Biodiversity from the bottom up: causes and consequences of resource species diversity

by

Anita Narwani
B.Sc., McGill University, 2003

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Supervisory Committee

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Abstract

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Species diversity may simultaneously be a cause and a consequence of variability in population, community and ecosystem properties. Ecology has traditionally focused on elucidating the causes of biodiversity. However, in the last decade and a half ecologists have asked the opposite question: What are the consequences of species diversity? The majority of these studies elucidated the effects of species diversity within single trophic levels. Incorporating trophic complexity is the next step in this research program. In this dissertation I investigated the causes of resource species diversity, as well as the impacts that resource diversity has on rates of consumption and the stability of population, community and ecosystem properties over time in planktonic food webs.

The high diversity of phytoplankton found in nature appears to defy the competitive exclusion principle, and elucidating the mechanisms which maintain this diversity continues to be a challenge. In general, variability in limiting factors is required to maintain non-neutral species diversity, but this variability can be generated by forces outside of the competitive community (i.e. exogenous), or may be the outcome of competitive interactions themselves (i.e. endogenous). Using microcosm experiments, I showed that endogenously generated variability in limiting factors was more effective at maintaining phytoplankton species diversity over the long-term, although the strength of this effect depended on the composition of the phytoplankton community.

Existing resource diversity has been proposed to generally weaken consumer-resource interaction strengths and limit consumer control of resource biomass. This is because more diverse resource communities are more likely to contain inedible, unpalatable, toxic or non-nutritious species. However, when resource communities contain multiple palatable species, diversity may also accelerate consumption. Using grazing experiments with multiple zooplankton consumer species, I found that the mechanism, direction and magnitude of modulation of consumption depended on the feeding selectivity of the consumer and the composition of the resource community. By altering consumer-resource interaction strengths in the short-term, resource species diversity may impact the stability of consumer-resource dynamics in the long-term. In separate microcosm experiments, I investigated the influence of resource species diversity, community composition and consumer feeding selectivity on population, community, and ecosystem properties over time. Diversity had positive effects on phytoplankton population biomass, resource community biomass, the rate of photosynthesis, the standing stock of particulate nutrients, and the generalist consumer's population density. It also stabilized resource community biomass and the stocks of particulate nutrients over time. Unexpectedly, diversity did not stabilize either of the consumer populations, regardless of feeding selectivity. This suggests that effects of diversity on resource community properties do not impact consumer dynamics linearly. Resource community composition was generally more important than resource species diversity in determining food web properties.

The importance of community composition in determining both the causes and consequences of resource diversity in these experiments points to the importance of species' traits and the outcomes of their interactions. I suggest that the use of complex adaptive systems theory and trait-based approaches in the future will allow a consideration of the feedbacks between the causes and consequences of species diversity in food webs.

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Dedication

To my parents and Ray, who gave me the peace and strength to persevere.

Chapter 1: Introduction

1.1 General Introduction

Definitions of ecology have evolved greatly since the term was first coined by Ernst Haeckel (1869), and this evolution reflects changes in our understanding of the natural world and an expansion in scope of ecological research. Haeckel (1869) defined ecology as (translated in Allee et al. 1949):

> ... '*the investigation of the total relations of the animal both to its inorganic and its organic environment*'.... '*the study of all those complex interrelations referred to by Darwin as the conditions of the struggle for existence*.'

This definition describes ecology as being focused on the individual organism and the forces which determine an individual's fitness under natural selection (Fig. 1.1 a). Andrewartha and Birch (1954) later defined ecology as the study of both biotic and abiotic factors governing the distribution and abundance of organisms. This definition reflects an expansion of focus from individual organisms to higher levels of biological organization including populations and communities (Fig. 1.1 b). A dramatic shift in the focus of ecology from the abundance and diversity of organisms to the structure and functioning of ecosystems began in the 1970s (Odum 1971, Fig. 1.1 c). Over time these two perspectives of ecology, one focused on the evolution, diversity and dynamics of organisms and the other on fluxes of material and energy between ecosystem compartments, have splintered into two relatively distinct fields: community ecology and ecosystem ecology.

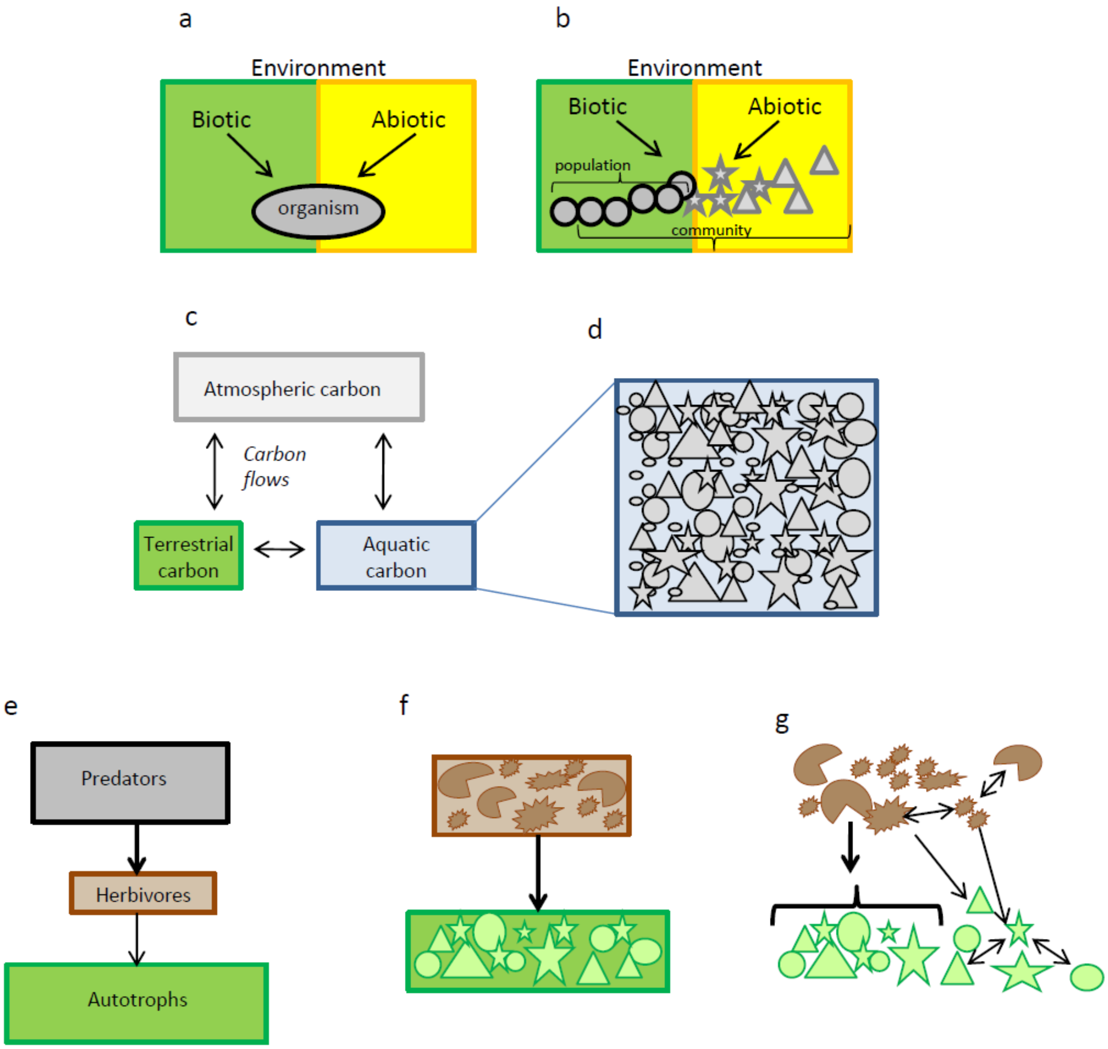

Figure 1.1. A schematic depicting changes in ecological perspective over time. **a.** The Haeckelian perspective, where the focus of ecology is on the influence of the environment on the organism. **b.** A broadening perspective including the consideration of populations and communities. **c.** Ecosystem ecology focuses on compartments of matter and energy and flows between them. **d.** Biodiversity and ecosystem function (BEF) research recognizes the potential for biotic influences on matter and energy. **e.** Early food web theory posits discrete, homogenous trophic levels; 'Green world hypothesis' (Hairston et al. 1960). **f.** Emerging inclusion of heterogeneity within trophic levels into food web concepts. **g.** Recognition of potential nonlinear and indirect effects of biodiversity in food webs.

In the last decade and a half, biodiversity-ecosystem functioning research (BEF) has made some progress in uniting these two fields by testing the influence of organisms on ecosystem structure and functioning (Chapin et al. 2000, Hooper et al. 2005, Fig. 1.1 d). Progress in theory has culminated in a recent theoretical synthesis of ecology which ties together the evolution of organisms, their interactions both with abiotic and biotic components of their environments, and their impacts on the functioning and stability of all levels of ecological organization from populations to ecosystems (Loreau 2010a). This view of organisms as dynamically adapting to, interacting with, and shaping both their biotic and abiotic environments is clearly reflected in a modern definition of ecology by the Cary Institute of Ecosystem Studies (2008):

> *'The scientific study of the processes influencing the distribution and abundance of organisms, the interactions among organisms, and the interactions between organisms and the transformation and flux of energy and matter.'*

1.2 Merging food web and biodiversity research

The importance of biotic diversity for the functioning and stability of communities and ecosystems has been a prolific area of research in recent years, spurred on in part by accelerating extinctions due to human activity (Pimm et al. 1995, Vitousek 1997). Prior to the recent focus on the impacts of species diversity, it had been recognized that the vertical structuring of food webs, i.e. the number of trophic levels or 'vertical diversity', could have large impacts on its properties. The 'green world hypothesis' (Hairston et al. 1960) proposed that predators limit herbivores via predation and release plants from suppression due to grazing (Fig. 1.1 e). Building on this hypothesis, trophic cascade theory predicted that food webs would be dominated by plant or herbivore biomass based on whether they had an even or odd number of trophic levels (Oksanen et al. 1981). While there is empirical support for the existence of trophic cascades (Estes and Palmisano 1974, Shurin et al. 2002), this view of food webs generally ignored the impacts of heterogeneity or diversity within trophic levels (Fig. 1.1 d). On the other hand, much of BEF research has tested the impacts of diversity on a single trophic level, ignoring the impact of vertical complexity (Duffy et al. 2007).

The limitations of such trophically simplified food web concepts have been recognized for some time (Strong 1992), and indeed differences among species within trophic levels may explain macroecological differences across ecosystems in the strength of trophic cascades, rates of flow of energy and matter across trophic levels, and food web topology (Shurin et al. 2006). Studies examining the effects of species diversity within a trophic level on community and ecosystem properties have generally found positive effects of diversity (Balvanera et al. 2006, Schmid et al. 2009, Cardinale et al. 2011). These effects have been attributed to one of two mechanisms, namely selection or complementarity (Loreau and Hector 2001). Selection occurs when a species which has a strong impact in monoculture comes to dominate mixtures, whereas complementarity arises out of niche differentiation or facilitation among species. The majority of the experiments on this topic to date have been conducted on primary producers (Balvanera et al. 2006, Cardinale et al. 2011). Very few studies have experimentally tested the impacts of diversity in a food web context, e.g. on rates of consumption, accumulation of biomass on neighbouring trophic levels, the stability of food webs, or the strength of trophic cascades (Balvanera et al. 2006, Duffy et al. 2007, Cardinale et al. 2011). However, the number of multi-trophic studies is growing (Hillebrand and Cardinale 2004, Finke and Denno 2005, Gamfeldt et al. 2005, Duffy et al. 2007, Jactel and Brockerhoff 2007, Jiang and Pu 2009, Srivastava et al. 2009).

There is a growing recognition of the need to consider biodiversity in a food web context and not just within trophic levels (Ives et al. 2005, Thébault and Loreau 2005, Duffy et al. 2007, Loreau 2010a, b, Fig. 1.1 f). Yet theoretical work on the impacts of biodiversity on ecosystem functioning and stability in food webs has not been developed to the same extent as that for single trophic levels. It has been proposed that selection and complementarity effects may be common both for producers and consumers, although the effects of these mechanisms may depend on whether their resources are biotic or abiotic (Ives et al. 2005, Duffy et al. 2007). The impacts of biodiversity on trophic interactions, neighbouring trophic levels, and food web dynamics is likely to depend on the trophic roles that organisms play either as consumers or resources (Duffy et al. 2007). For example, diversity at the resource trophic level may represent greater nutrition, variance in edibility, masking or dilution of edible resources, or altered total resource abundance for consumers (Petchey 2000, Duffy et al. 2007). Consumer diversity may represent greater niche complementarity in terms of resource specialization (and therefore greater resource consumption), a greater likelihood of intraguild predation, omnivory, or interference among species, or an increased likelihood of indirect, trait- or behaviourally-mediated effects on resources (Fig. 1.1 g). While differences in diversity effects across trophic levels have been proposed in theory, the data so far suggest that there are no differences in the impacts of diversity among trophic levels (Cardinale et al. 2006b).

The relative importance of species diversity at resource and consumer trophic levels, and the interactive effects of diversity at different trophic levels on food web properties is a burgeoning field and deserves much attention (Gamfeldt et al. 2005, Srivastava and Vellend 2005, Duffy et al. 2007, Dunne and Williams 2009, Srivastava and Bell 2009, Srivastava et al. 2009). In this thesis I focused specifically on the importance of resource species diversity for food webs. Resource diversity can dampen top-down control of biomass (Hillebrand and Cardinale 2004), and may be responsible for weakened trophic cascades (Strong 1992, Shurin et al. 2006). It has been hypothesized to stabilize food webs either by stabilizing resource biomass (Petchey 2000), by increasing the number of weak trophic interactions (McCann et al. 1998, McCann 2000), or by providing insurance for generalist consumers (MacArthur 1955, Yachi and Loreau 1999, Petchey 2000). However, resource diversity may also reduce the stability of consumer-resource interactions via the ‘paradox of enrichment’ (Rosenzweig 1971, McCauley et al. 1999), the synchronization of oscillations via generalist predation (Vandermeer 2006, Benincà et al. 2009), or the generally increased likelihood of unstable configurations of species interactions (May 1973).

1.3 Bottom-up effects of diversity in food webs

While it is almost common parlance that ‘diversity begets stability’, and heuristic theory has long posited the intuitive hypothesis that the diversity of resources should have positive impacts on the stability of the food web (MacArthur 1955, Elton 1958), empirical testing and formalization of this theory has lagged (Loreau 2010b, but see May 1973, McCann et al. 1998, Thébault and Loreau 2003, Thébault and Loreau 2005). Moreover, there are many reasons to expect that effects on the resource trophic level may not ‘cascade’ upwards through the food web linearly. First, resource heterogeneity may modify consumer-resource interaction strengths, and thereby produce unpredictable food web linkages (Kratina et al. 2007, Kratina 2009). Second, consumer-resource interactions may modify the relative abundance of individual resource species depending on the feeding selectivity of the consumer and trade-offs among resource species between competitive ability and resistance to consumption (Strong 1992, Mulder et al. 1999, Post et al. 2000, Thébault and Loreau 2003, Thébault and Loreau 2005, Tirok and Gaedke 2010). Accordingly, consumers may alter the mechanisms of coexistence among resources, and hence the effects of diversity, e.g. selection or complementarity within the resource trophic level (Post et al. 2000, Mouquet et al. 2002, Fox 2003, Tirok and Gaedke 2010). Finally, there may be multiple competing or synergistic effects of resource diversity on food web properties, the balance of which will determine the final impact of resource diversity.

My aim in this dissertation was to test the influence of resource diversity on consumer-resource interactions, and on food web dynamics, including population-level, community-level and ecosystem-level properties and stability. There has been a somewhat heated debate regarding appropriate methods to test the effects of diversity on ecosystem functioning on single trophic levels (Aarssen 1997, Huston 1997). Part of the debate centered on whether ‘selection effects’ of biodiversity are merely statistical artefacts resulting from greater sampling of a finite pool of species. However, selection effects require competitive dominance of species with particular traits (Loreau and Hector 2001, Fox 2005), and because they reflect the outcome of an ecological interaction (competition), they are now accepted to reflect more than just statistical artefacts (Loreau and Hector 2001, Cardinale et al. 2006a, Loreau 2010b, Cardinale et al. 2011). As a result of this debate, a number of methods have been devised to separate effects of individual species, or ‘community composition’, from those of species diversity per se (Cardinale et al. 2011). While this variance partitioning is useful from a phenomenological perspective, in fact all proposed biodiversity-ecosystem functioning/stability mechanisms (with the exception of statistical averaging, see Chapter 4) depend on species traits and ecological niches (Norberg 2004, Hillebrand and Matthiessen 2009, Merico et al. 2009, Loreau 2010b).

This highlights a theme which has emerged from this thesis and which is proposed by complex adaptive systems theory (Norberg 2004): namely, the effects of diversity on ecosystem functioning are likely inextricably linked to the traits of organisms and the ecological mechanisms which maintain the diversity of a community in the first place (Loreau 2010a). Therefore, while this dissertation's main focus was to study the effects of resource species diversity on trophic interactions and food web dynamics, I also aimed to address the mechanisms which maintain species diversity on the resource trophic level.

1.4 Model system and methods

I used controlled microcosm experiments to isolate and test the ecological impacts of the variables of interest in each chapter (Fraser and Keddy 1997, Drenner and Mazumder 1999). I used a planktonic freshwater model ecosystem, for which I individually cultured numerous phytoplankton species as resources and cladoceran zooplankton as consumers. I chose a planktonic experimental system for a number of practical reasons including the relatively short generation times of the organisms, the availability of organisms through culture collections and colleagues at other research institutions, and ease of culture and identification. The pool of species also represented substantial variation in traits of hypothesized ecological interest (e.g. size and growth rate for phytoplankton, and feeding selectivity for zooplankton (Thébault and Loreau 2005, Litchman and Klausmeier 2008, Litchman et al. 2010)). Furthermore, there is a large body of theoretical and empirical literature on this model ecosystem because the natural diversity of phytoplankton (Descamps-Julien and Gonzalez 2005) and the apparently strong top-down control of biomass by consumers in aquatic systems (Hairston et al. 1960) have baffled ecologists for a long time (e.g. Tilman 1982, Sommer 1984, Leibold 1989, Nisbet et al. 1991, Sommer 1992, Strong 1992, Hairston 1993, Kretzschmar et al. 1993, McCauley 1993, Sommer 1993, 1995, Leibold 1996, Murdoch et al. 1998, Nelson et al. 2001, Schippers et al. 2001, Steiner 2001, Downing and Leibold 2002, Steiner et al. 2005, Benincà et al. 2008, McCauley et al. 2008, Benincà et al. 2009, Jones et al. 2009, Downing and Leibold 2010, Fox et al. 2010, among others). Finally, I expect that planktonic food webs will be ideal systems with which to test mechanistic theory linking niche-based coexistence and ecosystem functioning and stability in the future. This is because many of the relevant species traits, trade-offs and interactions can be or have been measured (Tilman 1977, 1981, 1982, Huisman et al. 2001, Litchman et al. 2006, Litchman et al. 2007, Klausmeier et al. 2008, Litchman and Klausmeier 2008, Litchman et al. 2010)(see Chapter 5).

1.5 Relative importance of endogenous and exogenous mechanisms in maintaining phytoplankton species diversity

In order to investigate the effects of phytoplankton species diversity on food web properties and stability, it was first necessary to investigate how phytoplankton diversity is maintained over time. The competitive exclusion principle posed the pressing question of how biodiversity is maintained in nature. Many mechanisms have been proposed to explain diversity and to resolve what has become known as the ‘paradox of the plankton’ (Hutchinson 1961). Generally, these mechanisms invoke spatial or temporal variability in limiting factors, which enables species with unique ecological requirements and impacts to co-exist. In a seminal work, Chesson (2000b) described these mechanisms as ‘stabilizing’. He distinguished these from equalizing mechanisms which reduce or eliminate fitness differences among species, and therefore allow transient co-existence.

I propose a dichotomy among these mechanisms in order to enable empiricists to begin testing their relative importance. Specifically, the mechanisms can be categorized as being internally generated, or as depending on forces external to the competitive community. Here I tested whether the internal competitive dynamics of a phytoplankton assemblage, or externally generated resource variability (a disturbance) were more effective at maintaining species diversity over time. Niche theory suggests that species’ traits determine the outcome of competition and the likelihood of coexistence (Chase and Leibold 2003), and so we also tested whether the species composition of assemblages was important in determining the persistence of species diversity over time.

I employed controlled microcosm experiments in which I either imposed exogenous variability in nutrient availability via serial dilution, or allowed the communities to remain completely undisturbed. I found that species diversity was maintained most effectively in undisturbed microcosms in which only internal dynamics regulated coexistence. I also found that the community composition of the assemblage significantly interacted with the disturbance regime in determining species diversity. This confirmed the importance of internal dynamics and community composition in maintaining species diversity. Finally, I found that the treatments with the greatest diversity also had the greatest particulate organic carbon and were the most nutrient-limited, suggesting that internal mechanisms of coexistence may lead to greater resource use and biomass production.

1.6 Community composition and consumer identity determine the effect of resource species diversity on rates of consumption

Species diversity at the resource trophic level may affect the efficiency of the transfer of energy and matter to consumers via consumption. Experiments manipulating consumer presence or absence have suggested that resource species diversity should generally reduce top-down control of resource biomass (Hillebrand and Cardinale 2004, Edwards et al. 2010). The few studies which have carried out direct manipulations of resource diversity and measured consumption rates have shown both positive and negative impacts of resource diversity on rates of consumption, with no effect overall (Duffy et al. 2007).

In Chapter 3, I compiled a list of mechanisms by which resource diversity can impact rates of consumption. I proposed that resource diversity impacts consumption via different mechanisms depending on the consumer's feeding selectivity and the composition of species in the resource community. I used grazing experiments in which I manipulated resource diversity, community composition and consumer feeding selectivity to test the proposed mechanisms. I found that resource diversity most often had negative influences on rates of consumption, particularly for the specialist consumer, but that it could also accelerate rates of consumption when all resources were edible for the generalist consumer. I also confirmed that the mechanism by which resource diversity modulates consumption depends on the community composition and feeding selectivity of the consumer. Resource diversity may therefore modify trophic interaction strengths and consequently affect the stability of consumer-resource dynamics and food webs, which I explore further in Chapter 4.

1.7 Resource species diversity impacts the functioning and stability of food webs

Biodiversity experiments have shown that diversity can impact both the average and variability of populations and ecosystem functions in single trophic level ecosystems. Whether these impacts hold in food webs and across trophic levels is still unclear.

In Chapter 4, I tested the influence of resource species diversity on the stability of populations and ecosystem functions in food webs. I compared the effect of diversity to the effect of community composition. I also tested the ability of a number of proposed stabilizing mechanisms to explain stabilizing effects of resource diversity on resource community biomass. I separated the impacts of species richness, composition and community context on the average and variance in community biomass using Fox’s Price equation partitions (Fox 2006, Fox 2010). Finally, I confirmed that species’ traits had effects on dominance and diversity of the phytoplankton community, although I found that dominance did not have a strong effect on community stability.

Contrary to my expectations, I did not detect a significant effect of resource diversity on consumer population stability. I discuss potential reasons for this finding. In agreement with previous work on single trophic levels however, there was a stabilizing influence of resource diversity on resource community biomass and a number of ecosystem functions, while resource diversity negatively affected resource population stability. Among the stabilizing mechanisms tested, an increase in the average resource community biomass with diversity had the greatest effect. Nevertheless, community composition generally explained more variance in community biomass, ecosystem functions and stability than species diversity *per se*, again confirming the importance of species' traits.

In summary, Chapter 4 shows that resource diversity has positive effects on a number of food web properties and ecosystem functions, but indicates that these effects do not always linearly impact consumer population dynamics.

1.8 Summary and future directions

In Chapter 5, I summarize the main findings from each chapter and underscore the most compelling questions arising from each experiment. Overall, this thesis highlights the importance of community composition in determining the diversity, functioning and stability of communities. This emphasizes the importance of species' traits and interactions in determining both the causes and consequences of resource species diversity. I suggest that trait-based approaches and complex adaptive systems theory be employed to incorporate trait and interaction strength variance into food web models in the future. Such approaches also explicitly recognize that the processes which maintain (or eliminate) diversity ultimately determine the impacts that diversity has on population, community and ecosystem properties.

Chapter 2: Relative importance of endogenous and exogenous mechanisms in maintaining phytoplankton species diversity

Narwani, A., J. Berthin and A. Mazumder. 2009. Écoscience 16(4): 429-440.

2.1 Introduction

The competitive exclusion principle states that only a single competitor can survive on a single limiting resource (Volterra 1928). The principle has been extended to show that *n* species require at least *n* resources (MacArthur and Levins 1964), ‘limiting factors’(Levin 1970), or niches (Rescigno and Richardson 1965) to ensure indefinite and stable equilibrium coexistence in a homogeneous environment. The principle has inspired a search for mechanisms that maintain species diversity in nature despite competition’s tendency to reduce it, given the generally smaller number of limiting factors identified in most ecosystems (Hutchinson 1961, Connell 1978). These mechanisms have included limits to similarity and niche differentiation (MacArthur and Levins 1967, MacArthur 1969, Tilman 1982, Chase and Leibold 2003) disturbance of equilibrium species dynamics (Connell 1978, Huston 1979), density-independent mortality (Koch 1974a, Abrams 2001b, Steiner 2005), density- and frequency-dependent mortality (Janzen 1970, Connell 1978, Holt 1984), predation (Caswell 1978, Crowley 1979, Holt 1984), heterogeneity in the environment over space or time (Chesson and Huntly 1997, Chesson 2000a) storage-effects (Chesson and Warner 1981, Chesson 2000a), competition-colonization trade-offs (Levins and Culver 1971, Tilman 1994), and species equivalence or neutrality (Hubbell 2001, Scheffer and van Nes 2006). This list incorporates a great number of non-exclusive mechanisms, and there have been efforts to unite them all under a common synthetic framework.

Such a framework was most recently proposed by Chesson (2000b), who showed that mechanisms maintaining coexistence can work in two distinct ways: either they minimize fitness differences between species (these are equalizing mechanisms), or they increase the relative strength of intraspecific limitation over interspecific limitation (stabilizing mechanisms). This framework employs a modern definition of stable coexistence, which can be broadly equated with long-term persistence (DeAngelis and Waterhouse 1987). Such a view of stable coexistence is fundamentally different from that held by Volterra (1928) and Gause (1934) because it does not hinge on the existence of a stable equilibrium point and stabilizing mechanisms may depend upon population fluctuations. As a result, competition is not necessarily a destructive force, pushing the system towards dominance by a single species, but when competition is relatively nonlinear between species, it too can induce fluctuations and stabilize coexistence (Koch 1974b, Armstrong and McGehee 1980, Huisman and Weissing 1999, Abrams 2001b).

In this chapter we propose that, given Chesson's (2000b) new framework, the recognition of a second major dichotomy among mechanisms will aid empiricists in comparing their relative importance. Namely, mechanisms either depend on exogenous forces (e.g. variability in limiting factors), or they depend on internal competitive dynamics which can result in increased resource limitation or variability in limiting factors (Tilman 1982, Chesson 2000b). Exogenous variability in limiting factors can allow the expression of storage effects and relative nonlinearities in competitive ability among species (Chesson 2000b). Density-independent mortality, disturbances, nutrient pulses, heterogeneity in resource supply, density-dependent specialist predation, and frequency dependent predation all represent sources of environmental variability that are extrinsic to the assemblage of competitors and may enable coexistence. Intrinsic competitive dynamics on the other hand, may also promote non-equilibrium coexistence when competitive abilities are relatively nonlinear and produce intrinsic fluctuations in limiting factors (Armstrong and McGehee 1980). When the limiting factors are abiotic resources, competition among three or more species can produce "supersaturated" coexistence, or the coexistence of >*n* species on *n* resources. The likelihood of such coexistence has been debated (Huisman et al. 2001, Schippers et al. 2001). However, the probability of supersaturated coexistence can be high (up to ~70%) when competitors display intransitive competition. Intransitive competition occurs when three or more competitors form competitive networks rather than hierarchies, as in the common children's game of rock-paper-scissors (Huisman and Weissing 2001). In this scenario, no competitor is superior to all other competitors, but each competitor is superior to some, e.g. rock beats scissors, scissors beats paper, paper beats rock. Competitive intransitivity has been shown to exist and to enable coexistence in bacterial (Kerr et al. 2002, Kirkup and Riley 2004) and reef invertebrate communities (Buss and Jackson 1979), as well as among morphs of male lizard within a population (Sinervo and Lively 1996).

The relative importance of exogenous and endogenous mechanisms of coexistence in maintaining biodiversity is unknown. Temporal storage dynamics, in which coexistence is promoted by external environmental variability, have been demonstrated both in the lab (Descamps-Julien and Gonzalez 2005) and in the field

(Kelly and Bowler 2002), although spatial storage dynamics are predicted to occur more commonly (Chesson 2000a). Sources of exogenous variability such as disturbance and predation do not promote coexistence simply by reducing the strength of competition (Chesson and Huntly 1997), but rather, they do so also by allowing the expression of relative nonlinearity in competition and storage dynamics (Chesson 2000a). By contrast, with regard to internal dynamics, there have been numerous demonstrations of competitive exclusion in very simple, purely competitive systems (e.g. Gause 1934, Tilman 1977, 1981). Nevertheless, some more recent studies have shown that numerous species can coexist apparently indefinitely in purely competitive communities that are not subject to exogenous variability in limiting factors (Kerr et al. 2002, Roelke et al. 2003, Haddad et al. 2008). Our main aim here was to test the relative abilities of internally and externally driven dynamics to maintain species diversity.

Theory also predicts that the coexistence of multiple species should depend upon the traits of the species in the assemblage (Huisman and Weissing 2001, Chase and Leibold 2003). For instance, niche theory states that at equilibrium, species with similar requirements, but different impacts on their limiting factors will be more likely to coexist (Chase and Leibold 2003). Away from equilibrium, relative nonlinearity in competitive abilities, or storage effects are required, both of which entail particular differences in species' responses to limiting factors (Chesson 2000b). Huisman & Weissing (2001) showed that supersaturated coexistence is more likely when species consume the most of the resource for which they have intermediate requirements. Species' traits are therefore predicted to be important in determining the ability of species to coexist under both equilibrium and nonequilibrium conditions, and regardless of whether variability in limiting factors is generated internally or externally. As such, we also tested the effects of species identity and community composition on coexistence over time.

Specifically we addressed the following questions: 1) Is exogenous variability in limiting factors or are endogenously generated competitive dynamics more effective at maintaining species diversity in assemblages of phytoplankton? 2) Does the maintenance of species diversity depend on the species composition of the experimental community?

2.2 Methods

We tested the effects of external variability on species diversity by imposing density-independent mortality and fluctuations in resource availability on the communities. We compared the species diversity maintained in these treatments over time to that maintained in completely undisturbed, control treatments. We crossed these 'disturbance' levels by three different community compositions in order to determine the importance of the combination of species within communities on coexistence.

We created three unique phytoplankton community compositions by randomly assigning four species to each composition from a total pool of nine species (Table 2.1). In order to measure the growth rate of each species under our experimental conditions, we recorded the raw fluorescence (in raw fluorescence units, or RFUs) of well-mixed samples of each species daily for 18 days after an initial inoculation of batch monocultures. We measured raw fluorescence of each species with a Turner Designs Fluorometer™ and calculated their intrinsic maximal growth rates, $\mu_{\max}$ (day^{-1}):

$$\mu_{\max} = \frac{1}{T} \bullet \ln\left(\frac{P_t}{P_o}\right), \qquad [1]$$

where P_o = RFUs at the beginning of exponential growth, P_t = RFUs at the end of exponential growth, and T = days spent in exponential growth (Kilham et al. 1998).

Table 2.1. The four species introduced to each community composition. Inocula of phytoplankton species were obtained from the University of Texas Culture Collection (UTEX) and the Canadian Phycological Culture Centre at the University of Waterloo (CPCC).

Community composition	Species (Source and identifier)	Growth rate (day^{-1})
1	*Ankistrodesmus falcatus* (UTEX 101)	0.513
	Chlamydomonas reinhardtii (CPCC 84)	0.778
	Pseudokirchneriella subcapitata (CPCC 37)	0.281
	Staurastrum pingue (UTEX 1606)	0.204
2	*Rhodomonas minuta* (CPCC 344)	0.197
	Cryptomonas cf. rostratiformis (CPCC 343)	0.201
	Ankistrodesmus falcatus (UTEX 101)	0.513
	Fragilaria crotonensis (CPCC 269)	0.425
3	*Asterionella formosa* (CPCC 605)	0.231
	Fragilaria crotonensis (CPCC 269)	0.425
	Cyclotella sp. (CPCC 537)	0.703
	Cryptomonas cf. rostratiformis (CPCC 343)	0.201

The microcosms (500 mL Erlenmeyer flasks) each initially contained 250 mL of COMBO freshwater culture medium (Kilham et al. 1998). The phosphate and the nitrate concentrations in COMBO are 50 $\mu mol \cdot L^{-1}$ and 1000 $\mu mol \cdot L^{-1}$ respectively (Kilham et al. 1998). We inoculated equal cell (colony or filament) densities into the experimental microcosms using sterile technique. For the inoculations, we used exponentially growing monocultures of phytoplankton, which were maintained in serially-diluted batch culture. We measured the densities of each of the monocultures using a Bright-Line™ hemacytometer and either concentrated or diluted them to obtain suspensions with equal densities of ~30,000 cells$\cdot$mL^{-1}. To inoculate, we removed 20 mL of medium from each microcosm and replaced it with 5 mL of monoculture from each of four species using sterile technique. After inoculation, the assemblages grew in an Enconaire Environmental Growth Chamber™ at a constant temperature of 20ºC (max/min deviation of 1 ºC). They received 80 μmol photons$\cdot$m$^{-2}\cdot$s^{-1} of photosynthetically active radiation from cool-white fluorescent lights on a 12h light: 12h dark cycle. Throughout the experiment, the microcosms were shaken only before imposing disturbances and before sampling to ensure that representative communities were sampled.

Three community compositions were crossed by three disturbance levels in a factorial design. The three disturbance levels consisted of serial dilutions at 7-day intervals, 11-day intervals, and a treatment in which the microcosms were undisturbed for the duration of the entire experiment (97 days). The disturbed microcosms experienced density-independent death and nutrient replenishment. The undisturbed microcosms did not receive any nutrient replenishment for the full duration of the experiment. We imposed disturbance treatments by shaking the microcosms and then diluting the phytoplankton assemblages with autoclave-sterilized medium. Specifically, this involved the removal of 150 mL of the phytoplankton assemblage from the shaken Erlenmeyer flasks and replacement of this volume by fully-enriched sterile COMBO. We chose the duration of the two disturbance intervals because previous disturbance experiments have shown that peaks in diversity tend to occur at intervals between 5 and 28 days, with most peaks occurring at intervals between 7 and 10 days (Robinson and Sandgren 1983, Gaedeke and Sommer 1986, Sommer 1995, Floder and Sommer 1999, Floder et al. 2002). As such, we hoped to maximize the likelihood of detecting storage effects expressed as a result of fluctuating nutrient availability. Each community composition by disturbance treatment cross was replicated twice.

