(c \text{ or } cp) \to cp$, this perturbation is sufficient to cause a wave of coexistence to move throughout the lake where the predator is able to control the consumer. In panels C and D, the consumer numbers are reduced by the same total amount, but uniformly throughout the lake. This perturbation is insufficient to initiate a wave and the system rapidly returns to the state prior to perturbation (the result every 100 time units is plotted, but they are all superimposed since they correspond to the spatially homogeneous consumer monoculture state).

We should also note that if the parameter set was in the region $(c \text{ or } cp) \to c$ in Fig. 6, then perturbing the system would cause a wave of the consumer excluding the predator which would be more useful when the predator is the pest, as for Yellowstone Lake lake trout and cutthroat trout dynamics (as we saw in Fig. 5).

From the results presented in Fig. 7, we can see that it is better to focus population reduction efforts on small local area (by trawling or possibly a high effort trapping locally) rather than spreading the effort over a large area. The effort spread out across the lake does not cause enough disturbance and is insufficient to initiate a travelling wave of coexistence, so the pest consumer excludes the predator (Fig. 7B). Where the removal of the consumer was carried out at a high intensity, but locally, the perturbation was sufficient to initiate a travelling wave of coexistence allowing the predator to control the consumer. The minimum size of the local removal zone is related to the quantity $\sqrt{D_c/r_c}$ in Eqs. (22)–(24) and has been considered for a two-dimensional problem (Lewis and Kareiva, 1993).

4.4. *Range expansion of exotic species*

When considering biological control of a nuisance species, the arena of interaction may be contained, within a lake, or an orchard, for example. Then, under this restriction, a spatially independent model may be appropriate. However, when considering the range expansion of exotic species a spatially explicit framework is required because the distribution of the species are not homogeneous throughout

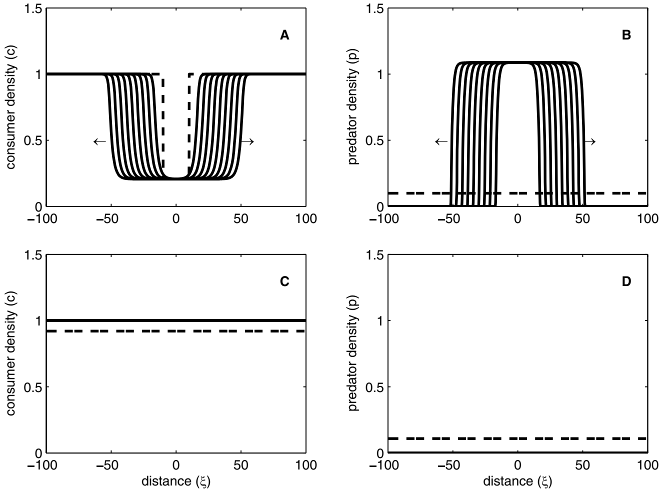

Fig. 7 Comparison of local versus lake-wide removal of a pest consumer. *Left-hand* panels show the consumer population density, while *right-hand* panels show the predator population density over space. Travelling wave solutions join (c_1, p_1) to $(1, 0)$, see Fig. 4A. Initial conditions are indicated by *dashed lines*, with solutions at time intervals of size 100. Parameter values used in all panels are $(\alpha_{pc}, a, h, r, \alpha_{cp}, \beta) = (0.50, 0.25, 0.43, 1.00, 6.00, 7.00)$ and $\epsilon = 1 \times 10^{-8}$. (A and B) Consumer removed by trawling in local area around $x \in [-10, 10]$. (C and D) Consumer removed by trapping uniformly around the lake. Predator are initially at a low uniform density ($p_0(x) = 0.1$) throughout the lake for both simulations. A wave of control is initiated by a local removal, while a similar effort lake-wide removal is insufficient to initiate control. Numerical solutions of (25)–(26) obtained using Matlab pdepe.

the landscape. The invader density is likely to be high behind a wave of expansion while the native competitor density will be higher in uninvaded areas. The spatial IGP model developed in this section can also be applied to help understand a species range expansion and the interaction with local species.

Examples of IGP for species undergoing range expansion are round gobies, raccoons, salamanders, amphipods, European green crabs (Grosholz and Ruiz, 1995) and daphnids (Table 1). Further examples of species undergoing range expansion can be found in Table 1.

As we have shown in previous sections, the consequences of IGP are often alternative stable states, which have implications in the management and control of invading species.

5. Discussion

In this paper, we have developed a dynamic model to describe the interactions between an intraguild predator and consumer. The predator and consumer compete for resources under exploitative competition, but the predator also consumes or kills the consumer. Coupling these interactions together, we derived a nonlinear ordinary differential equation model for IGP. We presented many examples in agricultural pest management, in the interactions between invasive and native species across a wide taxonomic range and species undergoing range expansion (Section 1, Table 1).

