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Plankton Population Dynamics: Effects of Climate Warming and Food Chain Length

by

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ABSTRACT

In ecological systems, temperature can be an important factor affecting individual growth and species distributions. With recent predictions for global climate warming, the question arises as to how temperature and biotic relationships interact to determine the dynamics of populations. In this thesis, I investigate the effect of temperature on the stability of a common freshwater predator-prey system consisting of *Daphnia pulex* and its phytoplankton prey. The dynamics are examined at 18°C and 25°C within three community types: a baseline community, a simplified community and in a 3 trophic level food chain. The predator-prey system was destabilized at the higher temperature in all communities and *Daphnia* extinction always occurred. This result was unaffected by simplification of the community, but was enhanced by the addition of the carnivore. I also examined the dynamics of 2 and 3 level food chains and the effect of the carnivore *Mesostoma ehrenbergii* on *Daphnia* population dynamics. *Mesostoma* influenced its prey population in a stage-structured manner and this response was temperature mediated.

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To

Ceddy, Tasha and Tika

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CHAPTER 1: Introduction

I - Climate Change

Predictions

There has been concern in recent years about the accelerating rate of increase of trace greenhouse gases in the atmosphere since the beginning of the industrial revolution (Ramanathan 1988). These gases which include CO_2, CH_4, H_2O vapour, N_2O, tropospheric O_3 and chlorofluorocarbons (CFC's), result in an increased trapping of infrared radiation in the atmosphere (Ramanathan 1988, Henderson-Sellers 1990). The increased energy in the Earth's atmosphere leads to a warmer and more active climate (Ramanathan 1988).

General circulation models (GCMs) have been used to forecast possible changes in the global climate. GCMs simulate the physical and dynamic processes of the atmosphere and oceans (Meehl 1984, Smith 1991). The major prediction of these models is a warming of the Earth's atmosphere over the next century at a rate 10 to 50 times faster than any natural rates observed in the past (Pain 1988, Roberts 1988, Botkin *et al.* 1991, Schneider 1993). Since 1840, the global mean temperature has increased by 0.5°C and the 1980's was the warmest decade on record (Cohen 1990, Mohnen and Wang 1992). A doubling of CO_2 levels since the mid-19th century is expected to lead to an increase of 3.5°C to 4.2°C in the global mean temperature over the next 50 years (Gribbin 1986).

The GCM predictions for climate warming are greatest in areas within 50° to 70°N (Ramanathan 1988). In the area bounded by 48° to 52°N and 90° to 100°W, the expected increase in temperature may be as high as 9°C in the summer (Schindler *et al.* 1990). This area includes the prairies of central Canada and the midwestern United States. Although precise predictions for local climatic change at a scale smaller than 500 miles cannot be made from GCMs (Meehl 1984, Vitousek 1992), it is clear that Canadian ecosystems may be exposed to a significant increase in atmospheric temperature.

The question arises as to how these changes will affect natural ecosystems. It has been recognized that temperature is probably the most important climatic factor in biological terms. At the physiological level, all metabolic rates are temperature dependent, even in organisms that thermoregulate (Ford 1982). An average temperature rise of even 1°C can be ecologically significant and can alter patterns of species interactions and dynamics (Peters 1989, Ayres 1993). Although natural systems have

experienced climatic temperature changes in the past, anthropogenically induced global warming will be more severe because: (1) the rates of temperature increase are expected to be much faster than has been observed historically and (2) natural communities may be more susceptible owing to habitat fragmentation brought about by urbanization which hinders species dispersal (Roberts 1988).

The effect of global climate warming on ecosystem dynamics still remains largely to be determined. General predictions that have been made include a northward shift of the geographic range of many species (Davis 1986, Graham and Grimm 1990). As the temperature increases, the overall productivity of ecosystems may increase at all trophic levels (Carpenter *et al.* 1992) although, a concomitant decrease in the diversity and stability of communities is also expected (Pain 1988a, b, Parsons 1989, Fogg 1991). Missing from such predictions is an examination of how species interactions will influence changes in diversity, productivity and stability (Kareiva *et al.* 1993).

Previous Studies

To date, three methods have been used to determine the potential impacts of a global temperature change on natural communities: paleoecological studies based on past climatic warming, correlative studies based on present day temperature shifts and finally mechanistic model development.

In a community context, the most common method uses the study of paleoecology to examine the effects of past climatic shifts. Such studies use fossil and palynological records from climate changes that have occurred during past interglacial periods of the Pleistocene, Holocene and late Quaternary (Davis 1989, Peters 1989, Graham and Grimm 1990, Clark 1993, Lindley *et al.* 1993). Generally, these studies reveal overall community shifts in diversity and structure and by their nature, are unable to assess changes in population dynamics. Conclusions from such studies indicate that as environmental conditions change due to global warming, it is highly unlikely that communities will simply change their geographic location as single units (Ford 1982, Graham and Grimm 1990, Harrison 1993). Rather, individual species will shift their geographic range at different rates (Webb 1987, Davis 1989, Graham and Grimm 1990, Schimel 1993).

The second method is also a correlative method and uses modern day perturbations in temperature (e.g. El Niño events) to examine how these temperature fluctuations influence species distributions over large geographical scales (George *et al.* 1990, Schindler *et al.* 1990, Fogg 1991). In related work, speculation as to the potential

effects of global warming have been done based on the physiological and ecological tolerance levels of individual taxonomic groups (Fogg 1991, Carpenter *et al.* 1992). These methods identify species dispersal routes and final distribution maps.

The final method, which is still mostly unexplored, involves the development of mechanistic models of population responses to temperature shifts (Leadley and Reynolds 1992, Kareiva *et al.* 1993, Wennergren and Landin 1993). This method couples information about the physiological changes resulting from temperature variation and population level responses in order to determine how population productivity, dynamics and stability are affected (e.g. Hill and Magnuson 1990, Magnuson *et al.* 1990, Shugart *et al.* 1992). There are important changes in physiology with temperature that occur at the individual level that are likely to affect population dynamics. While there is a large amount of information on the physiological effects of temperature, our understanding of how physiological changes influence the population dynamics or the dynamics of interacting populations is limited. When examining dynamics, it is also important to consider that interspecific interactions may influence the dynamics of a species of interest (Ayres 1993, Dunham 1993, Ives and Gilchrist 1993). Hill and Magnuson (1990) concluded that food web dynamics and interactions between populations were very important in determining the effects of increased temperature on individual populations. The climate change response will depend therefore, on the pattern of the temperature effect on the individual species and on the community structure (Ives and Gilchrist 1993). The difficulty arises in the parameterization of such models, especially for complex food webs, where there are many species interactions that are not well understood (Crawley 1990). Detailed investigations into the importance of abiotic and biotic interactions in communities is required before a full scale model can be developed for most natural systems.

In preliminary studies of the potential effects of global warming, it is necessary to understand the changes in population dynamics and stability that will occur in natural systems. Because of the rapid rate of warming expected, there is little time for fully detailed models to be constructed. Although a mechanistic description of changes in dynamics is the ultimate goal, such models are hard to construct and to parameterize on the time scales we are dealing with. Several workers have suggested that scaled-down microcosm experiments investigating population dynamics in controlled communities are a useful first step (Crawley 1990, Woodward 1992, Ayres 1993, Ives and Gilchrist 1993). An experimental approach can demonstrate the major effects of temperature increase on population dynamics. The use of mesocosms with structured treatments allows for the

detection of the important mechanisms which determine observed responses and the identification of areas where further explanations are required.

II - Goals, Hypotheses and Predictions

The System

In the Canadian prairies, the predicted rise of mean annual temperature by up to 9°C may have significant effects on the organisms in the area. Prairie wetlands and ponds are highly vulnerable systems and this vulnerability is of concern to conservationists. Aquatic systems are useful for preliminary studies of global warming for two reasons. First, the ambient temperature of shallow bodies of water closely mimics the air temperature (Cooper 1990); thus freshwater systems will be among the first to demonstrate the effects of global warming (Carpenter *et al.* 1992). Secondly, planktonic systems are useful for addressing more theoretical questions regarding the effects of temperature on population dynamics in various communities; questions that remain unanswered. Plankton dynamics have been well studied in the past (e.g. McCauley and Murdoch 1987, McCauley et al. 1990) and aquatic communities are widely used in manipulative experiments. Replicate populations can be established at different levels of temperature and, changes in their dynamics can be observed over a relatively short period of time (i.e. a few months).

There are a number of physical changes expected in freshwater systems owing to increases in water temperature: increased levels of evapotranspiration (Cooper 1990, Jacoby 1990, Schindler *et al.* 1990), increased nutrient turnover rates with higher rates of microbial decomposition (Saunders 1980, Blumberg and DiToro 1990, Cooper 1990), increased pelagic nitrification (Berounsky and Nixon 1990, Schindler *et al.* 1990), increased risks of acidification (Oppenheimer 1989), and decreased dissolved oxygen (Blumberg and DiToro 1990, Cooper 1990, Schindler *et al.* 1990, Carpenter *et al.* 1992). With global warming, a lengthened ice-free season is expected owing to earlier ice-out dates in the spring and to more frequent ice break-up during the winter (Schindler *et al.* 1990, Robertson *et al.* 1992). In addition, the frequency of large-scale environmental perturbations in all systems should increase (Pain 1988a, Walker 1991, Carpenter *et al.* 1992).

The Biological Community

The main objective of this thesis is to determine how the dynamics of an important predator-prey system in simple aquatic communities are affected by an increase in ambient temperature. The system consists of the herbivore *Daphnia pulex* (Leydig) and its phytoplankton prey.

As described previously, most studies to date have attempted to determine changes in community structure and diversity with global warming (Fogg 1991, Carpenter *et al.* 1992). There have been far fewer investigations into food chain dynamics; an approach that addresses questions of dynamics and stability of trophic-level populations (Murdoch 1993). The major goal of this study is to investigate the change in dynamics of trophic-level populations in an aquatic community under a hypothetical global warming scenario involving an increase in the mean ambient temperature.

A great deal of information regarding the effect of increasing temperature on the physiology of individual organisms has been collected (i.e. Andrewartha and Birch 1954, Wagner *et al.* 1984, Shanower *et al.* 1993). For ectothermic invertebrate populations especially, temperature plays a large role in both physiology and behaviour (Grant and Porter 1992). These individual physiological effects can translate into population level changes. Halbach (1970) determined that laboratory populations of rotifers were destabilized by increases in temperature. There was an increased frequency and amplitude of population fluctuations at higher temperatures even though food was supplied and non-dynamic. Pratt (1943) found a similar response in *Daphnia magna* populations. Past the single population level however, no known studies of interacting populations have been done to test the effect of increasing temperature on the dynamics of all populations involved. Thus, it is necessary to begin with a simple predator-prey system in order to determine how temperature influences dynamics (Ayres 1993).

There were three main objectives of this thesis. The first was to investigate how increasing ambient temperature would alter the population dynamics of a simple predator-prey system composed of *Daphnia* and their phytoplankton prey. The second was to determine how environmental complexity associated with the presence of zooplankton competitors and a diverse algal community would modify the response of the simple predator-prey system to temperature increase. The third objective was to determine how the presence of the predator of *Daphnia, Mesostoma ehrenbergii* (Focke 1836) (Turbellaria) would alter the temperature induced shift in the predator-prey dynamic. While the addition of the predator may affect the response to temperature, the contrast between two and three-level food chains can also be made to test some aspects of

food chain theory. In the next section, I present the hypotheses used to meet these objectives and some predictions.

Hypotheses

Hypothesis 1) Increasing the ambient temperature will alter the dynamics of the *Daphnia*-algal system.

Temperature has two main effects on biological systems. First, increases in temperature affect vital rates (e.g. rates of feeding, maintenance, conversion efficiency, reproduction, death), as seen in numerous physiological investigations (for phytoplankton: DiToro *et al.* 1975, Ahlgren 1987, Hanagata *et al.* 1992; for zooplankton: Hall 1964, Blazka 1966, Burns 1969, Bottrell 1975, Lampert 1977a, Vijverberg 1980, Neill 1981, Gulati *et al.* 1982, Orcutt and Porter 1984, Awaiss and Kestemont 1992, Cyr and Pace 1992). These changes alone can lead to a qualitative alteration of population dynamics as has been observed both theoretically (May 1976, Murdoch and McCauley 1985, Lawton 1987, McCauley and Murdoch 1987) and in the dynamics of laboratory populations of rotifers (Halbach 1970) and *Daphnia* (Pratt 1943).

The second effect of temperature is to increase the potential primary productivity of systems by increasing the rates of nutrient recycling by the microbial loop (Saunders 1980, Blumberg and DiToro 1990, Cooper 1990). This second effect, could also destabilize population dynamics and lead to paradox of enrichment behaviour in predator-prey systems (Rosenzweig 1971). The *Daphnia*-algal system possesses the essential biological ingredients for destabilization of dynamics via nutrient enrichment (McCauley and Murdoch 1990, Murdoch *et al.* 1992). Thus, owing to a change in population vital rates or an increase in environmental productivity, the dynamics of the plant-herbivore system should be destabilized by an increase in temperature.

Hypothesis 2) Food web simplification will alter the response to increased temperature in the predator-prey dynamic.

In most natural communities, there are several interacting populations at each trophic level. Both the phytoplankton and zooplankton are highly diverse assemblages and the potential effect of this diversity on the response of the predator-prey system to temperature is of interest.

Some investigations have suggested that species complexity may not play an important role. For example, similar dynamics of *Daphnia* and algae have been found in simple mesocosm lab communities as in complex field communities (McCauley and

Murdoch 1987, McCauley *et al.* 1988, McCauley and Murdoch 1990). The range of dynamics displayed by the *Daphnia*-algal interaction have been shown to be internally generated by the predator-prey interaction (McCauley 1993). Variability in dynamics was not found to arise predominantly from qualitative differences between habitats but rather, due to quantitative differences in parameters affecting the predator-prey interaction.

McCauley *et al.* (1988) concluded from the comparison of field and lab dynamics that the presence of additional species in the system could be modelled as part of the environment of the predator-prey interaction. The *Daphnia*-algal system is tightly coupled and can usually be modelled separately from the food web within which it is contained (Murdoch *et al.* 1992, Murdoch 1993). It remains to be determined whether community complexity affects the predator-prey responses to temperature and the trophic-level interactions under identical experimental treatments.

Hypothesis 3) The addition of a third trophic level will alter the response to increased temperature in predator-prey dynamics.

Predictions regarding the effect of the addition of a third trophic level on the stability of the predator-prey system can be made using food chain theory. It is expected that the effect of the carnivore population will be temperature-dependent. Increases in the potential primary productivity of the system are expected with increased temperature and may induce a different response, depending on the state of the system. According to the exploitation hypothesis (Oksanen *et al.* 1981), in a food chain with only one trophic level, increases in potential productivity of the environment result in direct increases in the biomass of primary producers and to no alteration of the stability of the population that follows logistic growth.

In predator-prey systems, increases in potential primary productivity lead to an increase in herbivore equilibrium biomass and in no change of the plant equilibrium. However, further increases in the rates of potential primary productivity can destabilize the system and cause predator-prey dynamics with large amplitude cycles as explained above (Rosenzweig 1971).

In a three-level food chain, food limited carnivores are expected to reduce the herbivore populations and release autotrophs from predatory control (Oksanen *et al.* 1981). In response to increases in potential productivity therefore, autotroph and carnivore biomass increase while herbivore biomass remains unchanged. In terms of stability of the plant-herbivore interaction therefore, the addition of a third trophic level

may stabilize the unstable, large amplitude cycles expected at high environmental productivity levels (Rosenzweig 1973). The response to the addition of a third trophic level will depend on the state of the predator-prey system to which it is added. This state is predicted to be temperature-dependent (see Hypothesis 1). The dynamics of the carnivore population may also provide some insight into the mechanism underlying the temperature-dependent effect of the third trophic level.

Depending on the change in dynamic observed with an increase in temperature, the addition of a third trophic level may play an important role in determining the response. A third trophic level acts to stabilize plant-herbivore dynamics when these are unstable (Rosenzweig 1973). Thus, one would expect that any destabilization of dynamics predicted for higher temperature treatments (hypothesis 1) to be stabilized by the addition of the third trophic level. However, it is uncertain whether this will occur in a system where the invertebrate carnivore is also subject to changes in vital rate parameters at the higher temperature. In addition, a carnivore population which is stage-structured, such as the one used here, may alter some the predictions that can be made from food chain theory (Oksanen *et al.* 1981).

III - Outline of Thesis

In the following chapter, I investigate the response of the *Daphnia*-algal interaction to an increase in water temperature and the influence of food web structure on observed dynamic shifts. The response to increased temperature in a baseline community type consisting of a predator-prey system is recorded. Any changes in the observed response due to simplification of the plankton communities is then examined to satisfy the second objective. Finally, changes in the response to temperature in the 2 trophic-level baseline community type are compared to those observed for the *Daphnia*-algal interaction in the 3-trophic level systems.

In chapter 3, I contrast the dynamics of the plant-herbivore system in the presence and absence of the third trophic level at the two temperatures. The coupling of the *Mesostoma-Daphnia* interaction is examined along with a detailed look at the *Mesostoma* population dynamics and life history. Species of this flatworm have demonstrated an ability to depress *Daphnia pulex* populations both in the lab (Rocha *et al.* 1990, Schwartz and Hebert 1982, Wrona and Koopowitz unpubl. manuscr.) and in natural ponds (Maly *et al.* 1980). *Mesostoma* has a generation time close to that of its prey (Heitkamp 1977), and therefore, it makes an ideal predator for studies of dynamics of all trophic levels over

several generations. There are no experimental studies to date examining the dynamics of three trophic levels in eukaryotic food chains where all levels are dynamic on similar time scales. This chapter examines the dynamics of *Mesostoma*, its effect on the plant-herbivore system and finally, how these responses may be mediated by temperature.

CHAPTER 2: The Effect of Temperature on Plankton Population Dynamics

Introduction

General Circulation Models (GCMs) of global climate change predict an increase in global mean temperature of 3.5 to 4.2°C over the next 50 years (Gribbin 1986). Moreover, this anthropogenically induced temperature increase is expected to occur at a rate 10 to 50 times faster than any natural changes observed in past climatological records (Pain 1988a, b, Roberts 1988, Botkin *et al.* 1991, Schneider 1993). In North America, the temperature rise is expected to be greatest in the midwestern United States and in the prairies of central Canada (Ramanathan 1988) where summer increases of up to 9°C are expected with doubling of atmospheric CO_2 (Schindler *et al.* 1990). The many wetlands and ponds in these areas are systems of great vulnerability and interest to conservationists. Shallow, low volume water bodies are among the first ecosystems expected to show the effects of global warming because the water temperature closely mimics ambient air temperature (Cooper 1990, Carpenter *et al.* 1992). Temperature is an important abiotic variable for all organisms. Some organisms have the capability to thermoregulate and to therefore buffer themselves against short-term changes in temperature. Other organisms, for example, aquatic invertebrates, are poikilothermic and their body temperature and metabolic rates fluctuate with changes in environmental temperature (Wennergren and Landin 1993). These temperature changes need not be large to have ecological consequences: for example, Ayres (1993) found in a study of a terrestrial plant-herbivore system, that a temperature increase of even 1°C could significantly alter population growth rates.

The question arises as to how these temperature changes will affect the population dynamics and stability of poikilothermic organisms living in shallow freshwater habitats. Increasing ambient temperature has the potential to alter the values of both the physiological rates of individuals and the vital rate parameters describing populations. The consequences of increasing ambient temperature on population stability in a plant-herbivore system has yet to be investigated under conditions where both populations are dynamic. Further, it is of interest to determine how other food web interactions such as the presence of competitors, predators or alternate prey may affect the shape of the response to temperature in the plant-herbivore interaction.

Among freshwater zooplankton, cladocerans are ubiquitously distributed and are often the major herbivores and carnivores present in these habitats (Mourelatos and Lacroix 1990). *Daphnia* spp. are typically the dominant cladocerans in lentic systems

(Goss 1978, Hebert 1978). Plankton systems are useful for answering questions regarding population dynamics for several reasons. Of the cladocera zooplankton, *Daphnia* spp. has been the most extensively studied (e.g. McCauley *et al.* 1990). They have relatively short generation times, making them ideal for studies of population dynamics and their ecological interactions (i.e. patterns of predation and competition) have been well studied (McCauley *et al.* 1990). The dynamics of lab and field populations are similar (McCauley and Murdoch 1987) and are usually scale-invariant above a certain system size (approximately 50 L) (Dibble 1993).

It has been demonstrated using simple population models, that significant qualitative changes in population dynamics can be induced merely by increases in the population growth rate '**r**' (May 1976). Changing other population level parameters have also been shown theoretically to alter dynamics and stability (Hastings and Powell 1991, Abrams and Roth 1994). Using an increase in temperature to change physiological rates is one way to alter population level parameters (May 1976). The physiology of *Daphnia* spp. has been well studied with respect to temperature and increasing temperature leads generally, to increases in most physiological rates (Table 2.1).

With many temperature-dependent physiological and developmental rates in daphnids, it becomes important to determine how processes and dynamics are affected at the population level. Alterations in population parameters describing *Daphnia*'s feeding, maintenance, conversion efficiency and death rates would be expected as a result of the physiological changes that have been described. Orcutt and Porter (1984) measured the population growth rate (**r**) of *Daphnia parvula* and found that increasing temperature over a sub-lethal range (10 to 25°C) led to a larger **r**. There have only been two key population dynamic studies with zooplankton raised at various temperatures (Pratt 1943, Halbach 1970). Pratt (1943) raised laboratory populations of *Daphnia magna* at 18°C and 25°C and noted a switch from stable population dynamics at the lower temperature to wildly fluctuating dynamics at 25°C. The instability at the higher temperature usually led to extinction of the *Daphnia* population. Halbach (1970) similarly noted that for rotifer (*Brachionus calyciflorus*) populations, the dynamics were destabilized with an increase in temperature. Sigmoid population growth seen at 15°C was replaced by successively larger amplitude and more frequent oscillations at 20°C and 25°C. It has been shown theoretically that the changes in dynamics observed in both cases can be attributed to the effect of temperature on physiological rates that determine the population growth rates and the time lags of the population (May 1976, Murdoch and McCauley 1985, Lawton

Table 2.1: Table showing the expected direction of effect of temperature increase on various physiological and life history traits of *Daphnia* species over a range of sub-lethal temperatures.

Process	Species	Direction of Effect	Source
Metabolic rate (O_2 consumption)	*D. magna*	positive	Obreshkove and Abramowitz (1932)
	D. pulex	positive	Ivanova (1965)
			Blazka (1966)
	D. pulicularia	positive	Blazka (1966)
	D. hyalina	positive	Blazka (1966)
Assimilation rate	*D. pulex*	positive	Lampert (1977a)
Filtering rate	*D. pulex*	positive	Burns (1969)
Frequency of molting	*D. galeata mendotae*	positive	Hall (1964)
Frequency of reproduction	*D. galeata mendotae*	positive	Hall (1964)
	D. pulex	positive	Craddock (1976)
Lifespan	*D. galeate mendotae*	negative	Hall (1964)
	D. parvula	negative	Orcutt and Porter (1984)
	D. hyalina	negative	Vijverberg (1980)
	D. cucullata	negative	Vijverberg (1980)
Egg development time	*D. parvula*	negative	Orcutt and Porter (1984)
	D. pulex	negative	Esslová (1959)
	Other cladocerans	negative	c.f. Bottrell (1975)
Age at first reproduction	*D. parvula*	negative	Orcutt and Porter (1984)
	D. pulex	negative	Craddock (1976)
Final body size	*D. hyalina*	negative	Vijverberg (1980)
	D. cucullata	negative	Vijverberg (1980)

1987, McCauley and Murdoch 1987). Therefore, a population can be destabilized to the point of extinction at a sub-lethal temperature without any structural changes in population or food web structure, by simple manipulation of vital rates with temperature.

Pratt (1943) and Halbach (1970) conducted population studies on single species of herbivores where prey populations were non-dynamic (i.e. a fixed amount of prey was added and under conditions where prey could not grow). *Ad libitum* levels of phytoplankton were present in the rotifer study (Halbach 1970), while an erratic phytoplankton supply schedule was used in the *Daphnia* study (Pratt 1943). The influence of temperature on the stability of a predator-prey system in which both prey and predators are dynamic remains to be determined and is important for explorations of global warming effects on natural systems (Ayres 1993).

In a phytoplankton-cladoceran system, changes in the vital rates of both the phytoplankton (DiToro *et al.* 1975, Ahlgren 1987, Hanagata *et al.* 1992) and zooplankton (see Table 2.1) are expected. A second indirect effect of temperature becomes important when examining predator-prey interactions: environmental potential productivity for the prey population (**K**). An increase in water temperature will affect the rates of decomposition and of nutrient recycling by microbes and increase the nutrient supply rate to the community (Saunders 1980, Blumberg and DiToro 1990, Cooper 1990). Thus, independent of temperature induced changes in phytoplankton or zooplankton vital rates, a destabilization response similar to the 'Paradox of Enrichment' (Rosenzweig 1971) may be expected because of an increase in **K** alone. Predator-prey systems modelled in continuous time have a tendency to oscillate (Hastings and Powell 1991) as does the underlying *Daphnia*-algal dynamic in natural systems (McCauley 1993). How these oscillations change with accelerated vital rates in both populations and with increases in environmental productivity is unknown, especially if rates of change are disproportionate between trophic levels.

The purpose of this chapter is to examine 3 major hypotheses concerning the effect of temperature on dynamics of planktonic systems:

(1) Increasing temperature will affect the dynamics of the *Daphnia*-algal system in a baseline community.
(2) Simplification of the food web will affect the response to temperature of the *Daphnia*-algal interaction.
(3) The addition of a third trophic level will affect the response to temperature of the *Daphnia*-algal interaction.

In the following section, I make some predictions regarding the dynamic responses to temperature of the *Daphnia*-algal systems and discuss the measurement of stability in experimental populations.

This study investigates the stability of an important aquatic plant-herbivore interaction under conditions of temperature change that may be expected with global warming. Based on changes in physiological rates and resultant population vital rates with temperature, both theoretical models of dynamics and the few single species population experiments that have been done suggest a destabilization of dynamics at the higher temperature. Increases in environmental productivity expected with increased temperature should also contribute to a less stable plant-herbivore dynamic at higher temperatures.

Stability is an important aspect of the dynamics of populations. The stability of populations has proven difficult to measure in experimental systems (Lawler and Morin 1993). For this reason, other indicators of local stability are often used (Connell and Sousa 1983, Pimm 1984, Lawler and Morin 1993). The most rigid definition states that a population is stable if it returns to, or remains at, a steady state value or a limit cycle following a perturbation event (Roughgarden 1979, Nisbet and Gurney 1982, Connell and Sousa 1983). Another measure that is often used is the maintenance of steady population densities regardless of whether any disturbing forces are present or not (Connell and Sousa 1983). Finally, the persistence of populations has also been used as a measure of stability (Holling 1973, Beddington *et al.* 1976). In natural systems, disturbances are rarely small enough to allow for local stability analysis. Rather, most perturbations carry populations outside of local stability boundaries (Hastings 1988). The question of biological interest is therefore usually one of global stability and the persistence of populations (Beddington *et al.* 1976) and involves the investigation of factors inducing fluctuating dynamics that may potentially lead to extinctions. In this study, the hypothesis that increasing temperature will affect the dynamics and stability of a common freshwater plant-herbivore system is tested. Stability in terms of the degree of fluctuation and the persistence of populations is of interest.

Simplification of the food web may have an effect on the response to temperature of the *Daphnia*-algal dynamic. Models of ecological systems are often restricted to examination of 2-species interactions in order to maintain mathematical tractability, despite the fact that most organisms live in more complex food web systems where competitors, and various sources of food are present (McCauley *et al.* 1988). May (1972) found that adding complexity to food webs by increasing connectance or the number of

species tended to destabilize the entire system. It has been argued however, that species not explicitly described in coupled predator-prey models can be treated as part of the environment, influencing only the average values of parameters (McCauley *et al.* 1988). For the *Daphnia*-algal interaction, McCauley and Murdoch (1987) found similar dynamics in field and mesocosm populations suggesting that predator-prey dynamics are internally generated through the coupled interaction between the consumer and its prey and this idea has been experimentally confirmed recently by McCauley (1993). It would be expected from these observations that altering community complexity within which the predator-prey interaction was embedded would lead to the same qualitative dynamics at a given temperature. Thus, the influence of food web complexity on the temperature response of the *Daphnia*-algal interaction is investigated here. Final changes in community species composition are also of interest.

In order to study the importance of food chain length on the temperature response of the plant-herbivore system, the response of the *Daphnia*-algal dynamic in the presence of the carnivore population will be investigated. Food chains in most fishless pond systems consist of at least 3 trophic levels: phytoplankton, herbivores and invertebrate carnivores. It has been demonstrated that the addition of a third trophic level can act to stabilize an unstable plant-herbivore interaction (Rosenzweig 1973, Wollkind 1976). We may expect therefore, that the addition of a carnivore to the system will counteract the destabilization predicted with an increase in temperature. However, the stability of the carnivore population may also be affected by temperature. It remains to be determined therefore, whether the destabilization expected in the *Daphnia*-algal interaction with an increase in temperature can be reversed by the addition of a carnivore population that also has elevated vital rates. Hastings and Powell (1991) have demonstrated that complex, chaotic dynamics can be obtained in a continuous time model of a 3-species food chain by simple manipulation of the parameters describing the handling times of the herbivore and carnivore trophic levels while Abrams and Roth (1994) have more recently found a similar destabilization by altering other parameters in the same model. *Mesostoma ehrenbergii* is a common flatworm predator of *Daphnia pulex* in northern temperate ponds (Göltenboth and Heitkamp 1977). It possesses a generation time close to that of *Daphnia* (Heitkamp 1977) and, as a poikilotherm, it has metabolic and population vital rate parameters that are readily changed by alterations in mean ambient water temperature (Heitkamp 1977, Kolasa 1987, Heitkamp 1988). Specific predictions cannot be made for the effect of food chain length on the plant-herbivore dynamic response to temperature because the interaction between the carnivore effects and temperature are not understood.

In order to predict changes in natural systems that may be expected with global warming, it will be necessary to conduct controlled studies of interacting populations in natural food chains and food webs. Ideally, questions of population dynamics under global warming scenarios can be approached by constructing models based on individual physiological (Dunham 1993, Murdoch 1993) and population vital rate (Ives and Gilchrist 1993) information. Using such models, we will be able to predict how both biotic and abiotic changes in community structure will affect population stability and community composition. There is however, a need to collect empirical data on species interactions above 2 trophic levels in order to completely parameterize mechanistic models of interacting populations. Standardized measurements of changes in population vital rates with temperature for 2 and 3 trophic levels under identical conditions have not been done (Crawley 1990). This information is required because it is likely that vital rates change disproportionately between different trophic levels. Controlled comparative experiments are useful for identifying areas where population interactions lead to unexpected results and where further mechanistic explanation is required (Crawley 1990, Woodward 1992, Ayres 1993, Ives and Gilchrist 1993).

The current study involves an investigation into the effect of increasing temperature to a level expected under current global change scenarios for the prairies of North America, on an important planktonic plant-herbivore system consisting of *Daphnia pulex* and phytoplankton. Experimental mesocosms are used as they provide a controlled method for monitoring population dynamics in aquatic communities. The response to temperature in the predator-prey dynamics are examined within several food web contexts in order to determine how it is affected by biotic interactions.

Materials and Methods

Experimental Setup and Design

Aquatic mesocosms were used to investigate the effects of temperature on simple communities. Freshwater systems are useful for preliminary studies of global change because they have been well studied in the past and a large body of biotic information is available. Mesoscosms provide a method of simulating some fundamental properties of natural ecosystems in order to investigate experimentally, properties of communities such as trophic level interactions, community succession, community metabolism and stability (Rees 1979). Although the mesocosm community may not be a direct analog of any natural communities, the major functional groups are represented. Populations in

mesocosms have been shown to display qualitatively and quantitatively similar dynamics to field populations (McCauley and Murdoch 1987, 1990).

