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Interactions between Chaoborus spp. and Mysis relicta and their
impact on pelagic crustacean zooplankton in mesocosms at the
Experimental Lakes Area.

submitted by

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in partial fulfillment of the requirements for the degree of

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**Interactions between *Chaoborus* spp. and
Mysis relicta and their impact on pelagic
crustacean zooplankton in mesocosms at the
Experimental Lakes Area**

by

Dalila Seckar

A Thesis submitted to the Faculty of Graduate Studies of

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Abstract

The objectives of this study were: 1) to compare and contrast the effects of variations in natural densities of two common freshwater predators of crustacean zooplankton, *Chaoborus* spp. and *Mysis relicta*; and 2) to determine whether the combined impacts of these predators together differed from their effects when alone. In deep (>10m) mesocosms, additions of *Chaoborus* and *Mysis* at natural densities did not result in large changes in zooplankton abundances, lengths, or biomass. Significant decreases in abundance were observed only for *Bosmina longirostris* and *Daphnia* spp. In small (~20L) enclosures, higher predator densities caused zooplankton declines over three days. Strong interactive effects between *Chaoborus* and *Mysis* were not detected in either the large or small enclosures. This suggests that the combined effects of these two predators can be predicted from their effects determined in isolation.

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1 Introduction

Pelagic invertebrate predators have potentially large impacts on abundance of crustacean zooplankton and community composition (e.g. Lane 1979; Threlkeld et al. 1980; Brabrand et al. 1986; Elser et al. 1987; Matveev and Martinez 1990; Wissel and Benndorf 1998; McNaught et al. 2004). Invertebrate predators of crustacean zooplankton are taxonomically diverse and include cyclopoid copepods, water mites (*Acari*), *Leptodora kindtii* (Focke) (Cladocera), *Chaoborus* spp. (Insecta), and *Mysis relicta* Lovén (Malacostraca). Typically, several different invertebrate predators may occur within individual lakes and regionally.

It is now widely recognized that invertebrate predators should be more broadly included in representations of aquatic food webs because they consume zooplankton (e.g. Fedorenko 1975a; Cooper et al. 1985; Chess and Stanford 1998; Branstrator and Holl 2000; Hart 2002), compete with fish for food (e.g. Gliwicz and Hillbricht-Ilkowska 1978; Lane 1979; Rieman and Falter 1981; Brabrand et al. 1986; Soto and Hurlbert 1991), and are directly eaten by fish (e.g. Luecke 1986; Næsje et al. 1991; Pothoven et al. 2000). As a result, variations in invertebrate predator densities or species composition may influence fish community biomass and water quality.

The Precambrian Shield underlies approximately half of Canada's landmass (Natural Resources Canada 2006) and contains an estimated one million lakes (Schindler 1991; Hebert 2007; Gouvernement du Québec 2008). Many are oligotrophic, with low availability of phosphorus (Dillon and Kirchner

1975) and are heavily fished by anglers (Economic Analysis and Statistics Policy Sector Fisheries and Oceans Canada 2007) and used as water sources. Many lakes on the Canadian Shield are being affected by anthropogenic activities such as eutrophication, climate change, contaminants, and over-fishing (Schindler 1998b). These activities frequently affect the abundance and species composition of invertebrate predators of crustacean zooplankton. An understanding of the implications of these changes is essential for developing better predictions of human impacts for the future.

Two of the most common invertebrate predators in lakes of the Canadian Shield are the phantom midge (*Chaoborus* spp.) and the opossum shrimp (*Mysis relicta*). The four larval instars of *Chaoborus* spp. consume phytoplankton, rotifers, and crustacean zooplankton (Moore 1988; Moore et al. 1994). *Chaoborus* are ambush (or "sit-and-wait") predators (reviewed in Cooper et al. 1985) that sense prey with mechanoreceptors located on the body surface (Pastorok 1980). *Mysis* are soft-bodied, shrimp-like invertebrates that consume zooplankton as well as phytoplankton and detritus (Grossnickle 1982). They are cruising predators (reviewed in Cooper et al. 1985) that use mechanoreception (Cooper and Goldman 1982) and possibly light (Ramcharan and Sprules 1986; Van De Meutter et al. 2005) to find and capture prey.