The ODE system describes a spatially homogeneous population. We used linear stability and phase plane analysis to determine stable states and under what conditions they occur. When the feeding efficiency (numerical response) of the predator on the consumer is high, but the effect on the consumer (functional response) is weak, coexistence is observed. If the predator is very efficient and predation greatly hinders the consumer population growth, then the predator is able to exclude the consumer. In the situation where the consumer population incurs a small predation effect, but the predator feeding efficiency is low, the consumer is able to exclude the predator. This is equivalent to the results without predation (i.e. competition only). Alternative stable states arise in two sets of circumstances. When the predator is a very inefficient feeder but the effect on the consumer is very detrimental, then single species predator or consumer monopolies arise (depending on the initial conditions). When the predator gains from predation on the consumer, but does not reduce the population growth of the consumer too much, bistability is also observed with coexistence or consumer excluding predator. This is qualitatively different to the bistability observed in previous models (Polis et al., 1989; Holt and Polis, 1997; Mylius et al., 2001).

We were able to find analytical expressions which determine the boundaries in parameter space of all these different system behaviours using the method of resultants (Bôcher and Duval, 1938; Allgower and Georg, 1990) which we highlighted as a little-used but useful method in population dynamics modelling.

Often, for example, in agricultural pest control, the objective is to for the predator to control the consumer, but in other examples (for invasive species) the predator may be the exotic (see examples in Table 1), in which case we would look to conditions for the consumer to exclude the predator. The stable states analysis provides us with a framework for determining the best course of action depending on the parameter regime of the particular system. Management options were divided into two categories, either an ongoing removal which would lead to the reduction of either or both species intrinsic growth rate (r_c and r_p) or a single event perturbation to the lake (e.g. trawling) which would remove a large density of consumer (or predator) at one time which has the potential to move the system into the basin of attraction of an alternative stable state (e.g. from the consumer excluding predator state to the coexistence state). The cost associated with different manipulations varies. In our model framework, the resource was not modelled explicitly. The impact of a one-time perturbation might be different under alternative modelling assumptions and model structure. Further work would need to be carried out to determine if there are any delayed density-dependent effects.

We then relaxed assumption U4 of population mixing and extended the framework to include spatial dynamics and focussed on within-lake dynamics of aquatic invaders. We considered the situation where alternative stable states arise (coexistence and consumer excluding predator). Travelling wave analysis determined the conditions for a forward moving wave (the coexistence state replacing the predator exclusion state) or wave reversal. We found that for certain parameter regimes, a lake-wide perturbation is not necessary, but a local removal of the consumer can be sufficient to cause a wave of coexistence throughout the lake or a wave of predator exclusion by consumer. The spatial analysis suggests more effective control measures than does the non-spatial case. Local removal may require less effort than an ongoing lake-wide removal (Hein et al., 2006). From our numerical experiments, the consumer population density remains low after trawling a small area (Fig. 7) and the wave of coexistence observed is due to the predator responding to the release from competition locally and then increasing in density to control the consumer. However, if the predator response is on a slow timescale, then practically, it might be necessary to maintain an area without the consumer (an exclusion zone) while the wave of coexistence is initiated. To find the analytical conditions for a forward or backward moving wave, we assumed the consumer moved much greater distances than the does the predator. Relaxing this assumption would make the analysis more complicated, but should not affect the outcome. The possibility of pattern formation (through long-range inhibition and short-range activation, e.g. Murray, 2003) has not been investigated. This a direction of further study.

The modelling approach utilised in this paper was based on a number of assumptions (Section 2). The assumption that all individuals of each species are identical (U1) is a simplification. Different size classes of each species exhibit different characteristics. Many species, especially fish, undergo ontogenetic niche shifts (Werner and Gilliam, 1984), allowing the juveniles to compete with the prey of adults. A two-size compartment structure has been considered for another model system, but the juvenile class reduces the predation effect on the consumer, and thus extends the parameter regime where coexistence is observed (Mylius et al., 2001). The largest consumers may escape predation because predator consumption of the consumer is gape limited (Persson et al., 1996), and many predators consume food in a particular size range depending on their body size (Polis et al., 1989, and references therein). A size-structured model including a class of consumer invulnerable to predation has been investigated (Mylius et al., 2001). The extra class reduces the overall risk of predation on the consumer population and extends the region of parameter space where coexistence is observed. Harvesting may preferentially remove individuals of a certain size (e.g. Suski and Philipp, 2004). A size-structured model would be appropriate to investigate this effect. Investigating a competitive bottleneck (where juvenile predators are prevented from maturing by competition) that may be facing juvenile predators would also require a similar model.

The environment was assumed to be constant throughout (U2). However, this is a simplification as there are likely to be patches of different habitat types, for example, agricultural rows, forest and urban patches, and aquatic habitats. Each habitat type confers a different food and shelter level (and thus a different predation risk). The relative contribution of each habitat type to the overall environment is likely to play a factor in the possible control of a nuisance species. These spatial heterogeneities could be incorporated into the model framework in a variety of ways including modifying the spatially explicit system of partial differential equations (Section 4) to require the intrinsic growth, predation rates and diffusion coefficients to be a function of habitat, or building a compartment model (each compartment representing a different habitat type) with differential growth and predation rates in each compartment.

Many systems, especially temperate ones, exhibit seasonal population dynamics and the assumption that populations reproduce continuously over time (U3) may not be valid. This is likely to have a smaller effect on the model outcome than population size-structure or the heterogeneous environment.

For invasive species, the effect of harvesting the biological control agent (either predator or consumer) has not been investigated. To include natural mortality, angling or harvesting mortality in the populations, we could modify Eqs. (4) and (5) by adding a mortality function. Two simple ways of including this are a proportional reduction of the population, or a constant reduction per unit time. Alternative harvesting strategies for aquatic systems are well documented (e.g. Clark, 1985, 1990).