Plankton communities were maintained in 750 L rectangular polyethylene tanks housed under constant conditions at the National Hydrology Research Institute in Saskatoon, Saskatchewan.

The tanks were half filled with dechlorinated tap water from the Saskatoon water supply on May 13, 1993. This water was filtered through a Fluval® Power Filter 403 (1200 L/hour) equipped with ammonia removing rocks and ultragrade carbon to remove chlorine. The tap water in each tank was filtered for 2 hours and left to stand for 4 days before any pond water was added. Pond water was obtained from a research pond belonging to the Saskatchewan Research Council (SRC) located about 1 km from the site of the experiments. The pond was constructed over 20 years ago. A full nutrient analysis of water samples from the SRC pond was done at the Limnology Laboratory at the University of Alberta in Edmonton (Table 2.2). The pond water was added to all tanks on May 17, 1993 (Julian Day 137).

Communities were reared at two temperatures: 18°C and 25°C. A 7°C temperature change was chosen to represent a likely mean temperature change under predicted global warming scenarios (Schindler *et al.* 1990). In addition, the two temperatures were chosen to ensure that both were non-lethal for *Mesostoma* (Heitkamp 1977) and this clone of *Daphnia pulex* (McCauley and Murdoch 1987, McCauley unpublished data). There were a total of 9 tanks at each temperature. The 18°C water temperature was maintained by keeping the ambient air temperature at 18°C using air conditioners in a sealed room. For the 25°C treatments, three 300 W aquarium immersion heaters were used per tank.

For the 18°C treatment, the water temperature upon inoculation with *Daphnia* was between 16°C and 18°C. For the 25°C treatment, there was a transient period in the increase of water temperature from 18°C to 25°C that took place over about a 20 day period (see Figure 2.1 for a typical temperature time-series). Table 2.3 compares the rates of increase for temperature in natural pond and lake systems in Alberta during spring warming with the rate of increase of temperature in the 25°C tanks. The rates of increase in the experimental tanks are lower than those typically seen in natural systems.

To investigate the effect of temperature on planktonic population dynamics, a baseline community type was set up. This community type was defined by the extent to which the pond water was filtered as it passed into the tanks. All biota smaller than

Table 2.2: Results of the nutrient analysis done on a water sample from the SRC pond collected on May 9, 1993 and analysed at the Limnology Laboratory at the University of Alberta, Edmonton.

Nutrient parameter	Value
NO_3+NO_2	6.5 µg/L
NH_4	0.6 µg/L
Total Kjeldahl Nitrogen	1123 µg/L
Soluble Reactive Phosphorus	4.7 µg/L
Total Phosphorus	129.2 µg/L
HCO_3	106.35 mg/L
CO_3	11.93 mg/L
Total Alkalinity	107.13 mg/L as CaCO3
Conductance	381 µmhos/cm
pH	8.85

Figure 2.1: Typical temperature values (in °C) for the 25°C (solid line) and the 18°C (dashed line) treatments for the duration of the experimental period. The values are taken from tanks 2c18-3 and 2c25-3.

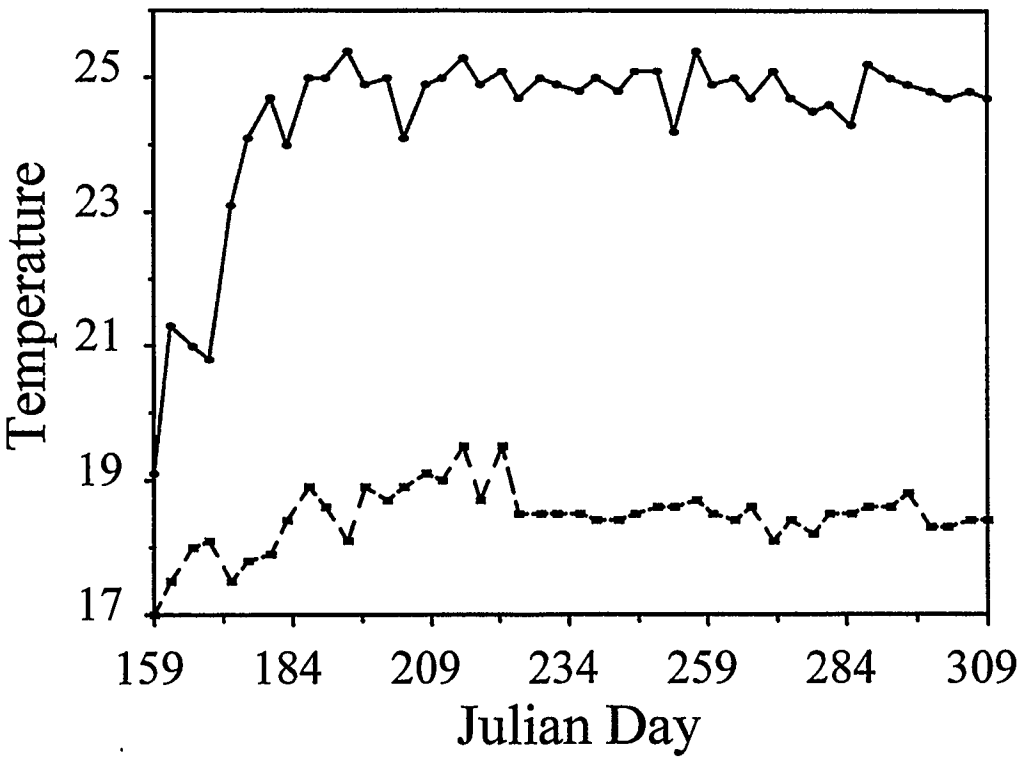

Temperature
25
23
21
19
17
159
184
209
234
259
284
309
Julian Day

Table 2.3: The rates of temperature change during spring warming for several natural aquatic systems in Alberta and for the experimental tanks in this study. Rates of change were calculated using the log-transformed temperature values.

System	Source	Depth of water (m)	Low Temp. (°C)	High Temp. (°C)	Number of Days	Rate of Change (day^{-1})
Pond	Lei and Clifford (1974)	2.5	3	15	26	0.062
Pond	Lei and Clifford (1974)	2.5	15	18	8	0.023
Pond	Davies and Everett (1977)	1.5	4	16	30	0.046
Pond	Davies and Everett (1977)	1.5	2.5	10	60	0.023
Lake	Gallup (1978)	5	4	10	60	0.015
Lake	Gallup (1978)	5	10	17	45	0.012
Tank 2c25-1		0.5	18.9	24.4	28	0.009
Tank 2c25-2		0.5	18.8	24.3	31	0.008
Tank 2c25-3		0.5	19	24.7	25	0.010
Tank 2s25-1		0.5	19.7	24.4	17	0.013
Tank 2s25-2		0.5	18.4	23.8	17	0.015
Tank 2s25-3		0.5	19.4	25.3	17	0.016
Tank 3c25-1		0.5	19.1	23.6	28	0.008
Tank 3c25-2		0.5	16.4	24.9	14	0.030
Tank 3c25-3		0.5	18.4	24.4	17	0.017

60 μm were able to pass through the Nitex® net. There were a total of 6 tanks containing the baseline community type with three replicate tanks at 18°C and three at 25°C. A single clone of *Daphnia pulex* (Leydig) was then added to all tanks over a series of inoculation dates. Ten adult *Daphnia* individuals were added to tank water contained within a 1 L Ehrlenmeyer flask. Each flask was suspended in its respective tank for 24 hours to allow the *Daphnia* to acclimate to the tank temperatures. *Daphnia* were then released into the tanks and the flasks were refilled and the process repeated over a period of 18 days (May 28 to June 15, 1993; Julian days 148 to 166). A total of 65 individuals were added per tank on 7 separate dates. Experience has shown that 15 to 20 days is required for D. *pulex* populations to become established in mesocosms (McCauley pers. comm.). These baseline communities consisted therefore of 2-trophic level food chains of *Daphnia pulex* and their phytoplankton prey within a community of herbivores and algae.

To test the hypothesis that community structure in terms of the presence of herbivore competitors and complexity of the algal species composition, can alter *Daphnia*-algal dynamics, simpler communities were also set up in 6 tanks (3 replicates at each temperature) by filtering the pond water using a smaller pore size. The goal was to exclude potential competitors such as rotifers or other cladocerans and to potentially simplify the phytoplankton species composition. Pond water for these plankton communities was filtered through the 60 μm Nitex® mesh as in the baseline communities. Subsequently, the water was further filtered through three successive Omnifilter™ drinking water filters equipped with taste/odour cartridges (20 μm mesh). *Daphnia* individuals were inoculated into these tanks using the same method and schedule as described for the baseline community type.

Three-trophic level systems were also created, to test the effect of the addition of a third trophic level on the response of the *Daphnia*-algal dynamics to temperature. Three replicate tanks at each temperature, containing baseline communities were inoculated with the carnivore species. *Daphnia pulex* were added in the same manner to these tanks as for the other treatments. The carnivore trophic level consisted of *Mesostoma ehrenbergii* (Focke 1836) (Turbellaria). *Mesostoma* produces 2 types of eggs: subitaneous and dormant. Subitaneous eggs contribute immediately to population growth within a growing season while dormant eggs are resting eggs that contribute only to the next year's population. *Mesostoma* was collected from a pond northwest of Calgary, Alberta. Individuals were added to the 3-level tanks using the Ehrlenmeyer flasks as was described for the *Daphnia*. Initially, 40 adults (mostly possessing subitaneous eggs) were

added on June 18, 1993. On 2 more dates, ending on June 26, 1993, a total of 110 juvenile *Mesostoma* were added to the 3-level treatment tanks.

Figure 2.2 shows the arrangement of tanks and their treatment classifications. Tanks were randomly assigned to treatments, except for the position of the baseline and simplified community treatments. These treatments had to be separated in order to avoid inadvertent splashing of water from the more complex baseline systems into the simpler community tanks. Plywood sheets that extended approximately 50 cm above the tanks were placed between adjacent tanks housing the simple and baseline communities to avoid accidental splashing. These sheets did not alter the local environments for the tanks nor create average environmental differences in light levels, since each tank was equipped with its own light source (see below). Equipment used for mixing water (paddles and buckets) was duplicated so that there was a separate set for the simpler and baseline systems.

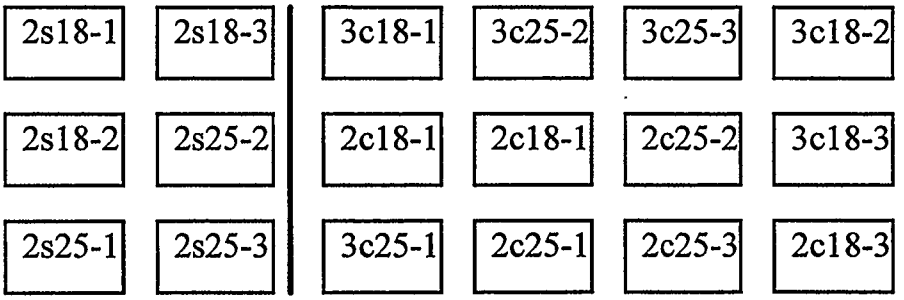
All tanks were equipped with an airstone that provided a constant air supply. The water temperature in each tank was monitored at each sampling date (Fig. 2.1 for a representative temperature series). Each tank was individually illuminated on a 12:12 hour light:dark regime by a bank of 4 Gro-Light® fluorescent tubes that was positioned 1m above the surface of the water. Water conductivity and pH were measured on each sampling date and remained relatively constant throughout the experimental period. Every week, 2 to 3 L of filtered and autoclaved pond water was added to all tanks. Due to evaporative water loss, approximately 20 to 40 L of distilled water was added to all tanks weekly, as required. These constant conditions were maintained throughout the entire experimental period (150 days) from June to early November 1993 (Julian day 169 to 309).

Sampling was done every Tuesday and Friday. Physical variables (pH, temperature and conductivity) were measured on each date. Samples for nutrient analysis (total phosphorus and total dissolved nitrogen) were taken once a month from 6 randomly chosen tanks. Nutrient analysis was done at the Water Quality Branch of Environment Canada in Saskatoon. Samples for phytoplankton, rotifers, crustacean zooplankton and *Mesostoma* were taken on each sampling date (see below). Each tank had its own set of sampling bottles. Before sampling, tanks were well mixed using a paddle.

Phytoplankton sampling

Three 1L samples of water were taken at mid-depth from three random locations in each tank. These samples were taken after mixing using 1L wide-mouthed Nalgene®

Figure 2.2: The layout of the tanks and their assigned treatments. The combination of letters and numbers inside the boxes indicates the treatment and the number following the dash indicates the replicate number. The first number indicates the length of the food chain. The complexity of the community is represented by the letters 's' (simplified) or 'c' (complex). The final 2 numbers indicate the temperature treatment in °C. The baseline community tanks begin with '2c' while the simplified community types begin with '2s' and the treatments containing the carnivore begin with '3c'. The vertical line between the second and the third columns indicates the placement of the plywood sheet used to prevent splashing.


2s18-1
2s18-3
3c18-1
3c25-2
3c25-3
3c18-2
2s18-2
2s25-2
2c18-1
2c18-1
2c25-2
3c18-3
2s25-1
2s25-3
3c25-1
2c25-1
2c25-3
2c18-3

bottles. The water was mixed in a bucket and a 125 mL subsample was poured into a flintglass bottle. These samples were preserved with Lugol's Iodine (Lund *et al.* 1958) solution and used for identification and enumeration of algal species. Table 2.4 lists the tanks and dates for which phytoplankton counts were done. Two dates were analysed for all tanks counted; an 'early' date during the peak *Daphnia* population biomass and the corresponding low phytoplankton period and, a 'late' date while *Daphnia* were declining and phytoplankton biomass was increasing. A 10 mL subsample was settled in a counting chamber for 12 hours and then examined using an inverted microscope. Half the chamber was counted at 100X power to determine the length and species composition of the large filamentous phytoplankton. Transects were also counted at 400X power in order to classify and count the smaller phytoplankton. Transects were completed when a minimum of 400 individuals were counted to reduce counting error to within 20% (Lund *et al.* 1958). Larger phytoplankton were measured and identified, while smaller phytoplankton were classified based on size and the possession of flagella. Calculations were then done based on the size and shapes of phytoplankton to determine biomass estimates for the major groups (Watson pers. comm.).

One 1 L phytoplankton sample was taken from the middle of each tank after mixing using a dark narrow-mouthed Nalgene® bottle for chlorophyll *a* analysis. Chlorophyll *a* was determined using a fluorometer and ethanol extraction (Waiser pers. comm.) for whole water samples and for size-fractionated subsamples (< 35 μm).

In addition to these quantitative measures of phytoplankton biomass, weekly observational notes were recorded on the state of each tank (periphyton, algal growth, clarity of water column, relative densities of *Daphnia*). Every 2 weeks, photographs were taken of every tank.

Zooplankton sampling

After stirring the tanks, four 1 L samples were taken using clear wide-mouthed Nalgene® bottles. Two samples were drawn from the upper portion of the tank (≈ 20 cm from the top) (upper samples) and two were drawn from ≈ 20 cm from the bottom (lower samples). Samples from each depth were combined and then filtered through a 35 μm mesh net. Zooplankton were anaesthetized with carbonated water and then preserved in a 4 % sugar-formalin solution. The filtrate was returned to the tanks. Samples were completely censused separately for each depth (upper and lower) and the major taxonomic groups of zooplankton identified using a dissecting microscope at 60X

Table 2.4: Dates of the phytoplankton counts and the tanks for which they were done. The 'Early Date' (Julian Day) indicates the count done for the period during which *Daphnia* biomass was high and phytoplankton biomass (estimated from chlorophyll *a*) was low and the 'Late Date' indicates the count done for the period during which the *Daphnia* populations were declining and the phytoplankton biomass was increasing.

Treatment and Tank	Early Date	Late Date
i) Baseline		
2c18-1	187	246
2c18-2	190	215
2c18-3	194	225
2c25-1	180	194
2c25-2	180	194
2c25-3	180	208
ii) 2-Level Simplified		
2s18-1	187	246
2s25-1	194	215
2s25-3	176	190
iii) 3-Level		
3c18-1	190	232
3c25-1	173	194
3c25-3	180	194

magnification. The density of *Daphnia pulex* was recorded for 5 size classes (S1 ≤ 0.8 mm, S2 = 0.8-1.0 mm, S3 = 1.0-1.4 mm, S4 = 1.4-2.0 mm, S5 ≥ 2.0 mm) and clutch size was recorded for each fecund adult. Rotifer counts were done by enumerating the entire contents of a 10 mL subsample that had been settled for four hours. Populations were counted using an inverted microscope at 400X magnification and rotifer individuals were identified to genus.

Mesostoma sampling

Mesostoma ehrenbergii adults prefer hard substrates, which makes simple pelagic sampling of the population difficult and inaccurate. For this reason, all tanks contained two PVC columns (Fig. 2.3), including the 2-level food chain treatment tanks to control for any structural differences the columns may have created in the 'pelagic' zone. These columns were as tall as the water depth and had several surfaces for *Mesostoma.*

Mesostoma were sampled by lowering a 20 cm diameter tube over the column. The base of the column consisted of a plate with 60 μm mesh covering 4 holes that allowed water to filter through as the columns were pulled from the tanks. This mesh trapped all individuals in the base of the columns. Sampling for *Mesostoma* occurred before tank water was mixed. The length of individuals as well as the number of subitaneous and dormant eggs were measured under a dissecting microscope. The egg types are easily distinguished through the clear body wall of *Mesostoma ehrenbergii.* Subitaneous eggs are translucent and contribute immediately to population growth while dormant eggs are black, resting eggs. All individuals were returned to their respective tanks after about 15 minutes, when sample processing was complete.

Data Analysis

A correlation analysis of the lower and upper sample *Daphnia* series showed the dynamics at the two depths were highly correlated (most r greater than 0.85) (Table 2.5), and as a result, the series were combined for ease of analysis. Temporal dynamics for total *Daphnia* biomass, the edible size fraction for phytoplankton, *Daphnia* demography and all other zooplankton present were examined. For the *Daphnia* demography data, individuals less than 1 mm (S1+S2) were classified as juveniles, individuals between 1 mm and 1.4 mm (S3) were classified as adolescents and individuals greater than 1.4 mm (S4+S5) were mature and were classified as adults (McCauley and Murdoch 1987). Individuals less than 1.4 mm are virtually never reproductive although, it is possible for

Figure 2.3: Schematic diagram of the sampling device used to census *Mesostoma ehrenbergii* populations. The diagram to the left represents the columns that were placed in all tanks and the diagram on the right represents the tube placed over the column during sampling.

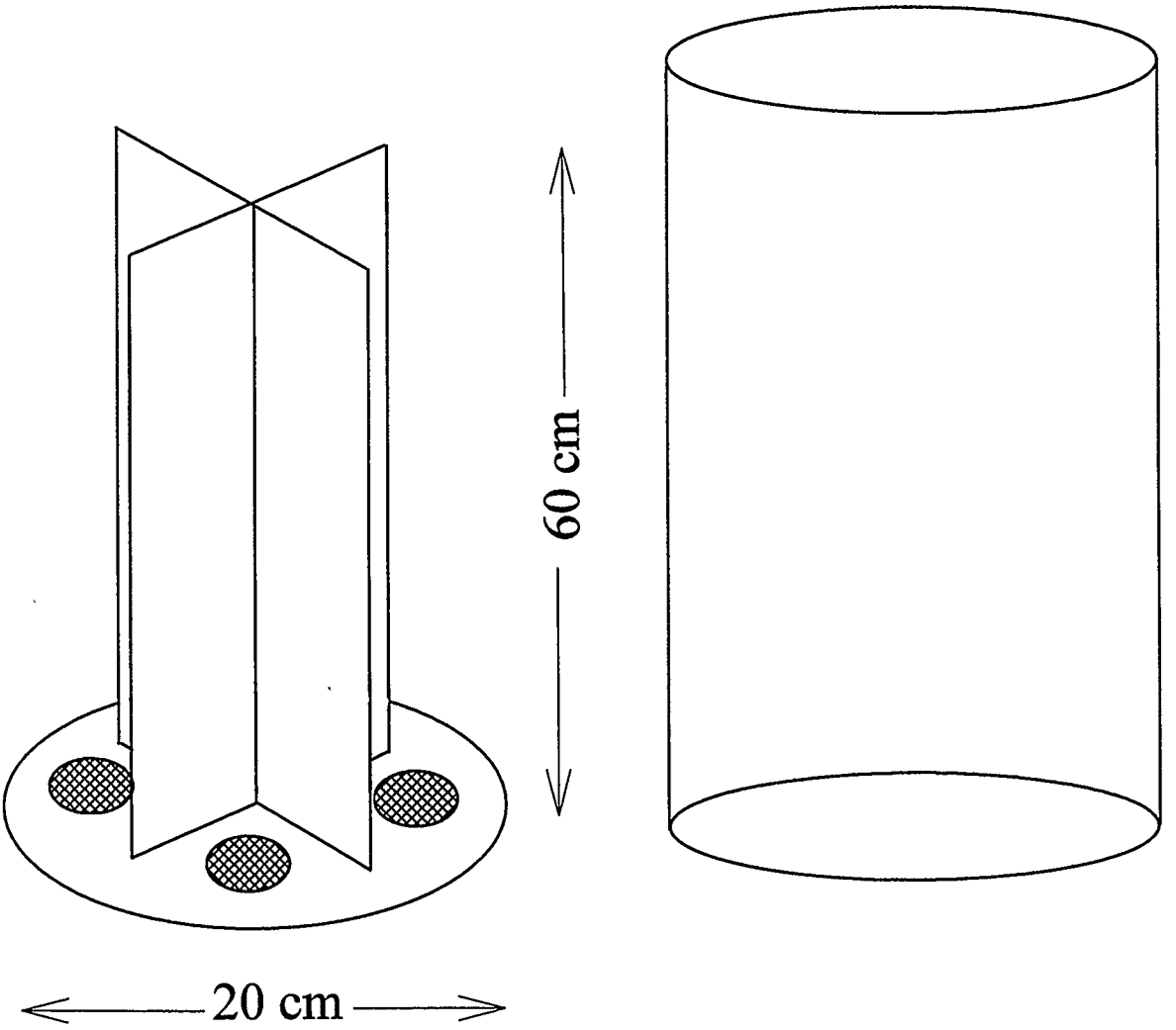

60 cm
20 cm

Table 2.5: Pearson correlation coefficients (r) for the lower and upper *Daphnia* log density time-series.

Baseline		Simplified		3-Level	
Tank	r	Tank	r	Tank	r
2s18-1	0.92	2c18-1	0.95	3c18-1	0.94
2s18-2	0.93	2c18-2	0.89	3c18-2	0.88
2s18-3	0.87	2c18-3	0.92	3c18-3	0.92
2s25-1	0.89	2c25-1	0.95	3c25-1	0.96
2s25-2	0.89	2c25-2	0.93	3c25-2	0.95
2s25-3	0.84	2c25-3	0.93	3c25-3	0.93

adults to also be non-reproductive, especially if food levels are low (McCauley and Murdoch 1987).

Due to the short time-series at 25°C, a formal time-series analysis to test for temperature effects was not feasible. Time is non-random and time-series data (i.e. repeated observations on an experimental unit) tends to violate the assumption of independence of observations in analysis of variance. For these reasons, time cannot simply be incorporated into an ANOVA design as a split factor (Mead 1988). There are 3 remedial measures that can be used to account for time-dependent observations: derived variables, response functions or multivariate analyses (Mead 1988). Using derived variables involves selecting variables objectively at particular points in time; or calculated averages of variables over time to detect patterns of treatment variation. Response functions are an extension of this idea and involve fitting functions to experimental units, and analysing the parameters from these functions within the original framework of the experimental design (Mead 1988). Finally, multivariate analyses such as repeated measures ANOVA can be used (Mead 1988). These methods involve treating time as a separate factor. This final method makes interpretation of multi-factor designs difficult however. In this chapter, the principal measure used to test for temperature differences was derived (response) variables. Features of the time-series were compared between treatments in a factorial ANOVA design. Descriptions of the response variables chosen are listed in Tables 2.6, 2.7 and 2.8.

A 2-way factorial ANOVA was done on each response variable to test for the effects of temperature and community complexity or food chain length. When necessary, the data was log transformed or arcsine transformed (for proportional data) to reduce heteroscedasticity. One 2-way ANOVA was done to test the combined effects of temperature and community complexity. Similarly, a separate analysis was done to test the interaction and main effects of temperature and food chain length. A full 3-way ANOVA combining all treatments into one analysis could not be done because the design was unbalanced since there was no 3-level simplified treatment.

Table 2.6: Descriptions of the response variables measured for the phytoplankton (where edible phytoplankton is the size fraction <35 μm) and the *Daphnia* biomass time-series. See text for further explanations.

Response Variable	Units	Description
Phytoplankton biomass		
Minimum edible biomass	(μg/L)	Average of the phytoplankton biomass values on the date of the first maximum *Daphnia* biomass and the date preceding it.
Absolute minimum edible biomass	(μg/L)	Absolute edible minimum biomass while *Daphnia* were present.
Date of absolute minimum	Julian day	Date on which the absolute edible minimum biomass occurred.
Maximum edible biomass	(μg/L)	The biomass value of the first maximum in phytoplankton biomass after *Daphnia* inoculation.
Date of maximum biomass	Julian day	Julian date on which edible maximum biomass occurs.
***Daphnia* biomass**		
Population growth rate	day^{-1}	The *Daphnia* population growth rate (the slope of the log biomass versus time relationship calculated from the date of inoculation to the first maximum biomass level).
First maximum biomass	mg/L	The first peak in total *Daphnia* biomass
Date of maximum biomass	Julian day	Date on which first maximum biomass occurs
Period of high biomass	days	Period of time beginning when total *Daphnia* biomass is > 0.5mg/L and ending with the last peak where biomass is still > 0.25mg/L
Start of high biomass	Julian day	Date at which *Daphnia* biomass first reaches levels > 0.5mg/L
Persistence time	days	Time period between day 159 (start of experiment) and the first of 2 consecutive dates on which there were zero values for *Daphnia* biomass followed by no later increases above 0.05mg/L

Table 2.7: Descriptions of the response variables measured for *Daphnia* demography and fecundity. See text for further explanations.

Response Variable	Units	Description
Age Class Densities		
Maximum density of juveniles/adolescents/adults	(#/L)	The first maximum density for each age class of *Daphnia* (Juvenile=S1+S2, Adolescent=S3, Adult=S4+S5) (c.f. McCauley and Murdoch 1987).
Date of juvenile /adolescent/adult maximum	Julian day	Date of first maximum density for each age class
Percent juveniles /adolescents/adults during decline		Percent of total density consisting of each age class during the defined decline period for the *Daphnia* population (period from the end of high biomass to the end of the population persistence time)
Egg Production		
Total reproductive days	days	The total number of days on which there were > 0 eggs/adult.
Proportion of existence time		# reproductive days / total # days *Daphnia* present
Number of reproductive bouts		Number of discrete bouts of reproduction; delimited by periods of 0 eggs/adult
Average length of bouts	days	Average duration of all the reproductive bouts
Ephippia Production		
Number of production days	days	The total number of days on which ephippial individuals were recorded
Proportion of existence time		# days of ephippia production / total days *Daphnia* present
Number of bouts		Number of discrete ephippial bouts (delimited by 0 ephippia/adult)
Average length of bouts	days	Average duration of all the ephippial bouts
Start of ephippia production	Julian day	First date on which ephippial individuals were recorded

Table 2.8: Descriptions of the response variables measured for all other zooplankton groups (i.e. Rotifers, *Ceriodaphnia* sp., *Alona* sp., and Ostracoda)

Response Variable	Units	Description
Peak density	(#/L)	The peak density of the entire time-series
Date of peak density	Julian day	Date on which this peak density occurs
Date of entry	Julian day	First date on which a density value greater than 0 was recorded
Average density	(#/L)	The average density over the entire time-series

Results

I - The Effect of Temperature in 2-Level Food Chains

Edible Phytoplankton and Total *Daphnia* Biomass

There was an inverse predator-prey relationship between *Daphnia* biomass and the edible phytoplankton biomass observed for all tanks (Fig. 2.4). At both temperatures, *Daphnia* population growth to peak biomass led to a large decline in chlorophyll *a* in the edible size fraction (< 35 μm). In general, when the average *Daphnia* biomass was high, phytoplankton biomass levels were low and vice versa. Decline of *Daphnia* populations occurred at both 18°C and 25°C, and in both cases this was accompanied by an increase in phytoplankton biomass. Quantitative characteristics of these changes differed with temperature and will be discussed later.

At 18°C, there was an extended period (≈ 47 days) during which *Daphnia* biomass was high and phytoplankton biomass was low. Following this period, there was a decline to low levels at which the *Daphnia* population persisted in most cases for the duration of the experimental period (excluding tank 2c18-3) (Fig. 2.4). Raising the temperature led to a change in the dynamic from one of an extended period of persistence (18°C), to one where a large population peak was followed by rapid decline to extinction (25°C). The major qualitative differences lie in the change in shape of the *Daphnia* dynamic and in the shift from persistence to extinction with an increase in temperature (Fig. 2.4).

In the higher temperature treatment, the *Daphnia* populations had already started to decline before the maximum temperature of 25°C was reached. The populations reached their peak densities and started to decline when the temperature was approximately 23 or 24°C.

Several response variables were chosen to characterize the dynamics and to test for temperature effects on quantitative aspects of the time-series (see Tables 2.6 to 2.8 for definitions). During the *Daphnia* population growth and colonization period at both temperatures, chlorophyll *a* in the edible size fraction (i.e. <35 μm) reached low levels (≈ 0.2 μg/L) by day 173 (Fig. 2.4). Temperature had no effect on the minimum edible biomass level measured as the minimum on the date of peak *Daphnia* biomass (P=0.2177) or as the first absolute minimum value of edible phytoplankton (P=0.6380) (Table 2.9). However, the decline to absolute minimum levels occurred 13 days earlier at 25°C (P=0.0165) (Table 2.9).

Figure 2.4: Total *Daphnia* biomass (——) and edible phytoplankton biomass (——) for the 3 replicate tanks in the 18°C and the 25°C baseline treatments.

