Interaction strength and the consequences of non-native omnivory

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May 2016

A thesis submitted to McGill University in partial fulfillment of the requirements for the degree of Doctor of Philosophy in Biology

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Dedication

I dedicate this thesis to all the women of colour in science whose shoulders I have had the privilege to stand on.

Sí se puede.

Thesis acknowledgments

From my first day as a PhD student through the trials of the qualifying exam to the last pages of this document, one constant has been my PhD supervisor, Gregor Fussmann. Thank you Gregor for your support in its many forms, for allowing me the autonomy to work on a diversity of projects and for helping me to develop into the scientist I am today. I would also like to thank all the members of my supervisory committee, Frédéric Guichard, Brian Leung and Stéphane Plourde for their advice and assistance with my research.

It is impossible to conduct research alone. To Rowshyra Castaneda, Sean Duffy, Pierre Joly and Gabriel St-Jean-Lavoie thank you for your assistance in the field and the laboratory in the pursuit of data. To my co-authors on the manuscripts in this thesis, Ianina Altshuler, Sean Duffy, Daniel Barrios-O'Neil and Katie Pagnucco, thank you for sharing your knowledge and embarking on this science journey with me. I would also like to thank the members of Fussmann lab and my officemates Luke Andersen-Trocmé and Genelle Harrison and Kristina Enciso and Johanna Bradie across the hall for the insightful lab meetings, resources and synthesis of ideas.

I am fortunate to have been involved in several collaborations have shaped and guided my research. To Etienne Low-Decarie, Cory Chivers, Justin Marleau, Holly Moeller, Eric Pedersen, Marissa Lee, Pamela Reynolds, Kes Schroer, Mehdi Cherif and Zofia Taranu thank you for all that each of you has taught me, I am a better scientist for having worked with you.

I submit that the product of a graduate degree is more than the bound chapters of a thesis. In between the experiments and simulations that make up the pages of this thesis I learned to become an improv comedian. The classes and shows at Montreal Improv taught me how to be a better listener, a more confident speaker and provided me with some of the most sustained laughs and the best of friends. To the members of the Montreal Improv community, thank you for being such a positive influence in my life and for providing me a second home, it was truly a place where everyone knows your name.

To my Lego family thank you for providing me a creative medium, for your encouragement and for making my dream of working for Lego come true.

I am grateful to for the funding for research and travel I received toward the pursuit of this degree. Thank you to the Quebec Centre for Biodiversity Science, Québec Océan, Centre for Applied Mathematics in Bioscience and Medicine and McGill University. Through your generous support I was able to attend workshops, conferences, conduct research and extend my classroom beyond the walls of McGill.

There is a shelf above the desk I have occupied in the years it has taken to complete my thesis. On this shelf are small objects that demarcate events and remind me of the people that have made my experience at McGill spectacular. There is a cork from the champagne bottle opened after I passed my qualifying exam. Thank you Aerin Jacob for the event where this cork is from, for your imitable support during so many formative times throughout my thesis and for helping me across the finish line. I've retained an Ohio State pen that sits on this shelf from Math Camp where Eric Pedersen, Justin Marleau and I slayed some equations. Thank you both for your statistical advice and friendship. I'm confident we have many more equations to solve together. The shelf is also covered with glitter that migrated from a memorable party at 4425 Mentana, the address that was my home for so many years. Thank you Bronwyn Rayfield for giving me a home in all its definitions and thank you David Ross for maintaining it with cheesecakes. There are business cards on the shelf from the many different establishments visited by the Breakfast Club, thank you Carly Ziter and Sylvia Wood for sharing this any many other meals, drinks and laughs that provided the fuel to execute my thesis. I am reminded of the TREE, every time I look at the picture on the shelf we took at Medieval Times. Thank you Brie Edwards, Laura Canty, Anna Simonsen, Russell Dinnage, Katrina Chu and especially Mr. Brand and Maggie Neff for your friendship and support. Allan, I still look forward to your chats each and every morning and Maggie thank you for being at my side for so many years and across many miles. And at the end of the shelf is a collection of unicorn items given to me by Katie Pagnucco. It now seems fitting that the items bestowed upon me by Katie bear a resemblance to a unicorn, for in many ways that is what you are – unique, beautiful and kind of magical. Thank you Katie for being at and the catalyst for many of the best days of my life.

Finally to my family, simply the most constant source of support for all the years I have pursued a greater understanding of science. Thank you for instilling in me the belief that I could become and achieve anything I wanted. I hope this achievement is a testament to all the struggles you endured to secure an education and a future for me. Los quiero mucho.

Abstract

This thesis concerns the intersection of food web theory and invasive species research. Omnivory defined as feeding at multiple trophic levels occurs in a plethora of terrestrial, marine and freshwater food webs, owing to the capacity of the omnivore to reduce the maximum and minimum population sizes of the consumer that it feeds on and the resource that both it and the consumer feed on. While both empirical and theoretical pursuits have determined that omnivory in native food webs is stabilizing, whether this stability is conferred by introduced omnivores remains unknown. In this thesis I use a combination of meta-analyses, experiments and theoretical approaches to illustrate that the impact of introduced omnivores and their effect on stability (i.e. persistence of the food web) is a function of interaction strength. The meta-analyses, which coalesced several introduced aquatic invertebrates studies, revealed that when comparing the impact between introduced omnivores and predators on recipient consumers, the impact is greater when omnivores are introduced. Further, the impact on the consumer in the recipient community is related to the interaction strength of the introduced species. Species with stronger functional responses had greater impacts on consumers in recipient communities. In the laboratory, I reproduced a food web subject to the introduction of an omnivore to quantify the growth rate of the consumer under different food web modules including omnivory. By using RNA:DNA ratios I determined that over the course of a 24-hour experiment growth rate and variation in growth rate was highest in the omnivory food web. Analyses of differences in growth rates and its variation across food web modules revealed that individual differences in consumer growth rates might be contributing to stability in food webs with omnivory by decreasing interaction strengths between predator and consumers. Finally, I used a modeling approach to analyze how interaction strength within the recipient community interacts with the strength of omnivory to determine the consequences of the introduction of the omnivore. The model revealed that the introduction of an omnivore could increase the persistence of a food web when strong consumer-resource interactions would otherwise drive it to extinction. Overall my thesis reveals the consequences of the introduction of omnivores depend on interaction strengths – not only the novel interactions formed between the omnivore and the recipient community but also the existing interaction strengths within that community.

Résumé de la thése

Cette thèse concerne l'intersection de la théorie de réseau alimentaire et de recherche en espèces envahissantes. L'omnivorie, définie à plusieurs niveaux trophiques, se trouve dans une multitude de réseaux alimentaires terrestre, marin et d'eau douce, en raison de la capacité de l'omnivore de réduire le maximum et le minimum des tailles de population du consommateur qu'il consomme et les ressources dont il et le consommateur se nourrissent. Tandis que les recherches empiriques et théoriques ont déterminé que l'omnivorie dans les réseaux alimentaires indigènes sont stabilisantes, si cette stabilité est conférée par l'introduction d'un omnivore reste inconnue. Dans cette thèse, j'utilise une combinaison de méthodes, incluant des méta-analyses, des expériences et de la théorie, pour illustrer l'impacte d'omnivores introduits et leurs effets sur la stabilité, (i.e. la persistance du réseau alimentaire), est une fonction de la force de l'interaction. Les méta-analyses, qui ont combiné plusieurs études d’invertébrés aquatiques introduits, ont révélé que quand on compare l’impact des omnivores introduits avec les prédateurs sur la communauté récipiendaire, l’impact est plus grand quand les omnivores sont introduits. De plus, l’impact sur le consommateur dans la communauté récipiendaire est relié à la force de l’interaction de l’espèce envahissante. L’espèce avec les plus fortes réponses fonctionnelles avait des plus grands impacts sur les consommateurs dans les communautés récipiendaires. Dans le laboratoire, j’ai reproduit un réseau alimentaire avec une introduction d’un omnivore pour quantifier le taux de croissance du consommateur sous différents modules de réseau alimentaire incluant l’omnivorie. En utilisant des ratios de ARN:ADN, j’ai déterminé qu’au cour d’un expérience de 24 heurs, le taux de croissance et sa variance étaient les plus élevés dans le réseau alimentaire omnivore. Les analyses des différences de taux de croissance et sa variation à travers les modules de réseau alimentaire ont démontré que les différences individuelles dans le taux de croissance du consommateur peuvent contribuer à la stabilité des réseaux alimentaires avec l’omnivore en réduisant les forces de l’interaction entre le prédateur et les consommateurs. Finalement, j’ai utilisé une méthodologie de modélisation pour analyser comment la force d’interaction dans la communauté récipiendaire interagit avec la force de l’omnivorie pour déterminer les conséquences de l’introduction de l’omnivore. Le modèle a révélé que l’introduction d’un omnivore peut augmenter la persistance d’un réseau alimentaire quand les fortes interactions de consommateur-ressource pourraient autrement le pousser à l’extinction. En général ma thèse révèle que les conséquences de l’introduction d’omnivores dépendent sur les forces d’interactions – non seulement les nouvelles interactions formées entre l’omnivore et la

communauté récipiendaire mais aussi les forces d’interaction existantes dans cette communauté.

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Preface

Thesis structure

This thesis is presented in a manuscript-based format and consists of the general introduction and three chapters each intended for peer-reviewed scientific journals. Appendix B contains two additional related manuscripts of which I am first author or joint first author; but they have not been included in the main thesis owing to their inclusion as chapters in the theses of co-authors.

Contributions of co-authors

This thesis is entirely comprised of original work and I am the first author on each manuscript presented here. I formulated the ideas, executed the experiments, collected the data and wrote for all the manuscripts, except where noted below. Gregor Fussmann contributed to design of the experiments and interpretation of results, assisted with the formulation of the model in Chapter 3 and he edited all of the manuscripts. For Chapter 1 Dr. Daniel Barrios-O'Neil collected the empirical data included in the analysis and contributed to the interpretation of the results. Stéphane Plourde co-developed the experimental design and Ianina Altshuler assisted with the laboratory analyses in Chapter 2.

Original contributions of knowledge

I used a combination of meta-analyses, experiments and theoretical approaches to study the intersection of food web theory and introduced species. The products of this thesis have contributed to the understanding of the impacts of introduced omnivores, a facet that had been lacking in the invasive species literature. Specific contributions are as follows:

General introduction: This manuscript is first a comprehensive review of the history of the study of omnivory. Inspired by the role that interaction strength played in unifying the omnivory-stability debate, we propose, through the use of case studies, that observed differences in the impact of introduced omnivores can be ascribed to differences in interaction strengths. This manuscript is the first to review the literature on introduced omnivores, applies food web theory in a novel context and provides testable predictions on the impacts of introduced omnivores.

Chapter 1: Recent work on functional response had postulated that introduced species that have stronger functional responses would have larger impacts on recipient communities. This chapter is the first to aggregate both published functional response and impact data to test this hypothesis. The results of this chapter suggest that indeed stronger functional responses will lead to greater impacts in the field. Because salient predictions are necessary to mitigate the impacts of introduced species, identifying this relationship provides a tool for forecasting impacts using traits that can be quantified empirically.

Chapter 2: Although food webs are reticulate they can often be simplified into basic modules. While extensive theoretical and empirical pursuits have demonstrated that omnivory, a basic module found repeatedly in nature, can mute oscillations in population sizes, much less is known about how omnivory and other basic modules affect individual growth rates and in turn; the stability of the food web. This chapter provided the first empirical construction of basic food web modules and the novel application of RNA:DNA ratios to quantify growth rates at the cellular level. The results of this chapter offer the first insights into how omnivory can stabilize a food web by increasing the variation in consumer growth rates.

Chapter 3: While many models have studied how the inclusion of different parameters, including stage structure and productivity, affect stability in food webs with omnivory, none have applied this concept to the study of introduced omnivores. Previous work has concluded that interaction strengths must be weak, but the characteristics of the recipient community have not been integrated into analyses. In this chapter I provide the first theoretical analysis of a food web with respect to introduced omnivores. I model a planktonic food web to determine how consumer-resource interactions strength and the strength of omnivory interact to affect the persistence of the food web. The results of the model add to the growing body of literature that under some contexts the introduction of an omnivore can be beneficial.

1 General Introduction

Interaction strength and the impact of introduced omnivores

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A version of this manuscript is in review at Journal of Animal Ecology

1.1 Abstract

There is presently discordance in the literature as to the impact of introduced species characterized as omnivores or individuals that feed on multiple trophic levels. While some studies indicate that, as a group, omnivores do not have a significantly greater impact than other trophic groups, others have documented devastating impacts of introduced omnivores on the diversity and abundance of their prey. Here we present a review of the study of omnivory and highlight the importance of interaction strength in unifying opposite sides of the omnivory-stability debate. We then argue, as with the omnivory-stability debate, that considering interaction strengths can help explain differences in impacts. We present several case studies to demonstrate that when interaction strengths are strong, introduced omnivores will have large impacts on native consumers owing to simultaneous competition and predation. However, when interactions strengths are weak stabilizing mechanisms prevail, introduced omnivores will have weak impacts and can potentially stabilize recipient food webs. Given the importance of predictions in mitigating the impacts of introduced species it is imperative that trophic connection be a variable considered in impact assessment.

1.2 Introduction

The study of omnivory (see Table 1.1 for a glossary of key terms) in food webs has had a contentious history. Once thought impossible to maintain in real ecosystems, omnivory is now regarded as pervasive across ecosystems because it confers stability to food webs (McCann and Hastings 1997, Arim and Marquet 2004). While much is known about how omnivory can contribute to the persistence of food webs, we know very little about how recipient communities respond to the introduction of species that form novel omnivorous links (Hall 2011b). Identified as one of the major drivers of global change, species introductions have the power to radically change recipient ecosystems and can force population declines, species extirpations and extinctions (Blackburn et al. 2004, Bellard et al. 2016, Clavero and García-Berthou 2016). Curtailing these impacts requires a predictive understanding of impact (Ricciardi et al. 2013). It is then imperative to synthesize existing knowledge on food webs and omnivory to provide insights into the conditions the introduction of omnivory could be stabilizing and when its introduction is deleterious. In this paper we review the relationship between omnivory and stability and argue that interaction strength has emerged as the pivotal parameter in determining the impacts (measurable change to the properties of an ecosystem by a non-native species) of an introduced omnivore on a recipient ecosystem (Ricciardi et al. 2013).

1.3 The study of omnivory

Omnivory can manifest as a simple arrangement of omnivore, herbivore and common resource (intraguild predation) or be embedded in a reticulate food web where the omnivore is feeding on multiple prey and resources (Kratina et al. 2012). In this paper we focus on the simple and tractable intraguild predation (IGP) module as a proxy for general omnivory. Omnivory should be very deleterious for the herbivore, hereafter referred to as the consumer, because the consumer is being subjected to simultaneous predation and competition from the omnivore. In fact, simulations of food webs with omnivory by Pimm and Lawton (1978) demonstrated that as the number of omnivorous links in a food web increased, the percentage of unstable (Table 1.1) model simulations increased and equilibrium return times among stable models increased. Monte Carlo simulations of food webs also found that the number of omnivorous links in real food webs is less than expected by chance (Pimm 1980). These results were corroborated empirically by an analysis of Cohen's (1978) food web database which found of the 58 food webs considered 24 had no omnivores. Yet, an analysis over 25 years later by Arim and Marquet (2004) found omnivory to be prolific. Between 58.4% and 86.7% of food webs analyzed in a subset of Cohen et al.'s (1990) expanded data set contained an omnivore-consumer pair sharing a common resource. Thompson et al. (2007), when looking for the prevalence of discrete trophic levels, found that secondary consumers could not be ascribed to integer trophic levels - a result indicative of feeding on multiple trophic levels. Here, food webs were better characterized as a "tangled webs of omnivores." Across taxa and diverse ecosystems empirical evidence mounted for the ubiquity of omnivory in food webs. Tropical fish (Winemiller 1990), zooplankton (Sprules and Bowerman 1988), bird (Hall and Raffaelli 1991), arthropod (Walter 1987), soil macro-invertebrate (Scheu and Falca 2000, Ponsard and Arditi 2000), desert (Polis 1991) stream (Woodward and Hildrew 2002) and marine (Menge and Sutherland 1987) food webs were all found to be replete with omnivores. The incongruence between early theoretical and subsequent empirical work was likely due to the exclusion of interaction strength (Table 1.1) in the models (Polis 1991, McCann et al. 1998) and low resolution in the early empirical data (Martinez 1991).

1.4 Stability and omnivory

The integration of interaction strength reconciled the omnivory-stability debate (Gellner and McCann 2012). Both empirical and theoretical pursuits have demonstrated that food webs with weak omnivory are more stable than food webs with less or no omnivorous interactions. Stability in this context is a measure of the ability of the food web to maintain its present condition or the time it requires to return to this condition after a perturbation (Kratina et al. 2012). McCann and Hastings (1997) demonstrated with the use of more biologically realistic models, incorporating nonlinear functional responses (Table 1.1), that in food webs with weak and intermediate interaction strengths, omnivore and resource are more likely to persist because the minimum population sizes are bounded further away from zero. Omnivory is stabilizing because 1) it can facilitate the persistence of the omnivore in cases where a predator cannot maintain positive densities on the consumer alone (feasibility stabilization) and 2) the consumption of the consumer or the resource by the omnivore reduces the strongly coupled and unstable interaction strength between the consumer and resource (overcompensation stabilization) (McCann 2012). Mechanistically, feasibility stabilization provides an additional resource while overcompensation stabilization mutes oscillations between the consumer and resource bounding them away further from zero. Generally, if a relatively weak interaction exists for each strong consumer–resource interaction, then the food web should be stabilized (McCann et al. 1998). However, both feasibility and overcompensation stabilization can destabilize the food web when the interaction strength between predator and the resource is strong. In this case, the predator will ultimately outcompete the consumer and drive it to extinction (McCann and Hastings 1997; Vandermeer 2006; McCann 2012) .

1.5 Weak omnivory in nature

Real ecosystems are rife with weak interactions. Data on interaction strength in real food webs indicate that they are characterized by many weak interactions and few strong interactions (Paine 1992, Wootton 1997). So, what mechanisms exist to weaken the interaction between omnivore and consumer or resource? Kratina et al. (2012) broke down these stabilizing mechanisms into five main categories: habitat complexity, anti-predator phenotypes of prey, adaptive feeding behaviour of omnivores, life history omnivory and interference between omnivores. Habitat complexity can weaken the omnivore-resource interaction by providing a physical refugium for the resource thereby decreasing encounter rates (Finke and Denno 2002, Janssen et al. 2007). Inducible defenses can weaken the omnivore-resource interaction strength by decreasing the palatability of the consumer or the resource (Holt and Polis 1997), while life history omnivory provides temporal refugia for consumers. Here, consumers and resources can outgrow predation by the omnivore or the omnivore experiences a diet shift (Mylius et al. 2001, Hin et al. 2011). When an omnivore feeds adaptively, switching between feeding on the resource with the greatest availability, it allows the depleted resource to recover. This behaviour weakens the interaction strength between the omnivore and the lower-density resource (Krivan 2000, McCann 2012). Weakening of interaction strength need not arise solely from the resource. As in interference competition, interactions between omnivores including cannibalism or aggressive behaviour can alter the rate of predation on resources (Amarasekare 2008).

While numerous theoretical and empirical studies have demonstrated omnivory is stabilizing (e.g. Lawler and Morin 1993; Fagan and Hurd 1994; Holyoak and Sachdev 1998) there has been little work on how omnivory arises (Eubanks et al. 2003). Because the evolution of omnivory is tantamount to its introduction and both are concerned with how the inclusion of an omnivore in the food web will affect its stability and persistence, the study of how omnivory evolves in native food webs may yield insights on the consequences for the introduction of omnivores.

1.6 The evolution of omnivory

Omnivory could conceivably arise in a native food web through two scenarios: A system with a predator embedded in a food chain with a consumer and resource evolves the ability to also consume the resource or one of two consumers competing for a common resource evolves to also consume its competitor (Fig. 1 in Vandermeer 2006). The latter scenario is unlikely because a system with two competitors and a single resource has a limited range of persistence (Armstrong & McGehee 1980). Mutual invasibility and a stable three-species coexistence is possible but a stabilizing mechanism is necessary. Diehl (2003) found the inclusion of flexible plant quality allowed both the omnivore and consumer to coexist in the transition from competitors to omnivory. The evolution of omnivory from a food chain is also stable but only when the conversion efficiency (how well the omnivore converts prey to more predators) or ostensibly resource quality is low (Diehl 2003). Models of both scenarios demonstrated weaker flows of energy and nutrients from the resource to the omnivore can help maintain omnivory.

The evolution of omnivory also necessitates the consumer turned omnivore has a broad feeding spectrum. Analyses of the evolution of omnivory in Heteropteran insects suggested that species that had larger host ranges where more likely to be omnivorous (Eubanks et al. 2003). Further, the evolution of omnivory may be contingent on conditions of the novel environment. In an evolutionary simulation model, the evolution of different feeding phenotypes was most sensitive to the ratio of the abundance of plant to prey resources. At low relative resource availability, omnivores dominated community composition. Absolute resource quality and resource availability had a less pronounced effect on the number of omnivores (Chubaty et al. 2014). The introduction of an omnivore, as with its evolution, may then depend on the diet breadth of the non-native omnivore, the relative abundance of resources in the recipient community and the strength of interactions. Both the diet breadth (Ehrlich 1989, Marchetti et al. 2004) and composition of the recipient community (Elton 1958, Stachowicz et al. 1999) have been shown to be important determinants in the success of the introduced species and the invisibility of the recipient community respectively, however only recently has interaction strength been the subject of empirical work to assess its role in the impact of introduced species (Dick et al. 2014). The inclusion of interaction strength, we argue, is pivotal to understanding the impact of introduced omnivores.

1.7 Introduced omnivores

The characteristics - ranging from micro- to macroscopic - of introduced species are likely good predictors of their impacts (Ehrlich 1989) and, therefore, have been the subject of intense study. For example, the ferocity of predation (Dick et al. 2013) and high fecundity of introduced species (Keller et al. 2007) have all been correlated with high impact. Trophic position has also been the subject of analysis, with some studies suggesting that piscvores are more likely to alter fish assemblages (Moyle and Light 1996). However, there is much less consensus on the impact of omnivores. Moyle and Light (1996) suggest omnivores, in the context of fish invasions, have had a relatively low impact on existing fish assemblages. Yet, there are many prominent cases of omnivores having large impacts on recipient communities. Crayfish introductions have led to population declines, extirpation and even extinction of native crayfish species; they have been documented to alter nutrient cycling and to reduce the biomass of basal resources (Lodge 1987, Lodge et al. 1994). Other omnivores including mysid shrimp, amphipods, the king crab and Eurasian rats have had similar devastating impacts on native species (Devin and Beisel 2007, Jones et al. 2008, St Clair 2011, Falk-Petersen et al. 2011, Bovy et al. 2014). These seemingly disparate effects where some omnivores have a low impact while others have a strikingly negative impact on native communities, are likely due to the differences in interaction strengths and the absence or presence of stabilizing mechanisms.

Because an omnivore shares a common resource with its prey its introduction could conceivably result in two outcomes. If interaction strengths are strong, omnivory models predict that the presence of the omnivore is unstable (McCann et al. 1998). Either the omnivore will drive the consumer to extinction or it will drive the resource to extinction depending on where the strong interaction is in the food web. These strong interactions can lead to the omnivore persisting with one of the resources or if it cannot be sustained on available resources, the extirpation of the omnivore. Alternatively, if interaction strengths are weak the introduction of an omnivore can have little impact to recipient community or even stabilize an unstable native consumer-resource interaction (Ricciardi et al. 2013). Thus, interaction strength is pivotal to understanding observed impacts in natural ecosystems, and systems with introduced species are no exception. In fact, in one of the few studies on the impacts of non-native omnivory, Hall (2011b) found that the consumption of the both the consumer and a common resource can increase the rate of spread of non-native omnivores but it is dependent on interaction strength. As the attack rate on the resource by the omnivore (i.e., interaction strength) increases, the rate of spread decreases.

1.8 Case studies

1.8.1 Weak interactions

Ontogenetic niche shifts allow fishes to participate in niche diversification. Juvenile fish often have disparate diet preferences to reduce competition between conspecifics. As fish age and grow, they also require larger prey (Werner and Gilliam 1984). In the context of omnivory, ontogenetic niche shifts is one of the stabilizing mechanisms discussed by Kratina et al. (2012). As a juvenile, a life-history omnivore competes with the species that becomes its prey later in life. Competition can hence limit the growth of young predators, while adult predators can suppress consumers and relieve the negative effects of competition on their younger conspecifics (Hin et al. 2011). The observed low impact of introduced fish omnivores therefore may be the manifestation of life history omnivory. Interactions between non-native omnivore fishes and native consumers are weakened by the consumption of non-native juveniles by conspecific native adults.

In aquaculture, mussels, capable of consuming both plant and animal prey, effectively become omnivores when they are suspended in long lines and can consume zooplankton unavailable to them when they are benthic animals. Although zooplankton are facing the double jeopardy of both predation and competition from mussels, zooplankton persist in mussel farms (Cherif et al. 2016). The impact of the introduction of mussels on zooplankton consumers has been low owing to the weakening of predatory and competitive interactions between the mussels and zooplankton. Zooplankton secure prey size refugia by outgrowing mussel predation while ontogenetic niche shifts in zooplankton can reduce competition between mussels and zooplankton (M. Granados *et al*. Appendix B).

1.8.2 Strong interactions

Crayfish introductions have been widespread and devastating for native consumers (Hobbs et al. 1989). In a meta-analysis, Twardochleb et al. (2013) determined non-native crayfish had greater negative effects on insects, snails and fish than native crayfish. Without any broad stabilizing mechanisms including life history omnivory, it appears that the strong interactions between crayfish and their resources are responsible for the observed population declines of native crayfish (Hogger 1988, Lodge et al. 2000).

The study of interaction strengths in non-native species has recently yielded a possible mechanistic explanation for the strong impacts of some omnivores. Dick et al. (2014) compared the functional response (the number of prey that an individual predator kills as a function of prey density) of a non-native species to a related (e.g. congener) native species feeding on the same prey and found that the non-native species has a consistently “stronger” functional response. Dick et al. (2013) further propose a positive correlation between the differences in functional response between the two species compared and impact of the non-native species in the field. Functional response here can be thought of as a measure of interaction strength given it quantifies how much of the resource the predator is consuming. Crayfish, amphipods and mysid shrimp have all been shown to have strong negative effects on recipient communities and all have demonstrated stronger functional responses relative to related native species (Alexander et al. 2012, Haddaway et al. 2012, Dick et al. 2014, Dodd et al. 2014). In summary, the introduction of non-native omnivores likely also introduces strong interactions, which tends to destabilize the food web.

1.9 Conclusion

Like any non-native species, the successful introduction of an omnivore requires the right combination of propagule pressure, resource availability and environmental conditions (Ricciardi et al. 2013). The impact of an omnivore, however, can be better understood through the integration of the role of interaction strength. Here we reviewed the study of omnivory, the literature on introduced omnivores and showed that differences in the documented impacts of introduced omnivores can be ascribed to interaction strengths in the novel food web. It is therefore imperative that future work on predicting the impact of non-native omnivores includes not only the characteristics of potential invaders but also the trophic links that can be formed in the new food web. Invasive species research can only benefit from the integration of food web theory into predictive models and impact assessment.

1.10 Acknowledgements

This research was funded by an NSERC Discovery Grant to G.F.F.

1.11 Tables

Table 1.1. Glossary of terms

Term	**Definition**[1]
Functional response	The number or biomass of prey that an individual predator consumes as a function of prey density
Impact	Reduction in abundance of a native species
Interaction strength	The likelihood of consumption of one species by another
Introduced species	A species not native to the community. We refrain from ascribing "invasiveness"
Omnivory	Feeding on multiple trophic levels
Stability	Decrease in the probability of extinction as a function of increasing the minimum population size

1. Note that definitions are given in the context of the present paper and that other authors may define the same terms differently.