We have only considered the interaction between one predator species and one consumer species. When IGP occurs across multiple trophic levels the outcomes can be unexpected. Many natural enemies of agricultural pests interact through IGP, such as *Georcoris* spp. and *Orius* spp. consuming spider mites on cotton (Rosenheim, 2005). Further examples are found in the literature (Rosenheim et al., 1999, 1993, 2004; Colfer et al., 2003). In many examples, the higher predator is a generalist and will consume both the intermediate predator and the consumer. The result for biological control may be the reduction of the intermediate predator (see also Fagan, 1997), while the pest species population increases. Further consideration of multiple species and trophic levels in the model framework are required to investigate this problem.

Our model differs in three important ways from previous approaches. Firstly, the resource is not modelled explicitly (for examples of models where the resource is explicitly considered, see Holt and Polis, 1997; Diehl and Feißel, 2000; Mylius et al., 2001; Diehl, 2003). This enhances the analytical tractability of the system. We are also able to interpret the invasibility criteria and the conditions for control ecologically. The more parsimonious model without a resource equation is sufficient to generate results qualitatively similar to those observed in some systems. However, in reality, there may be many more complex interactions between more species at different levels of the food web (including multiple resources, consumers, and predators). The reduction in model complexity from a multiple-dimensional system to a two-dimensional system is a simplification. While predictions can only be made at the complexity level of the model studied (see Bassingthwaighte et al., 2006, for a discussion), there are numerous studies finding that increasing model complexity often does not improve the fit to time series data and that there is very little loss of predictive ability (Stillman et al., 2000; Smets et al., 2002; Arhonditsis and Brett, 2004). We have included the minimum level of detail to describe our system and a more realistic model is being analysed elsewhere (Drury et al., manuscript in preparation).

Secondly, the results are qualitatively different from previous models that used a Type II predation functional response or a related nonlinear function (Polis et al., 1989; Holt and Polis, 1997; Mylius et al., 2001). Previous models allowed for coexistence of predator and consumer under a particular parameter regime, where the productivity (or resource carrying capacity) varied. The coexistence region overlapped with a region of bistability with alternative stable states of coexistence or predator excluding consumer. We also observed parameter regions of coexistence and of bistability, but the alternative stable states are coexistence or consumer excluding predator. Further work would be needed to compare dynamic outcomes of our model with time series population data in case study ecosystems.

Thirdly, the spatial framework has not been applied to IGP, and it has given us additional insights. We have shown that given a fixed control quotum, pest species removal over a local area is more effective than homogeneous removal throughout the interaction arena (within the area of parameter space where bistability is observed). Partial differential equation models have been employed in biological control and predator systems previously (Lewis and van den Driessche, 1993; Ashih and Wilson, 2001; Owen and Lewis, 2001; Hilker et al., 2005). The spatial approach allows us to extend the region in parameter space over which control is possible, but also to consider applications to range expansion.

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Appendix

Coefficients of polynomials $l(c)$ and $k(c)$ and the Sylvester matrix M.

The coefficients of the polynomial $l(c)$ in Eq. (16) are given by

$$l_3 = rh^2\left(1 - \alpha_{cp}\alpha_{pc}\right), \tag{A.1}$$

$$l_2 = h\left[\beta\alpha_{pc} + r\left(h\alpha_{pc} - \alpha_{cp}a - 2\alpha_{cp}\alpha_{pc} - h + 2\right)\right], \tag{A.2}$$

$$l_1 = r\left(1 + ha + 2\alpha_{pc}h + \beta\alpha_{pc} + \beta a - \alpha_{cp}a - \alpha_{cp}\alpha_{pc} - 2h\right), \tag{A.3}$$

$$l_0 = r\left(\alpha_{pc} + a - 1\right). \tag{A.4}$$

The coefficients of the polynomial $k(c)$ in Eq. (17) are

$$k_2 = 3rh^2(1 - \alpha_{cp}\alpha_{pc}) = 3l_3, \tag{A.5}$$

$$k_1 = 2h\left[\beta\alpha_{pc} + r\left(h\alpha_{pc} - \alpha_{cp}a - 2\alpha_{cp}\alpha_{pc} - h + 2\right)\right] = 2l_2, \tag{A.6}$$

$$k_0 = r\left(\alpha_{pc} + a - 1\right) = l_1. \tag{A.7}$$

The Sylvester matrix of the polynomials l and k (Allgower and Georg, 1990) is

$$M(l,k) = \begin{pmatrix} l_3 & l_2 & l_1 & l_0 & 0 \\ 0 & l_3 & l_2 & l_1 & l_0 \\ k_2 & k_1 & k_0 & 0 & 0 \\ 0 & k_2 & k_1 & k_0 & 0 \\ 0 & 0 & k_2 & k_1 & k_0 \end{pmatrix}. \tag{A.8}$$

References

Adisu, B., Freier, B., 2003. The potential of biocontrol agents for the control of *Diuraphis noxia* (Homoptera: Aphididae) in spring barley in the central highlands of Ethiopia. Biol. Agric. Horticult. 21(1), 35–51.