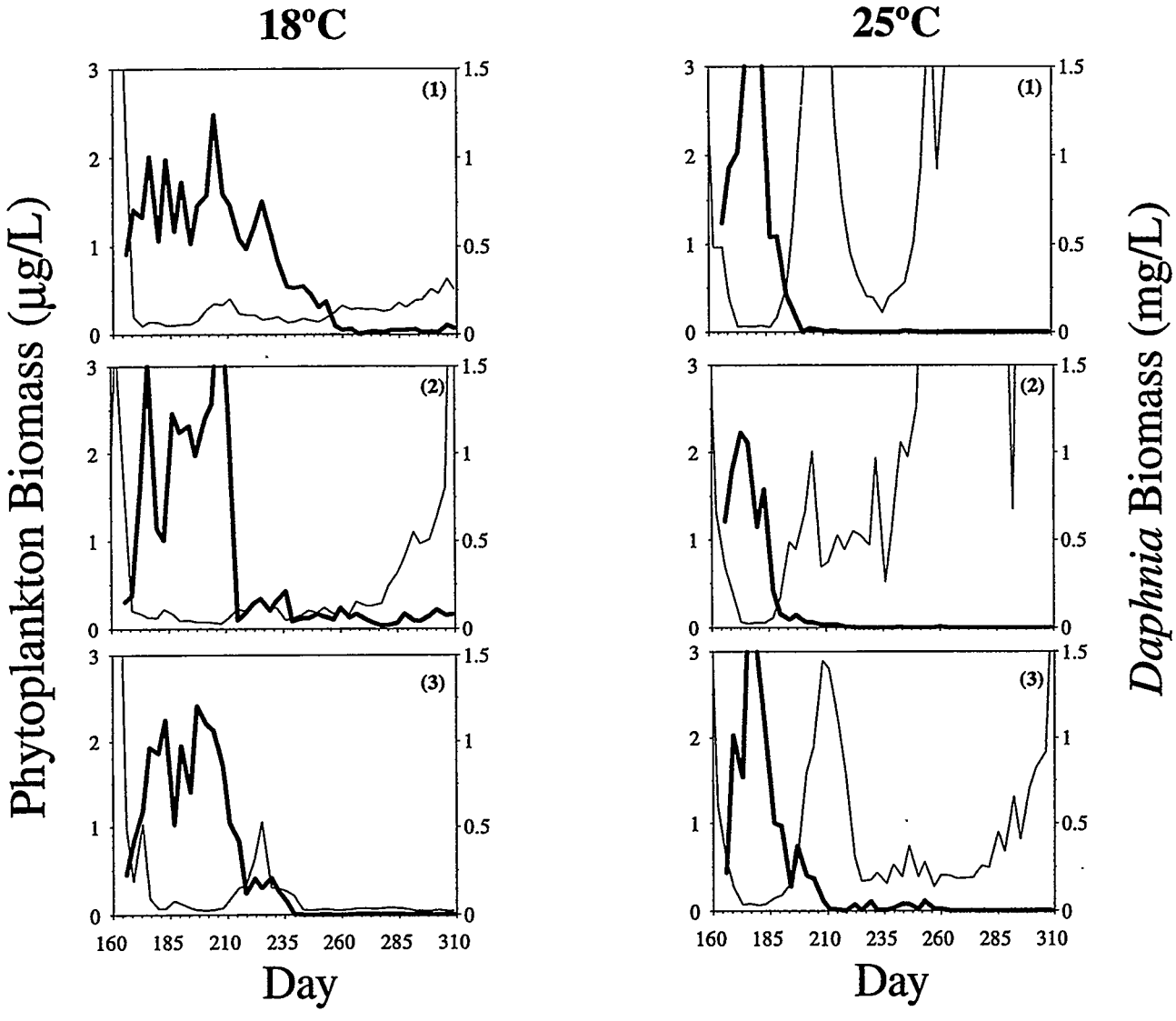

18°C
25°C
Phytoplankton Biomass (µg/L)
Daphnia Biomass (mg/L)
(1)
(2)
(3)
0
1
2
3
0
0.5
1
1.5
160
185
210
235
260
285
310
Day

Table 2.9: The response variable averages ± standard errors for *Daphnia* biomass and demography and for phytoplankton biomass at 18°C and 25°C for the baseline treatment. The definitions of the response variables are given in Tables 2.6 and 2.7.

Response Variable	18°C	25°C	*P* value
Phytoplankton Biomass			
Minimum edible biomass	0.113 ± 0.02	0.126 ± 0.06	0.2177
Absolute minimum edible biomass	0.137 ± 0.081	0.055 ± 0.006	0.6380
Date of absolute minimum	194 ± 10	181 ± 3	0.0165
Maximum edible biomass	0.57 ± 0.24	3.71 ± 1.29	0.0095
Date of maximum biomass	237 ± 11	189 ± 3	0.0005
***Daphnia* Biomass**			
First maximum biomass	1.22 ± 0.16	1.54 ± 0.22	0.2737
Date of maximum biomass	178.3 ± 2.3	177.3 ± 2.9	0.2490
Population growth rate	0.019 ± 0.006	0.032 ± 0.001	0.0073
Start of high biomass	172 ± 1.2	167 ± 1.2	0.0001
Period of high biomass	46.7 ± 13.7	23.3 ± 3.5	0.0038
Persistence time	129 ± 21.0	76.7 ± 14.3	0.0121
Age Class Densities			
Maximum juvenile density	58 ± 13.3	70 ± 17.3	0.1042
Date of juvenile maximum	174 ± 1.2	172 ± 1.2	0.0520
Maximum adolescent density	16.5 ± 4.0	21.9 ± 3.2	0.0272
Date of adolescent maximum	176 ± 0	174 ± 1.2	0.2145
Maximum adult density	34.7 ± 7.7	40.8 ± 8.4	0.7610
Date of adult maximum	178 ± 2.3	178 ± 2.3	1.0000
Percent juveniles during decline	11 ± 5.8	33 ± 2.9	0.0093
Percent adolescents during decline	10.6 ± 6.0	28.7 ± 4.0	0.0338
Percent adults during decline	78 ± 11	30 ± 2	0.0038
Egg Production			
Total reproductive days	105.3 ± 20.8	36.7 ± 15.0	0.0065
Proportion of existence time	0.87 ± 0.09	0.49 ± 0.14	0.0244
Number of reproductive bouts	5 ± 1.2	3.7 ± 1.8	0.0946
Average length of bouts	22.3 ± 4.1	10.7 ± 0.9	0.0080
Ephippia Production			
Number of production days	43.3 ± 11.0	29.3 ± 2.2	0.0125
Proportion of existence time	0.35 ± 0.05	0.45 ± 0.06	0.6938
Number of bouts	2.3 ± 0.9	2.3 ± 0.4	0.9615
Average length of bouts	20.6 ± 2.7	12.9 ± 1.7	0.0528
Start of ephippia production	173 ± 0	167 ± 1.2	0.0001

During the colonization period, *Daphnia* biomass increased to maximum levels (Fig. 2.4). The first peak in population biomass was greater at the higher temperature (Table 2.9). This difference was not significant however (P=0.2737), probably because one tank (2c25-2) did not reach high levels. The other two 25°C tanks had much higher peak levels than any of the replicates at 18°C (Fig. 2.4). Temperature had no effect on the timing of the *Daphnia* maximum which occurred around day 177 and 178 (P=0.2490) (Table 2.9). At either temperature, a comparison of the date on which the phytoplankton was reduced to low levels (≈ day 173) and the date of *Daphnia* peak biomass (day 177.5), demonstrates that phytoplankton biomass was reduced to low levels before the *Daphnia* population had reached its peak levels (Fig. 2.4) (i.e. *Daphnia* populations continued to increase for a period once the phytoplankton had been suppressed). Increasing temperature led to a significant difference in the *Daphnia* population growth rates measured as the slope of the log biomass values from inoculation levels to the peak biomass (P=0.0073) (Table 2.9). *Daphnia* also reached high biomass levels (defined as 0.5 mg/L) earlier as temperature was raised (P=0.0001). A biomass of 0.5 mg/L was chosen because the first date of sampling for some of the warmer tanks showed the populations had already reached biomass levels just below this level. Thus, a smaller value could not have been used to discriminate between treatments. This level was attained earlier, by day 167, in the high temperature treatment while at 18°C, it took until day 172 (Table 2.9).

Another characteristic of the *Daphnia* time-series measured was the period during which *Daphnia* were present at high biomass levels. The start of this period was defined as the first date on which *Daphnia* biomass reached a level of at least 0.5 mg/L for reasons already explained. The end of the period was defined as the last peak in the *Daphnia* time-series where the biomass level was still greater than 0.25 mg/L (Table 2.6). The length of this period was twice as long at 18°C (P=0.0038) lasting 47 days while at 25°C the period lasted only 23 days (Table 2.9).

The end of the period of high population biomass levels was characterized by extinction at 25°C and by population reduction at 18°C (Fig. 2.4). At 18°C, in the baseline communities, the *Daphnia* populations persisted at low densities for the duration of the experiment in all but one tank (2c18-3), where extinction occurred . The average persistence time of the *Daphnia* populations was significantly shorter at 25°C (P=0.0262) lasting 77 days, while at 18°C it lasted 129 days (where the experimental period was 150 days) (Table 2.9) It must be stressed that extinction occurred in only one tank at 18°C and, had the experiment not ended after 150 days, the average persistence of the

populations would have been even longer in this treatment. The qualitative difference of extinction versus persistence is the important result here.

When the *Daphnia* populations began to decline at both temperatures, phytoplankton biomass increased (Fig. 2.4). Algal biomass increased to maximum levels faster at 25°C (P=0.0005) and peak levels were higher (P=0.0095) at 25°C (Table 2.9).

In order to understand possible mechanisms for the decline of the *Daphnia* populations, detailed identification and enumeration of the phytoplankton species was done. The major phytoplankton groups present in all 18 tanks were: *Schizothrix calcicola*, *Oscillatoria limnetica*, *Anabaena lemmermannii* var. *minor*, *Gloeocystis ampla*, *Scenedesmus* spp., *Navicula* sp., *Synedra acus*, *Chrysamoeba* sp., *Chlorella* sp., and several groups of small flagellates (e.g. *Rhodomonas minuta*, *Gymnodinium* sp., *Kephyrion sitta* and *Chrysochromulina parva*, *Chromulina* sp.). Differences in phytoplankton composition between the 2 dates counted for each tank indicated a slight trend with temperature in the algal composition during the decline phase of the *Daphnia* populations (Table 2.10). For the baseline community type, larger losses in the proportion of biomass less than 35 μm were more common at 25°C (Table 2.10), and were usually associated with larger increases in the biomass of *Anabaena*. At 18°C, the only large change in the proportion of edible phytoplankton biomass (i.e. <35 μm) occurred in tank 2c18-3 where there was a 29% decline in edible phytoplankton biomass (Table 2.10). This was also the only tank at 18°C in which extinction of the *Daphnia* population occurred (Fig. 2.4).

In addition to the detailed phytoplankton enumeration, weekly observations on the tanks indicated that at the higher temperature, the extinction of *Daphnia* was usually accompanied by the growth of macroscopic filamentous algae while at 18°C, no filamentous growth was associated with the decline to lower levels. However, in all cases, periphyton growth on the sides and bottoms of the tanks was observed. A larger surface area, covered by a thicker layer of periphyton was noted in the higher temperature treatment.

Daphnia Demography

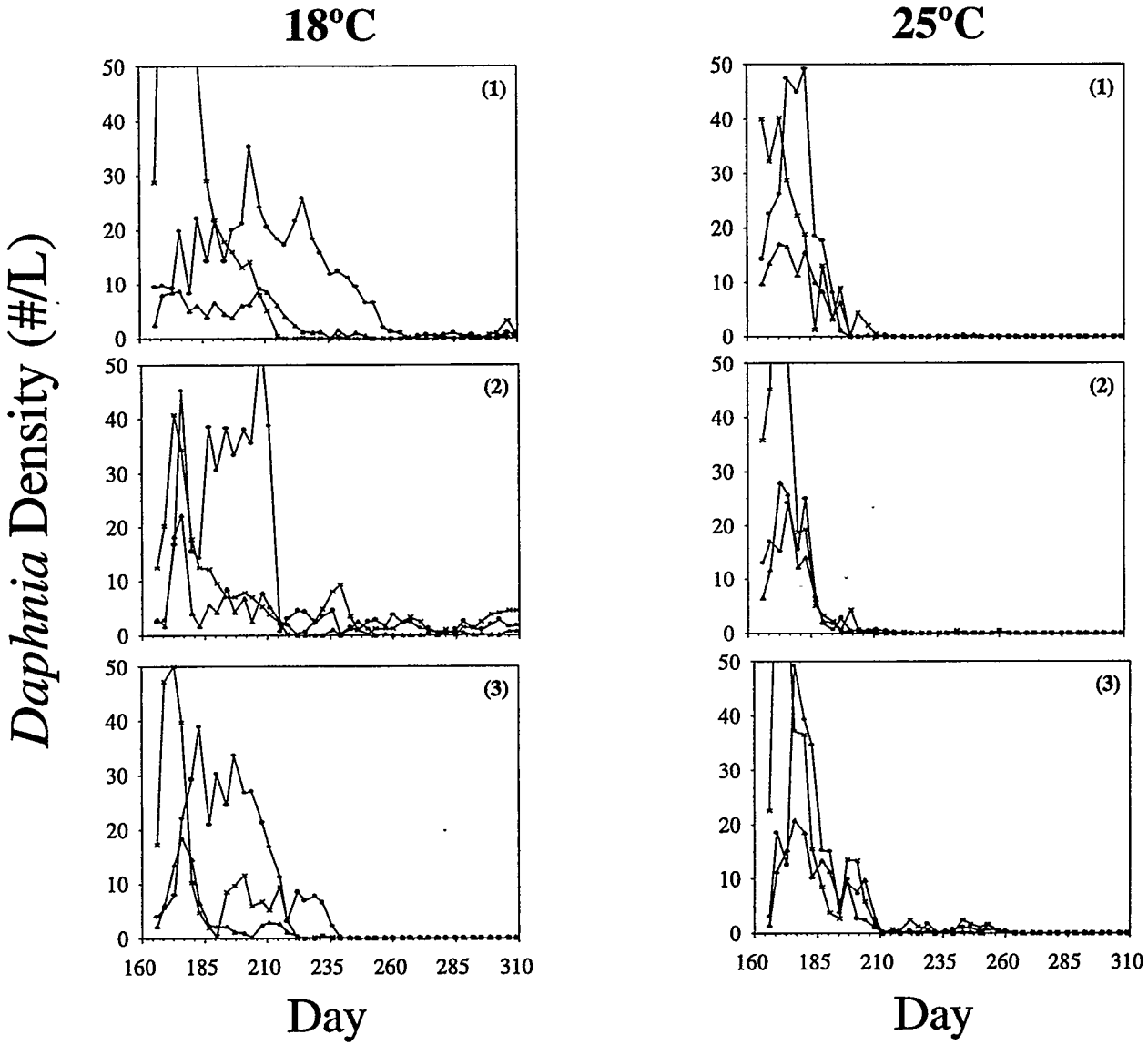
The demography data for each tank provides insight into the effect of temperature on different age classes of *D. pulex* (Fig. 2.5).

During the population growth phase, at both temperatures, the characteristic dynamic consisted of a large first cohort of juveniles with subsequent peaks in adolescent and adult densities. During this period of *Daphnia* increase, the main effect of

Table 2.10: Table showing the percent composition of the phytoplankton biomass by size class for the early and late Julian dates for the baseline community type. The percent change in the phytoplankton biomass composed of particles <35 μm between the early and late sampling dates are given.

Tank	Julian Day	Percent Composition					% Change in <35 μm
		<5	5 to 10	10 to 20	<35	>35	
2c18-1	187	76.0	10.4	10.7	97.6	2.3	
2c18-1	246	95.1	2.9	0	98	2	+ 0.4
2c18-2	190	81.6	6.2	7.3	95.2	4.8	
2c18-2	215	84.9	8.0	2.2	95.1	4.9	- 0.1
2c18-3	194	96.6	3.4	0	100.0	0	
2c18-3	225	36.3	34.8	0	71.1	29.0	- 29
2c25-1	180	93.6	6.4	0	100.0	0	
2c25-1	194	81.2	12.0	2	95.2	4.8	- 5
2c25-2	180	91.9	7.9	0	99.9	0	
2c25-2	194	38.1	10.3	7.9	56.3	44	- 44
2c25-3	180	74.7	7.6	17.6	100.0	0	
2c25-3	208	5.60	14.1	0	19.8	80.2	- 80

Figure 2.5: *Daphnia* density in the juvenile (—x—), adolescent (—△—) and adult (—●—) size classes for the 3 replicate tanks in the 18°C and the 25°C baseline treatments.


18°C
25°C
Daphnia Density (#/L)
(1)
(2)
(3)
0
10
20
30
40
50
160
185
210
235
260
285
310
Day

temperature was to lead to a slightly earlier date of peak density for all age classes at 25°C, although most of these differences were statistically non-significant (Table 2.9). The mean maximum densities attained by all age classes were greater for the high temperature treatment but only significantly so for the adolescent age class (P=0.0272).

At 18°C, following the initial peak densities for the *Daphnia* populations, there was a slight decline from maximum densities leading to a period (approximately 3 to 4 weeks) of relatively constant densities in all age classes and in egg production (Figs. 2.5 and 2.6). Overlapping of generations occurred during this period, making it difficult to follow the turnover of cohorts. The large decline in *Daphnia* populations was preceded by a short period of decreased egg production (days 215 to 271 in tank 2c18-1, days 208 to 215 in tank 2c18-2 and days 204 to 222 in tank 2c18-3) (Fig. 2.6). All age classes persisted at low densities following the population decline at 18°C (Fig. 2.5).

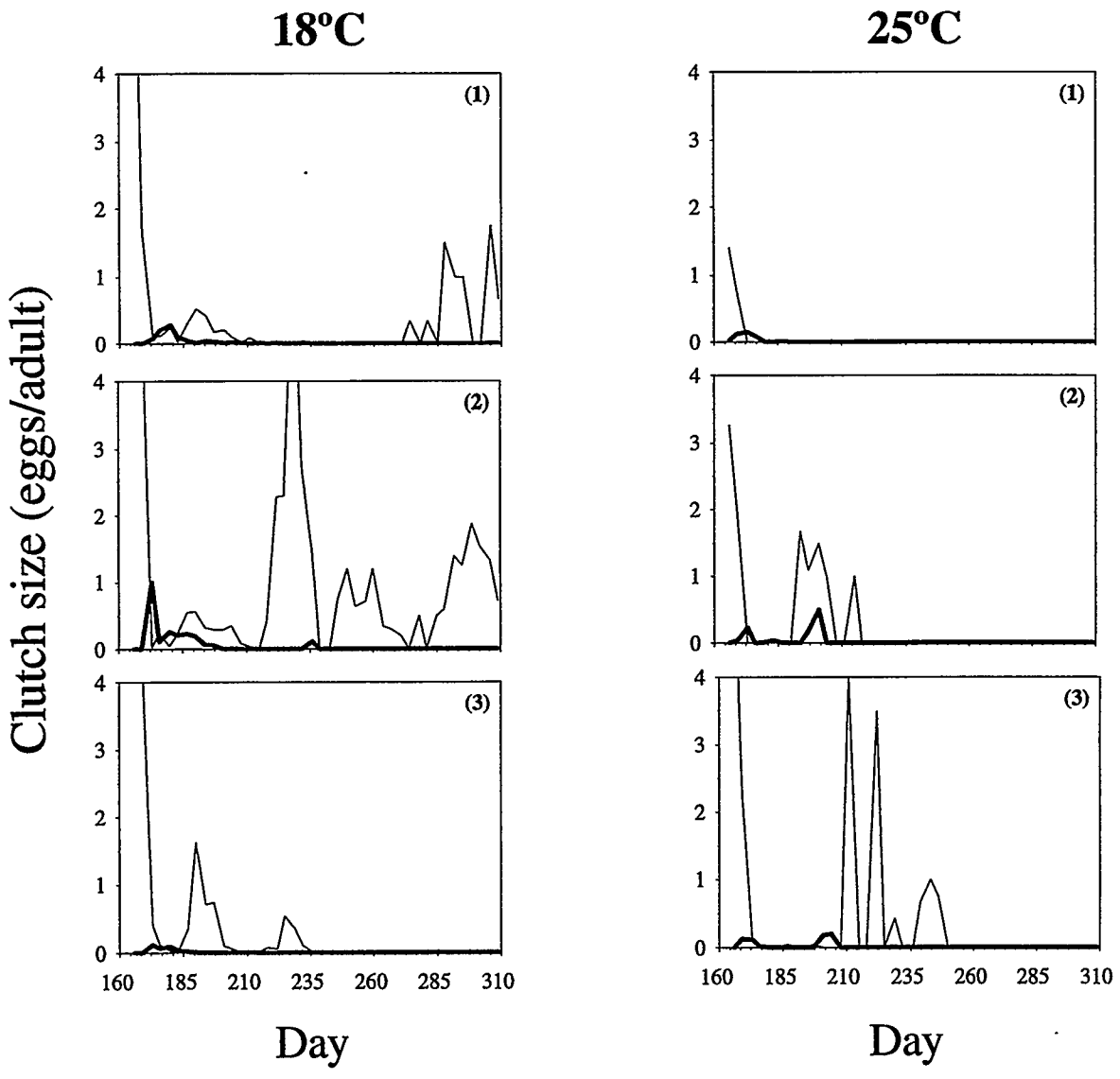
The pattern of *Daphnia* demography was altered by increasing the temperature. The constant density period for all age classes and the overlapping of cohort production seen at 18°C were absent at 25°C (Fig. 2.5). Rather, the growth and decline of cohorts can be distinctly followed in the 25°C treatments (Fig. 2.5). The initial bout of egg production (Fig. 2.6) by the *Daphnia* inoculant produced peak juvenile, adolescent and adult densities (Fig. 2.5). Subsequent to the initial burst of egg production at 25°C, clutch sizes were reduced to levels of 0 eggs per female (Fig. 2.6). With the large decline in the population, a second burst of egg production and juveniles occurred. Second peaks in adolescents and adults never occurred and extinction ensued (Fig. 2.5).

During the decline phase of the *Daphnia* populations, the demography patterns differed with temperature. At 18°C, the large decline in overall *Daphnia* biomass was during a period of time when the populations were dominated by adults (Table 2.9). To contrast, at 25°C, the *Daphnia* populations possessed a more even age distribution with approximately 30% of the population in each age class (Table 2.9). Increasing the temperature led to a significantly larger proportion of juveniles (P=0.0093) and adolescents (P=0.0338) in the population and a smaller proportion of adults (P=0.0038) during this period.

Daphnia Fecundity

As would be expected, given the shorter *Daphnia* time-series in the high temperature treatment, there were also fewer reproductive days (P=0.0065). There was no difference in the number of reproductive bouts with temperature (P=0.0946) (Table 2.9). The proportion of existence time that was reproductive was reduced from 0.87 to

Figure 2.6: Average number of eggs produced per adult (——) and ephippia per adult (▬▬) for the 3 replicate tanks in the 18°C and the 25°C baseline treatments.


18°C
25°C
Clutch size (eggs/adult)
(1)
(2)
(3)
0
1
2
3
4
160
185
210
235
260
285
310
Day

0.49 by increasing temperature (P=0.0244) (Table 2.9). The average length of the reproductive bouts was significantly shorter at the higher temperature (P=0.0080).

Resting egg (ephippia) production by *Daphnia* was also examined (Fig. 2.6). Ephippia production began 6 days earlier as the temperature was increased (P=0.0001) (Table 2.9). The period of time over which ephippia production occurred was shorter (P=0.0125) at the higher temperature, once again because the persistence time of the population was shorter. There was however, no significant difference in the proportion of the existence time spent producing ephippia ($\approx$ 0.40) with temperature (P=0.6938) (Table 2.9). There were the same number of bouts of ephippia production at both temperatures (P=0.9615) although the length of these bouts was shorter at 25°C (P=0.0528) (Table 2.9).

Other Zooplankton

Four major groups of other zooplankton were present in these tanks: rotifers (*Keratella quadrata* and *Lepadella* sp.), *Alona* sp., *Ceriodaphnia* sp. and Ostracoda (Table 2.11). Proliferation of the density of these groups only occurred following the decline or extinction of *Daphnia pulex*.

There was no significant difference in the average rotifer density with temperature (P=0.8930). A statistical difference did not occur because of very large rotifer populations in one 18°C tank (2c18-2) (Fig. 2.7). Temperature had no effect on the date of entry of rotifers into the system nor in the date at which rotifers reached their peak densities (Table 2.11).

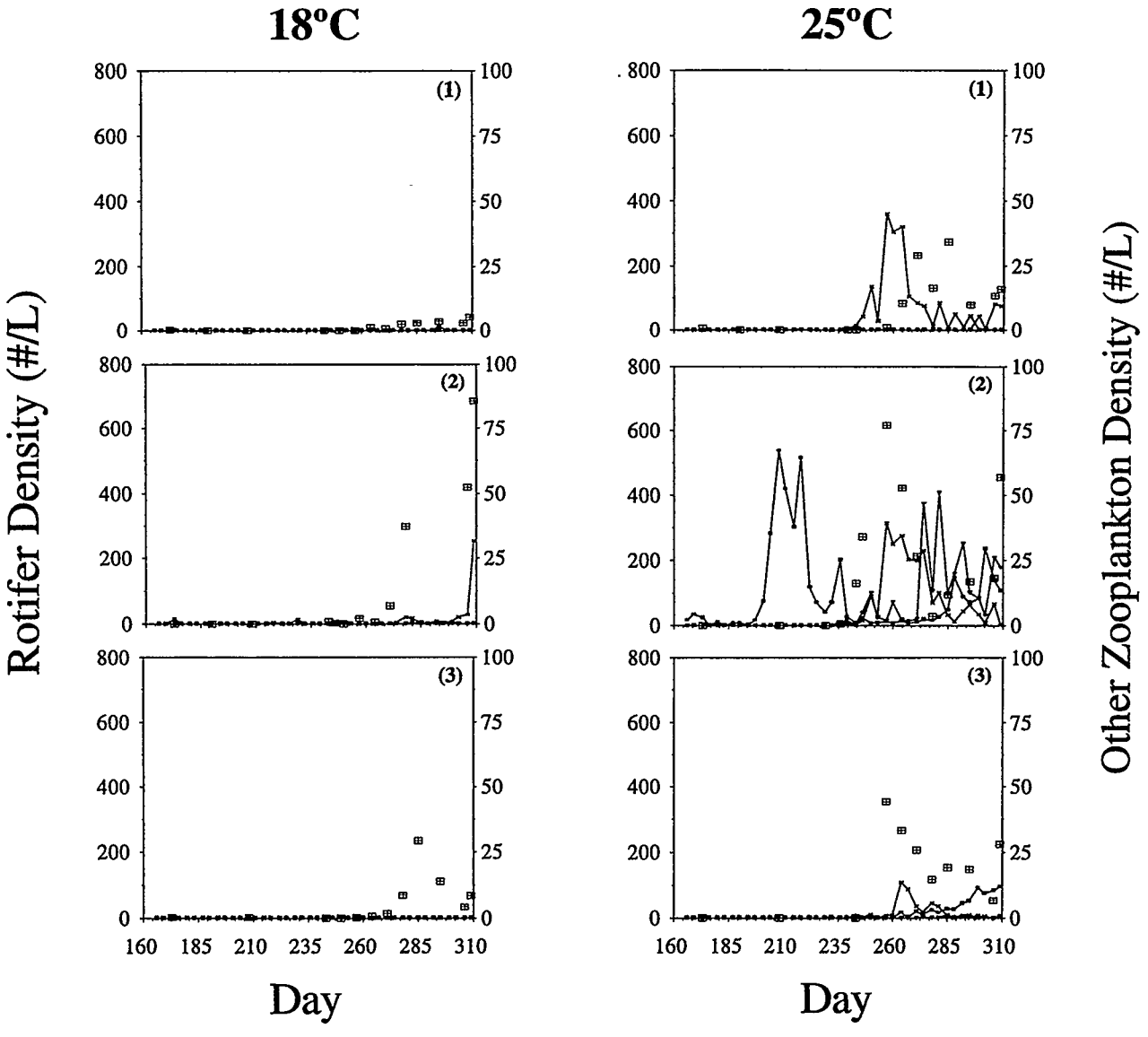
The presence of *Alona* in the tanks was much more consistent and common when temperature was increased (Fig. 2.7). They were present in all three 25°C tanks but, in only one 18°C tank (2c18-2) (Fig. 2.7). At 18°C the *Alona* density was very low for most of the series with a large increase to about 30 individuals per litre on the last sampling date (Fig. 2.7). With an increase in temperature, *Alona* reached higher densities for most of the latter half of the experimental period (Fig. 2.7). Thus, for *Alona*, the effect of temperature was to lead to a significantly higher average density at 25°C (P=0.0095) although, peak population density did not differ significantly (P=0.0827). The response of the *Alona* population was faster at 25°C for the date of maximum density (P=0.0103) although, the date of entry did not differ significantly with temperature (P=0.0606) (Table 2.11).

Ceriodaphnia were also more common at higher temperatures (Fig. 2.7). They were present in two tanks at 25°C (tanks 2c25-2 and 2c25-3) and in only one tank at 18°C

Table 2.11: The response variable averages ± standard errors for densities of other zooplankton for the baseline treatment at 18°C and 25°C. The definitions of the response variables are given in Table 2.8.

Response Variable	18°C	25°C	*P* value
1) Rotifers			
Peak density	632 ± 498	415 ± 103	0.0558
Date of peak density	148 ± 4	133 ± 5	0.1534
Date of entry	127 ± 3	125 ± 3	0.7976
Average density	151 ± 79	133 ± 29	0.8930
2) *Alona* sp.			
Peak density	10.6 ± 10.6	32.6 ± 9.7	0.0827
Date of peak density	155 ± .	130 ± 1.2	0.0103
Date of entry	137 ± .	123 ± 3	0.0606
Average density	0.4 ± 0.3	4.3 ± 1.6	0.0095
3) *Ceriodaphnia* sp.			
Peak density	0 ± 0	26.4 ± 20.7	0.0812
Date of peak density	.	129 ± 21	-
Date of entry	.	113 ± 11	-
Average density	0.02 ± 0.02	4.4 ± 3.6	0.2525
4) Ostracoda			
Peak density	0.75 ± 0.43	19 ± 16.1	0.2386
Date of peak density	148 ± 0.6	145 ± 2.3	0.4276
Date of entry	.	137 ± 9.8	-
Average density	0.01 ± 0.01	2.39 ± 2.27	0.3268

Figure 2.7: Density (#/L) of other zooplankton in the 3 replicate baseline community tanks at 18°C and 25°C representing rotifers (⊞), *Ceriodaphnia* sp. (—⊟—), *Alona* sp. (—✕—) and Ostracoda (—▽—).


18°C
25°C
Rotifer Density (#/L)
Other Zooplankton Density (#/L)
(1)
(2)
(3)
800
600
400
200
0
100
75
50
25
0
160 185 210 235 260 285 310
Day

(2c18-2). They appeared only on single dates in the 18°C treatment and always at densities lower than 2.5 individuals per litre. Increasing the temperature led to very large densities for *Ceriodaphnia* for most of the post-*Daphnia* experimental period (10 to 14 weeks) (Fig. 2.7).

Ostracoda were present at very low densities in the 18°C treatment (Fig. 2.7). At 25°C, densities were usually very reduced with proliferation to any significant degree in only one tank (2c25-2). High densities, up to 50 individuals per litre, were obtained in this tank and Ostracoda were present for about 6 weeks starting around day 246 (Fig. 2.7), long after the date of *Daphnia* extinction.

II - The Influence of a Simplified Phytoplankton and Zooplankton Community on the Temperature Response

Edible Phytoplankton and Total *Daphnia* Biomass

Simplification of the communities had very little effect on the qualitative responses of the *Daphnia* biomass and the edible phytoplankton to temperature (Figs. 2.8 and 2.4). Once again, there was a general inverse relationship between *Daphnia* and phytoplankton biomass at both temperatures (Fig. 2.8). The inoculation of *Daphnia* led to a decline in the phytoplankton biomass while the *Daphnia* biomass increased to peak levels. A proliferation of algae occurred upon decline of *Daphnia* in the simplified communities (Fig. 2.8), as in the baseline type (Fig. 2.4), especially at 25°C.

In the simplified communities at 18°C, there was an extended period during which *Daphnia* was present at high biomass and the phytoplankton was maintained at low levels; a response that was reduced as water temperature was increased (Fig. 2.8). At the higher temperature the populations always went extinct, while at 18°C the decline was merely to lower levels of persistence (Fig. 2.8). These responses to temperature were also observed in the baseline communities (Fig. 2.4). In the simplified communities, all populations of *Daphnia* persisted for the entire duration of the experimental period at 18°C (Fig. 2.8), while recall, one population went extinct in the baseline communities (Fig. 2.4).

Neither of the two response variables for minimum edible phytoplankton levels were significantly affected by increasing temperature (Table 2.12), similar to the response observed in the baseline communities (Table 2.9). The date on which the absolute minimum value occurred was again earlier at 25°C (P=0.0165) as observed in the baseline community type.

Figure 2.8: Total *Daphnia* biomass (——) and edible phytoplankton biomass (——) for the 3 replicate tanks in the 18°C and the 25°C simplified treatments.