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2 Chapter 1

Interaction strength and the impact of introduced omnivores: A meta-analysis of introduced aquatic invasive species

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2.1 Abstract

Omnivory, or the feeding on multiple trophic levels, has been heavily studied owing to its almost ubiquitous presence in food webs. Both empirical and theoretical studies have shown that the presence of omnivory in a food web can be stabilizing by reducing the coupling strength between consumer and resource. However, we know very little about the effects of omnivory in the context of species introductions. To examine whether omnivory operates according to theoretical predictions when introduced to a novel food web, we assembled a database on the impact of the introduction of omnivores and predators, for comparison, on native prey. Using a meta-analytical approach and effect sizes we first measured the impact of omnivores and predators on native prey. We also explored the effect of prey trophic level on effect size. Because many of the predictions of omnivory in food webs are predicated on the likelihood a predator will consume a prey, we used functional response as a proxy for interaction strength to determine the relationship between effect size and interaction strength. When using coarse, community scale information on native prey abundances we did not find a difference in effect size between omnivores and predators. However, using population level data we found that omnivores had significantly greater negative impacts on native prey. Omnivores in our meta-analysis also had stronger functional responses than predators, and negative effects increased with stronger functional responses suggesting strong interaction strengths in omnivores are exerting larger negative impacts. Our results fortify the importance of interaction strengths in understanding omnivory and we submit that integrating food web theory into the study and management of invasive species is not just important but vital to mitigating the effects of continued species introductions.

2.2 Introduction

Omnivory, broadly defined as feeding on multiple trophic levels, is prolific in food webs because it reduces the coupling strength in a consumer resource interaction and can also facilitate the persistence of the omnivore (McCann 2012). When interaction strength (likelihood of consumption of one species by another) is weak, omnivory can increase the probability of persistence (here defined as stability) of the food web by bounding prey densities further away from zero (McCann 2000). Dissections of food webs reveal as many as 87% of food webs have omnivory and are characterized by many weak interactions (McCann 2000, Arim and Marquet 2004). However, very little is known about how omnivory operates in the context of species introductions, an aspect that has been explicitly studied only in a few species (Kolar and Lodge 2001, Ricciardi et al. 2013). Here we provide a broader, cohesive analysis of this topic. We feel that understanding the role of omnivory in species introductions is necessary to predict and mitigate the effects of introduced species.

The nature of species introductions as a natural experiment allows us to use data on the impacts of species introductions to test some of the predictions of food web theory and omnivory (Gaston and Blackburn 1999). Because introduced species are in a novel environment the likelihood of stabilizing mechanisms (e.g. adaptive feeding, habitat complexity, anti-predator phenotypes) that weaken interaction strengths is low (Kratina et al. 2012, Ricciardi et al. 2013). The absence of these mechanisms allows us to compare the impacts of strong and weak interaction strengths in the published literature. Our predictions are couched in a simple, tri-trophic food web with omnivory, where the omnivore feeds on both the consumer, and the resource (i.e. intraguild predation). If introduced omnivores form weak interactions with native consumers and resources, theory posits that the link between omnivore and the common resource reduces the coupling strength between the consumer and resource by shunting some of the energy up the omnivore-resource pathway and mutes this potentially excitable (i.e. population sizes reaching large values and then being depleted towards extinction) consumer-resource interaction (McCann 2012). These weak interactions should therefore translate to lower impacts via larger consumer population sizes in the literature. However, if interaction strengths are strong, omnivores may have a greater impact on the consumer particularly given omnivores are both preying and competing with consumers (Polis et al. 1989, Polis and Holt 1992). In this case strong interactions would result in lower native consumer populations (McCann 2012). For clarity henceforth we eschew theoretical terminology and refer to the consumer in the food web as prey. To examine the impacts of omnivores and the role of interaction strength in said impacts we used a meta-analytical approach to (i) quantify the impact of introduced omnivores relative to introduced predators at two different assemblage scales, (ii) assess whether that impact is mediated by the trophic level of the prey and (iii) determine if the observed impacts can be ascribed to the interaction strength between the omnivore/predator and prey.

We first assembled a database of effect sizes from field and laboratory studies to determine whether omnivores or predators had larger impacts on native prey. We divided the database into population scale data (species and genus aggregation) and community scale data (order or lower aggregation) to assess whether differences in impact between omnivores and predators were dependent on the taxonomic aggregation. We expect that impacts and differences between omnivores and predators will be muted in the community dataset as it may aggregate species that are not prey of the omnivores or predators. This distinction will also help us assess the importance of scale in assessing impacts. To assess whether that impact is mediated by the trophic level of the prey we assigned each prey in the database to as either herbivore or a consumer categories. We expect prey that are herbivorous to be more negatively impacted by omnivores as their introduction exposes them to both predation and competition. To determine the role of interaction strength in impact we used functional responses as a proxy for a measure of interaction strength. The number of prey that an individual predator kills is a function of prey density and is defined as the functional response (Holling 1959, Juliano 2001). The shape and magnitude of the curve fitted on the plot of the number of prey consumed against the number of prey supplied quantifies the interaction strength between the predator and prey (Dick et al. 2014). Predators that have lower handling times and/or achieve higher maximum feeding rates will deplete prey resources more quickly (Holling 1965), and here refer to them as displaying "strong" functional responses or "strong" interaction strengths. Functional responses have been increasingly used in the invasive species literature to provide a mechanistic explanation for the observed effects of non-native species (Dick et al. 2013, Dodd et al. 2014). Studies that compared the functional response of a non-native species to a related (e.g. congener) native species using the same prey indicated that the non-native species has a consistently "stronger" functional response. Data also suggest that the greater the differences in functional response between the two species, the greater the impact of the invader in the field, although this effect was not explicitly quantified (Dick et al. 2013). We extend this methodology in our paper and hypothesize that introduced species with a strong functional responses will elicit stronger impacts on native prey.

Our synthesis of invasive species and food web theory not only allows us to test some broad predictions of food web theory on a scale much greater than the experimental microcosm scale it is often limited to, but also provides insights into how characteristics of non-native species, like functional responses, in concert with food web theory, can be used to better predict what species will have the greatest impacts. Humans increasingly dominate ecosystems and facilitate species' dispersal, which accelerates the rate of introduction events (Vitousek et al. 1997). Accurate and robust methods that anticipate the effects of these introductions will be necessary to mitigate the coming onslaught.

2.3 Materials and Methods

2.3.1 Data sources

We began assembling our dataset by searching the *Web of Science* (https://webofknowledge.com, Thompson Reuters) for publications describing the functional response of introduced species. Using keywords (e.g. functional, response, introduced, alien, invasive) we compiled publications on 19 introduced species. We returned to the *Web of Science* and systematically searched for publications on the impacts of the introduced species or their congeners on recipient communities (e.g. *Genus* OR *species* AND impact OR effect). This search of the literature and the references cited within yielded 22,755 studies. From these studies we applied the following criteria to ensure that studies in our dataset were comparable and captured trophic differences. (i) Impact is quantified as a change in the density or biomass of native species. (ii) Study must quantify the effect of a predatory interaction. (iii) Studies that quantify the effect of an omnivore must include the availability of a common resource in the experimental design (iv) Study includes the introduction of only one non-native species. (v) Prey species in the study must be native. (vi) Study uses non-native species that do not experience strong ontogenetic niche shifts. (vii) Study quantifies the effect of both the introduced species and a control treatment (absence of introduced species). (viii) Study treatments were replicated, reports a sample size and an assessment of the variance of treatment means was possible.

We first divided the studies that met these criteria into two categories based on taxonomic resolution of the prey. Studies providing the taxonomic family or higher resolution (e.g., genus or species) were assigned to the population data set, while studies providing taxonomic information at the order level or lower were added to the community data set. This classification allowed us to examine the effects of omnivory and predation at two scales. The population data set contained studies with similar species and is an approximation of the effects on a population of prey (e.g. *Physella* sp.). The community data set contained studies that aggregated the effects on a number of different species in the same order or higher taxonomic resolution (e.g. cladocerans). Because of the inclusion of several diverse species, the community data set allows us to analyze the effects of omnivory and predation at the prey community scale. We obtained a total of 54 unique studies for the population data set and 36 for the community data set; 16 omnivore/predator species were included in the meta-analysis. Our data set included both experimental and field surveys of stream, river and lake habitats. Because not all of the impact studies contained functional response data, we separately acquired functional response data for 8 different species represented in the data set from 9 different studies after the inclusion of an unpublished data set (Barrios-O'Neil, *unpublished data*). Although we did not obtain functional responses for all species in the meta-analysis due to the availability to data, all of the species have a taxonomically similar representative in the functional response data set. We extracted data from these studies using open source Image J software (Schneider et al. 2012) and the Figure Calibration plugin (Hessman 2009). For studies where prey density at multiple time points was reported, we recorded density at the last value provided and the measure of variance at this time point. When a measure of variance was not reported we estimated variance by extracting multiple values (e.g., across multiple years), the mean and calculating the standard deviation. Limited by the low diversity of species in functional response studies all the species in our meta-analysis were freshwater crustaceans.

2.3.2 Meta-analysis

Each prey in the population data set was assigned to either an “herbivore” or “consumer” category depending on what trophic level it feeds on. We used published sources (Balcer et al. 1984, Merritt and Cummins 1996, Johnson and Allen 2005) to assess whether each prey was herbivorous (herbivore) or predatory (consumer) to determine the effect of prey trophic level on prey impact. For both the population and community data sets, species were assigned to either predator or omnivore trophic categories using published information on their prey (Pichlová et al. 2001, Hooff and Bollens 2004, Strecker et al. 2006, Pichlova-Ptacnikova and Vanderploeg 2009, Fink et al. 2012, Haddaway et al. 2012, Bacela-Spychalska and Van Der Velde 2013, Pérez-Fuentetaja and Wuerstle 2014).

Mean abundances of prey species in the presence of the non-native species ($\bar{x}_P$) and without ($\bar{x}_A$) the non-native species were used to calculate the effect size as the standard mean difference (SMD or Hedges' g) owing to the presence of negative values (Rosenberg et al. 2013) where

$$SMD = \frac{\bar{x}_P - \bar{x}_A}{\sqrt{\frac{(n_P - 1)SD_P^2 + (n_A - 1)SD_A^2}{n_1 + n_2 - 2}}} \tag{1}$$

SMD weights each group's standard deviation (SD_i^2) by its sample size (n_i), a recommended approach when the groups are dissimilar in size (Hedges 1981). Given that the SMD is undefined in cases where the denominator is zero, a detection limit of 0.01 was added to all zero values (Iacarella et al. 2015). The meta-analysis were performed using the metafor package 1.9-7 (Viechtbauer 2010). We tested for adherence to the normality assumption and searched for publication biases (i.e. whether non-significant data is omitted) in our dataset by plotting a Q-Q plot (Wang and Bushman 1998). Visual inspection of the plots did not suggest the presence of publication biases or deviations from normality. Because we used multiple effect sizes from a single study we calculated the intra-class correlation coefficients (ICC) for both community and population datasets to determine the magnitude of non-independence of effect sizes within studies and species (ICC package 2.2.1; Wolak et al. 2012, Iacarella et al. 2015). Calculated ICCs indicated a lack of dependence between studies (ICC= -0.092) for the community data set and between studies (ICC=0.402) and species (ICC=0.231) for the population data set.

We fitted a mixed-effects model with non-native trophic level (i.e. omnivore or predator) as a moderator for the community data to assess the effect of trophic level on prey impact. For the population data set, prey trophic information allowed us to explore the effect of prey trophic level on effect size in addition to non-native species trophic level. We fitted a mixed-effects model with non-native trophic level to the population dataset and used a likelihood ratio test with a maximum likelihood estimation to test the interaction of non-native trophic and prey trophic level (Raudenbush and Bryk 1985). Forrest plots were produced using alternative parameterizations of the models without an intercept. All analyses were conducted in R (R Development Core Team 2015).

2.3.3 Functional responses

Functional response data (prey density provided and number of prey consumed) for each available species in our data set were obtained using Image J as above with the exception of the *Bythotrephes longimanus* data, which was obtained empirically and we did not need to extract values. For each predator-prey data set we first tested the appropriateness of a type I (non-saturating) or type II (saturating) functional response by plotting the proportion of prey consumed against prey density and fitting a linear model to the data. Data demonstrating a negative slope were fitted using the Rogers' random predator equation (Rogers 1972) for non-replacement of prey (Juliano 2001) where the prey consumed (N_e, equation 2) is a function of the prey density (N_0, equation 2) and a is the attack rate and h is handing time.

$$N_e = N_0(1 - e^{a(N_0 h)}) \tag{2}$$

We used the Lambert W function in the emdbook and the frair package to implement equation 2 to estimate the parameters a and h, owing to the presence of N_e on both sides of the equations (Bolker 2010, Pritchard 2014). Data sets demonstrating a type I functional response were fitted using equation 3, where a is attack rate using the frair_fit function in frair package as above (Pritchard 2014). For both Type I and II fits, prey consumed (N_e) was standardized to per predator, per day.

$$N_e = aN_0 + b \tag{3}$$

To standardize attack rate across experiments in both type I and type II functional responses, we divided a by the volume of the experimental areas (in liters) to generate an attack rate a, per liter. We subsequently divided this value by the length of the predator to arrive at an attack rate L^{-1} mm^{-1}. To incorporate the different sizes between predator and prey we divided the handing time, h, by the ratio of the prey to predator length in the type II functional response fits where handling time is incorporated.

Finally, to assess the relationship between interaction strength (measured as attack rate and handling time) and impact, bootstrapping was used to generate multiple estimates (*n* = 20) of the a and h parameters were standardized as above (Alexander et al. 2012). We subsequently ran a linear model with effect size (SMD) of each species represented in the functional response data set as the dependent variable and the different measurements of interaction strength as the explanatory variable. All analyses were conducted in R (R Development Core Team 2015).

2.4 Results

2.4.1 Meta-analysis

The population and community data sets yielded information on the impact of 12 and 15 species, respectively (Appendix A, Table A1-A2). Constrained by the availability of functional response data, all of the species in the analyses were freshwater crustaceans. We did not include any fish data given their strong ontogenetic changes with age (Werner and Gilliam 1984). While the community dataset did not indicate a difference in impact between predators and omnivores (mixed-effects model, QM= 1.161, p= 0.2812), we did detect a difference in the population data set (mixed-effects model, QM= 37.777, p<0.001). The population meta-analysis indicated that omnivores had a greater negative impact on their prey relative to predators as indicated by a larger negative effect size, where effect size measures the differences in prey abundance or density in the absence and presence of the non-native species (Fig. 2.1). However we did not find that the effect size was mediated by the trophic level of the prey as the model with the interaction did not show a significant effect of prey type on the effect size of the omnivores and predators (likelihood ratio test, p= 0.654).

2.4.2 Functional responses

We fitted a total of 34 functional response curves for four predator and four omnivore species, each of which was represented in the meta-analysis data set (Appendix A, Table A3). Linear regression of impact against attack rate indicated a negative relationship with stronger attack rates eliciting more negative impacts on prey (Fig. 2.3a, R^2 =0.141, p<0.05 (bootstrapped)). The linear regression of handling time against impact produced similar results - as handling time decreases, the effect size is increasingly negative (Fig. 2.3b, R^2 =0.163, p<0.01 (bootstrapped)). Omnivores also had significantly higher attack rates (t-test, p<0.001) but we found no difference in handling times between predators and omnivores (t-test, p=0.1384).

2.5 Discussion

We found that the introduction of omnivores has a greater negative impact on native prey relative to predators and that omnivores have higher attack rates. The results from the functional response analysis suggests that the higher impact of omnivores is likely driven by strong interaction strengths between introduced omnivores and their prey. Studies comparing the functional responses of introduced species and comparable native species have consistently found that introduced species have stronger functional responses (Dick et al. 2014). Studies of fishes (Alexander et al. 2014), amphipods (Bollache et al. 2008, Dodd et al. 2014) and crayfish (Haddaway et al. 2012) all recorded lower handing time or higher maximum feeding rates in the introduced species. Dick et al. (2014) speculate that these stronger functional responses are what are driving the success of introduced species. If successful invaders are generally characterized by stronger functional responses it is no surprise then that omnivores with strong functional responses have a higher impact given their wider prey breadth. Under omnivory the prey can be subjected to both predation and competition, a scenario made stable only when those interactions are weak (Holt and Polis 1997, McCann 2000).

The negative result in our taxonomically coarse, community data set suggests that the greater negative effects exacted by omnivores on native prey is muted at coarser scales. Although all of the native prey included at the community scale are potential prey, omnivores and predators will exercise feeding preferences (Ivlev 1961, Emlen 1966). At the community scale the strong interactions between omnivores and one prey are likely accompanied by weaker interactions between omnivores and other prey types. Our results thus suggest that the greater negative effect of omnivores may not scale up to a community effect because of the inclusion of multiple trophic links.

In this paper we utilized the expansive invasive species literature to test the theoretical predictions of interaction strengths and omnivory in food webs. Our results on the effects of omnivory are consistent with expectations based on the context-independent application of trophic theory. Here, instead of omnivory shunting some of the energy away from the predator-prey interaction up through the predator-resource pathway, strong interaction strengths, as evidenced by strong functional responses, caused decrease in the abundance of the native prey community. The higher impact was likely mediated through the combination of stronger predation or depletion of shared resources. Predators, in contrast, only exacted relatively weaker consumptive interactions on the prey and had lower impacts. Of interest here is the observed differences in interaction strengths between omnivores and predators, which may be indicative of a filtering effect in one of the stages of invasion whereby only omnivores with strong interaction strengths can invade (Williamson 2006). Theory further predicts that the impact of omnivores should be less on consumer prey where they are not subject to competition in addition to predation by the predators (Polis et al. 1989, Polis and Holt 1992). We found no interaction of prey type and predator trophic level on impact, however the mean impact on consumers was lower than on herbivorous prey, which suggests a trend toward the predicted stronger negative effect on herbivorous prey.

Across trophic levels our results show that as interaction strength increases, measured through attack rate and handling time, the impact on the prey increases -

indicating the strong relationship between interaction strength and impact (Fig. 2.3). While our study is not the first to investigate the role of omnivory in invasive species, previous studies have reported variable effects of omnivory on the recipient community. Studies of fishes have found invading that omnivores have little effect on recipient fish communities (Moyle and Light 1996) while other introduced omnivores like crayfish have had deleterious effects on resident consumers (Ricciardi et al. 2013). In our study we explicitly used species that do not undergo strong ontogenetic shifts to decrease the variability in impact due to size or age differences in the predators, which may be driving the variability in the measured impacts of omnivores (Ricciardi et al. 2013). Further our study is the first to incorporate a measure of interaction strength to explain the perceived differences between predators and omnivores.

2.5.1 Implication for invasive species management

Functional responses are increasingly seen as a valuable tool for invasive species prediction and management (Dick et al. 2014). Our study not only provides further evidence for the effectiveness of functional responses in invasive species research but also synthesizes this literature with theoretical approaches. Functional responses can be used as a measure of interaction strength and with knowledge of the recipient community used to predict the impacts of introduced omnivores. Although our study had limited taxonomical breadth, conceivably, omnivores with weak or weakened interaction strengths could have a markedly lower impact on the native prey and possibly confer the advantages of omnivory. Fishes with ontogenetic niche shifts, species introduced to habitats with prey refuges, inducible prey defenses all can act to weaken interaction strengths between omnivores and prey (Kratina et al. 2012). In fact, while the study introduction of non-native species has mostly focused on negative effects, some studies have reported benefits of introduced species (Henkanaththegedara and Stockwell 2014, Macneil and Dick 2014). Understanding not only the characteristics of the introduced species but also how those characteristics interact with the recipient community and their interaction strengths is crucial to understanding how introduced species will proliferate and impact communities. Our results suggest the most deleterious introduced species may be those with strong interactions with native prey and particularly those that engage in omnivorous interactions with prey that serve both as competitors and prey. These results could be integrated and extended into the management of non-native and invasive species to better predict the outcomes and mitigate impacts.

2.6 Data accessibility

The complete R script for the analysis performed in the paper and associated data can be found online as a GitHub repository at the following DOI: http://dx.doi.org/10.5281/zenodo.48148

2.7 Acknowledgements

We would like to thank Josie Iacarella for her assistance with the meta-analyses methodology. This study was funded by an NSERC Strategic Grant to G.F.F.

2.8 Supporting information

Additional supporting information can be found the following DOI: http://dx.doi.org/10.5281/zenodo.49303

Table A1. Community data and metadata on the impact of introduced species used in the meta-analysis

Table A2. Population data and metadata on the impact of introduced species used in the meta-analysis

Table A3. Taxa information and metadata for species used in the functional response analysis.

Appendix B. References for studies used in the analyses in the paper

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2.10 Figures

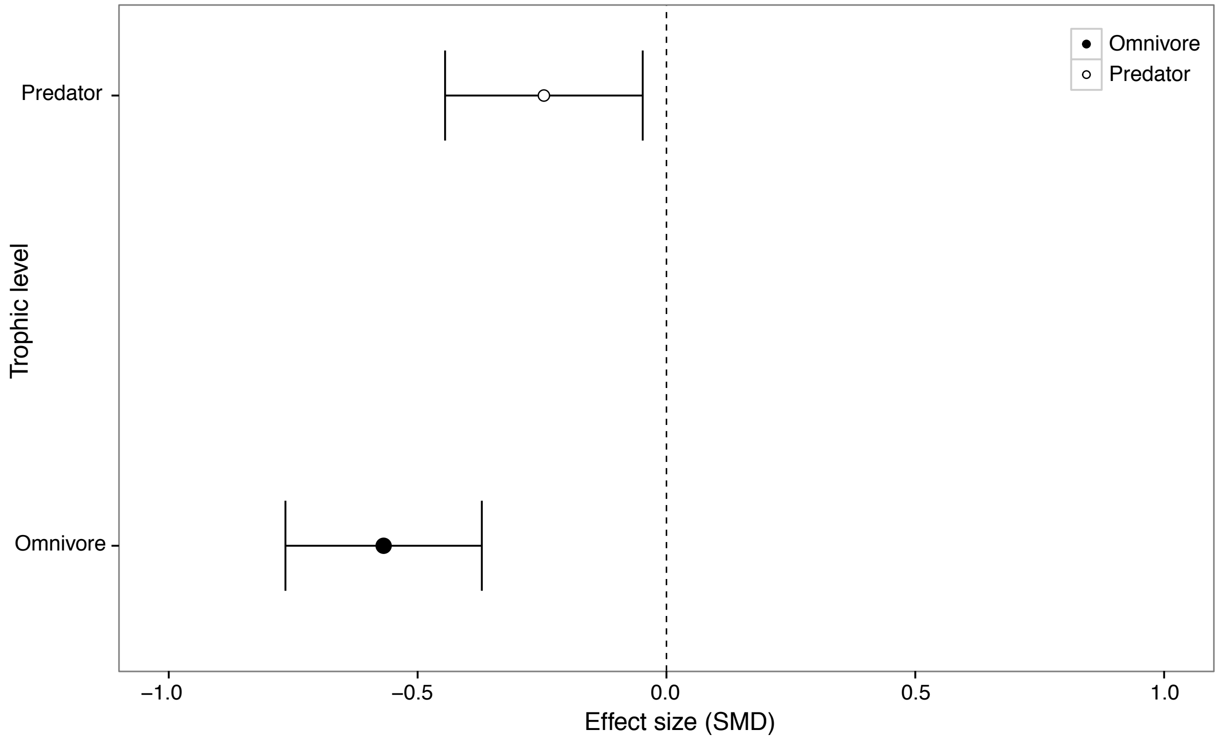

Figure 2.1. Forrest plot of the effect size (measured as the Standardized Mean Difference) of omnivores (closed circle) and predators (open circle) in the population data set. Differences in effect size are significantly different (mixed-effects model, QM= 37.777, p<0.001). The size of the points is indicative of the number of studies used to obtain the mean effect size: omnivore (81), predator (75). Error bars denote 95% confidence intervals.

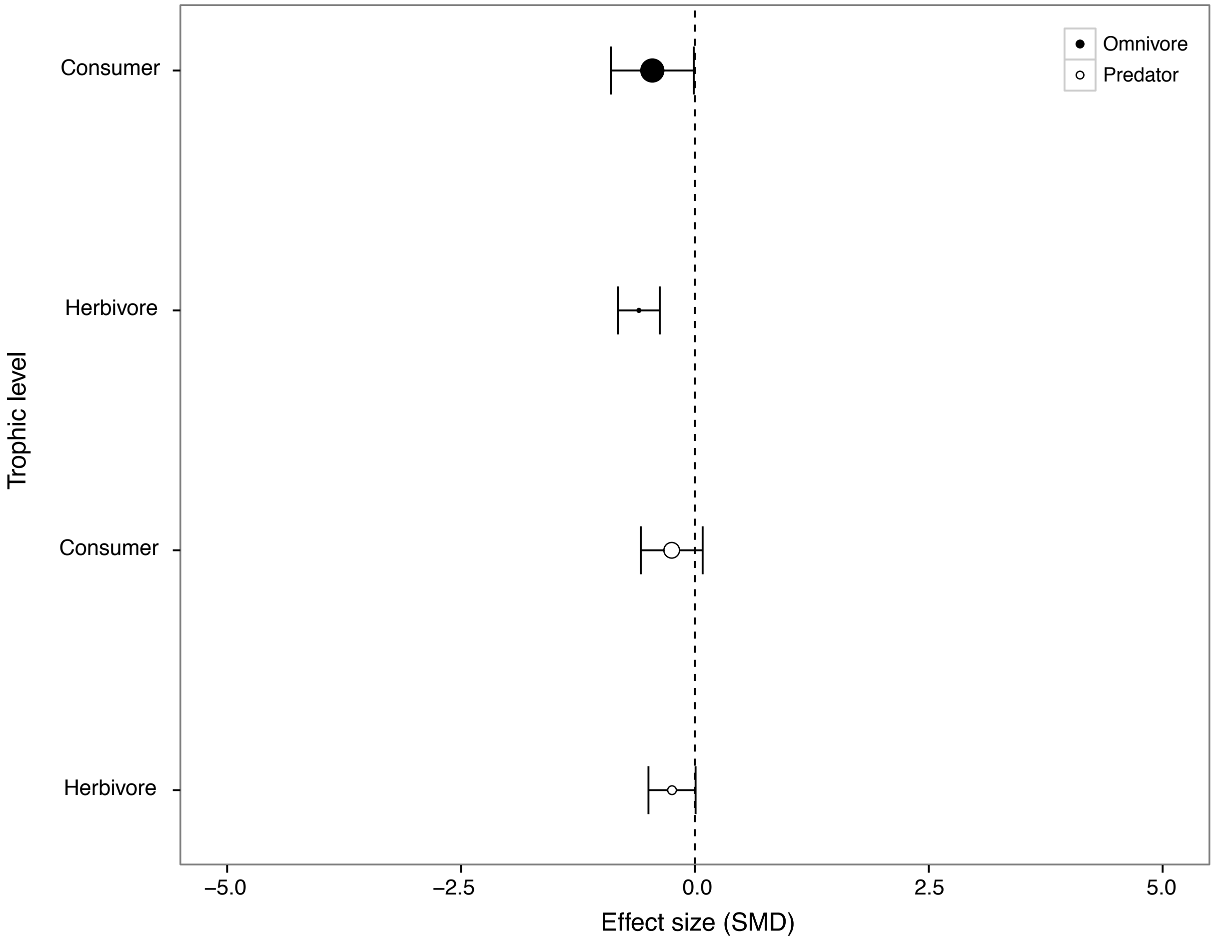

Figure 2.2. Forrest plot of the effect size (measured as the Standardized Mean Difference) of omnivores (closed circle) and predators (open circle) in the population data set separated by the trophic level of the prey they consumed. Differences in effect size among prey type are not significant (likelihood ratio test, p= 0.654). The size of the points is indicative of the number of studies used to obtain the mean effect size: omnivore-consumer (64), omnivore-herbivore (17), predator-consumer (46), predator-consumer (29). Error bars denote 95% confidence intervals.