Albuquerque, G.S., Tauber, C.A., Tauber, M.J., 1994. *Chrysoperla externa* (Neuroptera, Chrysopidae)—Life-history and potential for biological-control in Central and South America. Biol. Control 4(1), 8–13.

Allgower, E.L., Georg, K., 1990. Numerical Continuation Methods: An Introduction. Springer Series in Computational Mathematics. Springer-Verlag, Berlin.

Arhonditsis, G.B., Brett, M.T., 2004. Evaluation of the current state of mechanistic aquatic biogeochemical modeling. Mar. Ecol. Prog. Ser. 271, 13–26.

Ashih, A.C., Wilson, W.G., 2001. Two-sex population dynamics in space: Effects of gestation time on persistence. Theor. Popul. Biol. 60(2), 93–106.

Askari, A., Stern, V.M., 1972. Biology and feeding habits of *Orius tristicolor* (Hemiptera-Anthocoridae). Annal. Entomol. Soc. Am. 65(1), 96–100.

Bassingthwaighte, J.B., Chizeck, H.J., Atlas, L.E., 2006. Strategies and tactics in multiscale modeling of cell-to-organ systems. Proc. IEEE 94(4), 819–831.

Behnke, R.J. (1992). Native Trout of Western North America. American Fisheries Society, Bethesda, MD.

Bôcher, M., Duval, E.P.R., 1938. Introduction to Higher Algebra. Macmillan, New York.

Boustead, N.C., 1993. Detection and New Zealand distribution of *Myxobolus cerebralis*, the cause of whirling disease of salmonids. N. Z. J. Mar. Freshwater Res. 27(4), 431–436.

Brown, M.W., Schmitt, J.J., 1994. Population-dynamics of woolly apple aphid (Homoptera, Aphididae) in west Virginia apple orchards. Environ. Entomol. 23(5), 1182–1188.

Capelli, G.M., 1982. Displacement of northern Wisconsin crayfish by *Orconectes rusticus* (Girard). Limnol. Oceanogr. 27(4), 741–745.

Capelli, G.M., Magnuson, J.J., 1983. Morphoedaphic and biogeographic analysis of crayfish distribution in northern Wisconsin. J. Crustacean Biol. 3(4), 548–564.

Carlander, K.D., 1977. Handbook of Freshwater Fishery Biology, vol. 2, Life History Data on Centrarchid Fishes of the United States and Canada, 1st edition. Iowa State University Press, Ames.

Chesson, P., 2000. Mechanisms of maintenance of species diversity. Annu. Rev. Ecol. Syst. 31, 343–366.

Clark, C.W., 1985. Bioeconomic Modelling and Fisheries Management. Wiley, New York.

Clark, C.W., 1990. Mathematical Bioeconomics: The Optimal Management of Renewable Resources, 2nd edition. Wiley-Interscience, New York.

Colfer, R.G., Rosenheim, J.A., Godfrey, L.D., Hsu, C.L., 2003. Interactions between the augmentatively released predaceous mite *Galendromus occidentalis* (Acari: Phytoseiidae) and naturally occurring generalist predators. Environ. Entomol. 32(4), 840–852.

Congdon, B.D., McMurtry, J.A., 1988. Prey selectivity in *Euseius tularensis* (Acari, Phytoseiidae). Entomophaga 33(3), 281–287.

Cowie, R.H., 2001. Can snails ever be effective and safe biocontrol agents? Int. J. Pest Manage. 47(1), 23–40.

Crossman, E.J., 1995. Introduction of the lake trout (*Salvelinus namaycush*) in areas outside its native distribution: A review. J. Great Lakes Res. 21, 17–29.

de Roos, A.M., Persson, L., 2003. Competition in size-structured populations: Mechanisms inducing cohort formation and population cycles. Theor. Popul. Biol. 63(1), 1–16.

Didonato, G.T., Lodge, D.M., 1993. Species replacements among Orconectes crayfishes in Wisconsin lakes—The role of predation by fish. Can. J. Fish. Aquatic Sci. 50(7), 1484–1488.

Diehl, S., 2003. The evolution and maintenance of omnivory: Dynamic constraints and the role of food quality. Ecology 84(10), 2557–2567.

Diehl, S., Feißel, M., 2000. Effects of enrichment on three-level food chains with omnivory. Am. Nat. 155(2), 200–218.

Dorn, N.J., Wojdak, J.M., 2004. The role of omnivorous crayfish in littoral communities. Oecologia 140(1), 150–159.

Ebenman, B., Persson, L., 1988. Size-Structured Populations: Ecology and Evolution. Springer-Verlag, Berlin.

Engeman, R.M., Groninger, N.P., Vice, D.S., 2003. A general model for predicting brown tree snake capture rates. Environmetrics 14(3), 295–305.

Escudero, L.A., Ferragut, F., 2005. Life-history of predatory mites *Neoseiulus californicus* and *Phytoseiulus persimilis* (Acari: Phytoseiidae) on four spider mite species as prey, with special reference to *Tetranychus evansi* (Acari: Tetranychidae). Biol. Control 32(3), 378–384.

Fagan, W.F., 1997. Omnivory as a stabilizing feature of natural communities. Am. Nat. 150(5), 554–567.

Fife, P.C., McLeod, J.B., 1975. Approach of solutions of nonlinear diffusion equations to traveling wave solutions. Bull. Am. Math. Soc. 81(6), 1076–1078.