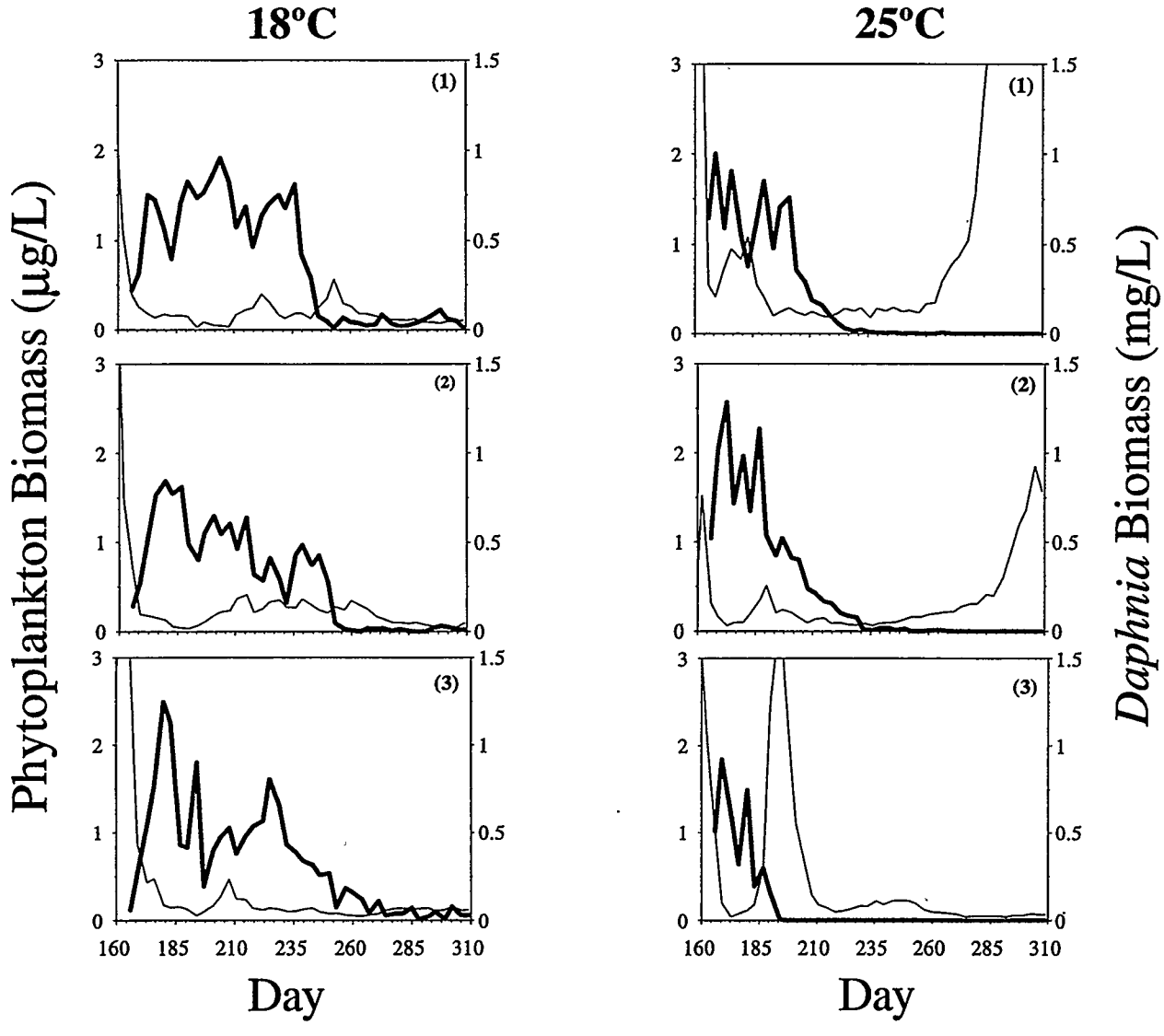

18°C
25°C
Phytoplankton Biomass (µg/L)
Daphnia Biomass (mg/L)
(1)
(2)
(3)
0
1
2
3
0
0.5
1
1.5
160
185
210
235
260
285
310
Day

Table 2.12: The response variable averages ± standard errors for *Daphnia* biomass and demography and for phytoplankton biomass at 18°C and 25°C for the simplified treatment. An asterisk (*) indicates an interaction term with community complexity as discussed in the text. The definitions of the response variables are given in Tables 2.6 and 2.7.

Response Variable	18°C	25°C	*P* value
Phytoplankton Biomass			
Minimum edible biomass	0.226 ± 0.05	0.522 ± 0.22	0.2177
Absolute minimum edible biomass	0.039 ± 0.01	0.17 ± 0.12	0.6380
Date of absolute minimum	193 ± 1	172 ± 1	0.0165
Maximum edible biomass	0.30 ± 0.13	1.72 ± 0.94	0.0095
Date of maximum biomass	215 ± 4	189 ± 3	0.0005
***Daphnia* Biomass**			
First maximum biomass	0.95 ± 0.16	1.04 ± 0.13	0.2737
Date of maximum biomass	177.7 ± 2.3	172.7 ± 2.3	0.2490
Population growth rate	0.009 ± 0.003	0.04 ± 0.003	0.0073
Start of high biomass	173 ± 0	166 ± 0	0.0001
Period of high biomass	71 ± 4	31 ± 5	0.0038
Persistence time	150 ± 0	77 ± 19	0.0121
Age Class Densities			
Maximum juvenile density	55.1 ± 5.4	94.8 ± 12.2	0.1042
Date of juvenile maximum	173 ± 0	169 ± 2	0.0520
Maximum adolescent density	12.7 ± 3.3	25.5 ± 0.6	0.0272
Date of adolescent maximum	174 ± 1	173 ± 2	0.2145
Maximum adult density	28.8 ± 5.1	27.5 ± 4.6	0.7610
Date of adult maximum	182 ± 3.5	181 ± 3.5	0.8637
Percent juveniles during decline	9.8 ± 1.7	15.4 ± 4.6	0.0093
Percent adolescents during decline	16.8 ± 5.8	10.1 ± 4	0.3725*
Percent adults during decline	73.4 ± 6.5	74.5 ± 2.3	0.9664*
Egg Production			
Total reproductive days	110 ± 2.5	38.7 ± 15.7	0.0065
Proportion of existence time	0.81 ± 0.02	0.58 ± 0.16	0.0244
Number of reproductive bouts	5.7 ± 1.2	2.7 ± 0.7	0.0946
Average length of bouts	20.9 ± 3.6	13.5 ± 2.1	0.0080
Ephippia Production			
Number of production days	61 ± 4	26 ± 6	0.0125
Proportion of existence time	0.45 ± 0.02	0.38 ± 0.03	0.6938
Number of bouts	2.7 ± 1.2	2 ± 0.6	0.9615
Average length of bouts	34.9 ± 14.1	13.4 ± 1.4	0.0528
Start of ephippia production	173 ± 0	168 ± 1	0.0001

For the *Daphnia* population growth period, the first maximum biomass was higher and occurred earlier with increased temperature although, neither of these differences were significant (Table 2.12). The population growth rate was significantly faster with temperature (P=0.0073) (Table 2.12). These same relationships with temperature were all observed in the baseline systems (Table 2.9). The temperature relationship for the *Daphnia* population growth period was not affected by simplification of the communities.

The period of time during which *Daphnia* was present at high biomass values began earlier (P=0.0001) and was shorter in the high temperature treatment (P=0.0038) (Table 2.12). However, the period was longer at both temperatures in the simple as compared to the baseline communities (Tables 2.12 and 2.9). Again, increasing water temperature led to a decreased persistence time (P=0.0121) although, it must be noted that no *Daphnia* populations went extinct at 18°C in the simplified systems (Fig. 2.8).

An increase in edible phytoplankton biomass occurred in the simplified communities upon decline of the *Daphnia* populations (Fig. 2.8). The effect of increasing temperature was to lead to a larger (P=0.0095) and earlier peak (P=0.0005) in the phytoplankton biomass response (Table 2.12). This was exactly what was seen in the more complex community types (Table 2.9). In contrast to the response in the baseline communities (Fig. 2.4) however, the largest increase in phytoplankton in the 25°C treatment was delayed in two of the three replicate tanks (Fig. 2.8). In tanks 2s25-1 and 2s25-2, very large and persistent increases in phytoplankton biomass did not occur until long after ($\approx$ 2 months) the *Daphnia* population had gone extinct (Fig. 2.8). Recall that in the baseline replicates at 25°C, the rise in edible phytoplankton occurred concomitant with the *Daphnia* population decline phase (Fig. 2.4).

Detailed phytoplankton identification and enumeration was done for several tanks in the simplified treatment (2s18-1, 2s25-2 and 2s25-3). Once again, the largest loss in phytoplankton biomass less than 35 μm with time occurred in a 25°C tank (Table 2.13). However, there was also a small loss of the biomass in the edible size fraction in the 18°C tank and a small gain in edible biomass in the other 25°C tank examined (Table 2.13). These ambiguous results mask any trends in phytoplankton size class succession over time that may be related temperature. Trends were more obvious in the baseline treatment (Table 2.10). Phytoplankton species composition was similar for both baseline and simplified community types.

Table 2.13: Table showing percent composition of the phytoplankton biomass by size class for the early and late Julian dates for the simplified community type. The percent change in the phytoplankton biomass composed of particles <35 μm between the early and late sampling dates are given.

Tank	Julian Day	Percent Composition <5	5 to 10	10 to 20	<35	>35	% Change in <35 μm
2s18-1	187	90.1	7.8	1.6	99.6	0	
2s18-1	246	44.6	5.4	39.0	89.0	11.0	- 11
2s25-1	194	86.4	5.1	0	91.5	8.5	
2s25-1	215	91.1	3.7	1.6	96.5	3.5	+ 5
2s25-3	176	94.0	6.0	0	100.0	0	
2s25-3	190	15.7	3.6	0.7	20.0	80.0	- 80

***Daphnia* Demography**

There were few differences in the temperature response of the *Daphnia* demography that were a result of simplifying the community. The dynamics at 18°C were very similar across community types with a large first cohort and initially, clear separation of age classes (Figs. 2.5 and 2.9). This period was followed by relatively constant densities for all age classes (Fig. 2.9). During the constancy period, unlike in the more complex systems, juvenile density did not show an overall declining trend and, in one tank (2s18-3), juvenile density actually increased markedly (Fig. 2.9). Again, a large decline in density occurred midway through the experiment and all age classes persisted at low densities (Fig. 2.9).

The dynamics changed in the same way in these simplified food webs as in the more complex ones in response to temperature (Figs. 2.5 and 2.9). At 25°C, the initial dynamic was the same in both systems with rapid growth and peaks in all age classes. There was clearer distinction between cohort age class peaks as the temperature was raised in both the simplified and baseline community types (Figs. 2.9 and 2.5). Extinction of *Daphnia* occurred at 25°C despite egg (Fig. 2.10) and juvenile production (Fig. 2.9) as observed in the baseline communities (Figs. 2.6 and 2.5).

In contrast to the demography pattern in the baseline communities during the decline phase of *Daphnia*, in the simplified communities, the population consisted of mostly adults (74%) at both temperatures ($P_{interaction}$=0.0204). (Table 2.12) The percent composition of adolescents in the simplified populations also did not differ significantly with temperature (P=0.3725), unlike the baseline community observations ($P_{interaction}$=0.0384) (Table 2.12). There were however, significantly more juveniles in the 25°C treatment during the decline phase (P=0.0093), as in the baseline communities. Thus, the major effect of simplification was to lead to a more similar population age class composition during the declines at both temperatures, with the exception of juveniles. Regardless of community complexity, the effect of increasing temperature on the demography during the decline phase was to lead to a significantly larger proportion of juveniles in the *Daphnia* population.

***Daphnia* Fecundity**

The same relationship with temperature for fecundity and ephippia production was observed regardless of community complexity (Figs. 2.10 and 2.6). Community complexity did not have a significant effect on the magnitude, nor on the direction of the responses of the fecundity variables to temperature (Tables 2.12 and 2.9).

Figure 2.9: *Daphnia* density in the juvenile (—x—), adolescent (—△—) and adult (—●—) size classes for the 3 replicate tanks in the 18°C and the 25°C simplified treatments.

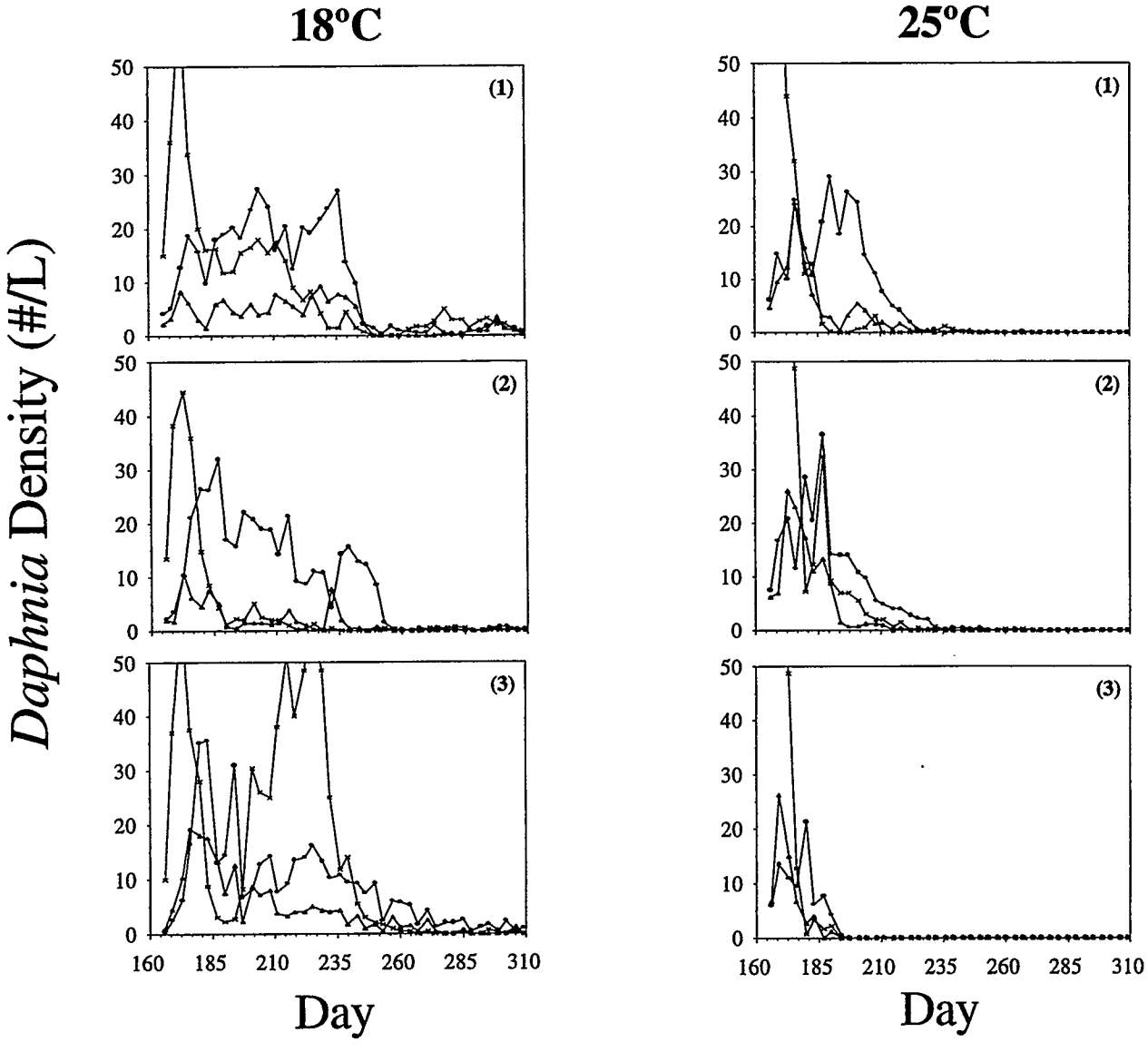
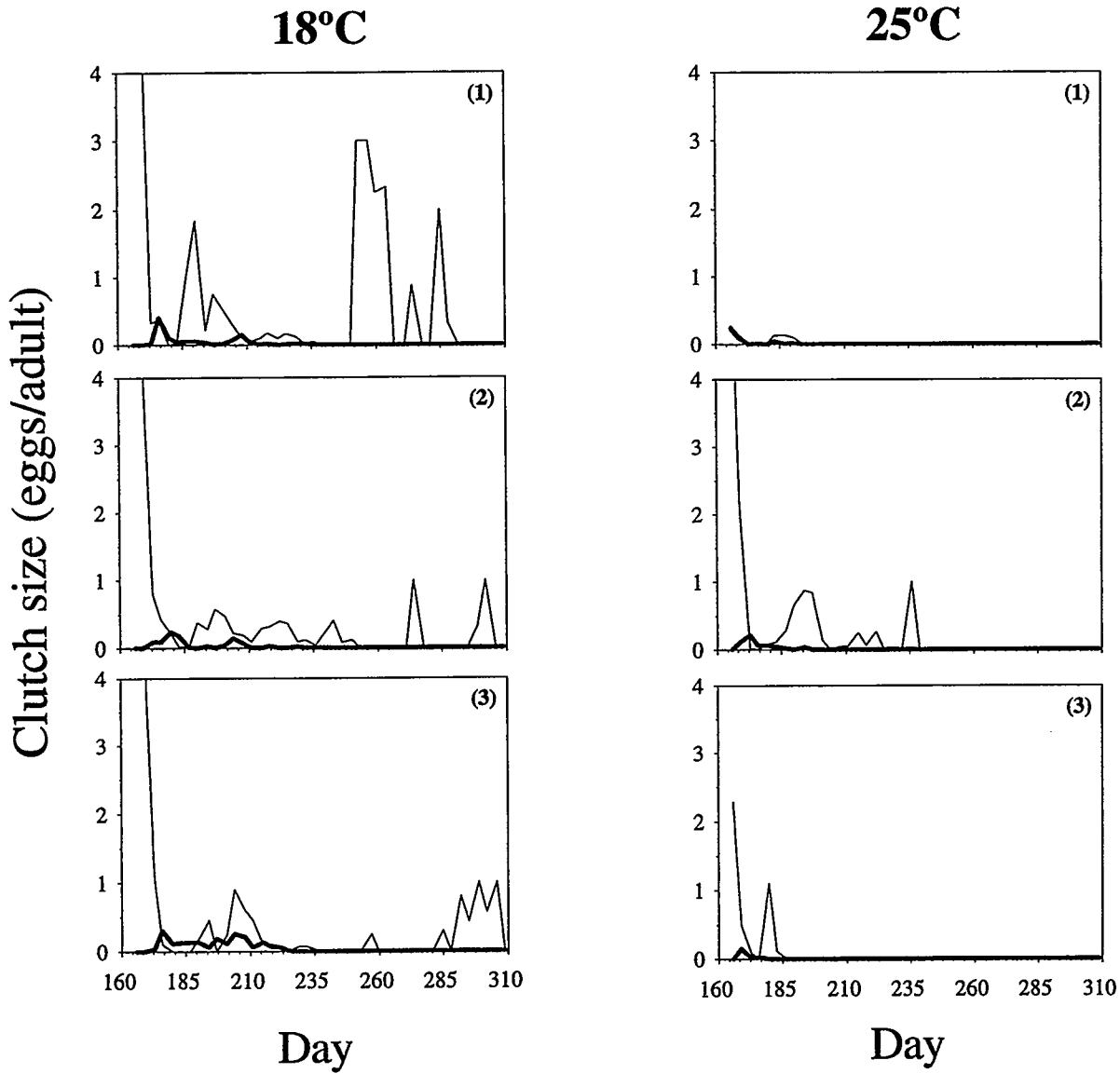

18°C
25°C
Daphnia Density (#/L)
(1)
(2)
(3)
0
10
20
30
40
50
160
185
210
235
260
285
310
Day

Figure 2.10: Average number of eggs produced per adult (——) and ephippia per adult (▬▬) for the 3 replicate tanks in the 18°C and the 25°C simplified treatments.


18°C
25°C
Clutch size (eggs/adult)
(1)
(2)
(3)
0
1
2
3
4
160
185
210
235
260
285
310
Day

Other Zooplankton

The major result to note for other zooplankton, was the presence of only rotifers in the simplified communities (Table 2.14). *Ceriodaphnia* sp., *Alona* sp., and Ostracoda were all excluded from these tanks. Thus, in terms of zooplankton species, these were simplified systems.

There were generally fewer rotifers present for shorter periods of time at both temperatures in these simplified systems as compared to the baseline treatment (Figs. 2.11 and 2.7). The temperature response was more dramatic in the simplified systems with larger average densities (P=0.0077) (Tables 2.14 and 2.11) persisting for a longer period of time (Figs. 2.11 and 2.7) as the temperature of the systems was increased.

III - The Effect of the Addition of a Third Trophic Level on the Temperature Response

Edible Phytoplankton and Total *Daphnia* Biomass

This section will report the effects of the addition of a third trophic level on the *Daphnia* and phytoplankton dynamics in terms of their responses to temperature.

Qualitatively, the response to temperature by the *Daphnia* and phytoplankton populations remained mostly unchanged when compared to the responses seen in the 2-level system (Figs. 2.12 and 2.4). All the characteristics of the *Daphnia*-algal interaction were the same with one large population peak and extinction at 25°C while prolonged persistence was the general trend at 18°C (Fig. 2.12). The major differences in the temperature response attributable to chain length were in terms of degree and time scales (Tables 2.15 and 2.9).

The temperature effect on the initial reduction of phytoplankton biomass to minimum levels was not influenced by food chain length. This was true for both the phytoplankton biomass level on the date of maximum *Daphnia* biomass and the absolute minimum level (Tables 2.15 and 2.9). As in the 2-level baseline communities, the absolute minimum level was reached significantly faster at 25°C (P=0.0446).

The growth rate of the *Daphnia* population during the colonization period was not significantly affected by temperature (P=0.1718) although it was faster in the higher temperature treatment (Table 2.15). This response differed from the significant temperature effect on population growth rate in the 2-level baseline systems (Table 2.9).

Table 2.14: The response variable averages ± standard errors for densities of other zooplankton for the simplified treatment at 18°C and 25°C. An asterisk (*) indicates a statistical interaction with community complexity as discussed in the text. The definitions of the response variables are given in Table 2.8.

Response Variable	18°C	25°C	*P* value
Rotifers			
Peak density	13 ± 10	172 ± 197	0.0558
Date of peak density	147 ± 8	146 ± 3	0.1534
Date of entry	136 ± 3	140 ± 1	0.7976
Average density	2 ± 1	42 ± 32	0.0077*

Figure 2.11: Density (#/L) of rotifers in the 3 replicate tanks in the 18°C and 25°C simplified treatments.

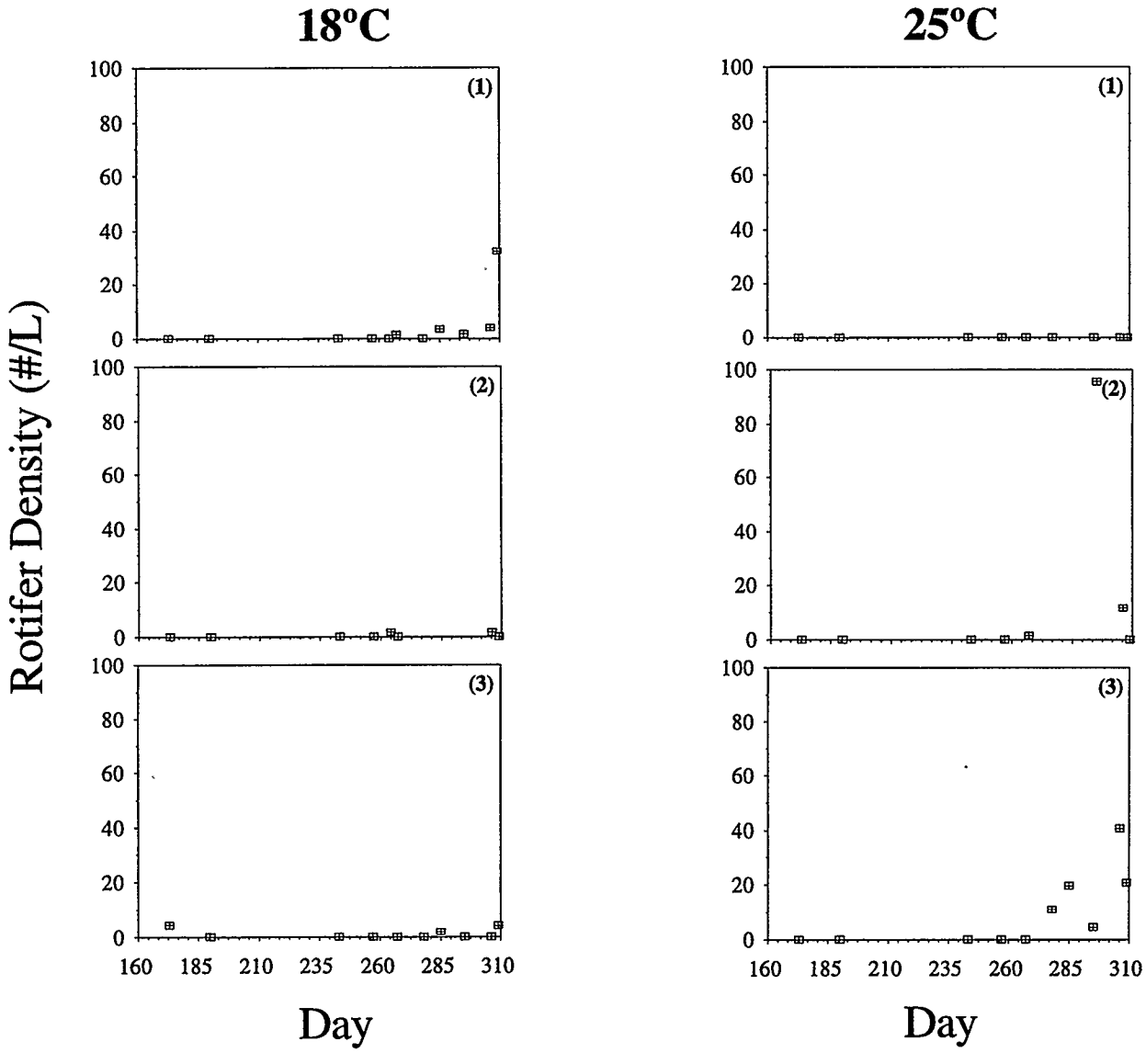

18°C
25°C
Rotifer Density (#/L)
(1)
(2)
(3)
0
20
40
60
80
100
160
185
210
235
260
285
310
Day

Figure 2.12: Total *Daphnia* biomass (——) and edible phytoplankton biomass (——) for the 3 replicate tanks in the 18°C and the 25°C 3 trophic level treatments.

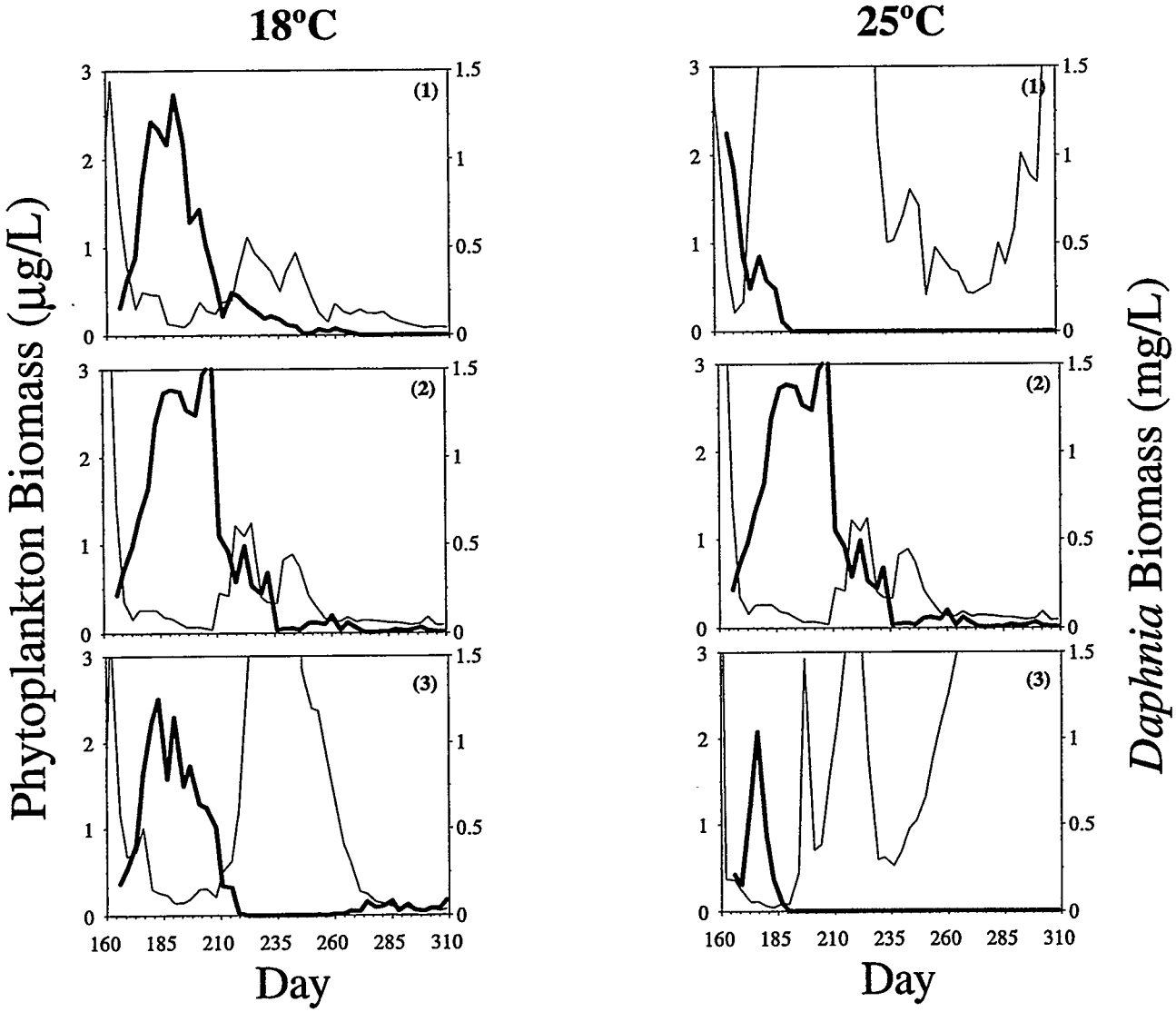

18°C
25°C
Phytoplankton Biomass (µg/L)
Daphnia Biomass (mg/L)
(1)
(2)
(3)
0
1
2
3
0
0.5
1
1.5
160
185
210
235
260
285
310
Day

Table 2.15: The response variable averages ± standard errors for *Daphnia* biomass and demography and for phytoplankton biomass at 18°C and 25°C for the 3 trophic level treatment. An asterisk (*) indicates a statistical interaction with food chain length as discussed in the text. The definitions of the response variables are given in Tables 2.6 and 2.7.

Response Variable	18°C	25°C	*P* value
Phytoplankton Biomass			
Minimum edible biomass	0.310 ± 0.089	0.630 ± 0.418	0.4623
Absolute minimum edible biomass	0.094 ± 0.029	0.103 ± 0.058	0.4735
Date of absolute minimum	197 ± 5	178 ± 5	0.0446
Maximum edible biomass	3.44 ± 2.27	5.27 ± 1.65	0.0161
Date of maximum biomass	226 ± 6	197 ± 2	0.0007
***Daphnia* Biomass**			
First maximum biomass	1.28 ± 0.05	1.13 ± 0.06	0.6574
Date of maximum biomass	184.3 ± 2.9	171.7 ± 2.9	0.0412
Population growth rate	0.012 ± 0.001	0.034 ± 0.023	0.1718
Start of high biomass	177.3 ± 1.3	169.3 ± 2.0	0.0026
Period of high biomass	36 ± 10	9 ± 3	0.0101
Persistence time	137 ± 13	35 ± 0	0.0001*
Age Class Densities			
Maximum juvenile density	64.6 ± 8.9	60.2 ± 17.7	0.9993
Date of juvenile maximum	174 ± 1	169 ± 2	0.0377
Maximum adolescent density	24.4 ± 2.8	18.2 ± 5.3	0.9432
Date of adolescent maximum	180 ± 0	172 ± 3	0.0119
Maximum adult density	42.8 ± 6.8	29.3 ± 3.3	0.6364
Date of adult maximum	185 ± 2	174 ± 4	0.0889
Egg Production			
Total reproductive days	82.7 ± 4.6	17.7 ± 2.0	0.0001
Proportion of existence time	0.65 ± 0.08	0.63 ± 0.08	0.9292
Number of reproductive bouts	4.7 ± 0.7	1.7 ± 0.3	0.0040
Average length of bouts	18.1 ± 1.6	11.2 ± 1.5	0.0004
Ephippia Production			
Number of production days	35.0 ± 7.0	17.7 ± 3.7	0.0013
Proportion of existence time	0.27 ± 0.04	0.63 ± 0.13	0.0007*
Number of bouts	1.67 ± 0.66	1.67 ± 0.66	0.9664
Average length of bouts	24.1 ± 3.9	12.1 ± 1.9	0.0048
Start of ephippia production	173 ± 0	169 ± 2	0.0028

The first peak in *Daphnia* biomass was not significantly affected by temperature in the 3-level chains (Table 2.15) as was observed in the 2-level systems (Table 2.9). The date of peak *Daphnia* density occurred significantly earlier as temperature was increased in the 3-level chains (P=0.0412) (Table 2.15), unlike the insignificant response in the baseline systems (Table 2.9).