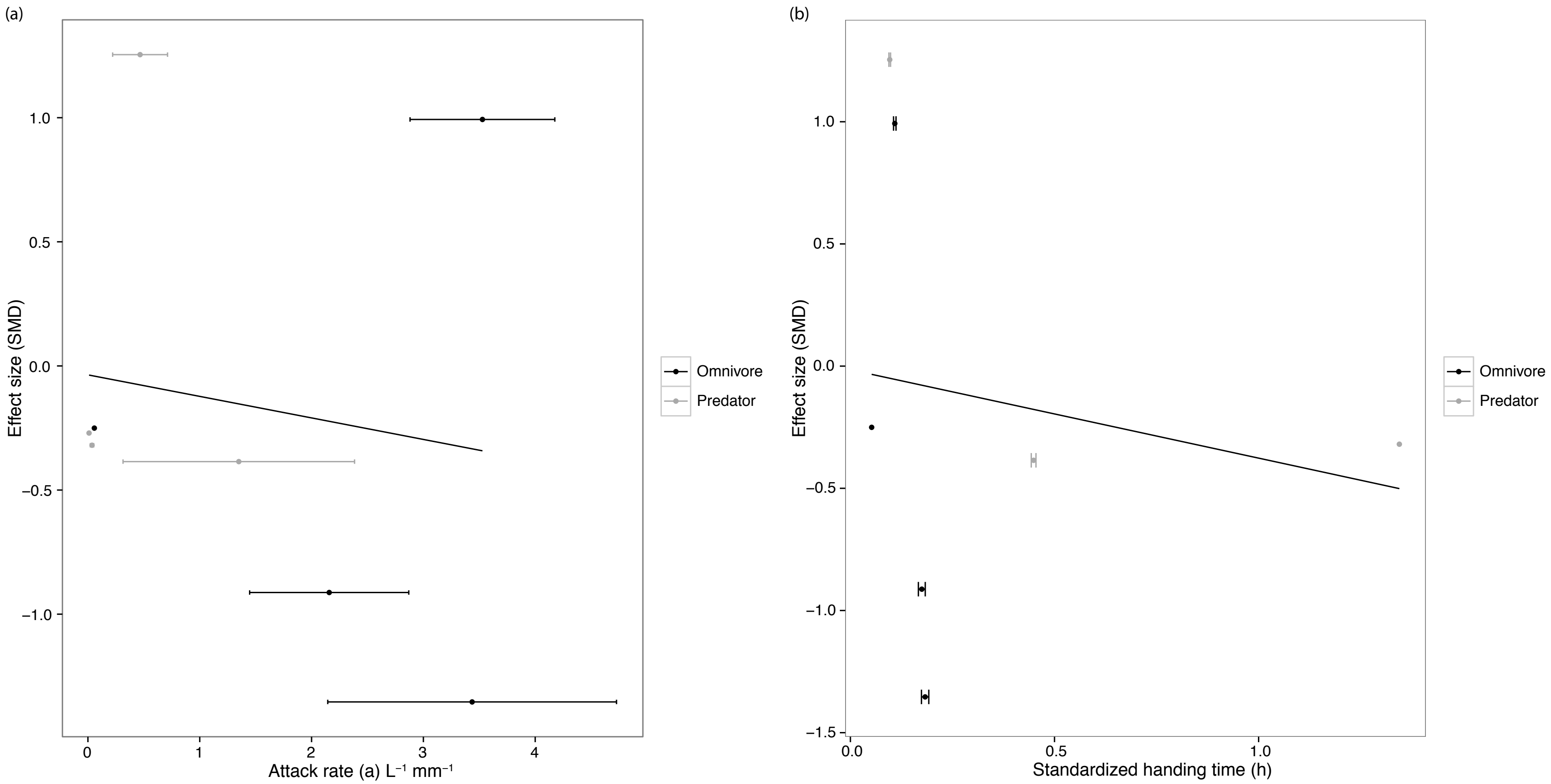

Figure 2.3. Linear regression of omnivores (black) and predators (grey) of (a) effect size (measured as the Standardized Mean Difference) against attack rate standardized by the length of the omnivore/predator and the size of the arena. Linear regression is significant using bootstrapped values ($R^2 = 0.141$, $p<0.05$). (b) effect size against handling time standardized by the ratio of the prey to predator length. Linear regression is significant using bootstrapped values ($R^2 = 0.163$, $p<0.001$). Error bars denote standard error.

2.11 Connecting statement

In the first chapter of the thesis I demonstrated that introduced omnivores have significant effects on recipient communities and that the impacts are tied to interaction strength. One community subject to the introduction of omnivores is the zooplankton and phytoplankton community that surround mussel farms. Mussels are normally confined to feeding on phytoplankton near the benthos (Gosling 2003). Once suspended on long lines in aquaculture, mussels are rendered omnivores consuming zooplankton while competing with zooplankton for a common phytoplankton resource. In Chapter 2 I empirically assembled the mussel-zooplankton-phytoplankton food web to determine how the growth rates of the zooplankton consumer differ among omnivory and other food web modules. Using a novel application of RNA:DNA ratios I quantified growth rates in six and 24-hour experiments. The results of this chapter extend the results from Chapter 1 by increasing our understanding of how omnivory can stabilize food webs beyond the fluctuation of population sizes. Interaction strength is an important parameter that controls the extinction of the food web and growth rates and their variation can be an important contributor.

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3 Chapter 2

Size and variation in individual growth rates among food web modules

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A version of this manuscript is in review at Ecosphere

3.1 Abstract

The complexity of food webs can be reduced to fundamental modules of trophic interactions that repeat to form reticulate webs. Omnivory, defined as feeding on more than one trophic level, is a module that is found in food webs more often than predicted by chance, likely because it confers stability. Yet little is known about how omnivory and other food web modules affect individuals in the food web. Here we constructed four different experimental food web modules using a blue mussel predator, zooplankton consumer and phytoplankton resource. By manipulating the predator's access to the consumer and providing resource subsidies, we produced exploitative competition, food chain and omnivory food web modules, and a consumer-resource interaction. We used RNA:DNA ratios to measure the growth rate of the consumer in each food webs. In 24-hour experiments, growth rates of the consumer in the omnivory food web were significantly higher and more variable than in the other modules. Our results suggest that higher growth rates and variation at the individual scale may weaken the strength of predator-consumer interactions and help explain the ubiquity of omnivory in real food webs.

3.2 Introduction

Graphical illustrations of food webs are reticulate representations of who-eats-whom interactions. Yet, dissected food webs reveal a basal architecture of simple, connected trophic modules (Holt 1995, Milo et al. 2002). These simple modules facilitate the study of complex food webs by representing the basic, distinct types of trophic interrelationships. In a multi-trophic, three-species food web, interactions can be arranged into distinct modules here we review three: (1) the food chain, where energy flux is transported up trophic levels (2) exploitative competition, where two consumers compete for a common resource and (3) omnivory, where the predator both preys upon and competes with the consumer (Fig. 1, McCann 2012). These simple theoretical models represent fundamental units of complex food webs.

In food webs, the frequency of these different trophic modules varies (Bascompte and Melián 2005). Of the three tri-trophic, three-species modules in food webs considered here, omnivory is over-represented and is detected more often than expected by chance (Bascompte and Melián 2005), although some contention about the prevalence of omnivory persists when not considering the influence of interaction strength (the likelihood of a predator consuming a resource) (Milo et al. 2002 and Williams and Martinez 2004). However, feeding on more than one trophic level seems ubiquitous across terrestrial and aquatic food webs (Winemiller 1990, Hall and Raffaelli 1991, Polis 1991, Arim and Marquet 2004, Thompson et al. 2007), likely because omnivory, when interaction strength is weak, removes energy from consumer-resource interactions that have the capacity to fluctuate rapidly (McCann 2012).

While many theoretical (Holt and Polis 1997, Vandermeer 2006) and empirical studies (Fagan 1997, Holyoak and Sachdev 1998) have explored how omnivorous interactions can stabilize (here defined as an increase likelihood of persistence) food webs by muting population changes, there is reason to believe that individual growth rates and its variability can also influence stability. Simulations of predator-consumer interactions by Moya-Laraño (2011) showed that individual variation in somatic growth rates of the predator could decrease the average strength of predator-consumer interactions, increase the variation in interaction strengths across species pairs, and increase the rates of omnivory. Simply stated, because body size is so strongly linked to prey type, more variation of predator body sizes results in more variation in predator-consumer interactions. This means that higher individual variation could promote food web stability by weakening resource-consumer interaction strengths and conferring the properties that make omnivory stabilizing. Since body growth rates also govern when individuals reach reproductive maturity, individuals with higher growth rates may produce more offspring over the course of their lives simply because it facilitates longer reproductive spans. Furthermore, since body growth rates also govern the availability of prey size refugia, consumers with high growth rates could outgrow their predators (Chase 1999). Both mechanisms could lead to larger consumer population sizes and reduced predator-consumer interaction strengths.

In this paper we explore how different tri-trophic food web modules affect (1) the growth rate of the consumer and (2) the variability of these growth rates to understand how both can ultimately influence food web stability. We experimentally constructed four food web modules: consumer-resource interaction, exploitative competition, food-chain and omnivory, each consisting of one predator, one consumer and one resource to assess the growth of the consumer and the variability of these growth rates in each of the modules. We used a blue mussel, zooplankton and phytoplankton system to build the modules (Fig. 1). Here, both the mussel and zooplankton feed on phytoplankton, while the mussel has the capacity to consume zooplankton. The blue mussel is an omnivore with an equal preference for phytoplankton or zooplankton irrespective of their relative densities; however, as blue mussels grow, they can accept a wider size range of zooplankton (M. Granados *et al*. Appendix B). We assessed the growth of the consumer, here zooplankton, in each of the food web modules using RNA:DNA ratios (Dagg and Littlepage 1972, Johannsson et al. 2009). We tested four hypotheses on the effects of food web structure on individual growth rates: 1. We expect competition between consumers should limit growth rates in the consumer-resource interaction and be more pronounced in the exploitative competition module where mussels are competing for the same resource as zooplankton. 2. In the food chain and omnivory modules individual consumers should benefit from reduced intraspecific competition and the increased resource availability that follows. 3. Growth rates should be highest in the food chain module where competition between the predator and the consumer is absent. 4. We expect that variation in growth rates should be highest in the food chain and omnivory modules where mussels could drive a bimodal distribution of zooplankton sizes through size selective predation and competition between zooplankton in the omnivory modules could drive that variation even higher.

3.3 Materials and methods

We manipulated the consumption of the resource and the consumer by the predator to produce four food web modules: omnivory, food chain, exploitative competition, the consumer-resource interaction plus a control containing only the consumer and resource (Fig. 1). Together they comprise five treatments.

We performed two sets of experiments lasting six hours and 24 hours to assess differences in response between the two time periods. Five hours had been previously shown as is the minimum time required to detect differences in RNA:DNA ratios thus we selected 6 and 24 hours to ensure detection of growth differences (Vrede *et al.* 2002). Each experiment was conducted in a series of trials (temporal replicates): three for the six-hour experiment and four for the 24-hour experiment. Each trial contained three replicates for each treatment. In the 24-hour experiment, the food-chain module resulted in the extinction of the consumer; consequently, only four treatments are presented for that experiment.

3.3.1 Experimental set-up

Fifteen microcosms were constructed from 15 L round plastic containers filled with 8 L of UV-treated, filtered seawater. Each microcosm was inoculated with combinations of 1. *Artemia franciscana* N2 nauplii (henceforth: "*Artemia*" or "the consumer"), 2. a non-axenic strain of the flagellated alga *Isochrysis galbana* (mean cell diameter 6.1 µm) (Prymnesiophyceae, henceforth: "phytoplankton" or "the resource"), and 3. a single planktivorous blue mussel, *Mytilus edulis* (shell length range 51 ± 2 mm (SE); henceforth "the predator"). *Artemia* eggs (supplier: Artemia International) were kept in a refrigerator at 5°C, then decapsulated and hatched in 10 L glass aquaria with aeration. The hatched *Artemia* were kept in the aquaria for 96 hours before the start experiment to obtain N2 individuals and without food to deplete their yolk reserves (Reeve 1963). *Artemia* are filter feeders that use setae on their swimming legs (phyllopods) to capture particles (Criel and Macrae 2002). Blue mussels are also filter feeders that can adjust their filtration rate depending on the concentration of particles in the water, where higher concentrations elicit higher filtration rates. Blue mussels can accept particles in the range of 1-1000 µm, although their highest retention efficiency is at 3 µm (Gosling 2003). While maximum filtration rate is related to mussel length (Gosling 2003), the small variance in the size range used in the experiment does not introduce an effect of size. *Isochrysis galabana* was obtained from NutrOcéan and cultured in 40 L vessels with aeration, while blue mussels were obtained from an aquaculture farm (Baie-des-Chaleurs Carleton, Quebec).

Each microcosm received an initial inoculation of 200 *Artemia* individuals ml^{-1}and 100,000 phytoplankton cells ml^{1}. These densities gave *Artemia* sufficient resources to grow but kept them below the threshold density that would arrest mussel filtering (Evjemo 1999). Experiments were conducted in chambers at 18°C without light to avoid stimulating phytoplankton growth and altering *Artemia* swimming behaviour.

3.3.2 Food web modules

We generated the different food web modules by manipulating the trophic link between the predator and the consumer, and/or the trophic link between the predator and the resource, except for the omnivory food web module where they remained intact (Fig. 3.1).

Consumer-resource: Both predator-consumer and predator-resource trophic links where removed by placing the predator in the 250 μm sleeve and adding resource subsidies, respectively (Fig. 3.1b). Because the average length of N2 nauplii in our experiment was 650 ± 40 μm, enclosing the predator in a 12 cm x 8 cm Nitex mesh sleeve with width of 250 μm stopped the consumer moving through the sleeve and being eaten by the predator. The addition of phytoplankton subsidies allowed us to remove the competitive interaction between the predator and the consumer by adding back the phytoplankton resource removed by the predator. For logistical ease, every three hours we determined the concentration in the microcosms using a Neubauer hemocytometer and added cells from the phytoplankton culture vessel. Additions were volume-corrected to bring the phytoplankton densities back to starting conditions. Because the amount of resource removed by the predator is much larger relative to the consumer is much larger relative to the consumer, the addition of subsidies allowed us to remove the competitive interaction between the predator and the consumer by adding back the phytoplankton resource removed by the predator (Gosling 2003).

Exploitative competition: To create the exploitative competition module we allowed the predator to consume the resource and did not add subsides, but we removed the predator-consumer trophic interaction by placing the predator in the 250 μm pouch (Fig. 3.1c).

Food chain: We created the food chain modules by providing phytoplankton subsidies to remove the predator-resource interaction and to allow predation on the consumer, we placed mussels in a 1000 μm sleeve, which allowed the infiltration of *Artemia* while controlling for the possible effects of a sleeve on the predator (Fig 3.1d).

Omnivory: For the omnivory module we did not manipulate any trophic links. Omnivory microcosms did not receive subsidies and mussels were placed in a 1000 μm mesh sleeve (Fig 3.1e).

We added an additional control treatment consisting of only *Artemia* and phytoplankton in the microcosm (Fig 3.1a). The inclusion of the control treatment allowed us to determine whether the trophic manipulations were successful by providing results in the absence of the predator. For all modules, mussels were transferred to sleeves in a basin with filtered seawater 24 hours prior to the experiment to allow acclimation to conditions.

At the end of each trial, we removed the mussel and took a 10 ml subsample of water to determine final phytoplankton densities. Subsequently, the contents of the microcosm were filtered through a 64 µm sieve and filtrate transferred to a 45 ml Falcon tube. We determined the number of *Artemia* remaining in the microcosm using a 15 mL subsample, used as a proxy for quantifying predation on *Artemia*. A second 15 ml subsample was taken, transferred to vials and stored at -80°C to determine RNA:DNA ratios.

3.3.3 RNA:DNA ratios

We quantified growth in the consumer (*Artemia*) by determining the RNA:DNA ratio in *Artemia* individuals across the treatments for both the six and 24-hour experiments. Because RNA is required for protein synthesis, the concentration of RNA in tissue is an index of cell growth (Speekmann et al. 2006). To make comparisons amongst modules the total amount of RNA must be normalized to a measure of cell size. Since the amount of DNA is constant per somatic cell, the ratio of RNA to DNA is an estimate of the magnitude of protein synthesis in a cell and ultimately the growth rate of the organism (Vrede et al. 2002, Johannsson et al. 2009). RNA:DNA ratios are an excellent method to obtain a measure of growth rate for short-term experiments because RNA synthesis occurs on a short time scale and thus responses to different treatments can be detected in as little as five hours (Vrede et al. 2002).

Twenty-four hours prior to the RNA:DNA analyses vials with *Artemia* individuals were transferred from the -80°C freezer to a -20°C freezer. To prevent the degradation of the RNA in the samples, we added sufficient RNA*later*-ICE (Ambion) to cover the each sample.

Three *Artemia* individuals were removed from each vial representing each food web module replicate and transferred to micro-centrifuge tubes. We repeated this three times for a total of nine micro-centrifuge tubes for each module and each trial. We used the mean across the nine micro-centrifuge tubes for each module for statistical purposes since each tube is not independent. We then added 350 µl of 1XTE buffer and homogenized the sample with a pellet mixer (see Vrede *et al.* 2002). Samples were incubated on a shaker table for an hour and then transferred to a black 96-well plate. We added 100 µl of RiboGreen reagent solution to each well and allowed it to incubate for an additional 30 minutes. The RiboGreen solution binds with RNA and DNA in the sample and fluoresces when excited by a mercury lamp. The fluorescence is subsequently converted to concentration using a standard curve (Vrede et al. 2002). The RNA and DNA standards were added to the 96-well plate and processed in tandem with the samples. Fluorescence was measured on a spectrofluorometer with a 96-well plate reader (Synergy I, BioTek). After the fluorescence measurements 25 µl of RNase solution was added to each well to degrade the RNA in the sample to measure the concentration of DNA remaining. Samples were incubated for an additional 30 minutes and the plate was re-read.

3.3.4 Statistical analyses

One-way ANOVAs were performed on the final phytoplankton and *Artemia* densities, and on the RNA:DNA ratios, with a Tukey HSD for pair-wise comparisons. A linear regression was used to determine the relationship between the RNA and DNA standards and fluorescence for the standard curve. We calculated the variance (spread of the points from the mean) in RNA:DNA ratios for each module using data pooled across all of the trials for the six and 24-hour experiments. In the calculation of the variance, each microcosm in each trial serves as a replicate. We performed a Bartlett's test for homogeneity of variance to determine whether the variances were significantly different across treatments. For the six-hour experiment we removed the omnivory module to perform the Bartlett's test the as there was insufficient replication, owing to loss of replicates. All statistical analyses were performed with R (R Core Team 2015).

3.4 Results

Because experiments were conduced in a series of trials, to retain independence for statistical analyses we averaged *Artemia* density, phytoplankton density and RNA:DNA results within each module for the three 6-hour experiments trials and for the four 24-hour experiment trials. This resulted in a total of three replicates for each control and module for the six-hour experiment, and four replicates for each control and module for the 24-hour experiments. For the 24-hour experiments, we removed the food chain module from subsequent analyses since the mussels consumed all the *Artemia*.

3.4.1 Phytoplankton

3.4.1.1 Six-hour experiment

Adding phytoplankton subsidies to form the consumer-resource and food chain modules resulted in no significant difference in final phytoplankton densities between the control and the consumer-resource module (Tukey HSD, p=0.07) and a significant higher density in the control treatment and the food chain module (Tukey HSD, p=0.04, Appendix A Fig. A.1a). We observed significantly lower final phytoplankton densities in the exploitative competition and omnivory modules relative to the control (Tukey HSD, p<0.01).

3.4.1.2 24-hour experiment

We found a significant difference between final phytoplankton densities in the control and the consumer-resource, exploitative competition and omnivory modules (Appendix A Fig. A.1b, Tukey HSD, p<0.01). Among the manipulated modules, the final phytoplankton density was significantly higher in the consumer-resource module (Tukey HSD, p<0.01). We did not detect a significant difference between the exploitative competition and the omnivory module (Tukey HSD, p=0.99).

3.4.2 Artemia

3.4.2.1 Six-hour experiment

Given that predation was allowed to proceed in the food chain and omnivory modules, final *Artemia* densities were significantly lower than in the control (Appendix A Fig. A.2a, Table A.1). However, the consumer-resource and exploitative modules were not significantly lower (Appendix A Fig. A.2a, Table A.1). There was no significant difference between the food chain and omnivory modules (TukeyHSD, p=0.755).

3.4.2.2 24-hour experiment

Similarly, we found significantly lower *Artemia* densities in the omnivory treatment relative to the control, consumer-resource and exploitative competition modules where predation was allowed to proceed (Appendix A Fig. A.2b, Table A.2). We found no significant difference in *Artemia* densities between the control and the consumer-resource or exploitative competition modules.

3.4.3 RNA:DNA ratios

3.4.3.1 Six-hour experiment

Over the course of six hours, we were unable to detect any differences in *Artemia* RNA:DNA ratio between the different modules considered including the control (Fig. 3.3a, Appendix A Table A.1). Variance was highest in the exploitative competition module but was relatively similar across the other modules (Fig. 3.4a, Bartlett's test p= 0.136).

3.4.3.2 24-hour experiment

In the 24-hour experiment, we found that the *Artemia* in the omnivory module had significantly higher RNA:DNA ratios relative to those in the other modules and the control (Fig. 3.3b, Supplementary material Appendix A Table A.2). We found no differences in the *Artemia* RNA:DNA ratio between consumer-resource, exploitative competition and control modules. Variance was also much higher in the omnivory module (Fig. 3.4b, Bartlett's test p<0.001).

3.5 Discussion

We were able to construct three food web modules and the consumer-resource interaction that appears within each of the food webs. The results demonstrated that in both the six and 24-hour experiments predation on *Artemia* in the consumer-resource and exploitative competition modules was not significantly different from the control. With the addition of resource subsidies, we expected the consumer-resource and food chain final phytoplankton densities to not differ from the controls – where the decline in density corresponds to the consumption of phytoplankton only by *Artemia*. With the exception of the food chain module, we successfully achieved the desired differences in phytoplankton densities in the 6-hour experiment. In the 24-hour experiment, while the final phytoplankton density in the consumer-resource interaction was significantly lower than in the control, the density was still significantly higher than the two other food web modules where subsidies where not provided. Although we detected a difference in phytoplankton density between the control and the consumer-resource modules in the 24-hour experiment, the density was measured at the end of the experiment once the mussels had a three-hour period to consume the phytoplankton.

3.5.1 Magnitude of growth rates

Although a previous study suggested that differences between treatments including diet can be detected in as little as 5 hours, we were unable to detect differences in RNA:DNA ratios in the 6-hour experiment (Vrede et al. 2002). Other studies suggest that it is insufficient time for organisms to integrate treatment differences and express them through differential RNA production and experimental periods of 24-hours or more are required (Gorokhova 2003, Speekmann et al. 2006, Gusmão and McKinnon 2009). The 24-hour results suggested that growth was greatest in the omnivory module. Although *Artemia* in the omnivory module was subjected to simultaneous competition and predation, at the individual scale the predation by the mussel on *Artemia* likely reduced intraspecific competition. Laboratory experiments with *Artemia* and the diatom *Phaeodactylum tricornuum* suggest that *Artemia* filtering rate increases with decreasing *Artemia* density (Braun 1980). *Artemia* here may be responding to physical or chemical cues from the mussel or conspecifics and increasing their filtering rate to escape predation by size refugia (Balcionas and Lawler 2011). Increased filtering coupled with higher resource availability, due to decreased intraspecific competition, likely led to higher RNA:DNA ratios, a proxy for higher growth rates (Vrede et al. 2002). Other studies have also detected higher RNA:DNA ratios in arthropods in response to increased food availability or quality (Vrede et al. 2002, Speekmann et al. 2006, Gusmão and McKinnon 2009). The results also suggest competition in the omnivory module was weak relative to the strong influence of predation.

The density of *Artemia* individuals remained constant and intraspecific competition was not relaxed in the consumer-resource and the exploitative competition modules. While the food chain module may have conferred the benefit of decreased intraspecific competition to *Artemia*, the effect was apparently negated by increased predation by the mussel on *Artemia*. As previously mentioned, the filtration rate of mussels is very much tied to the density of particles in the water (Gosling 2003). The extirpation of *Artemia* in the food chain microcosms was likely facilitated by the addition of algal subsidies, which increases the density of particles in the water, and consequently the filtering rate of mussels. The higher filtering rate thereby increases the predation rate on *Artemia* as it is more likely that the consumer will be captured. This effect is also visible in the densities of phytoplankton in the 6-hour experiments where despite the addition of subsidies, the density of phytoplankton was significantly lower than the control.

3.5.2 Variation in growth rates

Variation in RNA:DNA ratios was relatively constant across the modules, with the exception of the omnivory module in the 24-hour experiment where variance was significantly different (Figure 3.4b). This result could be driven by size selection predation in the mussel predator. Because mussels are filter feeders, their inhalant siphons will accept a range of prey sizes but will be most efficient at filtering median sizes that are not too small or too large to escape predation (Davenport et al. 2000, Gosling 2003, Lehane and Davenport 2006). This size preference could be driving the observed variation through a type of character displacement in the omnivore module and perhaps in the food chain module were predation not driving the consumer to extinction and obfuscating the result. Competition for phytoplankton may be contributing to the variance but it is weak relative to predation as competition in the consumer-resource or exploitative competition module did not result in high variance.

3.5.3 Implications for stability

Theoretical and empirical studies of food webs have consistently found omnivory to be a module that can confer stability to the food web (Kratina et al. 2012). However, our understanding of how different food web modules affect individual consumers' growth in the food web is scant. Interestingly the extirpation of the consumer in the food chain module suggests that in filter feeders the food chain module may be unstable when the resource is at a high density owing to the filtering rate being governed by particle density. Therefore any benefit conferred by the high resource density to the consumer would be outweighed by the negative effect of increased predation. We also found that omnivory could be beneficial at the individual level by facilitating faster and more variable growth rates in the consumer. Higher and more variable growth rates may have wide implications for food web persistence and stability. Individuals with higher growth rates may benefit from the advantages conferred by a larger body size including faster movement and higher dispersal rates (McCann et al. 2005), producing more and larger offspring (Blueweiss et al. 1978, Peters 1986) and facilitate escape from predation (Chase 1999). Increased growth rates at the individual scale may translate to larger population sizes through higher reproductive output per individual which could increase the probability of persistence where predation on the consumer is low (McCann and Hastings 1997). High and more variable growth rates also promotes the weakening of predator-consumer interactions as consumers with higher growth rates can escape predation and participate in cannibalism which reduces the interaction strength between consumer and resource. Further, the wide range of growth rates promotes a higher diversity of resource use by the consumer and consequently more trophic links in the food web which weakens interaction strengths throughout the food web thus promoting stability (McCann and Hastings 1997, McCann et al. 1998, Vandermeer 2006). Future explorations of food web modules should consider the effects of not only community and population scale effects but also how individual differences can scale up to contribute to food web stability and persistence.