Fife, P.C., McLeod, J.B., 1977. Approach of solutions of nonlinear diffusion equations to traveling front solutions. Arch. Ration. Mech. Anal. 65(4), 335–361.

Fritts, T.H., Rodda, G.H., 1998. The role of introduced species in the degradation of island ecosystems: A case history of Guam. Annu. Rev. Ecol. Syst. 29, 113–140.

Fuller, P., 2000. Nonindigenous fishes—*Oncorhynchus mykiss*. Technical report, Nonindigenous Exotic Species. US Geological Survey.

Gadomski, D.M., Venditti, D.A., Robinson, T.C., Beeman, J.W., Maule, A.G., 2004. Distribution and relative abundance of fishes in littoral areas of Chief Joseph Reservoir, Columbia River. Northwest Sci. 78(1), 48–58.

Garvey, J.E., Rettig, J.E., Stein, R.A., Lodge, D.M., Klosiewski, S.P., 2003. Scale-dependent associations among fish predation, littoral habitat, and distributions of crayfish species. Ecology 84(12), 3339–3348.

Grafton-Cardwell, E.E., Ouyang, Y., 1993. Toxicity of 4 insecticides to various populations of the predacious mite, *Euseius tularensis* Congdon (Acarina, Phytoseiidae) from San-Joaquin Valley California citrus. J. Agric. Entomol. 10(1), 21–29.

Grafton-Cardwell, E.E., Ouyang, Y., Striggow, R.A., 1999. Predacious mites for control of citrus thrips, *Scirtothrips citri* (Thysanoptera: Thripidae) in nursery citrus. Biol. Control 14(1), 29–36.

Greenwood, R.J., 1981. Foods of prairie raccoons during the waterfowl nesting season. J. Wildlife Manage. 45(3), 754–760.

Grosholz, E.D., Ruiz, G.M., 1995. Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Marine Biol. 122(2), 239–247.

Grosholz, E.D., Ruiz, G.M., Dean, C.A., Shirley, K.A., Maron, J.L., Connors, P.G., 2000. The impacts of a nonindigenous marine predator in a California bay. Ecology 81(5), 1206–1224.

Hadeler, K.P., Lewis, M.A., 2002. Spatial dynamics of the diffusive logistic equation with a sedentary compartment. Can. Appl. Math. Q. 10(4), 473–499.

Hagler, J.R., Cohen, A.C., 1991. Prey selection by invitro-reared and field-reared *Geocoris punctipes*. Entomol. Exp. Appl. 59(3), 201–205.

Hagler, J.R., Naranjo, S.E., 1994. Determining the frequency of heteropteran predation on sweetpotato whitefly and pink-bollworm using multiple elisas. Entomol. Exp. Appl. 72(1), 59–66.

Hagler, J.R., Jackson, C.G., Isaacs, R., Machtley, S.A., 2004. Foraging behavior and prey interactions by a guild of predators on various lifestages of *Bemisia tabaci*. J. Insect Sci. 4(1), 1–13.

Hairston, N.G., 1980. Species packing in the salamander genus *Desmognathus*—What are the interspecific interactions involved. Am. Nat. 115(3), 354–366.

Hairston, N.G., 1986. Species packing in *Desmognathus* salamanders—Experimental demonstration of predation and competition. Am. Nat. 127(3), 266–291.

Hamr, P., 2001. Orconectes. In: Holdich, D.M. (Ed.), Biology of Freshwater Crayfish, 1st edition. Blackwell, Oxford, pp. 585–608.

Hein, C.L., 2004. Rusty Crayfish (*Orconectes rusticus*) Population Dynamics During Three Years of Intensive Removal in Sparkling Lake, Wisconsin. M.S. thesis, University of Wisconsin – Madison, Madison.

Hein, C.L., Roth, B.M., Ives, A.R., Vander Zanden, M.J., 2006. Fish predation and trapping for rusty crayfish *Orconectes rusticus*) control: A whole-lake experiment. Can. J. Fish. Aquatic Sci. 63(2), 383–393.

Hilker, F.M., Lewis, M.A., Seno, H., Langlais, M., Malchow, H., 2005. Pathogens can slow down or reverse invasion fronts of their hosts. Biol. Invasions 7(5), 817–832.

Hoffmann, M.P., Frodsham, A., 1993. Natural Enemies of Vegetable Insect Pests. Cooperative Extension, Cornell University, Ithaca, NY.

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.

Holt, R.D., Polis, G.A., 1997. A theoretical framework for intraguild predation. Am. Nat. 149(4), 745–764.

Holyoak, M., Sachdev, S., 1998. Omnivory and the stability of simple food webs. Oecologia 117(3), 413–419.

Jensen, G.C., McDonald, P.S., Armstrong, D.A., 2002. East meets west: Competitive interactions between green crab *Carcinus maenas*, and native and introduced shore crab *Hemigrapsus* spp. Mar. Ecol. Prog. Ser. 225, 251–262.

Jordan, D.W., Smith, P., 1988. Nonlinear Ordinary Differential Equations, 2nd edition. Oxford Applied Mathematics and Computing Science Series. Clarendon Press, Oxford.