I compared and contrasted the effects of variations in natural densities of *Chaoborus* spp. and *Mysis relicta* on crustacean zooplankton. In addition to comparing the effect of each predator in isolation, I also examined whether the combined impacts of the predators together differ from their effects when alone.

Such analyses are crucial to understanding the effects of changes in the abundance of these taxa in lakes affected by natural or anthropogenic disturbances. Below, I briefly review information on the predatory behaviour of *Mysis* and *Chaoborus*, multiple predator effects, and variations in densities of these predators in Canadian Shield lakes.

1.1 Effects of Chaoborus and Mysis on crustacean zooplankton

Many studies suggest that variations in densities of *Chaoborus* or *Mysis* can strongly affect zooplankton community structure. For example, high densities (0.2-1/L) of *Chaoborus flavicans* larvae suppressed *Daphnia* and copepods in shallow ponds where low densities (up to 0.2/L) did not (Hanazato 1990). Sutor et al. (2001) found that *Bosmina* and calanoid copepod lengths were shorter when higher densities (0.3-0.5/L) of fourth-instar *Chaoborus trivittatus* (Loew) were present in deep enclosures. Following the introduction of *Mysis* to Lake Selbusjøen, cladoceran biomass declined from 26mg/m³ to 3.5mg/m³ (Langeland et al. 1991). In paired *in situ* chambers in Lake Michigan, *Mysis* consumed nauplii, cyclopoid copepodids, and cladocerans at high rates (Bowers and Vanderploeg 1982).

The independent impacts on zooplankton of *Chaoborus* and *Mysis* on zooplankton have not been directly compared on the same zooplankton community. Based on differences in their predatory behaviours (ambush or cruising), size, and within-lake distribution, several generalizations can be made.

Chaoborus is an ambush predator that most frequently captures active prey. Smyly (1980) found that the more active *Cyclops abyssorum* Sars was

eliminated in trials with *Chaoborus flavicans* (Meigen), while *Mesocyclops leuckarti* (Claus), was less vulnerable because it interspersed swimming with clinging to surfaces. In contrast, actively swimming prey are typically more evasive or are able to escape predation by *Mysis* (Cooper and Goldman 1980; Folt 1985; Nero and Sprules 1986a). For example, the calanoid copepod, *Epischura nevadensis* Lilljeborg, is more susceptible to *Mysis* predation than the calanoid, *Diaptomus tyrelli* Poppe, because it has weaker escape responses (Cooper and Goldman 1980). Most cladocerans are highly susceptible to *Mysis* predation because they are not as strong swimmers compared to copepods and lack post-contact defences (Nero and Sprules 1986a). The cladoceran *Diaphanosoma* may be an exception because of its faster swimming speed and superior escape behaviours (Nero and Sprules 1986a).

Although both predators grow through a range of sizes, *Mysis* typically achieve larger sizes than *Chaoborus*. Fourth instar *Chaoborus flavicans* larvae typically consume medium-length zooplankton (~1mm) (Vinyard and Menger 1980; Smyly 1980; Elser et al. 1987; Lüning-Krizan 1997). Small mysids consume smaller prey while large mysids can consume small and large prey (Cooper and Goldman 1980). In a survey of Ontario lakes, total zooplankton biomass and biomass of zooplankton larger than 1mm were both lower in lakes with *Mysis* (Almond et al. 1996). The shape of zooplankton prey also influences whether they are easily consumed by invertebrate predators. Fourth instar *Chaoborus flavicans* larvae eat most prey “head-first” and the shape of copepods makes them easier to consume than *Daphnia*, which are irregular in cross-

section (Luecke and Litt 1987; Jin and Sprules 1988). Thus, prey shape may be more representative of susceptibility to predators than prey length.