We sampled 15 mL of each experimental microcosm after shaking at low speed for one minute. We did this every two weeks for the first month, and then at one-month intervals until 97 days had passed. We fixed the 15 mL samples with 150 µL (1% by volume) of Lugol's iodine solution. We then concentrated the samples to 4 mL by settling for 10 hours and removing 11 mL of supernatant. We counted species-specific cell densities in the concentrated samples with a Bright-Line™ hemacytometer. For species with densities > 100,000 cells·mL^{-1}, we counted only the middle quadrat with a volume of 0.1 µL. Otherwise, we counted the number of cells in the entire counting chamber, with a volume of 0.9 µL. The counting procedure was replicated six times for each sample. We did not replace the sample volume removed from the microcosms with fresh medium because this would have introduced a pulse of nutrients and would therefore have interfered with the disturbance treatments. All of the microcosms therefore decreased in volume by a total of 75 mL over the course of the experiment. As such, the intensity of the disturbances increased after each sampling interval from a reduction in density of 60% to 63.8% to 68.2% and finally 73%.

On the final sampling date we took samples from each microcosm for organic carbon and nutrient analyses to determine the level of resource limitation. We measured total organic carbon, total phosphorus and total nitrogen from unfiltered samples. We calculated the particulate portion of carbon and nutrients as the total concentration minus the dissolved fraction. We filtered samples through Whatman™ GF/F glass microfiber filters to measure the dissolved organic carbon in the filtrate. We immediately ran these samples using a TOC-V-CPH Total Organic Carbon Analyzer™. We used Fisherbrand™ 0.45 µm nitrocellulose filters when filtering for the analysis of dissolved nitrogen and phosphorus and we froze these samples for analysis within four weeks of sampling. We measured phosphorus as orthophosphate (PO_4^{3-}) by the molybdenum blue-ascorbic acid method (Clesceri et al. 1998). We measured inorganic nitrogen using cadmium-reduction of nitrate to nitrite, followed by quantification of nitrite according to the sulphanilamide method (Clesceri et al. 1998).

We used cellular biovolume as a measure of biomass. We calculated the biovolume of each species by measuring the relevant cellular dimensions and entering these into previously described geometric formulae for their cell volumes (Hillebrand et al. 1999). We multiplied cell counts by cell biovolumes to achieve population biovolumes.

We used the Shannon Index as a measure of diversity (Shannon and Weaver 1949):

$$H' = -\sum p_i \bullet \ln p_i \,, \qquad [2]$$

where p_i is the relative abundance of species i. We derived p_i from biovolume, B, as $\frac{B_i}{B_{total}}$. We used biovolume (instead of abundance) in the Shannon Index so that the weighting of each species on the index would better reflect its ecological impacts (e.g. depletion of nutrients or ability to support consumers).

We calculated evenness as:

$$E = \frac{H'}{H'_{\max}} \,, \qquad [3]$$

where H' is the Shannon diversity index, and $H'_{\max}$ is the maximum value of H', and:

$$H'_{max} = \ln S, \quad [4]$$

where S represents species richness. The Shannon Index reflects both the number of species in a community and the evenness of their abundance (Magurran 2004). However, its usage and meaningfulness have been debated. In order to demonstrate how this metric was related to dominance in our communities, we also calculated Simpson’s Dominance Index:

$$D = \sum_i p_i^{\ 2} \quad [5]$$

D is the probability that any two individuals taken at random from the community are of the same species. This essentially represents the variance of the species’ abundance distribution (Magurran 2004).

We tested the effects of disturbance, community composition, and their interactions over time on phytoplankton diversity (H´) using a repeated measures analysis of variance (rm-ANOVA). In order to derive estimates for three missing data points, we used linear interpolation between bracketing data. In two cases, a missing value occurred at the beginning of a time series, in which case we used the subsequent values. We found that the effects of disturbance and community composition interacted with time (Table 2.3b), which made the interpretation of their main effects questionable (Underwood 1997). As a result, we compared only the data on the final sampling dates (day 97), in a factorial analysis of variance (ANOVA). We used a natural log transformation on H´ to ensure homogeneity of variances.

We found that greater nutrient limitation occurred in the undisturbed microcosms by the end of the experiment (see Results), and we wanted to test whether the effects of disturbance on diversity could be explained by the degree of nutrient limitation. To do this, we used the ratio of particulate organic carbon to particulate phosphorus (POC:PP) as a measure of nutrient limitation (Hecky and Kilham 1988), and we entered this into a single factor ANOVA as a covariate, with disturbance as a fixed effect. We also separately entered the ratio of particulate organic carbon to particulate nitrogen (POC:PN), because it appeared that nitrogen may have been more limiting than phosphorus (Fig. 2.5b, c). We compared these results to the ANOVAs without the covariate to determine whether the inclusion of the covariate eliminated disturbance from the model as a significant explanatory variable.

We tested whether disturbance level had an effect on particulate organic carbon (POC) with an ANOVA. We ln-transformed the POC data to meet the assumption of homogeneity of variances. We used a Tukey post-hoc comparison to determine which disturbance treatments differed. We also tested whether disturbance had an effect on the particulate organic carbon to particulate nitrogen molar ratios (POC:PN) and particulate organic carbon to particulate phosphorus molar ratios (POC:PP). Again, we ln-transformed the molar ratios to meet the assumption of homogeneity of variances. We tested whether the effects of disturbance on nutrient limitation depended on the phytoplankton diversity of the community by entering H´ into the explanatory model as a covariate and checking whether it affected the significance of disturbance as an explanatory factor. We used SPSS v 17.0 for all numerical analyses (SPSS Incorporated, Chicago, Illinois, USA).

2.3 Results

The highest mean species richness (S), diversity (H´, Fig. 2.1), and evenness (E) occurred in the undisturbed microcosms (Table 2.2). The lowest values occurred under the 7-day disturbance treatment. The same pattern was evident when we compared the effects of disturbance on diversity within each community composition (Fig. 2.2).

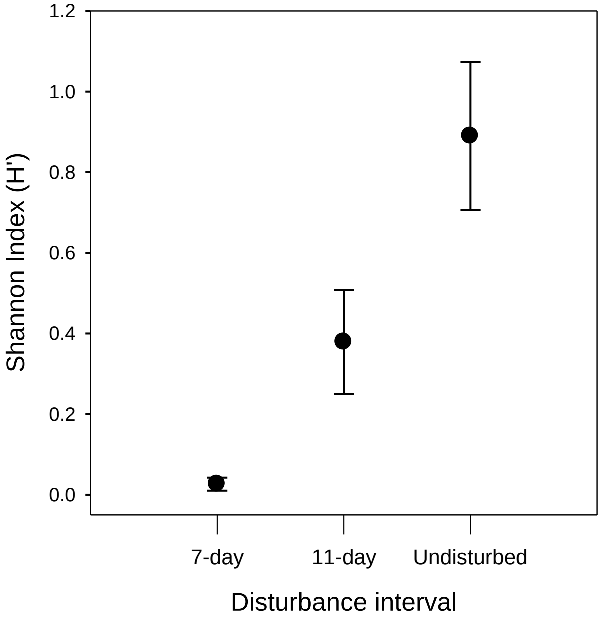

Figure 2.1. The Shannon diversity index (H´) as a function of the disturbance interval. Each point represents the mean H´ of each disturbance treatment on the final sampling day. Bars represent one standard error (n=3).

Table 2.2. Mean evenness, richness, and carbon: nitrogen: phosphorus ratio (C:N:P) of each disturbance treatment at the termination of the experiment (t = 97 days). Standard errors are shown in parentheses (n=6).

Disturbance treatment	Evenness (E)	Species richness (S)	C:N:P
7-day	0.028 (0.013)	2.333 (0.333)	32:11:1
11-day	0.346 (0.082)	2.833 (0.167)	50:7:1
Undisturbed	0.618 (0.087)	4.167 (0.307)	131:13:1

The rm-ANOVA revealed that community composition, disturbance and their interaction all had significant between-subjects effects on diversity (Table 2.3a, Fig. 2.3). Time had significant within-subjects interactions with disturbance and community composition on diversity (Table 2.3). As a result, the main effects of disturbance and community composition could not be clearly interpreted (Underwood 1997). An ANOVA for the effects of disturbance and community composition on diversity for day 97 showed that there was a significant interaction between disturbance and community composition (Table 2.3c, Fig. 2.2a). Increasing the disturbance interval caused an increase in diversity for all of the community compositions. However, the strength of the increase between consecutive disturbance levels varied among community compositions (Fig. 2.2a). The increase in diversity between the 7-day and 11-day interval was weaker for community composition 1 than for compositions 2 and 3, but it was stronger for composition 1 than for compositions 2 and 3 between the 11-day and undisturbed treatments. Because the disturbance treatments had the same qualitative effects (i.e. in terms of direction, though not in magnitude) on all of the community compositions, we judged it to be meaningful to interpret the main effect of disturbance on diversity, despite the significant interaction with community composition (Quinn and Keough 2002).

A single factor ANOVA showed that disturbance had a significant effect on diversity for day 97 (Table 2.3d). The Dunnett’s post-hoc comparison showed that the 7-

day disturbance level had a significantly lower diversity than the undisturbed treatment (P<0.001). There were positive correlations between phosphorus limitation and diversity (H´ versus POC:PP; R=0.568, P=0.017), and between nitrogen limitation and diversity (H´ versus POC:PN; R=0.521, P=0.039). Nevertheless, disturbance was a significant predictor of diversity, but phosphorus limitation was not, when phosphorus limitation (POC:PP) was included in the model (Table 2.3e). Similarly nitrogen limitation (POC:PN) was not a significant predictor and did not eliminate disturbance as a significant predictor (disturbance $F_{2,12}$=4.469, P=0.035 with POC:PN in the model). This indicates that the effect of disturbance on species diversity was not the result of correlated nutrient limitation.

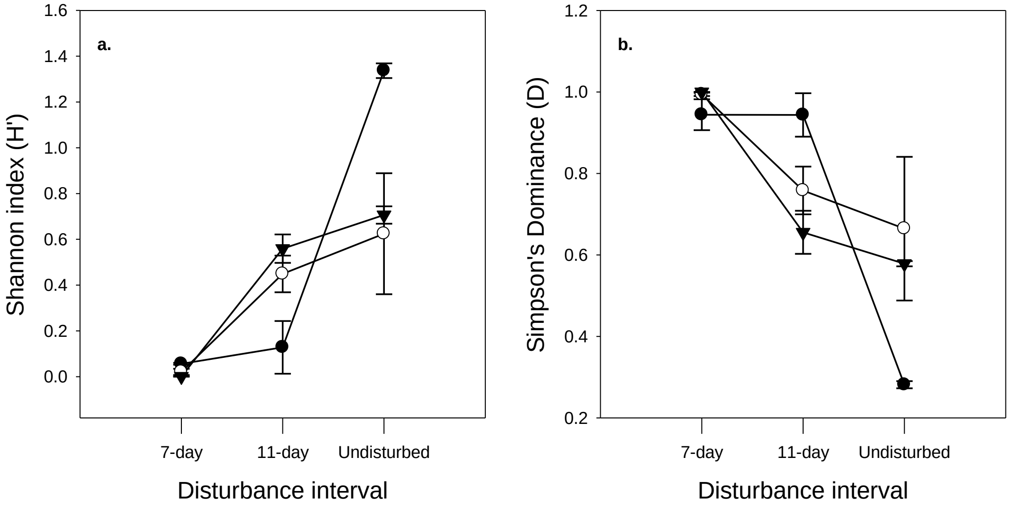

Figure 2.2. An interaction plot of the effects of disturbance and community composition on **a.** the diversity (H´) and **b.** the dominance (D) of the microcosms on day 97. Closed circles represent community composition 1, open circles represent composition 2, and closed triangles represent composition 3. Error bars represent ± 1 SE of the mean for each composition x disturbance treatment cross (n=2).

Table 2.3. a. Results of the repeated measures-ANOVA between-subject effects on species diversity, measured as the Shannon index (H'). **b.** Repeated measures-ANOVA within-subject effects. **c.** Results of the factorial ANOVA examining the effects of disturbance, community composition and their interactions on H' for day 97. **d.** Results of the one-way ANOVA examining the effect of disturbance on ln(H'+0.001) for day 97. **e.** As for part **d**, except phosphorus limitation (POC:PP) was included in the model as a covariate.
CC = community composition, Dist = disturbance.

Source	Type III sum of squares	Degrees of freedom	Mean square	F	P
a.					
CC	1.482	2	0.741	19.129	0.001
Dist	2.409	2	1.205	31.097	<0.001
CC*Dist	1.014	4	0.253	6.542	0.009
Error	0.349	9	0.039		
b.					
Time	1.361	4	0.340	9.034	<0.001
Time*CC	1.739	8	0.217	5.770	<0.001
Time*Dist	1.650	8	0.206	5.476	<0.001
T*CC*Dist	1.470	16	0.092	2.439	0.013
Error (Time)	1.356	36	0.038		
c.	R^2=0.941				
CC	0.061	2	0.031	1.439	0.287
Dist	2.260	2	1.130	52.964	<0.001
CC*Dist	0.750	4	0.188	8.791	0.004
Error	0.192	9	0.021		
d.	R^2=0.686				
Dist	56.664	2	28.332	16.423	<0.001
Error	25.877	15	1.725		
e.	R^2=0.718				
Dist	12.393	2	6.196	5.001	0.025
POC:PP	2.386	1	2.386	1.926	0.189
Error	16.108	13	1.239		

The effects of composition and disturbance on Simpson’s Dominance Index (D) were inversely related to the effects on diversity (Fig. 2.2 a & b). Overall, there was high dominance for the 7-day interval, lower dominance in compositions 2 and 3 under the 11-day interval, and the lowest dominance for all compositions in the undisturbed treatment (Fig. 2.2 b). The rm-ANOVA for the effects of disturbance and composition over time on dominance violated the assumption of sphericity. The Greenhouse-Geisser correction for this violation detected significant interactions between time and disturbance ($F_{3.855,17.347}$=4.203, P=0.015), as well as between time and community composition ($F_{3.855,17.347}$=4.705, P=0.01). As a result, we used an ANOVA to test for effects of disturbance and community composition on dominance on day 97.

Disturbance interval and the interaction between disturbance and community composition had significant effects on dominance ($F_{Disturbance;2,9}$ = 36.331, P<0.001, $F_{Interaction;4,9}$=6.164 , P=0.001), while composition did not have a significant main effect ($F_{2,9}$=1.187, P =0.349). We removed community composition from the model, and conducted a Dunnett's post-hoc test. This confirmed the significant main effect of disturbance ($F_{2,15}$=15.126, P<0.001), and showed that the undisturbed treatment had significantly lower dominance than the 7-day and 11-day disturbance treatments (Dunnett's P<0.05, Fig. 2.2b). Note that the P-values for this test should be evaluated cautiously because the data did not have equal variances, and this could not be improved by any transformation (Levene's Test $F_{2,15}$ = 4.146, P = 0.037).

Changes in diversity and dominance over time depended both on the disturbance level and on the community composition (Fig. 2.3). Diversity increased for all treatments between the inoculation of the microcosms (t=0) and the first sampling at 14 days, while dominance decreased. After 14 days, however, diversity declined for all microcosms exposed to the 7-day and 11-day disturbance levels, although the decline was less rapid for the 11-day disturbance treatment (Fig. 2.3 a & b). Conversely, dominance increased in the 7-day and 11-day treatments (Fig. 2.3 d & e).

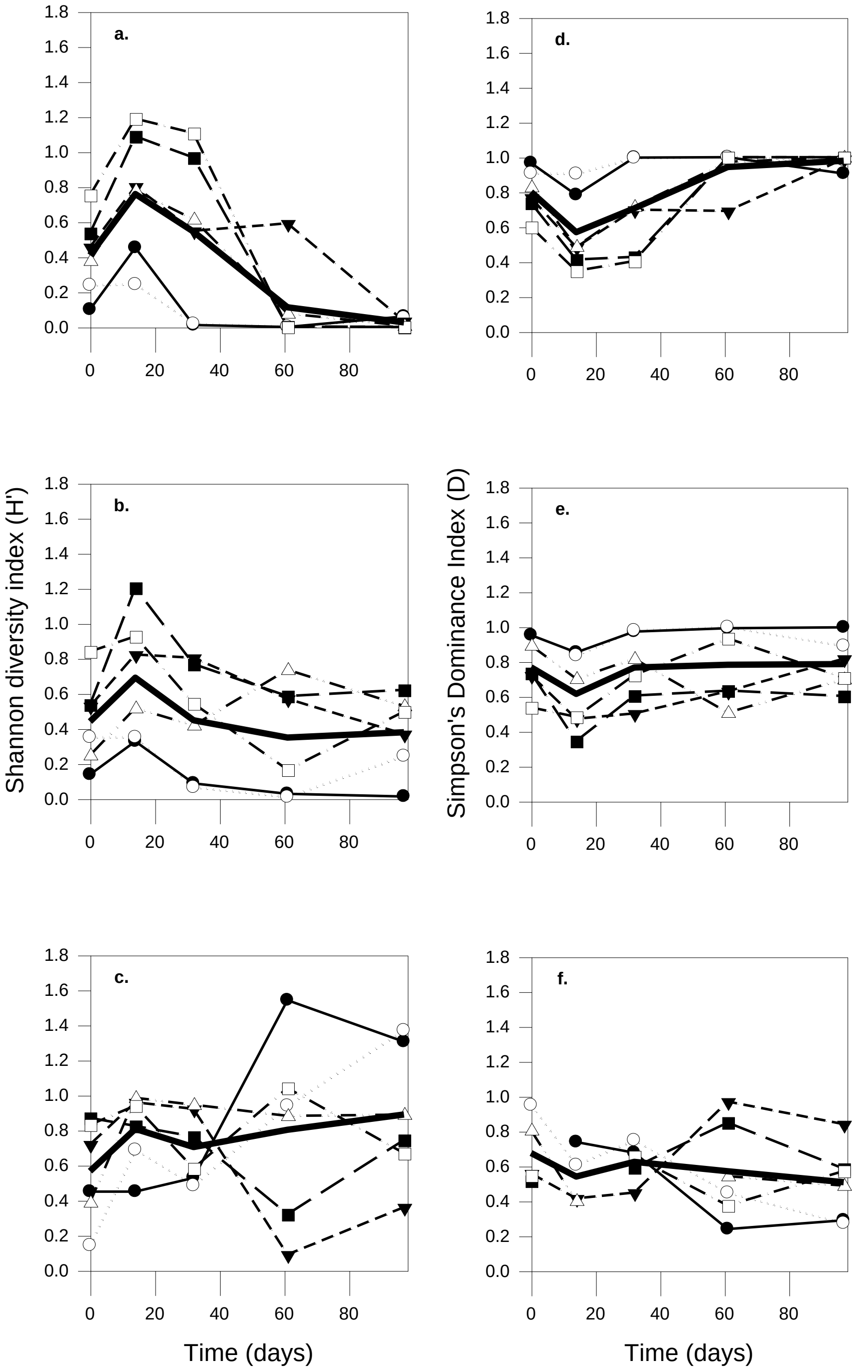

Figure 2.3. Shannon diversity index (H´) (**a.-c.**) and (**d.-f.**) as a function of time for individual replicates under the 7-day disturbance (**a., d.**), 11-day disturbance (**b., e.**), and undisturbed (**c., f.**) treatments. Each panel shows both replicates of all three phytoplankton community compositions (CCs). CC1 is represented by circles, CC 2 is represented by triangles, and CC 3 is represented by squares. The open and closed symbols signify separate replicates of the same treatment. The thick solid line represents the mean H´ across all treatments and replicates at a given time.

Changes in diversity and dominance in the undisturbed microcosms after 14 days were more variable, with some replicates increasing in diversity and decreasing in dominance, others remaining stable, and yet others declining in diversity while increasing in dominance (Fig. 2.3 e & f).

In all of the compositions receiving the 7-day disturbance treatment, the distribution of relative species abundance changed during the first month of the experiment (Fig. 2.4). At day 97, however, *Chlamydomonas reinhardtii* accounted for 95.0% or more of the total biomass in each microcosm. Species relative abundance distributions varied over a longer period of time in some of the microcosms exposed to the 11-day disturbance treatment (Fig. 2.4). For composition 1, *C. reinhardtii* established itself as the dominant after 14 days, and accounted for more than 94% of the total biomass at 97 days in both replicates, much like the dynamics for this composition under the 7-day disturbance interval. In compositions 2 and 3, the relative abundance of each species fluctuated over a longer period of time, with *Cryptomonas cf. rostratiformis* becoming established as the dominant for both compositions at 97 days. For these compositions, *Ankistrodesmus falcatus* also accounted for an average of at least 12% of the biomass at the termination of the experiment, indicating that *C. cf. rostratiformis* had not completely excluded this species. The relative abundances of species in the undisturbed microcosms continued changing throughout the experiment for all compositions. Competitive exclusion had not occurred in any undisturbed microcosm after 97 days (Fig. 2.4).

Species that were not included in the inoculated community compositions occurred in one or more of the replicates of each treatment by the final sampling date

(Appendix 2.1, Fig. 2.3). *Cyclotella sp.* was the most common invader, followed by *C. reinhardtii* and *A. falcatus*. *C. reinhardtii* only invaded microcosms receiving the 7-day disturbance treatment, and *A. falcatus* invaded microcosms receiving both the 11-day disturbance and undisturbed treatments. An unidentified species occurred in a single sample from an undisturbed microcosm with community composition 3 (Fig. 2.3).

The invasions of the 7-day disturbance treatments by *C. reinhardtii* caused the community composition and the disturbance treatments to become confounded because all of the 7-day disturbance treatments became dominated by the same species by the end of the experiment (Fig. 2.4). In order to determine whether our results depended on this effect, we eliminated the 7-day disturbance level from the explanatory model. However, this did not alter the main results; there was a significant interaction between community composition and disturbance, as well as a significant main effect of disturbance (linear model for untransformed H´, $F_{\text{Interaction, 2,6}}$ =11.459, P=0.009; $F_{\text{Dist, 1,6}}$ =24.473, P=0.003), while the main effect of composition was not significant ($F_{\text{CC, 2,6}}$ =1.199, P=0.365). We also detected a significant effect of disturbance within community composition 1 ($F_{2,3}$=108.582, P=0.002, Fig. 2.4), the only composition in which *C. reinhartdtii* was present from the time of inoculation. The undisturbed treatment had a significantly higher diversity at day 97 than either of the disturbed treatments for this composition (P=0.002 for both Dunnett’s post-hoc comparisons). This indicates that the presence of *C. reinhardtii* was not the only reason for the low diversity found in the 7-day disturbance treatments, because diversity was maintained in the undisturbed microcosms of composition 1 despite containing this species.

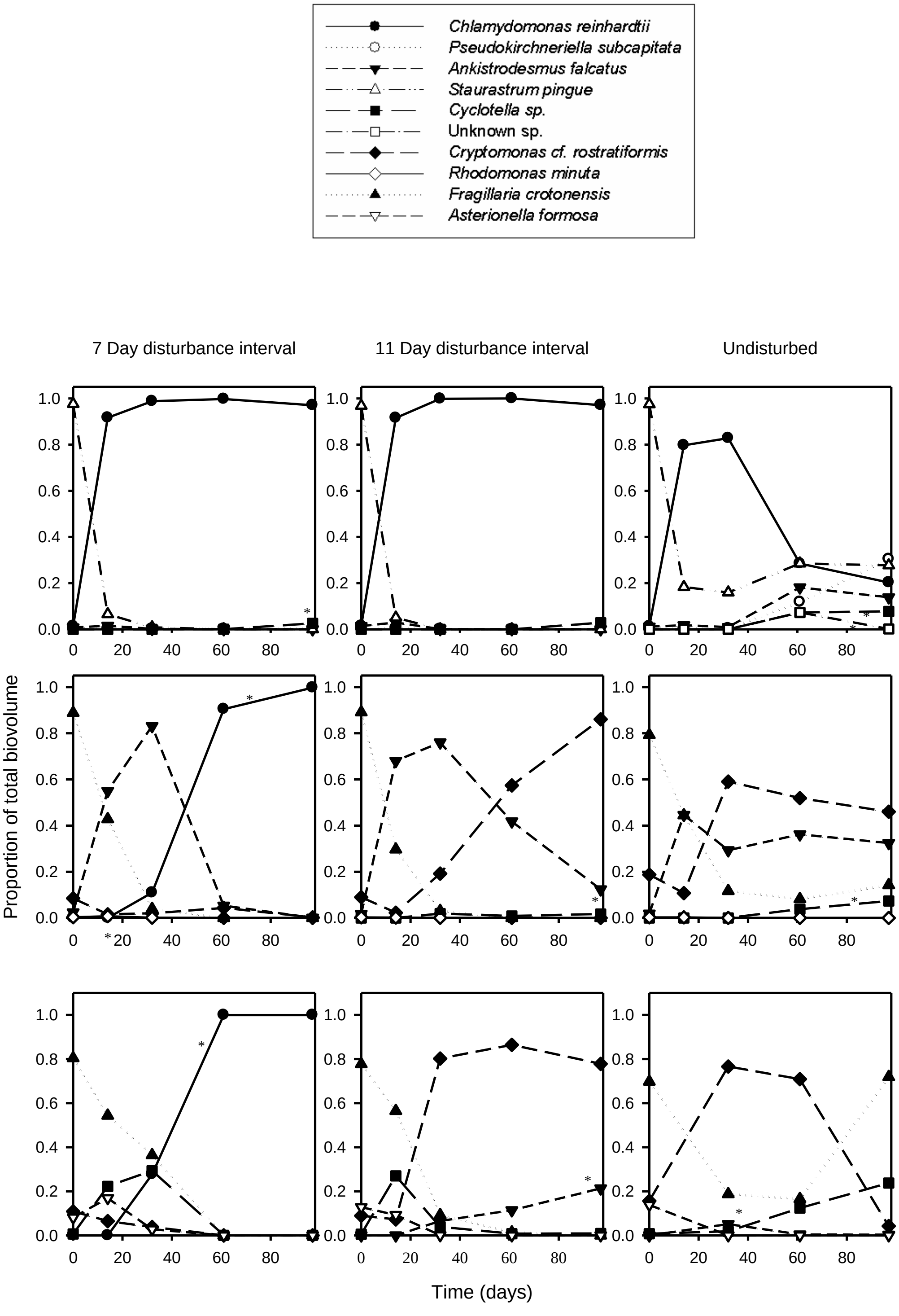

Figure 2.4. Species-specific relative biovolume under the 7-day, 11-day and undisturbed treatments, respectively from left to right. Community composition (CC) 1 is in the top panel, CC 2 in the middle, and CC 3 on the bottom. An asterisk (*) signifies a contaminant (**Appendix 2.1**). Relative biovolume is averaged across the two replicates for each community composition x disturbance treatment cross (see **Table 2.2**).

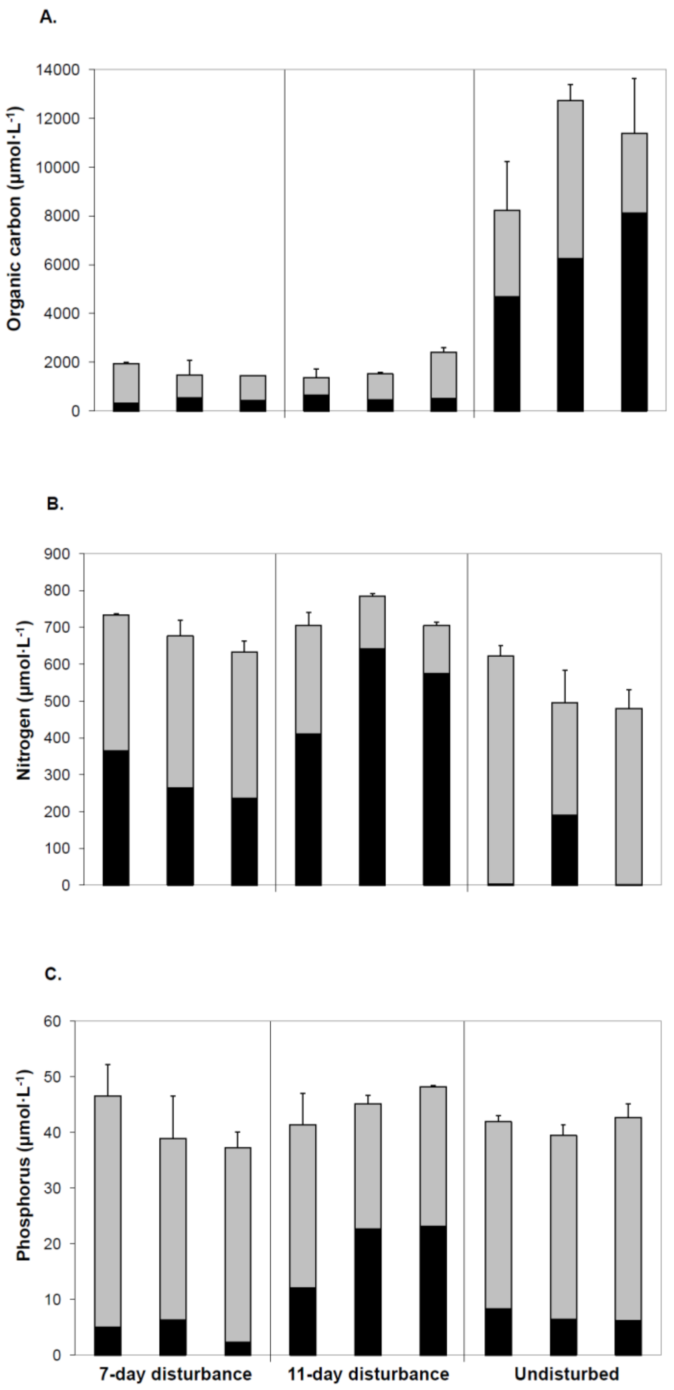

Figure 2.5. Average **a.** Organic carbon, **b.** nitrogen and **c.** phosphorus concentrations (μmol·L^{-1}) sampled from the microcosms on day 97. Grey shading represents the particulate fraction and black shading represents the dissolved fraction. Values for each bar represent the mean of two replicates for each community composition x disturbance treatment cross. Community compositions increase from left to right in each panel, starting at community composition 1. Error bars represent ± 1 S.E. of the total concentration.

Disturbance had a significant effect on ln-transformed particulate organic carbon (ln-POC) ($F_{2,14}$=14.196, P<0.001, Fig. 2.5a). The ln-POC of the undisturbed treatment was significantly different from the 7-day and 11-day disturbance treatments (Tukey's post-hoc comparisons, P<0.05). The undisturbed treatment also had the greatest proportion of particulate nitrogen (Fig. 2.5b). By contrast, both the 7-day and undisturbed treatments had similarly high particulate phosphorus levels, while the 11-day disturbance treatment had the lowest level of particulate phosphorus (Fig. 2.5c). Disturbance had a significant effect on the ln-POC:PN molar ratios ($F_{2,13}$=4.693, P=0.029) and ln-POC:PP molar ratios ($F_{2,14}$=12.354, P=0.001). Specifically, the average POC:PN and POC:PP molar ratios were both lowest for the 7-day disturbance treatment and highest for the undisturbed treatment (Table 2.2). Including H´ in the explanatory model eliminated disturbance as a significant effect on nutrient limitation for both phosphorus and nitrogen (the P-value for disturbance increased from P=0.001 to P=0.061 for ln-POC:PP, and from P=0.029 to P=0.516 for POC:PN when H´ was included).

2.4 Discussion

Our results demonstrate that greater diversity can be maintained in undisturbed assemblages of phytoplankton than in assemblages experiencing periodic, externally-forced, fluctuations in density and nutrient availability. This indicates that, at least in our experimental system, endogenously generated competitive dynamics were more effective in maintaining high species diversity than exogenously generated variability in resource availability. Community composition and disturbance also had significant interactive effects on diversity. While the greatest diversity always occurred in undisturbed microcosms, the form of the increase in diversity from the 7-day disturbance treatment to the undisturbed treatment depended on the identity of species within each assemblage (Fig. 2.2).

Disturbances are generally considered to be discrete events that result in the loss of biomass or liberation of resources (Grime 1977). Many studies have tested the importance of disturbance on maintaining species diversity and two prominent hypotheses have been proposed regarding the relationships between disturbance and diversity. The intermediate disturbance hypothesis (IDH) predicts a unimodal relationship between disturbance and diversity because intermediate frequencies of disturbance revert communities to intermediate states of succession (Grime 1973, Connell 1978, Hastings 1980). The IDH has been supported by some experimental tests both in the lab (Robinson and Sandgren 1983, Gaedeke and Sommer 1986, Sommer 1995, Floder et al. 2002) and in the field (Floder and Sommer 1999). The second hypothesis, known as the dynamic equilibrium model, proposes that diversity is determined by the interaction between growth rates and the frequency of disturbance (Huston 1979). The highest diversity is predicted to occur at low to moderate growth rates and frequencies of disturbance. The diversity-disturbance relationship is also predicted to depend on productivity because this may affect growth rates (Kondoh 2001). Currently, there is some experimental support for this hypothesis (Proulx et al. 1996, Proulx and Mazumder 1998, Worm et al. 2002, but see Scholes et al. 2005). Disturbances do not promote coexistence by reducing the strength of competition (Chesson and Huntly 1997). Instead, they create temporal environmental heterogeneity, which act as limiting factors or niches along which species can differentiate (Chesson and Huntly 1997, Chase and Leibold 2003). In producing heterogeneity in limiting factors, disturbances can allow the expression of storage effects or competitive relative nonlinearities, which enable coexistence (Koch 1974a, Chesson 2000a).

Generally, the vast majority of the ecological literature on diversity-disturbance relationships postulates a peaked relationship (Connell 1978, Huston 1979, Mackey and Currie 2001). On the other hand, the full gamut of possible disturbance-diversity relationships has been observed (Mackey and Currie 2001), including monotonically decreasing (Haddad et al. 2008), increasing (Sommer 1993), and U-shaped (Floder and Burns 2004) relationships. A positive relationship might be detected when the upper end of a peaked relationship is not sampled; i.e. the frequency of disturbance can increase infinitely, but the highest levels of disturbance are not well-represented. Conversely, a negative relationship could be generated by neutral dynamics (Hubbell 2001). In this case disturbance reduces the population density of species and could lead to greater extinctions due to demographic stochasticity. A negative relationship could also be detected if internal dynamics, including intransitive and nonlinear competition, more effectively maintained species diversity than disturbance. In this case disturbance would effectively disrupt the internal dynamics that maintain diversity. We observed such a negative relationship in our study (note: our figures have disturbance interval and not frequency on the x-axis). We are unaware of any explicit mechanism that can generate a U-shaped relationship. This rarely-observed relationship may be the outcome of more than one mechanism acting at once.