Jude, D.J., Reider, R.H., Smith, G.R., 1992. Establishment of *Gobiidae* in the Great Lakes Basin. Can. J. Fish. Aquatic Sci. 49(2), 416–421.

Jules, E.S., Kauffman, M.J., Ritts, W.D., Carroll, A.L., 2002. Spread of an invasive pathogen over a variable landscape: A nonnative root rot on Port Orford cedar. Ecology 83(11), 3167–3181.

Kain, D., Nyrop, J., 1995. Predatory Mites of Insect Identification Fact Sheet, vol. 23. Cooperative Extension, Cornell University, Ithaca, NY.

Kamler, J.F., Ballard, W.B., Helliker, B.R., Stiver, S., 2003. Range expansion of raccoons in western Utah and central Nevada. West North Am. Nat. 63(3), 406–408.

Kareiva, P., 1990. Population-dynamics in spatially complex environments—Theory and data. Philos. Trans. R. Soc. Lond. Seri. B Biol. Sci. 330(1257), 175–190.

Keddy, P.A., Shipley, B., 1989. Competitive hierarchies in herbaceous plant-communities. Oikos 54(2), 234–241.

Kershner, M.W., Lodge, D.M., 1995. Effects of littoral habitat and fish predation on the distribution of an exotic crayfish, *Orconectes rusticus*. J. North Am. Benthol. Soc. 14(3), 414–422.

Kideys, A.E., 1994. Recent dramatic changes in the Black-Sea ecosystem—The reason for the sharp decline in Turkish anchovy fisheries. J. Mar. Syst. 5(2), 171–181.

Kideys, A.E., Moghim, M., 2003. Distribution of the alien ctenophore *Mnemiopsis leidyi* in the Caspian Sea in August 2001. Mar. Biol. 142(1), 163–171.

Kideys, A.E., Kovalev, A.V., Shulman, G., Gordina, A., Bingel, F., 2000. A review of zooplankton investigations of the Black Sea over the last decade. J. Mar. Syst. 24(3/4), 355–371.

Kot, M., 2001. Elements of Mathematical Ecology. Cambridge University Press, Cambridge, UK.

Kristensen, E.A., Closs, G.P., 2004. Anti-predator response of naïve and experienced common bully to chemical alarm cues. J. Fish Biol. 64(3), 643–652.

Lariviere, S., 2004. Range expansion of raccoons in the Canadian prairies: Review of hypotheses. Wildl. Soc. Bull. 32(3), 955–963.

Lennon, J.T., Smith, V.H., Williams, K., 2001. Influence of temperature on exotic *Daphnia lumholtzi* and implications for invasion success. J. Plankton Res. 23(4), 425–434.

Lewis, M.A., Kareiva, P., 1993. Allee dynamics and the spread of invading organisms. Theor. Popul. Biol. 43(2), 141.

Lewis, M.A., van den Driessche, P., 1993. Waves of extinction from sterile insect release. Math. Biosci. 116(2), 221–247.

Limburg, D.D., Rosenheim, J.A., 2001. Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). Environ. Entomol. 30(3), 595–604.

Lodge, D.M., Beckel, A.L., Magnuson, J.J., 1985. Lake-bottom tyrant. Nat. Hist. 94(8), 32–36.

Lodge, D.M., Kratz, T.K., and Capelli, G.M., 1986. Long-term dynamics of three crayfish species in Trout Lake, Wisconsin. Can. J. Fish. Aquatic Sci. 43(5), 993–998.

Lodge, D.M., Kershner, M.W., Aloi, J.E., Covich, A.P., 1994. Effects of an omnivorous crayfish (*Orconectes rusticus*) on a fresh-water littoral food-web. Ecology 75(5), 1265–1281.

MacNeil, C., Montgomery, W.I., Dick, J.T.A., Elwood, R.W., 2001. Factors influencing the distribution of native and introduced *Gammarus spp.* in Irish river systems. Arch. Hydrobiol. 151(3), 353–368.

MacNeil, C., Dick, J.T.A., Johnson, M.P., Hatcher, M.J., Dunn, A.M., 2004a. A species invasion mediated through habitat structure, intraguild predation, and parasitism. Limnol. Oceanography 49(5), 1848–1856.

MacNeil, C., Prenter, J., Briffa, M., Fielding, N.J., Dick, J.T.A., Riddell, G.E., Hatcher, M.J., Dunn, A.M., 2004b. The replacement of a native freshwater amphipod by an invader: Roles for environmental degradation and intraguild predation. Can. J. Fish. Aquatic Sci. 61(9), 1627–1635.

Martinez, P.J., Chart, T.E., Trammell, M.A., Wullschleger, J.G., Bergersen, E.P., 1994. Fish species composition before and after construction of a main stem reservoir on the White River, Colorado. Environ. Biol. Fishes 40(3), 227–239.

MathWorks Inc., 2004. MATLAB: The Language of Technical Computing, version 7. MathWorks, Natick, MA.

McMullen, R.D., Jong, C., 1970. The biology and influence of pesticides on *Campylomma verbasci* (Hemiptera: Miridae). Can. Entomol. 102, 1390–1394.

Michaud, J.P., 1999. Sources of mortality in colonies of brown citrus aphid, *Toxoptera citricida*. Biocontrol 44(3), 347–367.