3.6 Acknowledgements

The authors thank P. Joly, G. St-Jean-Lavoie and S. Duffy for their assistance with the experiments and A. Jacob for suggestions on improving the manuscript. We gratefully acknowledge Québec-Océan and the Quebec Centre for Biodiversity Science for scientific and financial support. This research was supported by an NSERC Strategic Project grant, Fisheries and Oceans Canada, Resources Aquatiques Québec and Société de Développement de l'industrie Maricole Inc.

3.7 Data Accessibility

The complete R script for the analysis, and associated data, can be found online as a GitHub repository: http://dx.doi.org/10.5281/zenodo.16536

3.8 Supporting information

Additional supporting information may be found in Appendix A:

Table A.1. Tukey HSD pair-wise comparison results from one-way ANOVAs for the 6-hour experiment.

Table A.2. Tukey HSD pair-wise comparison results from one-way ANOVAs for the 24-hour experiment.

Figure A.1. Phytoplankton densities for each configuration and control at the conclusion of (a) the 6-hour experiment and (b) the 24-hour experiment. For the 6-hour experiment, control and consumer-resource phytoplankton densities were significantly than exploitative competition and omnivory configurations (Table A.1). In the 24-hour experiment the exploitative competition and omnivory configurations had lower phytoplankton densities relative to the consumer resource and control configurations. Letters denote significant differences and error bars indicate standard error.

Figure A.2. *Artemia* densities for each configuration and control at the conclusion of (a) the 6-hour experiment and (b) the 24-hour experiment. *Artemia* densities were significantly lower in food chain and omnivory configurations (Table A.1) in the 6-hour experiment. For the 24-hour experiment only the omnivory configuration had significantly lower *Artemia* densities (Table A.2). Letters denote significant differences and error bars indicate standard deviation.

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3.10 Figures

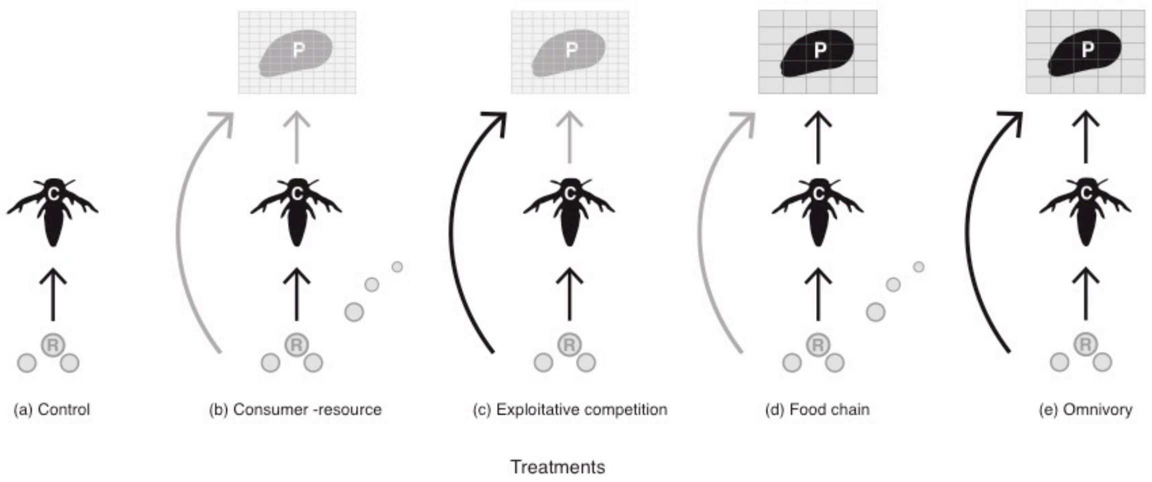

Figure 3.1. Five treatments in the experiments. We constructed the different treatments (four food web modules + control) by adding of phytoplankton subsidies and/or manipulating the mesh size of the Nitex mussel sleeves. The predator, P, is a blue mussel; the consumer, C, is *Artemia*; and the resource, R, is phytoplankton. Opacity is used to denote an interaction that was removed by experimental manipulation. (a) Control microcosms only contained *Artemia* and phytoplankton. (b) Consumer-resource microcosms received phytoplankton subsidies and mussels were placed in a 250 μm mesh sleeve. (c) Exploitative competition microcosms received no subsidies and mussels were placed in a 250 μm mesh sleeve. (d) Food chain microcosms received phytoplankton subsidies and mussels were placed in a 1000 μm mesh sleeve. (e) Omnivory microcosms did not receive subsidies and mussels were placed in a 1000 μm mesh sleeve.

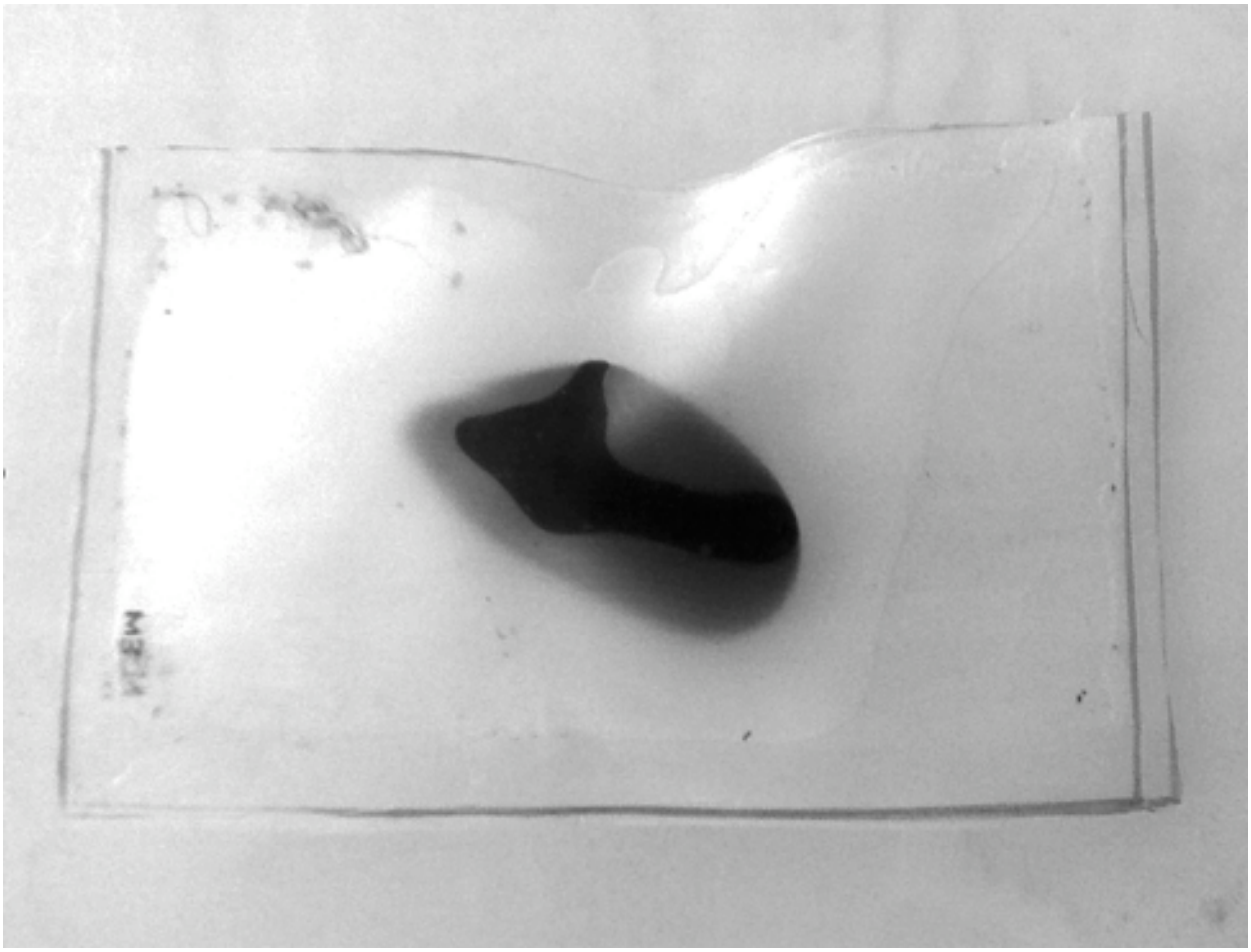

Figure 3.2. Blue mussel, *Mytilus edulis,* in 250µm Nitex sleeve to prevent predation on *Artemia*.

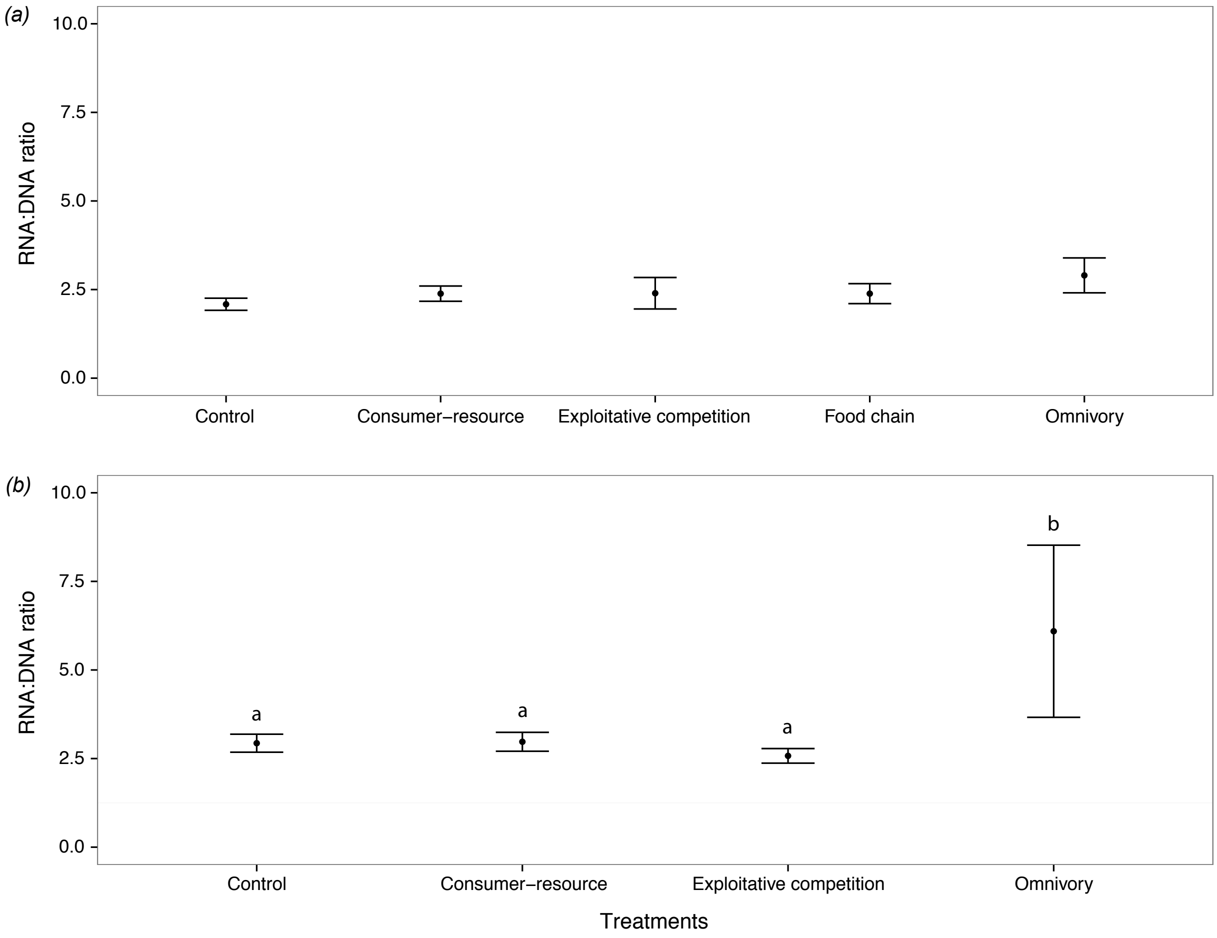

Figure 3.3. RNA:DNA ratios for each module and control at the conclusion of (a) the 6-hour experiment and (b) the 24-hour experiment. We found no significant difference between modules in the 6-hour experiment (Table A.1). However, in the 24-hour experiment RNA:DNA ratios were significantly higher in the omnivory module (Table A.2). Letters denote significant differences and error bars indicate standard error.

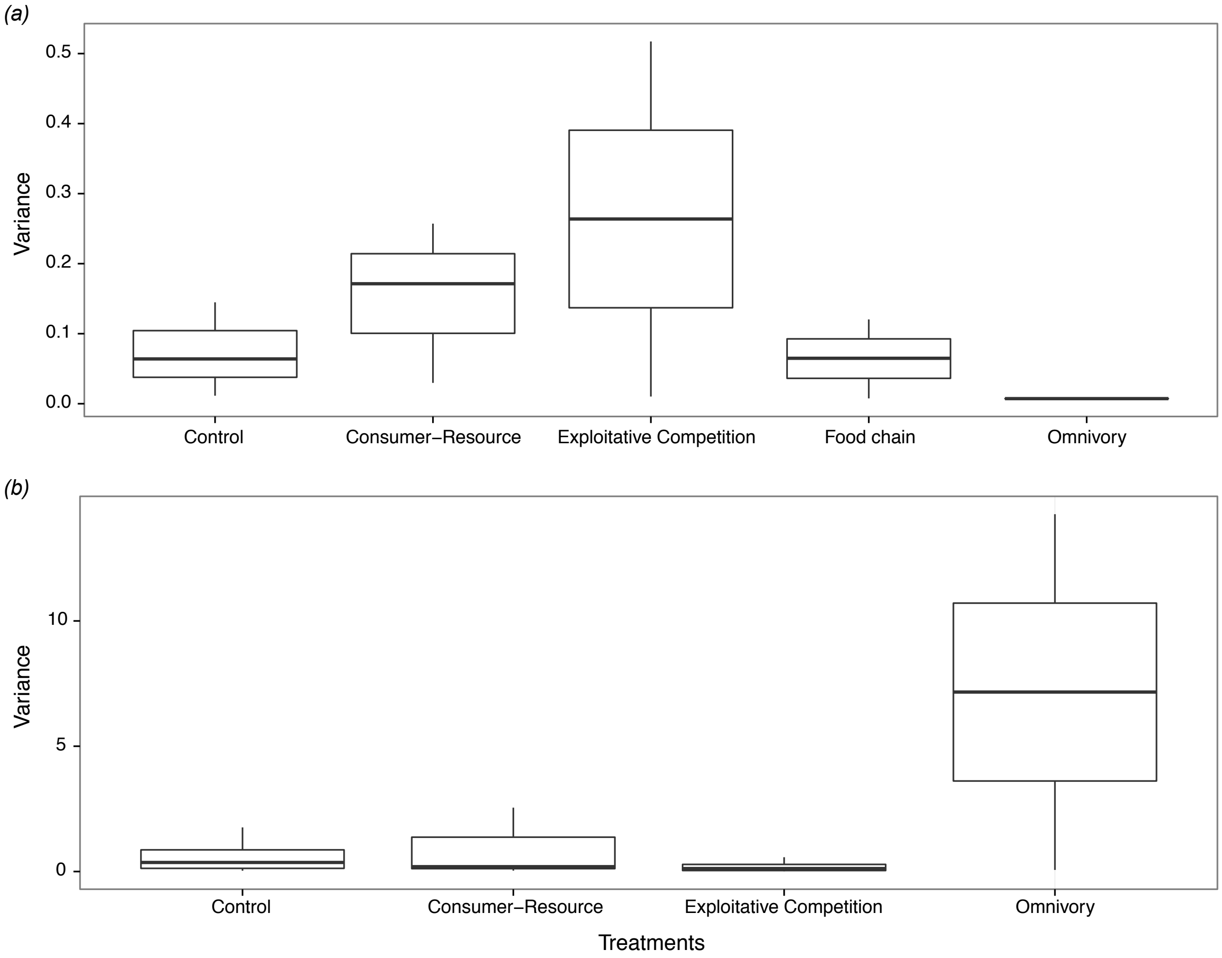

Figure 3.4. Box plot of the variance or the average distance from the mean of RNA:DNA ratios in (a) the six-hour experiment and (b) the 24-hour experiment. The upper whisker extends from the hinge (i.e. top/bottom of the box) to the highest value that is within 1.5 * IQR of the hinge, where IQR is the inter-quartile range, or distance between the first and third quartiles. The lower whisker extends from the hinge to the lowest value within 1.5 * IQR of the hinge. The variance was homogenous across treatments in the six-hour experiment (Bartlett test, p=0.136), but not in the 24-hour treatment (Bartlett test, p<0.001).

3.11 Connecting statement

In the previous two chapters, I demonstrated the importance of interaction strength in the determining the impact on the recipient community. While the focus of these chapters and previous research has been on the properties of the omnivore, the characteristics of the recipient community are important determinants of the stability of a food web with an introduced omnivore (McCann et al. 1998, Kratina et al. 2012). In the following chapter I use a modeling approach to investigate the role of consumer-resource interaction strength in mitigating the impact of an introduced omnivore. I build on a previous Rosenzweig-McArthur model and a planktonic food web to determine when the introduction of an omnivore can destabilize a food web by driving its constituents to extinction and when its introduction could confer stability to an excitable consumer-resource interaction. For clarity, I would like to remark that, in the preceding chapter, "growth rate" was used to refer to the individual, somatic rate of growth of an organism, whereas in chapter 4 the term is used for the intrinsic rate of increase of a population (*r*).

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4 Chapter 3

Introduced omnivores can increase stability in a tri-trophic model

Authors: Monica Granados and Gregor F. Fussmann

4.1 Abstract

Although introduced species are often considered to exert only negative impacts on recipient communities, the introduction of a species also provides new resources, interactions and can even act as habitat for species this community. In the right context the introduction of a species can have positive effects on the recipient community. In this paper we used mathematical models to investigate the potential positive benefit of the introduction of a species. Because omnivory can stabilize consumer resource interactions by decreasing their coupling strength in native food webs, we varied the strength of the consumer-resource interaction by introducing different strengths of omnivory and determined whether the persistence of a food web increased. When parameterizing for a planktonic food web, our results suggest the introduction of an omnivore could increase the persistence of the food web, but only at weak to intermediate omnivory. Our findings indicate that recipient communities with strong consumer-resource interactions could therefore benefit from the introduction of an omnivore provided the interactions between the omnivore-consumer and omnivore-resource do not eliminate the consumer.

4.2 Introduction

Introduced species can have very deleterious consequences on recipient communities, but in the right context introduced species might have positive effects. Introduced species can decrease the availability of resources, reduce the abundance and diversity of native species and spur their extinction (Blackburn et al. 2005, Vila et al. 2011, Twardochleb et al. 2013). Recent analyses across major taxa (i.e. mammal, birds) have found that the introduction of non-native species is a leading cause of species extinctions worldwide (Wilcove et al. 1998, Bellard et al. 2016, Clavero and García-

Berthou 2016). However, there is a growing body of literature documenting cases where the introduction of a species provided a benefit to a native species or the recipient community. A review of the invasive species literature revealed that non-native species can facilitate native species in a myriad of ways (Rodriguez 2006). Non-native species are potentially able to create new habitats that increase resource availability and prey refugia, act as pollinators, release prey from predation and competition, provide nutrient enrichment and they themselves can serve as trophic subsidies (Rodriguez 2006). More generally, it has been suggested that non-native species can promote conservation and restoration by supplying habitat, ecosystem services, increasing heterogeneity and replacing the roles of lost species (Schlaepfer et al. 2011). The number of beneficial interactions involving non-native species is also expected to increase as introductions continue to increase (Schlaepfer et al. 2011).

In this paper we use mathematical modeling to simulate the outcome of a concrete, parameterized invasion scenario. We look at a potential benefit of introduced species. Here we ask: Could the introduction of an omnivore increase the persistence of a recipient community? Although we know that introductions of non-native species and the subsequent predatory and competitive interactions can have positive effects on native species (Crossland 2000, Roemer et al. 2002, Grosholz 2005, Macneil and Dick 2014), the two types of interaction have not been studied in concert through omnivory. Broadly defined as feeding on multiple trophic levels, omnivory can be reduced to a food web module that has an omnivore species both competing with and preying on a consumer – a configuration termed intraguild predation (IGP) (Polis et al. 1989). In IGP the consumption of the shared resource by the omnivore reduces the coupling strength between consumer and resource and may thereby decouple and stabilize the dynamics of this food web configuration. The reduction in coupling strength can mute oscillations in the population sizes of the consumer and resource by limiting the population size of the resource and consequently the consumer (McCann 2012). This is the dynamical scenario that we seek to analyze in the context of the introduction of species that act as omnivores.

In terrestrial and aquatic food webs feeding on more than one trophic level seems ubiquitous (Winemiller 1990, Hall and Raffaelli 1991, Polis 1991, Arim and Marquet 2004, Thompson et al. 2007), likely because of omnivory's capacity to stabilize excitable consumer resource interactions when interaction strength is weak (McCann and Hastings 1997). It follows then, that the stabilizing properties of omnivory should translate to an invasion scenario, where an introduced omnivore shunts some of the energy from the consumer-resource interaction up to predator-resource pathway and increases the local minima and decreases the local maxima of predator and resource as long as omnivory is weak. Although models have examined the relationship between the strength of omnivory and stability (McCann and Hastings 1997, Vandermeer 2006) – including studies that have integrated productivity (Amarasekare 2006, 2008), stage-structure (Hin et al. 2011), and anti-predator defense (Urbani and Ramos-Jiliberto 2010) – none have explored the role of introduced omnivores in increasing stability.

Here we use a model formulation similar to McCann and Hastings (1997), a simple tri-trophic food web with IGP. We model the introduction of an omnivore into a planktonic food web by increasing the interaction strength between the omnivore and the consumer across different strengths of omnivory to determine whether the introduction of an omnivore can increase the stability of a native consumer-resource interaction across increasing consumer-resource interaction strengths here simulated through attack rates. Planktonic food webs have been subjected to multiple introductions owing to their vulnerability to introduction vectors including ballast water, aquarium trade and recreational fishing boats (Hulme 2009). Following convention we measure stability as an increase in persistence of the omnivore, consumer and resource. Our models suggest that when consumer-resource interaction strengths are prohibitively high to allow the persistence of the consumer, the introduction of an omnivore can raise the floor of the local minima but only for weak to intermediate omnivory.

4.3 Methods

4.3.1 Food web model

We used the following three species Rosenzweig-McArthur model (Rosenzweig 1973) with omnivory modified from Fussmann and Heber (2002):

$$\frac{\mathrm{d}R}{\mathrm{d}t} = Rr\left(1 - \frac{R}{K}\right) - \frac{a_{CR}R}{1 + b_{CR}R}C - (1 - \Omega)\frac{a_{PR}R}{1 + b_{PR}R + b_{PC}C}P$$

$$\frac{\mathrm{d}C}{\mathrm{d}t} = e\frac{a_{CR}R}{1 + b_{CR}R}C - \Omega\frac{a_{PC}C}{1 + b_{PR}R + b_{PC}C}P - m_c C \tag{1}$$

$$\frac{\mathrm{d}P}{\mathrm{d}t} = e(1 - \Omega)\frac{a_{PR}R}{1 + b_{PR}R + b_{PC}C}P + e\Omega\frac{a_{PC}C}{1 + b_{PR}R + b_{PC}C}P - m_p P$$

where b_{ij} is the inverse of the half-saturation constant of species i preying on species j, r is the instantaneous growth rate of the resource and the type-II functional response of the predator includes a parameter, Ω, that controls the preference for either resource, R, or consumer, C; accordingly. Carrying capacity is K, the attack rate of species i on j is denoted by a_{ij} and mortality of species i is represented by m_i.

4.3.2 Parameterization

Our parameters correspond to a paper by Fussmann and Heber (2002) where the growth rates and attack rates are consistent with those found in plankton food webs and all of the population sizes are relative to the carrying capacity, K, of the resource. We selected the morality rates that would generate limit cycles in the consumer-resource submodel across the consumer attack rate, a_{CR}, range considered. We set initial starting densities for the predator, consumer and resource at 0.5, except when we modeled the consumer-resource subsystem; in this case the predator initial density was set to zero to exclude the predator from the simulations all other parameters were consistent across the simulations. Predator and consumer conversions efficiencies, e, were set to 1. All of the parameters used in the paper are listed in Table 3.1.

4.3.3 Numerical simulations

All of the simulations were conducted in R (R Development Core Team 2015) using the deSolve package (Soetaert et al. 2010). We varied two parameters a_{CR} and Ω in the model to determine 1. How attack rates affect the local minima of the consumer and resource 2. How the strength of omnivory mediates the effect of consumer attack rates on stability.

4.4 Results

We found that, for weak ($\mathit{\Omega}$ =0.7) to intermediate omnivory ($\mathit{\Omega}$ =0.5), the presence of an omnivore enhanced persistence of the resource as the interaction strength between consumer and resource increased (Fig. 4.1). In the absence of the predator, the resource minima approached zero as a_{CR} increased (Fig. 4.1a), however when an omnivore was introduced the floor of the resource population size was raised producing a bifurcation at weak and intermediate omnivory at attack rates a_{CR}, between 6.5-7.5. As a_{CR} is increased, however, we observe a period doubling cascade toward chaotic dynamics (Fig. 4.1b,c). At strong omnivory Ω =0.3, the resource went extinct at strong interaction strengths (Fig. 4.1d). In the absence the predator, as for the resource, the increase in the attack rate a_{CR}resulted in a decrease of consumer minima (Fig. 4.2a). With the inclusion of the predator the introduction of an omnivorous link at weak (Ω =0.7) to intermediate omnivory (Ω =0.5), produced two local minima across the range of attack rates, a_{CR}, considered. One minimum falls lower than the minimum of the system when the predator is absent while one is greater; this occurs at attack rates, a_{CR}, between 7.2-9.0 for weak omnivory (Ω =0.7, Fig. 4.2b) and 6.5 -9.0 when omnivory is intermediate (Ω =0.5, Fig 4.2c). At strong omnivory (Ω =0.3) the consumer is extinct across most of the range of a_{CR} considered (Fig 4.2d).

4.5 Discussion

Our model suggests that for weak to intermediate omnivory in planktonic food webs the introduction of an omnivore could increase the persistence of a food web with strong consumer-resource interaction strengths. Our results are consistent with the model results of McCann and Hastings (1997) and McCann et al. (1998) which found that omnivory was stabilizing only for weak to intermediate interaction strengths and similarly concluded, when omnivory is strong the consumer is driven to extinction irrespective of the consumer-resource interaction strength as the predator depletes the resource (Figure 4.2d). When omnivory is weak or intermediate, the presence of the predator feeding on both consumer and resource increases the mortality of the consumer and resource. This increase in mortality acts to dissipate energy from the consumer-resource interaction, decreasing growth of the consumer population and its ability to deplete the resource population. The increase in the minimum population size of the resource is reflected in the increase in local minima relative to the model with only the consumer-resource subsystem. For the consumer, the introduction of the omnivore has primarily a negative effect on its population density because one of the resulting minima falls lower than the minimum observed in the absence of the predator. Likely the lower minimum would increase the probability of extinction as consumer population sizes near closer to zero (McCann and Hastings 1997). However, the second minimum is higher than the single minimum in the absence of the predator (Fig. 4.2b, c), and this higher minimum exists over a particularly wide range of attack rates, a_{CR}, for intermediate levels of omnivory (Fig. 4.2c). If the limit cycle oscillations are sufficiently slow and/or the consumer can find temporary rescue from predation to bridge periods of low density, these higher minima may contribute to larger overall consumer population sizes and the persistence of the food web.