Our results suggest that the internal competitive dynamics occurring within three different phytoplankton assemblages were more effective at maintaining species diversity than the environmental temporal heterogeneity in resource availability produced by two different frequencies of disturbance (Fig. 2.2). Other recent studies have also found relatively long-term coexistence of multiple species in purely competitive communities (e.g. Kerr et al. 2002, Roelke et al. 2003, Haddad et al. 2008), although they did not compare the importance of internal versus external dynamics *per se*. There are at least three potential mechanisms that could lead to internally-mediated competitive coexistence. The first two mechanisms require either that the phytoplankton in our experiment were competing for three or more abiotic resources and display relative nonlinearity in competitive abilities for these limiting factors (Armstrong and McGehee 1980, Huisman and Weissing 1999, 2001), or that they are ordered in an intransitive competitive hierarchy or network (Huisman and Weissing 2001, Kerr et al. 2002). There has as yet been no experimental demonstration that relative nonlinearity in competitive abilities promotes coexistence in internally-regulated assemblages, and this remains an important avenue for future research. By contrast, however, Kerr (2002) experimentally demonstrated that when bacteria compete locally in a game of ‘rock-paper-scissors’ (competitive intransitivity), that a greater number of species than the number of limiting resources may coexist. The third mechanism is the limitation of the community by as many limiting factors as there are species (Tilman 1982).

The undisturbed microcosms in our experiment were effectively closed systems (i.e. dissolved nutrients were not replaced from an exterior source), and it is therefore likely that they were limited by a larger number of resources than the disturbed microcosms. Indeed the nutrient analysis showed that the phytoplankton were more limited with respect to nitrogen and phosphorus in the undisturbed than the disturbed microcosms (Table 2.2). However, when the level of nutrient limitation was added into the ANOVA as a covariate, it was not a significant explanatory variable, and the effect of disturbance remained significant, indicating that the importance of disturbance was not mediated by its effect on nutrient limitation (Table 2.3). The level of nutrient limitation did not explain the higher species diversity in the undisturbed microcosms. Furthermore, Tilman’s (1982) predictions are relevant to communities at equilibrium and the only communities which appeared to have reached equilibrium with certainty were those which were disturbed most frequently (Fig. 2.3), whereas the undisturbed communities continued to vary in relative species abundances until day 97. Such non-equilibrium dynamics are more similar to those predicted in cases of relatively nonlinear competition and intransitivity (Huisman and Weissing 2001, Roelke et al. 2003). It is possible, however, that because the microcosms were closed systems, the identity of limiting resources varied over time as different species came to dominate. This in turn, may have prevented equilibrium in a system that would have approached equilibrium if nutrients were continuously replenished. We cannot discriminate between these possibilities further here, but what is clear from our study is that internal dynamics more effectively maintained species diversity than exogenous variability. Direct testing to tease apart the importance of different internal mechanisms would be a valuable avenue for future research.

Depending on the disturbance regime, some compositions were less likely to be dominated by a single species over time than others. This stands in direct contrast to predictions from neutral models which predict that species traits are unimportant in determining community diversity or coexistence (Hubbell 2001). A recent grassland experiment showed that the ability of communities to maintain species diversity in a disturbed landscape depended on the degree of functional complementarity among species (Questad and Foster 2008). Also, microcosm experiments have shown that species' intrinsic growth rates are important in determining responses to disturbance (Haddad et al. 2008). Niche theory predicts that species' characteristics such as their requirements for, and impacts upon, resources are important in determining community composition via species sorting (Chase and Leibold 2003). Also, Huisman and Weissing (2001) predicted that supersaturated coexistence would be more likely to occur in communities where species showed competitive intransitivity than in those which did not. Furthermore, the storage effect and relative nonlinearity require particular differences in species' traits in order to promote coexistence (Chesson 2000b). Numerous theoretical approaches therefore predict the importance of species traits and hence community composition on coexistence that we have demonstrated here.

The effect of community composition in determining coexistence depended on the level of disturbance of the microcosms. In the 7-day disturbance treatments, regardless of the community composition, the microcosms came to be dominated by a single species, *C. reinhardtii*, whereas in the undisturbed microcosms, there was greater variability in the final outcome of competitive dynamics, which depended on the original community composition. This indicates that disturbance was a strong homogenizing force among communities, causing "community convergence" *sensu* Houseman et al. (2008). Similar homogenizing effects of disturbance have been found in grassland (Collins and Smith

2006) and pond communities (Chase 2003). The alternative interpretation of the significant interaction between composition and disturbance is that the effects of disturbance depended on the community composition. For instance, in the 7-day and 11-day disturbance treatments, fast growing species more quickly dominated communities (Table 2.1, Fig. 2.3), whereas slower growing species, and potentially also better competitors for limiting nutrients, were better able to persist in the undisturbed microcosms. This agrees with the results of Haddad et al. (2008) who showed that the persistence of species in the face of disturbance could be predicted most effectively by their intrinsic rates of increase.

The occurrence of invasions indicates that even the undisturbed microcosms were not completely ‘closed’ to propagules of new species. Nevertheless, because the invaders were competitors (and not predators, parasites or resources) they fit into the class of organisms that by definition take part in endogenous dynamics. As a result, the invasions did not prevent us from asking whether endogenous or exogenous mechanisms are more important for maintaining species diversity. Microcosms were randomized in space (in the culture chamber) and in time (during sampling) and so we are confident that the propagule supply should have been unbiased with respect to the number or identity of species. We observed that with only one exception, microcosms experienced no more than one invasion, and so there was no evidence that the frequency of invasions differed among treatments (Appendix 2.1). If the invasions had been associated with an unmeasured external source of structure or variation upon which storage effects and nonlinearities could be expressed, this would have made the disturbance treatments more similar, making the difference that we observed among treatments conservative. Invaders in the 7-day disturbance treatment either remained at low density or became dominant (Fig. 2.4), whereas in the undisturbed microcosms they became a part of relatively even communities.

With respect to the effect of community composition on diversity, we expected that the invasions would have reduced differences in community composition, thereby diminishing any effect of composition on diversity. Accordingly, we found that *C. reinhardtii* invaded and came to dominate all of the 7-day disturbance interval microcosms. This prevented the detection of any potential effects of the original community composition for this disturbance treatment. It appears that disturbance interval selected for the establishment of particular invader species, causing community convergence (Collins and Smith 2006, Houseman et al. 2008). Unfortunately, community convergence in the 7-day treatments caused community composition and the disturbance treatment to be conflated. Nevertheless, when we controlled for the invasions of *C. reinhardtii* by removing the 7-day disturbance interval from our analysis or by considering only composition 1 in which this species was always present, our conclusions were not altered. The undisturbed microcosms still had higher species diversity and displayed stronger effects of community composition on diversity. This confirmed our expectation that endogenous mechanisms maintaining diversity depend on the species traits present in the community.

In conclusion, we have shown that competition for resources among phytoplankton species can enable greater coexistence in closed systems than in systems experiencing externally generated variability in resource availability over time. We recommend that greater attention be paid to the potential for internal competitive dynamics to maintain species diversity, and that similar studies be conducted in other experimental systems to determine the generality of our findings. Historically, the emphasis in biodiversity studies has been placed on the importance of external forces in generating long-term coexistence, but theory and a growing body of empirical work now suggest that internal dynamics may be equally (and in some cases more) important than external variability in maintaining biodiversity in some communities. Coexistence in our experimental communities also depended on the interaction between the composition and disturbance level. This confirmed the predicted importance of species' traits in maintaining biodiversity in our experimental communities.

Chapter 3: Community composition and consumer identity determine the effect of resource species diversity on rates of consumption

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3.1 Introduction

After more than a decade of active research on the importance of species diversity for ecosystem functioning, it has been shown that diversity affects multiple ecosystem functions (reviewed in Balvanera et al. 2006, Cardinale et al. 2006a). Most of this work has investigated the impact of diversity on a single trophic level (reviewed in Hooper et al. 2005). However, species diversity is also predicted to have impacts on the strength of trophic interactions (McCann et al. 1998), and dynamics across trophic levels (Duffy 2002, Ives et al. 2005, Thébault and Loreau 2005, Duffy et al. 2007). While some early experiments incorporated multiple trophic levels (e.g. Naeem and Li 1997, Downing and Leibold 2002), only recently have experiments been designed that directly investigate the impacts of species diversity across trophic levels.

Experiments testing the impact of resource diversity on consumer effect sizes have generally shown that consumer effects are reduced (Hillebrand and Cardinale 2004, Edwards et al. 2010). However, ‘consumer effects’, measured in terms of consumer abundance, consumer control of resource biomass, or total consumption, can be the result of consumption over the short-term or population-level responses over multiple generations (e.g. resource abundance declines due to competition, or predator abundance increases). Previous studies have rarely separated consumption effects from population responses, and so the relative importance of each has not yet been elucidated (Edwards et al. 2010). Among the few direct tests of the influence of resource species diversity on rates of consumption, neutral effects (DeMott 1998), positive effects (Pfisterer et al. 2003, Toscano et al. 2010), and negative effects (DeMott 1999, Kratina et al. 2007, Wyckmans et al. 2007) have been demonstrated. The variability in the effect of resource diversity likely stems from the importance of the palatability of the resource species in the community and the feeding selectivity of the consumer (suggested in Duffy 2002, Thébault and Loreau 2005, Jactel and Brockerhoff 2007). We expect that depending on these factors, different mechanisms determine the effect of diversity on rates of consumption.

There are number of mechanisms by which the presence of other species could modify the rate at which a consumer consumes any particular resource (Table 3.1). The simplest mechanism, Dilution, occurs when species diversity increases but the resource species are all equally palatable and all else remains constant. In this case, the absolute consumption rate of a focal species is diminished proportionally to its decline in relative abundance (DeMott and Kerfoot 1982), but the ‘prey risk’, or rate of consumption per prey, remains unchanged (Table 3.1). Complementarity occurs when resource diversity is largely palatable. In this case, diversity may provide better nutrition (Pfisterer et al. 2003, and reviewed in Duffy et al. 2007) or improve ease of detection or capture, causing accelerated consumption (Sterner et al. 1993). Preference occurs when a consumer displays selectivity among resource species, consuming relatively more of a preferred resource when it is available (DeMott and Kerfoot 1982, Kerfoot and Kirk 1991). Hindrance occurs when the consumption of an edible resource is reduced by the presence of other species. For instance, poor quality or toxic resources may reduce foraging rates (Sterner and Hessen 1994). Consumers may also waste time handling inedible resource species (Kratina et al. 2007), or be confused by heterogeneity in infochemicals (Vos et al. 2001).

In this chapter, we test the importance of community composition and consumer identity in determining the effect of resource species diversity on rates of consumption. We examined the evidence for each of the mechanisms in Table 3.1 for three consumers that vary in diet breadth. We expected that the most generalist species would be the most likely to experience Complementarity and that the relative specialists would be more likely to experience Hindrance and Preference.

Table 3.1. Mechanisms and the predicted effects of resources diversity on clearance rates (per capita consumption or prey risk, in $\mu l \cdot [\mu g \cdot hr]^{-1}$). Contrasts are between clearance rates in monoculture and polyculture compositions either on the focal species, *C. reinhardtii*, or the whole phytoplankton community.

	Clearance rate measured on:	
Mechanism	*C. reinhardtii*	Whole community
Dilution	Not altered	Not altered
Complementarity nutrition, facilitation,	Increased	Increased
Preference	Increased/Reduced Not altered	Not altered Increased/Reduced
Hindrance unpalatability, low quality, toxicity, confusion	Reduced	Reduced

3.2 Methods

We measured effects of resource species diversity on the clearance rates of three freshwater cladoceran zooplankton species. *Daphnia pulex* is the largest and most generalist consumer, *Bosmina longirostris* is the smallest and most selective, and *Ceriodaphnia reticulata* is intermediate in both respects (Burns 1968, Bogdan and Gilbert 1987). While all three species are filter-feeders, Bosmina species can also grasp medium-sized particles (5-25 µm) (DeMott 1982), and can select particles on the basis of taste (Kerfoot and Kirk 1991). *D. pulex* and *C. reticulata* are thought to reject particles from their food groove only when they exceed their gape (DeMott 1982): ~45 µm in size for *D. pulex* (Burns 1968), and likely < 35 µm for *C. reticulata* (Burns 1968, Bogdan and Gilbert 1987).

We factorially manipulated resource community composition, resource density and consumer identity. The resource trophic level was composed of either a monoculture or a polyculture (four species) of phytoplankton, and there were four polyculture community compositions spanning a range of expected palatability for the consumers based on size (Table 3.2). The monoculture resource was *Chlamydomonas reinhardtii*, an edible green alga routinely used in grazing experiments (Bogdan and Gilbert 1987). The polycultures all contained this (focal) species. There were also two *C. reinhardtii* densities: low (2,000 cells$\cdot$mL^{-1}) and high (8,000 cells$\cdot$mL^{-1}), which allowed us to employ both substitutive and additive designs. There were 40 experimental treatments (including controls, i.e. no consumers), and each was replicated five times.

Table 3.2. Resource community compositions. Inocula of phytoplankton species were obtained from the University of Texas Culture Collection (UTEX) and the Canadian Phycological Culture Centre at the University of Waterloo (CPCC). The median of 25 measurements of the greatest axial linear dimension (GALD) for each species is given. All values are for individual cells unless they are followed by ‘*f*’, which denotes that the length is for multicellular filaments. *A. formosa* occurs as a single cell or as multicellular radial colonies, often with between six or eight cells. We expected (black) and found (grey) that the phytoplankton species were palatable for the following consumer species: D = *Daphnia pulex*, C= *Ceriodaphnia reticulata*, B = *Bosmina longirostris*. Parentheses indicate that a species that was expected to be palatable for a consumer but was not. Palatability was assessed as a relative clearance rate of ≥1 compared to *C. reinhardtii*. All species were edible by *D. pulex*: average clearance rate ≥1 µl·[µg·hr]$^{-1}$.

Community composition	Species (Source and identifier)	Median GALD (µm)	Expected to be palatable for:
Monoculture (M)	*Chlamydomonas reinhardtii* (CPCC 84)	6.6	DBC
Palatable (Pa)	*Chlamydomonas reinhardtii* (CPCC 84)	6.6	DBC
	Pseudokirchneriella subcapitata (CPCC 37)	5.2	DBC
	Rhodomonas minuta (CPCC 344)	6.2	DBC
	Cyclotella sp. (CPCC 537)	7.1	DBC
Mixture 1 (Mix1)	*Chlamydomonas reinhardtii* (CPCC 84)	6.6	DBC
	Rhodomonas minuta (CPCC 344)	6.2	DBC
	Cryptomonas cf. rostratiformis (CPCC 343)	20.3	DBC
	Asterionella formosa (CPCC 605)	45.4	D
Mixture 2 (Mix2)	*Chlamydomonas reinhardtii* (CPCC 84)	6.6	DBC
	Cryptomonas cf. rostratiformis (CPCC 343)	20.3	DBC
	Staurastrum pingue (UTEX 1606)	34.0	(D)(C)
	Ankistrodesmus falcatus (UTEX 101)	44.7	DBC
Unpalatable (Un)	*Chlamydomonas reinhardtii* (CPCC 84)	6.6	DBC
	Staurastrum pingue (UTEX 1606)	34.0	(D)(C)
	Asterionella formosa (CPCC 605)	45.4	D
	Fragilaria crotonensis (CPCC 269)	124.6 *f*	-

Phytoplankton species were grown in batch monocultures in COMBO medium and the zooplankton species were grown in batch cultures with the green alga *Scenedesmus acutus* (Kilham et al. 1998). We adjusted concentrations of phytoplankton cultures to achieve stocks with densities of 20,000 natural units (cells, filaments or colonies, hereafter 'NU')$\cdot$mL^{-1} for all species and a second stock of 80,000 NU$\cdot$mL^{-1} for *C. reinhardtii*. We created the experimental community compositions by adding 1 mL of each required stock to 10 mL test-tubes. The experimental test-tubes received either 32 *B. longirostris*, 12 *C. reticulata* or two *D. pulex*, to account for differences in biomass among the species. The animals were rinsed for ~6 hours in sterile medium before being transferred into experimental test-tubes in random order. The experiment ran on a rotating-shaker in a dark culture chamber at 20°C for 12 hours. We inspected the test-tubes for dead zooplankton before preserving the samples with Lugol's Iodine solution. We discarded samples containing dead animals. Replicates were conducted in blocks over time due to space limitation on the rotator shaker.

We counted phytoplankton and zooplankton densities, and measured the length of the zooplankton using an inverted light microscope. We used length-weight regressions to estimate the mass of consumers (Dumont et al. 1975). We converted counts of natural units (NU) to cell densities using estimates of average cells$\cdot$NU^{-1} to account for changes in filament or colony size for multicellular species in grazed treatments relative to controls. We calculated the rate of consumption per prey, per unit mass of consumers, as a clearance rate (μl$\cdot$[μg$\cdot$hr]$^{-1}$):

$$F = [\ln(cells_{c} \cdot cells_{g}^{-1}) \cdot v] \cdot [t \cdot b]^{-1} \qquad [1]$$

where t is the duration of grazing (hours), $cells_c$ and $cells_g$ are the cell densities in the control and grazed treatments respectively after time t, v is the volume, and b is the grazer biomass (μg).

We used linear mixed effects models to analyze the data. We fitted the models separately for each consumer species using maximum likelihood. We calculated the loglikelihood (logLik), Akaike's Information Criteria (AIC) and the AIC corrected for small sample size (AIC_c) for a set of nested models (Burnham and Anderson 2002). The full model included the main effects of community composition and density, their interaction, the biomass of the consumers as a covariate, and blocks as a random effect. We included consumer biomass in order to account for potential effects of consumer interactions on clearance rates. The nested models were sequentially simpler and we removed factors in the following order: biomass, the interaction between density and composition, density, and composition. The best model was that which had the lowest AIC_c (Burnham and Anderson 2002). We tested for the significance of the factors in the best model by performing a Likelihood Ratio Test against the next simplest model in the nested set (Galwey 2006). A fixed effect in the best model was significant if the likelihood of the model containing it was significantly greater than the likelihood of the next simplest model omitting it (Likelihood Ratio Test $P \leq 0.05$). When community composition had a significant effect, we performed Dunnett's post-hoc comparisons to compare clearance rates between the polyculture compositions and monoculture.

In the framework of mechanisms that we present (Table 3.1), Dilution is the statistical null hypothesis. When resource density does not affect clearance rates, i.e. the density gradient is within the linear portion of the consumer's functional response, all of the data, including both additive and substitutive contrasts, can be used to test the mechanisms. This is because consumption rates are calculated on a per prey (or ‘prey risk’) basis. We used one of two types of posterior contrasts to test the hypothesized mechanisms (Table 3.1). When density had a significant effect, we separated the effects of density and diversity by using the substitutive contrasts. In this case, we ran post-hoc user-defined contrasts, with a family-wise error rate of α= 0.05 between the clearance rates in monoculture at high density and the polyculture compositions at low density. When density did not have a significant effect, we used Dunnett’s post-hoc comparisons with all of the data. We performed statistical analyses using the nlme and multcomp packages in v. 2.9.2 of R software, (R Development Core Team, 2009).

3.3 Results

Community composition had a significant influence on clearance rates, both on *C. reinhardtii* (the focal species) and on the whole community of phytoplankton, for all three consumers (Fig. 3.1, Table 3.3). The best models always included community composition as an explanatory factor (lowest AIC_c was never Model 5), and community composition was a significant factor for all of the consumers (Loglikelihood Ratio Test for comparisons of models 4 & 5, Table 3.3). For *D. pulex* and *C. reticulata*, the community composition was the only significant factor explaining clearance rates (Table 3.3, Loglikelihood Ratio Tests comparing models 4 & 5; Figs. 3.1 a & b, e & f). For *B. longirostris*, both community composition and density were significant explanatory variables (Table 3.3, Loglikelihood Ratio Tests comparing models 3 & 4 and 4 & 5).

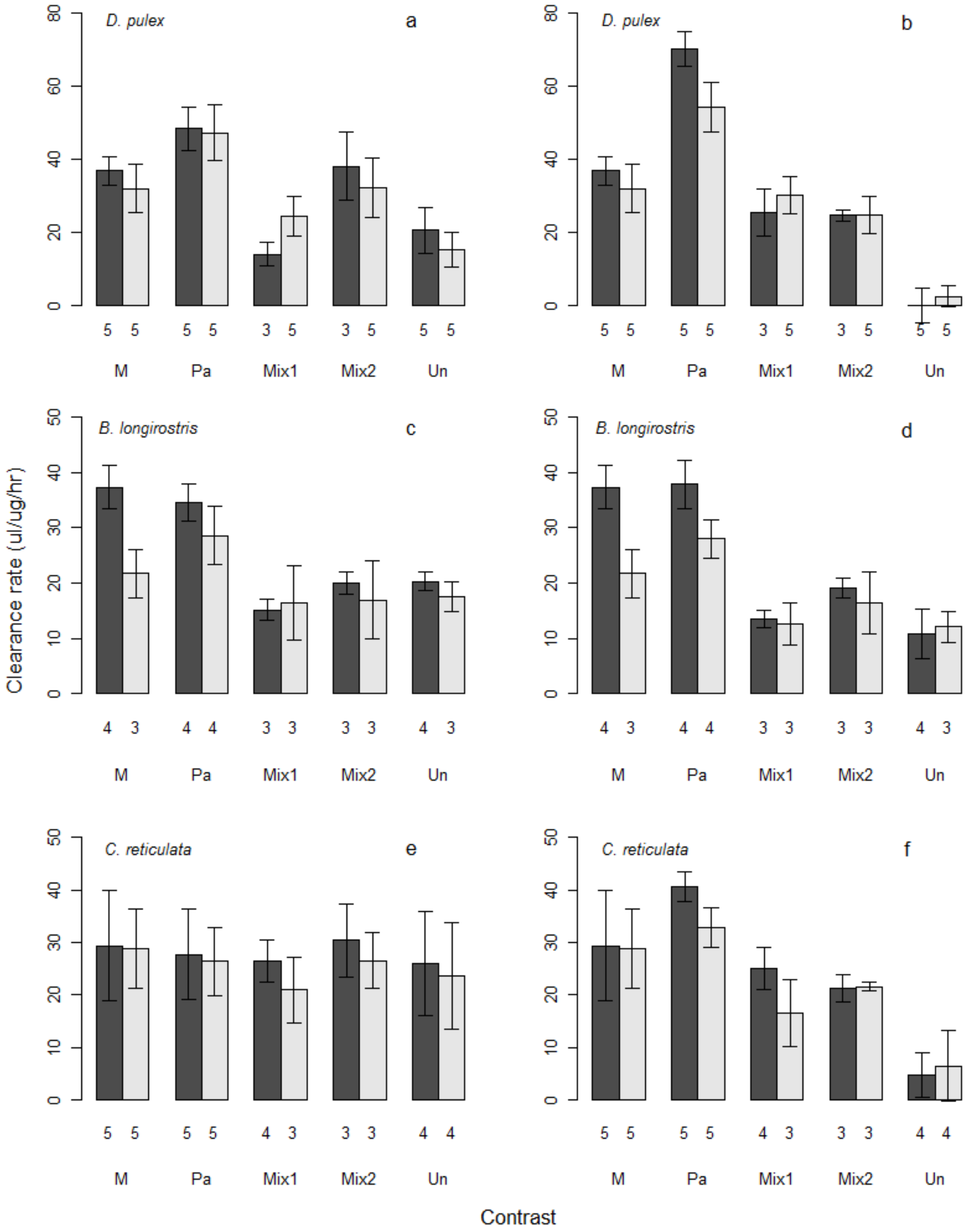

Figure 3.1. Clearance rates on *C. reinhardtii* (**a.**, **c.** & **e.**) and the entire phytoplankton community (b., d. & f.). From top to bottom, panels show average clearance rates for *D. pulex* (**a.** & **b.**) *B. longirostris* (**c.** & **d.**), and *C. reticulata* (**e.** & **f.**). Bars represent one standard error. 'M' signifies the monoculture, 'Pa' signifies the palatable composition, 'Mix1' and 'Mix2' signifiy the mixtures of palatable and unpalatable species, and 'Un' signifies the unpalatable composition. Dark grey and light grey bars indicate low and high *C. reinhardtii* densities respectively. Final treatment sample sizes (n) are shown below the category axis.

The clearance rate of *B. longirostris* was lower at high density than at low density in monoculture (Fig. 3.1 c), indicating a nonlinear functional response. For clearance rates of *B. longirostris* on the whole community, incorporating consumer biomass into Model 3 significantly improved the fit (AICc = 240.9119, Loglikelihood Ratio Test model 3 v. model 3 + Biomass P = 0.0047), suggesting that consumer interactions affected total consumption. The generally high density of *B. longirostris* may have resulted in consumer interactions in all treatments, reducing clearance rates overall.

The polycultures most commonly caused declines in consumption relative to the monoculture (Fig. 3.2). In seven of the twelve Dunnett's post-hoc comparisons done for both the clearance on *C. reinhardtii* and on the whole community, clearance rates declined significantly (Fig. 3.2). The direction and magnitude of change in the clearance rate depended on the identity of the consumer, the composition of the phytoplankton community, and on whether the clearance rates under consideration were on the focal species or the whole community.

There was evidence in support of all four mechanisms presented in Table 3.1 (Fig. 3.2, Table 3.4). The clearance rates of the three consumers however were not affected by the same subset of mechanisms, and the mechanisms by which any given phytoplankton community composition affected clearance rates depended on the consumer's identity. *D. pulex* was affected by all of the mechanisms except Dilution (Table 3.4). In the palatable composition, its clearance rates on both *C. reinhardtii* and the whole community were accelerated (Fig. 3.2 a & b), indicating the action of Complementarity (Table 3.1).

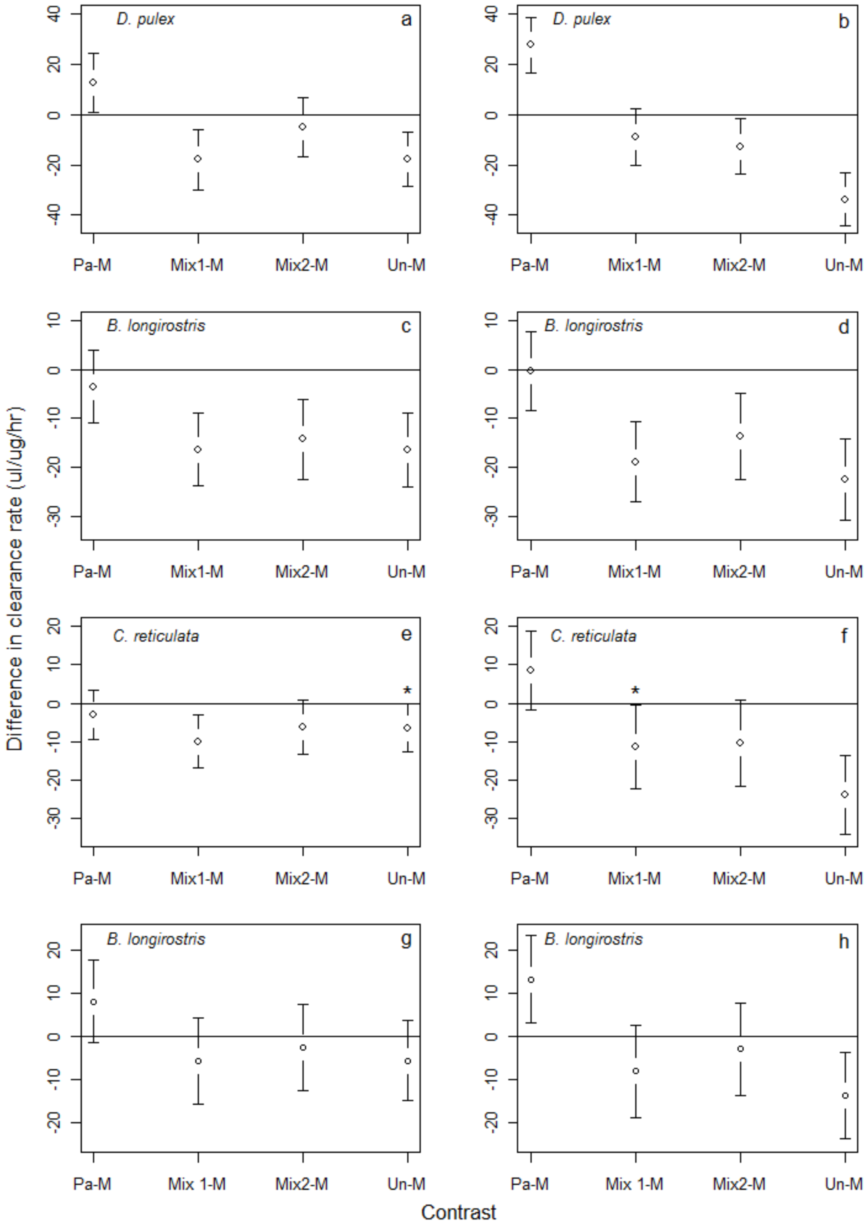

Figure 3.2. a-f. Dunnett's post-hoc comparisons between the average clearance rate in resource polyculture and monoculture, ± 95% confidence intervals. From top to bottom, panels show comparisons for *D. pulex*, *B. longirostris*, and *C. reticulata*. Confidence intervals not overlapping zero indicate a significant difference at $\alpha = 0.05$ (signified by an asterisk when unclear). Comparisons from left to right on the category axis are for the following polyculture compositions: palatable (Pa-M), mixture 1 (Mix1-M), mixture 2 (Mix2-M), unpalatable (Un-M). Left panels (**a.**, **c.**, **e.** & **g.**) indicate comparisons of clearance rates on *C. reinhardtii*, and right panels (**b.**, **d.**, **f.** & **h.**) on the whole community. **g & h.** Substitutive contrasts between the average clearance rate of *B. longirostris* in polyculture compositions (at low density) and monoculture (at high density), ± 95% confidence intervals.

In mixture 1, clearance on *C. reinhardtii* declined, but the total clearance rate was unaffected, indicating Preference against *C. reinhardtii*. In mixture 2, clearance on *C. reinhardtii* was unaffected, but the total clearance rate declined, indicating Preference for *C. reinhardtii*. In the unpalatable composition, the clearance rates for both *C. reinhardtii* and the whole community declined, indicating the influence of Hindrance.

For *B. longirostris*, all of the community compositions except the palatable composition caused a decline in the clearance rates on *C. reinhardtii* and the whole community (Figs. 3.2 c & d). This was mainly explained by the increase in total food density with increased diversity that occurred in the additive contrasts. When we used only the substitutive contrasts, the reduction in clearance rates largely disappeared (Figs. 2 g & h). *B. longirostris* was affected by Dilution and Preference (Table 3.4). Clearance rates were unaltered in mixtures 1 and 2, failing to reject Dilution as the null mechanism (Table 3.1). In the palatable composition, the total clearance rate was accelerated but on *C. reinhardtii* it was unaltered (Figs. 3.2 g & h), indicating Preference against *C. reinhardtii*. In the unpalatable composition, the clearance rate on *C. reinhardtii* was unaltered but on the whole community it was reduced, indicating Preference for *C. reinhardtii*.

C. reticulata was affected only by Dilution and Hindrance (Table 3.4). In the palatable composition and mixture 2, its clearance rates on *C. reinhardtii* and the whole community were unaltered compared to that in monoculture (Figs. 3.2 e & f), failing to reject the action of Dilution. In mixture 1 and the unpalatable compositions, the clearance rates on *C. reinhardtii* and the whole community both declined (Figs. 3.2 e & f), indicating the action of Hindrance.

Table 3.3. Results of model comparisons. Model identity (Model), degrees of freedom (df), Akaike's Information Criterion (AIC), Akaike's Information Criterion corrected for small sample size (AIC$_c$), Loglikelihood (logLik), the models compared using the Likelihood Ratio Test (Test), Likelihood Ratio (Ratio), and the P value of the Likelihood Ratio Test (P) are presented. Bold indicates the best model. Italics indicate models containing only factors that were significant according to Likelihood Ratio Tests at α=0.05.

Model	df	AIC	AIC$_c$	logLik	Test	Ratio	P
D. pulex – C. reinhardtii							
1	13	372.2387	383.6137	-173.1193	-		
2	12	370.5959	380.0504	-173.2979	1 v 2	0.3572	0.5501
3	8	366.5726	370.4645	-175.2863	2 v 3	3.9767	0.4092
4	7	364.8481	**367.7955**	-175.4241	3 v 4	0.2756	0.5996
5	3	392.6159	393.1873	-193.3079	4 v 5	35.7677	<0.0001
D. pulex – total phytoplankton							
1	13	356.4787	367.8537	-165.2394	-	-	-
2	12	354.5462	364.0007	-165.2731	1 v 2	0.0675	0.7950
3	8	357.6274	361.5193	-170.8137	2 v 3	11.0812	0.0257
4	7	357.1215	**360.0689**	-171.5608	3 v 4	1.4941	0.2216
5	3	424.6478	425.2192	-209.3239	4 v 5	75.5263	<0.0001
B. longirostris – C. reinhardtii							
1	13	238.1485	256.3485	-106.0743	-	-	-
2	12	238.1410	252.9981	-107.0705	1 v 2	1.9925	0.1581
3	8	236.0461	**241.8061**	-110.0230	2 v 3	5.9051	0.2063
4	7	245.9787	250.2864	-115.9894	3 v 4	11.9326	0.0006
5	3	259.8749	260.6749	-126.9375	4 v 5	21.8962	0.0002
B. longirostris – total phytoplankton							
1	13	228.1559	246.3559	-101.0779	-	-	-
2	12	239.8096	254.6667	-107.9048	1 v 2	13.6537	0.0002
3	8	239.4050	**245.165**	-111.7025	2 v 3	7.5954	0.1076
4	7	246.7634	251.0711	-116.3817	3 v 4	9.3584	0.0022
5	3	270.5357	271.3357	-132.2678	4 v 5	31.7723	<0.0001
C. reticulata – C. reinhardtii							
1	13	290.7531	304.2346	-132.3765	-	-	-
2	12	288.7605	299.9034	-132.3803	1 v 2	0.0075	0.9312
3	8	284.8399	**289.3399**	-134.4199	2 v 3	4.0794	0.3954
4	7	286.3954	289.7893	-136.1977	3 v 4	3.5556	0.0593
5	3	291.3300	291.9786	-142.6650	4 v 5	12.9346	0.0116
C. reticulata – total phytoplankton							
1	13	323.6307	337.1122	-148.8154	-	-	-
2	12	321.7394	332.8823	-148.8697	1 v 2	0.1087	0.7416
3	8	317.0282	321.5282	-150.5141	2 v 3	3.2888	0.5107
4	7	316.5838	**319.9777**	-151.2919	3 v 4	1.5555	0.2123
5	3	345.9517	346.6003	-169.9758	4 v 5	37.3679	<0.0001

Table 3.3 continued.