Michaud, J.P., Belliure, B., 2001. Impact of syrphid predation on production of migrants in colonies of the brown citrus aphid, *Toxoptera citricida* (Homoptera: Aphididae). Biol. Control 21(1), 91–95.

Miller, R.J., Addison, J.T., 1995. Trapping interactions of crabs and American lobster in laboratory tanks. Can. J. Fish. Aquatic Sci. 52(2), 315–324.

Momot, W.T., 1992. Further range extensions of the crayfish *Orconectes rusticus* in the Lake Superior Basin of northwestern Ontario. Can. Field Nat. 106(3), 397–399.

Momot, W.T., Gowing, H., 1972. Differential seasonal migration of crayfish, *Orconectes virilis* (Hagen), in Marl Lakes. Ecology 53(3), 479–483.

Momot, W.T., Hartviksen, C., Morgan, G., 1988. A range extension for the crayfish *Orconectes rusticus*—Sibley Provincial Park, northwestern Ontario. Can. Field Nat. 102(3), 547–548.

Morin, P., 1999. Productivity, intraguild predation, and population dynamics in experimental food webs. Ecology 80(3), 752–760.

Munro, A.R., McMahon, T.E., Ruzycki, J.R., 2005. Natural chemical markers identify source and date of introduction of an exotic species: Lake trout (*Salvelinus namaycush*) in Yellowstone Lake. Can. J. Fish. Aquatic Sci. 62(1), 79–87.

Murray, J.D., 2003. Mathematical Biology, 3rd edition. Springer-Verlag, New York.

Mylius, S.D., Klumpers, K., de Roos, A.M., Persson, L., 2001. Impact of intraguild predation and stage structure on simple communities along a productivity gradient. Am. Nat. 158(3), 259–276.

Noble, R.L., 2002. Reflections on 25 years of progress in black bass management. In: Philipp, D.P., Ridgway, M.S. (Eds.), Black Bass: Ecology, Conservation, and Management. American Fisheries Society, Bethesda, MD, pp. 419–432 (Symposium 31).

Noble, R.L., Jones, T.W., 1999. Managing fisheries with regulations. In: Kohler, C.C., Hubert, W.A. (Eds.), Inland Fisheries Management in North America, 2nd edition. American Fisheries Society, Bethesda, MD, pp. 455–477.

Olsen, T.M., Lodge, D.M., Capelli, G.M., Houlihan, R.J., 1991. Mechanisms of impact of an introduced crayfish *Orconectes rusticus*) on littoral congeners, snails, and macrophytes. Can. J. Fish. Aquatic Sci. 48(10), 1853–1861.

Ouyang, Y., Grafton-Cardwell, E.E., Bugg, R.L., 1992. Effects of various pollens on development, survivorship, and reproduction of *Euseius tularensis* (Acari, Phytoseiidae). Environ. Entomol. 21(6), 1371–1376.

Owen, M.R., Lewis, M.A., 2001. How predation can slow, stop or reverse a prey invasion. Bull. Math. Biol. 63(4), 655–684.

Persson, L., Andersson, J., Wahlstrom, E., Eklov, P., 1996. Size-specific interactions in lake systems: Predator gape limitation and prey growth rate and mortality. Ecology 77(3), 900–911.

Polis, G.A., Holt, R.D., 1992. Intraguild predation—The dynamics of complex trophic interactions. Trends Ecol. Evol. 7(5), 151–154.

Polis, G.A., Myers, C.A., Holt, R.D., 1989. The ecology and evolution of intraguild predation—Potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20, 297–330.

Pree, D.J., Archibald, D.E., Morrison, R.K., 1989. Resistance to insecticides in the common green lacewing *Chrysoperla carnea* (Neuroptera, Chrysopidae) in southern Ontario. J. Econ. Entomol. 82(1), 29–34.

Rissler, L.J., Wilbur, H.M., Taylor, D.R., 2004. The influence of ecology and genetics on behavioral variation in salamander populations across the Eastern Continental Divide. Am. Nat. 164(2), 201–213.

Robinson, A.T., Bryan, S.D., Sweetser, M.G., 2003. Habitat use by nonnative rainbow trout, *Oncorhynchus mykiss*, and native Little Colorado spinedace, *Lepidomeda vittata*. Environ. Biol. Fishes 68(2), 205–214.

Rojo, S., MarcosGarcia, M.A., 1997. Syrphid predators (Dipt.: Syrphidae) of gall forming aphids (Hom.: Aphididae) in Mediterranean areas: Implications for biological control of fruit trees pests. Entomophaga 42(1/2), 269–276.

Rosenheim, J.A., 2005. Intraguild predation of *Orius tristicolor* by *Geocoris spp.* and the paradox of irruptive spider mite dynamics in California cotton. Biol. Control 32(1), 172–179.

Rosenheim, J.A., Wilhoit, L.R., Armer, C.A., 1993. Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. Oecologia 96(3), 439–449.

Rosenheim, J.A., Kaya, H.K., Ehler, L.E., Marois, J.J., Jaffee, B.A., 1995. Intraguild predation among biological-control agents—Theory and evidence. Biol. Control 5(3), 303–335.

Rosenheim, J.A., Limburg, D.D., Colfer, R.G., 1999. Impact of generalist predators on a biological control agent, *Chrysoperla carnea*: Direct observations. Ecol. Appl. 9(2), 409–417.