In our model the predator attack rate was relatively low compared to the attack rates between consumer and resource (Table 4.1). Although the parameterization is consistent with growth and attack rates in planktonic food webs, many introduced species are characterized by their strong interactions in recipient communities (Fussmann and Heber 2002). Increasingly, functional responses are being recognized as important predictors of the impact of introduced species. In comparative experiments successful invasive species demonstrated stronger functional responses than similar congener species (Dick et al. 2014). It is possible then that many of the successful invasive species form strong interactions between native consumers, which would likely drive the consumer and resource to extinction. However, outside experimental conditions stabilizing mechanisms that weaken interactions strengths between the introduced omnivore and native consumer and resource may exist that permit the persistence of the food web after the introduction of an omnivore (Granados et al. Appendix B). Our model suggests that conditions do exist that permit the introduced omnivore have a positive benefit on the recipient community. However, it is contingent on the conditions being appropriate for omnivore to increase stability.

4.6 Data Accessibility

The complete R script for the model can be found online as a GitHub repository: http://dx.doi.org/10.5281/zenodo.50352

4.7 Acknowledgements

This research was funded by an NSERC Discovery Grant to G.F.F. We thank Just Marleau for helpful comments that have improved this manuscript.

4.8 Tables

Table 4.1. Table of parameters used in the model.

Parameter	Description	Value[1]
r	Resource instantaneous growth rate	4 (day^{-1})
α_{pc}	Attack rate of predator on consumer	2 (individuals day^{-1})
α_{pr}	Attack rate of predator on resource	0.5 (individuals day^{-1})
α_{cr}	Attack rate of consumer on resource	varied (6-9 individuals day^{-1})
b_{pc}	1/half saturation constant of predator on consumer	2
b_{pr}	1/half saturation constant of predator on resource	0.5
bc_{r}	1/half saturation constant of consumer on resource	5
m_p	Mortality rate of the predator	0.20586 (day^{-1})
m_c	Mortality rate of the consumer	0.84617 (day^{-1})
e	Conversion efficiencies	1
K	Carrying capacity	1
Ω	Predator preference for consumer or resource	varied (0.3-0.7)

1. Parameter values taken from Fussmann and Herber (2002).

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4.10 Figures

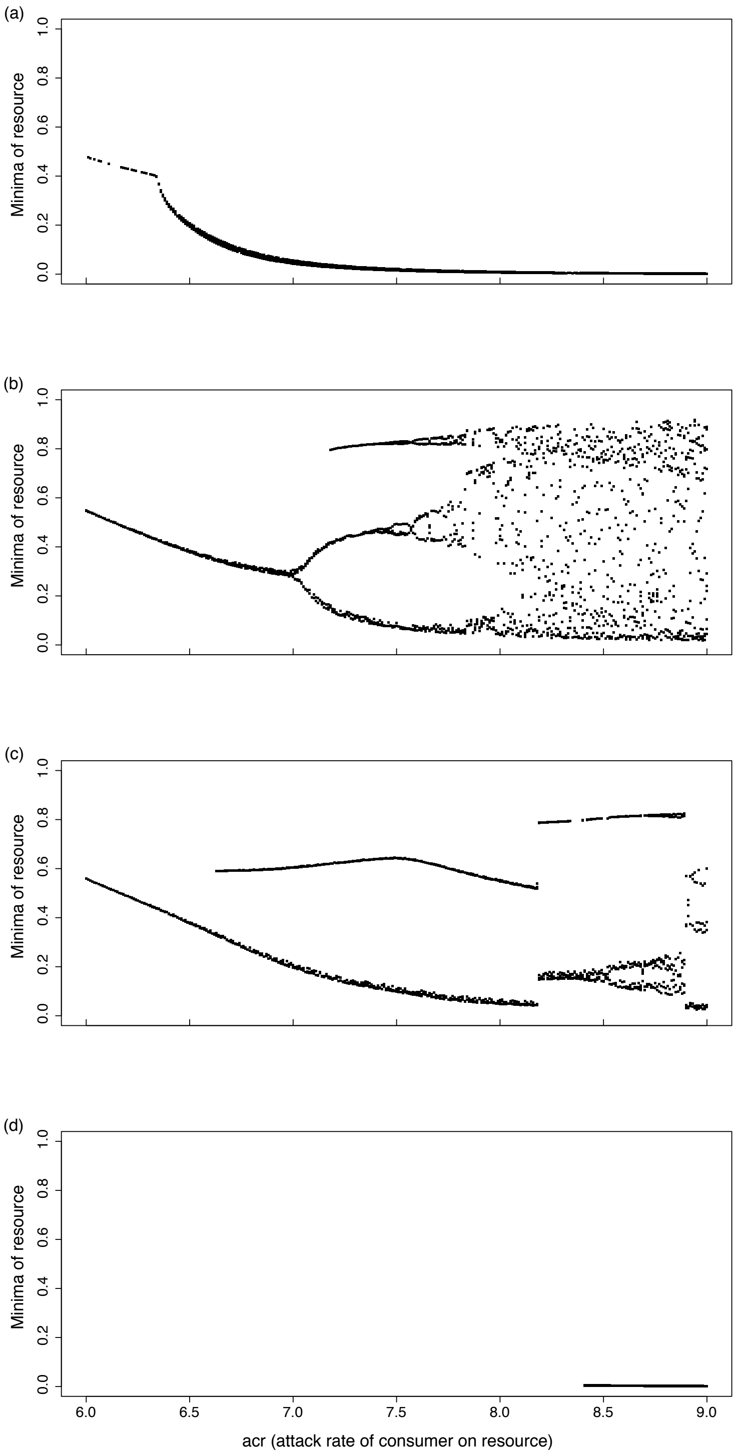

Figure 4.1. Minima of resource $\boldsymbol{R}$ as the attack rate of the consumer on the resource increases. Parameter values are shown in the text (a) Predator is absent (b) Omnivory is weak $\boldsymbol{\Omega}$ = 0.7. (c) Intermediate omnivory, $\boldsymbol{\Omega}$ = 0.5. (d) Omnivory is strong $\boldsymbol{\Omega}$ = 0.3.

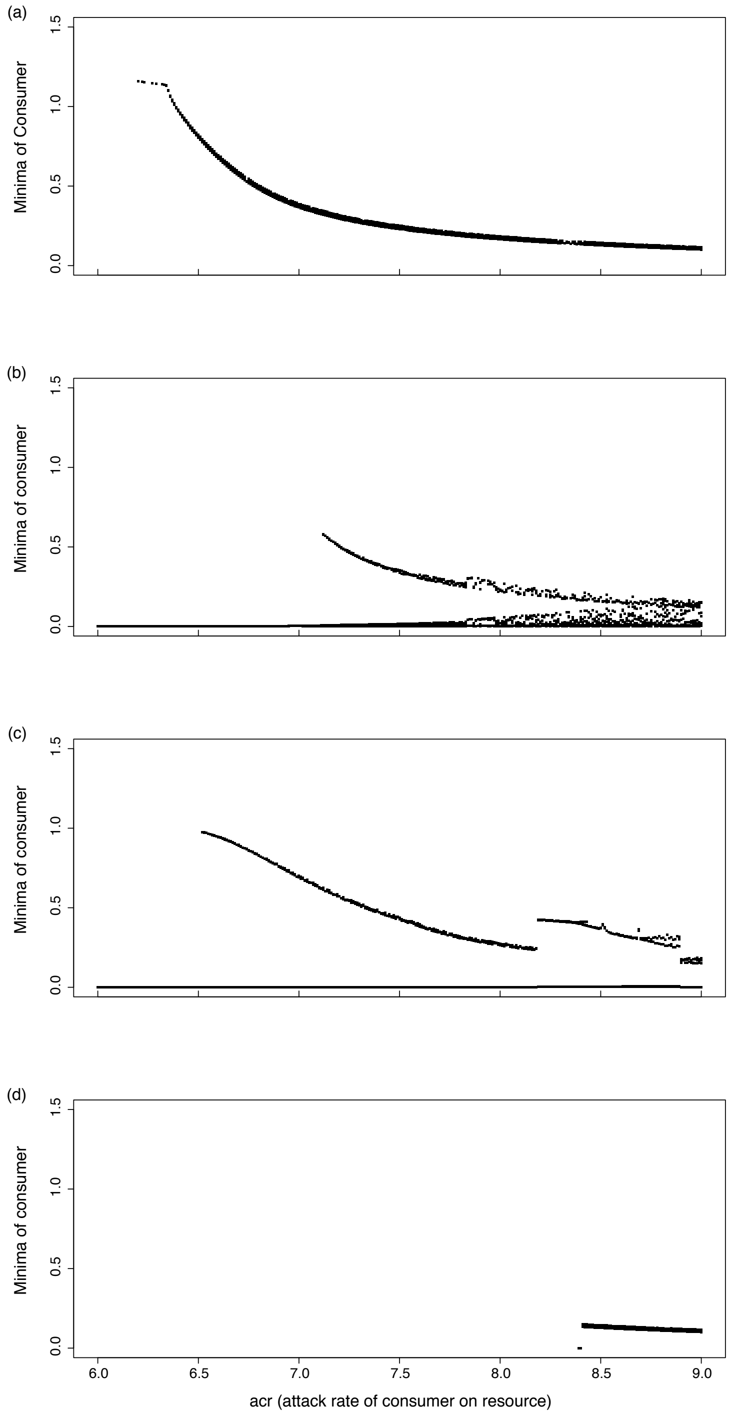

Figure 4.2. Minima of consumer C, as the attack rate of the consumer on the resource increases. Parameter values are shown in the text (a) Predator is absent (b) Omnivory is weak Ω = 0.7. (c) Intermediate omnivory, Ω = 0.5. (d) Omnivory is strong Ω = 0.3.

5 General conclusion

5.1 Overview

In this thesis I have demonstrated that as predicted by the theoretical work of McCann and Hastings (1997) on food webs with omnivory, interaction strength is a pivotal parameter in determining the impact of introduced omnivores. By investigating different interaction strengths within the food web, between predator and consumer, among consumers and between consumer and resource, I provide tangible predictions on the consequences of the introduction of non-native omnivores. In Chapter 1 I showed that the impact of an introduced species is tied to the interaction strength between the predator and the consumer. Omnivores in the data set had stronger interactions with and larger negative impacts on consumers relative to predators. Introduced omnivores with stronger interactions as measured by their functional response are then expected to have greater impacts on recipient communities. In Chapter 2 I experimentally investigated a food web where an omnivore has been introduced *in situ*. Here I showed that omnivory could affect interaction strength by increasing the variation in growth rates. Introduced omnivores that promote higher variation in growth rates of the consumer, through selective predation, are predicted to reduce interaction strengths in the food web. Finally in Chapter 3 I focused on how the consumer-resource interaction affects the impact of an introduced omnivore. I determined that the interaction between the consumer and resource is an important aspect that contributes ultimately to the impact of an introduced omnivore. When the interaction between consumer and resource is strong the introduction of an omnivore can be stabilizing. Together this thesis provides methods that can be integrated into a robust discipline dedicated to providing tools to decision makers to stem the negative impacts of introduced species.

5.2 Future directions

Currently, most quantitative models use as parameters characteristics of the introduced species and quantitative measures of the introduction process (e.g., propagule pressure) (Kolar and Lodge 2001). However, potential interactions between introduced species and the recipient community are seldom considered, likely because of the difficulty in making predictions on interactions that have yet to occur. The results from Chapter 1 however, provide a method to make predictions on potential interactions that can be measured empirically. Future impact assessments should integrate interaction strength into models to understand the impacts of introduced species not only from the interactions of species pairs, but of the food web as a whole.

The focus of most studies on the stability of food has been on the magnitude of population fluctuations across time. The results of Chapter 2 suggest that the growth rates of individuals in the food web can also have effects that reverberate up to population size fluctuations. Further empirical work should quantify how variation in growth rates translates to persistence.

Finally, in Chapter 3 I demonstrate that whether an introduced omnivore has a destabilizing effect depends also on characteristics of the recipient community. While previous research has shown that characteristics of the recipient community such as its diversity is an important determinant in invasibility and establishment, the interactions of species in the recipient community are not variables considered in predictive models (Levine and D’Antonio 1999). Future work should integrate available information not only about the predicted interaction between the introduced species and native species, but also how the present interactions in the recipient community will combine with the novel interactions. Overall I advocate for more integration of food web theory into invasive species research.

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Appendices

5.4 Appendix A

Supplemental material for Chapter 2

Table A.1. Tukey HSD pair-wise comparison results from one-way ANOVAs for the 6-hour experiment.

Table A.2. Tukey HSD pair-wise comparison results from one-way ANOVAs for the 24-hour experiment.

Figure A.1. Phytoplankton densities for each configuration and control at the conclusion of (a) the 6-hour experiment and (b) the 24-hour experiment. For the 6-hour experiment, control and consumer-resource phytoplankton densities were significantly than exploitative competition and omnivory configurations (Table A.1). In the 24-hour experiment the exploitative competition and omnivory configurations had lower phytoplankton densities relative to the consumer resource and control configurations. Letters denote significant differences and error bars indicate standard error.

Figure A.2. *Artemia* densities for each configuration and control at the conclusion of (a) the 6-hour experiment and (b) the 24-hour experiment. *Artemia* densities were significantly lower in food chain and omnivory configurations (Table A.1) in the 6-hour experiment. For the 24-hour experiment only the omnivory configuration had significantly lower *Artemia* densities (Table A.2). Letters denote significant differences and error bars indicate standard deviation.

Table A.1. Tukey HSD pair-wise comparison results from one-way ANOVAs for the 6-hour experiment.

Module	Treatment				
Final phytoplankton density	control	consumer-resource	exploitative competition	food chain	ominvory
control	-	0.077	<0.05	<0.05	<0.05
consumer-resource		-	0.316	0.991	0.135
exploitative competition			-	0.532	0.971
food chain				-	0.254
ominvory					-
Final Artemia density					
control	-	0.430	0.299	<0.001	<0.001
consumer-resource		-	0.998	<0.001	<0.001
exploitative competition			-	<0.001	<0.001
food chain				-	0.712
ominvory					-
RNA:DNA ratio					
control	-	0.783	0.968	0.859	0.409
consumer-resource		-	0.992	1.000	0.952
exploitative competition			-	0.999	0.806
food chain				-	0.893
ominvory					-

Table A.2. Tukey HSD pair-wise comparison results from one-way ANOVAs for the 24-hour experiment

Module	Treatment			
Final phytoplankton density	control	consumer-resource	exploitative competition	ominvory
control	-	<0.001	<0.001	<0.001
consumer-resource		-	<0.001	<0.05
exploitative competition			-	0.999
ominvory				-
Final Artemia density				
control	-	0.859	0.998	<0.001
consumer-resource		-	0.924	<0.001
exploitative competition			-	<0.001
ominvory				-
RNA:DNA ratio				
control	-	0.989	0.902	<0.001
consumer-resource		-	0.769	<0.001
exploitative competition			-	<0.001
ominvory				-

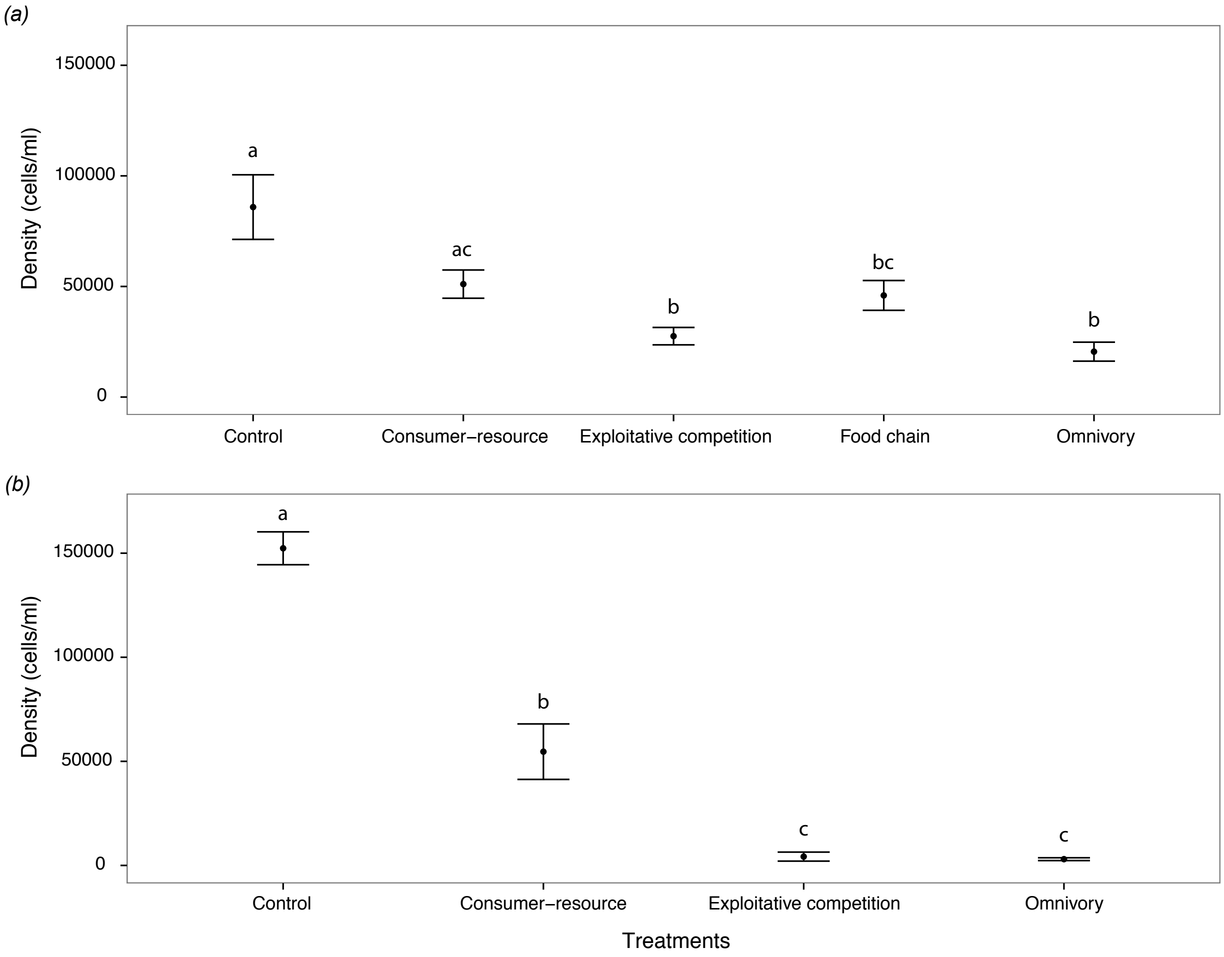

Figure A.1. Phytoplankton densities for each configuration and control at the conclusion of (a) the 6-hour experiment and (b) the 24-hour experiment. For the 6-hour experiment, control and consumer-resource phytoplankton densities were significantly higher than exploitative competition and omnivory configurations (Table A.1). In the 24-hour experiment the exploitative competition and omnivory configurations had lower phytoplankton densities relative to the consumer resource and control configurations. Letters denote significant differences and error bars indicate standard error.

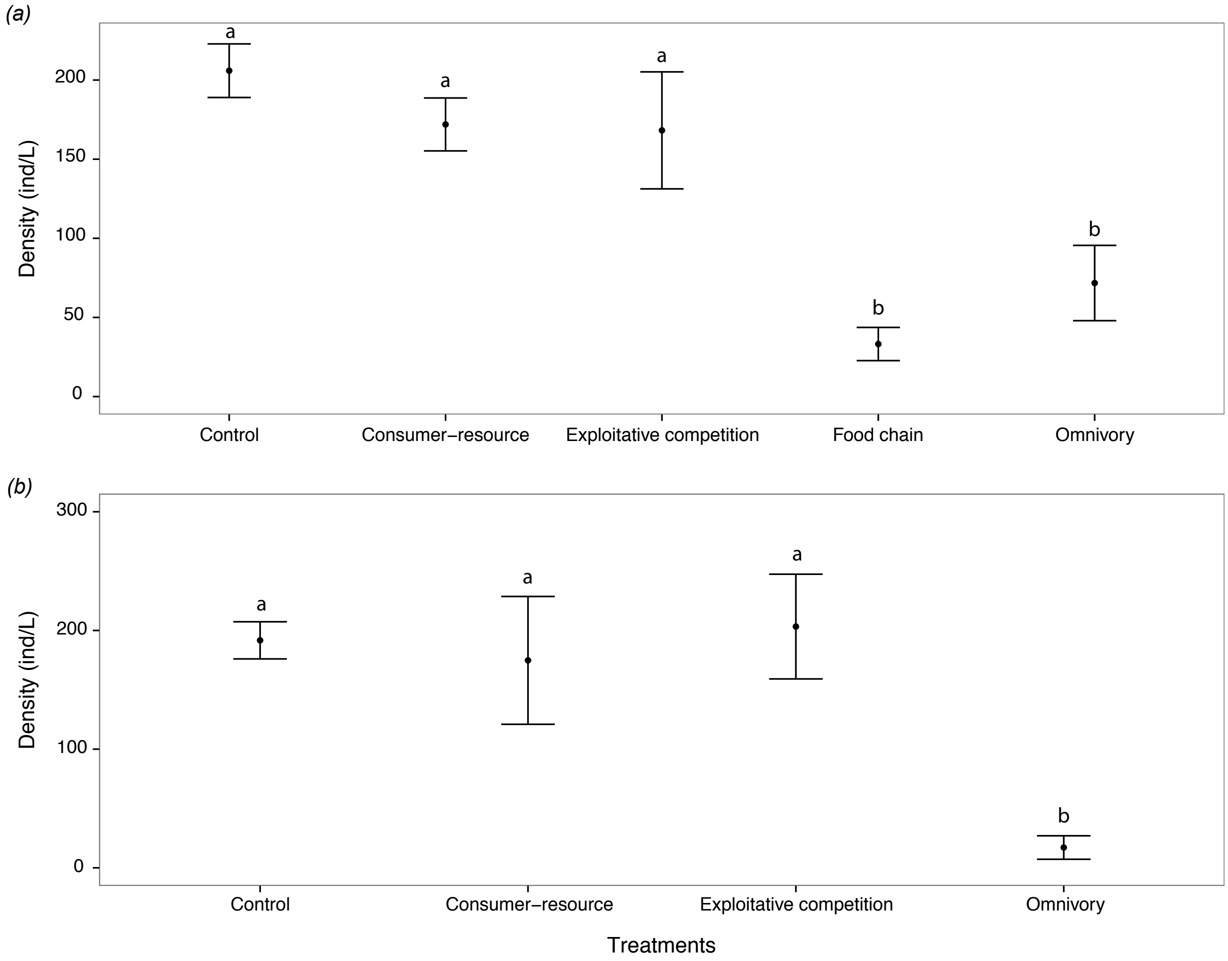

Figure A.2. *Artemia* densities for each configuration and control at the conclusion of (a) the 6-hour experiment and (b) the 24-hour experiment. *Artemia* densities were significantly lower in food chain and omnivory configurations (Table A.1) in the 6-hour experiment. For the 24-hour experiment only the omnivory configuration had significantly lower *Artemia* densities (Table A.2). Letters denote significant differences and error bars indicate standard deviation.

5.5 Appendix B

Appendix B contains two manuscripts under review at peer-reviewed journals. They are included in this thesis as both are extensions of my thesis work on the consequences of the introduction of omnivory and were carried out concurrently with my thesis work. “Stabilizing mechanisms in a food web with an introduced omnivore” uses food web subject to the introduction of omnivores to determine the importance of interaction strength on the impact of these introduced omnivores. “Consequences of consumer origin and omnivory on trophic cascades and stability in an experimental food web” experimentally tests some of the hypothesis proposed in this thesis by comparing the stability of food web with introduced omnivores versus predators.

Stabilizing mechanisms in a food web with an introduced omnivore

Authors: Monica Granados, Sean Duffy, Christopher W. McKindsey and Gregor F. Fussmann

A version of this manuscript in review at Ecology and Evolution

Abstract

Intraguild predation (IGP) is an omnivorous food web configuration in which the top predator consumes both a competitor (consumer) and a second prey that it shares with the competitor. This omnivorous configuration occurs frequently in food webs but theory suggests that, it is unstable unless stabilizing mechanisms exist that can decrease the strength of the omnivore and consumer interaction. Although these mechanisms have been documented in native food webs, little is known about whether they operate in the context of introduced species. Here we study a marine mussel aquaculture system where the introduction of omnivorous mussels should generate an unstable food web that favours the extinction of the consumer, yet it persists. Using field and laboratory approaches we searched stabilizing mechanisms that could reduce the interaction strengths in food web. Field data suggested that while mussels have an effect on the composition and abundance of copepods, stable isotope results indicated that, *in situ*, stage structure facilitated the availability of prey refugia and reduced competition between the mussel omnivore and zooplankton consumers. We however found no evidence of prey switching. Our food web study suggests that the impact of an introduced omnivore may not only depend on its interaction with native species but also on the availability of coexistence mechanisms that alter the strength of those interactions.

Introduction

Intraguild predation (IGP) is a specific case of omnivory where predator and prey compete for a common resource. Under IGP, the consumer is subject to strong predatory and competitive interactions and is usually excluded (Holt & Polis 1997; Krivan & Diehl 2005). Yet, dissections of trophic interactions in food webs suggest that this type of omnivory is widespread (Arim & Marquet 2004; Thompson et al. 2007) when the interactions in the food web are weak (McCann et al. 1998). Stabilizing mechanisms are thus believed to exist in nature, which alter the strength of interactions between constituents of the food web (Polis et al. 1989). Kratina et al. (2012) breakdown these stabilizing mechanisms into five main categories: habitat complexity, anti-predator phenotypes of prey, adaptive feeding behavior of omnivores, life history omnivory and interference between omnivores. In each, the stabilizing mechanism reduces the probability of consumption of the prey thus altering the strength of the interaction. While stabilizing mechanisms have been documented in native food webs (Janssen et al. 2007; Finke & Denno 2002; Rickers et al. 2006; Rudolf & Armstrong 2008) very little is known about their existence in food webs with introduced species.

Because interaction strength governs whether omnivory has a positive, stabilizing impact or a deleterious, extinction effect on food webs, interaction strength can be used to predict and understand the impact of introduced omnivores. If an introduced omnivore forms strong interactions with the native consumer and its shared resource its introduction can lead to the extinction and reductions of consumers and resources. A notable example is the introduction of the omnivorous rusty crayfish, *Orconectes rusticus* - their introductions have directly led to the decline of both macroinvertebrate consumers and shared common resources (Lodge et al. 1994; McCarthy et al. 2006). Recently, strong functional responses, which measure the intensity of predation, have also been positively associated with greater impacts among introduced omnivores in recipient communities (Dick et al. 2014). Yet should these strong interactions be attenuated by stabilizing mechanisms we would expect a decrease in impact of the introduced omnivore and persistence of the consumer.

Here we examine the recent introduction (<30 years ago) of the omnivorous blue mussel, *Mytilus edulis*, to the Havre-aux-Maisons Lagoon (HAM) for the purposes of aquaculture (Richard et al. 2006). The blue mussel is generally regarded as a microphagous filter feeder. However, it also has the capacity to consume zooplankton, where pre-adult life stages are most vulnerable to predation (Lehane & Davenport 2006a; Jonsson et al. 2009). Significant ingestion of zooplankton by mussels has been recorded both experimentally with *Artemia* nauplii as proxies (Davenport et al. 2000) and in natural systems (Nielsen & Maar 2007). Because naturally occurring mussels are benthic organisms, confined to consuming resources present in the water above substrates, the potential for competition and predation between mussels and zooplankton is limited (Maar et al. 2008). In contrast, off-bottom or suspended mussel aquaculture places mussels in the water column using a series of lines as substrate that span the upper reaches of the pelagic zone, which facilitates zooplankton predation by mussels (Lehane & Davenport 2002; Maar et al. 2007). Under aquaculture conditions, where dense mussel populations are in contact with zooplankton, the potential for omnivory becomes appreciable. Suspended in lines, the mussel operates as the omnivore with zooplankton as the consumer and micro/nanoplankton (i.e. phytoplankton, heterotrophic protists; seston) as the common resource. In this paper we use this mussel aquaculture food web to determine 1. Whether consumers persist at sites where the omnivorous mussel has been introduced 2. Search for stabilizing mechanisms that may be reducing the interaction strength between the omnivore and the consumer. Given that mussels can selectively filter-feed by increasing feeding currents and valve gapes (Gosling 2003; Riisard 1991) and zooplankton growth proceeds in distinct ontogenetic stages (Johnson & Allen 2005), we tested for the presence of adaptive predator feeding behaviour and stage structure as stabilizing mechanisms.