Models

1) Clearance ~ Composition*Density + Biomass | Block
2) Clearance ~ Composition*Density | Block
3) Clearance ~ Composition + Density | Block
4) Clearance ~ Composition | Block
5) Clearance ~ Mean | Block

Table 3.4. Mechanisms which are supported by results from the grazing experiments based on expectations in Table 3.1. ‘Preference for’ indicates a preference for *C. reinhardtii* and ‘Preference against’ indicates a preference against *C. reinhardtii*.

	Polyculture community composition			
Species	Pa(latable)	Mix(ture) 1	Mix(ture) 2	Un(palatable)
D. pulex (All data Fig. 2a & b)	Complementarity	Preference against	Preference against	Hindrance
B. longirostris (Substitutive Fig. 2g & h)	Preference against	Dilution	Dilution	Preference for
C. reticulata (All data) Fig. 2e & f)	Dilution	Hindrance	Dilution	Hindrance

3.4 Discussion

Previous work has suggested that increased resource species diversity can cause an increase (Pfisterer et al. 2003, Gamfeldt et al. 2005) or a decrease (Hillebrand and Cardinale 2004, Kratina et al. 2007, Edwards et al. 2010) in the transfer of energy between trophic levels (Jactel and Brockerhoff 2007). This study demonstrates that consumer identity and resource community composition determine the direction and magnitude of the effect of species diversity on rates of consumption. Community composition has been shown to have significant effects on a variety of other ecosystem functions, and in some cases, has been more important than species diversity (Pfisterer et al. 2003, Ives and Cardinale 2004, Jactel and Brockerhoff 2007). As such, the diversity of traits encompassed by the species in a community may generally be more important than the number of species *per se* (Hillebrand and Matthiessen 2009).

Overall, resource community composition had significant effects on both the clearance rate of the focal species, *C. reinhardtii*, and the whole phytoplankton community for all three consumers. In agreement with most studies, the majority of high diversity community compositions caused reduced consumption (Hillebrand and Cardinale 2004, Jactel and Brockerhoff 2007, Edwards et al. 2010). Nevertheless, consumers were influenced by different mechanisms depending on the community composition. This suggests that while generalizations about the types of mechanisms that affect consumers with different feeding habits may emerge, the accuracy of predictions for any given community may be limited, particularly in cases of nonlinear modulation such as Complementarity or Hindrance (Abrams 2001a).

As expected, *D. pulex* was the only consumer species that displayed an effect of Complementarity (Table 3.4). However, the action of Complementarity depended on the particular combination of phytoplankton species, and not just their palatability. For instance, the species in mixture 1 were palatable for *D. pulex* but did not cause Complementarity. It had been shown that diverse resource communities may lead to larger consumer effects for generalists (Jactel and Brockerhoff 2007, Toscano et al. 2010), but this is the first demonstration that this effect depends on the composition of the resource community. Complementarity may have arisen as a positive interaction among the cell shapes or cell-surface chemistries of the different species, facilitating capture, or it may have arisen via improved nutrition (Duffy et al. 2007). For instance, Cryptomonads have a relatively high content of long-chained polyunsaturated fatty acids (Ahlgren et al. 1990), whereas fast-growing species like *C. reinhardtii* and *Cyclotella sp*. may provide the high phosphorus content that cladocerans require (Sterner and Hessen 1994). Indeed, food of greater nutritional value can cause elevated clearance rates in Daphnia within 20 hours (Sterner et al. 1993). Despite being a generalist however, *D. pulex* was affected by Hindrance in the unpalatable composition (Table 3.4). When a single unpalatable species was present (mixture 2), no effect of Hindrance was detected, suggesting that the number of unpalatable species may be important. Similarly, Kratina et al. (2007) found that two inedible resource species caused a greater reduction in consumption than either of the resources alone.

Resource diversity affected the two relatively specialist consumers differently (Table 3.4). It generally reduced consumption rates for *B. longirostris* (although mainly due to the additive design). Preference and Dilution affected consumption rates in this species. Contrary to expectation, *B. longirostris* was not affected by Hindrance, indicating that species with active food selection behaviour may be less susceptible to interference by unpalatable resources as those which simply reject unpalatable resources. By contrast, *C. reticulata* was affected by Hindrance and Dilution, indicating that diversity can impact the consumption rates of even relatively specialized consumers via different mechanisms, depending on their feeding behaviours.

In conclusion, the mechanism by which resource diversity modulates rates of consumption depends on the consumer’s feeding selectivity and the composition of the resource community. The mechanism of modulation determines the direction and magnitude of the effect of the resource community on rates of consumption. We manipulated the size and therefore the palatability of the species in the resource community to investigate these mechanisms. However, other properties such as nutrition (Sterner et al. 1993), chemical (DeMott 1999) and mechanical defences, infochemicals (Vos et al. 2001), and behaviour (Toscano et al. 2010) may also influence the palatability of resource species and therefore rates of consumption in diverse communities. We expect that incorporating these properties and mechanisms into food web models will improve our understanding of complex community dynamics.

Chapter 4: Resource species diversity impacts the functioning and stability of planktonic food webs

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4.1 Introduction

The impact of species diversity on the stability of populations, communities and ecosystems has long been a central question in ecology (MacArthur 1955, Elton 1958, May 1973, Tilman 1996). There are many definitions of ecological stability and the influence of species diversity can depend both on the type of stability and the level of ecological of organization being investigated (Tilman 1996, Steiner et al. 2005, Thébault and Loreau 2005, Ives and Carpenter 2007). Historically, concepts of stability have centered on mathematical notions of equilibrium (e.g.May 1973), in which a system is stable if it returns to equilibrium after a disturbance, or if the rate of return is rapid (McCann 2000). Stability may also refer to the complexity of the dynamical behaviour, with high stability being conflated with a stable point equilibrium, and low stability with chaos (McCann and Hastings 1997, Post et al. 2000, Fussmann and Heber 2002). However, the prevalence of variable, non-equilibrium population dynamics in nature has led empiricists to resort to a less restrictive notion of stability (McCann 2000). In the last 15 years, empirical research on the topic has largely focused on the influence of diversity on stability, defined as the inverse of variability (or the coefficient of variation, CV) (Tilman 1996, Steiner et al. 2005, Romanuk et al. 2006, Vogt et al. 2006, van Ruijven and Berendse 2007, Isbell et al. 2009a, Romanuk et al. 2009).

Defined in this way, diversity may have different impacts on the stability of populations and aggregate community properties (Lehman and Tilman 2000, Steiner

2001). Diversity may increase the stability (1/CV, or μ/σ) of aggregate community properties on a single trophic level either by increasing the mean total function (μ), or reducing the variability of function (σ) over time (Lehman and Tilman 2000). Diversity can increase the total function (μ) (overyielding) via resource use complementarity, facilitation, or a selection effect (Loreau and Hector 2001, Fox 2005) and/or decrease the variance (σ^2) of the function by reducing the summed variances or summed covariances of the functioning of individual species. Increasing diversity will reduce summed variances when the variance in each species' level of functioning scales with its mean as a power function with an exponent, z, greater than 1 (i.e., statistical averaging, or the "Portfolio effect") (Doak et al. 1998, Tilman et al. 1998). Diversity can also reduce the variability of aggregate properties by reducing the summed covariances among populations (i.e., the 'Insurance Hypothesis', Ives et al. 1999, Yachi and Loreau 1999, Leary and Petchey 2009). However, insurance effects are predicted to reduce the stability of individual populations as diversity increases (Lehman and Tilman 2000).

The majority of empirical studies on the influence of diversity on stability have focused on effects on a single trophic level (Tilman et al. 2006, Hector et al. 2010), although the number of multitrophic studies is growing (Jiang and Pu 2009, Schmid et al. 2009). In support of theory, grassland biodiversity experiments have shown that plant species diversity tends to increase and stabilize aggregate community biomass over time but destabilize population-level biomass in single trophic level ecosystems (Tilman et al. 2006, van Ruijven and Berendse 2007, Hector et al. 2010). More generally, species diversity has been found to have positive effects on average levels of a variety of ecosystem functions including nutrient uptake, resource use efficiency, carbon fixation, respiration, decomposer activity, secondary production, and resistance to disturbance (Bell et al. 2005, Balvanera et al. 2006, Cardinale et al. 2006a, Worm et al. 2006, Ptacnik et al. 2008, Schmid et al. 2009), and may stabilize them as well (Ptacnik et al. 2008).

The impacts of species diversity on populations, ecosystem functions and stability in multi-trophic ecosystems however, may differ substantially from those in single trophic level systems, (Thébault and Loreau 2005, Duffy et al. 2007, but see Ives et al. 2005). For example, predators are often mobile, consume their prey in a density-dependent fashion, may overexploit their prey or forage adaptively (Murdoch 1969), and may display complex feeding relations including omnivory, interference, and intraguild predation (Holt and Polis 1997, Holyoak and Sachdev 1998, Duffy et al. 2007). Theory has also suggested that generalist consumers may have synchronizing impacts on community biomass, whereas specialist consumers may promote compensation (Tirok and Gaedke 2010). These aspects of trophic interactions are hypothesized to have impacts on food web structure and stability (Rosenzweig 1971, Holt and Polis 1997, McCann et al. 1998, McCann 2000, Kondoh 2003, Rooney et al. 2006). Trophic interaction strengths are also known to impact food web stability, with weak interactions stabilizing food webs (McCann 2000, Williams and Martinez 2004, Kratina 2009, O'Gorman and Emmerson 2009, Rip et al. 2010a). Trophic interaction strengths can be modified by species diversity and community composition in the resource trophic level (Kratina et al. 2007, Narwani and Mazumder 2010). As a result, food web structure, functioning and stability may depend on resource diversity, as well as the feeding selectivity of the consumer, and competition-resistance trade-offs among resources (Holt and Polis 1997, Ives et al. 1999, Thébault and Loreau 2003, Yoshida et al. 2003, Thébault and Loreau 2005).

Numerous aquatic food web studies have manipulated whole food web diversity by manipulating diversity at multiple trophic levels and generally have found that diversity stabilizes community properties but can have contrasting effects on population stability (McGrady-Steed and Morin 2000, Kolasa and Li 2003, Steiner et al. 2005, Steiner et al. 2006, Vogt et al. 2006, Jiang et al. 2009). Such experiments however, did not address the relative importance of the diversity of resources and consumers (but see Gamfeldt et al. 2005, Srivastava et al. 2009). Despite the abundant theory demonstrating the particular importance of bottom-up effects of diversity on food web properties and stability (MacArthur 1955, Elton 1958, Pimm 1991, Fussmann and Heber 2002, Thébault and Loreau 2003, Thébault and Loreau 2005), very few studies have empirically tested the influence of resource diversity on the stability of consumer populations (Luckinbill 1979, Petchey 2000, Gonzalez and Descamps-Julien 2004), community dynamics (Hairston et al. 1968, Haddad et al. 2011) or ecosystem functions in food webs. To our knowledge, no experimental work has yet investigated bottom-up effects of diversity on all three levels of ecological organization.

There are a number of mechanisms by which resource species diversity may affect the stability and availability of resources, and therefore the stability of consumer populations (Petchey 2000). 1) **Resource availability**. Increased resource species diversity may lead to an increase in total resource biomass due to selection or complementarity (Loreau and Hector 2001), which could have positive effects on generalist consumer abundance (Haddad et al. 2011). However, greater resource biomass may also destabilize generalist consumers via the paradox of enrichment (Rosenzweig 1971, Luckinbill 1979). Impacts of selection, facilitation or complementarity on specialist consumers would be tied to impacts on their particular resources, assuming no indirect effects or interaction modifications by non-prey species (Luckinbill 1979). 2) **Resource reliability**. Greater diversity may lead to greater stability of total resource biomass via statistical averaging (Doak et al. 1998, Tilman et al. 1998) or insurance effects (Ives et al. 1999, Yachi and Loreau 1999). This would result in more stable populations of generalist consumers due to the increased reliability of resources (MacArthur 1955), but less stable populations of specialists due to greater variability of individual resources (insurance effects, Haddad et al. 2011). 3) **Resource composition effects**. Diverse resource communities are more likely to contain a species, or group of species, with any particular combination of traits via sampling effects. For example, diverse communities may be more to likely to contain inedible species ("Variance in edibility" hypothesis Leibold 1989). This may stabilize consumer populations (Vos et al. 2001), by reducing consumer foraging efficiency , or by competing with edible species for limiting nutrients, thereby lowering their carrying capacity (Kretzschmar et al. 1993, Grover 1995, McCauley et al. 1999). However, inedible species also decrease the total biomass of consumers (μ), increasing their risk of stochastic extinctions. Conversely, when resource species are all edible (and/or consumers are generalists), diversity may increase the rate of resource capture via indirect effects or complementarity among resource species (Narwani and Mazumder 2010, Toscano et al. 2010), resulting in increased growth and total biomass. Increased consumption could be either stabilizing or destabilizing depending on its relative impacts on consumer biomass and variability.

In this chapter, we tested the effects of resource species diversity, resource community composition, and consumer feeding selectivity on the density and stability of resource and consumer populations. We also tested the impacts of these factors on the average and variability of a number of community properties and ecosystem functions including primary producer biomass (measured as total community biovolume and chlorophyll-a), total community biomass (measured as total particulate carbon), total nutrient accumulation (measured as particulate nitrogen and phosphorus), and the rate of primary production (we used δ13C as a proxy for rate of carbon fixation) (Fry 1996, Brutemark et al. 2009).

Changes in ecosystem functioning and stability with increasing species diversity can be additive (i.e. the average of the contributions of the individual species in monoculture), they can result from dominant effects of individual species, or they can result from modifications of the contributions of individual species to functioning when in a diverse community (Mulder et al. 1999, Fox 2006, Fox 2010). We tested whether the lower resource community biovolume and variance that we found in monocultures relative to the polycultures depended upon species number (Species Richness Effects, SREs), the identity of species in the polyculture communities (Species Composition Effects, SCEs), or changes in the functioning of individual monoculture species when in polyculture (Context Dependence Effects, CDEs). We employed Fox's Price partitions for the mean and variance of functions (Fox 2006, Fox 2010) to partition these effects of diversity.

Finally, the impacts of species diversity on the functioning and stability of ecosystems are likely related to the outcomes of species' interactions and mechanisms of coexistence (Mulder et al. 2001, Mouquet et al. 2002, Isbell et al. 2009a, b, Zhang et al. 2009, Tirok and Gaedke 2010). For example, competitive exclusion by a high-functioning (low-functioning) species would lead to a positive (negative) selection effect (Mulder et al. 2001, Isbell et al. 2009b). Conversely, co-existence among species via niche partitioning (competition) would lead to a positive effect of complementarity. We expected that species' traits would determine the outcome of species' interactions in polyculture, the level of dominance or diversity, and thereby influence the stability of ecosystem functioning (Walker et al. 1999, Mulder et al. 2001, Zhang et al. 2009). For example, communities with high variability in traits relating to niche partitioning would show high diversity (Chase and Leibold 2003). Size differences among species may reflect a competition-resistance trade-off, with smaller individuals being better able to compete for nutrients while larger individuals are better able to compete for enemy-free space in the presence of consumers (Leibold 1989, but see Fox 2003). Such trade-offs may enable greater phytoplankton co-existence via stabilizing mechanisms (Chase and Leibold 2003, Tirok and Gaedke 2010). Conversely, communities with high variability in traits related to competitive ability for a single limiting resource would show strong dominance. Greater variability in such traits among species is likely to hasten competitive exclusion by diminishing equalization stability (Chesson 2000b, Tirok and Gaedke 2010). We tested whether species' traits could explain the degree of resource algal community dominance, and indirectly, stability.

This work is unique compared to the majority of previous biodiversity-ecosystem functioning and stability experiments for a number of reasons. First, we focused on the bottom-up effects of diversity. Second, we investigated the effects of diversity on three levels of ecological organization. Third, we tested some stabilizing mechanisms of species diversity. Fourth, we compared the relative importance of species diversity, community composition, and changes in individual species' contributions, in determining the average and stability of resource community biomass. Fifth, we investigated the relationship between variability in species' traits, species' average coexistence over time, and community biomass stability.

4.2 Methods

4.2.1 Experimental design and sampling

The experimental design consisted of four monoculture and four polyculture phytoplankton community compositions (Table 4.1), and these community compositions were crossed by two consumer species. The two consumers were the cladoceran freshwater filter-feeders *Daphnia pulex* and *Ceriodaphnia dubia*. The monoculture phytoplankton species were edible for both consumers. The polycultures each contained five phytoplankton species and the compositions of the four communities were chosen so as to comprise a gradient in palatability for the two consumers. *D. pulex* is larger than *C. dubia* and is therefore able to consume larger particles (~45 μm in diameter as opposed to 35 μm or less for *C. dubia*), making it a relative generalist. Community composition 1 contained species that were all edible for both consumers. The number of inedible species in each community (according to size, one axis > 40 μm) increased from composition 1 to 4 (Table 4.1). Each treatment was replicated three times, yielding a total of 48 microcosms.

Table 4.1. Resource community compositions. Inocula of phytoplankton species were obtained from the University of Texas Culture Collection (UTEX) and the Canadian Phycological Culture Centre at the University of Waterloo (CPCC). The diameter estimates are in μm of 'estimated spherical diameter' (ESD). These estimates were determined from ≥ 195 natural units of each species using a Bench Top Model FlowCAM®.

Composition	Species (Source & Identifier)	Diameter (ESD)
Monoculture 1	*Scenedesmus acutus* (CPCC 10)	7
Monoculture 2	*Pseudokirchneriella subcapitata* (CPCC 37)	8
Monoculture 3	*Cyclotella sp.* (CPCC 537)	8
Monoculture 4	*Rhodomonas minuta* (CPCC 344)	11
Polyculture 1	*Scenedesmus acutus* (CPCC 10)	7
	Pseudokirchneriella subcapitata (CPCC 37)	8
	Cyclotella sp. (CPCC 537)	8
	Rhodomonas minuta (CPCC 344)	11
	Cryptomonas erosa (CPCC 446)	16
Polyculture 2	*Cyclotella sp.* (CPCC 537)	8
	Cryptomonas erosa (CPCC 446)	16
	Ankistrodesmus falcatus (UTEX 101)	37
	Staurastrum Pingue (UTEX 1606)	44
	Fragilaria crotonensis (CPCC 269)	123
Polyculture 3	*Pseudokirchneriella subcapitata* (CPCC 37)	8
	Rhodomonas minuta (CPCC 344)	11
	Stichococcus bacillaris (CPCC 177)	12
	Asterionella formosa (CPCC 605)	42
	Pediastrum simplex (CPCC 431)	62
Polyculture 4	*Ankistrodesmus falcatus* (UTEX 101)	37
	Asterionella formosa (CPCC 605)	42
	Staurastrum pingue (UTEX 1606)	44
	Pediastrum simplex (CPCC 431)	62
	Fragilaria crotonensis (CPCC 269)	123

Microcosms consisted of 2L media bottles containing sterile COMBO medium. Prior to inoculation, we measured the density and average biovolume (estimated as the equivalent spherical diameter, ' ESD') of ≥ 85 natural units (cells, colonies or filaments) of each monoculture in the species pool at stationary phase using a Bench Top Model FlowCAM® (Fluid Imaging, Yarmouth, ME, USA). Experimental monocultures then received a biovolume of 500,000 μm ESD of the appropriate species, and polycultures received 100,000 μm ESD of each species in the mixture. We inoculated the phytoplankton one week prior to the addition of zooplankton (week 0). *D. pulex* treatments received 9 individuals and *C. dubia* treatments received 14 individuals. The microcosms were placed randomly into an environmental growth chamber at 20 °C on a 12 h light: 12 h dark cycle.

We swirled the microcosms daily and collected 250 mL samples weekly for twelve weeks, replacing samples with sterile COMBO medium. Two observers checked each microcosm for the presence of zooplankton prior to sampling. When zooplankton were extinct, we replaced them at the original low density. Replacements of zooplankton were intended to overcome the effects of stochastic extinctions at low density. Re-additions of consumers at low density did not substantially alter community dynamics; communities which could not support consumers continually experienced extinctions regardless of re-additions, while for communities in which zooplankton re-established after extinction, inoculation densities represented less than 2% of the maximum abundance (Zooplankton time series data, Appendix 4.1). If zooplankton were present at low density (<10 animals), we visually counted all of the animals in the microcosm or else the number of animals in the 250 mL sample. When there were greater than eight animals in the sample, we preserved a 40 mL subsample in sugared-buffered formalin (10%) for enumeration under a microscope. On weeks 5 and 9, we re-inoculated all of the microcosms with 1/10th of the original phytoplankton densities. These extremely low densities ensured that propagules of the species within each community were present. This allowed for potential density-dependent increases (invasions from rarity) of species, again overcoming the potential reductions in diversity due to stochastic extinctions, without imposing mass effects, or disturbing successional dynamics (Phytoplankton relative abundance data, Appendix 4.2).

Upon sampling, we took 10 mL subsamples for phytoplankton enumeration using the FlowCAM® within 48 hours. We filtered 60 mL subsamples onto Whatman® GF/F grade glass microfiber filters (Whatman PLC, Maidstone, Kent, UK) and stored them at -20 °C for later chlorophyll-a analysis. We extracted the chlorophyll-a in 95% ethanol by shaking for 20 minutes and refrigerating for 24 h at 4 °C in the dark. We measured the chlorophyll-a using a Turner Designs Triology™ Laboratory Fluorometer (Turner Designs Inc., Sunnyvale, CA, USA) calibrated to manufacturer-recommended standards.

In addition to consumer and resource dynamics, we also monitored a number of ecosystem-level variables over time. We measured particulate organic carbon, nitrogen and $\delta^{13}C$ (as a proxy for the rate of primary production) by filtering an 80 mL subsample from each microcosm onto ashed Whatman® GF/C grade glass microfiber filters. We dried the filters in an oven at 60 ^{o}C for 12-24 h and measured nutrient levels and carbon isotopes using an ECS 4010 CHNSO Elemental Analyzer (Costech Analytical Technologies Inc., Valencia, CA, USA) coupled to a Delta V continuous flow stable isotope ratio mass spectrometer (Thermo Fisher Scientific Inc., Waltham, MA, USA). We took 20 mL subsamples for particulate phosphorus analysis, filtering 10 mL through 0.45 μm nitrocellulose filters for the measurement of dissolved phosphate, and 10 mL of the unfiltered sample for the measurement of total phosphate. Particulate phosphate was calculated as the total minus the dissolved phosphate. We digested the subsamples using potassium persulfate in an autoclave, and measured the ortho-phosphate on a QuickChem® 8000 nutrient autoanalyzer (Lachat Instruments, Loveland, CO, USA).

4.2.2 Data analysis

We used nested ANOVAs to explore treatment effects, with zooplankton species identity, resource diversity and phytoplankton community composition (nested within diversity) treated as fixed effects. We asked whether these factors had significant effects on the mean and variability (CV) of zooplankton density, chlorophyll-a, average algal population biovolume, total phytoplankton community biovolume, total particulate carbon, nitrogen, and phosphorus. We also asked whether these factors affected the average $\delta^{13}C$ signature. We used data transformations when necessary to improve normality and homoscedasticity. When consumer identity had a significant interaction with resource community composition or diversity, we analyzed the data for each consumer separately (Table 4.2).

The organismal and ecosystem variables measured from within a given microcosm were unlikely to be independent. We used Principle Components Analysis (PCA) to explore relationships among all dependent variables and to partition the variability into orthogonal variables. We included all variables (transformed when necessary), including the average and CV of chlorophyll-a, zooplankton density, carbon, nitrogen, phosphorus, and average $\delta^{13}C$, and we report PCs 1 & 2.

We tested mechanisms by which resource biomass could be stabilized in polycultures. We estimated the exponent (z) of the population biovolume mean-variance scaling relationship to determine whether statistical averaging contributed to community stability (Tilman et al. 1998, Steiner et al. 2005). We also tested whether the total population biovolume, summed variances, or summed covariances varied among treatments (Lehman and Tilman 2000). Problems with using population covariance as a measure of synchrony have been noted (Isbell et al. 2009a), and so we also calculated synchrony *sensu* Loreau & de Mazancourt (2008):

$$\frac{{\sigma_T}^2}{(\sum_i \sigma_i)^2} \qquad [1]$$

${\sigma_T}^2$ is the variance of the whole community biovolume and σ_i is the standard deviation of the biovolume of species *i* over time. This metric will display high 'synchrony' when species' biomass dynamics are positively related, but also when community biomass dynamics are dominated by individual species. By contrast, dominance in a community can actually reduce the stabilizing impacts of statistical averaging or an insurance effect (Doak et al. 1998, Yachi and Loreau 1999, Gonzalez and Descamps-Julien 2004). We calculated the Simpson index, *D*, as a measure of dominance (Magurran 2004):

$$D = \sum_i {p_i}^2 \qquad [2]$$

where p_i is the proportion of species *i*, by biovolume, in a given microcosm. We entered average dominance, summed variance, summed covariance, synchrony and mean biovolume into a multiple regression to determine which factors were most important in explaining the CV in total community biovolume.

We tested whether the average realized dominance and diversity of the phytoplankton communities was related to variability among species with respect to three species traits. We measured the average biovolume of at least 85 natural units and the total population biovolume at carrying capacity for monocultures of each species using a FlowCAM® before commencing the experiment. We had measured the growth rate of each species in preliminary studies by measuring in vivo fluorescence for every species except *P. simplex*. For this species we used an estimate from the literature (Rojo et al.

2008).We calculated the variability (coefficient of variation) in estimated spherical diameter (ESD)(CVsize), carrying capacity monoculture biovolume (CVmb) and growth rate (CVgr) among all species within each polyculture composition (Isbell et al. 2009b). As a measure of dominance, we calculated the Simpson index, *D*, and as a measure of diversity, we calculated the Shannon index, H′ (Magurran 2004):

$$H' = -\sum p_i \bullet \ln p_i \qquad [7]$$

where p_i is the proportion of total biovolume made up of species *i*. We tested whether the dominance or diversity of phytoplankton communities in polyculture was related to the coefficient of variation of the three traits using a multiple linear regression.

We found that the average resource community biovolume and summed variance were greater in polyculture than in monoculture. We used the Price equation to partition the effect of species diversity on the time-averaged total phytoplankton community biovolume (Fox 2006) and summed variance (Fox 2010). This partitions the total effect of diversity (*ΔT*) on the mean or variance of community biovolume among the effects of species richness *per se* (the average effect of species ‘loss’, *SRE*), species composition effects, e.g. the ‘loss’ of particularly productive or variable species (*SCE*), and context dependence effects (*CDE*) whereby the biomass or variance of individual species differs between monoculture and polyculture.

$$\Delta T = SRE + SCE + CDE \qquad [3]$$

$$SRE = \bar{z} \cdot \Delta s \qquad [4]$$

$$\Delta s = s' - s \qquad [4\text{ a}]$$

$$\bar{z} = \sum \frac{1}{s} \cdot z_i \qquad [4\text{ b}]$$

$$SCE = \sum (w_i - \bar{w}) \cdot (z_i - \bar{z}) \qquad [5]$$

$$CDE = \sum w_i \cdot \Delta z_i \qquad [6]$$

$$\Delta z_i = z_i' - z_i \qquad [6\text{ a}]$$

The partition compares ‘pre-loss’ and ‘post-loss’ communities, which in this chapter are polycultures and monocultures, and have s (= 5) and s' (= 1) number of species respectively. For a given comparison between a high diversity (‘pre-loss’) and low diversity (‘post-loss) microcosm, species in the ‘post-loss’ community are weighted such that $w = 0$ if they were not originally inoculated into the composition and $w = 1$ if they were originally inoculated into the composition (and $\overline{w}$ = mean community weight). Individual species’ biovolume or variance are symbolized as z_i, with post-loss values denoted as z_i', and the mean community biovolume or variance denoted as $\overline{z}$. We compared each monoculture replicate to all polyculture replicates in which the monoculture species was originally inoculated. For each monoculture-polyculture comparison, there were nine contrasts (3 monoculture replicates by 3 polyculture replicates). With seven possible comparisons between monoculture and polyculture compositions, we had 63 total contrasts.

We performed statistical analyses using v. 2.9.2 of R software (R Development Core Team 2009) and used the car package for analysis of variance with type III sums of squares.

4.3 Results

4.3.1 Effects of resource diversity on consumers, ecosystem functions and their stability

Resource diversity had a positive effect on the density of the generalist consumer, *D. pulex*, (Fig. 4.1 a, Table 4.2 a), but not the specialist (Fig. 4.2 a, Table 4.2 a). Contrary to our predictions, diversity did not significantly stabilize the population density of either consumer species (Figs 4.1 b and 4.2b, Table 4.2 a), although there was a trend toward greater stability with diversity for the generalist (Fig. 4.1 b). Resource diversity stabilized and increased the phytoplankton community biovolume (Figs 4.3 a & b), while it destabilized and increased the average of resource population biovolume (Figs 4.3 c & d). Resource diversity had positive effects on the mean level of the majority of community properties and ecosystem functions, regardless of the consumer treatment (Figs 4.1 c, e, g & k and 4.2 c, e, g, i & k, Table 4.3 a). Diversity also stabilized ecosystem-functions, though not consumer density, by reducing their coefficients of variation (Figs 4.1 d, f, h & j and 4.2 d, f, h & j, Table 4.3 b, effects for phosphorus are marginally non-significant).

More specifically, resource diversity had a significant positive effect on chlorophyll-a for both consumers (Figs 4.1 c and 4.2 c, Table 4.2 b), and a negative effect on the CV of chlorophyll-a (Figs 4.1 d and 4.2 d). The trends in the particulate carbon (Table 4.2 c), the CV of carbon (Figs 4.1 e & f and 4.2 e & f), particulate nitrogen and the CV of nitrogen (Figs 4.1 g & h and 4.2 g & h) mirrored the trends in chlorophyll-a and the CV of chlorophyll-a respectively (Fig. 4.3). Diversity significantly increased the mean, but reduced the CV of both carbon and nitrogen for both consumers (Figs 4.1 e-h and 4.2 e-h, Table 4.2 c & d). Treatment effects on particulate phosphorus were qualitatively similar to those of carbon and nitrogen, though the data were more variable (Figs 4.1 i & j and 4.2 i & j, Table 4.2 e). Diversity had positive effects on δ^{13}C for both consumers (Figs 4.1 k and 4.2 k, Table 4.2 f).