The presence of a carnivore did not alter the fact that increasing temperature significantly shortened the period during which *Daphnia* was present at defined high biomass values (Tables 2.15 and 2.9). The high *Daphnia* biomass period started earlier (P=0.0026) and was significantly shorter (P=0.0101) when the temperature was increased in the 3-level food chains (Table 2.15).

The persistence times of the *Daphnia* populations were again affected by temperature as in the 2-level systems (Tables 2.15 and 2.9). There was however, a statistical interaction in the temperature response with food chain length ($P_{interaction}$=0.0151). For 2 of the 3 replicates at 18°C, there was no true date of extinction because the populations persisted until the end of the experimental period (Julian day 309). This necessitated choosing 150 days as the end of the persistence of these populations. However, if the experiment had continued, the persistence time would have been longer and the likelihood of a more significant response would be higher. Adding a carnivore to the system at 18°C had no effect on the persistence time of the *Daphnia* population. At 25°C however, the presence of the carnivore led to much faster extinction of the herbivore than in the 2-level system (Fig. 2.13). The addition of a third trophic level led to a more pronounced response to temperature increase (Fig. 2.13).

The decline of *Daphnia* occurred concomitant with a large increase in the algal biomass (Fig. 2.12). As in the 2-level systems (Table 2.9), the response of the phytoplankton was earlier (P=0.0007) and greater (P=0.0161) at the higher temperature in the 3-level chains (Table 2.15).

Phytoplankton identification and enumeration during the growth and decline phases of the *Daphnia* population indicated a different response with temperature than in either of the 2-level systems (Tables 2.10 and 2.13). There were large declines in the less than 35 μm group over time at both 18°C and 25°C (Table 2.16). The taxonomic composition of the algal samples was not affected by the presence of the third trophic level.

Figure 2.13: Interaction diagram showing the *Daphnia* population persistence times at 18°C and at 25°C in the 2-level baseline and 3 trophic level systems where the experimental period lasted 150 days.

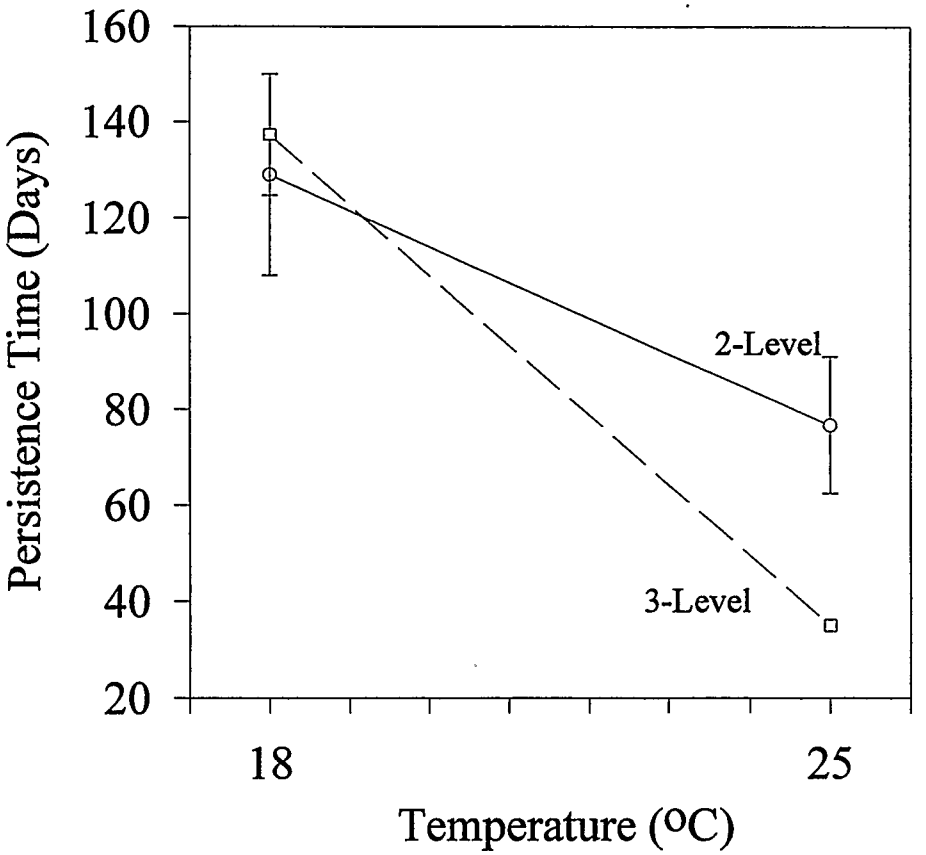

160
140
120
100
80
60
40
20
Persistence Time (Days)
2-Level
3-Level
18
25
Temperature (°C)

Table 2.16: Table showing percent composition of the phytoplankton biomass by size class for the early and late Julian dates for the 3 trophic level community type. The percent change in the phytoplankton biomass composed of particles <35 μm between the early and late sampling dates are given.

Tank	Julian Day	Biomass (µg/L) <5	5 to 10	10 to 20	<35	>35	% Change in <35 µm
3c18-1	190	1.2	11.2	1.7	99.9	0.1	
3c18-1	232	1.5	18.2	45	64.7	35.3	-35
3c25-1	173	94.1	2.8	0	96.9	3.1	
3c25-1	194	33.1	7.4	1.8	42.3	57.7	-55
3c25-3	180	260.9	30	0	100.0	0	
3c25-3	194	58.8	14.4	0.8	74.0	26	-26

***Daphnia* Demography**

As in the 2-level baseline system, the responses were faster and the densities fluctuated more at the higher temperature (Fig. 2.14). There were exceptions to the dynamics of the *Daphnia* age classes at each temperature however, that can be attributed to the presence of the *Mesostoma* predator (Figs. 2.5 and 2.14). These are discussed in detail in chapter 3.

At 18°C, as in the 2-level chains, there was a large first cohort produced, with initially, clear separation of age classes (Figs. 2.5 and 2.14). Again, this was followed bya more constant period during which overlapping of generations occurred (Fig. 2.14). The notable difference in the presence of the predator was a persistent declining trend in the densities of all age classes (Figs. 2.14 and 2.5).

At 25°C, the dynamics were similar to those in the 2-level systems (Fig. 2.5). The recruitment from eggs through to juveniles and adolescents was discernible for the first generation (Figs. 2.14 and 2.15). There were no differences in the peak densities attained by any of the age classes with temperature (Table 2.15). The major difference in *Daphnia* demography attributable to food chain length was the presence of only one peak in each age class before extinction (Fig. 2.14). In the 2-level baseline system, second or even third peaks in age class densities preceded extinction at the higher temperature (Fig. 2.5). Additional effects of *Mesostoma* on *Daphnia* demography are discussed in chapter 3.

***Daphnia* Fecundity**

As in the 2-level food chains (Table 2.9), there were significantly fewer reproductive days (P=0.0001) and the average duration of the reproductive bouts was shorter (P=0.0004) as temperature was increased (Table 2.15 and Fig. 2.15). Contrary to the temperature responses for the 2-level treatment (Table 2.9), there were significantly fewer reproductive bouts (P=0.0040) at the higher temperature and there was no significant difference in the proportion of days present spent in egg production with temperature (P=0.9292) (Table 2.15).

The relationship of ephippia production to temperature was unaltered by the lengthening of the food chain for most responses measured including: total number of days spent producing ephippia, the number of bouts, the average length of bouts of ephippia production and the start of ephippia production (Tables 2.15 and 2.9). The only interaction of the temperature response with food chain length was for the proportion of the existence time spent producing ephippia ($P_{interaction}$=0.0047). This value was

Figure 2.14: *Daphnia* density in the juvenile (–x–), adolescent (—△—) and adult (—●—) size classes for the 3 replicate tanks in the 18°C and the 25°C 3 trophic level treatments.

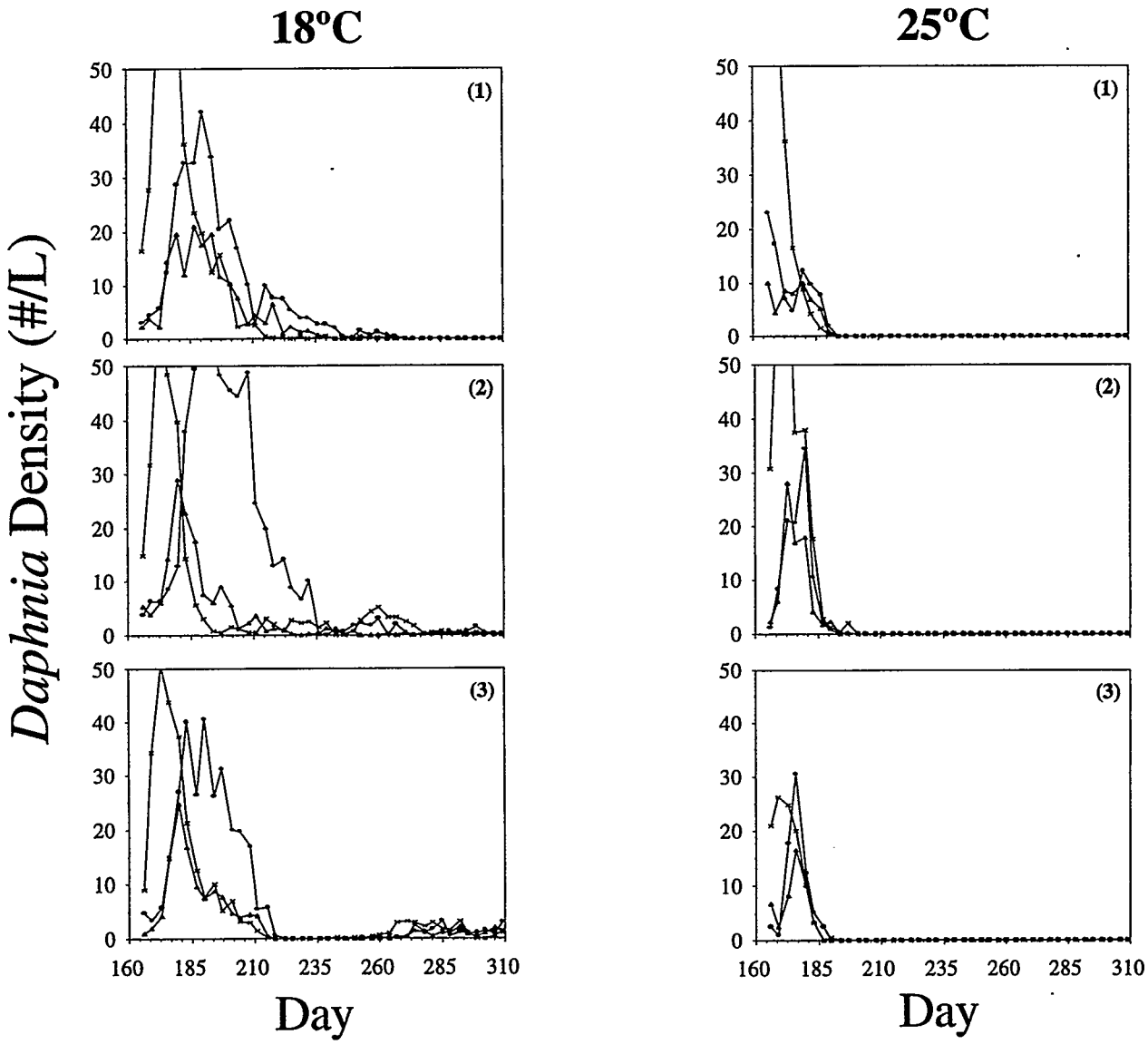
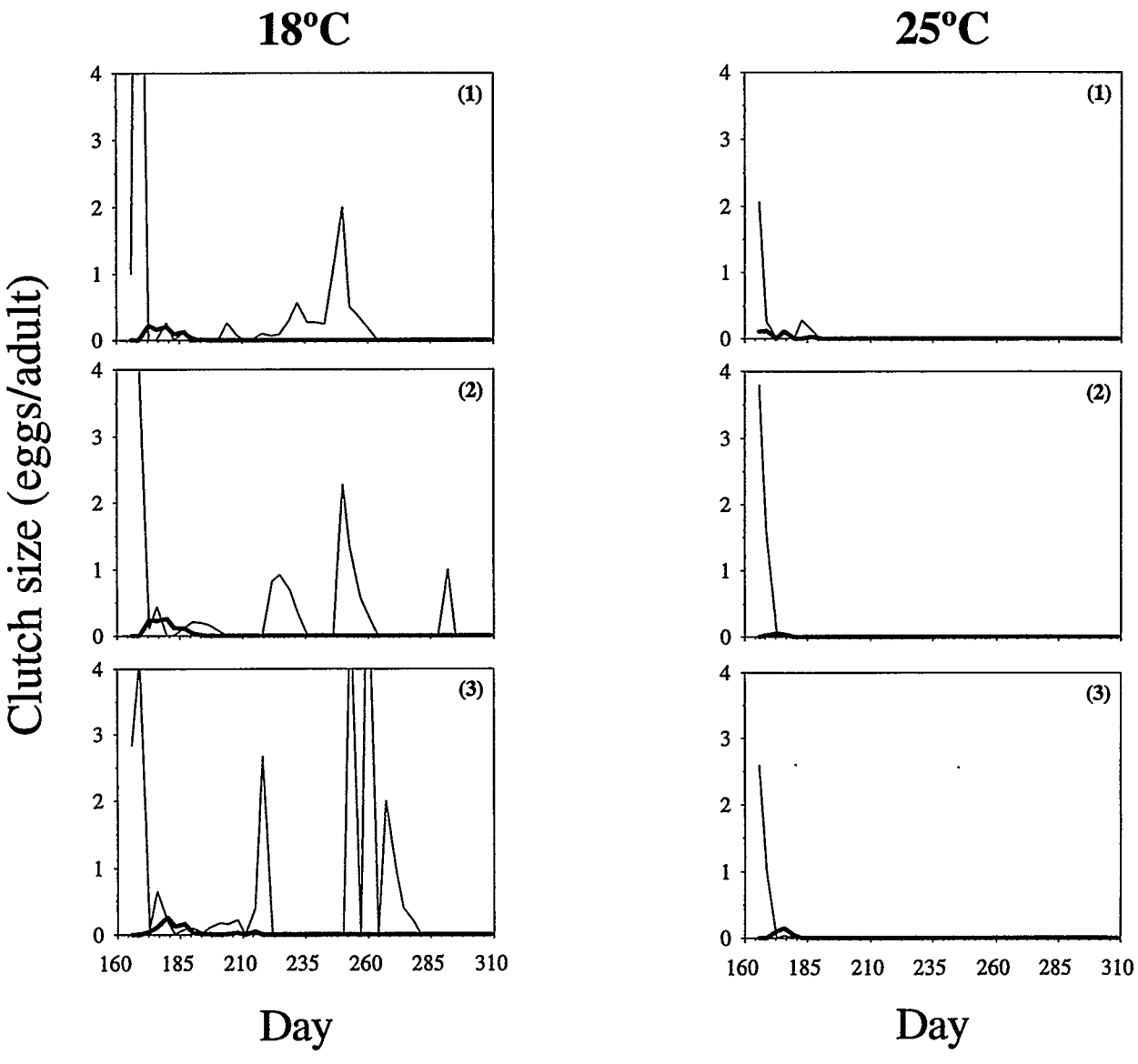

18°C
25°C
Daphnia Density (#/L)
(1)
(2)
(3)
0
10
20
30
40
50
160
185
210
235
260
285
310
Day

Figure 2.15: Average number of eggs produced per adult (——) and ephippia per adult (▬▬) for the 3 replicate tanks in the 18°C and the 25°C 3 trophic level treatments.


18°C
25°C
Clutch size (eggs/adult)
(1)
(2)
(3)
0
1
2
3
4
160
185
210
235
260
285
310
Day

significantly greater at 25°C (P=0.0007) in the presence of the carnivore (Table 2.15), unlike the insignificant response to temperature in the baseline 2-level food chains (Table 2.9).

Other Zooplankton

All groups of other zooplankton in the 2-level systems (Fig. 2.7) were also present in at least one of the 3-level tanks (Fig. 2.16). Once again, the main effect of increasing temperature was to lead to higher densities and to prolong the persistence of most other zooplankters (Figs. 2.16 and 2.7).

Ostracoda were completely absent from all the tanks at 18°C (Fig. 2.16). Thus the very large densities in 2 of the 3 tanks at 25°C represent an increase attributable to temperature as in the 2-level systems.

Ceriodaphnia were almost completely absent from both temperature treatments in the 3-level systems and never reached densities above 1.5 individuals per litre (Fig. 2.16). This was a large difference from the pattern seen in the baseline 2-level chains where the higher temperature treatment led in 2 cases to very high densities and to the prolonged presence of *Ceriodaphnia* (Fig. 2.7). Since *Ceriodaphnia* were also absent from the third tank in the 2-level treatment, it is unclear whether the virtual absence of *Ceriodaphnia* from the 25°C 3-level treatment is attributable to the presence of *Mesostoma* or to between tank variability.

Alona sp. showed a response to temperature that was independent of food chain length. Again, much higher average densities (P=0.0006) were maintained for a longer period of time at the higher temperature (Table 2.17 and Fig. 2.16).

The responses of rotifers to temperature were influenced by the addition of the carnivore. In the 3-level food chains, the maximum rotifer density did not differ with temperature (P=0.5132), unlike the significant difference in the baseline 2-level food chains. The date for the entry of rotifers into the 2 and 3-level systems differed slightly in their responses to temperature ($P_{interaction}$=0.0535) with the date of entry occurring significantly earlier at 25°C only in the 3-level systems (P=0.0048) (Tables 2.17 and 2.11). The peak rotifer density was reached earlier (P=0.0029) at 25°C in the 3-level chain only (Tables 2.17 and 2.11). Likewise, for the average rotifer density , there was a significant effect of temperature only in the 3-level systems ($P_{interaction}$=0.0110) with a lower average density at the higher temperature (P=0.0001) (Table 2.17).

Figure 2.16: Density (#/L) of other zooplankton for the 3 replicate tanks in the 3 trophic level systems at 18°C and at 25°C, representing rotifers (⊞), *Ceriodaphnia* sp. (—⊟—), *Alona* sp. (—x—) and Ostracoda (—▽—).

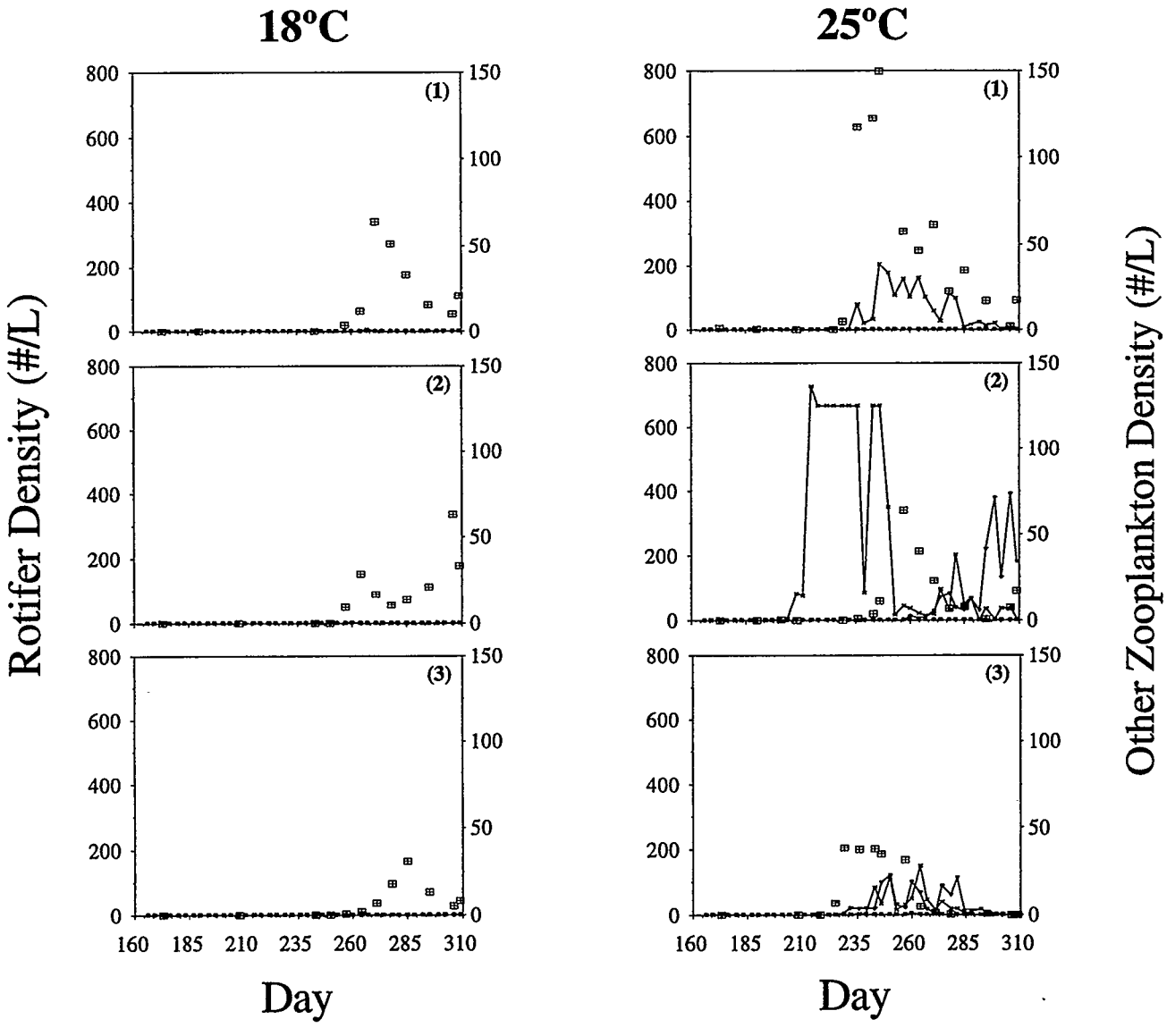

18°C
25°C
Rotifer Density (#/L)
Other Zooplankton Density (#/L)
(1)
(2)
(3)
800
600
400
200
0
150
100
50
0
160 185 210 235 260 285 310
Day

Table 2.17: The response variable averages ± standard errors for densities of other zooplankton for the 3 trophic level treatment at 18°C and 25°C. An asterisk (*) indicates a statistical interaction with food chain length as discussed in the text. The definitions of the response variables are given in Table 2.8.

Response Variable	18°C	25°C	*P* value
1) Rotifers			
Peak density	281 ± 58	448 ± 18	0.5132
Date of peak density	144 ± 5	122 ± 4	0.0029
Date of entry	129 ± 0	115 ± 2	0.0048*
Average density	65 ± 6	14 ± 0	0.0001*
2) *Alona* sp.			
Peak density	0.7 ± 0.3	67.5 ± 34.5	0.0260
Date of peak density	134 ± 2	121 ± 7	0.0421
Date of entry	134 ± 0	113 ± 5	0.0606
Average density	0.02 ± 0.01	14.2 ± 5.4	0.0006
3) *Ceriodaphnia* sp.			
Peak density	0 ± 0	0.34 ± 0.33	0.0599
Date of peak density	.	130 ± 0	-
Date of entry	.	.	-
Average density	0.004 ± 0.003	0.012 ± 0.01	0.2072
4) Ostracoda			
Peak density	0 ± 0	32 ± 21	0.0024
Date of peak density	.	137 ± 8	-
Date of entry	.	122 ± 6	-
Average density	0 ± 0	3.8 ± 2.1	0.0863

Discussion

Temperature had several important effects on the *Daphnia*-algal interaction. With an increase in temperature, prolonged persistence and overlapping of generations in the *Daphnia* dynamic was replaced by a dynamic consisting of a population peak followed by rapid decline. The second major qualitative effect of temperature was the extinction of all *Daphnia* populations at the higher temperature while in most cases at 18°C (7 of 9 tanks), the populations persisted for the duration of the experimental period. Alterations of the food web (i.e. simplification or lengthening of the main food chain), did not alter these main qualitative effects of temperature but, significantly modified quantitative aspects of these temperature responses.

The evidence suggests that the inoculated *Daphnia* populations overshot their equilibrium density at both temperatures; peak *Daphnia* biomass occurred after the minimum level of edible phytoplankton was reached. This indicates that there was a delay in the response of the *Daphnia* population to the level of food available and that the ability to overshoot carrying capacity was unaffected by temperature.

The *Daphnia* dynamics were similar in simplified and baseline communities. This is probably because, in the baseline communities, potential competitors of *Daphnia* did not become important until after the *Daphnia* populations had declined. There was therefore, little overlap in the time period during which potential competitors were present and during which they could affect the *Daphnia* dynamics in the baseline tanks. *Daphnia* were able to control the food supply in the tanks and thereby limit the recruitment of other species. The filtration method used to simplify the plankton community was effective. All large zooplankton species present in the baseline community types (i.e. *Alona* sp., *Ceriodaphnia* sp. and Ostracods) were excluded from the simplified systems. The differences in phytoplankton biomass levels, especially with the delayed increase in biomass upon *Daphnia* decline in the simplified system, suggest that the phytoplankton community, during the period while *Daphnia* were present, consisted of smaller sized individuals. Despite this difference, the major groups of phytoplankton near the beginning of the experiment were predominantly small (5 to 10 μm) flagellate and non-flagellate types. In all community types, *Daphnia* were able to regulate food resources despite some differences in initial conditions.

The predator enhanced the instability with temperature by further reducing persistence times of the *Daphnia* population at the higher temperature. Only one cohort of *Daphnia* was produced in the presence of the predator as opposed to 2 or 3 cohorts in

the 2-level systems. The results indicate that there is a much higher probability of destabilized *Daphnia* population dynamics at higher temperatures, and that this effect is enhanced by longer food chains. Further aspects of the dynamics and the effects of *Mesostoma ehrenbergii* are discussed in Chapter 3.

The most important results in terms of *Daphnia* population stability were the unstable dynamics and the extinctions observed at the higher temperature regardless of community structure. Across community types, at 18°C, the populations existed for an average of 50 days at high biomass levels and then generally continued to persist at low densities. At the low food levels observed in the mesocosms at 18°C, 50 days can represent 2 generations of *Daphnia pulex* (Paloheimo and Taylor 1987). The populations at the higher temperature existed for only an average of 20 days at high biomass levels and this period was always followed by extinction. There are thus two forms of decline to explain, one for each temperature treatment. The decline at 18°C was probably caused by a different mechanism. Periods of low clutch sizes ($\approx$ 0 to 0.5 eggs/adult) that are probably related to low food per head values preceded the decline at 18°C. Low fecundity values in the range of 1.5 to 2.5 eggs per adult female have been observed in natural populations of *Daphnia* in summer, when food levels are low (Hebert 1978). Thus, the large decline seen at 18°C is probably due to the senescence of second generation adults that are replaced by a cohort of lower density (i.e. recruitment limitation). The *Daphnia* population continued to persist at low biomass levels. The age structure of the population during the decline period supports the senescence hypothesis, as most of the population consisted of adults at 18°C. In contrast, at 25°C the *Daphnia* populations always declined to extinction. Despite high fecundity levels in the baseline communities around the time when the populations were declining, extinction still occurred. During the decline at 25°C, the populations always consisted of a higher proportion of immature *Daphnia* and in the baseline treatment, a lower proportion of adults. Extinction appears to be a result of the failure of juvenile *Daphnia* to mature at 25°C. The immature populations declined to extinction.

Stability, measured as the constancy of numbers, was also affected by temperature. The populations were less stable at higher temperatures with a constancy period in all population age classes being replaced by fluctuating densities. Increases in population fluctuations in zooplankton with temperature increase have been observed by Pratt (1943), and Halbach (1970) although, under conditions where algal food was supplied and non-dynamic. At the higher temperature, there were few cohorts to work with, but, the separation of cohorts was more obvious than at the lower temperature.

There were pulses in all age class densities and egg production that could be followed at 25°C while at the lower temperature, there was steady recruitment and overlapping of generations. Pratt (1943) found similarly, a loss of the overlapping of generations in the demography for *Daphnia magna* when temperature was raised from 18°C to 25°C.

Several mechanisms can be proposed for the greater instability both in terms of fluctuations in population density and in terms of the population persistence times with an increase in temperature in all community types. The first mechanism involves the direct effect of temperature on the parameters describing the feeding, maintenance, conversion efficiency and death rates for the *Daphnia* populations and time lags for the *Daphnia*-algal interaction. Changes in these parameters can act to destabilize population dynamics by leading to larger amplitude fluctuations under structurally identical conditions (May 1976, Murdoch and McCauley 1985, McCauley and Murdoch 1987, Lawton 1987). Dynamic instability due to the effect of temperature alone would lead to the prediction that with increases in vital rate parameters, larger amplitude and more frequent cycles would be expected (May 1976) as observed empirically by Pratt (1943) and Halbach (1970). These larger amplitude cycles increase the likelihood of extinction due to stochastic processes as the population trajectory approaches zero density more closely and more often.

Evidence for the direct effect of temperature playing a role in the instability here is in the quantitative changes in the series for the *Daphnia* and phytoplankton biomass with temperature. *Daphnia* were able to suppress phytoplankton biomass to very low levels faster at the higher temperature. The phytoplankton biomass was driven to absolute minimum levels much faster at the higher temperature. In addition, *Daphnia* population growth rates were significantly faster at 25°C and the population reached defined high biomass levels faster with an increase in temperature. Orcutt and Porter (1984) also found a higher intrinsic rate of increase in populations of *Daphnia parvula* with an increase in temperature. The average length of reproductive bouts was shorter at the higher temperature but, there were equal numbers of bouts at both temperatures. This can be indicative of a population that is cycling to a greater degree with dominance-suppression cycles (c.f. McCauley and Murdoch 1987) occurring more rapidly at the higher temperature. Dynamic instability due to the effect of temperature alone may therefore provide an explanation for the extinction of *Daphnia* populations at the higher temperature.

There are however, other possible mechanisms that could have given rise to the instability. The increase in temperature may have led to the direct starvation of *Daphnia*.

Lab experiments on individual *Daphnia pulex* (Lampert 1977b) have shown that at constantly supplied low food levels, *Daphnia* are unable to meet the increased metabolic costs induced by higher temperatures and their net production rate (%/day) is negative. At 25°C, in Lampert's (1977b) work, *Daphnia pulex* individuals were unable to persist at food levels less that 0.1 mg C/L (or about 2.4 µg/L chlorophyll *a* - based on a conversion factor incorporating the carbon content to dry weight and a species specific constant representing the percent of dry weight consisting of chlorophyll *a*). At 18°C, however, *Daphnia pulex* had positive production values for food levels down to approximately 0.04 mg C/L (or 0.96 µg/L chlorophyll *a*) (Lampert 1977b). When food supply is also dynamic, as in this study, it is uncertain whether this relationship still holds. Phytoplankton exists on a shorter time scale than *Daphnia* and it is therefore the rate of turnover of phytoplankton biomass in addition to the biomass levels that is important for *Daphnia* survival under dynamic conditions (McCauley *et al.* 1988). If the rate of phytoplankton turnover is sufficiently fast, it may still support high biomass levels of *Daphnia* despite low food levels.