Rosenheim, J.A., Glik, T.E., Goeriz, R.E., Ramert, B., 2004. Linking a predator's foraging behavior with its effects on herbivore population suppression. Ecology 85(12), 3362–3372.

Roth, B.M., Hein, C.L., Vander Zanden, M.J., 2006. Using bioenergetics and stable isotopes to assess the trophic role of rusty crayfish (*Orconectes rusticus*) in lake littoral zones. Can. J. Fish. Aquatic Sci. 63(2), 335–344.

Ruzycki, J.R., Beauchamp, D.A., Yule, D.L., 2003. Effects of introduced lake trout on native cutthroat trout in Yellowstone Lake. Ecol. Appl. 13(1), 23–37.

Schaeffer, J.S., Bowen, A., Thomas, M., French, J.R.P., Curtis, G.L., 2005. Invasion history, proliferation, and offshore diet of the round goby *Neogobius melanostomus* in western Lake Huron, USA. J. Great Lakes Res. 31(4), 414–425.

Schoener, T.W., 1974. Competition and the form of habitat shift. Theor. Popul. Biol. 6(3), 265–307.

Schoener, T.W., 1976. Alternatives to Lotka-Volterra competition: Models of intermediate complexity. Theor. Popul. Biol. 10(3), 309–333.

Schroder, A., Persson, L., De Roos, A.M., 2005. Direct experimental evidence for alternative stable states: A review. Oikos 110(1), 3–19.

Secord, D., 2003. Biological control of marine invasive species: Cautionary tales and land-based lessons. Biol. Invasions 5(1/2), 117–131.

Short, B.D., Bergh, J.C., 2004. Feeding and egg distribution studies of *Heringia calcarata* (Diptera: Syrphidae), a specialized predator of woolly apple aphid (Homoptera: Eriosomatidae) in Virginia apple orchards. J. Econ. Entomol. 97(3), 813–819.

Smets, I., Bernaerts, K., Sun, J., Marchal, K., Vanderleyden, J., Van Impe, J., 2002. Sensitivity function-based model reduction—A bacterial gene expression case study. Biotechnol. Bioeng. 80(2), 195–200.

Stein, R.A., 1977. Selective predation, optimal foraging, and predator–prey interaction between fish and crayfish. Ecology 58(6), 1237–1253.

Stillman, R.A., McGrorty, S., Goss-Custard, J.D., West, A.D., 2000. Predicting mussel population density and age structure: The relationship between model complexity and predictive power. Mar. Ecol. Prog. Ser. 208, 131–145.

Suski, C.D., Philipp, D.P., 2004. Factors affecting the vulnerability to angling of nesting male largemouth and smallmouth bass. Trans. Am. Fish. Soc. 133(5), 1100–1106.

Tamaki, G., Weeks, R.E., 1972. Efficiency of three predators, *Geocoris bullatus, Nabis americoferus* and *Cocinella transversogutata*, used alone or in combination against three insect prey species, *Myzus persicae, Ceramica picta*, and *Manastra configurata*, in a greenhouse study. Environ. Entomol. 1, 258–263.

Tauber, M.J., Tauber, C.A., 1983. Life-history traits of *Chrysopa carnea* and *Chrysopa rufilabris* (Neuroptera, Chrysopidae)—Influence of humidity. Ann. Entomol. Soc. Am. 76(2), 282–285.

Tenhumberg, B., Poehling, H.M., 1995. Syrphids as natural enemies of cereal aphids in Germany—Aspects of their biology and efficacy in different years and regions. Agric. Ecosyst. Environ. 52(1), 39–43.

Thistlewood, H., 1990. Seasonal abundance of the mullein plant bug, *Campylomma verbasci* (Hemiptera: Miridae), on apple and mullein in the Okanagan Valley. Can. Entomol. 122, 1045–1058.

Vanderploeg, H.A., Nalepa, T.F., Jude, D.J., Mills, E.L., Holeck, K.T., Liebig, J.R., Grigorovich, I.A., Ojaveer, H., 2002. Dispersal and emerging ecological impacts of Ponto-Caspian species in the Laurentian Great Lakes. Can. J. Fish. Aquatic Sci. 59(7), 1209–1228.

Waide, R.B., Reagan, D.P., 1983. Competition between West-Indian anoles and birds. Am. Nat. 121(1), 133–138.

Walter, D.E., 1987. Trophic behavior of mycophagous microarthropods. Ecology 68(1), 226–229.

Walter, D.E., 1999. Cryptic inhabitants of a noxious weed: Mites (Arachnida: Acari) on *Lantana camara* L. invading forests in Queensland. Aust. J. Entomol. 38, 197–200.

Werner, E.E., Gilliam, J.F., 1984. The ontogenetic niche and species interactions in size structured populations. Ann. Rev. Ecol. Syst. 15, 393–425.

Wright, S.J., 1981. Extinction-mediated competition—The anolis lizards and insectivorous birds of the West-Indies. Am. Nat. 117(2), 181–192.

Zhang, R.Z., Ren, L., Wang, C.L., Lin, R.H., Tian, C.Y., 2004. Cotton aphid predators on alfalfa and their impact on cotton aphid abundance. Appl. Entomol. Zool. 39(2), 235–241.