Table 4.2. Results of nested ANOVA for effects of species diversity (‘Diversity’), phytoplankton community composition (nested within diversity, ‘Phyto’) and consumer species identity (‘Zoop’) on the average and coefficient of variation of **a.** zooplankton density, **b.** chlorophyll-a, **c.** particulate carbon, **d.** particulate nitrogen, **e.** particulate phosphorus and **f.** δ^{13}C. Transformations are indicated in parentheses when they were necessary to improve normality or homoscedasticity. Significant interactions among phytoplankton community composition and zooplankton consumer species are shown, followed by separate results for each consumer species.

a. ZOOPLANKTON DENSITY

	Sum Sq	Df	F value	P	R^2
Mean (Square-root transformed)					
Diversity/Phyto*Zoop	383.700	6, 32	4.953	0.001	
D. pulex					0.951
Diversity	65.190	1, 16	10.338	0.005	0.503
Diversity/Phyto	348.710	6, 16	9.217	<0.001	0.448
C. dubia					0.826
Diversity	0.012	1, 16	0.001	0.981	<0.001
Diversity/Phyto	1486.500	6, 16	12.695	<0.001	0.826
CV					
Diversity/Phyto*Zoop	2.674	6, 32	3.242	0.013	
D. pulex					0.610
Diversity	0.378	1, 16	2.099	0.167	0.051
Diversity/Phyto	4.125	6, 16	3.823	0.015	0.559
C. dubia					0.805
Diversity	0.048	1, 16	0.502	0.489	0.006
Diversity/Phyto	6.220	6, 16	10.909	<0.001	0.799

b. CHLOROPHYLL-a

Mean ($\log_{10}$ transformed)					
Diversity/Phyto*Zoop	1.960	6, 32	6.880	<0.001	
D. pulex					0.886
Diversity	2.383	1, 16	35.366	<0.001	0.251
Diversity/Phyto	6.016	6, 16	14.881	<0.001	0.635
C. dubia					0.921
Diversity	2.200	1, 16	79.793	<0.001	0.396
Diversity/Phyto	2.915	6, 16	17.619	<0.001	0.525
CV ($\log_{10}$ transformed)					
Diversity/Phyto*Zoop	0.448	6, 32	4.539	0.002	
D. pulex					0.834
Diversity	0.165	1, 16	11.230	0.004	0.117
Diversity/Phyto	1.016	6, 16	11.513	<0.001	0.717
C. dubia					0.807
Diversity	0.681	1, 16	37.455	<0.001	0.451
Diversity/Phyto	0.537	6, 16	4.917	0.005	0.356

c. PARTICULATE CARBON

Mean (log$_{10}$ transformed**)**					
Diversity/Phyto*Zoop	3.710	6, 32	4.578	0.002	
D. pulex					0.825
Diversity	0.557	1, 16	16.045	0.001	0.175
Diversity/Phyto	2.065	6, 16	9.918	<0.001	0.649
C. dubia					0.806
Diversity	0.459	1, 16	28.159	<0.001	0.342
Diversity/Phyto*Zoop	0.622	6, 16	6.365	0.001	0.463
CV					
Diversity/Phyto*Zoop	0.466	6, 32	2.575	0.038	
D. pulex					0.703
Diversity	0.428	1, 16	11.123	0.004	0.116
Diversity/Phyto	0.657	6, 16	2.844	0.044	0.587
C. dubia					0.638
Diversity	0.136	1, 16	6.246	0.023	0.252
Diversity/Phyto	0.670	6, 16	5.280	0.004	0.386

d. PARTICULATE NITROGEN

Mean (log$_{10}$ transformed)					
Diversity/Phyto*Zoop	0.863	6, 32	4.348	0.003	
D. pulex					0.772
Diversity	0.344	1, 16	16.401	0.001	0.139
Diversity/Phyto	0.501	6, 16	3.989	0.012	0.633
C. dubia					0.716
Diversity	0.441	1, 16	9.764	0.007	0.291
Diversity/Phyto*Zoop	2.011	6, 16	7.412	0.001	0.425
CV					
Diversity/Phyto*Zoop	0.901	6, 32	3.892	0.005	
D. pulex					0.833
Diversity	0.314	1, 16	11.531	0.004	0.121
Diversity/Phyto	1.851	6, 16	11.343	<0.001	0.712
C. dubia					0.671
Diversity	0.732	1, 16	14.657	0.001	0.301
Diversity/Phyto	0.897	6, 16	2.994	0.037	0.369

e. PARTICULATE PHOSPHORUS

Mean (log$_{10}$ transformed**)**					
Diversity	0.107	1, 32	3.277	0.080	0.042
Zoop	0.347	1, 32	10.616	0.003	0.135
Diversity/Phyto	0.599	6, 32	3.056	0.018	0.233
Diversity*Zoop	0.081	1, 32	2.490	0.124	0.032
Diversity/Phyto*Zoop	0.394	6, 32	2.011	0.093	0.153
CV					
Diversity	0.170	1, 32	3.8250	0.059	0.034
Zoop	0.380	1, 32	8.543	0.006	0.077
Diversity/Phyto	2.645	6, 32	9.904	<0.001	0.533
Diversity*Zoop	0.029	1, 32	0.647	0.427	0.006
Diversity/Phyto*Zoop	0.318	6, 32	1.189	0.337	0.064

f. δ13C

Mean					
Diversity/Phyto*Zoop	23.1	6, 32	2.654	0.033	
D. pulex					0.930
Diversity	52.2	1, 16	44.082	<0.001	0.193
Diversity/Phyto	198.8	6, 16	27.986	<0.001	0.736
C. dubia					0.927
(violated normality)					
Diversity	146.9	1, 16	85.368	<0.001	0.390
Diversity/Phyto	202.5	6, 16	19.610	<0.001	0.537

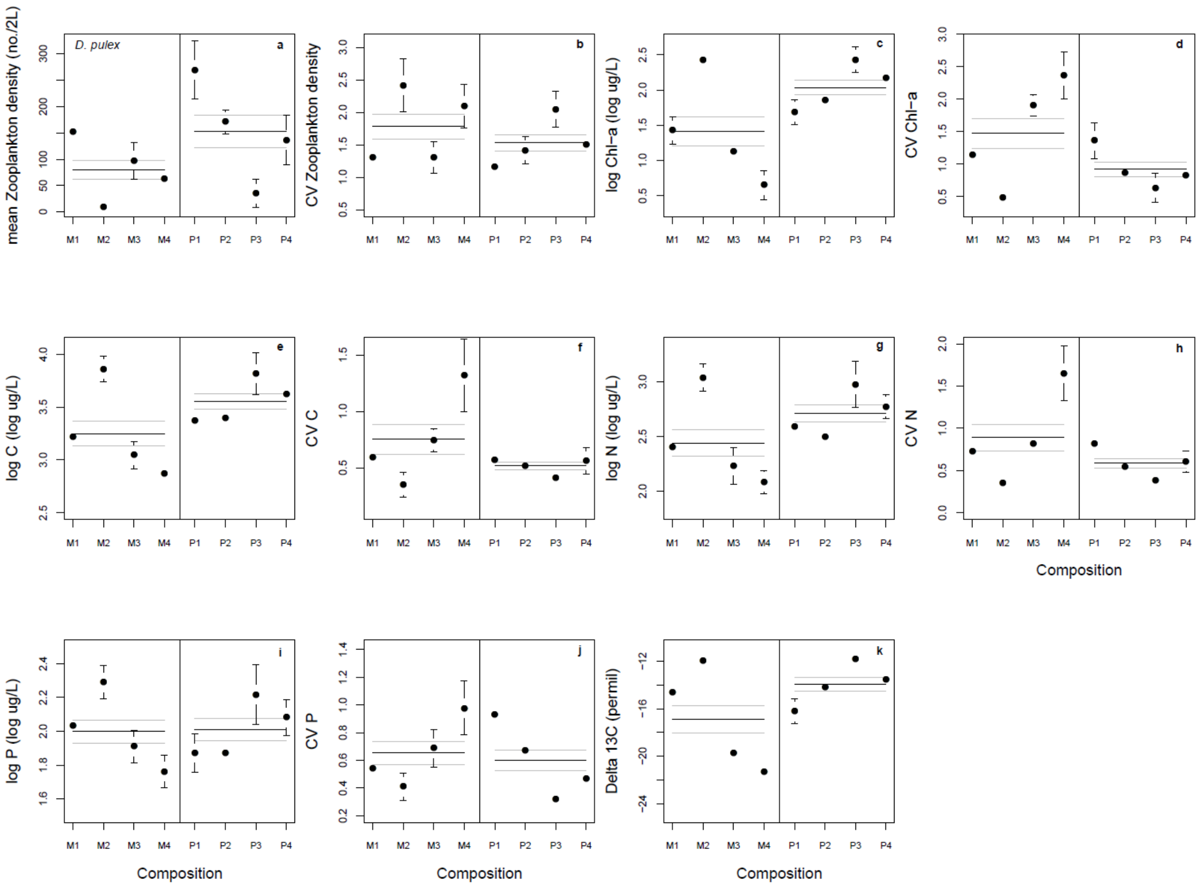

Figure 4.1. Effects of resource species diversity and community resource composition for microcosms containing the consumer *Daphnia pulex*. Effects on the mean and co-efficient of variation (CV) are plotted for: zooplankton density (**a & b**), chlorophyll-a (**c & d**), particulate carbon (C) (**e & f**), particulate nitrogen (N) (**g & h**), particulate phosphorus (P) (**i & j**) and δ^{13}C (**k**). Monocultures are represented by 'M' and polycultures by 'P' in the category axis labels (see **Table 4.1**). The mean value for each community composition is plotted as a dot ± standard error (S.E.) bars (n=3). Mean values for monocultures and polycultures are plotted as black horizontal lines ± S.E. bars (grey horizontal lines) (n=12).

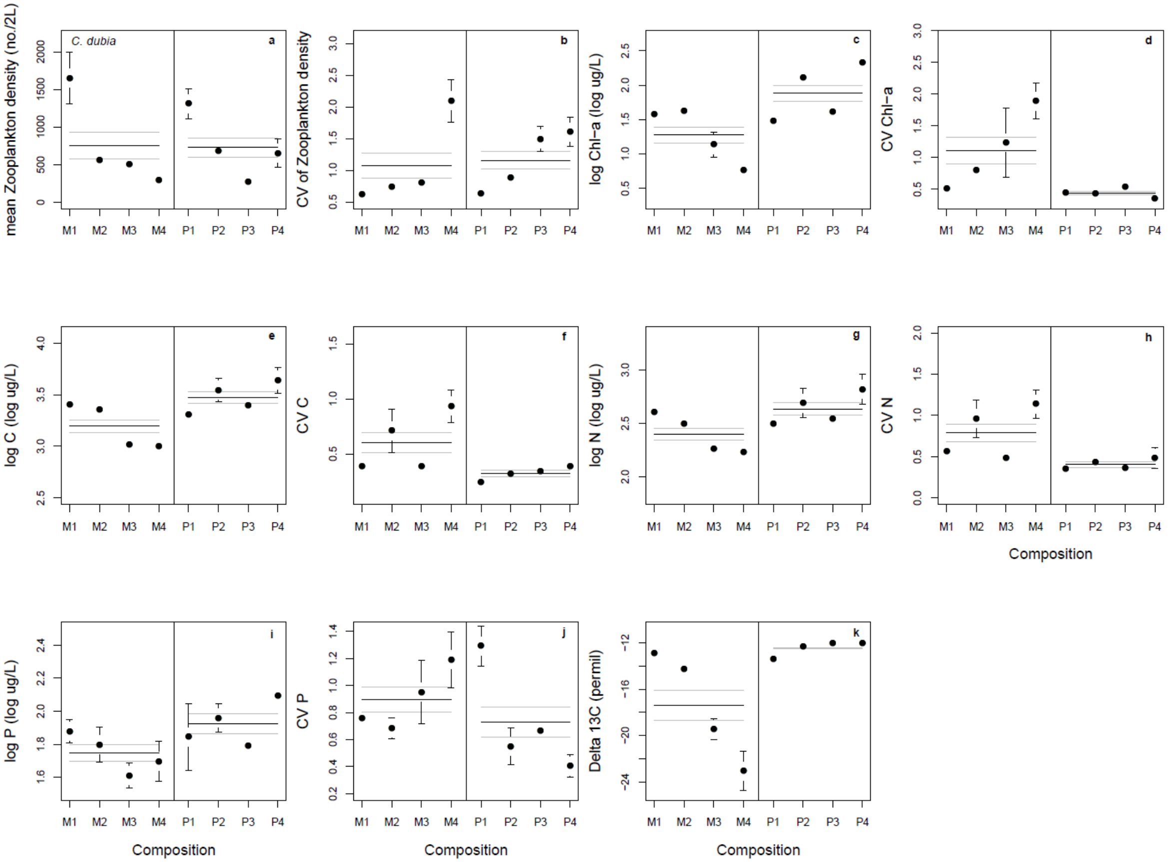

Figure 4.2. Effects of resource species diversity and resource community composition for microcosms containing the consumer *Ceriodaphnia dubia*. Effects on the mean and co-efficient of variation are plotted for: zooplankton density (**a & b**), chlorophyll-a (**c & d**), particulate carbon (C) (**e & f**), particulate nitrogen (N) (**g & h**), particulate phosphorus (P) (**i & j**) and δ^{13}C (**k**). Monocultures are represented by ‘M’ and polycultures by ‘P’ in the category axis labels (see **Table 4.1**). The mean value for each community composition is plotted as a dot ± standard error (S.E.) bars (n=3). Mean values for monocultures and polycultures are plotted as black horizontal lines ± S.E. bars (grey horizontal lines) (n=12).

Table 4.3. Summary of effects of resource species diversity on the dependent variables measured. Positive effects are indicated by a '+' and negative effects are indicated by a '-'. Significance at α=0.05 is indicated with an asterisk. Marginally non-significant effects, 0.05 < P <0.1, are indicated with 'm-ns'. Non-significant effects (P>0.10) are indicated with 'ns'. No discernible effect (no trend) is indicated with a "0".

Dependent variable	*D. pulex*	*C. dubia*
Mean		
Zooplankton density	+ *	**0**
Chlorophyll-a	+ *	+*
Carbon	+ *	+*
Nitrogen	+ *	+*
Phosphorus	+ m-ns	+ m-ns
δ13C	+*	+*
CV		
Zooplankton density	- ns	**0**
Chlorophyll-a	- *	- *
Carbon	- *	- *
Nitrogen	- *	- *
Phosphorus	- m-ns	- m-ns

Resource community composition had significant effects on the average and CV of consumer density for both the specialist and generalist consumers (Table 4.2 a, Figs 4.1 a & b and 4.2 a & b). Composition explained more of the variance in consumer density and variability than species diversity, except in the case of mean density for *D. pulex* (Table 4.2 a). The generalist, *D. pulex,* had its greatest abundance and stability in polyculture 1 (Figs 4.1 a & b, Table 4.1), in which all species were in the edible size fraction and which was dominated by *S. acutus* (Appendices 4.1 e and 4.2 a). The generalist had its lowest abundance and stability in monoculture 2 (Appendix 4.1 b), followed closely by polyculture 3 (Appendix 4.1 g), which were both generally dominated by the phytoplankton species *P. subcapitata* (Figs 4.1 a & b, Appendix 4.2 c).

The specialist, *C. dubia*, had its greatest density and stability in monoculture 1, followed closely by polyculture 1, which were both dominated by the species *S. acutus* (Figs 4.2 a & b, Appendix 4.2 a). The specialist's density was the lowest in monoculture 4 and polyculture 3. To determine whether the average proportion of edible phytoplankton in the polycultures determined zooplankton density for each consumer in polyculture, we regressed the average zooplankton density on the average proportion of edible phytoplankton species (<40 μm average ESD). There was a positive effect of the relative edible biovolume for the specialist (slope=880.900, t=2.852, d.f.=10, P=0.017, R^2= 0.449), but not for the generalist (slope=190.400, t=1.416, d.f.=10 P=0.187, R^2=0.167). Consumer density (square-root transformed) was negatively correlated with total chl-a for the generalist (R=-0.549, t=-3.082, d.f.=22, P=0.005), but not the specialist (R=0.066, t = 0.315, d.f.=22, P=0.756). Edible resource biovolume increased with species diversity in both consumer treatments ($F_{D.\ pulex\ 1,16}$ = 37.449, P<0.001; $F_{C.\ dubia\ 1,16}$ = 65.142, P<0.001) and was significantly affected by community composition ($F_{D.\ pulex\ 6,16}$ =9.050 , P<0.001; $F_{C.\ dubia\ 6,16}$ =49.624, P<0.001, Fig. 4.4 h).

The density of the generalist grazer, *D. pulex* was negatively related to the proportion of edible algal biovolume over time within polycultures 3 and 4 (Appendices 4.3 a & c). The decline in relative edible biovolume indicates that species larger than 40 μm increased with *D. pulex* density, suggesting compensatory dynamics among edible and inedible fractions of algal biomass with fluctuations in *D. pulex* density. Such compensation however, was not generally evident for *C. dubia* treatments. In polycultures 2 and 4, peaks in the specialist's density were not concurrent with large reductions in edible biovolume (Appendices 4.3 a & c). In polyculture 3 however, *C. dubia* density increased rapidly before week 3 (Appendix 4.3 b), and then declined with the proportion of edible biovolume by week 4, after which both the consumer density and proportion of edible biovolume remained low. In this transition, the decline of an edible species, *P. subcapitata*, was compensated for by the increase in of an inedible species, *P. simplex* (Appendix 4.2 c).

Resource community composition also had significant effects on average chlorophyll-a (Figs 4.1 c & 4.2 c), carbon (Figs 4.1 e & 4.2 e), nitrogen (Figs 4.1 g & 4.2 g), phosphorus (Figs 4.1 l & 4.2 l), and δ^{13}C (Figs 4.1k & 4.2k) for both consumer treatments (Table 4.2 b-f). Note that for *C. dubia*, model errors for δ^{13}C were not normally distributed so the P value should be evaluated cautiously (Anderson-Darling A=0.815, P=0.030). Particulate carbon, nitrogen, phosphorus and δ^{13}C were all positively related to chlorophyll-a concentration, and generally negatively related to zooplankton density (Fig. 4.3). For the generalist, monoculture 2 and polyculture 3 had the highest chlorophyll-a, carbon, nitrogen, phosphorus and δ^{13}C (Figs. 4.1 c, e, g, l & k). Otherwise levels dropped from monoculture 1 to 4 in order, and increased from polyculture 1 to 4 in order (Figs. 4.1 c, e, g, l & k). The CV of all of these community properties and ecosystem functions was negatively related to their mean levels (Fig. 4.3), suggesting that their variances increased less than their means with diversity. As a result, monoculture 1 and polyculture 3 had the lowest CV in these functions for the generalist (Figs 4.1 d, f, g, h & j). For the specialist, polyculture 4, the treatment with the greatest number of inedible species, had the greatest average chlorophyll-a, nutrients and rate of photosynthesis (Figs 4.2 c, e, g, l & k). However, the inverse relationship between mean abundance and variance, and the coupling among ecosystem functions were not as strong for this consumer, with more idiosyncratic effects of each composition for each function (Figs. 4.2 d, f, h & j). In all cases, except for the CV of chlorophyll-a for *C. dubia*, composition explained more variability than species diversity (Table 4.2 b-e).

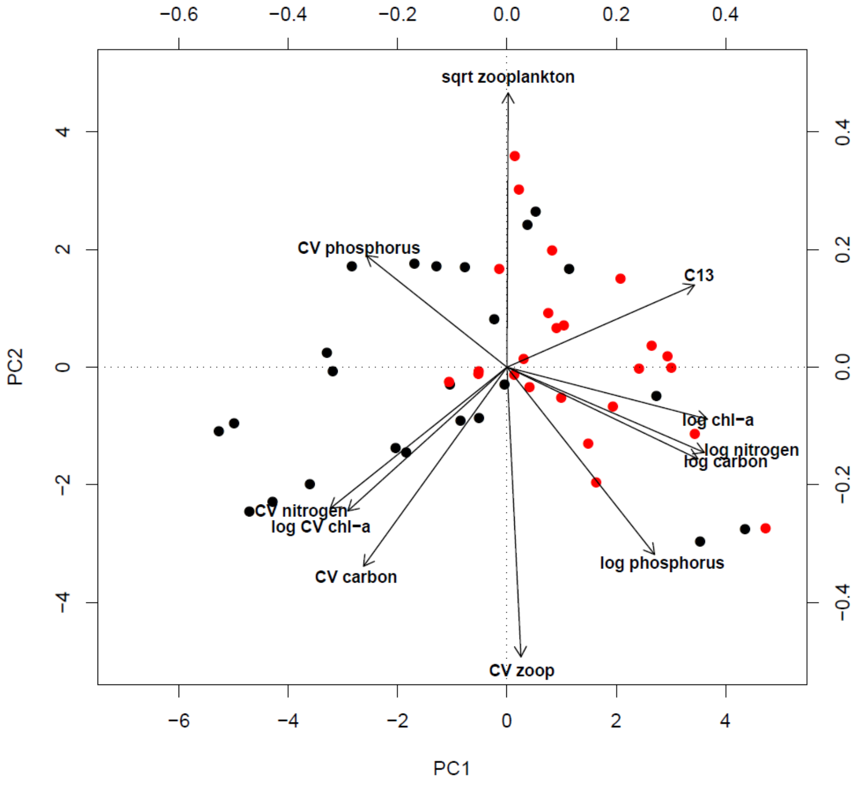

Figure 4.3. Biplot of principal components (PCs) 1 (53.1%) and 2 (22.5%) from all measured dependent variables. Dots represent microcosm scores on the PCs plotted. Black dots represent monocultures and red dots represent polycultures. Arrows represent the strength of the loadings of the dependent variables on each PC. PCs are orthogonal, and as such when variables are orthogonal in the PC space, variance plotted is independent. When variables are clustered they are positively related, and when they are at a 180° angle, they are negatively related. The two principal components explain 75.6% of all of the variation in the dependent variables.

4.3.2 Effects of resource diversity on resource community stability

The two measures of phytoplankton community biomass, total biovolume and chlorophyll-a, were positively related (log-log correlation Pearson’s R=0.775). The stability of most community properties and ecosystem functions were positively related to chlorophyll-a and so we tested for stabilizing effects of phytoplankton population biovolume on aggregate properties and ecosystem functions via impacts on total resource community biovolume. Diversity tended to cause a decline in the CV of total phytoplankton community biovolume for both consumers (Fig. 4.4 a). The effect of resource composition on the CV of community biovolume depended on consumer identity (log-transformed, interaction $F_{6,32}$=3.300, P=0.012). For the generalist, the decline in the CV of community biovolume was significant ($F_{1,16}$ =5.729, P=0.029, Fig. 4.4 a), but it was not significant for the specialist ($F_{1,16}$ =1.499, P=0.239, Fig. 4.4 a). Community composition had significant effects for both consumers ($F_{D.\ pulex\ 6,16}$ =9.760, P<0.001; $F_{C.\ dubia\ 6,16}$ =13.520, P<0.001). Mean community biovolume increased with diversity (log transformed, $F_{1,32}$=165.222, P<0.001), and there were significant main effects of composition ($F_{6,32}$=29.302, P<0.001) and consumer species ($F_{1,32}$=4.892, P=0.034) (Fig. 4.4 b). Conversely, the mean CV of population biovolume increased with diversity ($F_{1,32}$=100.277, P<0.001), and was affected by community composition ($F_{6,32}$=12.728, P<0.001) and consumer species ($F_{1,32}$=6.430, P,0.016) (Fig. 4.4 c). The average population biovolume also increased with diversity (log transformed, $F_{1,32}$=4.569, P<0.001), and was affected by composition ($F_{6,32}$=29.4729, P<0.001) and consumer species ($F_{1,32}$=4.807, P=0.036) (Fig. 4.4 d).

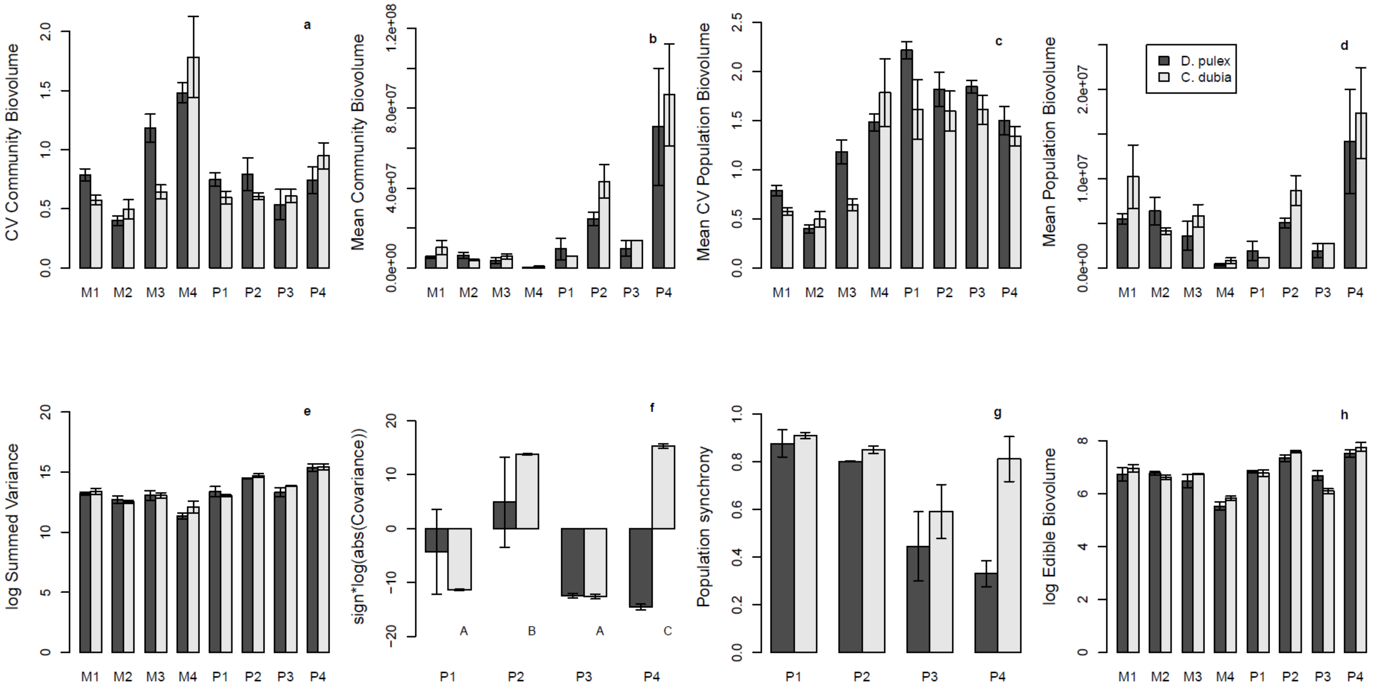

Figure 4.4. a. The coefficient of variation of total phytoplankton community biovolume over time. **b.** The mean phytoplankton community biovolume over time. **c.** The phytoplankton population coefficient of variation over time, averaged across populations within a microcosm. **d.** The mean phytoplankton population biovolume over time. **e.** The log of the sum of population variances within a microcosm. **f.** The log of the absolute value of the mean covariance among pairs of phytoplankton species within a microcosm over time, multiplied by the sign of the covariance. **g.** The synchrony (sensu Loreau and de Mazancourt 2008) among pairs of populations of phytoplankton within a microcosm over time. Letters indicate significantly different compositions for *C. dubia*. **h.** The log of the mean edible biovolume (<40 μm in longest axis length) within a microcosm. All functions were taken over a 12 week time period. Bars represent the mean across replicates (n=3) and the error bars display ± 1 S.E.. Dark bars represent values for *Daphnia pulex*, and light bars represent values for *Ceriodaphnia dubia*.

The mean variance scaling exponent, z, equalled 1.726 ($F_{1,134}$=4078.7, P<0.001, R^2=0.968), suggesting that statistical averaging should stabilize community biomass if community biomass does not increase with species diversity and is evenly distributed among species (Lehman & Tilman 2000). However, we found that both the community and average population biovolume increased with diversity (Figs 4.4 b & d), and that biomass was unevenly distributed among resource species (Fig. 4.6 c), reducing the influence of this stabilizing mechanism. Furthermore, the summed community variance increased with diversity (log-transformed, $F_{1,32}$=119.710, P<0.001), indicating that statistical averaging was not stabilizing (Fig. 4.4 e). The summed community variance was also affected by community composition ($F_{6,32}$=18.943, P<0.001).

The covariance of phytoplankton population biovolume in polyculture depended on the interaction between the consumer species and resource composition (sign*log(absolute value (covariance)), $F_{3,16}$=7.795, P=0.002). For the generalist, there was no significant effect of composition ($F_{3,8}$=2.368, P=0.147), but for the specialist there was ($F_{3,8}$=2279.762, P<0.001) (Fig. 4.4 f). There was also a significant interaction effect of consumer and composition on synchrony ($F_{3,16}$=3.512, P=0.040, Fig. 4.4 g). Composition had a significant effect on synchrony for the generalist ($F_{3,8}$=10.387, P=0.004) and a marginally non-significant effect for the specialist ($F_{3,8}$=3.502, P=0.069) (Fig. 4.4 g). The synchrony and covariance data are generally in agreement, showing that polyculture 2 had positive temporal coherence among species, polyculture 3 showed compensation among species, and that polyculture 4 showed compensation for *D. pulex,* but synchrony for *C. dubia* treatments (Figs 4.4 f & g). The main discrepancy was for polyculture 1, which showed a negative summed covariance for *C. dubia* (no significant covariance for *D. pulex*), but high synchrony. This is because monoculture 1 was heavily dominated by a single species, *S. acutus* (Appendix 4.2 a) for most of the time series causing high synchrony, but there was one peak in density of *P. subcapitata* in each time series, at which *S. acutus* declined causing negative covariance.

In a multiple regression, the CV of community biovolume for polycultures (log-transformed) was strongly affected by average community biovolume (partial regression coefficient = -0.939, $P<0.001$, $R^2=0.376$) and the summed variance (coefficient=0.476, $P<0.001$, $R^2=0.403$). The transformed covariance did not have a significant effect (coefficient=0.001, $P=0.164$, $R^2=0.005$), whereas synchrony had a positive effect (coefficient=0.243, $P<0.001$, $R^2=0.113$). Dominance had a negative effect, but it did not explain much variation in the coefficient of variation of community biovolume (coefficient=-0.341, $P<0.001$, $R^2=0.058$).

4.3.3 Price Equation partition of biodiversity effects on the mean and variance of community biovolume

We used the Price equation to partition the total effects of diversity on average community biovolume and variability. Species richness effects (SREs) are the expected (average) reductions in biovolume or variance resulting from the ‘loss’ of four species (comparing monoculture to polyculture). SREs do not depend on the monoculture of contrast and are always negative (Fox 2006, Fox 2010). The largest SREs occurred for P2 (Figs 4.5 b & f), reflecting the larger and more variable populations that occurred in this composition relative to the other two polycultures. Species composition effects (SCEs) reflect impacts of the losses of particular species with respect to the random expectation. If a monoculture species is productive or variable in polyculture relative to the other species in the mixture, then SCEs are positive and vice versa. Generally, the SCEs were negative, indicating that the monoculture species tended to have relatively low biovolume and variability in polyculture. The positive SCEs of M1 compared to P1 for both consumers, and M2 compared to P3 for *D. pulex* (Figs 4.5 c & g) indicate that these monoculture species were dominant and variable in polyculture. Context dependence effects (CDEs) reflect a difference in the biovolume or variance of a particular species between monoculture and polyculture. In all except one case, monoculture species were more productive in monoculture than in polyculture, likely reflecting negative interactions among phytoplankton species in polyculture, and compensation for species 'loss' in monoculture (Fig. 4.5 d, Fox 2006). However, M1 was less productive in monoculture than in P1 in the presence of *D. pulex*, reflecting positive effects of other phytoplankton species on this species (Fig. 4.5 d). In most cases, monoculture species were also more variable in monoculture than in polyculture (Fig. 4.5 h). There were two exceptions: M1 was less variable in monoculture than in P1 in the presence of *D. pulex* and M2 was less variable in monoculture than in P3. Overall, polycultures were more productive and variable than the monocultures, reflected by ΔT (Figs 4.5 a & e). There was one exception: M1 compared to P1 for *C. dubia*, in which case the monoculture biovolume and variance was greater than in the polyculture. In this case, SCA was dominant in polyculture (positive SCE), but was more productive in monoculture (positive CDE). The correlation between effects on the mean and variability of biovolume in Figure 4.5 likely reflect the influence of mean-variance scaling (Fox et al. 2010).

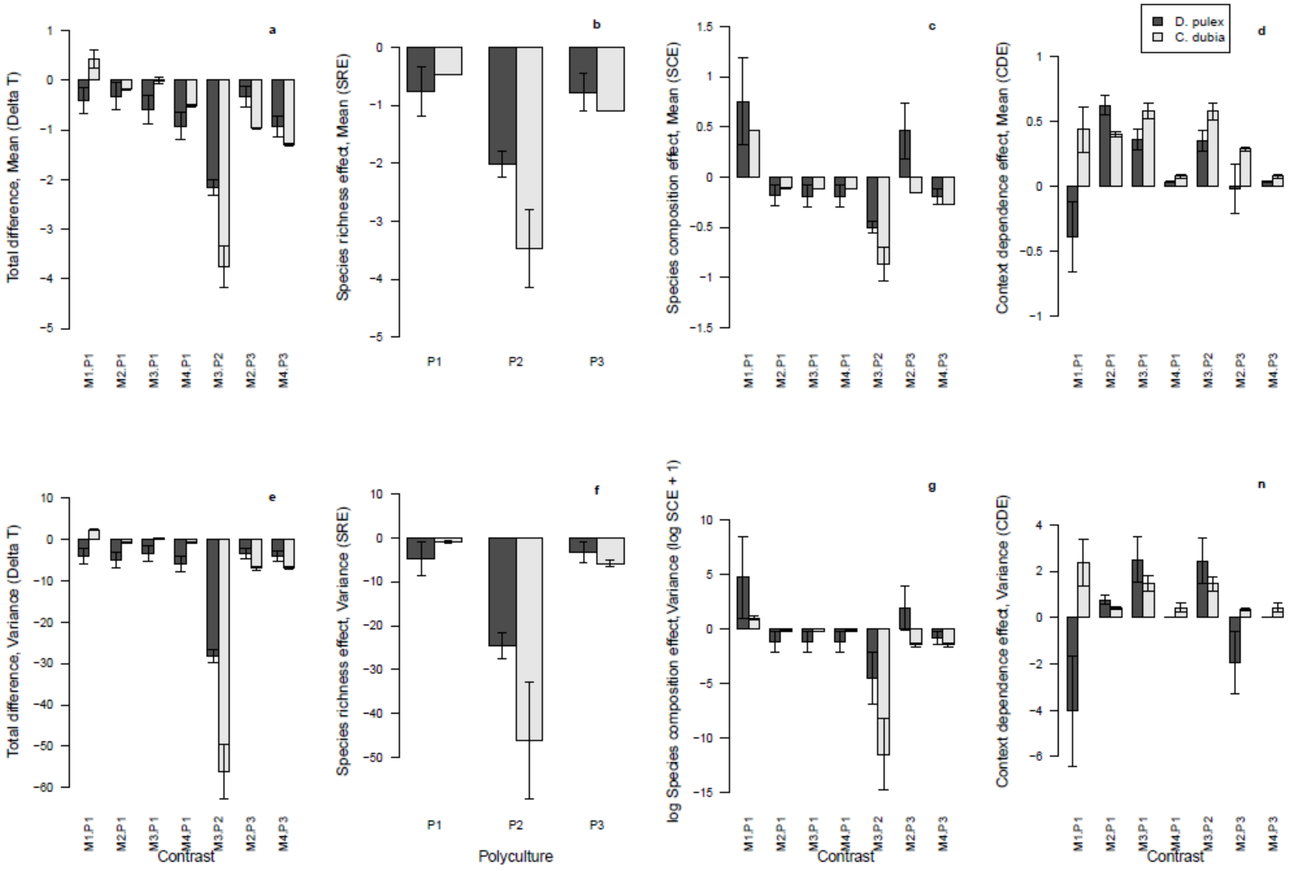

Figure 4.5. Price equation partition of the difference in the whole community biovolume (**a-d**) and the variance in whole community biovolume (**e-h**) between ‘post-loss’ (polyculture) and ‘pre-loss’ (monoculture) microcosms. ΔT represents the total difference in mean (**a-d**) or variance (**e-h**) in biovolume between pre-loss and post-loss microcosms, with negative values indicating greater values in polyculture than monoculture. SREs represent the average effect of species loss on the mean or variability of community biovolume. SCEs represent the effects of changes in species composition. CDEs represent changes in mean or variance of biovolume of individual monoculture species when in polyculture.

4.3.4 Phytoplankton community dominance & diversity: The role of species' traits

Most polyculture microcosms lost phytoplankton species over time, but they all maintained two or more species for the duration of the experiment and had an average of more than three species (Figs 4.6 a & b, Appendix 4.2). There were no contaminations, so all monocultures contained only one species throughout the experiment. The polycultures differed significantly in terms of dominance (D^2 (transformed by squaring), composition $F_{3,16}$=20.698 , $P<0.001$, Fig. 4.6 c), and diversity (log-transformed H′, composition $F_{3,16}$=40.697, $P<0.001$, Fig. 4.6 d). Dominance was greatest for P1 and declined monotonically from P1 to P4 (Fig. 4.6 c), and vice versa for diversity, H′ (Fig. 4.6 d) for both consumers. Polyculture 1 was heavily dominate by *S. acutus* for the majority of the time series under both consumers (Fig 4.5 c, Appendix 4.2 a). Polyculture 2 had greater diversity over time and showed some compensation between *S. pingue* and *A. falcatus* when *D. pulex* was the consumer (Fig 4.5 c, Appendix 4.2 b). Polyculture 3 showed a transition from dominance by *A. formosa* to dominance by *P. subcapitata* at about week 2 under *D. pulex* in two microcosms, but compensatory dynamics between *P. subcapitata* and *P. simplex* in another. For *C. dubia*, there was an early transition to dominance by *P. simplex* in all microcosms, with ~10% of biomass made up by *P. subcapitata* over the longer-term (Appendix 4.2 c). Polyculture 4 showed the highest diversity for both consumer treatments and compensatory dynamics between *P. simplex* and *A. falcatus* in two *D. pulex* microcosms (Appendix 4.2 d). However, there appeared to be no discernible pattern in fluctuations among species in microcosms with *C. dubia* (Appendix 4.2 d).