Variations in the migratory behaviour of *Mysis* and *Chaoborus* may also affect their impact on zooplankton communities. Both *Mysis* and *Chaoborus* exhibit strong vertical migratory behaviours and the most probable explanation is avoidance of predatory fish (Beeton and Bowers 1982). Early *Chaoborus* instars are found near the lake surface throughout the day and night (e.g. LaRow and Marzolf 1970),(Sardella and Carter 1983; Voss and Mumm 1999) whereas instars III and IV migrate vertically into the epilimnion at night (Luecke 1986). Larvae are in proximity to sediments during the day and their nocturnal ascent is initiated with diminishing light intensity (Swift and Forward 1988). *Mysis* also spend daylight hours associated with the sediments and ascend into the water column at dusk (Beeton and Bowers 1982). They usually aggregate below the thermocline and descend when light intensity increases (Beeton and Bowers 1982). *Mysis*, therefore, has a greater impact on prey in the hypolimnion (Nero and Sprules 1986a) and zooplankton may avoid areas where *Mysis* are aggregated (Schulze and Brooks 1987). Zooplankton may also display diurnal migrations in response to fish (Lampert 1987; Gliwicz 1994; Loose and Dawidowicz 1994; Young and Watt 1996) and invertebrate predators (Neill 1990; Peacor et al. 2005; Boeing et al. 2006). For example, after *Chaoborus* were removed from Gwendoline Lake (following the addition of fish), *Diaptomus kenai* Wilson ceased migration (Neill 1990). Once *Chaoborus* was added to

mesocosms with *Diaptomus*, the copepod was located in the surface waters during the day and migrated to the bottom at night (Neill 1990).

1.2 Impacts of multiple predators on prey communities

While both *Chaoborus* and *Mysis* can be found in the same lake (Hamilton 1971; Nordin et al. 2008), the impacts of these predators on zooplankton have not been examined together. When different predators occur together, they can have a risk enhancing or risk reducing impact on prey, as compared to their impacts alone. Risk enhancement occurs when prey defences used to avoid one predator make them more susceptible to the other predator (Sih et al. 1998). For example, if a prey species tries to avoid *Mysis* by increasing escape movements, it could increase encounters with the sit-and-wait *Chaoborus*. Risk enhancement could also occur if the predatory activities of the two predators occur most intensely in different parts of the water column. For example, if *Mysis* predation occurs primarily in the hypolimnion and *Chaoborus* predation in the epilimnion, effective spatial refuges will be reduced when both predators are present. Risk reduction may occur when prey have generalized responses that decrease susceptibility to multiple predators or when predators interfere with each other (Sih et al. 1998). For example, some zooplankton may develop spines or alter their behaviour in ways that make it difficult for both *Mysis* and *Chaoborus* to consume them. Predator interference includes consumption of one predator by another (intraguild predation) or reduced feeding caused by the presence of the other predator.

1.3 *The distribution of Chaoborus and Mysis in Holarctic lakes*

In north temperate lakes, *Mysis* is limited primarily to proglacial lakes (Roff et al. 1981), whereas adult *Chaoborus* are aerial and can widely disperse (Berendonk and Bonsall 2002). The density of *Chaoborus* spp. in Canadian Shield lakes is frequently lower than in other studied lakes, while the density of *Mysis* in Canadian Shield lakes is lower than in the Laurentian Great Lakes. *Chaoborus* often are abundant in eutrophic lakes (e.g. Liljendahl-Nurminen et al. 2002) and increases in lake productivity increase survival of early instars (Neill and Peacock 1980). *Chaoborus* are intolerant of UV light that penetrates to greater depths in clear lakes of the Canadian Shield (Carter et al. 1980; Persaud and Yan 2003; Wissel et al. 2003a). The abundance of *C. punctipennis* (Say) is greater in shallower lakes (Wissel et al. 2003a), while abundances of *Mysis relicta* are greater in large, deep lakes (Carpenter et al. 1974; Beattie and Clancey 1991; Gal et al. 2006). *Mysis* does not tolerate low dissolved oxygen levels (Sherman et al. 1987) and mortality increases above 17°C (Rudstam et al. 1999).

While densities of *Chaoborus* are typically less than 2000/m² or 1/L in lakes on the Canadian Shield (Pope et al. 1973; Yan et al. 1985; Persaud and Yan 2001; Malkin et al. 2006), abundances elsewhere can be dramatically higher. In a deep African lake, Lake Malawi, *C. edulis* Edwards reached densities of up to 5000/m² in June, 1993 (Irvine 1997). In the multi-basin Lake Hiidenvesi, Finland, the abundance of *C. flavicans* fluctuated between 1000/m² and 13000/m² (Liljendahl-Nurminen et al. 2002). A small fishless German lake had densities of up to 11 larvae/L (Wissel and Benndorf 1998).