Interestingly, in the higher temperature treatment, edible phytoplankton was reduced to a low level faster, while metabolic demands of *Daphnia* would have been elevated (e.g. Lampert 1977b, Goss 1978, Makarewicz and Likens 1979). In addition, as the temperature of the water continued to increase during the temperature transient, so would have the metabolic requirements of *Daphnia*. Therefore, it would be more unlikely that *Daphnia* could sustain their metabolic requirements in the low food environment at 25°C. At the higher temperature, during the decline period, the *Daphnia* population consisted of mostly immature individuals and extinction was preceded by an inability of juveniles to mature in most cases. Small daphnids can survive at lower food densities than large ones and there exists a threshold size above which no further growth can occur at low food densities (Kooijman 1986). It is likely that growing juveniles died upon reaching a threshold size at 25°C under conditions of increased metabolic requirements and low food levels.

At both temperatures, edible chlorophyll *a* was reduced during the *Daphnia* growth phase, to levels well below those required for positive production in Lampert's (1977b) work . Despite this, *Daphnia* extinction rarely occurred at 18°C. *Daphnia* equilibrium density is determined by the intrinsic per capita growth rate of the phytoplankton in addition to the standing crop of prey (McCauley *et al.* 1988). The differential survival of *Daphnia* with temperature suggest that turnover rates of the phytoplankton did not increase with temperature to a degree where the increased *Daphnia*

turnover rates could be maintained. Hill and Magnuson (1990) predicted that productivity increases for phytoplankton should be slightly larger than those for zooplankton under a 3 to 7°C global warming scenario and that therefore, zooplankton would be able to maintain positive production. The results of this study suggests to the contrary, that in some systems, productivity increases in phytoplankton may not be high enough to sustain the increased zooplankton growth rates under a global warming scenario.

In a dynamic system, one would expect that with the decline of the *Daphnia* populations, a concomitant increase in phytoplankton would allow for a recovery of the *Daphnia* biomass. Increases in phytoplankton biomass were seen but, only relatively small increases in *Daphnia* biomass. This suggests a further mechanism for the greater instability at the higher temperature. In temperate freshwater systems, a change in algal community structure occurs over the growing season with a dominant edible phytoplankton community being replaced by less edible species such as blue-greens (Schindler 1970, Arnold 1971, Lampert *et al.* 1986, Sterner 1989a). Several reasons for such a shift have been proposed including the suggestion that such a change occurs because of the grazing effects of zooplankton which alters the dominance in the algal competitive arena (Porter 1977, McCauley and Briand 1979). In nutrient-rich systems, the growth of less edible species may be favoured over that of the more edible ones (Smith 1982, Watson and McCauley 1988, Watson *et al.* 1992). In addition, higher temperatures have been shown to promote the growth of less edible species such as blue-greens (Patrick 1974). All of these factors combine to lead to the likely possibility that the recovery in phytoplankton seen in this study actually represented an increase in less edible species which could not support the growth of *Daphnia.* This is supported by the finding that in the higher temperature treatment, the increase in phytoplankton that accompanied the decline in *Daphnia* was more likely to consist of a large proportion of less edible species such as *Anabaena lemmermannii* var. *minor* and *Schizothrix calcicola* than at the lower temperature. Note, this mechanism may be less important than the proposed instability and starvation hypothesis because of the same extinctions observed in the baseline and simplified communities and the timing in the response of the phytoplankton. There was a less obvious trend in the shift in algal community composition in the simplified treatment and the proliferation of phytoplankton biomass and macroscopic inedible algae occurred much later in the simplified communities.

It is impossible to completely tease apart the cause of the instability seen at the higher temperature because this was not a completely mechanistic study. Rather, several

new hypotheses can be proposed. Instability and extinction may have been caused by: 1) the direct effect of temperature on vital rate parameters, 2) starvation of individuals under the combined low food and high temperature conditions or, 3) a shift in the algal community structure following the suppression by the herbivore *Daphnia* to inedible species that was more pronounced at higher temperatures. The evidence actually points to a combination of explanations, and it remains to be determined which of these factors plays the greatest role in causing instability. It is possible that the greater instability could have arisen due to an alteration of vital rates and productivity with temperature to the point where extinction could occur by the starvation of a *Daphnia* population which could not be supported by the turnover rate of the phytoplankton. Extinction was assured by the large amplitude fluctuation and by a shift in algal community structure to less edible species which could not support *Daphnia* growth. Regardless of the mechanism however, an important conclusion to draw is that increasing temperature leads to instability and decreased persistence in the *Daphnia*-algal interaction.

Community Composition

In addition to changes in the *Daphnia*-algal interaction, alteration in the composition and size-structure of the zooplankton community was observed. At 25°C, the rapid extinction of the large-bodied *Daphnia pulex* allowed the colonization of the system by smaller crustaceans. Such an effect at temperatures ≥ 25°C has been predicted by Moore and Folt (1993) based on physiological information. Larger cladocerans such as *Daphnia* occur rarely in the subtropical and tropical zones (Hebert 1978) and data comparing southern and northern latitude zooplankton communities have shown that in the tropical zones, smaller species are favoured (Fernando 1980, Bays and Crisman 1983). Limiting food at higher temperatures may lead to disproportionately greater inability of larger individuals to meet metabolic requirements (Lampert 1977b). This may explain why smaller-bodied zooplankton such as *Alona* sp., *Ceriodaphnia* sp. and Ostracoda were able to colonize and persist in the system at 25°C while they were largely excluded from the 18°C systems, probably because of the superior competitive ability of the larger-bodied *Daphnia pulex* (Sterner 1989b).

Implications

This study suggests several important implications for the potential effects of global warming on prairie pond systems. These systems are expected to be among the first ecosystems to display the effects of global temperature increase because of their

small size and their tendency to mimic air temperature (Carpenter *et al.* 1992). The change in temperature in these systems should be more important, ecologically speaking, than any other changes expected with anthropogenic changes to atmospheric conditions (i.e. increased CO_2 levels). The results of this study indicate that prairie pond systems consisting of an array of herbivore species feeding on phytoplankton may lose some of their larger and more dominant zooplankton herbivores. This loss is due to instability in the population dynamics leading to extinction that may be caused by changes in vital rate parameters, by starvation effects, by shifts in algal community structure to less edible species or, a combination of all these factors. The resulting communities consist largely of nuisance blue-green algae with populations of small zooplankton. Zooplankton assemblages consisting of smaller-sized zooplankton have lower community grazing rates than those dominated by larger-bodied species such as *Daphnia* (Bogdan and Gilbert 1982, Gulati *et al.* 1982, Zánkai and Ponyi 1986). These zooplankton are unable to significantly reduce the biomass levels of the primary producers in these systems as has been demonstrated for *Daphnia* populations (Murdoch and McCauley 1985, Goulden and Hornig 1980). Initial simplification of the plankton communities does little to alleviate these effects. Instead, the final system consists of algae with only rotifers present as herbivores.

The results are even more striking for 3-trophic level systems where an invertebrate carnivore is present. Most fishless ponds in the prairies have a third trophic level consisting of an invertebrate carnivore. In these systems, the instability induced by temperature is even more dramatic, with extinction of the major herbivore occurring faster than in the 2-trophic level systems. In these systems, extinction of both the dominant herbivore and the carnivore trophic levels occurred. The smaller zooplankton remaining upon extinction of *Daphnia* were too small-bodied to maintain the carnivore population. Again, in these communities, a large inedible phytoplankton and algal community with small zooplankton species were the final outcome, with these changes occurring even more rapidly.

CHAPTER 3: The Population Dynamics of 2 and 3-Level Food Chains

Introduction

In both terrestrial and aquatic systems, few studies have examined the stability of population dynamics at all trophic levels as food chains are lengthened (c.f. Lawler and Morin 1993). Rather, empirical food chain studies have generally focused on predictions for equilibrium trophic level biomass generated by Oksanen *et al.* (1981) and earlier by Hairston, Smith and Slobodkin (1960) (c.f. Elliot *et al.* 1983, Carpenter *et al.* 1985, 1987, Vanni 1987, Kitchell and Carpenter 1988, Persson *et al.* 1988, Leibold 1989, Hansson and Carpenter 1993, Hansson *et al.* 1993, Schmitz 1994). In aquatic systems, most investigations of food chain dynamics have involved vertebrate predators such as fish (Briand and McCauley 1978, Elliott *et al.* 1983, Carpenter *et al.* 1985, McQueen *et al.* 1986, Carpenter *et al.* 1987, Vanni 1987, Kitchell and Carpenter 1988, Kerfoot and DeAngelis 1989, Leibold 1989, Lazzaro *et al.* 1992, Persson *et al.* 1992, Post and McQueen 1987, Hansson and Carpenter 1993, Persson *et al.* 1993, Mazumder 1994) or invertebrates such as *Chaoborus* spp. larvae (e.g. Dodson 1970, Neill 1981, Carpenter and Kitchell 1987, Hanazato and Yasuno 1989), and *Notonecta* sp. (e.g. Murdoch and Scott 1984, Dodson and Havel 1988). These organisms have long generation times compared to their planktonic prey. The population dynamics are generally not of concern in these studies where biomass levels are averaged, usually over a single season to assess changes in equilibrium levels among systems. Owing to the large differences in generation times, McCauley *et al.* (1988) suggested that in modelling the dynamics of plants and herbivores in these systems, the carnivore does not require explicit dynamic representation. Rather, the carnivore can simply be represented by a change in the rates, constants or time lags in the plant-herbivore model descriptions.

Few empirical studies to date have examined a 3-trophic level system where the dynamics of all trophic levels occur on similar time scales and where the dynamics of all interacting populations are of interest (e.g. Lawler and Morin 1993). The objective of this chapter is to examine how the addition of a third trophic level alters the plant-herbivore dynamics of *Daphnia pulex* and phytoplankton, using the predator *Mesostoma ehrenbergii*.

In the north temperate zone, *Mesostoma ehrenbergii* (Focke 1836) is a typhloplanid flatworm that occurs in many semi-permanent and permanent pond habitats (Göltenboth and Heitkamp 1977, Heitkamp 1988, Blaustein and Dumont 1990, Wrona and Koopowitz unpubl. manuscr.). It has a generation time close to that of *Daphnia*

(Heitkamp 1977). These flatworms reproduce quickly, producing up to 6 generations in a 6 month growing season (Heitkamp 1977), making them ideal predators for studies of population dynamics in 3-level planktonic food chains. *Mesostoma* sp. show a preference for cladoceran prey (Schwartz and Hebert 1982, MacIsaac and Hutchinson 1985, Blaustein and Dumont 1990, Rocha *et al.* 1990) and can have a numerical impact on pelagic zooplankton, particularly *Daphnia pulex* (Maly *et al.* 1980, Schwartz and Hebert 1982, MacIsaac and Hutchinson 1985, Rocha *et al.* 1990).

The reproductive life history of *Mesostoma* spp. has been well studied (Fiore 1971, Heitkamp 1972, 1977, Mead 1978, Kolasa 1987, Hebert and Beaton 1990). The reproductive potential of these organisms is high as they can produce clutches of 10 to 20 eggs per individual every 10 days (Rocha *et al.* 1990). Two types of eggs are produced by *Mesostoma* spp.: subitaneous and dormant. Subitaneous eggs are soft-shelled and contribute immediately to the population growth (Kolasa 1987). These eggs are a product of self-fertilization and, in a lifetime, a single individual may produce 2 to 3 clutches consisting of on average, 18 eggs (Kolasa 1987). Dormant eggs are black, hard-shelled resting eggs and are the product of sexual reproduction (Hebert and Beaton 1990). Preferential production of dormant eggs over subitaneous ones may be a product of low prey densities (Mead 1978), high flatworm population densities (Fiore 1971, Heitkamp 1972) or low temperatures (Heitkamp 1977). The sole production of dormant eggs heralds the end of a population for a particular season (Fiore 1971). The resting eggs require a period of 3 months at 4°C to break diapause (Heitkamp 1977); however, a complete understanding of the environmental factors affecting diapause remains unknown.

Populations of *Mesostoma* are size-structured and are composed of non-reproductive juveniles (< 2 to 6 mm total body length), and the larger reproductive adults (6 to 15 mm total body length). There are important behavioural differences in foraging between these size classes or stages. Juvenile *Mesostoma* tend to be active prey searchers spending more time swimming through the water column while adults are generally sit-and-wait predators, especially in the dormant egg production phase (pers. obs., Wrona and Koopowitz unpubl. manuscr.). Actively searching *Mesostoma* either cruise the pelagic zone and dart at prey within 5 mm or descend through the water column to encounter swimming prey (Schwartz and Hebert 1982). It has been suggested that the mechanism for detection of prey is related to the turbulence generated by swimming cladocerans (MacIsaac and Hutchinson 1985). *Mesostoma* may also act as ambush predators by producing mucous nets within which to capture swimming prey (Schwartz

and Hebert 1982). In addition to these different prey search strategies, *Mesostoma* also show preferences for different sizes of prey. All size classes of *Mesostoma ehrenbergii* feed preferentially on juvenile *Daphnia magna* (Wrona and Koopowitz unpubl. manuscr.). Adult *Mesostoma* also consume adult *D. magna* while juveniles can rarely handle these large prey items. It is uncertain how the results based on *D. magna* would transfer to other *Daphnia* species, such as the smaller-bodied *Daphnia pulex*. Schwartz and Hebert (1982) have demonstrated that *Mesostoma ehrenbergii* adults can handle and consume both adult and juvenile *Daphnia pulex*. To date, few studies have examined the dynamics of *Mesostoma* populations (i.e. Heitkamp 1972), or the ability of *Mesostoma* to influence the structure of its prey populations.

It is difficult to make predictions regarding the effect of the addition of a trophic level of *Mesostoma ehrenbergii* on the stability of a predator-prey system consisting of *Daphnia pulex* and phytoplankton, especially given the potential for size-structured interactions. The difficulty arises in making predictions because the second and third trophic levels are stage-structured populations. Theoretical investigations of food chain dynamics and stability are based on unstructured population models (i.e. Rosenzweig 1973, Wollkind 1976, Oksanen *et al.* 1981, Hastings and Powell 1991, Abrams and Roth 1994). However, these models may still provide some insight into predicted effects of adding a third trophic level on dynamics. Until recently, most examinations of food chain stability have involved local stability analysis and the identification of stable equilibria using isocline analysis (Rosenzweig 1973, Wollkind 1976, Oksanen *et al.* 1981). Abrams and Roth (1994) and Hastings and Powell (1991) have recently presented an examination of the global stability properties of a 3-trophic level system by detailed investigation of the dynamics on all trophic levels. Using this approach, it has been demonstrated that predictions for trophic level abundances from the exploitation hypothesis cannot be used for dynamically unstable food chains, and that stability theory based on 2-trophic level systems cannot adequately predict dynamics of the herbivore-carnivore interaction in a 3-trophic level system (Abrams and Roth 1994). From theory, the addition of a third trophic level to an unstable 2-level one should stabilize the plant-herbivore dynamic (Rosenzweig 1973, Oksanen *et al.* 1981). According to Abrams and Roth (1994) however, the dynamics of all three trophic level populations are particularly sensitive to the carrying capacity of the environment for the autotroph population at the base of the food chain. Complete model guidance for a food chain system such as the one used here is not available.

The dynamics of the populations on all three trophic levels in a simple aquatic food chain are investigated in this study, in terms of how the addition of a third trophic level alters the dynamics of the predator-prey interaction and the size structure of the herbivore population and by investigation of the dynamics of the third trophic level itself (Objective 1). Since reproductive allocation patterns of *Mesostoma* are temperature dependent (Heitkamp 1977) and could potentially affect the predator's numerical response, dynamics of 2 and 3-trophic level food chains are examined at 18°C and 25°C to determine whether the effect of the predator is temperature mediated. Detailed examination of the carnivore demography can provide valuable insight into the mechanisms driving observed effects at 18°C and 25°C (Objective 2). The food chains consist of a community of phytoplankton autotrophs, the common herbivore *Daphnia pulex* and its invertebrate predator *Mesostoma ehrenbergii*.

In addressing the first objective of this study, predictions can be made regarding the effect of the carnivore population on the plant-herbivore system at 18°C and 25°C. From food chain theory, the addition of a third trophic level may stabilize an unstable plant-herbivore system (Rosenzweig 1973). However, raising water temperature may affect this response by changing the vital rates of all three poikilothermic trophic levels and these may have consequences for population stability. By changing population vital rate parameters, it has been demonstrated theoretically, that the dynamics of a single population can be destabilized (May 1976, Murdoch and McCauley 1985, Lawton 1987, McCauley and Murdoch 1987). Thus, without a qualitative change in the model describing the populations, a qualitative change in dynamics can occur (Murdoch and McCauley 1985). Experimentally, a similar destabilization of dynamics with temperature has been observed in single species studies (Pratt 1943, Halbach 1970). The change in dynamics has been attributed to the increase in vital rate parameters with increased temperature (Halbach 1984). Most parameters describing the vital and physiological rates for phytoplankton (DiToro *et al.* 1975, Ahlgren 1987, Hanagata *et al.* 1992), *Daphnia* (Esslová 1959, Hall 1964, Ivanova 1965, Blazka 1966, Burns 1969, Craddock 1976, Lampert 1977a, Vijverberg 1980, Orcutt and Porter 1984,) and *Mesostoma* (Heitkamp 1972, 1977, Schwartz and Hebert 1982, Kolasa 1987, Heitkamp 1988) increase with temperature within a sublethal range. What is unknown is the relative effect of temperature on various parameters determining the dynamics of a single trophic level. Predicting changes in dynamics with temperature becomes increasingly difficult as trophic levels with more temperature dependent parameters are added. An increase in the population growth rate (**r**) and the carrying capacity (**K**) for the bottom trophic level, can

be shown theoretically, to lead to increased fluctuations in the dynamics of the bottom two trophic levels (Abrams and Roth 1994). How a dynamic carnivore trophic level affects the stability of a plant-herbivore system at two different temperatures needs to be investigated. These theoretical predictions have yet to be tested in a controlled experimental setup where the dynamics of all populations are monitored. The results described here investigate the effect of the addition of a third trophic level on the dynamics of a predator-prey system at two different temperatures. The effect of the carnivore on the herbivore population will likely depend on the pattern of the size structure of both the carnivore and the herbivore populations. This will also be investigated here.

The second objective of this study is to describe the dynamics of the carnivorous *Mesostoma ehrenbergii* population at the two temperatures. An explanation for the effect of the predator on the stability of the plant-herbivore dynamic at 18°C and 25°C may lie in the influence of temperature on the carnivore population. *Mesostoma* has a plastic reproductive strategy that is determined in part by the water temperature (Heitkamp 1977). Subitaneous eggs are produced only at a high rate at temperatures above 20°C (Heitkamp 1977). For the two temperature treatments therefore, it would be expected that *Mesostoma* would display a stronger numerical response at 25°C than at 18°C. A change in life history strategy and in the size structure with temperature may have important consequences at the population and food chain level.

Materials and Methods

Experimental Design

The data discussed in this chapter were obtained from the same experimental setup as discussed in the Methods section of Chapter 2. Results are from the 2 and 3-trophic level baseline communities with the simplified communities excluded from the analyses. The effect of lengthening the food chain on the dynamics of the plant-herbivore interaction are investigated at 18°C and 25°C. New results are presented on the detailed demography and fecundity of both *Daphnia pulex* (Table 3.1 for descriptions) and *Mesostoma ehrenbergii* (Tables 3.1 and 3.2 for descriptions). Additionally, the effect of temperature on the life history and dynamics of *Mesostoma* are discussed. *Mesostoma* producing dormant eggs are hereafter referred to as dormant individuals. These individuals are dormant only in terms of their reproductive status.

Table 3.1: Descriptions of the new response variables measured for the phytoplankton and *Daphnia* biomass time-series. See text for further explanations.

Response Variable	Units	Description
Phytoplankton Biomass		
Mean biomass during high *Daphnia* period	µg/L	Mean phytoplankton biomass during the defined high biomass period for *Daphnia* (see Chapter 2).
***Daphnia* Biomass**		
Mean biomass in high period	mg/L	Mean *Daphnia* biomass during the defined high biomass period for *Daphnia* (see Chapter 2).
***Daphnia* Demography**		
S5, S4, S3 or (S1+S2) / total density		Size class density as a proportion of total *Daphnia* density during the defined juvenile *Daphnia* decline phase.
S5/(S4+S5)		Relative abundance of S5 individuals in the mature reproductive class during the defined juvenile *Daphnia* decline phase (see text). The value for S4 individuals is not recorded as it is equal to 1 minus the S5 value.
S3/(S1+S2+S3)		Relative abundance of S3 individuals in the immature reproductive class during the defined juvenile *Daphnia* decline phase (see text). The value for S1+S2+S3 individuals is not recorded as it is equal to 1 minus the S3 value.
Juvenile, S3, S4 or S5 Decline rate	day^{-1}	Slope of the linear regression fit to the log transformed densities during the size class decline period. At 18°C, this analysis was only done for juveniles (S1+S2).
***Daphnia* Fecundity**		
Egg Production		
Mean clutch size	eggs/ adult	Sum of the number of eggs/adult divided by the number of observations during the population existence period.
Ephippia Production		
Mean clutch size	ephippia/ adult	Sum of the number of ephippia/adult divided by the number of observations during the population existence period.

Table 3.2: Descriptions of the response variables measured for the *Mesostoma* time-series. See text for further explanations.

Response Variable		
Date of extinction	Julian day	Date on which the first 0 in *Mesostoma* density was recorded.
% juveniles/subitaneous or dormant egg adults during *Daphnia* decline		Percent of total *Mesostoma* density consisting of each stage class during the period of *Daphnia* decline (period from end of high biomass to extinction - see Chapter 2).
Maximum total density	(#/sample)	Maximum value of the entire *Mesostoma* total density series.
Date of maximum density	Julian day	Date on which the maximum *Mesostoma* density occurs.
Maximum juvenile/subitaneous adult or dormant adult density	(#/sample)	Maximum value of the *Mesostoma* density series for each stage class.

Three replicate tanks containing food chains of 2 and 3-trophic levels at each temperature (for a total of 12 tanks) were established. All tank identification and sampling techniques were identical to those discussed in Chapter 2. *Mesostoma* sampling started on Julian day 180 although individuals were inoculated on 3 dates from Julian day 169 to 177. All results presented are from the period beginning with *Mesostoma* inoculation.

Data Analysis

As discussed in chapter 2, several remedial measures can be used to account for time in data. All three methods: derived variables, response functions, and multivariate analysis are used in this chapter. Derived variables are most common. Response functions and multivariate analysis (repeated measures ANOVA) are used for selected measurements.

Derived (response) variables from the phytoplankton and *Daphnia* series, were analysed in a 2-way ANOVA with food chain length and temperature as factors (Table 3.1). Data was log or arcsine (proportional data) transformed prior to analysis when necessary to reduce heteroscedasticity. To test for the effect of temperature on features of the *Mesostoma* dynamics (Table 3.2), t-tests were used. New response variables were calculated for the *Daphnia* demography data (Table 3.1). The individual size classes were used in the analysis as S1+S2 (< 0.8 mm to 1 mm), S3 (1 mm to 1.4 mm), S4 (1.4 mm to 2.0 mm) and S5 (> 2.0 mm) (c.f. McCauley and Murdoch 1987). The abundances of size classes relative to total *Daphnia* density and to age class densities (S1+S2 = juveniles, S3 = adolescents and S4+S5 = adults) were calculated during the period defined by the decline of the juveniles (Table 3.1). The decline period of juveniles was defined as the period delimited by the last peak in density and the first density of 0. The depths at which samples were taken was a co-factor in the initial analyses for the demography data. Depth had no effect on the observed responses and the data was pooled for the final analysis (all $P > 0.1$).

A repeated measures ANOVA (multivariate analysis) was carried out to test for differences in the time-series for the phytoplankton data. Finally a response function was fit to the *Daphnia* demography data during the decline phase. For each age class, the decline began on the date of the last peak in age class density and ended at the first 0 density recorded. For this period, a linear regression was fit to the log transformed age class density for all ages at 25°C and for only the juvenile age class at 18°C. The slope

parameters of the fitted regression lines provided estimates of the rates of decline and these were compared in the 2-way ANOVA.

Results

I - The Effect of *Mesostoma* on the *Daphnia*-Phytoplankton Interaction at 18°C and 25°C

18°C Treatment

A change in the plant-herbivore interaction resulting from the addition of the third trophic level at 18°C occurred in the phytoplankton dynamics (Fig. 3.1). In the presence of the predator, the phytoplankton dynamic demonstrated a much more prominent rebound following the decline of the *Daphnia* population. High algal biomass levels persisted to a greater degree in the 3-level food chains (Fig. 3.1).

There was little qualitative change in the total *Daphnia* biomass dynamic induced by the addition of the predator. The *Daphnia* populations persisted at high levels for a period of time representing approximately 2 generations at 18°C in both food chain types (Fig. 3.1). This period was accompanied by low phytoplankton levels for the edible size fraction whether the predator was present or not and the inverse relationship between *Daphnia* and phytoplankton biomass was upheld at both chain lengths. The presence of the predator reduced the number of large fluctuations in the *Daphnia* population during the high biomass period (Fig. 3.1). Regardless of food chain length, there was a decline in *Daphnia* biomass after approximately 40 days although, the populations generally continued to persist at lower levels. Extinction of *Daphnia* occurred once at each chain length in the 18°C treatment (tanks 2c18-3 and 3c18-1). Additionally, in one tank containing the carnivore (3c18-3), there were zero values recorded for the *Daphnia* population biomass for a period of 2 to 3 weeks. During this time, the *Mesostoma* population went extinct and *Daphnia* were able to recolonize the system (Fig. 3.1). Phytoplankton biomass levels responded dramatically to the decline and subsequent increase in the *Daphnia* population in this tank (Fig. 3.1).

Phytoplankton biomass was reduced to lower initial levels for the minimum level measured on the date of peak *Daphnia* biomass in the 2-level food chain (P=0.0407) (Table 3.3). The absolute minimum in edible phytoplankton biomass and the date on which it occurred were not significantly affected by chain length (Table 3.3) (P=0.8301

Figure 3.1: Total *Mesostoma* density (—●—), *Daphnia pulex* biomass (———) and edible phytoplankton biomass (—|—) over the entire experimental period at 18°C for the 3 replicate tanks in the 2-level and 3-level treatments.

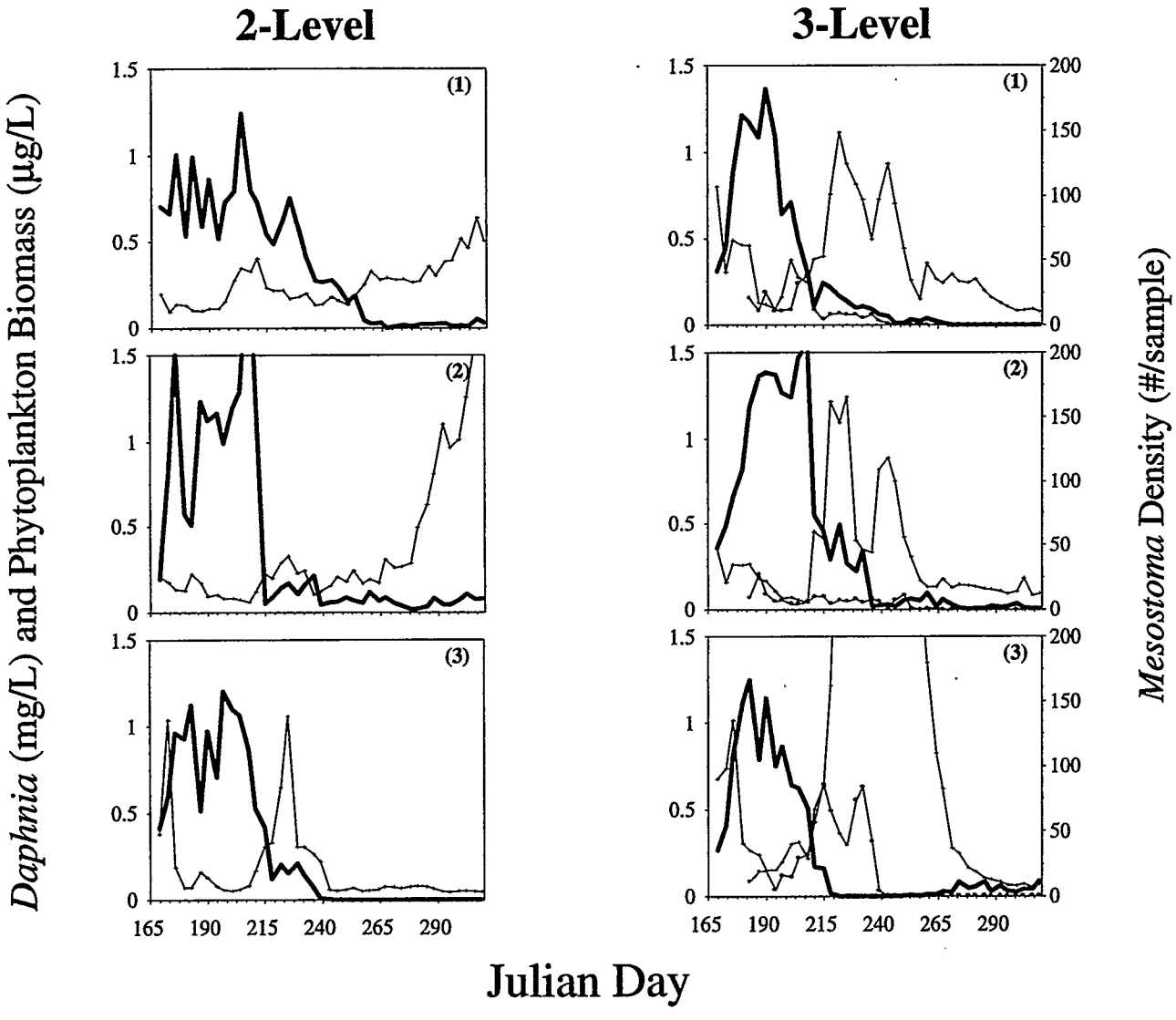

2-Level
3-Level
(1)
(2)
(3)
1.5
1
0.5
0
200
150
100
50
165
190
215
240
265
290
Daphnia (mg/L) and Phytoplankton Biomass (µg/L)
Mesostoma Density (#/sample)
Julian Day

Table 3.3: The response variable averages ± standard errors for the *Daphnia* and phytoplankton time-series for the 2-level and 3-level treatments at 18°C. An asterisk (*) indicates a statistical interaction with temperature as discussed in the text. All other *P*-values are based on the main effects due to chain length from the 2-way ANOVA. The definitions of the response variables are given in Table 3.1.