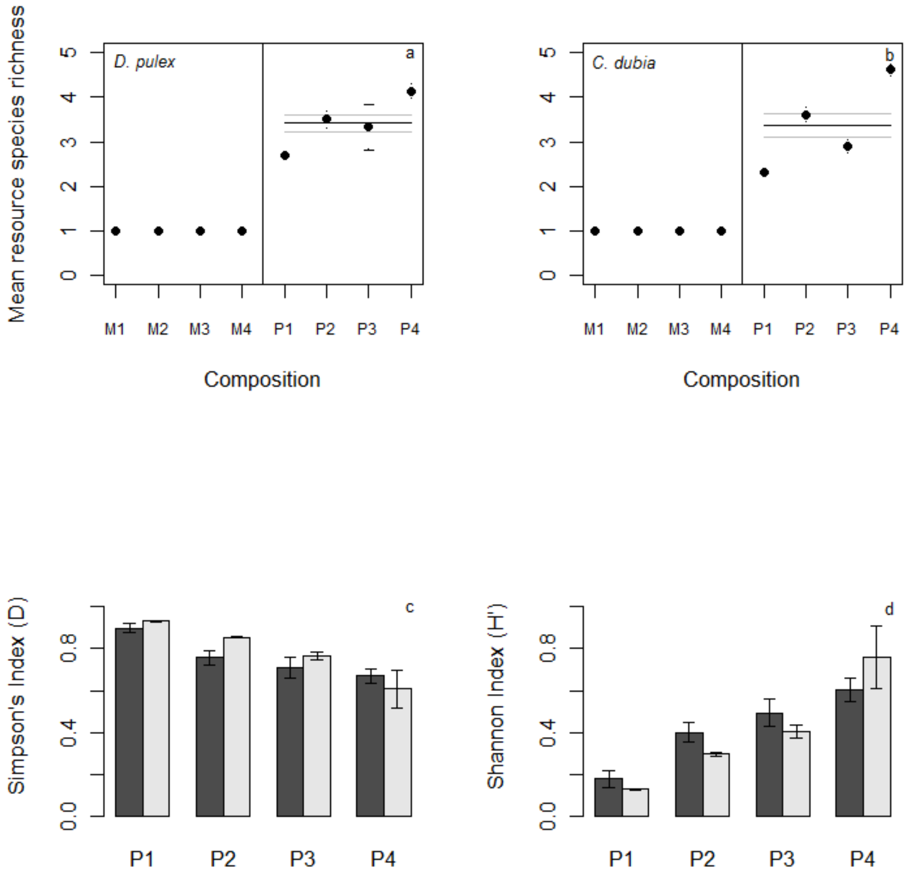

Figure 4.6. a. Mean species richness for microcosms containing *Daphnia pulex*, **b.** Mean species richness for microcosms containing *Ceriodaphnia dubia*, **c.** Mean Simpson's Dominance Index, D, for all four polyculture compositions, **d.** Mean Shannon Diversity index H′, for all four polyculture compositions. Bars represent ± 1 S.E. Black bars represent microcosms with *Daphnia pulex* and grey bars represent microcosms with *Ceriodaphnia dubia* as the consumers.

We entered the CV of growth rate (gr), carrying capacity biovolume (mb) and size into multiple linear regressions for dominance (D) and diversity (H′). The CVgr and CVsize both had positive effects on dominance (D) (partial regression coefficient=0.379 & 0.395 and adj. R^2= 0.109 & 0.114, respectively and P<0.001), while CVmb had a negative effect (partial regression coefficient=-0.223 and adj. R^2= 0.234, P<0.001). The variables had the opposite effect on diversity (H′), where CVgr and CVsize had negative effects (partial regression coefficient=-0.659 & -0.811 and adj. R^2= 0.143 & 0.208, respectively, $P<0.001$) and CVmb had a positive effect on H′ (coefficient=0.446, and adj. R^2= 0.402, $P<0.001$). Across polycultures, species' relative biovolumes tended to increase with growth rate, decrease with size, and did not appear to vary consistently with monoculture biomass (Appendix 4.4).

4.4 Discussion

We found that the bottom-up effects of resource species diversity on community biomass, ecosystem functioning and stability were generally positive. Resource diversity enhanced mean resource community biovolume, chlorophyll-a, carbon, nitrogen and $\delta\ ^{13}C$, regardless of consumer feeding selectivity (see also Steiner 2001). Diversity also stabilized these functions over time, in support of previous findings from single trophic-level experiments in grasslands (Tilman et al. 2006, Hector et al. 2010) and in aquatic food webs (Steiner et al. 2005, Vogt et al. 2006). By contrast, resource diversity did not significantly stabilize consumer density for either the generalist or specialist consumer. This suggests that while species diversity at the bottom of a food web may have significant impacts on community properties and ecosystem functioning, these impacts do not necessarily affect the dynamics of consumers in a linear fashion (see also Steiner 2001, Fox 2003).

Resource species diversity is predicted to stabilize consumer populations either by increasing the availability of resources (overyielding, Lehman and Tilman 2000, Petchey 2000), ensuring long-term availability of edible species (insurance effects, Yachi and Loreau 1999, Petchey 2000), reducing the strength of trophic interactions (McCann 2000, Kratina et al. 2007, Narwani and Mazumder 2010), or reducing the carrying capacity of edible resources (Kretzschmar et al. 1993, McCauley et al. 1999). Nevertheless, there are also a number of ways in which resource diversity may destabilize consumers. Increased total resource abundance may lead to a paradox of enrichment (Rosenzweig 1971). The stability of particular resource species may decline due to reduced abundance or increased variability resulting from stronger or more numerous competitive interactions (Lehman and Tilman 2000, Haddad et al. 2011). Finally, trophic interaction strengths may actually increase with resource species diversity depending on community composition (Narwani and Mazumder 2010), and this could destabilize consumer-resource dynamics (McCann 2000, Rip et al. 2010a).

Contrary to our expectations and despite a stabilizing effect of diversity on algal community abundance, neither of the consumer population densities was stabilized by diversity. This may reflect compensatory dynamics among edible and inedible phytoplankton species. Compensation can stabilize total algal biomass while consumer density continues to cycle out of phase with edible algal biovolume, similar to ‘cryptic’ population cycles in the context of rapid evolution (Yoshida et al. 2007, Jones et al. 2009). For *D. pulex*, such compensation appeared to occur in compositions 2 and 4, in which consumer density oscillated out of phase with the proportion of edible algal biovolume (Appendices 4.3 a & c). *C. dubia* however, did not display similar coupled oscillations in mixture. However, in polyculture 3 both *D. pulex* and *C. dubia* densities were dramatically reduced over time, concurrent with an increase in dominance by a particular phytoplankton species, suggesting poor edibility or quality of this dominant phytoplankton species. In the *C. dubia* treatment, this species was *P. simplex*, which is inedible due to its large size. In the *D. pulex* treatments, this dominant was *P. subcapitata*, which is in the edible size fraction. Nelson et al. (2001) show that low consumer and high algal biomass can result from low food quality, however, *P. subcaptiata* did not appear to have particularly low food quality based on bulk particulate C:N and C:P ratios (Appendix 4.5, assuming nutrient dynamics are determined primarily by phytoplankton), and so we are currently unaware of why *D. pulex* could not control this species. Nevertheless, in both cases, a phytoplankton species escaped grazer control, and either reduced the carrying capacity of other edible species (Kretzschmar et al. 1993, Murdoch et al. 1998), or competitively eliminated them altogether. As a result, consumer abundance was reduced while total algal abundance was relatively high.

D. pulex density increased with resource diversity but its stability did not increase significantly, indicating that variability in its density also increased with diversity. *D. pulex* is a generalist and can consume the majority of the species in our species pool. As expected, its density was positively related to total resource biomass, which increased with resource diversity. *D. pulex* may also have benefitted from complementarity among resources species, for example via a nutritional effect (DeMott 1998, DeMott et al. 1998, Petchey 2000, Duffy et al. 2007). However, increased resource availability may have been destabilizing via the paradox of enrichment (Rosenzweig 1971). Also, some resource communities were dominated by individual species, and on average, resource population variability increased with diversity, suggesting that increased variability in *D. pulex* may have resulted from interactions with individual resource species (Luckinbill 1979). Supporting this idea, Fox's (2010) Price equation partition on population variances showed that the dominant species in polycultures 1 and 3 (*S. acutus* and *P. subcapitata*, respectively), were more variable in polyculture than they were in monoculture (Fig. 4.5 h). Finally, earlier work has shown that in communities with multiple palatable resource species, *D. pulex* may have an elevated rate of consumption (Narwani and Mazumder 2010). This may have strengthened consumer-resource interactions, destabilizing temporal dynamics (McCann 2000, Rip et al. 2010a).

By contrast, neither *C. dubia* mean density nor variability were significantly affected by resource species diversity (see also Steiner 2001). The specialist's density was positively related to the average fraction of edible biovolume among polycultures. This dependence on the edible fraction could have been responsible for decoupling trends in zooplankton and total phytoplankton dynamics. For example, in polyculture 3, the community was dominated by inedible species, so community algal abundance was moderately high, while zooplankton abundance was low. Nevertheless, edible phytoplankton species dominated the biomass of the other polycultures (Appendices 4.3 a & c), the biovolume of edible species increased with diversity, and while total algal abundance tended to be high in these polycultures, *C. dubia* abundance was relatively low in polycultures 2 and 4. It is possible that the dominant species, *A. falcatus*, was unpalatable or was a low quality food item for *C. dubia*, limiting the positive effect of its high biovolume on the consumer's abundance and stability (Nelson et al. 2001). The C:N and C:P molar ratios of particulate matter indicate that only polyculture 4 may have been exceptionally phosphorus limited (Appendices 4.4 b & d). Data from the grazing experiment (Chapter 3, Table 3.2), however suggest that *A. falcatus* is palatable for Ceriodaphnia. Another possibility is that the low density of inedible species in these compositions lowered the specialists' density due to interference with grazing of edible species (Kretzschmar et al. 1993). Indeed, previous work has shown that increasing the number of inedible resources can reduce the rate of consumption in a Ceriodaphnia species (Narwani and Mazumder 2010). Overall, the results suggest that there was a decoupling of total algal biomass dynamics and *C. dubia* density due to the presence of inedible species in three out of four polycultures.

Our results contrast with those of one other study that has investigated bottom-up effects of diversity on consumer population stability for consumers with varying feeding selectivities (Haddad et al. 2011). In a grassland biodiversity experiment, Haddad et al. (2011) found that there was often no significant effect of resource diversity on generalist herbivores, but that specialists were generally destabilized by diversity. They concluded that this was likely due to increased variances in populations of palatable resources required by specialist consumers. Previous aquatic microcosm studies have provided mixed results. Some have shown no significant effect of resource diversity on consumer abundance (Fox 2004), or declines in abundance (Steiner 2001, Fox 2004, Gonzalez and Descamps-Julien 2004), and stability has either not been affected by diversity (Gonzalez and Descamps-Julien 2004), or has been positively affected (Hairston et al. 1968, Petchey 2000). Clearly, greater attention to the mechanisms by which resource diversity may impact consumer dynamics is warranted.

The community properties and ecosystem functions that we measured in this experiment were closely tied to phytoplankton community biomass (chlorophyll-a). Resource community biomass was most strongly stabilized by an increase in the average resource community biomass with an increase in diversity (see also Tilman et al. 2006, Jiang et al. 2009, Hector et al. 2010). While the mean-variance scaling relationship suggested that diversity should have reduced summed variances (z>1), summed variances increased with diversity. Uneven species distributions and higher average population biovolumes may have prevented a stabilizing effect in polycultures (Doak et al. 1998, Tilman et al. 1998). Dominance decreases the impact of statistical averaging (Doak et al. 1998) and static dominance by one species reduces the importance of an insurance effect on stability (Yachi and Loreau 1999, Gonzalez and Descamps-Julien 2004). However, if the dominant species tends to have high biomass and stability, it may increase the biomass and stability of the phytoplankton community, and the community as a whole (Petchey 2000, Gamfeldt et al. 2005, Steiner et al. 2005). In this experiment, dominance was likely positively related to stability through the influence of dominant, stable, fast-growing species, such as *S. acutus* and *P. subcapitata* (Figs 4.6 d, h). Finally, the stabilizing effect of compensatory dynamics among species depended on the community composition. Asynchrony was stabilizing in polyculture 3 for both consumers, and in polycultures 2 and 4 for *D. pulex* (Gonzalez and Descamps-Julien 2004, Isbell et al. 2009a, Hector et al. 2010), reflecting compensatory dynamics between edible and inedible species (Appendix 4.3 b & c)(Gonzalez and Loreau 2009). Conversely, synchrony among species was destabilizing in polycultures 2 and 4 for *C. dubia* (Zhang and Zhang 2006, Romanuk et al. 2010, Tirok and Gaedke 2010). We did not find any evidence to support the hypothesis that generalists are more likely to cause synchrony in resource dynamics than specialists (Tirok and Gaedke 2010).

Community composition of phytoplankton influenced all of the population, community and ecosystem functions that we measured, confirming the importance of particular species' interactions and individual species' traits (Walker et al. 1999, Downing and Leibold 2002, Downing 2005). As opposed to previous studies which have generally chosen compositions randomly (Downing and Leibold 2002, Downing 2005, Steiner et al. 2005, Hector et al. 2010), we chose community compositions to reflect a range in palatability for the consumers. Theory predicts that trade-offs among species in competitive abilities will determine their ability to show niche partitioning and insurance effects (Yachi and Loreau 1999), and that in the presence of consumers, the trade-off between competitive ability and resistance to grazing may be particularly important in determining the magnitude and stability of both primary and secondary production (Leibold 1989, Thébault and Loreau 2005). Conversely, 'prey reliability' mechanisms would only be expressed when resource species are edible (MacArthur 1955, Petchey 2000).

The effects of individual compositions on consumers and community and ecosystem properties reflect the balance between the impact of resource species interactions on coexistence and individual species' effect traits (Hillebrand and Matthiessen 2009). For example, polyculture 1 was dominated by *S. acutus* for both consumers, and the high density and low variability of both consumers in this composition were likely due to dominant effect of this species via a selection effect (Fig. 4.5 c, Steiner et al. 2005, Weis et al. 2008). Nevertheless, both the abundance of *D. pulex* and the biovolume of *S. acutus* were greater in polyculture 1 than in the *S. acutus* monoculture, signalling a positive effect of complementarity among phytoplankton species (Gamfeldt et al. 2005). *D. pulex* attained its lowest density in monoculture on *P. subcapitata* and had a similarly low density in polyculture 3, which was generally dominated by this species, suggesting that this species' traits dominated this composition's effects (e.g. poor quality, unpalatability, toxicity or environmental effects - on pH for example). For both consumers, polyculture 4 had the greatest level of coexistence among resource species. In this community, ecosystem functions may have benefited from niche partitioning and insurance effects resulting from competition-resistance trade-offs.

The Price Equation partition separated the total difference in the average and variability of functioning between monocultures and polycultures into portions expected on average due to random loss of species (Species Richness Effects, SREs), the loss of particular species (Species Composition Effects, SCEs), or changes in monoculture species' contributions (Context Dependence Effects, CDEs). Monocultures were less productive and less variable than polycultures in all except one contrast. This general reduction in biomass and variability in monocultures was due both to random loss of species, and the loss of dominant species in polyculture (negative SCEs) (Mulder et al. 1999). However, monoculture species tended to be more productive and variable in the absence of competitors (see also Jiang et al. 2009). This trend supports findings by Fox (2006), suggesting that when dominant species are lost from polycultures, sub-dominant species can compensate by showing positive context dependence effects (i.e. SCEs and CDEs are negatively correlated). Conversely, *S. acutus* both dominated polyculture 1 in the presence of *D. pulex* and had lower biomass in monoculture than polyculture. This suggests that intraspecific competition was stronger than interspecific competition for this species, or that there was an effect of facilitation by other species in mixture (Mulder et al. 2001, Cardinale et al. 2002, Cardinale et al. 2007, Romanuk et al. 2010). Both *S. acutus* and *P. subcapitata* were dominant in particular mixtures in the presence of *D. pulex* and showed greater variances in polyculture than monoculture. The larger variance may have resulted from larger average biomass for *S. acutus* in polyculture 1, but for *P. subcapitata* in polyculture 3, it likely also resulted from negative covariances or asynchrony. So while the properties of dominant species may have dominant impacts on community properties, their properties depend on the composition of the community in which they are found (Mulder et al. 1999).

Variability among species in the three traits that we measured had significant impacts on measures of community dominance and diversity. Variability in size and growth rate had positive effects on dominance and negative effects on diversity, suggesting that there was unidirectional selection for these traits in this environment (Gause 1934, Tilman 1982, Walker et al. 1999, Isbell et al. 2009b). Haddad et al. (2008) found that intrinsic growth rate was the best predictor of species' responses to disturbance and productivity, suggesting that that weekly sampling and nutrient replacement may have been strong selective forces in our experiment. We expected that variability in size would reflect the degree of niche partitioning in the presence of the consumer and would promote diversity (Litchman and Klausmeier 2008, Litchman et al. 2010). Contrary to expectation, variability in size positively affected dominance, with the size of the dominant varying among compositions and consumer treatments. For example, *P. subcapitata* (the smallest species in the composition) generally dominated polyculture 3 in the presence of *D. pulex*, but *P. simplex* (the largest species) dominated this community for *C. dubia*, suggesting that size determined fitness, depending on the identity of the consumer (Mulder et al. 1999). In this case, a lack of variability may confer equalizing stability in plankton communities (Chesson 2000b, Isbell et al. 2009b, Zhang et al. 2009). However, average dominance may also be high if species oscillate in abundance, with selection shifting rapidly between extremes of a trait distribution. Rapid oscillations in consumer abundance could cause selection to shift rapidly back and forth between grazing resistance and competitive ability. Variability in monoculture biomass among species was negatively related to community dominance and positively related to diversity, suggesting that this trait either promoted negative selection effects or niche partitioning (Isbell et al. 2009a, b). In support of a negative selection effect, *S. capricornutum* had relatively low monoculture biomass compared to the other species in mixture and yet dominated polyculture 3 under *D. pulex* (Mulder et al. 2001, Isbell et al. 2009a). However, variability in monoculture biomass may also have promoted niche partitioning under fluctuating nutrient conditions via a gleaner-opportunist trade-off if opportunists have higher monoculture biomass than gleaners under nutrient-replete conditions (Leibold 1989, Litchman and Klausmeier 2001). Certainly, greater investigation of the mechanisms by which various species' traits influence diversity under particular environmental conditions is needed.

Dominance did not have a large effect or explain much of the variability in the stability of phytoplankton community biomass. This may be because selection and complementarity have opposing influences on dominance and diversity, while both can lead to increased stability. Furthermore, not all mechanisms of coexistence via niche complementarity are equally likely to promote overyielding and hence stability (Mouquet et al. 2002, Fox 2003), and in particular, consumer-mediated mechanisms of coexistence are predicted to be less likely to produce overyielding (Fox 2003, but see Jiang et al. 2009). Unfortunately, we were unable to directly partition biodiversity effects into selection and complementarity effects (Loreau and Hector 2001) and so cannot conclusively determine whether these three traits had direct impacts on diversity via equalizing effects or indirect effects via selection or complementarity (Isbell et al. 2009b).

While selection and complementarity on the resource trophic level may affect food web properties, methods to distinguish these two mechanisms developed for single-trophic level communities cannot be directly applied in multi-trophic systems (suggested in Petchey 2000, Downing and Leibold 2010). Selection and complementarity on a single trophic level can be separated because the contribution of each species to the total can be directly observed and compared to that in monoculture (Loreau and Hector 2001, Fox 2006). In multi-trophic systems, the contribution of a species to any given function cannot be directly observed without tracing species-specific ‘losses’ to consumers. As such, it is impossible to determine whether selection, complementarity or a nutritional effect were responsible for a biodiversity effect. This is because individual resource species’ contributions to consumer biomass may change depending on community context ('context dependence effects', Fox 2006), and individual species’ traits (e.g. 'trait-dependent complmentarity', Fox 2005). New methods capable of mass-balance accounting of biomass flows among species must be developed to distinguish selection and complementarity in multi-trophic ecosystems. This may be simpler in terrestrial ecosystems where turnover times are longer and evidence of consumption is left behind in the plant tissues. In other systems, this may include the use of species-specific biochemical labels (e.g. isotopes, fluorescently-labelled antibodies, or qPCR).

In summary, resource species diversity had positive effects on the abundance and stability of resource community biomass and a number of ecosystem functions in these multi-trophic ecosystems. While diversity is clearly important for the functioning and stability of food webs, we did not detect straight-forward bottom-up impacts on consumer stability, suggesting that resource diversity may have both stabilizing and destabilizing impacts on some consumers. Finally, community composition generally had a greater impact on food web properties than resource diversity, indicating that biodiversity-ecosystem functioning and stability research would benefit from greater focus on species' interactions and functional effect traits.

Chapter 5: Summarizing discussion, unresolved questions and future directions

The main objective of this thesis was to investigate the influence of resource species diversity on trophic interactions and population, community and ecosystem properties in food webs. I also investigated the mechanisms responsible for maintaining resource species diversity over time. In the following section I summarize the fundamental findings of each chapter and point to the most compelling unresolved issues for future research. One theme in particular emerged from all of the chapters, namely the importance of community composition. Much of biodiversity-ecosystem functioning (BEF) research has actively sought to investigate the impacts of species diversity, separate from the impacts of individual species or species combinations. This thesis has shown community composition to be important across the board. It was a significant factor determining the species diversity of resource communities over the long-term, as well as the impacts of species diversity on population, community and ecosystem properties. This suggests that species' traits and interactions are directly linked to the mechanisms maintaining diversity and the effects of diversity on population, community and ecosystem properties. In this section, I highlight the potential for complex adaptive systems theory and trait-based ecology to close this gap and move BEF research from the realm of phenomenological description to mechanistic prediction.

5.1 Summary and unresolved questions

In Chapter 2, I found that phytoplankton species diversity was better maintained by endogenously generated ecological mechanisms than by exogenously generated variability in resource availability caused by periodic disturbance. The community composition of the communities interacted with the disturbance regime to determine species diversity in the long-term. This confirmed that species traits are important in determining the outcome of competitive interactions.

The actual mechanism(s) responsible for maintaining diversity in this chapter were unresolved. We discussed some of the possible mechanisms of endogenously generated non-equilibrium coexistence, including variability in the identity of limiting resources over time, intransitive competition, and non-linear competition or storage dynamics. Huisman & Weissing (2001) present a theoretical examination of the potential for endogenously generated nonequilibrium dynamics and supersaturation (coexistence of >n species on n resources) in phytoplankton communities, given scenarios of different trade-offs between competitive abilities and resource requirements. The most physiologically likely trade-off scenario, in which species showed trade-offs in their ability to consume multiple nutrients, and in which resource requirements declined with competitive ability for a given resource, showed supersaturated coexistence ~9% of the time. Interestingly, species did not always oscillate, suggesting neutral coexistence. Intransitive competition generated supersaturated coexistence most frequently. Such competition occurred when species displayed cyclic competitive abilities for different resources. This means that they were strong competitors for resources for which they had moderate requirements, but were moderate competitors for resources for which they had strong requirements. Determining how frequently such trade-offs occur and testing predictions of coexistence based on trade-offs would be a fruitful next step. Finally, while a few experiments have demonstrated that storage effects can promote coexistence when there is externally generated variability in limiting factors (Caceres 1997, Kelly and Bowler 2002, Descamps-Julien and Gonzalez 2005), similar tests should be conducted to extend this to endogenously generated variability. Similarly, the ability of competitive relative non-linearity to generate temporal variability in resource availability within purely competitive communities, and hence promote coexistence, has yet to be tested. Methods for quantifying the stabilizing effects of competitive relative non-linearity and storage effects are outlined in Chesson (2003).

Evolutionary experiments on adaptive radiation suggest that there are at least two other possible mechanisms of endogenous coexistence. First, it is possible that species experienced facilitative interactions. For example species may form biochemical processing chains, or cross-feeding networks, in which some species are able to consume, or otherwise benefit from the waste or bi-products of other species (Heard 1994, Rosenzweig et al. 1994). Rosenzweig et al. (1994) found that genetic diversity evolved in a homogeneous environment with a single limiting resource from an isogenic strain of *E. Coli*. Novel genotypes evolved to consume products of incomplete glucose metabolism including acetate and glycerol. I am unaware of any such cross-feeding interactions among the phytoplankton used in this thesis. However, it is possible that useful cellular bi-products such as ammonium were removed or diluted during disturbances. Experiments measuring species' per capita population growth rates under intra- versus interspecific competition could be conducted to test for the potential effects of facilitation, whereby interspecific competition is weaker than intraspecific competition. Second, heterogeneous environments created by the phytoplankton in the absence of microcosm mixing may have enabled coexistence among species. Repeatable adaptive radiations of three unique morphs of *Pseudomonas fluorescens* have been shown to occur in unmixed microcosms containing a single isogenic strain (Rainey and Travisano 1998). These radiations were prevented when microcosms were mixed. Among the evolved strains, one morph specialized on the medium-surface interface, one on the media column, and another on the microcosm floor. Any purely physical spatial heterogeneity within our microcosms would have been identical among disturbance treatments. However, disturbance treatments reduced phytoplankton cell densities, along with potentially correlated spatial heterogeneity in limiting factors such as light, oxygen, or carbon dioxide. Testing for the endogenous generation of spatial heterogeneity within the microcosms in the future would simply require homogenization by constant shaking.

In Chapter 3, I showed that the effects of resource species diversity on rates of consumption depended on the resource community composition and the feeding selectivity of the consumer. The mechanism by which resource diversity modified rates of consumption also depended on community composition and consumer feeding selectivity. While diversity tended to cause reductions in rates of resource consumption, particularly for specialist consumers, it was also able to cause increased rates of consumption for the generalist species when all of the resource species were palatable. These findings are of general significance for community ecology because they may have implications for the effects of resource diversity on the trophic structure of food webs, trophic cascade strength, consumer-resource dynamics, and food web stability (Leibold 1989, McCann et al. 1998, McCann 2000, Thébault and Loreau 2003, Thébault and Loreau 2005, Shurin et al. 2006, Rip et al. 2010b). I explored some of these questions further in Chapter 4.

Some questions regarding how resource diversity modifies consumption rates remain unresolved. In the grazing experiments in Chapter 3 all high diversity compositions had four species. As a result, we were unable to discern the form of the relationship between the number of resource species and consumption. For example, changes in consumption with diversity may be linear, sigmoidal or saturating. Meta-analyses on consumer effect sizes provide support for a negative saturating function in most cases, with effect sizes of consumers declining towards zero as resource diversity increases (Hillebrand and Cardinale 2004, Jactel and Brockerhoff 2007, Edwards et al. 2010). These studies, however, did not manipulate resource diversity, and generally did not investigate the influence of palatable resource diversity per se. Elucidating the shape of this relationship is a crucial next step. An interesting follow up would be to add species sequentially and in all possible combinations to determine whether the addition of individual palatable, or unpalatable, species have similar and additive impacts, or whether species' impacts are synergistic and context-dependent. Also, species were added at equal densities, except for the focal species, *C. reinhardti*. The density and evenness of individual resource species may impact consumer effect sizes (Hillebrand and Cardinale 2004, Kratina et al. 2007) and other ecosystem functions (Hillebrand et al. 2008). Kratina et al. (2007) showed that both the density and diversity of non-prey species can have unique impacts on the rate of consumption of a hypotrich ciliate predator, *Euplotes aediculatus*. Further investigation is warranted to determine how species' density and diversity interact to modify consumption for all of the mechanisms that I outline in Chapter 3. For example, do species' preferences change given changes in resource availability? Does complementarity rely on the dominant influence of one particular species or on the interactions among evenly distributed species?

In Chapter 4, I showed that resource species diversity caused an increase in a number of population, community and ecosystem properties including generalist consumer biomass, producer biomass, the rate of photosynthesis, and the stocks of particulate carbon, nitrogen and phosphorus. Diversity also stabilized producer biomass and the stocks of particulate nutrients. Contrary to expectations however, consumer biomass was not stabilized for either the generalist or specialist consumer. For the generalist, this was due to a balance between stabilizing forces that increased the mean density of the consumer, and destabilizing forces which increased variability. For example, total resource abundance increased with diversity, likely resulting in a stabilizing increase in the generalists' density. However, an increase in rates of consumption with palatable resource diversity (Chapter 3) may have been destabilizing by increasing the strength of the consumer-resource interaction. For the specialist, diversity had no detectable effect on mean density or stability. This suggests that specialist species may not be strongly affected by community properties, but by the abundance of their focal resources.

Among the most intriguing insights from Chapter 4 is that resource diversity can have impacts on ecosystem properties without influencing the dynamics of consumer populations. If consumer and resource dynamics can be decoupled, this raises the question of whether consumers have any impact on the relationship between resource diversity and ecosystem function. Mulder et al. (1999) presented three hypotheses regarding the influence that consumers may have on ecosystem function (Fig. 5.1). First, consumers may modify the effect of resource species diversity on ecosystem function in a linear fashion by simply by reducing resource biomass (Figs. 5.1 a & b). Second, they may alter the mechanisms of coexistence and the relative abundance of resource species, and thereby alter ecosystem function (Fig. 5.1 c). Third, they may impact ecosystem functioning directly (Fig. 5.1 c). In addition to these mechanisms, I have shown that resource diversity can modify rates of consumption depending on community composition and consumer identity (Figs. 5.1 d & e). Variability in trophic interaction strengths among resource species may alter the abundance of individual species, the outcome of competition, the evenness of resource species biomass, and the presence of compensatory or synchronous dynamics over time in the presence of consumers (Fig. 5.1 d & e). These community properties may in turn affect ecosystem functions and stability. Indeed, Jiang et al. (2009) found that resource diversity had no effect on resource community biomass stability and destabilized population stability in the absence of consumers, but that weak trophic interactions in the presence of consumers caused an increase in both population and community stability with resource diversity. Conversely, consumer-resource interaction strengths may be relatively uniform in certain community compositions (e.g. possibly for polyculture 1 in Chapter 4), or for generalist consumers (e.g. *D. pulex* in Chapter 4). In this case, the presence of consumers may not substantially alter the outcome of competition among resources. In such cases, consumers would linearly impact ecosystem functions simply by removing resource biomass (e.g. Fig. 5.1 b & e). Unlike Mulder et al. (1999), I found no evidence to support a direct effect of consumers on the ecosystem functions tested (Fig 5.1 c). However, these hypotheses remain to be tested directly. This would require experiments similar to the diversity experiments in Chapter 5 to be conducted both in the presence and absence of consumers (see Jiang et al. 2009).

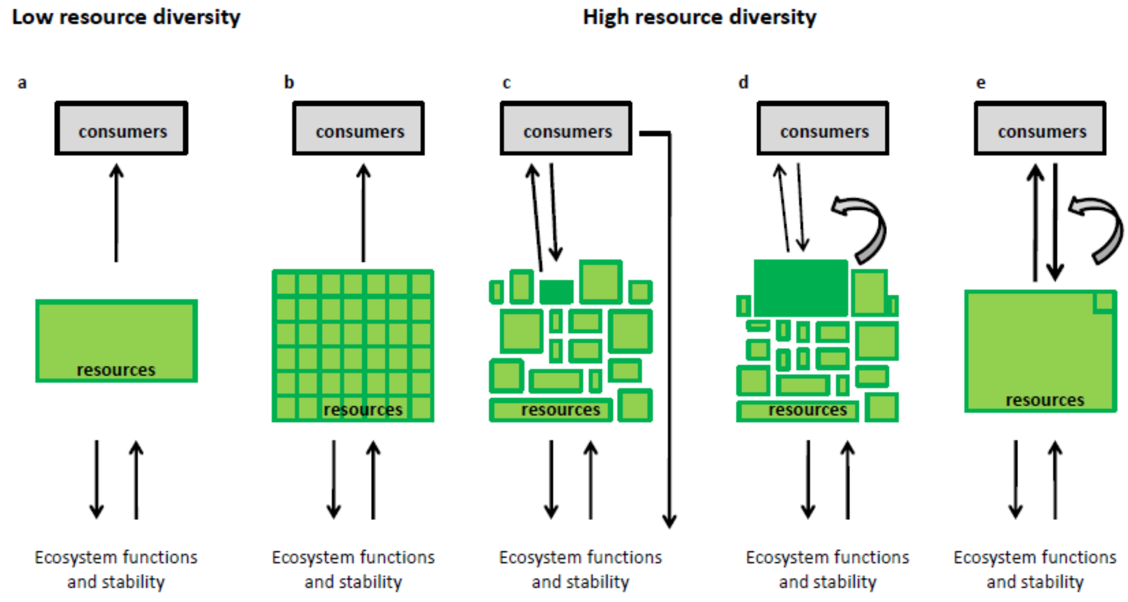

Figure 5.1. A schematic diagram depicting how resource diversity affects ecosystem functioning and stability in the presence of consumers. Panels **a-c** are redrawn from Mulder et al. (Mulder et al. 1999). In panels **a.** and **b.** consumers are affected by the relationship between resource diversity and ecosystem function, but do not affect the relationship. In panel **c.**, consumers affect ecosystem function directly but also by modifying the diversity and relative abundance of species. Panels **d.** & **e.** are schematics incorporating interaction strength modification by resource diversity, and the effects of community composition. Panel **d.** represents the possibility for low dominance and compensatory dynamics among species, and panel **e.** represents the dominance and synchronous dynamics among resource species.

The ubiquitous importance of community composition in this thesis emphasizes the importance of species traits and community context in determining the outcomes of species interactions as well as their impacts on population, community and ecosystem properties. Most biodiversity and ecosystem functioning studies to date have used random species combinations. However, the relevance of such experiments for predicting the effects of diversity given realistic extinction processes and the outcomes of species sorting are questionable (Gross and Cardinale 2005, Larsen et al. 2005, Srivastava and Vellend 2005, Savage et al. 2007, Staddon et al. 2010). The data from this thesis and previous work suggest that species' impacts on ecosystem function are often non-linear because the outcomes of species interactions are context-dependent. This limits the insight that can be gained from experiments using random species combinations for any particular ecosystem, and makes predicting the impacts of biodiversity losses a more difficult task. It implies that multi-species models need to be carefully parameterized by data from individual ecosystems on a case by case basis in order to be predictive. Below, I propose that complex adaptive systems theory and trait-based approaches are currently the best solutions to dealing with this complexity in a comprehensive, simplified and predictive manner (Hillebrand and Matthiessen 2009).

5.2 Future directions: complex adaptive systems theory and trait-based approaches

Complex adaptive systems theory is a generalized theory which stems from three basic premises: 1) diversity exists, 2) there are localized interactions among components of the diversity, and 3) selection among components occurs based on localized interactions (Norberg et al. 2001, Norberg 2004). These principles apply to the process of natural selection within populations and to species sorting within communities alike (Merico et al. 2009). Species can be described according to their traits, e.g. minimum resource requirements, maximum growth rate, size, edibility etc. (Litchman et al. 2007, Savage et al. 2007, Litchman and Klausmeier 2008, Merico et al. 2009, Litchman et al. 2010). Species experience trade-offs among traits that are important for their fitness and can be described by their position along trade-off curves (Merico et al. 2009). For example, phytoplankton may experience a trade-off between the ability to compete for nitrogen and resistance to consumption (Litchman and Klausmeier 2008, Litchman et al. 2010). Selection then occurs among species based on the state of their environment, e.g. in a low nutrient environment with few consumers, good competitors win (Merico et al. 2009). Selection then causes changes in trait-distributions over time, with the trait distribution being determined by the strongest selective agent (Litchman and Klausmeier 2008). Changes in trait distributions likewise can cause changes in aggregate community traits such as total resource or community biomass, the abundance of particulate nutrients, or the pH of the environment (Hillebrand and Matthiessen 2009). Changes in trait distributions, and the resulting changes in community and ecosystem-level traits, may alter the identity or strength of the selective forces. For example, an increase in the average edibility of phytoplankton species may cause an increase consumer density, shifting the source of selection from nutrient availability to consumer density.