The interaction strength between omnivore and consumer can be mediated through age/stage structure and ontogeny (stage-structured omnivory), where omnivorous interactions are subject to change as both prey and predator increase in size or age during the course of their development (Rudolf & Armstrong 2008; Olson et al. 1995; Browne & Rasmussen 2009). Adaptive feeding is defined as a behaviour, where an increase in resource density or decrease in consumer density leads to increased rates of consumption of the resource and decreased rates of consumption of the consumer by the omnivore predator (McCann et al. 2005). The behaviour is adaptive because less energy is required to prey on the resource at greater densities. Prey switching at high resource density releases the consumer from predation at low density and promotes persistence (Krivan & Diehl 2005; Gismervik & Andersen 1997; McCann 2012).

We first sampled the HAM assess consumer abundance and composition between farm and reference sites. In the HAM, we analyzed the stable isotope signature of mussel and plankton samples to elucidate whether the strength of predation changed with mussel size and whether adult stages of the consumer experienced a size refugium that affords them reduced predation. We also used the stable isotope data to determine whether the diet overlap between mussels and the consumer changes as they mature, which can lead to reduced competition. Finally, we performed a laboratory experiment to investigate how mussels consume a common resource versus consumer and whether they exhibit prey switching. We tested the hypothesis that omnivory in mussel aquaculture food webs depends on the relative abundance of consumer and common resource by offering varying proportions of these two prey types and quantifying their relative uptake using selectivity indices.

Materials and methods

Copepod community composition

Our field site was located in the HAM, Îles de la Madeleine, Quebec. The surface area of HAM is 30 km^2, with a mean depth of 3 m and about 5 to 6 m in the aquaculture sites (Richard et al. 2006). The tides are small (ca. 0.6 m), and frequent strong winds drive water mixing and renewal (Minagawa & Wada 1984). The lagoon is currently used for long-line mussel aquaculture. We selected two sites within the mussel aquaculture farm and two reference sites outside the farm to characterize the consumer, here zooplankton, community and assess the impact of mussel grazing. Individuals in the subclass copepoda dominate the HAM zooplankton community and thus we limited the characterization of the community to copepods. We collected copepods using a 73µm plankton net, with a diameter of 50cm, towed to a depth of three feet in August 2009. Each farm and reference site was sampled three times between lines and next to the line for a total of six tows for each site. We identified copepods to genus and classified to one of three stage classes: adult, copepodite or nauplii under a dissecting microscope. Data from the sites was pooled to the site level to assess the difference between farm and reference sites. Count data was used to produce a two-dimensional ordination plot using non-metric multidimensional scaling (NMDS) using a Bray-Curtis similarity measure with site as a grouping factor. We also conducted an analysis of similarities (ANOSIM) with site as the grouping factor to quantify the between and within group similarities. Count data was converted to density in individuals L^{-1}. We performed a two-way ANOVA on the density data with site and stage class as fixed factors to assess differences in copepod density between sites and across age classes. Differences between site and stage class were analyzed using Tukey's HSD post-hoc test.

Trophic position field study

Generally, there are three age classes of mussels (0+, 1+, and 2+ year old mussels) growing in different regions of a farm. We selected the 1+ and 2+ sites to sample randomly to obtain a large size range of mussels. *Mytilus edulis* were collected off mussel socks on 23-Aug-2010 and 02-Sep-2010. Throughout this period, multiple plankton net tows (75 µm) and water samples (<60 µm, using a Niskin bottle) were taken at 3 m depth from random positions within sites of the farm dedicated to the different age groups of mussels. Tow contents were immediately frozen for subsequent isotope analysis.

Each mussel collected was measured in mm (shell length) after which the mantle tissue was dissected. Seston <60 µm was collected on GF/F filters (pre-combusted at 450 ^{o}C for 12 hours) by filtering one litre of each water sample. Copepods from the plankton net tows were separated into adult and naupliar stages under a dissecting microscope. Nauplii were concentrated onto pre-combusted GF/F filters to accumulate sufficient organic material. All samples were dried in a lyophilizator for at least 24 hours.

The stable isotope signatures (δ^{13}C and δ^{15}N) for *Mytilus edulis* mantle tissue, adult copepods, nauplii and seston were measured by the University of New Hampshire Stable Isotope Laboratory using a Delta Plus XP Mass Spectrometer interfaced to a Costech ECS4010 Elemental Analyzer. The δ^{13}C and δ^{15}N values are expressed as deviations from a standard in parts per thousand ($^{o}/_{oo}$) and calculated as:

$$\delta^{13}C \text{ or } \delta^{15}N = [\ (R_{sample} - R_{standard}) \ / \ R_{standard}\ ] \times 10^{33} \qquad (1)$$

where R is the ratio of ^{13}C/^{12}C or ^{15}N/^{14}N. Trophic position is directly related to δ^{15}N and each trophic step corresponds to a change of roughly 3.4 $^{o}/_{oo}$ (Minagawa & Wada 1984; Zanden & Rasmussen 2001), whereas the source of the food is generally determined by similarities in δ^{13}C signatures. Lipids are depleted in ^{13}C and variable lipid storage between species can alter the interpretation of δ^{13}C values (McConnaughey & McRoy n.d.). Post et al. (2007) showed that lipid content is strongly related to C:N ratios for aquatic organisms. The δ^{13}C signatures of all our samples were corrected for lipids using the following equation from Post et al. (2007):

$$\delta^{13}C_{normalized} = \delta^{13}C_{untreated} - 3.32 + 0.99 \times C{:}N \qquad (2)$$

where C:N is the mass ratio of carbon and nitrogen in the sample. Although the authors suggest a different equation to correct for lipids in photosynthetic organisms, we applied Eq. 2 to the δ^{13}C values of the seston since we considered the samples to be mainly heterotrophic protists (Trottet et al. 2006). $\delta^{15}N$ values are not affected by lipid content and do not require transformation.

$\delta^{15}N$ data was tested for homogeneity of variance (Levene's test) and normality (Shapiro-Wilk test) to satisfy the assumptions of parametric statistical analyses. We analyzed the differences between the $\delta^{15}N$ signature of each length and potential prey items by calculating the mean $\delta^{15}N$ for each tissue type and the 95% confidence intervals (CI) around each mean for each site. To determine whether larger mussels had higher $\delta^{15}N$ than copepod nauplii, we split mussels into two categories - greater or less than the upper bound 95% CI of the mean $\delta^{15}N$ for copepod nauplii. We selected the higher $\delta^{15}N$ bound between the two sites to have a more conservative estimate of the upper bound. This new binary variable was then used to generate a logistic regression using a generalized linear mixed model fit by maximum likelihood using a binomial distribution with site as a random factor. The logistic regression describes the relationship between mussel length and the probability mussel $\delta^{15}N$ is greater than copepod nauplii $\delta^{15}N$. To quantify this relationship we calculated the exponent of the slope coefficient. We repeated this procedure using the lower bound of the 95% CI around the mean $\delta^{15}N$ for adult copepods to determine the relationship between mussel length and the probability mussel $\delta^{15}N$ is significantly less than copepod adult $\delta^{15}N$. We did not generate a logistic regression for seston because the $\delta^{15}N$ was of both mussels and copepod was greater than seston $\delta^{15}N$ in all the samples. Since the trophic position of blue mussels was our primary interest, $\delta^{13}C$ data was not included in the statistical analysis and was just presented to support the $\delta^{15}N$ data.

Adaptive feeding laboratory experiment

The experiment was performed at the Maurice Lamontagne Institute in Mont-Joli, Quebec, Canada. *Mytilus edulis* (shell length range 53 ± 3 mm) were obtained from an aquaculture farm in baie des Chaleurs (Carleton, Quebec). Mussels were maintained in controlled conditions prior to experimental trials; each mussel was glued to a line and suspended in 200 litre flow through basins supplied with unfiltered raw St. Lawrence estuary seawater (6-9^{o}C) taken from off-shore of the research institute. A non-axenic strain of the flagellated alga, *Isochrysis galbana* (Prymnesiophyceae, supplier: NutrOcéan), was used as the common resource. The algae were grown in 30 litre batch cultures at 21°C using Guillard's f/2 medium (Guillard 1975). The cultures were drained every three days and replenished with fresh medium to keep the algae in an exponential phase of growth. The average cell diameter of the algae was 6.1 µm and the dry weight was 5×10^{-5} µg/cell, estimated from Fidalgo et al. (1998). Nauplius larvae of *Artemia franciscana* (Anostraca, Crustacea) were used as the consumer in the experiment. Nauplii were hatched daily by suspending eggs in aerated filtered seawater, 22 hours before the start of experimental trials. Un-hatched eggs were siphoned off from the cultures. The average length of *Artemia* nauplii was 454 µm and the dry weight was 1.0 µg individual^{-1}, estimated from Abreu-Grobois et al. (1991).

Twelve-litre plastic buckets filled with eight litres of 0.2 micron UV treated seawater (6°C, salinity = 26 PSU) each received one mussel. Each mussel was suspended in the centre of an experimental bucket by hanging it from a dowel resting across the rim. Mussels were provided one of seven diet treatments varying in biomass proportion of *algae:Artemia* (100:0, 90:10, 75:25, 50:50, 25:75, 10:90, 0:100). The total biomass of each diet treatment was the same (4000 μg dry weight). To prepare diet mixtures, the densities of algae and *Artemia* cultures were estimated by counting the individuals from a subsample. From this, we calculated the volume needed from each culture to make up the diet treatments. Control buckets without mussels received the diet mixture as well. Diet treatments were replicated six times for buckets with and without mussels (84 buckets total). Although we aimed for the diet proportions listed above during preparation, the actual diet mixtures measured at the start of the experiment were used for the analysis. The experimental trials were run for one hour in an incubated room at 9°C without light to avoid stimulating algal growth and altering *Artemia* swimming behaviour. Gentle aeration kept the water in each bucket homogenized. The mussels were acclimated to their experimental conditions 24-hour period prior to the initiation of each trial. During this acclimation period mussels were fed their prescribed experimental dietary treatment.

At the start and end of experimental runs, we took 10 mL water samples from all treatment and control buckets and measured raw fluorescence using a Turner Designs Trilogy Fluorometer. Raw fluorescence values were converted using a standard curve to estimate the density of algae. *Artemia* were collected at the end of the experiment by straining the contents of each bucket using a 64 μm filter and fixing them in 70 % ethanol. These samples were counted under a dissecting microscope to determine *Artemia* density.

Clearance rates on algae and *Artemia* were used to measure the grazing activity by mussels and is defined as the volume of water cleared of a given prey type per unit time per mussel (volume time^{-1} mussel^{-1}). Specific clearance rate (F_i) for the ith prey type was calculated according to Coughlan (1969) as:

$$F_i = (V / \Delta t) (\ln [C_{0i} / C_{ti}]) \qquad (3)$$

where V is the volume of water in each bucket and Δt is the elapsed time. When calculating clearance rates for algae (F_{Iso}), C_{0i} and C_{ti} are the algal concentrations at time 0 and time t in buckets with mussels. To account for algal growth and sedimentation (consumption by zooplankton is negligible given newly hatched *Artemia* do not feed [41]), we calculated the mean clearance rate on algae in control buckets with no mussels for each diet mixture and subtracted the corresponding mean from each F_{Iso} value of the same diet. For clearance rates on *Artemia* (F_{Art}), C_{0i} and C_{ti} are the nauplii concentrations in control and treatment buckets respectively. We assumed no growth in the *Artemia* population given the short duration of the experiment and the moulting rate of *Artemia* [42].

The selectivity coefficient (S_i) for the ith prey type was calculated as:

$$S_i = F_i / \sum F_i \qquad (4)$$

where a value of S_i above or below 0.5 indicates feeding preference or avoidance, respectively (Chesson 1978; Vanderploeg & Scavia 1979). Changes in selectivity across diets were analysed using linear regression. If the regression was not significant, the selectivity data from all mixed diets was pooled and the t-statistic was used to test for significant deviations from random feeding (S_i = 0.5). Selectivity data met the assumptions of normality (Shapiro-Wilk test) and homogeneity of variance (Breusch-Pagan test).

Results

Copepod community composition

The ordination qualitatively demonstrates the copepod community between farm and reference sites were distinct (Figure 1a). In an ordination, where distance on the plot is inversely related to similarity, farm sites group together and reference sites are closer to each other than to farm sites. The ANOSIM indicated that farm and reference sites copepod community composition was significantly different (p=0.014, R=0.325). The Tukey HSD results on the density data indicated copepod density was greater in reference sites (Figure 1b, ANOVA, p=0.032).

Trophic position field study

Clear trophic structure was demonstrated by the $\delta^{15}N$ data with seston at the base of the food web, followed by copepod nauplii and adult copepods occupying the highest trophic position at both site 1+ and 2+ (Figure 2). Mussels demonstrated a linear increase in $\delta^{15}N$ with length - with smaller mussels feeding closer to the base of the food web and larger mussels farther up, but lower than adult copepods. Results from the linear regression looking at intraspecific changes in trophic position revealed a significant positive relationship between $\delta^{15}N$ and mussel shell length for both sites 1+ and 2+ (site 1+ $R^2 = 0.254$, site 2+ $R^2 = 0.104$, $P < 0.001$), indicating that larger mussels occupied a higher trophic position (Figure 2). In both site 1+ and 2+ the seston mean and CI did not overlap with the mean and CI of any of the other tissue types. In site 1+ no mussel had a greater $\delta^{15}N$ that the lower bound of the CI around the mean $\delta^{15}N$ and in site 2+ only two mussels had a greater $\delta^{15}N$ than the lower bound. The logistic regression of mussel length and the binary variable created by categorizing mussel $\delta^{15}N$

by the nauplii CI upper bound indicates a positive relationship between mussel length and likelihood of the $\delta^{15}N$ value being greater than the copepod nauplii $\delta^{15}N$ (Figure 3). The exponent of the logistic regression of 1.06 indicates the probability the $\delta^{15}N$ of mussels is greater than the $\delta^{15}N$ of nauplii increases by 1.06 for every increase in unit of mussel length. The exponent of logistic regression of mussel length and the lower bound of the 95% CI around the mean of adult copepods of 0.978 indicates that a one unit increase in mussel length decreases the probability that mussel $\delta^{15}N$ is less than adult $\delta^{15}N$ by 1.02.

The mean (± SD) $\delta^{13}C$ signatures from the original dataset widely ranged from –24.61 ± 0.47 $^{o}/_{oo}$ (seston <60 μm) to –20.60 ± 0.51 $^{o}/_{oo}$. After mathematical lipid correction, $\delta^{13}C$ values increased and became more aligned; with the farthest outlying seston values being shifted the most (Table S1). This lends credence to the assumption that all the organisms analysed were part of one food chain supported by the same carbon pool. The sample variance in $\delta^{13}C$ values was amplified as a result of lipid correction as well.

Adaptive feeding laboratory experiment

Our target-feeding ration in each bucket was 4000 μg of total biomass (dry weight). However, based on the initial densities of *Artemia* and algae, the estimated mean (± SE) total biomass per bucket was 4588 ± 110 μg. On average, 60 to 70 % of the prey populations remained at the end of each experimental run. We found no pseudofeces in the containers at the end of each experimental run, indicating that mussels successfully ingested all the *Artemia* nauplii that were removed from the buckets.

The mean (± SE) specific clearance rates on algae and *Artemia* from unmixed diet treatments (i.e. 100 % algae or 100 % *Artemia*) were 2.24 ± 0.41 L h^{-1} $mussel^{-1}$ and 4.52 ± 0.59 L h^{-1} $mussel^{-1}$, respectively. Selective feeding appeared to decrease with increasing proportions of algae, although this trend was not significant ($R^2 = 0.094$, $P = 0.127$) (Figure. 4). When pooling the selectivity data from all mixed diets, mussels exhibited significant deviations from random feeding ($t = 6.43$, $P < 0.001$) with *Artemia* taken up in greater proportions than what was offered (mean ± SE of $S_{Artemia} = 0.69 \pm 0.03$) (Figure. 4).

Discussion

The present study combined field sampling and laboratory experimentation to characterize the consumer prey of omnivorous mussels in the HAM, assess ontogenetic niche shifts in this food web and the presence or absence of prey switching. In our experiment we established that *Artemia* can be part of the mussels' diet and have a significant impact on copepod communities i*n situ*, that the *Artemia* can even be positively selected over the common resource and that the preference for the *Artemia* does not change with the relative proportion of the two prey types. While we did not detect adaptive feeding in our experimental system, we identified potential stabilizing mechanisms in the *in situ* sampling. Here stable isotope signatures revealed stage-structured omnivory and associated prey size refugia, along with ontogenetic niche shifts of the consumer. These coexistence mechanisms essentially released copepods from occupying the position of the consumer by restricting the omnivore - consumer relationship to the interaction between very large mussels and the larvae of copepods.

We propose these coexistence mechanisms potentially allow the zooplankton to sustain itself as postulated by theory (Kratina et al. 2012).

Adaptive feeding by mussels

Our experiment showed that the mussels were selectively ingesting *Artemia* and "avoiding" algae, i.e., for all experimental algae:*Artemia* ratios *Artemia* was taken up in higher proportions than present in the prey mix (Figure. 4). More importantly, mussels showed no evidence for adaptive feeding, i.e., mussels consistently preferred *Artemia* nauplii over algae, independent of the ratio of the two prey objects (Figure. 4). There was a tendency toward increased selectivity for *Artemia* with higher *Artemia* proportions in the prey mix but this trend was not statistically significant. Consequently, we did not detect a behavioural coexistence mechanism in mussels. Both Gismervik and Andersen (Gismervik 1997) and Krivan and Diehl (2005) found that adaptive feeding improved the conditions for the consumer to persist however this behaviour appears to be absent in our experimental omnivorious food web. We extrapolate these results to the *in situ* food web where these manipulations would prove exceedingly difficult to perform. While adaptive feeding is absent in this food web, ontogenetic niche shifts and coincident prey size refugia were successfully detected.

Trophic relationships

Field data indicated the presence of mussels have a very real and significant impact on copepods in the HAM. The reduction in copepod density and difference in composition in the farm sites suggests that mussels are indeed participating in omnivory. Although it is likely that the zooplankton community is benefiting from migration events from sites where mussels are absent, the differences in composition between farm and reference sites suggests the persistence of zooplankton can not be explained by just source-sink dynamics. In the mussel aquaculture food web the consumer benefits from a reduction in competitive and predatory interactions. Stage-structured predation limited predatory interactions to the largest mussels with the earliest larval stages of the copepods. The smallest size class of mussels and copepod nauplii have similar $\delta^{15}N$ signatures and likely compete for seston, while the larger mussels were at a significantly higher trophic level (Figure. 2). The elevated $\delta^{15}N$ signatures in larger mussels suggest they are consuming considerable amounts of copepod nauplii (Figure. 2). The simultaneous feeding on seston and copepod nauplii dilutes the $\delta^{15}N$ signatures in larger mussels. If larger mussels had fed solely on copepod nauplii, $\delta^{15}N$ signatures would be expected to be higher. Additionally, the significant positive relationship between $\delta^{15}N$ and mussel shell length (Figure. 3) suggests a gradual shift towards stronger omnivory as farmed mussels increase in size.

The inclusion of only the naupliar stage of copepods into the mussel diet likely creates a size refuge for adult copepods. Size refugia allow potential prey to outgrow predation (Hin et al. 2011) and in food webs with omnivory size refugia can decrease the interaction strength between predator and prey as well as the niche overlap with competitors (Woodward & Hildrew 2002). The isotope data indicates that adult copepods were rarely (or never) ingested by mussels despite being very well represented in aquaculture farms (Cherif et al. *in press*). The calanoid *Acartia* sp. is the dominant large zooplankton species of HAM (Cherif et al. 2016) and is a copepod with a strong escape response, even in the naupliar form (Green et al. 2003; Titelman 2001).

Acartia adults experience significantly lower predation rates by mussels compared to other copepods (Lehane & Davenport 2006b; Jonsson et al. 2009).

Ontogenetic niche shifts in copepods reduced competition between adult copepods and mussels. Adult copepods sampled in this study tend to feed on dinoflagellates, other algae, ciliates, and copepod nauplii (Lonsdale et al. 1979). The mixed diet explains the lack of separation between copepod life stages. Interestingly, adult copepods occupied a higher trophic position than the largest mussels (Figure. 2). Since copepods cannot prey on mussels the result suggests that organisms from higher trophic levels (such as nauplii) make up a greater proportion of the adult copepods' diet than of the large mussels'. This greater reliance on copepod nauplii suggests that adult copepods have less niche overlap with larger mussels and therefore experience reduced competition. Ontogenetic niche shifts, as demonstrated above, have been shown to promote the maintenance of omnivory both empirically (Rudolf & Armstrong 2008) and theoretically (Hin et al. 2011). We conclude that copepods in the mussel aquaculture food web shift their ontogenetic niche when they mature from the naupliar to adult stages, which reduces competitive interactions with mussels.

Implications for introduced species

Initially the introduction of an omnivore with its simultaneous predation and competition would appear to be devastating to recipient communities, particularly consumers. While there are many documented introductions with deleterious effects, as in native food webs, stabilizing mechanisms could reduce interaction strengths in food webs with introduced omnivores (Lodge et al. 1994; Dick & Platvoet 2000; Hall 2011b;

Hall 2011a). Our study suggests that these stabilizing mechanisms may reduce the impact of the introduced omnivores allowing for the persistence of the food web.

Species introductions have the power to radically change recipient ecosystems and can force population declines, species extirpations and extinctions (Clavero & García-Berthou 2016; Blackburn et al. 2004; Bellard et al. 2016). Curtailing these impacts requires a predictive understanding of impact (Ricciardi et al. 2013). Here we show that an understanding of factors that can alter the strength of the novel interactions formed by the introduced species is necessary to assess the consequences of the introduction of an omnivore and the impact of aquaculture.

Data Accessibility

The complete R script for the analysis performed in the paper and associated data can be found online as a GitHub repository at the following DOI: http://dx.doi.org/10.5281/zenodo.58303

Acknowledgments

We thank Simon Bourgeois, Fred Hartog, Sarah Pease and Pauline Robert for their help with field and laboratory work. We also thank the staff of Maurice-Lamontagne Institute, Moules de culture des Îles and Le ministère de l'Agriculture, des Pêcheries et de l'Alimentation du Québec for logistical support.

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Figures

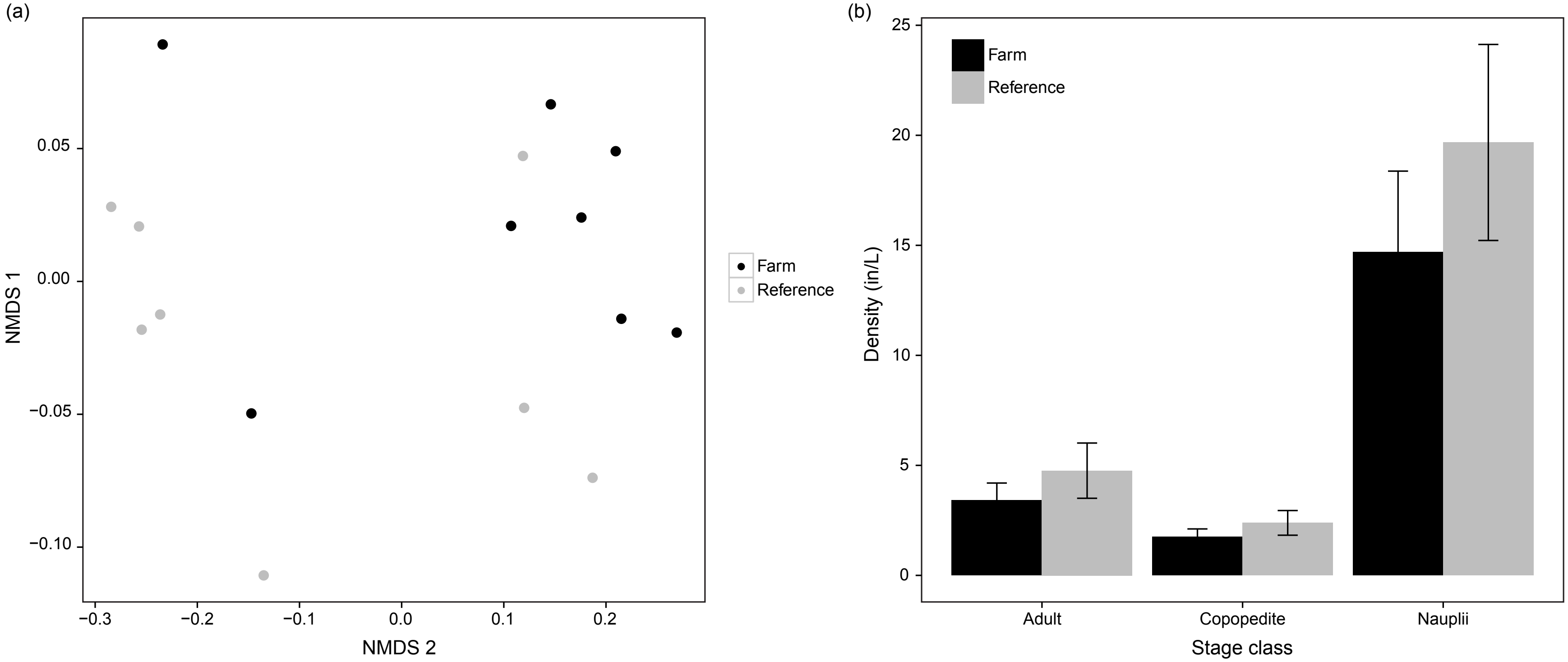

Figure 1. A. NMDS plot of farm and reference sites based on of zooplankton species and life stage composition. ANOSIM result indicates the composition between the two sites is significantly different (p=0.016). B. Bar plot of zooplankton density in farm and reference sites for each zooplankton life stage. Error bars denote standard error. Reference sites had significantly higher densities (ANOVA, p=0.031).