Response Variable	2-level	3-level	*P*-value
Phytoplankton Biomass			
Minimum edible biomass	0.11 ± 0.02	0.3 ± 0.09	0.0407
Absolute minimum edible biomass	0.14 ± 0.08	0.09 ± 0.03	0.8301
Date of absolute minimum	194 ± 11	197 ± 5	0.9539
Mean biomass during high *Daphnia* period	0.165 ± 0.023	0.325 ± 0.038	0.2345
Maximum edible biomass	0.57 ± 0.24	3.44 ± 2.27	0.0634
***Daphnia* Biomass**			
Mean biomass in high period	0.565 ± 0.232	0.913 ± 0.031	0.3250
Persistence time	129 ± 21	137 ± 13	0.6723*
***Daphnia* Demography**			
S5/total density	0.274 ± 0.04	0.157 ± 0.03	0.0120
S4/total density	0.294 ± 0.03	0.414 ± 0.02	0.0017
S3/total density	0.132 ± 0.01	0.195 ± 0.03	0.0278
(S1+S2)/total density	0.300 ± 0.06	0.234 ± 0.02	0.2455
S5/(S4+S5)	0.450 ± 0.02	0.275 ± 0.03	0.0002
S3/(S1+S2+S3)	0.367 ± 0.03	0.550 ± 0.05	0.0036
Juvenile decline rate	0.057 ± 0.01	0.119 ± 0.01	0.0391
***Daphnia* Fecundity**			
Egg Production			
Number of bouts	5.3 ± 1.1	4.7 ± 0.7	0.2320
Duration of bouts	21.6 ± 3.5	18.1 ± 1.6	0.3867
Proportion of existence time producing eggs	0.84 ± 0.06	0.65 ± 0.08	0.4014
Mean clutch size	0.19 ± 0.05	0.16 ± 0.02	0.6127
Ephippia Production			
Proportion of existence time producing ephippia	0.40 ± 0.05	0.27 ± 0.04	0.0322
Mean clutch size	0.009 ± 0.003	0.007 ± 0.001	0.3089
Start of ephippia production	173 ± 0	173 ± 0	0.3322

and P=0.9539 respectively). During the high *Daphnia* biomass period, the mean phytoplankton biomass was higher in the presence of the predator although, not significantly so (P=0.2345). Repeated measures ANOVA also showed no significant effect of chain length on the phytoplankton biomass time-series during this period (P>0.1). The increase in phytoplankton biomass concomitant with the decline of the *Daphnia* population was much more prominent, reaching higher levels (but no significantly higher levels) in the 3-level food chains (P=0.0634). In the 2-level food chains, the phytoplankton dynamic was generally less variable with a small increase (mostly indistinguishable from other peaks in the series) upon decline of the *Daphnia* population (Fig. 3.1). The one exception was tank 2c18-3 where there was extinction of *Daphnia*, followed by a large peak in phytoplankton biomass (Fig. 3.1).

The average *Daphnia* biomass levels were not affected by chain length (P=0.3250). The *Daphnia* populations persisted in almost all cases for the entire duration of the experimental period (150 days) whether the predator was present or not (Table 3.3). Full extinction of *Daphnia* occurred in one tank in each of the 2-level (2c18-3) and 3-level (3c18-1) treatments (Fig. 3.1). The *Daphnia* populations were almost driven to extinction in another tank (3c18-3) where *Mesostoma* were present. In this case however, *Daphnia* were able to repopulate the tank (Fig. 3.1). At 18°C, all *Mesostoma* populations went extinct before the end of the experimental period and before the single *Daphnia* population extinction seen in the 3-level treatment (Fig. 3.1).

The influence of *Mesostoma* on *Daphnia* is not evident from total *Daphnia* biomass (Fig. 3.1). Rather, *Mesostoma*'s main effect was to alter the size structure of the *Daphnia* populations (Table 3.3). For the period defined by the decline of juvenile (S1+S2) *Daphnia*, there was a significant effect of the predator on the size structure of the population. First, the relative abundances of all size classes were taken as a function of total *Daphnia* density during this period (Table 3.3). The proportion of S5 individuals in the population was significantly lower when *Mesostoma* was present (P=0.0120), while the proportion of S4's (P=0.0017) and S3's (P=0.0278) were higher. Second, the relative abundance for the different size groups (S1, S2, S3, S4 and S5) of *Daphnia* in their stage classes (either non-reproductive = S1+S2+S3, or reproductive adults = S4+S5) was calculated over the same period. These values were significantly altered by the presence of *Mesostoma* for all size groupings (Table 3.3). There were significantly fewer S5's in the 3-level food chains as a function of adult density (S4+S5) (P=0.0002). There were also fewer S1+S2's in the 3-level chains as a function of juvenile density (S1+S2+S3) (P=0.0036). *Mesostoma* altered the *Daphnia* population size structure mainly by

reducing the proportion of the population in the largest size class (S5) while increasing the relative abundance of individuals in the mid sizes (S3 and S4). The presence of the carnivore also altered the rate of decline of the *Daphnia* juvenile age class (Table 3.3). The juveniles declined at a significantly faster rate in the presence of the predator (P=0.0391). These results suggest that both very large *Daphnia* (S5's) and the very small neonates (S1+S2's) were preferentially attacked by the *Mesostoma* population over the time period when juveniles were declining.

Fecundity of *Daphnia* was not affected by chain length including: the total number of reproductive bouts (P=0.2320), the average duration of the reproductive bouts (P=0.3867), the proportion of time spent producing eggs (P=0.4014), and the average clutch size (P=0.6127) (Table 3.3). There was no increase in reproductive effort by S4 *Daphnia* individuals that could explain the higher proportion of S3's in the presence of *Mesostoma* (Fig. 3.2). Ephippia production occurred for approximately 40% of the existence time in the 2-level food chains and for only 27% of the existence time in the 3-level food chains (P=0.0322). This meant only a difference in the number of non-zero days of ephippia production however, and no difference in the mean ephippial clutch size (P=0.3089). In both cases, ephippia production started at the same time, on day 173.

25°C Treatment

At the higher temperature, the plant-herbivore dynamics were qualitatively similar whether *Mesostoma* was present in the system or not (Fig. 3.3). A large single population peak in *Daphnia* accompanied by a single nadir in the phytoplankton biomass was observed in both 2 and 3-level food chains. Again, the inverse relationship of the *Daphnia* and phytoplankton biomass was qualitatively unaltered by chain length (Fig. 3.3). The only major difference in the *Daphnia* series became apparent following the large peak in biomass. In the 2-level chain, a second very small peak in *Daphnia* biomass was observed in all replicate tanks while in the presence of *Mesostoma*, this peak was absent in most cases (Fig. 3.3). Tank 3c25-2 showed one small further increase. Again, a very large increase in phytoplankton biomass was observed upon the decline of the *Daphnia* population. This increase occurred and persisted to the same relative degree in both 2 and 3-level food chains (Fig. 3.3).

The minimum phytoplankton level coincident with *Daphnia* peak biomass was significantly lower in the 2-level food chain at 25°C (P=0.0407) as seen at 18°C (Table 3.4). In the 2-level chains, the minimum levels were similar, around 0.12 μg/L at both temperatures. Although there was not a significant statistical interaction, in the 3-level

Figure 3.2: The *Daphnia* fecundity data for the 18°C 2-level and 3-level treatments where number of eggs per S4 adult (—■—) and number of eggs per S5 adult (—┼—) are represented.

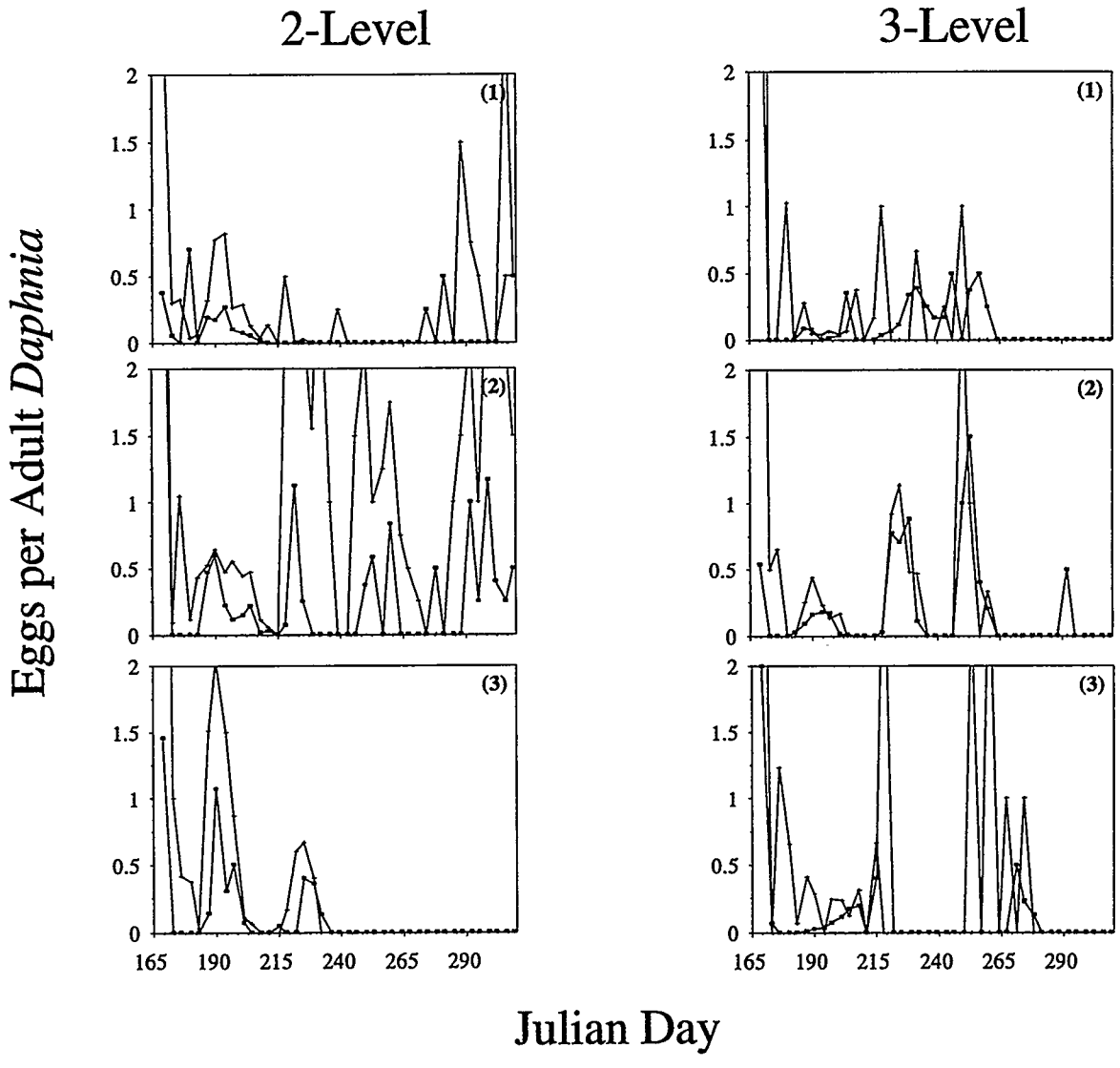

2-Level
3-Level
Eggs per Adult *Daphnia*
(1)
(2)
(3)
0
0.5
1
1.5
2
165
190
215
240
265
290
Julian Day

Figure 3.3: Total *Mesostoma* density (—●—), *Daphnia pulex* biomass (———) and edible phytoplankton biomass (—+—) over the entire experimental period at 25°C for the 3 replicate tanks in the 2-level and 3-level treatments.

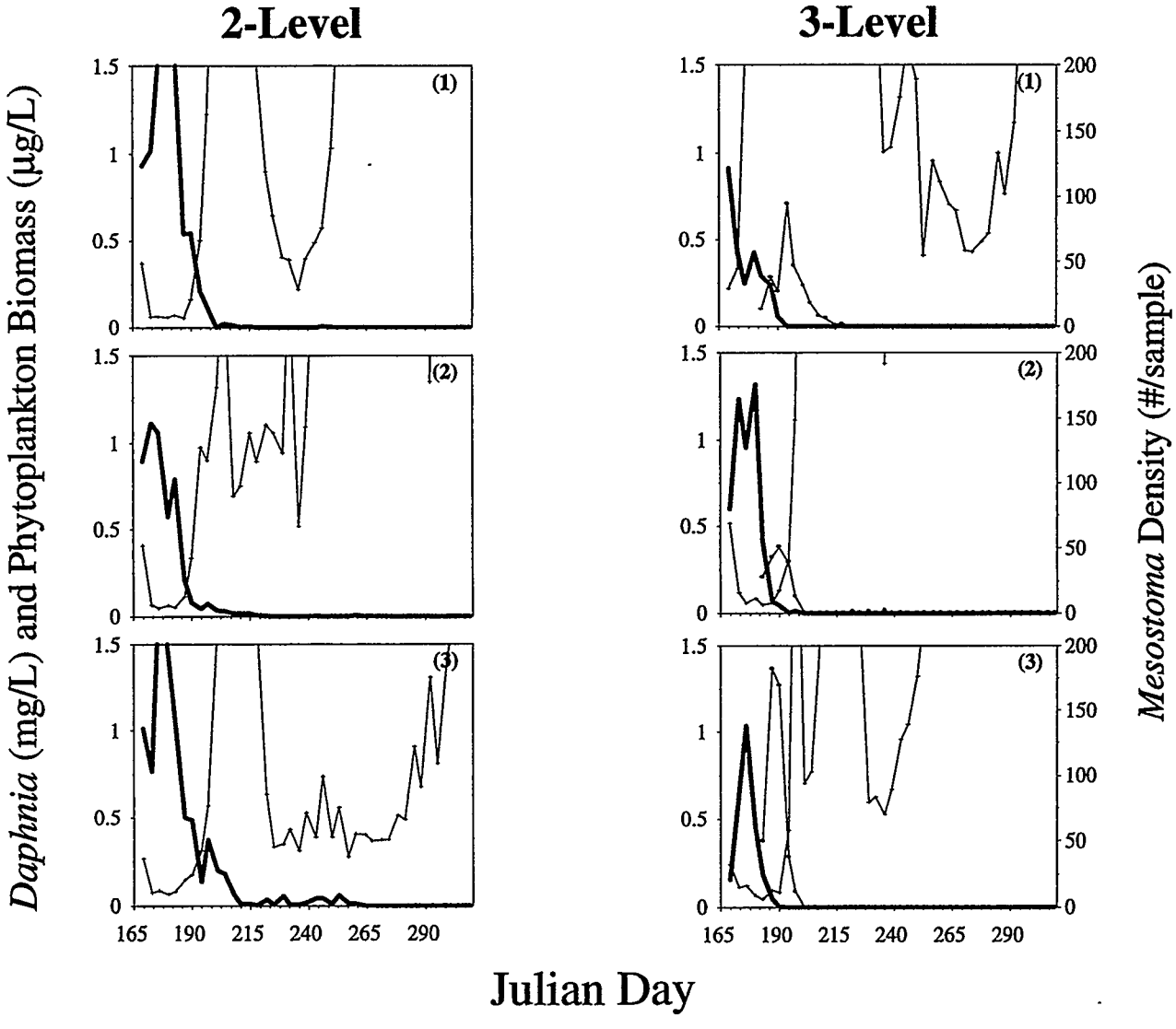

2-Level
3-Level
(1)
(2)
(3)
1.5
1
0.5
0
200
150
100
50
165
190
215
240
265
290
Daphnia (mg/L) and Phytoplankton Biomass (µg/L)
Mesostoma Density (#/sample)
Julian Day

Table 3.4: The response variable averages ± standard errors for the *Daphnia* and phytoplankton time-series for the 2-level and 3-level treatments at 25°C. A asterisk (*) indicates a statistical interaction with temperature as discussed in the text. All other *P*-values are based on the main effects due to chain length from the 2-way ANOVA. The definitions of the response variables are given in Table 3.1.

Response Variable	2-level ± SE	3-Level ± SE	*P*-value
Phytoplankton Biomass			
Minimum edible biomass	0.13 ± 0.06	0.63 ± 0.42	0.0407
Absolute minimum edible biomass	0.05 ± 0.01	0.103 ± 0.06	0.8301
Date of absolute minimum	181 ± 3	178 ± 5	0.9539
Mean biomass during high *Daphnia* period	0.214 ± 0.01	0.488 ± 0.33	0.2345
Maximum edible biomass	3.72 ± 1.29	5.27 ± 1.65	0.0634
Total *Daphnia* Biomass			
Mean biomass in high period	0.9 ± 0.06	0.8 ± 0.12	0.3250
Persistence time	77 ± 14	35 ± 0	0.0044*
***Daphnia* Demography**			
Juvenile decline rate	0.107 ± 0.011	0.214 ± 0.006	0.0091
S3 decline rate	0.086 ± 0.017	0.126 ± 0.012	0.2788
S4 decline rate	0.124 ± 0.006	0.140 ± 0.023	0.7075
S5 decline rate	0.151 ± 0.035	0.158 ± 0.006	0.9153
***Daphnia* Fecundity**			
Egg Production			
Number of bouts	3.17 ± 1.24	1.67 ± 0.33	0.2320
Duration of bouts	12.1 ± 1.7	11.2 ± 1.5	0.3867
Proportion of existence time producing eggs	0.53 ± 0.14	0.63 ± 0.08	0.4014
Mean clutch size	0.12 ± 0.05	0.14 ± 0.03	0.6127
Ephippia Production			
Proportion of existence time producing ephippia	0.41 ± 0.05	0.63 ± 0.13	0.0324
Mean clutch size	0.008 ± 0.003	0.009 ± 0.002	0.3089
Start of ephippia production	167 ± 1	169 ± 2	0.3322

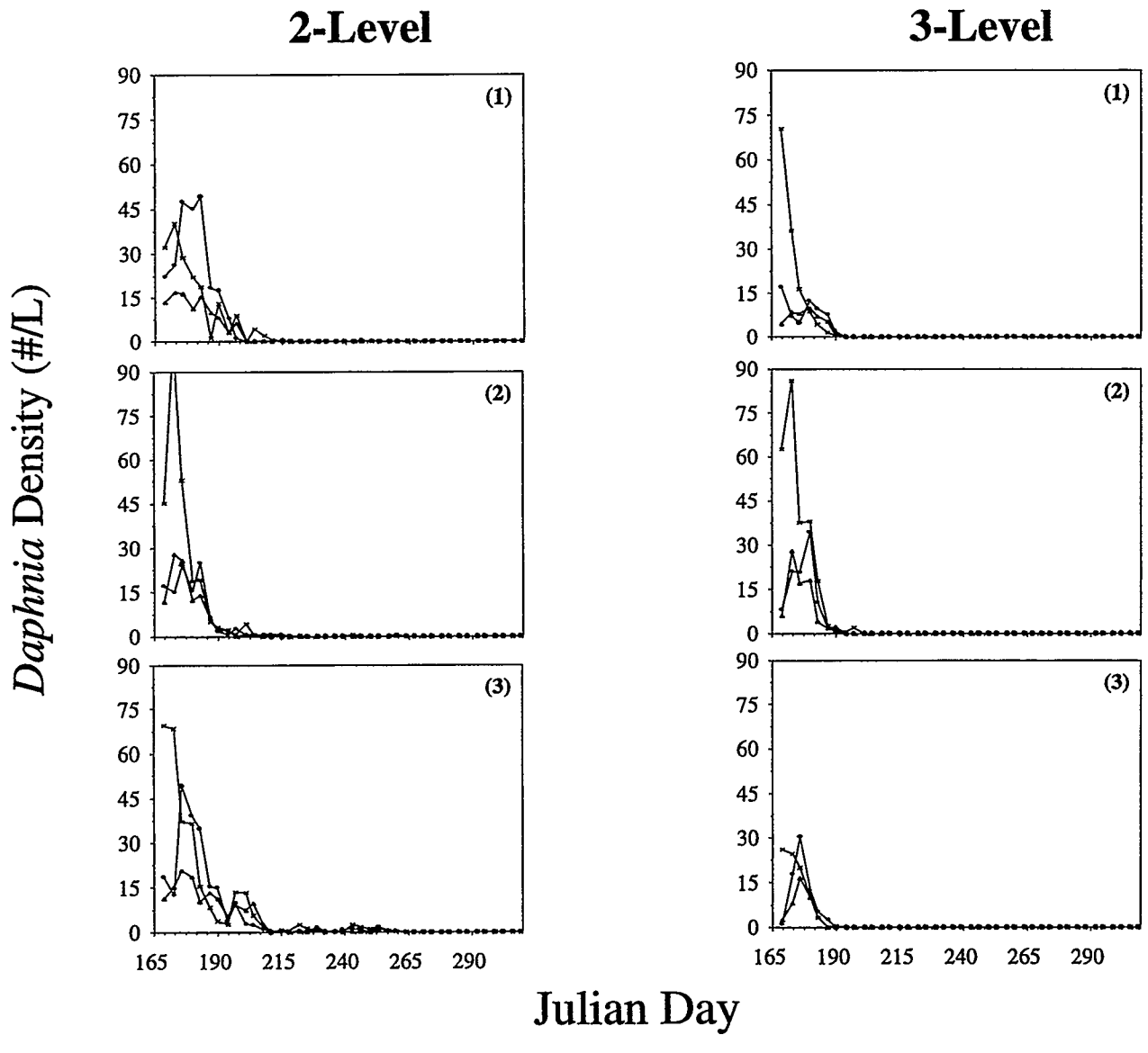
chains, the minimum levels were more than double at 25°C as compared to 18°C (Tables 3.3 and 3.4). There was again, no difference in the first absolute minimum phytoplankton level nor, in the timing of this minimum at 25°C (Table 3.4). For the period during which *Daphnia* biomass levels were high, there was no difference in the mean levels of phytoplankton biomass (P=0.2345) and repeated measures ANOVA showed no effect of chain length on the phytoplankton time-series (P>0.1). Following the decline in the *Daphnia* populations to extinction, edible phytoplankton increased to very high levels, these levels being higher, but not significantly so, in the presence of the carnivore (P=0.0634).

The mean *Daphnia* biomass was not affected by chain length (P=0.3250). In the presence of the predator at 25°C however, *Daphnia* population persistence was affected (P=0.0044). While in the 2-level food chains the populations persisted for 77 days, the addition of the carnivore led to a much shorter persistence time (35 days) in all replicate tanks ($P_{interaction}$=0.0151). Decreased persistence of the *Daphnia* populations in the presence of *Mesostoma* was only observed at 25°C. In all cases at 25°C, the *Daphnia* populations went extinct before *Mesostoma* did while at 18°C, the opposite ordering of extinctions was observed (Fig. 3.3).

Daphnia demography was unaltered by the addition of *Mesostoma* during the peak *Daphnia* biomass period with clear separation of the age classes at both chain lengths (Fig. 3.4). Later, the rate of juvenile (S1+S2) decline was faster when *Mesostoma* was present (P=0.0091). These rates did not differ for any other size classes (Table 3.4). None of the egg production response variables differed significantly with chain length (Table 3.4). *Mesostoma* significantly affected the proportion of time spent producing ephippia which increased from 0.41 to 0.63 when the food chain was lengthened (P=0.0324), opposite of the result obtained at 18°C ($P_{interaction}$=0.0047). However, there was still no difference in the average ephippia clutch size (P=0.3089).

The major effect of adding *Mesostoma* on *Daphnia* demography at 25°C was to prevent a second burst of *Daphnia* juveniles following the major population peak (Fig. 3.4). In the 2-level food chains, a second and occasionally, several more bursts in *Daphnia* population biomass occurred after the first major population peak (Fig. 3.3). No such further increases in the *Daphnia* population were observed when *Mesostoma* was added to the system, with extinction of the *Daphnia* population occurring on day 194 in all cases. The only case where one small increase in juvenile *Daphnia* density occurred was in tank 3c25-2 (Fig. 3.4). This was also the one tank where *Mesostoma* peak densities were lowest (Fig. 3.3).

Figure 3.4: The *Daphnia* demography data for the 25°C 2-level and 3-level treatments where juvenile S1+S2 (—×—), adolescent S3 (—Δ—) and adult S4+S5 (—●—) densities are represented.


2-Level
3-Level
(1)
(2)
(3)
90
75
60
45
30
15
0
165
190
215
240
265
290
Daphnia Density (#/L)
Julian Day

II - The Effect of Temperature on *Mesostoma* Dynamics

The *Mesostoma* density was relatively constant at 18°C, with populations persisting at levels between 10 and 25 individuals/sample for most of the experiment (Fig. 3.1). In one case (tank 3c18-3), *Mesostoma* density broke this pattern owing to a very large numerical response following the *Daphnia* peak, that nearly drove the *Daphnia* population extinct. In tank 3c18-1, a burst in juvenile *Mesostoma* production occurred, again following peak *Daphnia* biomass and this *Daphnia* population eventually went extinct (Fig. 3.1). In the third tank, *Mesostoma* and *Daphnia* coexisted with the only break in stable densities for *Mesostoma* occurring just after inoculation, when there was a burst in juvenile production, while *Daphnia* were at their peak densities.

The overall *Mesostoma* dynamic at 25°C was very different from the more constant one observed at 18°C. In all cases, there was a single large peak in total *Mesostoma* density following the peak in the *Daphnia* populations (Fig. 3.3). Peak densities in the *Mesostoma* populations at 25°C were double those at 18°C but, this was not a significant difference (Table 3.5), owing to small peak densities in tanks 3c25-2 (Figs. 3.3 and 3.1). The date on which the maximum total *Mesostoma* densities occurred also did not differ significantly with temperature (P=0.2120) although the largest peaks were seen earliest at 25°C (Fig. 3.3). At 18°C, the variability in the date of maximum density was greater (Table 3.5), with tank 3c18-2 having an earlier maximum than any others. For the different age classes of *Mesostoma*, the only difference in peak density was for the juveniles (Fig. 3.5 and Table 3.5). Their peak density was greater at the higher temperature (P=0.0540) reaching an average value of 93 individuals per sample at 25°C while only reaching 25 individuals per sample at 18°C. Tank 3c18-2 had the lowest peak juvenile *Mesostoma* density of the 25°C treatment tanks (Fig. 3.5).

The demography pattern for *Mesostoma* was affected by temperature. A pattern emerges in the life history of the *Mesostoma* individuals at 18°C that can be observed by examining the percent composition graphs (Fig. 3.6) and the demography graphs (Fig. 3.5). Both juveniles and adults (mostly subitaneous) were inoculated into these systems. A build-up of individuals producing subitaneous eggs occurred with increases in the proportion of subitaneous adults (Fig. 3.6). Reproduction ensued (Fig 3.7), mostly owing to subitaneous egg production. Following the decline in subitaneous egg production, all individuals reverted to dormant egg production at 18°C (Fig. 3.6).

The demography pattern for *Mesostoma* individuals differed somewhat at 25°C (Figs. 3.5 and 3.6). At 25°C, there was a rapid numerical response shortly after inoculation with a transition from approximately 50% to over 90% of the *Mesostoma*

Table 3.5: The response variable averages ± standard errors for the *Mesostoma* time-series at 18°C and 25°C. The definitions of the response variables are given in Table 3.2.

Response Variable	18°C	25°C	*P*-value
Maximum total density	50 ± 10	109 ± 23	0.2035
Date of maximum density	203 ± 5	190 ± 1	0.2120
Maximum juvenile density	25 ± 2	93 ± 21	0.0540
Maximum subitaneous adult density	27 ± 10	11 ± 1	0.5137
Maximum dormant adult density	9.7 ± 1.0	12.3 ± 1.3	0.4223
% juveniles during *Daphnia* decline	27 ± 12	69 ± 2	0.0196
% subitaneous during *Daphnia* decline	67 ± 14	16 ± 1	0.0031
% dormant during *Daphnia* decline	6 ± 3	15 ± 2	0.0657
Date of extinction	252 ± 4	209 ± 4	0.0119

Figure 3.5: The stage structure of the *Mesostoma* population where juvenile density (—|—), subitaneous adult (—●—) and dormant adult (—A—) densities are shown for the 3-level 18°C and 25°C treatments.

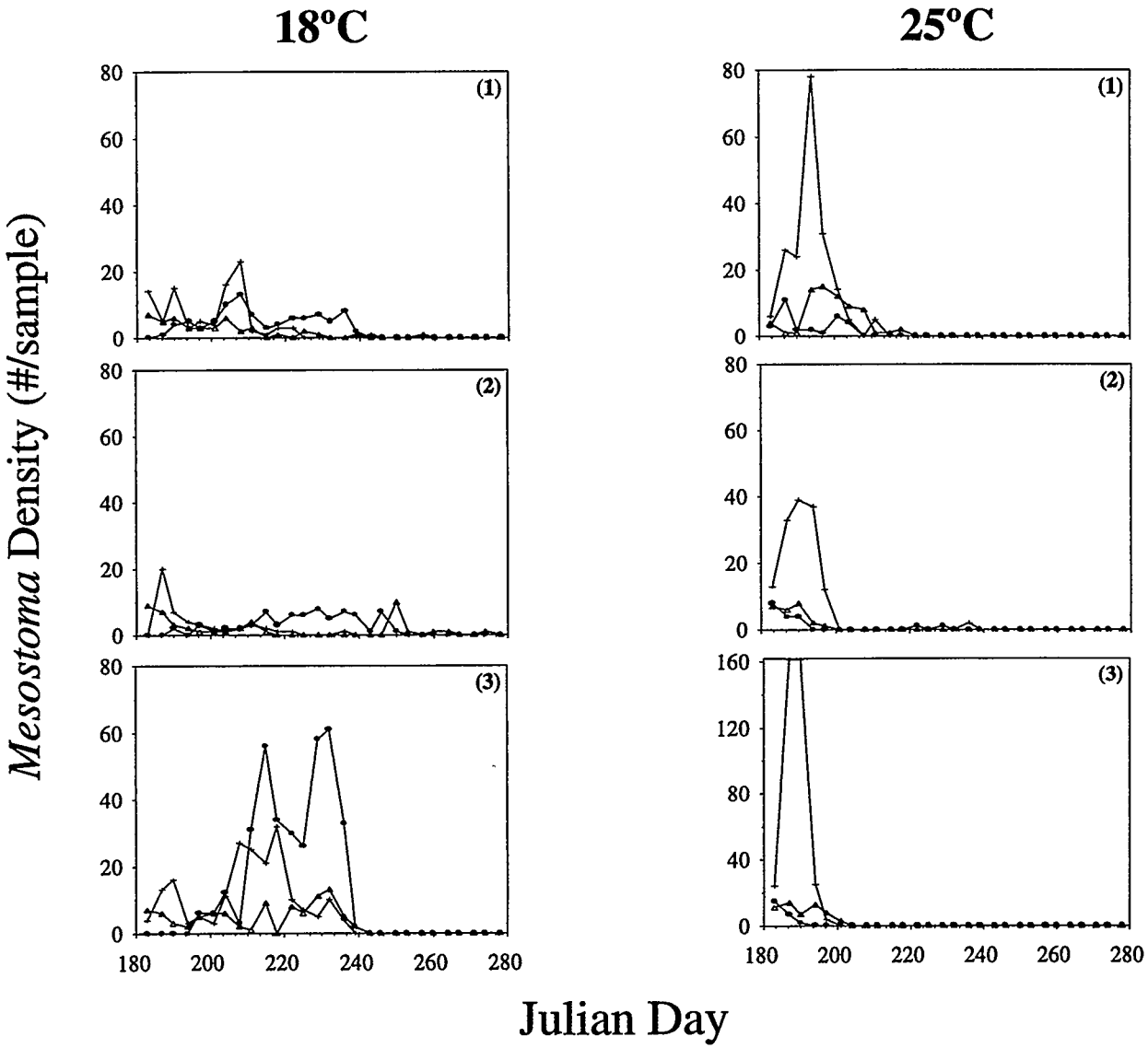

18°C
25°C
(1)
(2)
(3)
Mesostoma Density (#/sample)
Julian Day
0
20
40
60
80
120
160
180
200
220
240
260
280

Figure 3.6: The stage structure of the *Mesostoma* population where the proportion of total density composed of juveniles (☐), subitaneous adults (▤), and dormant adults (▧) are represented for the 3-level, 18°C and 25°C treatments.