The merits of such an approach are numerous. First, it directly addresses the link between forces that maintain diversity in a system and the effects of diversity on population, community and ecosystem properties (including stability). Second, as a result of considering interactions among group trait distributions, and not the multitude of interactions among individual species, it can vastly simplify the models used to make predictions (Litchman and Klausmeier 2008, Merico et al. 2009, Litchman et al. 2010). Third, it can incorporate changes in species' interactions strengths by making them a function of trait distributions (Litchman et al. 2007, Litchman and Klausmeier 2008, Merico et al. 2009, Litchman et al. 2010). For example, if trophic interaction strengths are largely based on allometric scaling, then they could be formulated as a function of the size ratio between consumer and resources (Litchman and Klausmeier 2008, Litchman et al. 2010). Fourth, it can dynamically incorporate shifts in the agents of selection and can include both top-down and bottom-up controls of both trait diversity and ecosystem functioning (Savage et al. 2007, Merico et al. 2009).

The success of complex adaptive systems theory and trait-based approaches depend on a number of requirements. First, complex adaptive systems theory requires that diversity exists, and does not incorporate any mechanisms to regenerate diversity once it is lost. Such mechanisms may include storage effects, immigration or speciation, but as it stands, this framework only deals with selection among existing variants. Second, the predictive ability of complex adaptive systems theory relies on the accurate identification and measurement of species traits that respond to selective agents (‘response traits’), as well as of the trade-offs among them (Litchman et al. 2007, Litchman and Klausmeier 2008, Hillebrand and Matthiessen 2009). Third, determining the effects of species’ trait distributions on populations, community and ecosystem properties also depends on describing the relationship between species’ response and effect traits (traits that determine the effect that a species has on a particular function, e.g. respiration rate) (Hillebrand and Matthiessen 2009). This relationship may be a one-to-one relationship in some cases (e.g. resource biomass), but may be a negative (e.g. nutrient availability) or nonlinear relationship in others (Hillebrand and Matthiessen 2009). Finally, creating a predictive theory also relies on identifying the important selective agents and interacting food web or ecosystem (including environmental variability) components. Obviously, these are not insubstantial challenges. However, I expect that this will be the most promising avenue forward in transforming biodiversity and ecosystem function research into a predictive science, capable of incorporating the complexity of the natural world.

5.3 Conclusion

In this thesis, I investigated both the causes and consequences of resource species diversity in model planktonic ecosystems. Using microcosm experiments, I was able to show that in the absence of consumers, phytoplankton species diversity is more effectively maintained by endogenously generated variability in limiting factors than externally generated fluctuations in resource availability (Chapter 2). Using short-term grazing experiments, I demonstrated that resource species diversity has impacts on rates of consumption for multiple consumers, with the magnitude, direction and mechanism of modulation being determined by the resource community composition and the feeding selectivity of the consumer (Chapter 3). Over the long-term I found that resource diversity had positive effects on many community and ecosystem properties, as well as their stability (Chapter 4). In line with previous studies on single-trophic levels, diversity stabilized total resource community biomass and particulate nutrient concentrations, but destabilized resource population dynamics. However, resource diversity did not impact the stability of consumer populations, regardless of feeding selectivity, indicating that resource diversity can decouple consumer and resource dynamics. In Chapters 3 and 4, I used statistical techniques to infer potential mechanisms by which diversity impacted rates of consumption and ecosystem properties. However, in many cases direct tests of proximate mechanisms have yet to be conducted.

The importance of community composition was a common theme throughout this thesis and suggests that species traits and community context are important in determining the outcome of species interactions and their impacts on population, community and ecosystem functions. The processes which maintain species diversity and the impacts of species diversity should no longer be studied separately. I recommend the use of complex adaptive systems theory and trait-based approaches to unite these related fields in the future. Finally, the experiments in this thesis were conducted in controlled environments with relatively few species compared to natural ecosystems. These simple communities allowed the examination of individual causal factors in each chapter, but the relative importance of these factors in more complex and natural ecosystems will require further investigation.

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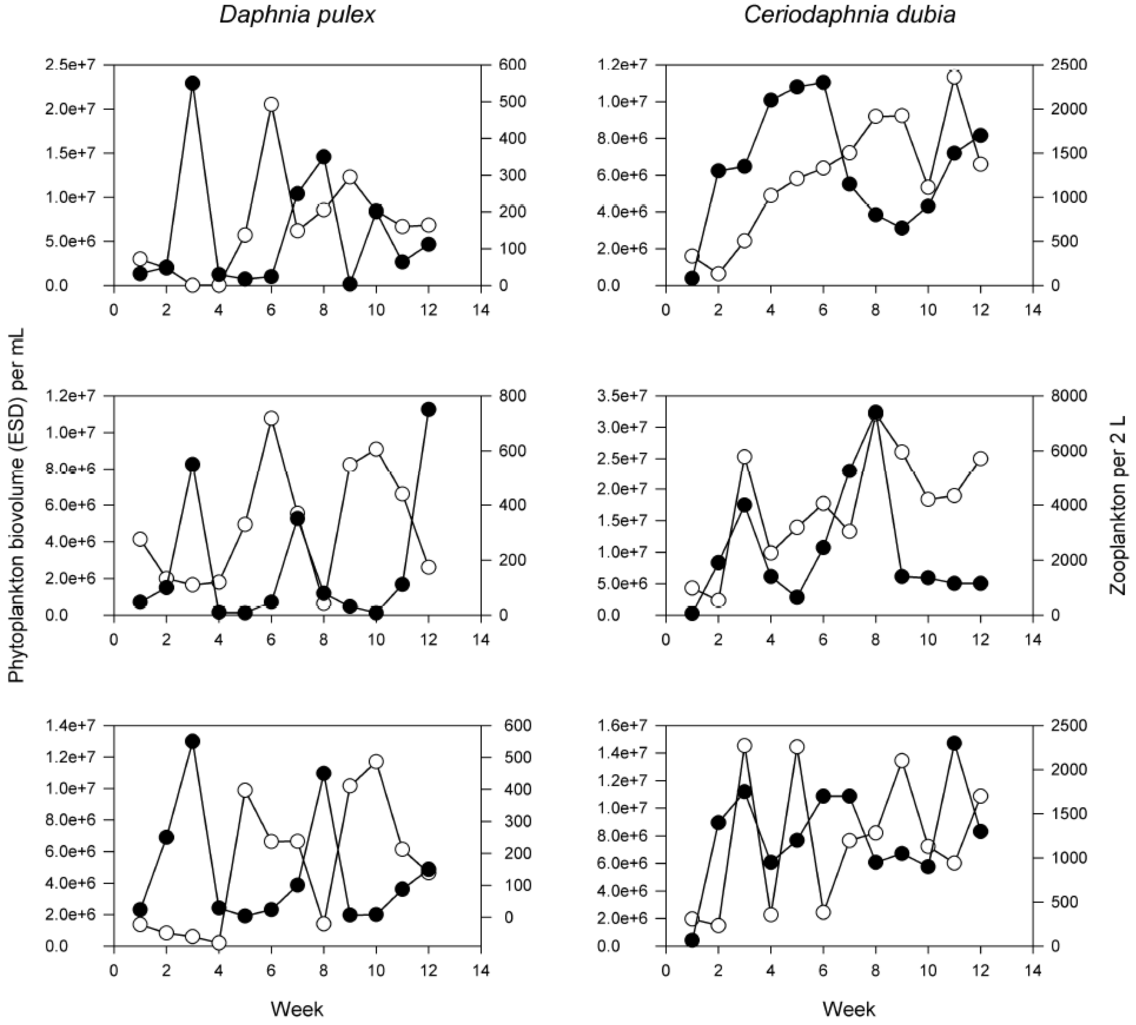
Appendix 2.1. Contaminations of microcosms

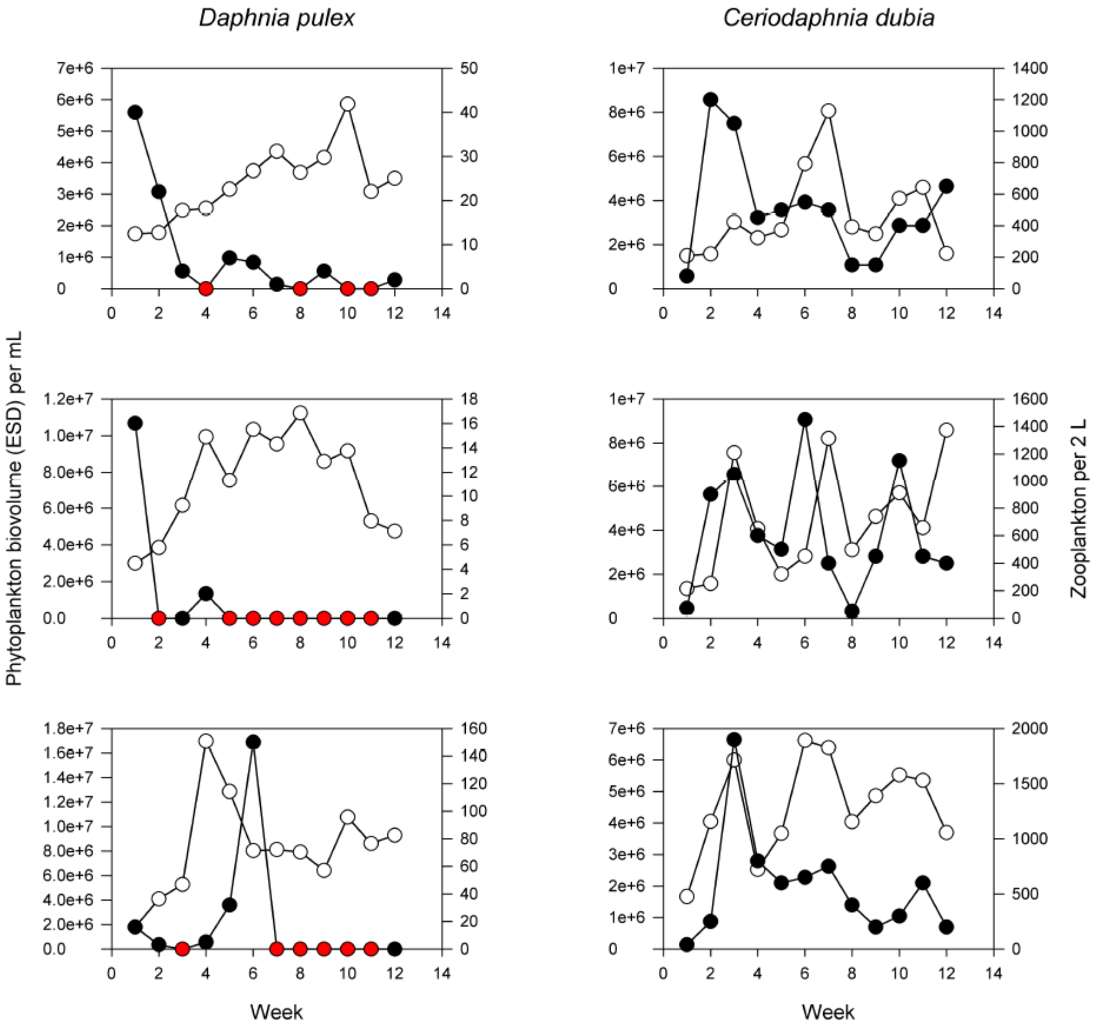
Appendix 2.1. Replicate numbers from Chapter 2's microcosm experiment and the species that invaded them. Species all initially appeared at various sampling dates after 14 days.

Replicate	Disturbance treatment	Community composition	Contaminant
1	7-day	1	*Cyclotella sp.*
2	7-day	1	*Cyclotella sp.*
3	7-day	2	*Chlamydomonas reinhardtii*
4	7-day	2	*Chlamydomonas reinhardtii*
5	7-day	3	*Chlamydomonas reinhardtii*
6	7-day	3	*Chlamydomonas reinhardtii*
7	11-day	1	*Cyclotella sp.*
8	11-day	1	*Cyclotella sp.*
9	11-day	2	*Cyclotella sp.*
10	11-day	2	*Cyclotella sp.*
11	11-day	3	*Ankistrodesmus falcatus*
12	11-day	3	*Ankistrodesmus falcatus*
13	Undisturbed	1	*Cyclotella sp.*
13	Undisturbed	1	*Unknown species*
14	Undisturbed	1	*Cyclotella sp.*
15	Undisturbed	2	*Cyclotella sp.*
16	Undisturbed	2	*Cyclotella sp.*
17	Undisturbed	3	*Ankistrodesmus falcatus*

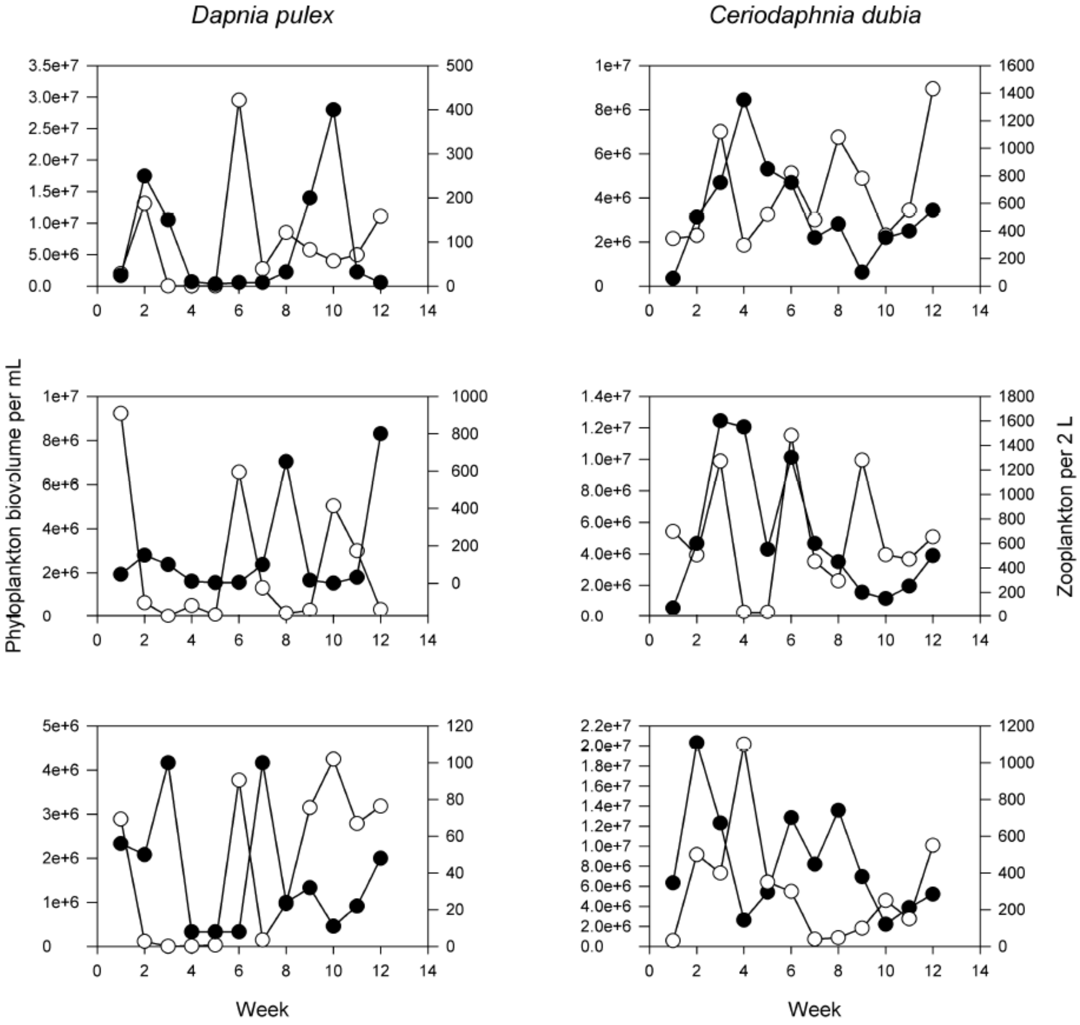
Appendix 4.1. Phytoplankton and zooplankton dynamics over time



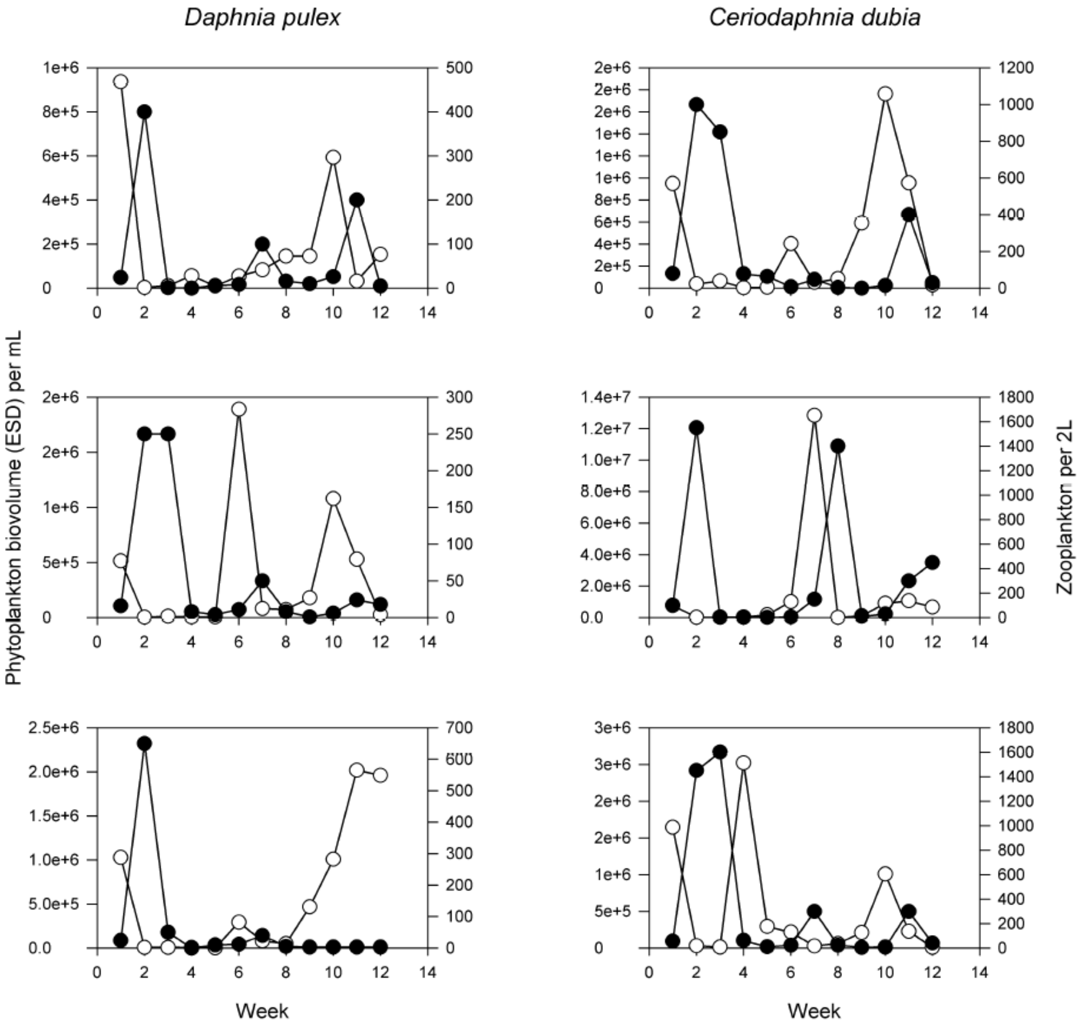
Appendix 4.1 a. Phytoplankton and zooplankton dynamics over time in monoculture 1 from Chapter 4’s microcosm experiment. Phytoplankton are represented by open symbols and plotted on the left y-axis, and zooplankton are represented by closed symbols and plotted on the right y-axis. Weeks in which no zooplankton were observed and were re-inoculated at the original density are indicated with red-filled circles (none in this panel). Each panel shows the dynamics of one microcosm over time, with three replicates per treatment.



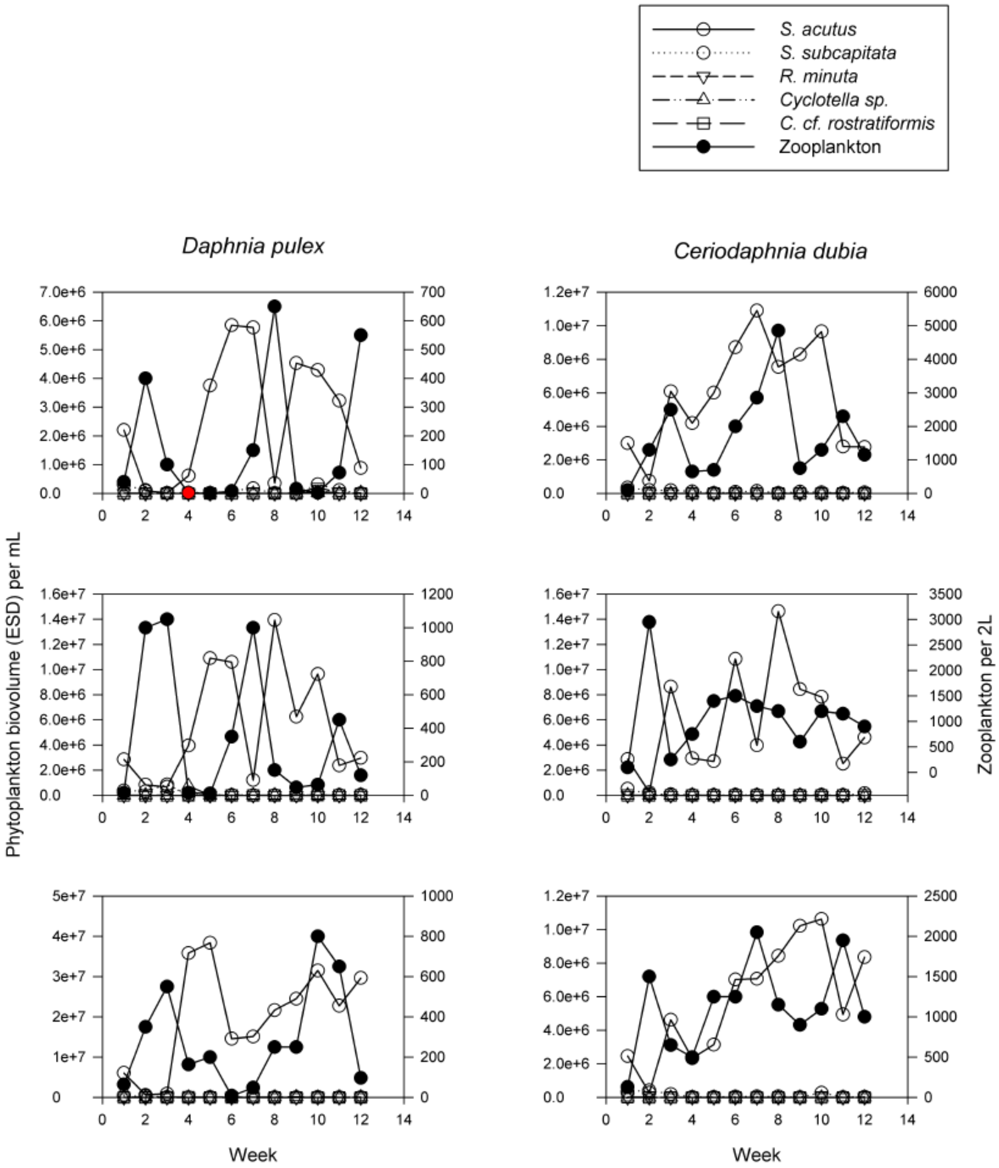
Appendix 4.1. b. Phytoplankton and zooplankton dynamics over time in monoculture 2. All else is as in Appendix 4.1a.



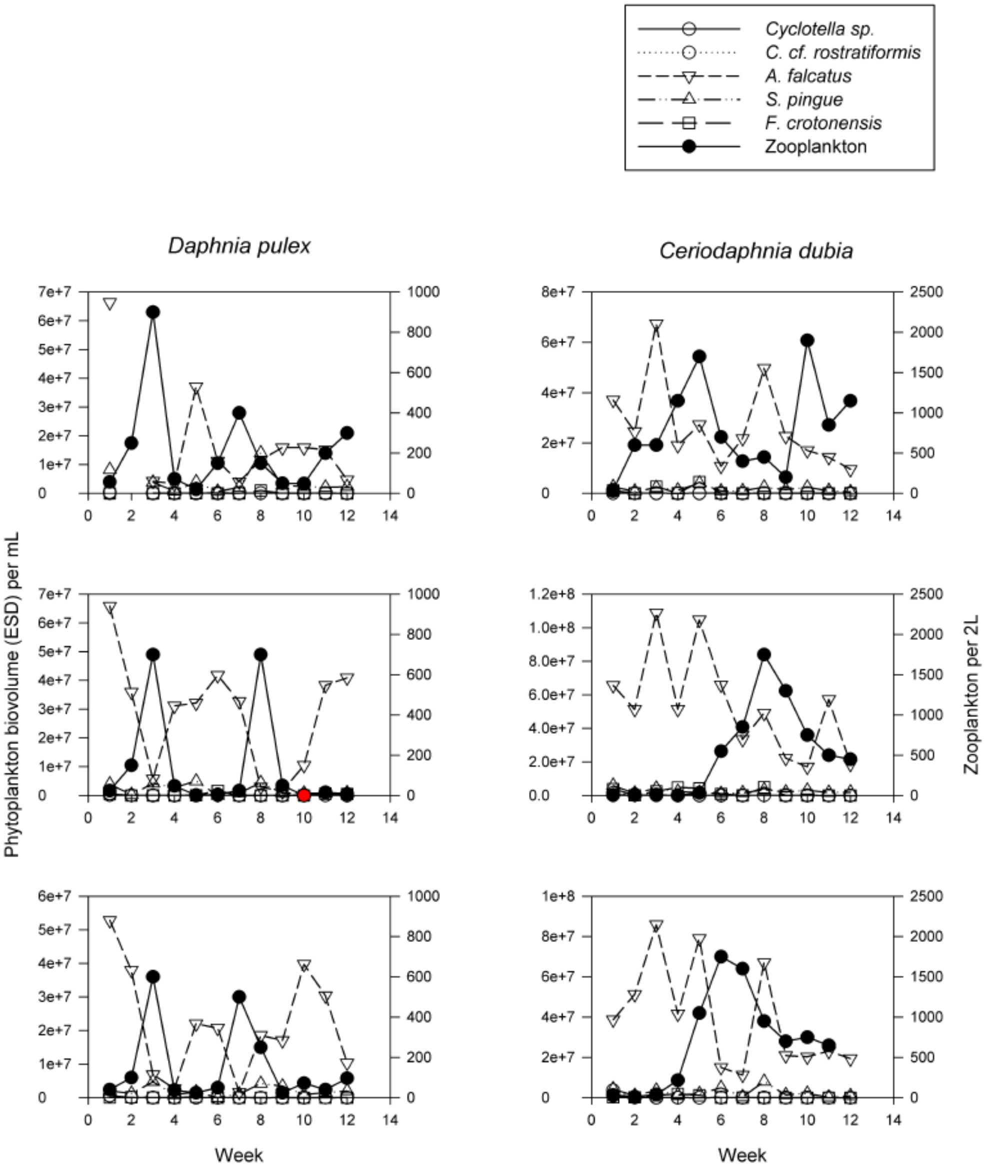
Appendix 4.1. c. Phytoplankton and zooplankton dynamics over time in monoculture 3. All else is as in Appendix 4.1a.



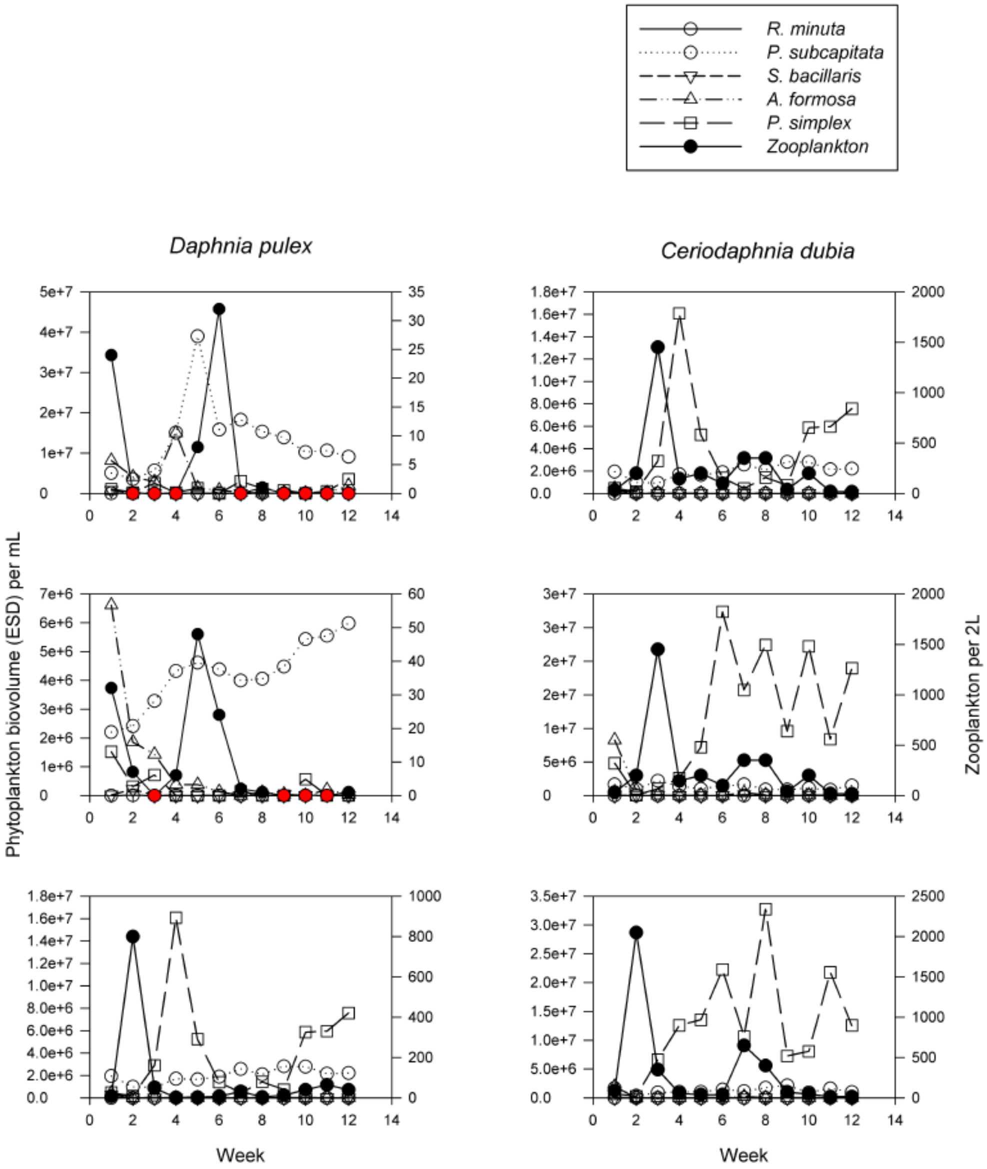
Appendix 4.1. d. Phytoplankton and zooplankton dynamics over time in monoculture 4. All else is as in Appendix 4.1a.



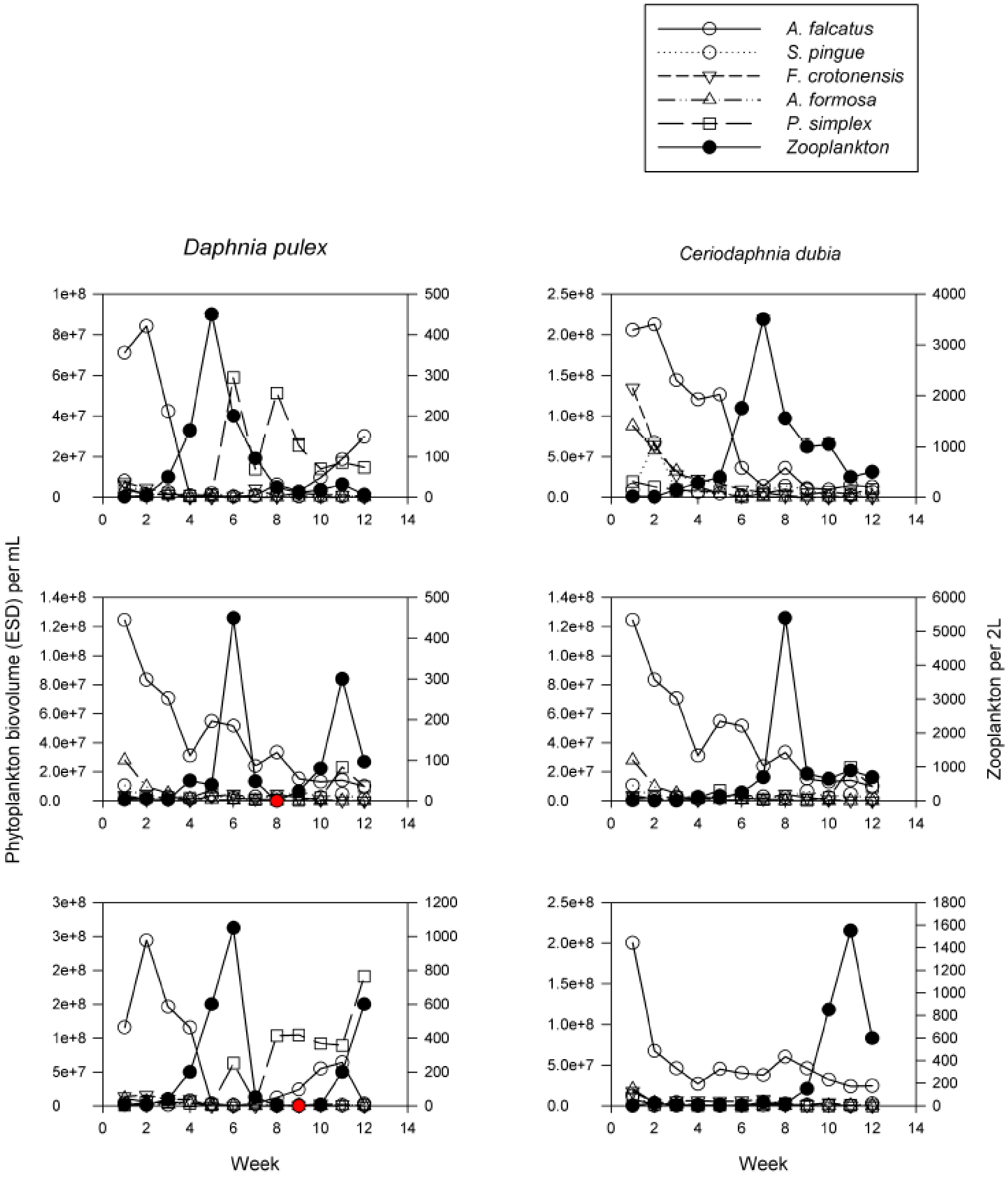
Appendix 4.1. e. Phytoplankton and zooplankton dynamics over time in polyculture 1. Relative biovolumes of phytoplankton species are shown in Appendix 4.2. All else is as in Appendix 4.1a.