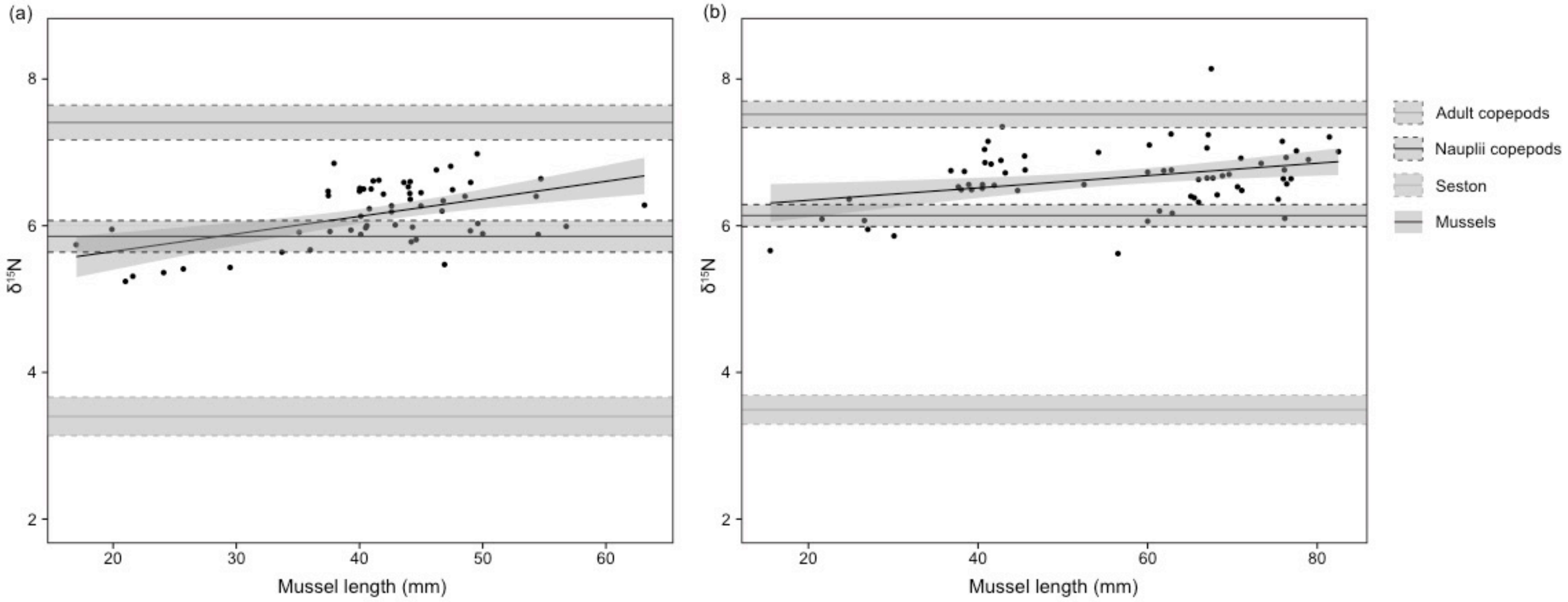

Figure 2. Plot of δ^{15}N against mussel size fitted with a linear model (δ^{15}N ~ mussel length) for A. Site 1+ and B. Site 2+. Horizontal lines are the mean δ^{15}N for adult copepods, copepod nauplii and seston in dark grey, black and grey, respectively with 95% confidence intervals plotted around the means in dashed lines.

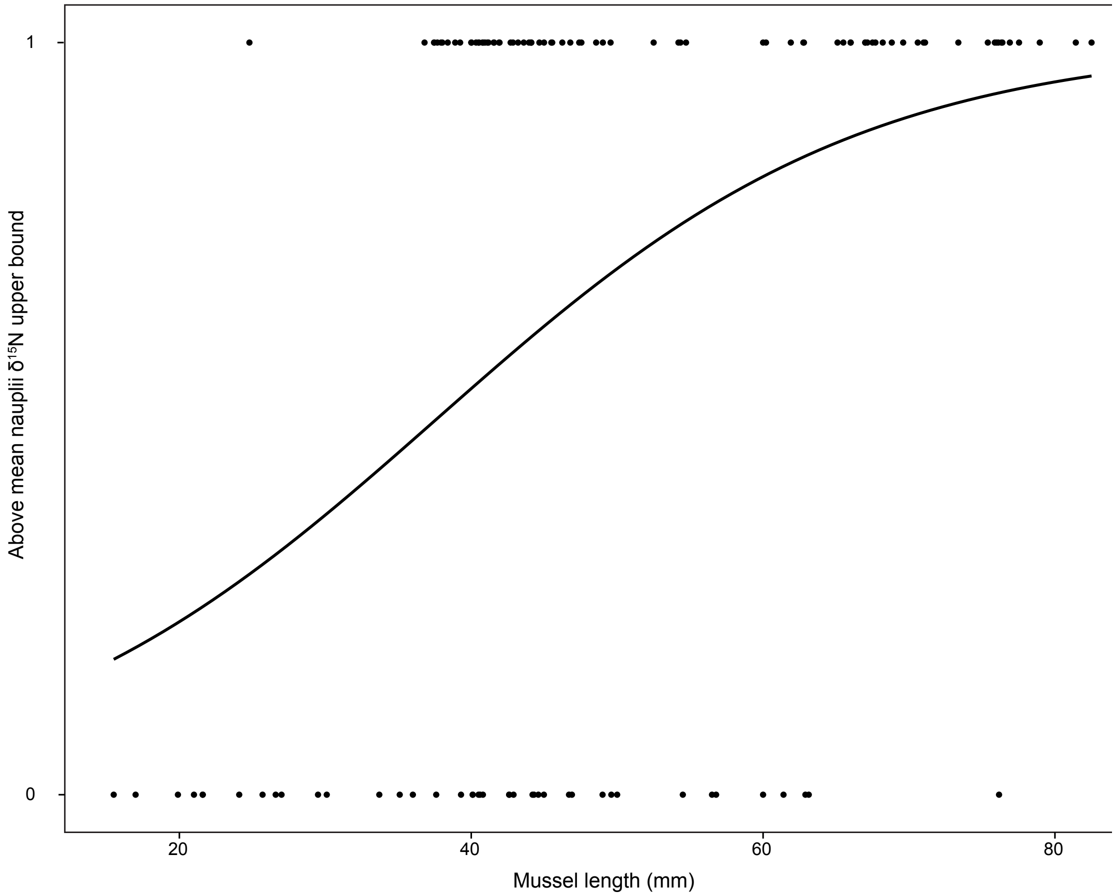

Figure 3. Logistic regression of mussel length and a binary variable created by assigning mussels into categories based on whether their $\delta^{15}N$ value was great less than (0) the upper bound of the 95% confidence interval around the mean copepod nauplii. A one-unit increase in mussel length increases the probability mussel δ^{15}N will be greater than nauplii δ^{15}N by 1.06 (GLMM).

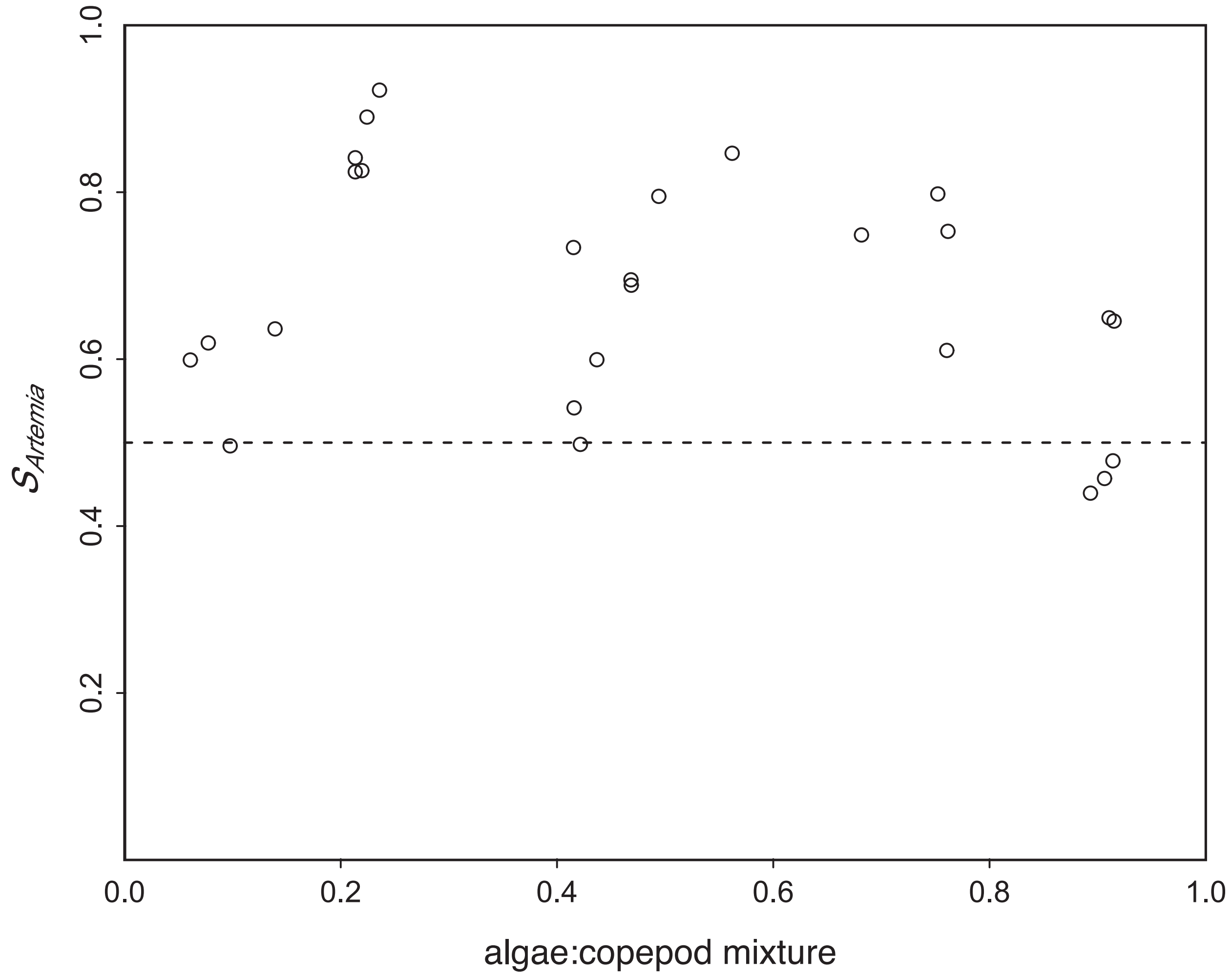

Figure 4. Selectivity of mussels (*Mytilus edulis*) for nauplii (*Artemia franciscana*) ($S_{Artemia}$) in feeding trials. Diets with different fractions of algae (*Isochrysis galbana*) vs. nauplii were offered (fraction values are based on proportion of biomass). Total biomass of the algae and nauplii was constant across all mixtures. The dashed line denotes no feeding preference by mussel for either prey. $S_{Isochrysis}$ values are not shown since they mirror $S_{Artemia}$ values ($S_{Isochrysis} = 1 – S_{Artemia}$) and the regression result is the same for both.

Consequences of consumer origin and omnivory on trophic cascades and stability in an experimental food web

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Summary

1. Food web stability is a fundamental characteristic of ecosystems that is influenced by the nature and strength of species interactions. Theory posits that omnivory positively affects food web stability. Non-native predators are hypothesized to alter stability and trophic cascades, owing to potentially higher consumption rates and prey naïveté. However, these hypotheses have not yet been tested together in a phylogenetically-controlled experiment.
2. The goal of this study was to test the interactive effects of secondary consumer origin (native/non-native) and trophic level (predator/omnivore) on stability and trophic cascades in a tri-trophic food web using a factorial mesocosm experiment.
3. We used four congeneric species of crayfish as secondary consumers: two species from native populations (*Orconectes propinquus* and *O. virilis*), and two highly invasive species from non-native populations (*O. limosus* and *O. rusticus*). Each mesocosm contained one crayfish, which acted as either an omnivore (feeding on snails and algae) or a predator (feeding on snails exclusively). Half of the crayfish were converted to predators through the surgical removal of setae to prevent algal consumption.
4. We found that, across all species, omnivores consumed a greater proportion of snails than predators, which led to higher benthic algal densities in mesocosms containing omnivores. Snail consumption was not affected by consumer origin.
5. Temporal variation in benthic algal density decreased in the presence of omnivorous crayfish compared to a predator of the same species, providing

the first phylogenetically-controlled empirical evidence that omnivores can increase stability.

Introduction

Food web stability (here defined as temporal constancy) is a fundamental characteristic of ecosystems (Worm & Duffy 2003) that is influenced by the strength of interactions between species (Lawler & Morin 1993; Morin & Lawler 1995). In food webs, interaction strengths are the likelihood of consumption of one species by another (McCann, Hastings & Huxel 1998). Weak interactions dampen oscillations between consumers and their food resources through lower consumer attack rates, which bound the population of consumers from explosive growth, thereby reducing the probability of extinction (Sala & Graham 2002). Therefore, communities dominated by weak interactions among species are expected to be more stable than those dominated by strong interactions (May 1973; McCann *et al.* 1998; Kokkoris, Troumbis & Lawton 1999). Empirical evidence suggests that natural food webs are indeed characterized by many weak interactions and a few strong interactions (Paine 1992; Fagan & Hurd 1994; Wootton 1997).

The presence of omnivores, typically defined as organisms that feed on more than one trophic level (Pimm & Lawton 1978; Pimm 1982), can have profound effects on food web stability. Omnivores reduce the strength of consumer-resource links by shunting some of the energy up the omnivore-resource pathway and away from the consumer-resource pathway (McCann et al. 1998). Increasing the number of omnivores in a system reduces the likelihood of strong interactions between trophic levels (Polis & Strong 1996) and can enhance the persistence of food webs (Holyoak and Sachdev

1998). Finke and Denno (2005) found that increasing the proportion of omnivores within the predator assemblage reduced the ability of predators to suppress herbivore populations, which resulted in reduced plant productivity. This same mechanism has been demonstrated to inhibit trophic cascades in both theoretical (McCann *et al.* 1998; Hart 2002) and empirical studies (Finke and Denno 2004).

The form of omnivory that has been the focus of theoretical and empirical investigations on omnivory and stability is intraguild predation (IGP), where an omnivore feeds on an intermediate consumer in addition to one of the IG prey's resources (Polis, Myers & Holt 1989; Holt & Polis 1997). Here, the consumption of the intermediate consumer or the resource by the omnivore reduces the strongly coupled interaction between the consumer and resource (McCann 2012). Dynamics of simple three- or four-species food webs with and without omnivores (especially IGP) have been examined experimentally and show omnivory is stabilizing (Lawler & Morin 1993; Morin & Lawler 1995). However, these early experiments did not directly manipulate the strength of food web interactions involving omnivores, so the potential stabilizing effects of omnivory could not be tested directly.

One of the only direct experimental tests of food web stability as a function of the degree of omnivory was conducted on arthropod assemblages by Fagan (1997), who found that a high degree of omnivory stabilized community dynamics following disturbance. However, because the omnivore and predator species used in this experiment comprised different genera, the effects of omnivory on community stability are confounded by potential species effects. Phylogenetically-controlled experiments of omnivory on stability are required for this theory to be substantiated.

There are reasons to expect that predator origin also has an influence on foodweb stability. Non-native predators tend to have stronger negative effects than native predators on native prey assemblages (Salo et al. 2007; Paolucci et al. 2013). These effects are thought to be the result of prey naïveté (Cox and Lima 2006). Invasive non-native species also tend to have higher resource consumption rates (Bollache *et al.* 2008; Morrison & Hay 2011; Dick *et al.* 2013) and could conceivably reduce stability by rapidly depleting resource abundance, leading to unstable predator-prey oscillations. Barrios-O'Neill et al. (2014) suggested that non-native species may destabilize food webs by being stronger interactors than similar native species, or by eliminating other species, consequently increasing the average interaction strength within a food web Moreover, stronger consumer-resource interactions involving non-native predators could magnify trophic cascades (e.g. Flecker and Townsend 1994; Kipp and Ricciardi 2012). However, the effects of non-native predators on the stability of primary production have not been investigated.

Here, we factorially manipulated secondary consumer origin (two species from native populations, two species from non-native populations) and secondary consumer trophic level (predator or omnivore) in freshwater mesocosms, to examine the effects of secondary consumer origin and trophic level on trophic cascades and stability in a tri-trophic food web (Figure 1). We tested four hypotheses: 1) Predators cause stronger trophic cascades than omnivores; 2) Omnivores increase stability at the resource level; 3) Non-native consumers elicit stronger trophic cascades than native consumers; and 4) Non-native consumers reduce the temporal stability of populations of primary producers.

Materials and methods

Study species

Non-native crayfish are commonly introduced in freshwater ecosystems, where they can replace native species (Lodge 1987, Lodge et al. 2000), cause complex indirect effects (Nystrom, Bronmark & Graneli 1996; Lodge *et al.* 2000) that can lead to changes in the structure of communities and food webs (Taylor & Redmer 1996; Wilson *et al.* 2004), and ramifying effects on aquatic food webs by significantly reducing macroinvertebrate grazer densities so as to facilitate increased primary production (Charlebois & Lamberti 1996). Four congeneric crayfish species were used in this experiment: two species from native populations (northern clearwater crayfish *O. propinquus*, and northern crayfish *Orconectes virilis*) and two species from non-native populations (spiny-cheek crayfish *O. limosus*, and rusty crayfish *O. rusticus*). *Orconectes limosus* and *O. rusticus* both have extensive invasion histories and have caused significant impacts on recipient communities (Olsen *et al.* 1991; Kozák *et al.* 2007; Hirsch 2009; Nilsson *et al.* 2012). Although *O. virilis* occurs naturally in many regions of the USA and Canada, it has been introduced to other regions in North America (Hobbs, Jass & Huner 1989; Phillips, Vinebrooke & Turner 2009; Larson *et al.* 2010) as well as the United Kingdom (Ahern, England & Ellis 2008). By comparison, *O. propinquus* has a limited invasion history (Hill and Lodge 1999).

Experimental design

This study was comprised by a 4 x 2 factorial experiment, where the following two factors were manipulated: secondary consumer species, henceforth crayfish [four levels: two native species (*O. propinquus* and *O. virilis*), and two non-native species (*O. limosus* and *O. rusticus*); and secondary consumer trophic level [two levels: omnivore and predator] using outdoor freshwater mesocosms (114-L plastic containers, 81 x 51.4 x 44.5 cm) located at McGill University in Montreal, Quebec. All mesocosms were arranged adjacent to each other in a single row, across which treatments were distributed randomly. Each mesocosm received 4 L of gravel as sediment to foster natural biogeochemical cycling processes. A refuge (PVC pipe, 10 cm length x 5 cm diameter) was also added to each mesocosm, to reduce crayfish stress. Eight 10 cm x 10 cm tiles that were divided into quadrats were attached to the bottom of each mesocosm using magnets to keep them stationary during the experiment. The tiles were used as substrate on which benthic algae would grow, and from where we would collect algal samples for analysis. Mesocosms were covered with 2 mm^2 vinyl mesh to reduce colonization by macroinvertebrates, to minimize diurnal temperature variations, and to prevent crayfish from escaping. On 15 July 2013, mesocosms were filled with 64 L of dechlorinated tap water, and benthic algae were allowed to grow on tiles for 21 days prior to the start of experiments. All experimental mesocosms contained snails (*Physella* spp.), which acted as primary consumers of benthic algae, as well as prey for crayfish. Each treatment combination was repeated four times, for a total of 32 mesocosms.

Organism collection

Eight *O. rusticus* (mean carapace length ± 1SE, 25.26 ± 0.43 mm) were collected from Little Rouge River in Ontario (43°50’8.8794”N, 79°11’37.5354”W) on 29 July 2013, eight *O. propinquus* (26.68 ± 0.58 mm) and eight *O. virilis* (30.48 ± 0.85 mm) were collected from Blue Chalk Lake in Ontario (45°12’1.764”N, 78°56’50.352”W) on 30 July 2013, and eight *O. limosus* (21.66 ± 0.69 mm) were collected from the St. Lawrence River near Parc René-Lévesque at Lachine, Quebec (45°25’40.5624”N, 73°40’41.1882”W) on 2 August 2013. Snails (*Physella* spp.) were also collected from the St. Lawrence River near Parc René-Lévesque from 31 July – 3 August 2013.

Procedures for predator conversion

Crayfish feed on both vegetation and animals to a sufficient degree to be classified as omnivores, and exhibit a specificity in feeding structures for different resources (Holdich 2002). In order to have phylogenetically-equivalent crayfish “predators” to compare against omnivores, crayfish were manipulated in order to prevent them from effectively consuming algae and therefore rendering them a default predator.

The transformation of the crayfish omnivores to predators was achieved by manipulating the “filter proper”, which is comprised of the acuminate setae on the 1st maxilliped and maxillae (Budd, Lewis & Tracey 1978; Holdich 2002). Setae from the 1st-3rd maxillipeds, maxilla, maxillule and mandible were removed under a microscope using microdissection scissors while crayfish were under anesthesia (clove oil at 1 ml/L). Crayfish selected as omnivores were also anesthetised and placed under a microscope for the same duration as the full predator conversion procedure; this was intended to reduce any manipulation effects on subsequent crayfish behaviour. Dissections were performed from 31 July to 3 August 2013, after which the crayfish were kept in separate tanks during the recovery period prior to the beginning of the experiments. The date of the procedure was randomised across species. The manipulation of arthropod mouthparts has been used primarily in several studies to control for predation (e.g., Schmitz et al. 1997, Nelson et al. 2004). However, in these other studies, mouthparts were altered so as to prevent consumption of all prey, whereas in the present study, mouthparts were manipulated to allow consumption of only certain resources.

On 5 August 2013, 70 snails and a single crayfish were added to each experimental mesocosm; this was considered the starting point of the experiment.

Sampling benthic algal density and snail abundance

The experimental period lasted 61 days (5 August – 6 October 2013). Benthic algal density was sampled every second day for a total of 31 benthic algal samples for each mesocosm. To collect benthic algae, a single quadrat from a single tile from the bottom of each mesocosm was scraped on each sampling day. The quadrat measured on each sampling day was chosen randomly for each mesocosm. The benthic algae that was removed was added to 30-mL of dechlorinated tap water, and the concentration of chlorophyll-*a* in each sample was determined using fluorometry (FluoroProbe, bbe-Moldaenke, Kiel, Germany). Chlorophyll-*a* concentration was used as a proxy measure of benthic algal density. Data was collected from a total of four replicates from all crayfish species for each treatment combination except for the *O. rusticus* predator treatment, where data was collected from only three mesocosms due to crayfish mortality.

At the end of the experiment on 07 October 2013, the remaining snails were counted and recorded for final densities. The final abundance of snails in each mesocosm was later determined in November 2013.

Statistical analyses

All statistics and figures were performed using R (R Core Team 2015). To measure snail predation rate across crayfish species, the day at which 75% of snails were consumed in each mesocosm (LD75) was estimated by fitting a binomial model with a logit link function to the snail density time series data. A two-way analysis of variance (ANOVA) was then performed on mean LD75 using origin and trophic level as fixed factors. Since there was no significant effect of origin on mean LD75, and because species identity integrates origin, an ANOVA with trophic level and species as fixed factors was subsequently used. Owing to the high degree of spatial variation within tiles of the mesocosms, the rolling mean of algal density starting with the second sampling day (averaging across every three sampling days) was taken and subsequent analyses were performed on the homogenized data. The effects of trophic level and origin on algal density were tested in a generalized additive model (GAM; mgcv R package; Wood 2015). Models were ranked according to their second-order Akaike's information criterion (AIC_c; Burnham & Anderson 2002). Each model's support was estimated using difference in AIC_c with respect to the top-ranked model (ΔAIC_c). Each model's weight (w_i) can be interpreted as the probability that that model is the best model, given the data and the set of candidate models. A locally-weighted scatterplot smoothing (LOESS) regression was applied to scatterplots of benthic algal density over time to visualize trends in the benthic algal time series data and the vis.gam function (mgcv R package; Wood 2015) to visualize benthic algal density across time for each trophic level in three-dimensional space (symbolised as "s(Day)" in Equation 1 and Table 1).

In order to assess treatment effects on the stability of benthic algal density, analyses were focussed on temporal stability using measures of the coefficient of variation (CV) within plots across time (Pimm 1991; Tilman et al. 2006; Ives and Carpenter 2007). CV, equal to the standard deviation divided by the mean, is a scale-independent measure of variability that is used in ecological studies (Haddad et al. 2011); Schindler et al. 2010; Howeth and Leibold 2010; Kratina et al. 2012). A one-way ANOVA was used to determine the effects of crayfish origin and trophic level on the CV of benthic algal density. Because there was no effect of origin, an ANOVA with trophic level and species as fixed factors was subsequently used.

Results

Snail abundance

The abundance of snails at the end of the experiment was significantly affected by crayfish trophic level (ANOVA, $P = 0.021$) and crayfish species (ANOVA, $P < 0.001$; Figure 2; see Figure S1 in Supporting Information for estimated snail abundances over time in each treatment). Across all species, omnivores consumed 75% of snails in the mesocosm (i.e., reached LD75) faster than predators (ANOVA, $P = 0.02$). However, binomial models revealed that consumption rate was not significantly affected by crayfish origin (ANOVA, $P = 0.644$). *Orconectes rusticus* and *O. virilis* reached LD75 faster than *O. limosus* and *O. propinquus* (Figure 2, Table S1 in Supporting Information).

Evidence for a trophic cascade

Across all species, benthic algal densities were higher in the omnivore treatments than the predator treatments (Figure 3). The top-ranked model included only trophic level as the predictor (Table 1). Equation 1 was used for all benthic algal analyses with origin dropped, as it was not significant in the model.

$$Algal\ density \sim s(Day,) + Trophic \qquad (1)$$

Coefficient of variation

There was no significant difference in the coefficient of variation (CV) between native and non-native crayfish species (ANOVA, $P = 0.867$). However, the CV did differ significantly between predator and omnivore trophic levels, with a higher CV in the predator treatment (Figure 4, ANOVA, *P* = 0.034), as predicted. There was also a significant difference in the CV between *O. rusticus* and *O. limosus* (Tukey HSD, *P* = 0.038).

Discussion

Effects of crayfish trophic level, origin and body size on trophic cascades

Contrary to our hypothesis, omnivorous crayfish consumed snails at a higher rate than predaceous crayfish. The heightened consumption of snails by omnivores led to increased abundances of benthic algae, signifying a trophic cascade. This is contrary to a previous study on salt-marsh communities (Finke and Denno 2005), which suggested that omnivory dampened the indirect effects on primary producers compared to strict predators that fed on herbivores alone. In the study by Finke and Denno (2005), omnivores reduced herbivores by only 50% and predators reduced herbivores by 99%; whereas in our study, omnivores consumed more herbivores than did the predators. It is certainly possible for an omnivore to illicit trophic cascades, if it reduces herbivore abundances enough to relieve grazing pressure on the resource; this has been demonstrated by Lodge et al. (1994) in an enclosure experiment using *O. rusticus* and snails. While we might expect an omnivore to have a lower dampening effect on trophic cascades compared to a predator, this expectation changes if the omnivore consumes more snails than the predator, as was the case in our study. In our experiment, the omnivorous crayfish were free to prey on both snails and the resource, and through their reduction of snail densities, omnivores had an indirect positive effect on primary production. Meanwhile, the predatory crayfish that had undergone the manipulation may have reduced their consumption of snails compared to omnivorous crayfish, and therefore, did not have perceptible effects on primary production. Predatory crayfish, although unable to consume benthic algae, may have still attempted to collect algae, and through these wasted efforts, reduced their overall predation rates on snails. In addition, the manipulation of predatory crayfish mouthparts may have impeded their ability to detect snails, given that these mouthparts possess chemoreceptors (Hodgson 1958; Thomas 1970; Ameyaw-Akumfi 1977; Giri & Dunham 1999).

Neither benthic algal densities nor snail abundances were affected by crayfish origin. Although there were no significant differences in mean body size across crayfish species, (see Figure S2 in Supporting Information). The two largest species, *O. virilis* and *O. rusticus*, consumed both benthic algae and snails at a significantly higher rate than the two smaller species. Previous studies have shown that large crayfish can have greater negative impacts on both benthic algal biomass and benthic invertebrates (McCarthy et al. 2006). In addition, while *O. virilis* is native to our study system, it has an invasion history in North America and Europe, where it has had major ecosystem-level impacts (Hobbs *et al.* 1989; Phillips *et al.* 2009; Larson *et al.* 2010). In its invaded range, *O. virilis* has had adverse effects on the abundance and diversity of aquatic plants (Lorman & Magnuson 1978; Chambers *et al.* 1990) and benthic macroinvertebrates in ponds and streams (Moody & Sabo 2013), which, in addition to larger body size, may explain why we observed stronger consumptive effects of *O. virilis* in our experiments compared to *O. propinquus*.