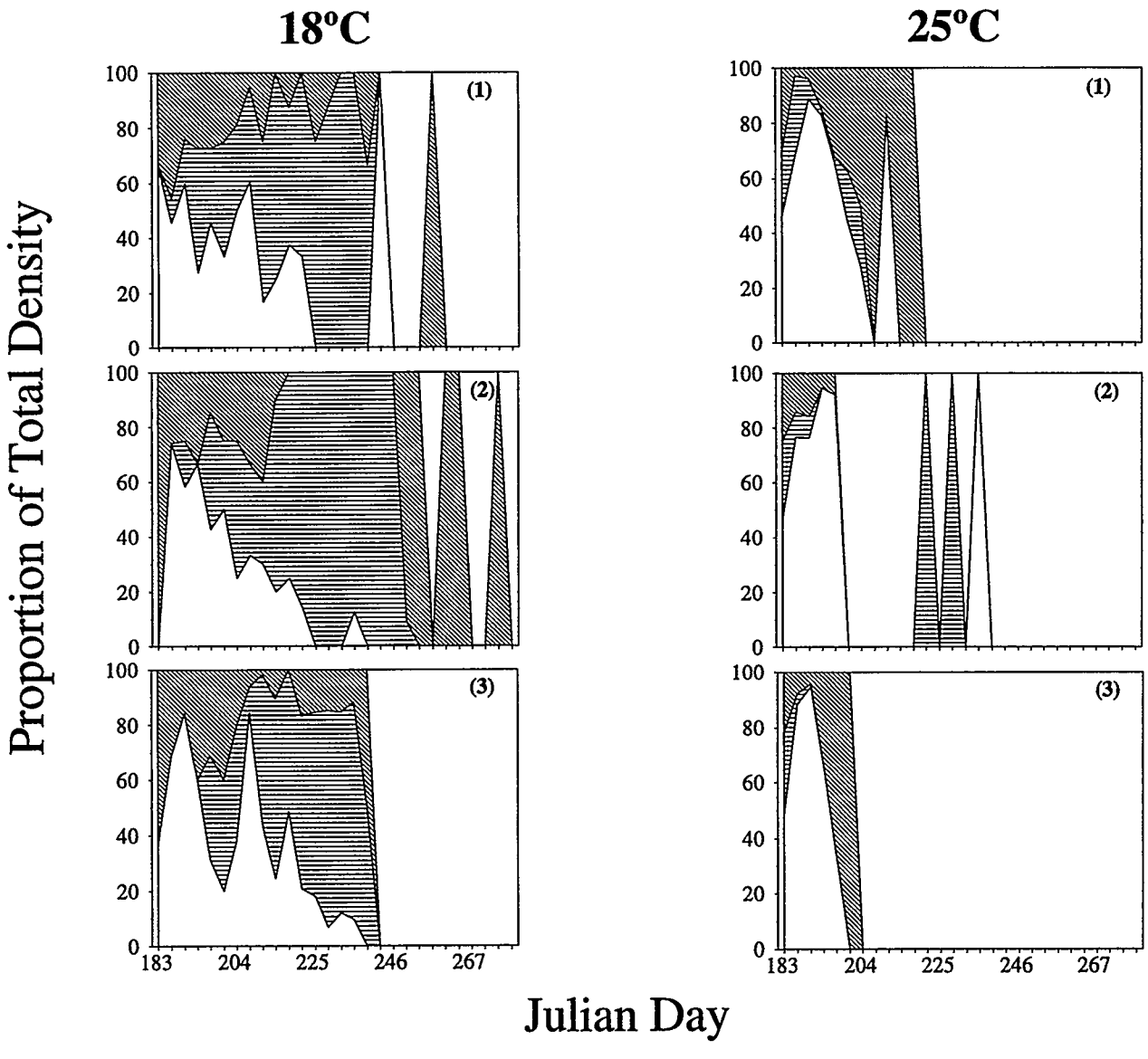
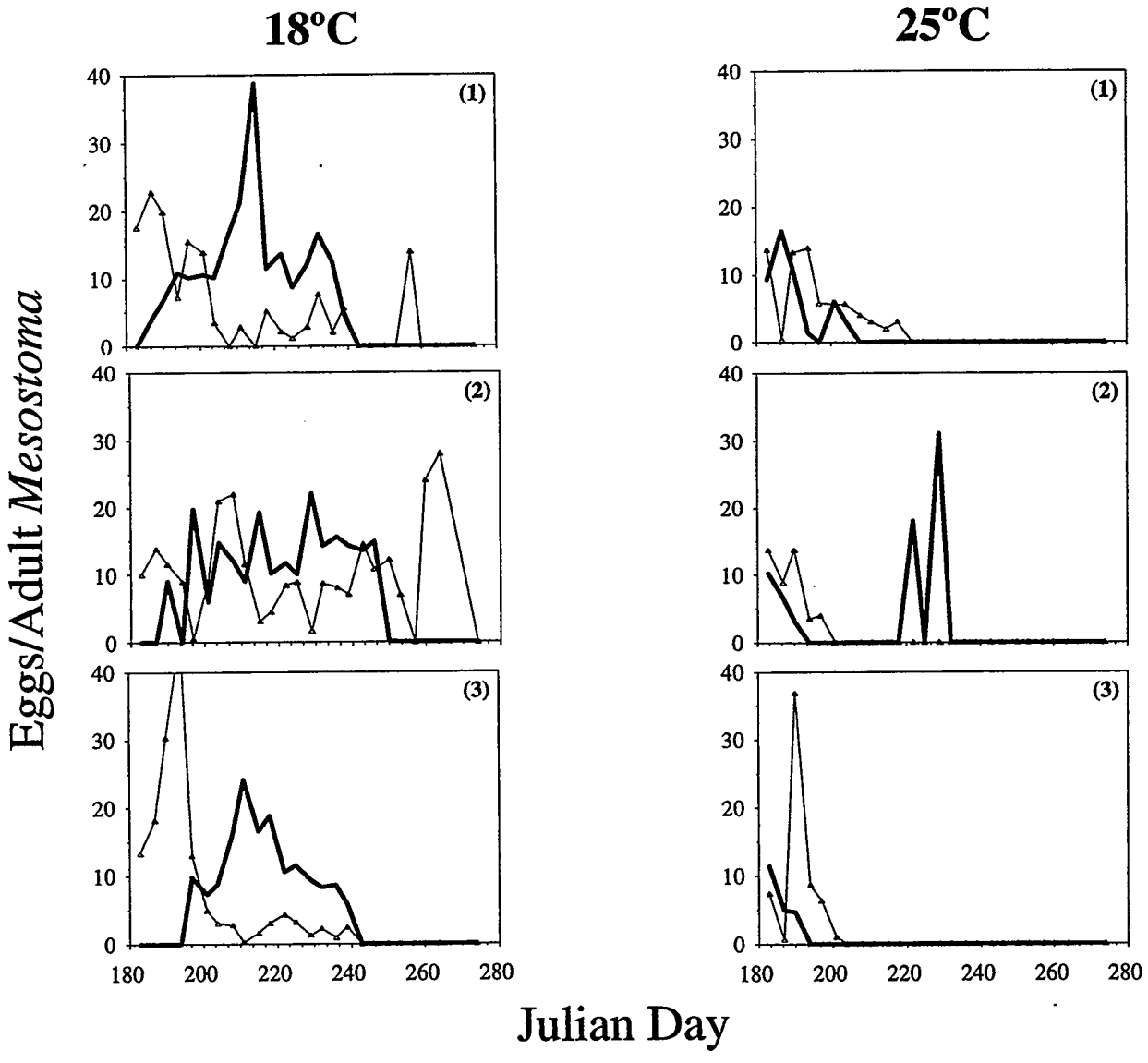

18°C
25°C
Proportion of Total Density
(1)
(2)
(3)
100
80
60
40
20
0
183
204
225
246
267
Julian Day

Figure 3.7: The fecundity data for *Mesostoma* during the time period of *Mesostoma* existence where (———) is the number of subitaneous eggs per adult and (—A—) is the number of dormant eggs per adult for the 3-level treatment at 18°C and 25°C.


18°C
25°C
(1)
(2)
(3)
Eggs/Adult Mesostoma
Julian Day
0
10
20
30
40
180
200
220
240
260
280

population being composed of juveniles on day 190 (peak *Mesostoma* density) (Fig. 3.6). The major difference with temperature in the *Mesostoma* demography was the very large increase in juvenile *Mesostoma* density (Fig. 3.5). This burst of juveniles was preceded by a larger clutch size of subitaneous *Mesostoma* at 25°C than at 18°C (Fig. 3.7). Figure 3.8 shows that adults producing subitaneous eggs were dominant in the adult carnivore population earlier at 25°C. Apparently, the inoculant of both juveniles and adults were able to produce a large cohort of young individuals following the period of high *Daphnia* biomass. After *Daphnia* extinction however, the large cohort of tank-born juveniles passed directly into dormant egg production (Fig. 3.6). Subitaneous adults appeared to lay only one clutch of eggs before passing into dormancy (Fig. 3.7).

The individuals dominating the *Mesostoma* population during the *Daphnia* decline phases at 18°C were mostly subitaneous adults (67%) followed by juveniles (27%) (Fig. 3.5). To contrast, at 25°C, during the decline period, this pattern was reversed. At 25°C, a larger proportion (69%) of the *Mesostoma* population consisted of juveniles (P=0.0196) and there was a smaller proportion (16%) of subitaneous adults (P=0.0031) (Table 3.5).

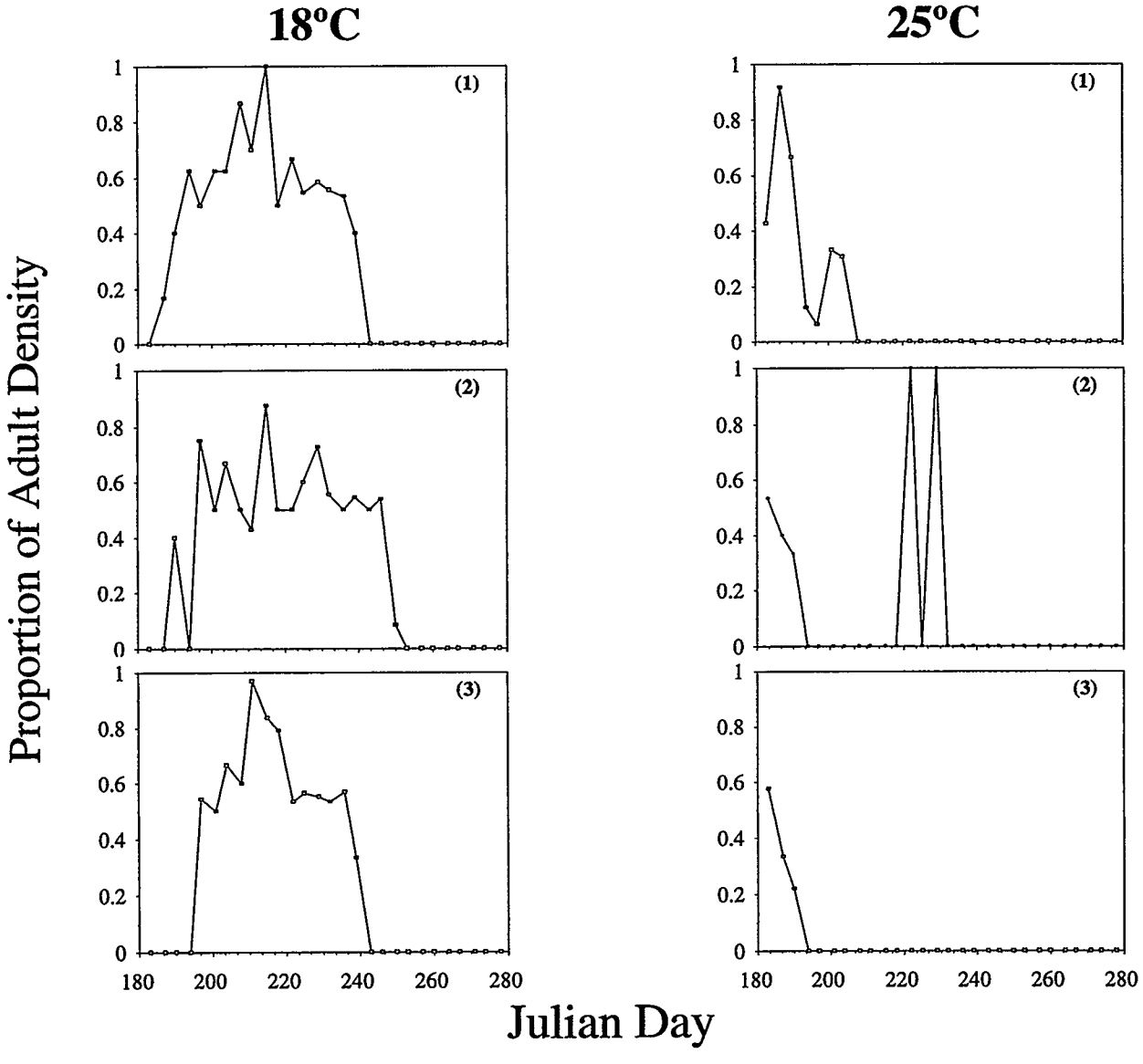
The date of *Mesostoma* extinction was significantly earlier at 25°C (P=0.0119). In all cases at 25°C, *Mesostoma* went extinct after the *Daphnia* populations (Fig. 3.3). At 18°C, the opposite pattern was observed with *Mesostoma* extinctions occurring earlier in all cases (Fig. 3.1).

Discussion

The dynamics of populations and the interactions between trophic levels differed with temperature. At 18°C, only small changes in the *Daphnia* dynamic resulted when *Mesostoma* was added to the system. There was a change in the size structure of the *Daphnia* population with the largest and smallest individuals being preferentially taken by the carnivore. There was also a response to the addition of *Mesostoma* in the phytoplankton with higher minimum phytoplankton biomass levels in the presence of the carnivore. The most obvious effect of the carnivore was the very large and persistent increase in phytoplankton upon decline of the *Daphnia* populations. The *Daphnia* populations declined at both food chain lengths to low levels at 18°C.

In all cases, at 18°C, the main effect of *Mesostoma* on the *Daphnia* population was to lead to a shift in the size structure. Both the carnivore and herbivore populations in this study are size-structured. Different size classes of *Mesostoma* show preference for different sizes of prey (Schwartz and Hebert 1982, Wrona and Koopwitz, unpubl.

Figure 3.8: The proportion of the adult *Mesostoma* population consisting of subitaneous individuals


18°C
25°C
(1)
(2)
(3)
Proportion of Adult Density
Julian Day
0
0.2
0.4
0.6
0.8
1
180
200
220
240
260
280

manuscr.). Juvenile *Mesostoma* prefer smaller prey (Wrona and Koopowitz, unpubl. manuscr.) and adult *Mesostoma* can handle both large and small prey. It is uncertain which prey item an adult *Mesostoma* will preferentially choose when given the choice between large and small *Daphnia pulex* and whether this choice is dependent on energetic constraints. Although there was no change in overall *Daphnia* biomass induced by the predator, there was a reduction in the proportion of the population consisting of the largest (S5) *Daphnia* individuals and a compensatory increase in the adolescent (S3) size class. There was also a faster decline rate for juvenile *Daphnia* and since there was no change in reproductive rates, the loss in juveniles was not due simply to a loss of reproductive adults from *Mesostoma* feeding. Rather, these results suggest that both juvenile and adult *Daphnia* were being fed on by the carnivore. Although there was a significantly shorter period of time spent producing ephippia in the presence of the predator, there was no change in clutch sizes for either eggs or ephippia. *Mesostoma* also induced a faster decline rate for neonate *Daphnia* at 18°C. For the period of the *Daphnia-Mesostoma* interaction, the *Mesostoma* population consisted of all size classes. The size structure of the carnivore population allowed for very large *Daphnia* adults to be handled by the adult *Mesostoma* and the very small *Daphnia* neonates to be handled by the juvenile *Mesostoma*. Thus, the size structure of the *Mesostoma* population probably induced the observed shift in *Daphnia* population structure to the middle size class with a reduction in the smallest and largest sizes.

For stability measured as the constancy of numbers, both *Mesostoma* and *Daphnia* populations were more stable at 18°C than at the higher temperature. For *Daphnia* this was true in both 2 and 3-level food chains. The addition of *Mesostoma* led to a reduction in the magnitude and number of large population fluctuations in *Daphnia* during the high *Daphnia* biomass period. Stability of the *Daphnia* populations, in terms of their persistence time, was also unaltered by the addition of the carnivore. The *Daphnia* biomass was not affected by the carnivore and this is due to a change in population size structure which allows for the population to compensate for any loss in biomass in the very large and very small size classes. These results suggests that *Mesostoma* is a donor-controlled predator (Fretwell 1987) at 18°C. Donor-controlled predators have little impact on their prey populations and only do so when the prey are at very high biomass levels (Fretwell 1987, DeAngelis 1992). In this case, *Mesostoma* was unable to control its prey biomass because of the compensatory ability of the *Daphnia* population. Once the *Daphnia* populations had been reduced to lower biomass levels (as was observed in all 18°C systems), the *Mesostoma* populations declined to extinction.

Extinction of the carnivore population always occurred before *Daphnia* extinction and thus was probably not the driving force behind the one case of *Daphnia* extinction observed. *Daphnia* extinction also occurred once in the absence of the predator at 18°C.

There is an indication that *Mesostoma* can have an influence on *Daphnia* biomass at 18°C. One *Daphnia* population (tank 3c18-3) was nearly driven to extinction by *Mesostoma* and in this case the *Mesostoma* population displayed a different pattern than any others at 18°C. From the *Mesostoma* demography data, it is clear that the decline in *Daphnia* was due to a pronounced numerical response that led to large *Mesostoma* densities. A large cohort of juvenile and subsequent subitaneous carnivores led to very effective reduction of the *Daphnia* population. However, full extinction of *Daphnia* did not occur and the few individuals remaining were able to repopulate the tank. Recolonization by *Daphnia* was facilitated by the extinction of the *Mesostoma* population following a conversion to dormant egg production. Dormant egg production by the carnivore may have been induced by low levels of prey (Mead 1978). *Mesostoma* producing dormant eggs are less active than either juveniles or subitaneous egg producers (Wrona and Koopowitz unpubl. manuscr.), and are a final stage as far as further population growth is concerned (Fiore 1971). Lower searching efficiency by dormant *Mesostoma* would have given *Daphnia* a spatial refuge within which to build up the population. A prediction from the exploitation hypothesis (Oksanen *et al.* 1981) of food chain theory was upheld during the period of *Daphnia* decline and recolonization in tank 3c18-3. According to the exploitation hypothesis, the predicted response for an increase in carnivore biomass is a decline in herbivore levels with a concomitant increase in autotroph biomass. During the period of time when measured *Daphnia* densities were zero, a very large increase in phytoplankton biomass occurred. Upon recolonization of the system by *Daphnia*, as the system returned to a 2-trophic level food chain, an increase in *Daphnia* biomass led to a reduction in phytoplankton biomass.

Mesostoma had no effect on the overall population stability, measured as the *Daphnia* population persistence time at 18°C. In 2 of 3 tanks both in 2 and 3-level food chains, the *Daphnia* populations persisted for the entire duration of the experimental period. In all cases, the *Daphnia* populations actually persisted for a longer period of time in the presence of the carnivore although, not significantly longer. This relationship was reversed with an increase in temperature. At the higher temperature, the obvious effect of the carnivore was to significantly reduce the time to extinction for the *Daphnia* population. There is an interaction between food chain length and temperature in terms of the stability of the *Daphnia* populations and this suggests a switch in *Mesostoma* from

donor-controlled predation to predation that exerts a controlling (or top-down) influence over the biomass of the prey population.

In both 2 and 3-level food chains, extinction of the *Daphnia* populations occurred at the higher temperature. The addition of *Mesostoma* at 25°C had an effect on phytoplankton biomass levels that would be expected from the predictions of the exploitation hypothesis (Oksanen *et al.* 1981). Minimum phytoplankton levels were significantly lower in the 2-level food chains where *Daphnia* populations were not limited by predation from above. The *Daphnia* population was inherently unstable in the 2-level system at 25°C and there are several possible reasons for this observed effect as discussed in detail in chapter 2. The effect of temperature alone on the vital rate parameters, a shift in algal community structure with *Daphnia* feeding or, a possible starvation of *Daphnia* individuals under dynamic food conditions could have led to the observed instability. The instability of the *Daphnia* population was enhanced however at 25°C by adding the carnivore to the system, contrary to predictions from food chain theory (Oksanen *et al.* 1981).

Comparing *Mesostoma* dynamics at 18°C and 25°C provides some insight into how changes in the carnivore population with temperature were responsible for the faster extinction of *Daphnia* in the 3-trophic level systems at the higher temperature. At 25°C, *Mesostoma* generally reached higher densities than those seen at 18°C. Peak densities in the *Mesostoma* populations at 25°C were double those at 18°C although, there was not a significant difference because of very large peak densities in one 18°C (3c18-3). Only juvenile *Mesostoma* density reached significantly higher levels, earlier at 25°C. The *Mesostoma* populations consisted of predominantly juvenile individuals at 25°C as opposed to all life stages at 18°C. This suggests that there was an earlier and larger numerical response in the *Mesostoma* populations at 25°C than at 18°C. Mechanisms can be proposed for the greater numerical response and the more rapid production of juveniles at the higher temperature.

The first mechanism involves the life history pattern of *Mesostoma* and temperature. Studies of *Mesostoma ehrenbergii* and related species of *Mesostoma* have demonstrated that temperature can play a major role in determining the progression of reproductive stages (Heitkamp 1972, 1977, Kolasa 1987, Heitkamp 1988). Subitaneous egg production occurs to a high rate only at temperatures above 20°C while dormant production is predominant at lower temperatures (Heitkamp 1977, 1988). However, this relationship also depends on the eggs from which individuals developed. Individuals born from dormant eggs (i.e. first individuals of the new growing season) always produce

a subitaneous clutch of eggs, regardless of temperature (Heitkamp 1977). Individuals born from subitaneous eggs produce dormant or subitaneous eggs depending on the environmental conditions as described (Heitkamp 1977, 1988). Using 20°C as the boundary, a higher proportion of subitaneous egg production would be expected in the 25°C treatment than in the 18°C treatment. This could be represented by either larger subitaneous clutch sizes or by a larger proportion of individuals in the population producing subitaneous eggs. Unfortunately, most of this data is not available because the numerical response resulting in the large increase in juveniles at 25°C occurred before sampling of *Mesostoma* was underway. From the first sampling date, it is apparent however, that subitaneous egg production was greater initially at 25°C than at 18°C. In addition, a higher proportion of adults were subitaneous earlier at 25°C. Owing to changes in life history in terms of viviparous versus resting egg production, a greater realized numerical response would be expected at 25°C than at 18°C.

Based on physiological data for *Mesostoma*, a faster numerical response would be expected at the higher temperature. For the poikilothermic *Mesostoma*, metabolic rates and population vital rates are temperature dependent (Heitkamp 1972, Heitkamp 1977, Kolasa 1987). As temperature is increased, the duration of life, the generation time and the development rate of juveniles decreases (Kolasa 1987, Heitkamp 1977). For the closely related *Mesostoma lingua*, the Q_{10} rates for most important life-rate measures are between 2 and 4 (Heitkamp 1972). These relationships with temperature would allow for the faster numerical response observed in the 25°C treatment simply by allowing for faster development of eggs and juveniles.

The physiological data on *Mesostoma* indicates that the very large and rapid numerical response observed with an increase in ambient temperature may be due to a shift in the predominant life history pattern and vital rates respectively. The realization of the increased numerical response was likely due to shorter development times and to a predominance of subitaneous egg production. This provides a mechanism for the more unstable *Mesostoma* dynamic at 25°C with large populations fluctuations.

What remains to be explained is how the change in the *Mesostoma* demography acted to further destabilize the unstable 2-level *Daphnia* dynamic at 25°C. There are three reasons that together, explain the change in the *Daphnia-Mesostoma* coupling with temperature: the very large increase in the juvenile *Mesostoma* density, the timing of this increase and the change in the underlying *Daphnia* dynamic with temperature.

With regard to the first mechanism, a large population of mostly juveniles was able to lead to faster extinction of *Daphnia* mainly through their effect on juvenile

Daphnia. Based on the size structure of the predator and prey populations, it would be expected that juvenile *Mesostoma* would preferentially prey on juvenile *Daphnia*. The decline rate of only the juvenile age class was altered by the presence of the predator at 25°C. In addition, following the first *Daphnia* population crash, further increases in juvenile density observed in the 2-level chains were absent from the 3-level food chains. The one case where a further increase in juvenile *Daphnia* density occurred was in the tank where *Mesostoma* juvenile density was the lowest. This suggests that *Mesostoma* was able to extinguish the *Daphnia* population by the removal of new recruits. A large population of mostly juvenile *Mesostoma* could have had a large impact on the *Daphnia* population for another reason. Juvenile *Mesostoma* are more mobile and use a cruising search technique while adults tend to be sit-and-wait predators (Wrona and Koopwitz, unpubl. manuscr.). More mobile juveniles would be expected to have a higher encounter rate with pelagic *Daphnia* than their more sedentary adult counterparts. Therefore, populations of *Mesostoma* with high densities of juveniles would be expected to induce higher death rates on the pelagic herbivore than populations with lower densities of juveniles such as those seen at 18°C. A population of very mobile predators can be much more destabilizing for the dynamics of a predator-prey system than less active ones (McCauley *et al.* 1993).

The second and third mechanisms together provide further explanations for the change in the coupling of carnivore and herbivore. The timing of the large increase in *Mesostoma* density was affected by temperature both in terms of the very high densities of juveniles produced and in terms of subitaneous egg production. At 25°C, owing to changes in life history or to population vital rates, the *Mesostoma* population was able to respond to high *Daphnia* biomass levels faster. In addition, the underlying *Daphnia* dynamic was unstable at 25°C whether *Mesostoma* was present or not. Therefore, there are periods of major decline in the *Daphnia* population that are more likely to occur as the temperature is increased. Because of the faster response of *Mesostoma* to *Daphnia* biomass levels, an increase in the *Mesostoma* population is more likely to occur concomitant with a large decline in *Daphnia* biomass, thereby adding to the mortality factor during a period when the density dependent *Daphnia* reproductive rates are already low.

To summarize therefore, the large effect of *Mesostoma* on *Daphnia* at 25°C can be attributed to several interacting factors. A further destabilization of the *Daphnia* dynamic would be expected in the presence of the predator at higher temperatures owing to the fact that *Daphnia* periods of decline are more likely at higher temperatures and that

Mesostoma is able to respond faster and to a higher degree with subitaneous egg and juvenile production. *Mesostoma* is able to lead to faster *Daphnia* extinction by removal of new recruits to the population. Thus, at the higher temperature, characteristics of the *Daphnia* dynamics, *Mesostoma* life history, population size structure and the interaction of these make the faster extinction of *Daphnia* more likely. This is the most likely mechanism for the greater instability (faster extinction) observed in the *Daphnia* population at the higher temperature in the presence of a third trophic level.

This study has several important implications for investigations into food chain stability and for the potential effects of global warming in natural systems. In the past, it has been demonstrated that few predators exert control over *Daphnia pulex* population dynamics that is important enough to be modelled explicitly rather that as part of the environment of the *Daphnia*-algal interaction (McCauley *et al.* 1988, Murdoch 1992). This study has shown that the importance of a carnivore in this system depends on the ambient temperature for some species. With an increase in temperature, a switch from relatively unimportant donor-control to more explicit control over the *Daphnia* dynamics by the carnivore was observed. This suggests that dynamics occurring in natural systems over the growing season may change as the temperature of the water changes. Dynamic effects of some invertebrate carnivores may only become important when water temperature is high.

From theory, it has been predicted that the addition of a third trophic level to an unstable plant-herbivore system should act to stabilize the dynamics (Rosenzweig 1973, Wollkind 1976). This was the general outcome of the dynamics at 18°C with slight reductions in population fluctuations. At 25°C however, the dynamics of the already unstable *Daphnia*-algal interaction were further destabilized by the addition of the carnivore. This suggests that other features of the carnivore and the environment may be important in formulating predictions. The life history and the values of population parameters of the carnivore existing within a particular set of environmental conditions may change the expected stability response.

The effect of temperature on all trophic level populations and the interactions between these groups play an important role in the outcome expected from global warming. Many pond communities where fish are absent are composed of 3-trophic level food chains with invertebrate carnivores. At lower temperatures, all 3 trophic levels are more likely to coexist for extended periods of time. Increasing the temperature may lead to a destabilization of the entire system because of changes at all trophic levels. The extinction of all trophic levels above the primary producers may be the outcome.

Daphnia are an important food source to many organisms and their disappearance from prairie pond systems is likely as mean ambient temperatures are increased, especially in systems where predators such as *Mesostoma* are present and are also influenced by the same environmental conditions.

CHAPTER 4 - Conclusions

In this thesis, I examined the influence of temperature on the dynamics of the *Daphnia pulex* and phytoplankton predator-prey system under several community conditions. The major result, regardless of community composition, was a destabilization of the plant-herbivore dynamic as predicted by theory (May 1976, Murdoch and McCauley 1985, Lawton 1987, McCauley and Murdoch 1987) and observed by Pratt (1943) and Halbach (1970) for single species laboratory populations of zooplankton. Extinction of *Daphnia* always occurred at 25°C, while persistence was found at 18°C. Three mechanisms were proposed for the destabilization and extinction of *Daphnia* at 25°C:

(1) The direct effect of temperature on the parameters describing the vital rates for *Daphnia* and its algal prey leading to large amplitude fluctuations.

(2) The starvation of *D. pulex* individuals as a result of the prey being reduced to very low levels with productivity rates that could not support turnover rates of the herbivore.

(3) A shift in algal community structure, to less edible species, as a result of *Daphnia* feeding, that could not support the growth of *Daphnia*.

Further detailed experiments are needed to differentiate among these possible mechanisms, and could be done by monitoring the growth of marked individual *Daphnia* under conditions of dynamic food. Monitoring the growth of both the edible and inedible fractions of phytoplankton is necessary at 18°C and 25°C under conditions where *Daphnia* are present and where they are absent.

The major qualitative and quantitative responses to temperature observed in the baseline community type were not significanlty altered by simplification of the system (i.e. exclusion of competitors of *Daphnia* and a simplification of the phytoplankton assemblage). The response to temperature of the *Daphnia*-algal interaction was also examined in the presence of a third trophic level consisting of the flatworm *Mesostoma ehrenbergii*. This invertebrate carnivore has a generational time scale similar to *Daphnia* (Heitkamp 1977) and can therefore show a numerical response to its prey population density. In the 3-level food chains, the destabilization of the *Daphnia* populations with temperature was enhanced, with extinction occurring even faster than in the 2-level chains.

Regardless of initial community composition at 25°C, the final algal communities consisted predominantly of large blue-green algal blooms. Final zooplankton

assemblages contained only small-bodied species (rotifers in the simplified communities and rotifers, *Ceriodaphnia* sp., *Alona* sp. and Ostracods in all others) that were incapable of controlling the algal biomass. To contrast, at 18°C, almost all *Daphnia* populations persisted for the duration of the 5 month experimental period with an absence of very large algal blooms and significant densities of potential competitors (excluding rotifers).

In the second part of this thesis, I examined aspects of food chain dynamics by contrasting the population dynamics of all trophic levels in 2 and 3-level food chains at 18°C and 25°C. Few studies have examined population dynamics in food chains in which higher trophic levels are also dynamic.

At 18°C, the stage-structured predator induced a change in the size structure of the *Daphnia* population, although there was no change in overall biomass levels. *Mesostoma* had little effect on the overall *Daphnia* population at 18°C and acted as a donor-control predator. At 25°C, the effect of *Mesostoma* was pronounced and, the carnivore induced faster extinction of *Daphnia*. The carnivore exerted control over the density of the *Daphnia* population mainly by removing juveniles.

There were several possible factors which could have contributed to the differential controlling influence of *Mesostoma* with temperature. These involved a change with temperature in the predominant reproductive strategy and in the development time of *Mesostoma* leading more quickly to a carnivore population dominated by highly mobile juveniles. Changes in carnivore life history combined with an unstable underlying *Daphnia* dynamic at 25°C, would make the coincidence of a large population decline in *Daphnia* and a very large and fast numerical response in the carnivore more likely. This was the proposed mechanism for the faster extinction of *Daphnia* observed in the presence of the carnivore at 25°C. These results suggest that the importance of an invertebrate carnivore population in natural systems may depend on the temperature of the system. Further details of *Mesostoma* feeding and its influence on *Daphnia* populations need to be investigated.

If predictions from general circulation models are accurate, prairie wetlands will experience substantial increases in temperature. Many of these communities lack fish predators and therefore, most planktonic interactions involve invertebrate poikilotherms. Temperature increases are predicted to lead to substantial changes in community composition and structure. This study has shown that predicted responses to temperature from single species studies may be altered by interactions between adjacent trophic levels. In pond systems, the loss of major herbivores is expected with an increase in

water temperature. Final community composition consists of small-bodied zooplankton assemblages which are incapable of controlling a large amount of algal biomass.

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