Appendix 4.1. f. Phytoplankton and zooplankton dynamics over time in polyculture 2. Relative biovolumes of phytoplankton species are shown in Appendix 4.2. All else is as in Appendix 4.1a.

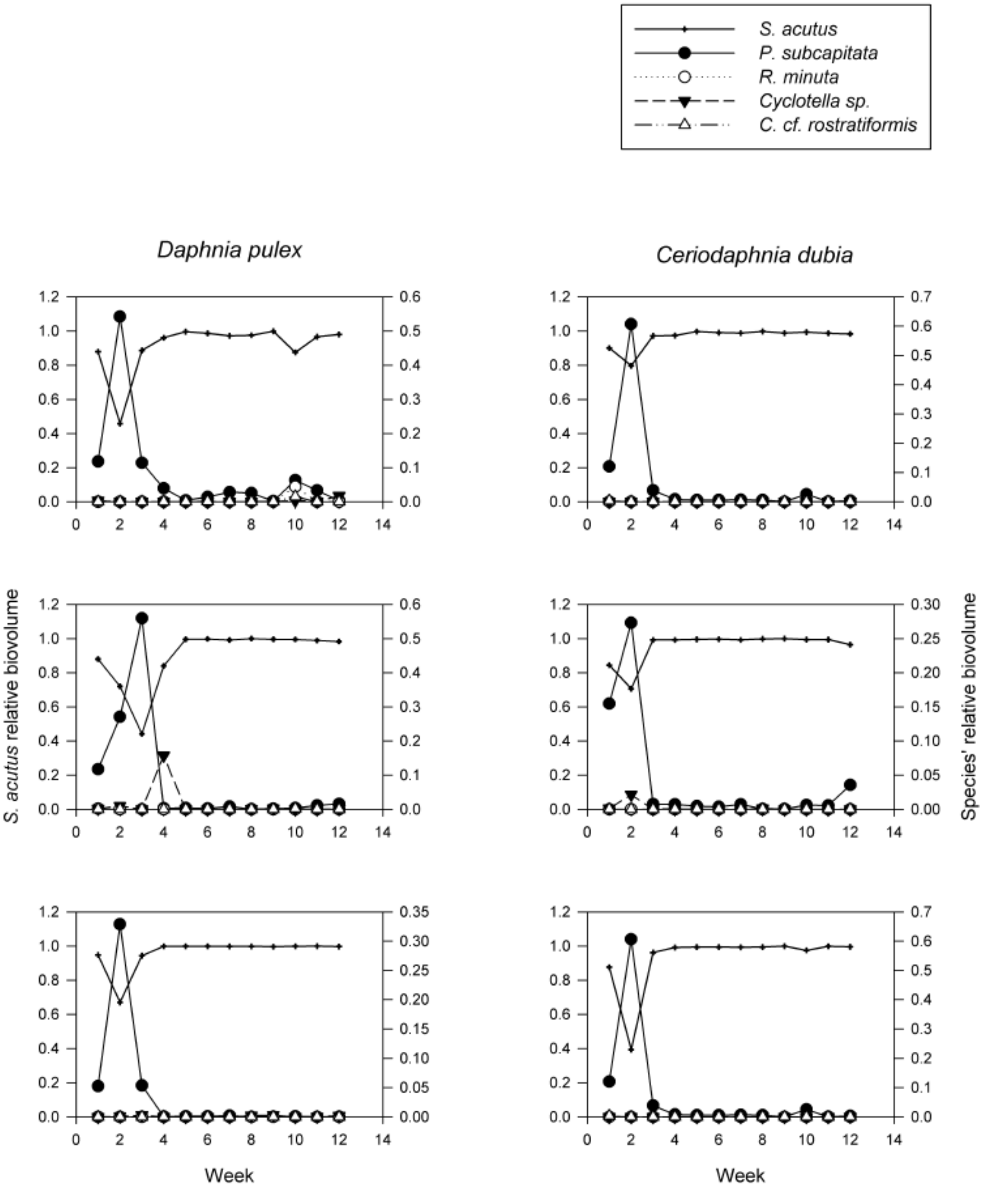


Appendix 4.1. g. Phytoplankton and zooplankton dynamics over time in polyculture 3. Relative biovolumes of phytoplankton species are shown in Appendix 4.2. All else is as in Appendix 4.1a.

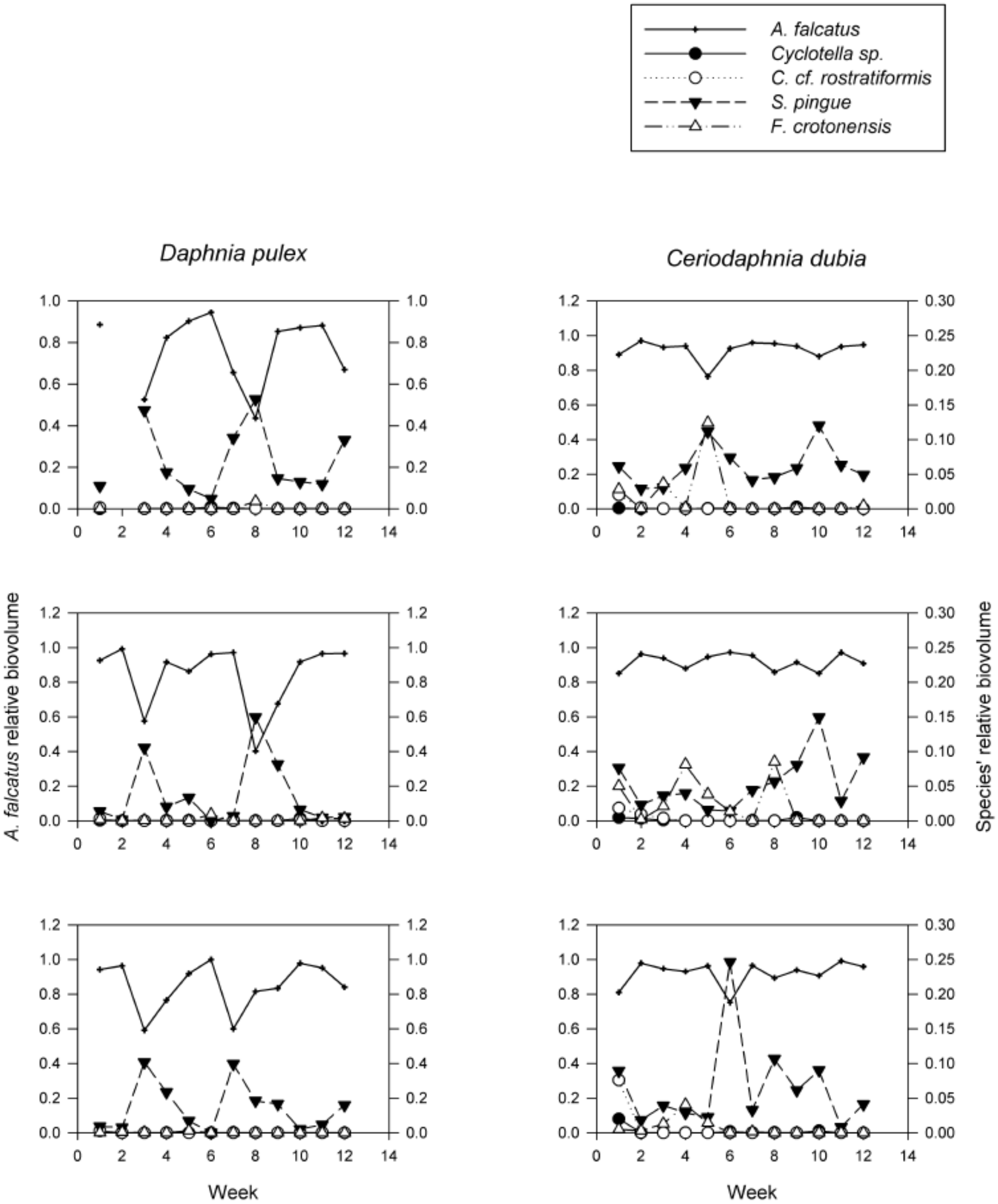


Appendix 4.1. h. Phytoplankton and zooplankton dynamics over time in polyculture 4. Relative biovolumes of phytoplankton species are shown in Appendix 4.2. All else is as in Appendix 4.1a.

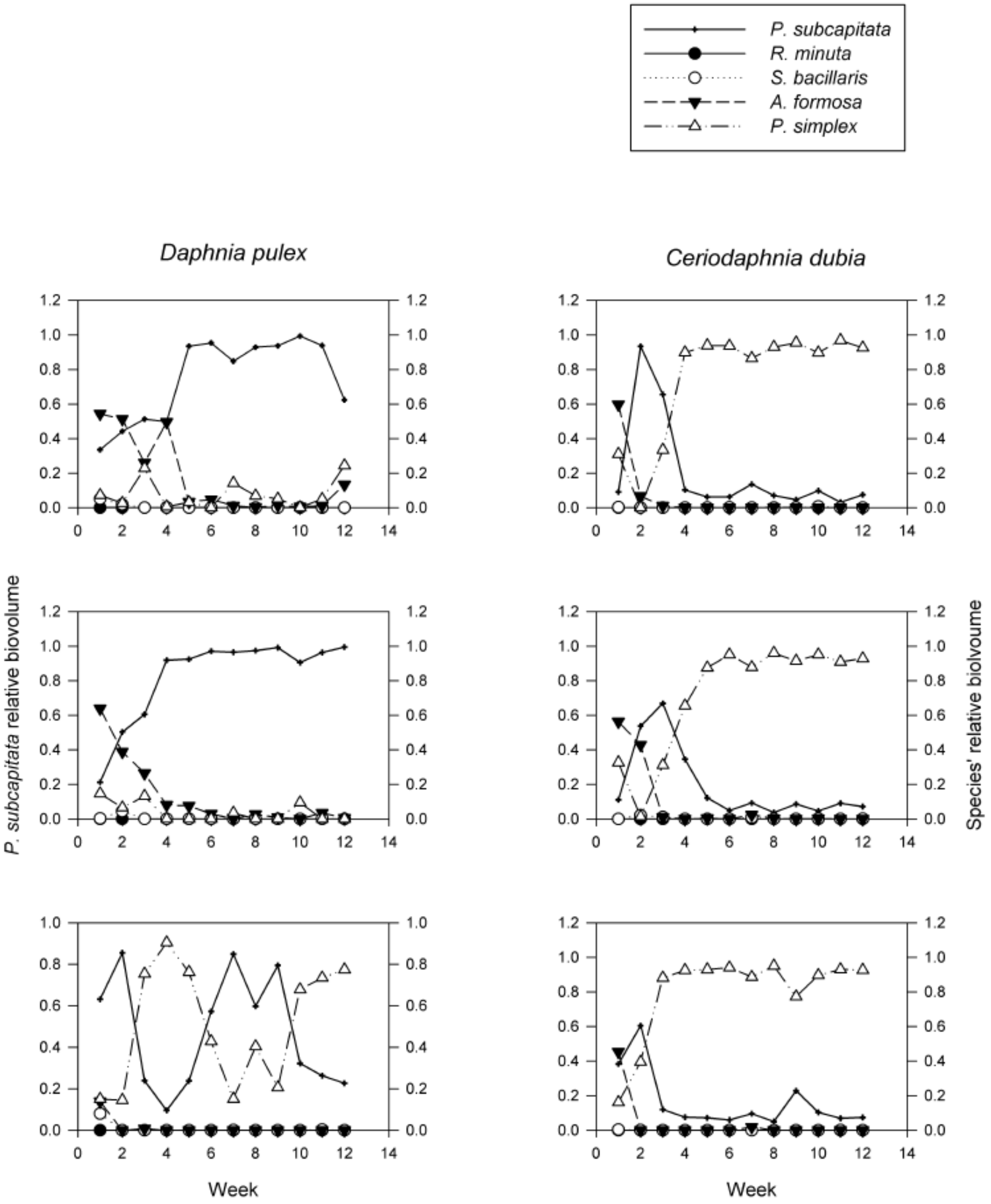
Appendix 4.2. Phytoplankton relative abundance over time



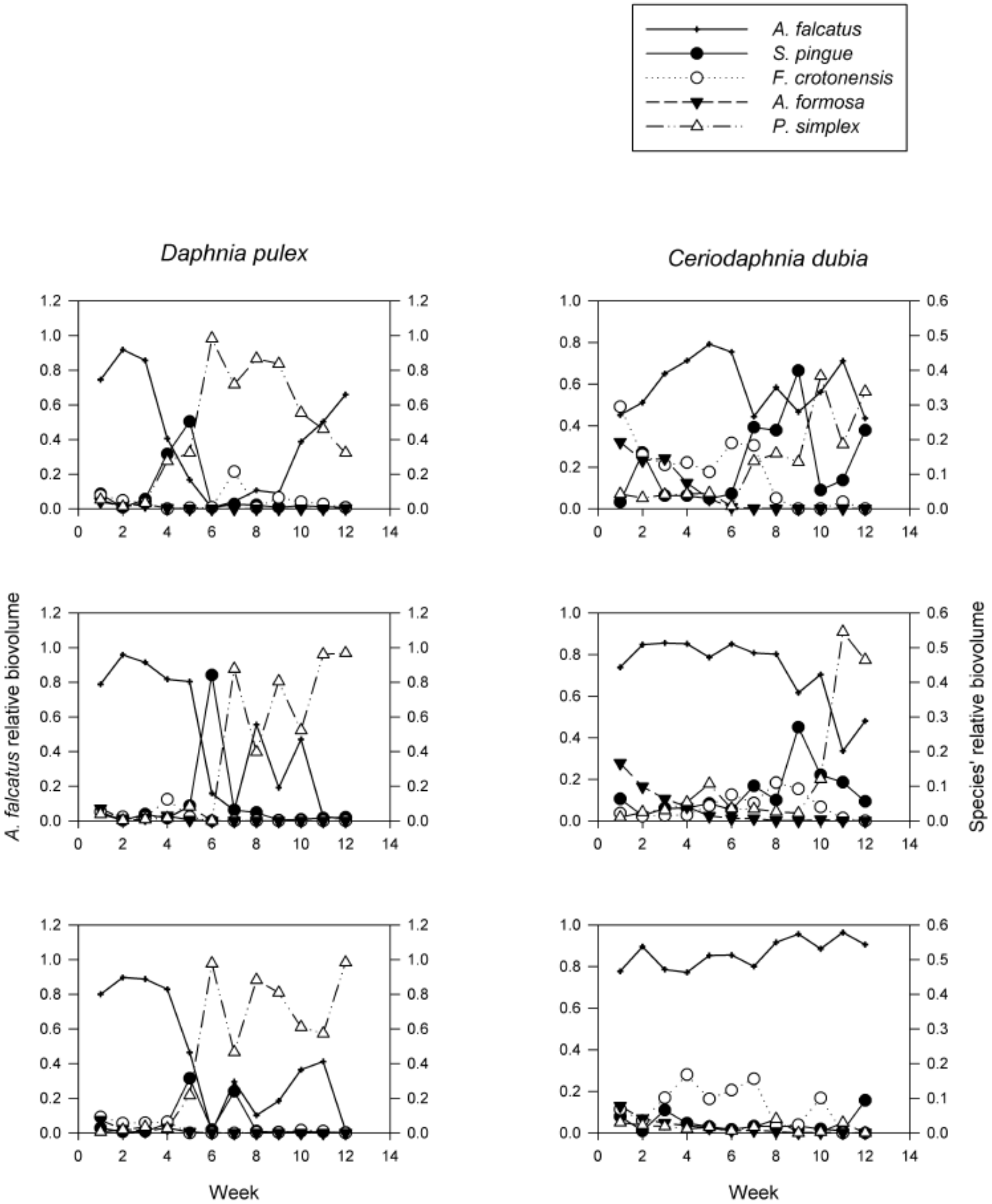
Appendix 4.2. a. The fraction of the total biovolume made up by each species of phytoplankton over time in polyculture 1 from Chapter 4's microcosm experiment. The species with the small cross-hair symbol is plotted on the left axis, and all other species' fractional biovolumes are plotted on the right axis. Each panel shows the dynamics of one microcosm over time.



Appendix 4.2. b. The fraction of the total biovolume made up by each species of phytoplankton over time in polyculture 2. All else is as in Appendix 4.2a.

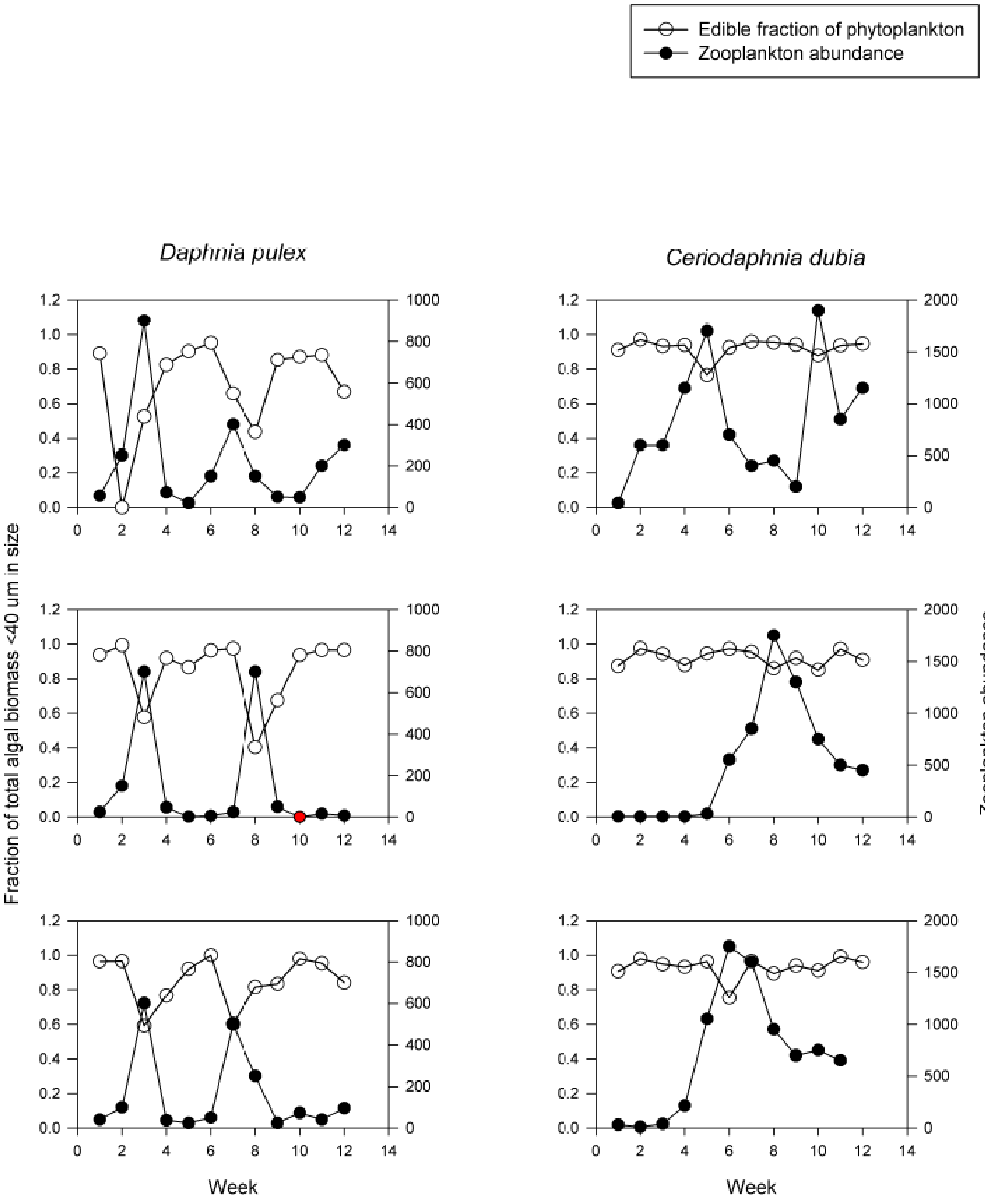


Appendix 4.2. c. The fraction of the total biovolume made up by each species of phytoplankton over time in polyculture 3. All else is as in Appendix 4.2a.

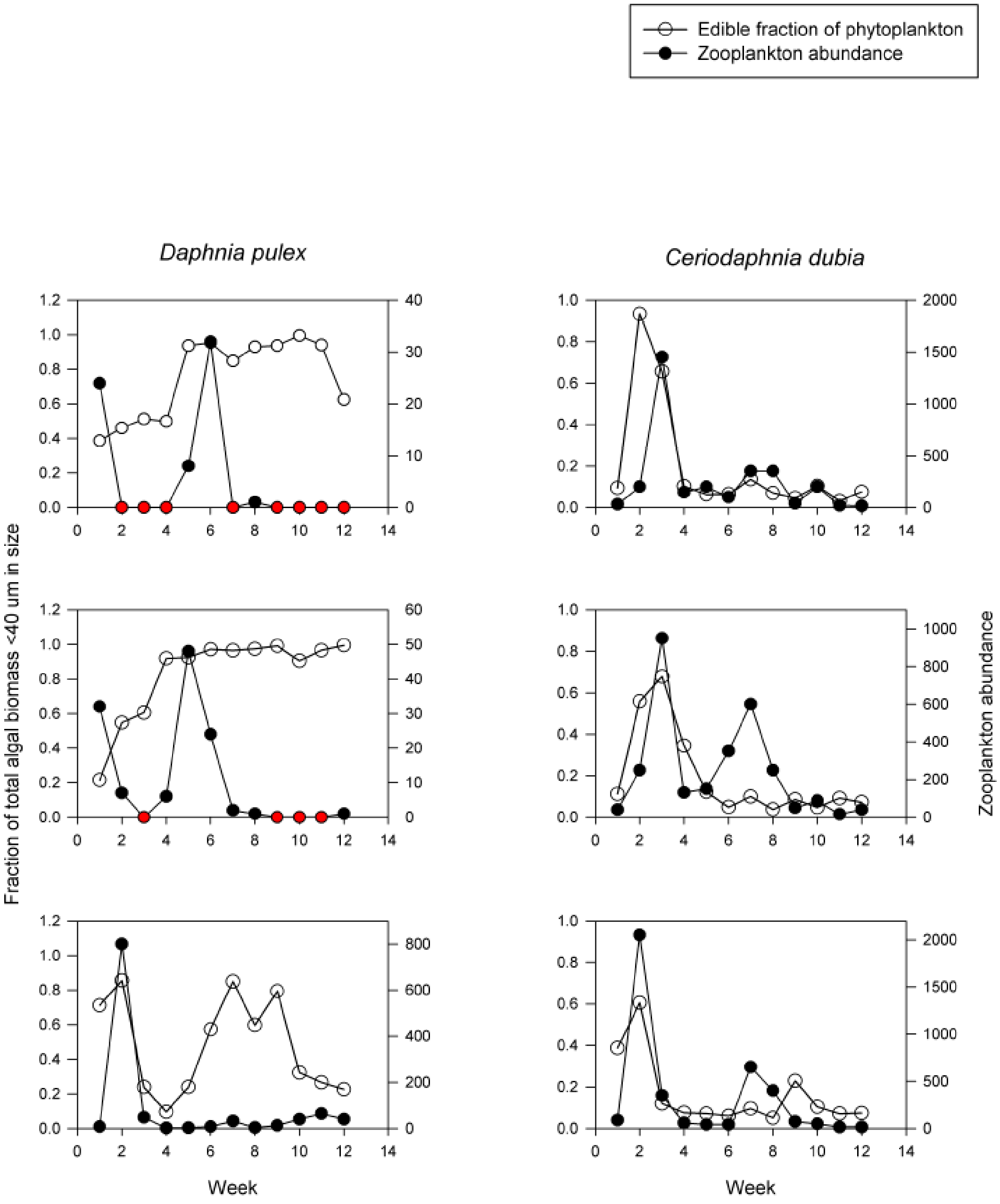


Appendix 4.2. d. The fraction of the total biovolume made up by each species of phytoplankton over time in polyculture 4. All else is as in Appendix 4.2a.

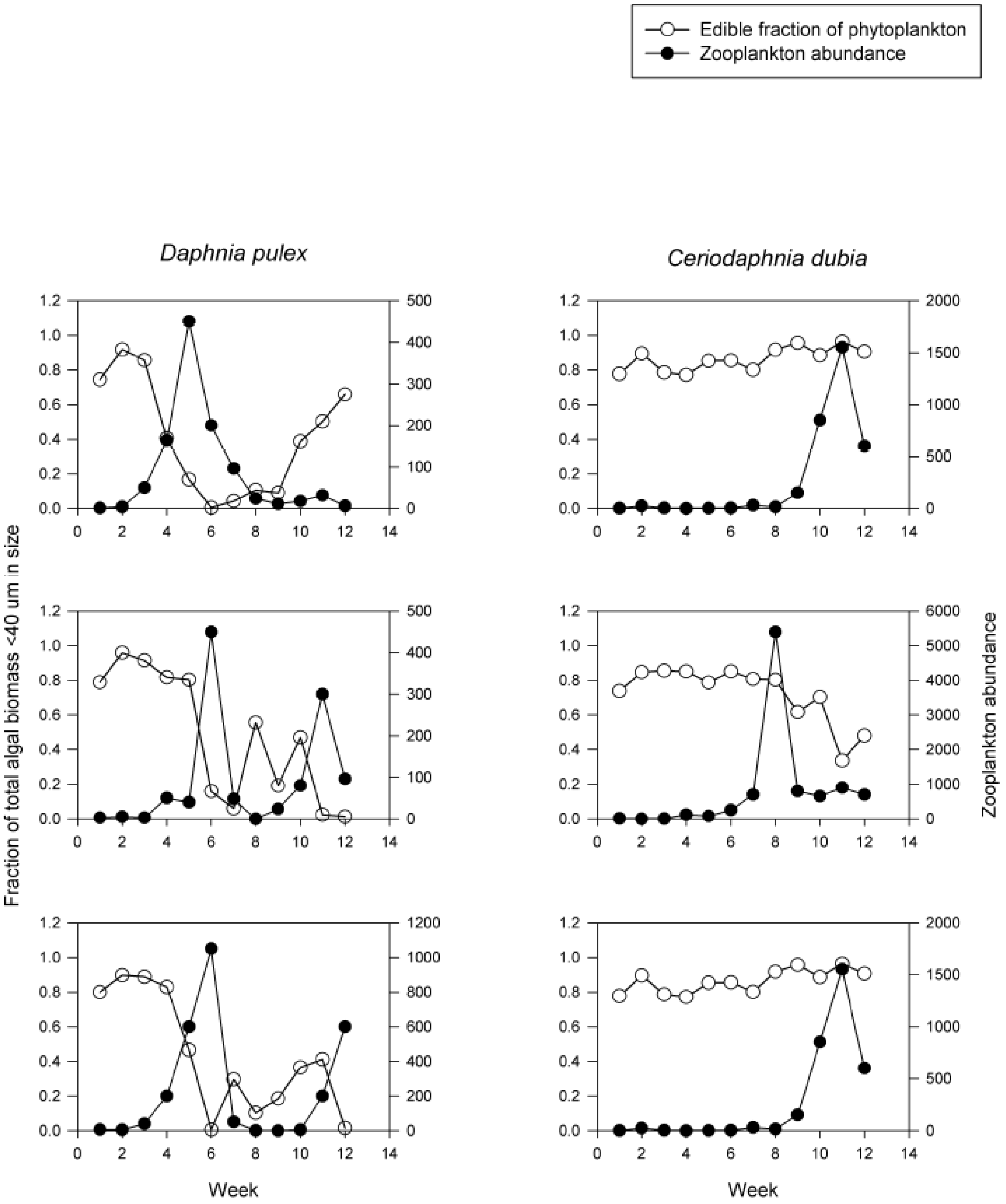
Appendix 4.3. Zooplankton density and fraction of edible phytoplankton over time



Appendix 4.3. a. Fraction of the total phytoplankton biovolume that is edible (>40 um) and zooplankton abundance in polyculture 2 over time for Chapter 4’s microcosm experiment. Open symbols represent phytoplankton which are plotted on the left y-axis and closed symbols represent zooplankton and are plotted on the right y-axis.

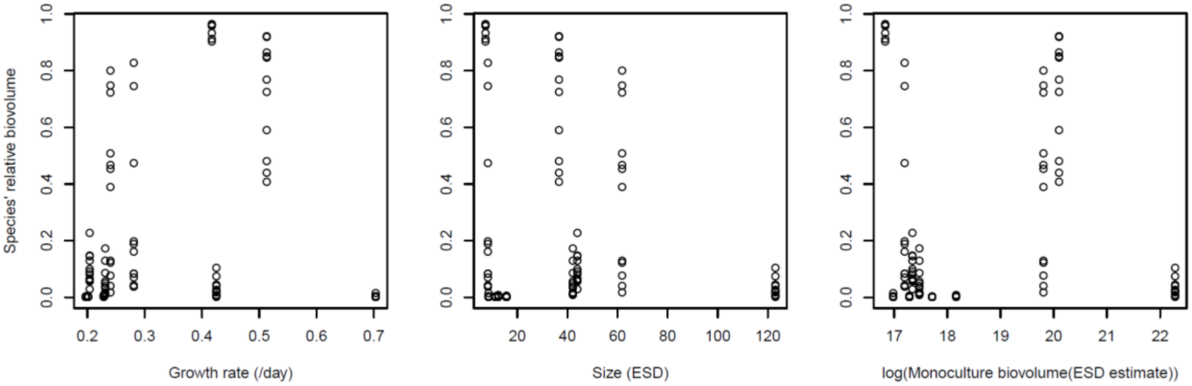


Appendix 4.3. b. Fraction of the total phytoplankton biovolume that is edible (>40 um) and zooplankton abundance in polyculture 3 over time. All else is as in Appendix 4.3 a.



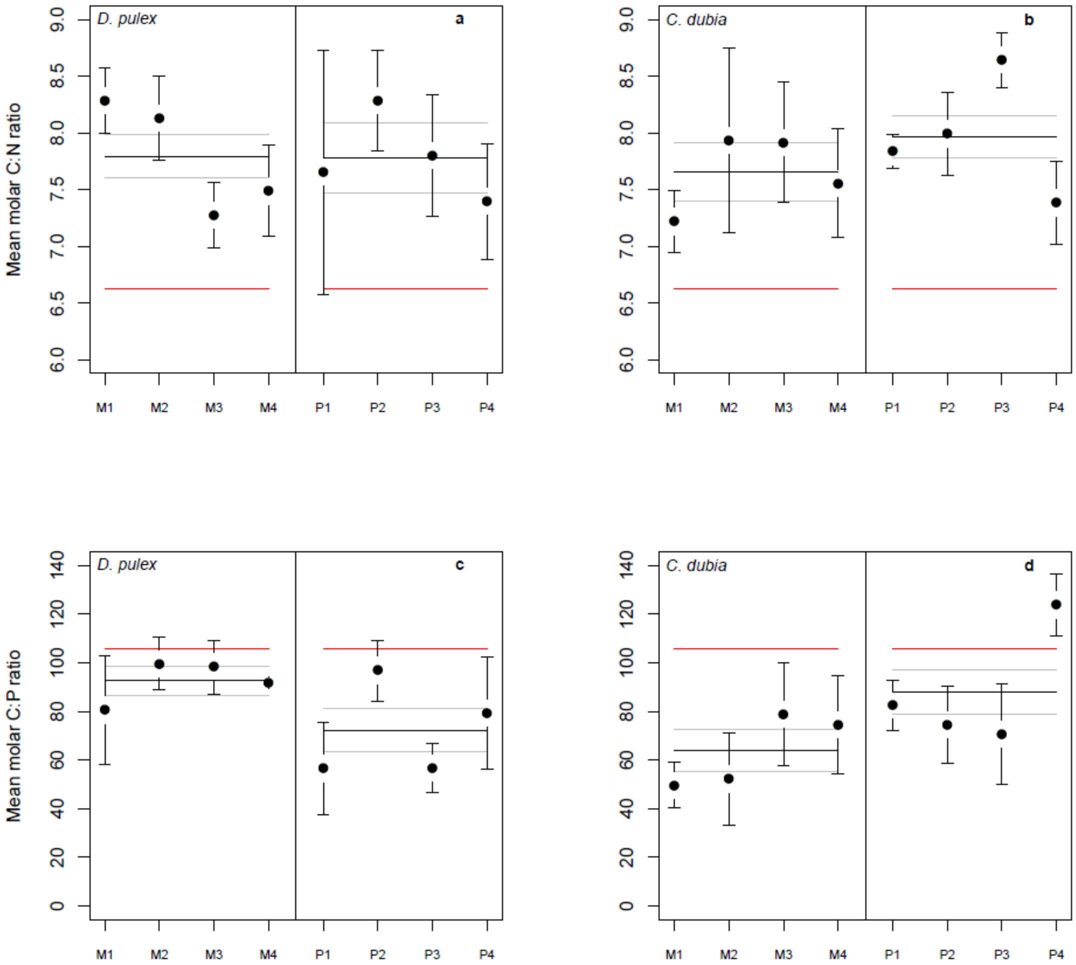
Appendix 4.3. c. Fraction of the total phytoplankton biovolume that is edible (>40 um) and zooplankton abundance in polyculture 4 over time. All else is as in Appendix 4.3 a.

Appendix 4.4. Species' traits and relative abundance



Appendix 4.4. The proportional biovolume of individual species in polyculture microcosms. Relative biovolume is plotted against each species' maximum growth rate (day^{-1}), estimated size (equivalent spherical diameter, ESD), and the log of the estimated monoculture biomass (log(cumulative biovolume)) respectively, from left to right.

Appendix 4.5. C:N and C:P



Appendix 4.5. The mean C:N (**a** & **b**) and C:P (**c** & **d**) molar ratios of the total particulate organic matter averaged over time for *Daphnia pulex* (**a**) and *Ceriodaphnia dubia* (**b**) in Chapter 4's microcosm experiment. Error bars indicate ± 1 S.E., black lines across panels indicate the average across monoculture or polycultures, and grey lines indicate ± 1 S.E. of the mean across diversity treatments. The red line indicates the Redfield ratio (6.625 for C:N and 106 for C:P).