At the end of the experiment, all individuals of *O. rusticus* that had undergone predator-conversion had subsequently regenerated the setae on their maxillipeds, a phenomenon not observed in the other three species. Although crayfish of all sizes are capable of growing new appendages (Skinner 1985), to our knowledge no previous study has documented the regeneration of crayfish maxilliped setae. In addition to their higher growth rates, propensity for achieving high densities, and competitive ability (Lodge, Beckel & Magnuson 1985; Hill, Sinars & Lodge 1993), this remarkable plasticity in *O. rusticus* may contribute to its invasion success.

Effects of crayfish trophic level and origin on stability

Theory suggests that omnivory increases stability by weakening interaction strengths that otherwise create large oscillations in organismal populations (McCann & Hastings 1997; McCann *et al.* 1998; McCann 2000). Although two previous studies found empirical evidence of omnivory increasing stability (Fagan 1997; Holyoak & Sachdev 1998), our study provides the first phylogenetically-controlled test of this phenomenon. We propose two non-exclusive hypotheses for why temporal stability of benthic algae was higher in mesocosms containing predatory crayfish than mesocosms containing omnivorous crayfish. Firstly, although predatory crayfish consumed fewer snails than omnivorous crayfish, they still consumed a higher ratio of snails to algae, given that crayfish grazing was eliminated, or at least substantively reduced, as a result of the surgical manipulation. It may be that the ratio of snails to algae being consumed by each crayfish is a more important predictor of stability rather than overall consumption rate of either trophic level. Secondly, although our original intent in manipulating crayfish to be predators was to eliminate the predator-resource interaction to compare against an omnivorous food web that contains weak interaction strengths between consumer and resources, we ultimately created a food web with very weak or absent interactions between predator and consumer and between predator and resource. The reduction, or ostensibly the elimination, of trophic links between the predator and the remainder of the food web allowed us to instead compare the effects of an omnivore food web against a food web with only a consumer-resource interaction. Consistent with predictions, the predator treatment with only the consumer and resource interacting is an excitable and less stable interaction than the omnivore treatment, as demonstrated by the significantly higher CV in our experiment. In the omnivore food web, CV was lower as the presence of both the omnivore-consumer and omnivore-resource trophic links increased the mortality of both the consumer and resource, thereby reducing the coupling strength between consumer and resource (McCann 2012). The reduction of this coupling strength translated into lower fluctuations in the resource population. Here, the resource population was not depleted – a pattern that was captured in the CV. Thus, our study demonstrated the ability of an omnivore to increase temporal stability in the resource compared to a weak-interacting predator of the same species.

Stability was not affected by crayfish origin in our study, contrary to one of our hypotheses. We expected that non-native crayfish would reduce stability through higher consumption rates compared to native crayfish (Barrios-O'Neill *et al.* 2014). Instead, we found that the CV was significantly lower in mesocosms containing the two larger crayfish species (*O. rusticus* and *O. virilis*) relative to smaller crayfish species (*O. limosus* and *O. propinquus*), indicating that larger crayfish were consuming snails at a higher rate. By effectively reducing the grazing activity of the snails and subsequently depressing oscillations in snail and resource abundance, larger crayfish increased the stability of the algal population.

In summary, our study provides the first phylogenetically-controlled empirical evidence of the ability of omnivores to increase food web stability compared to a conspecific predator. We found evidence for trophic cascades and increased stability in food webs in the presence of omnivores, but the omnivore's origin had no effect. These results suggest that, in the context of ever-increasing species introductions, the strength of interactions may depend on the relative size of the introduced species.

Data Accessibility

The complete R script for the analysis performed in the paper and associated data can be found online as a GitHub repository at the following DOI: http://dx.doi.org/10.5281/zenodo.30671

Acknowledgements

We thank Rowshyra Castañeda, Sian Kou-Giesbrecht, and François Vincent for their assistance with the experiment, Brie Edwards, Keith Somers and Ron Ingram for their support in the collection of crayfish and Zofia Taranu for her input on the statistical analyses. This study was funded by the National Sciences and Engineering Research Council of Canada, and the Canadian Aquatic Invasive Species Network.

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Tables

Table 1. Summary of models predicting mean algal density, ranked based on AIC$_c$ values.

Model Rank	Model	K	AIC$_c$	ΔAIC$_c$	w_i
1	Mean algae density~ s(Day)+Trophic level	4	4795.42	0	0.49
2	Mean algae density~ s(Day)+Trophic level+Origin	5	4795.88	0.46	0.37
3	Mean algae density~ s(Day)+Trophic level*Origin	4	4797.56	2.14	0.15
4	Mean algae density~ s(Day)	3	4825.64	30.22	<0.001
5	Mean algae density~ s(Day)+Origin	4	4826.65	31.23	<0.001

Figures

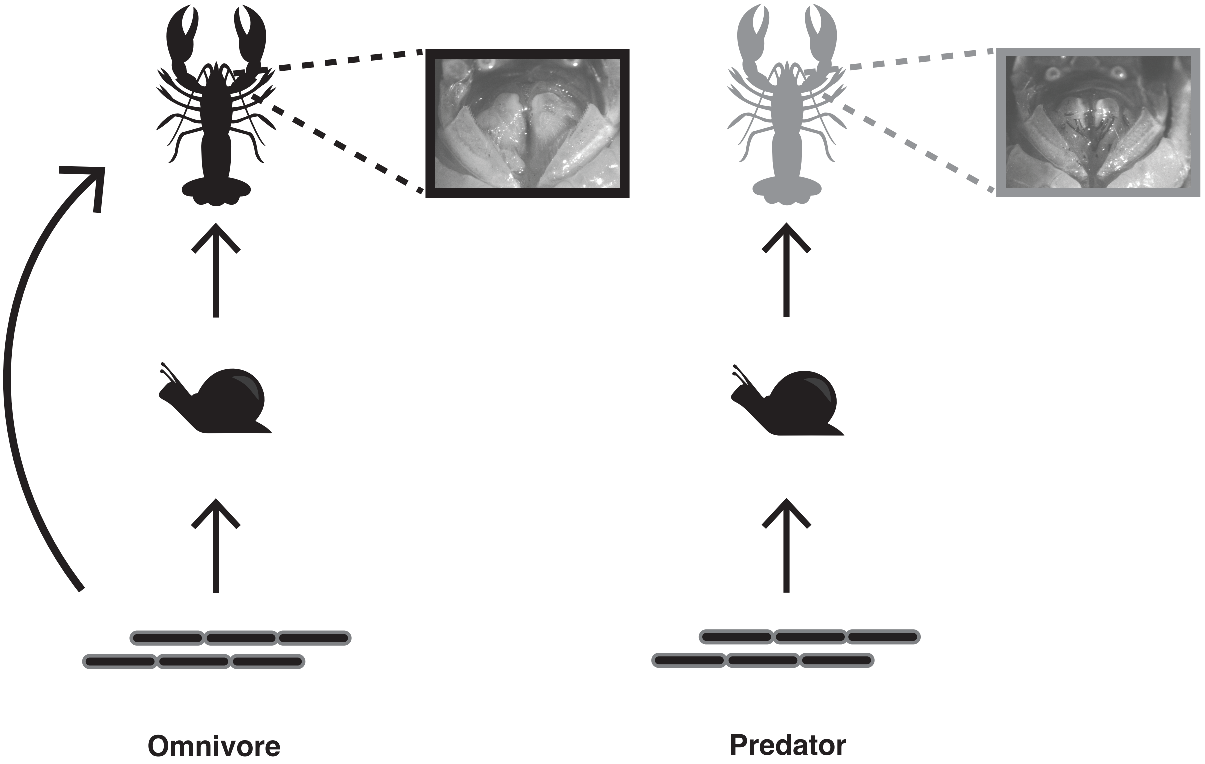

Figure 1. Food web modules used in the experiment. Omnivore (black) crayfish both consumed and competed with snails for a common resource (benthic algae). Predator (grey) crayfish only consumed snails, which in turn consumed benthic algae. Insets depict the removal of setae in the predator treatment to prevent the consumption of benthic algae.

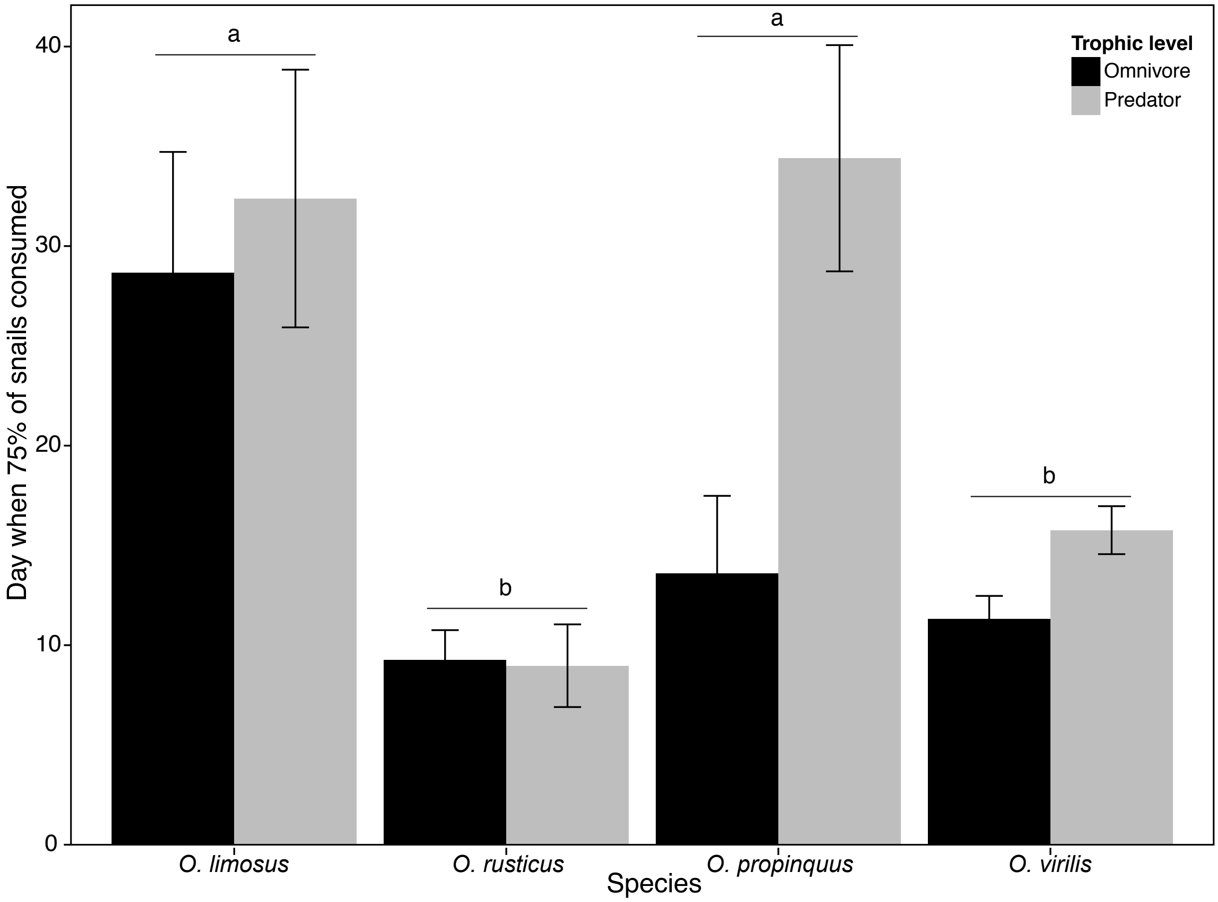

Figure 2. Mean day each species consumed 75% of the snails available in each mesocosm (LD75). Across all species, omnivores consumed 75% of snails in the mesocosm (i.e., reached LD75) faster than predators (ANOVA, *P* = 0.021).

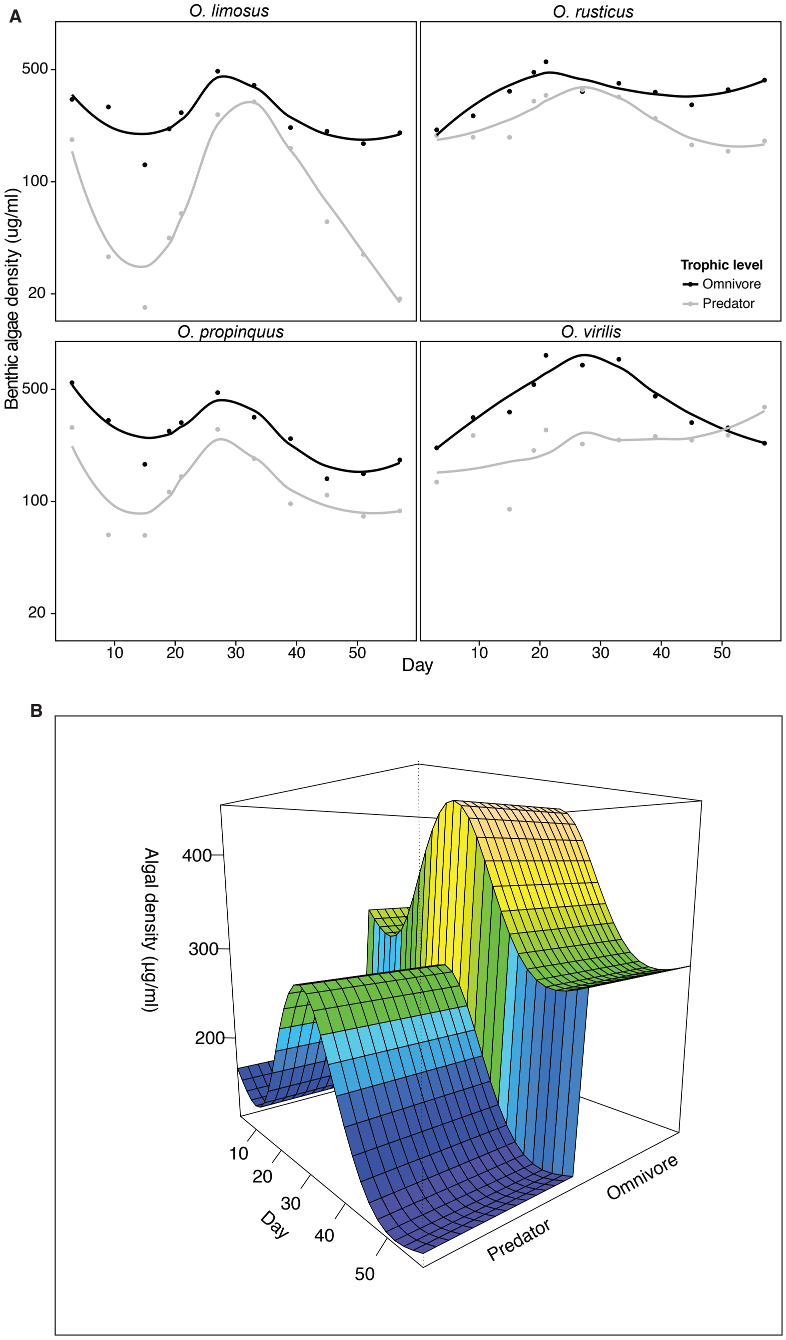

Figure 3. A. Benthic algal densities (µg/ml) across time for each species plotted by omnivore (black) and predator (grey) treatments. The smoothing line is a locally weighted scatterplot smoothing (LOESS) regression. Densities were significantly greater in the omnivore treatment and in the high feeding guild (GAM, $P < 0.001$). B. Predicted benthic algal densities from a GAM model using the same smoothing function for trophic level.

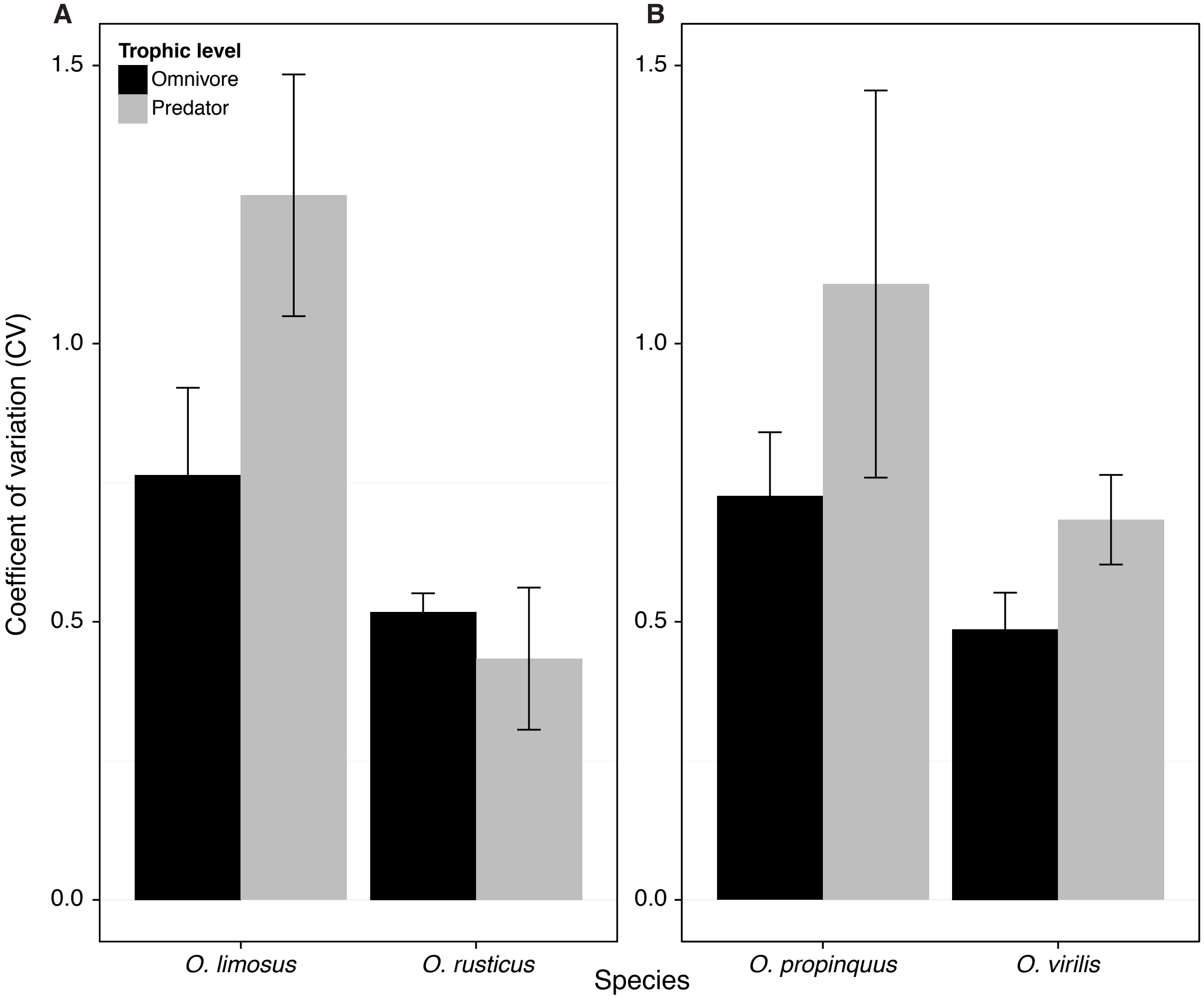

Figure 4. Coefficient of variation (standard deviation/mean) for benthic algal density across the experiment for A. non-native species and B. native species. The omnivore treatment is denoted in black and the predator treatment in grey. Error bars denote standard error calculated from the variation between mesocosm replicates. Coefficient of variation is significantly higher in the predator treatments (ANOVA, $P = 0.034$).

Supporting Information

Table S1. LD75* Tukey HSD results from a two-way ANOVA with trophic level and species as fixed factors.

Species	O. Limosus	O. Propinquus	O. Rusticus	O. Virilis
O. Limosus	-	0.415	<0.001	<0.05
O. Propinquus		-	<0.05	0.08
O. Rusticus			-	0.738
O. Virilis				-

1. Day when 75 of snails in mesocosm were consumed by the crayfish

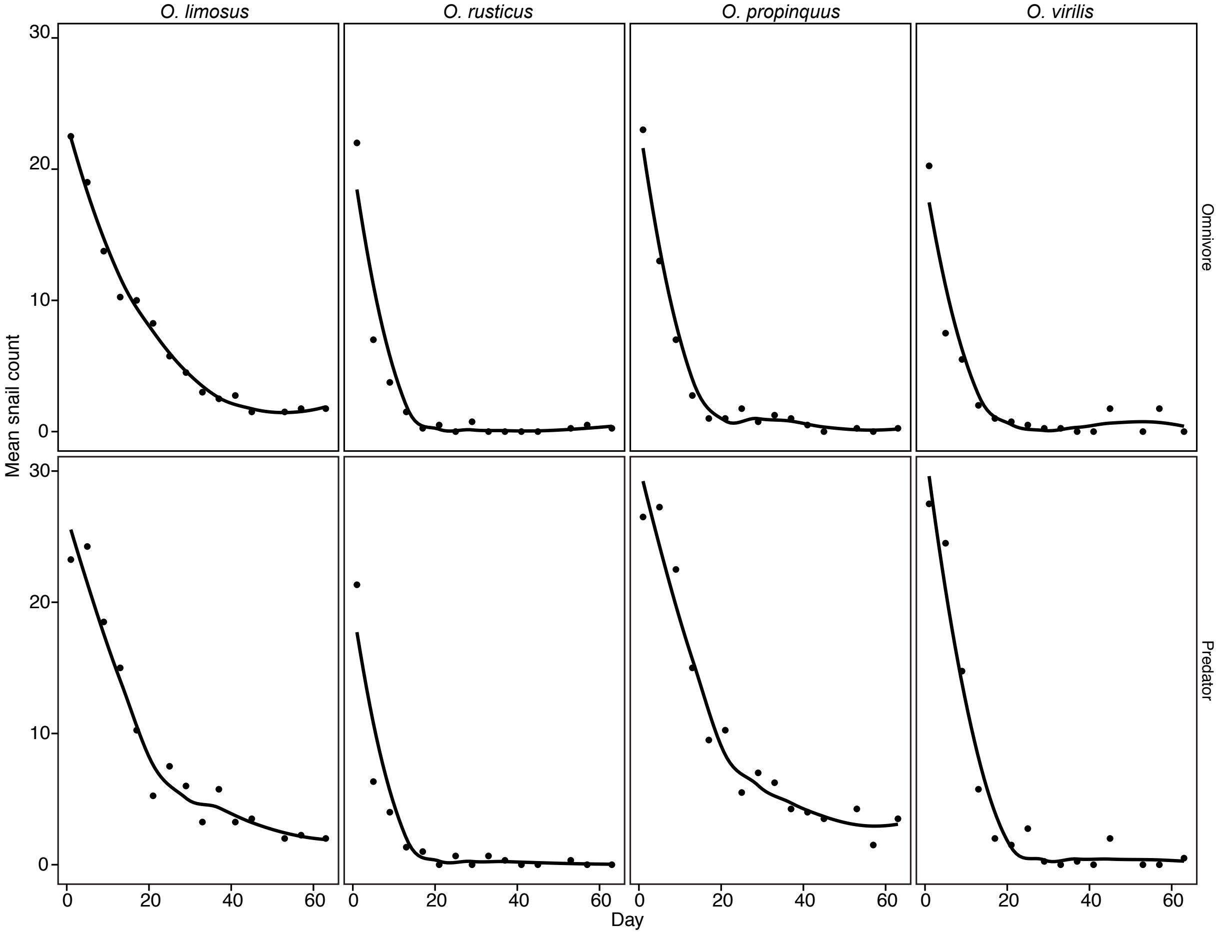

Figure S1. Mean snail abundances, averaged across species x trophic level replicates, across time for each species in the experiment. The smoothing line is a locally weighted scatterplot smoothing (LOESS) regression.

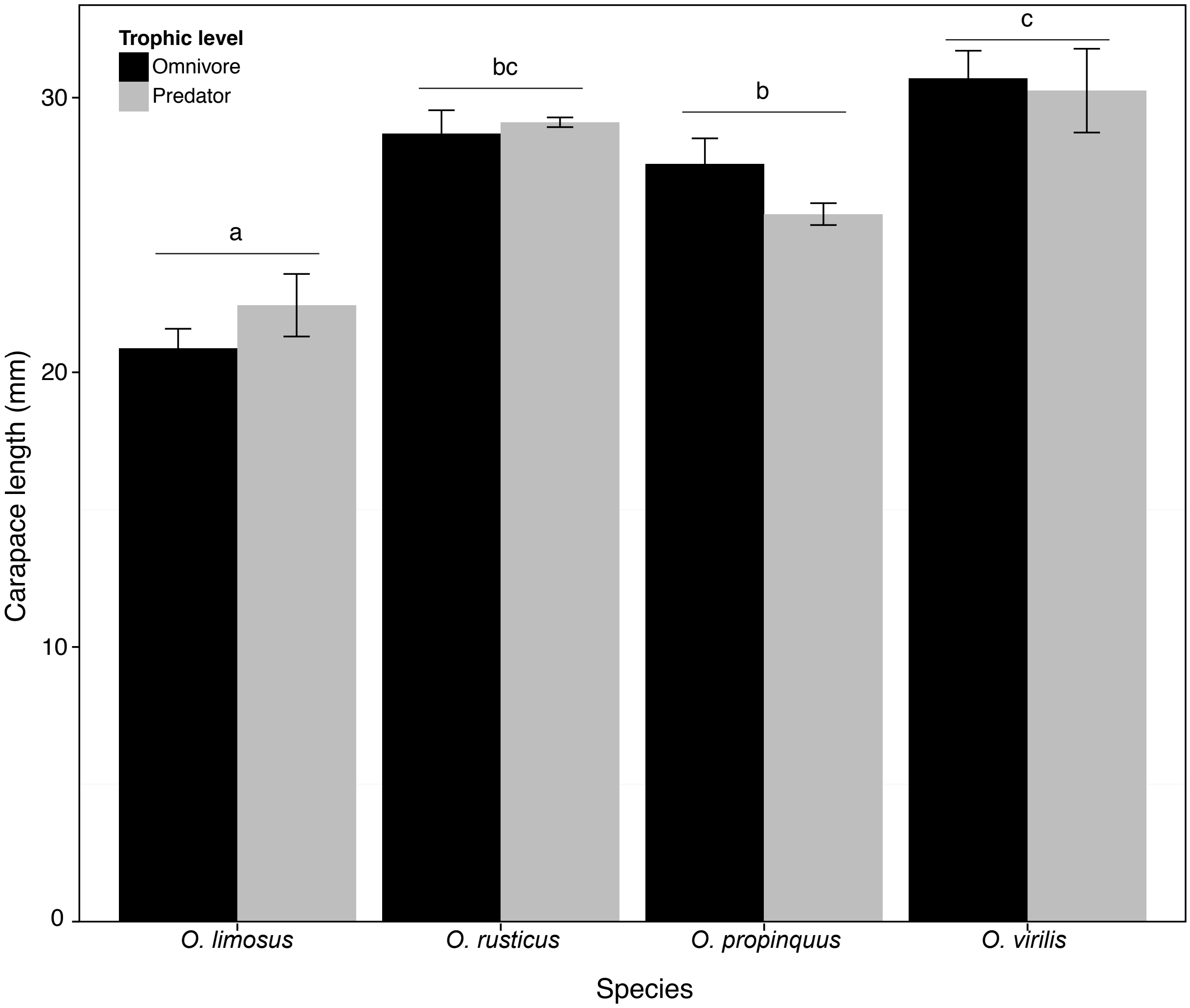

Figure S2. Mean carapace length (mm) for each crayfish species in the experiment. Error bars denote the standard error around the mean. *O. rusticus*, *O. virilis* and *O. propinquus* were significantly longer than *O. limosus* (ANOVA, Tukey HSD, *P* < 0.001). *O. virilis* was significantly larger than *O. propinquus* (ANOVA, Tukey HSD, *P* < 0.05).