While high densities of *Mysis* have been reported from lakes following their introduction (e.g. over 4860/m² in 1978 in Lake Tahoe: Rieman and Falter 1981), *Mysis* densities are commonly lower. In Lake Breter Luzin, Germany, Scharf and Koschel (2004) found *Mysis* abundance averaged 113/m² over the season. The mean abundance of *Mysis* in Lake Mjøen, Norway was approximately 200/m² during 1976 to 1980 (Kjellberg et al. 1991). In North America, the mean abundance of *Mysis* was reported as 267/m² in 1995 and 1996 in Lake Ontario (Gal et al. 2006) and 35/m² in 1997 and 1998 in Lake Michigan (Pothoven et al. 2000). Nero (1981) reported abundances of 313/m² and 149/m² in Lakes 305 and 239, respectively, at the Experimental Lakes Area (northwestern Ontario) in 1979 and 1980.

Mysis and *Chaoborus* may be sensitive to anthropogenic disturbances. For example, a whole-lake acidification experiment in Lake 223 at the Experimental Lakes Area (ELA) in northwestern Ontario resulted in the elimination of *Mysis* (Nero and Schindler 1983). The dominant invertebrate predators in Lake 223 are now *Chaoborus* spp. (M. Paterson, unpublished data). Similarly, lake eutrophication may result in lowered oxygen levels that *Mysis* is unable to withstand (Sherman et al. 1987). In contrast to *Mysis*, *Chaoborus* is highly tolerant of low hypolimnetic oxygen concentrations (Scholz and Zerbst-Boroffka 1998) and low pH (Price and Swift 1985). Alternately, the abundance of *Chaoborus* larvae often declines when fish are introduced to previously fishless lakes (e.g. Northcote et al. 1978). Large changes in crustacean zooplankton community structure often occur coincident with changes in densities of

invertebrate predators in impacted lakes but it is often unclear whether these changes are the direct result of the impacts or indirect responses to changes in invertebrate predation. A full understanding of the relative impacts of *Chaoborus* and *Mysis* on crustacean zooplankton is essential to appreciate the effects of different anthropogenic impacts on Canadian Shield lakes.

1.4 Study objectives

The objectives of this study were to address the following questions concerning the effects of *Mysis* and *Chaoborus* on pelagic crustacean zooplankton in an oligotrophic Canadian Shield lake: 1) Do variations in natural densities of *Chaoborus* and *Mysis* have different impacts on crustacean zooplankton abundance, species composition, biomass, or behaviour? 2) Are the combined effects on crustacean zooplankton of *Chaoborus* and *Mysis* different from their summed independent effects? Answers to these questions will help provide better predictions of the effects of anthropogenic disturbances that specifically affect these taxa. In addition, human activities most strongly affect higher trophic levels such as invertebrate predators (Duffy 2002). A generalized understanding of the effects of changes in the diversity of predators is currently being sought to better understand responses to human impacts (Worm and Duffy 2003; Duffy et al. 2007).

The study objectives were addressed using a series of manipulations in mesocosms in oligotrophic Lake 239 at the Experimental Lakes Area (ELA) in northwestern Ontario. Most of these manipulations utilized deep enclosures (>10m) that allowed predators and prey to maintain natural vertical migrations

and provided experimental replication. Predators and prey were added at densities corresponding to those in lakes typical of the surrounding area to better emulate the processes in oligotrophic Canadian Shield lakes.

An initial experiment was carried out in the summer of 2004 in which densities of *Chaoborus* and *Mysis* were manipulated alone and together in deep enclosures. In this experiment, some enclosures were lost due to the development of holes in the enclosure walls or accidental introduction of fish. As a result, the experiment was repeated in 2005. In each experiment, crustacean zooplankton were sampled weekly to determine changes in species composition, abundance, length of individuals, and biomass. On one date in each year, vertical distributions of zooplankton and predators were examined from one enclosure of each treatment. A short experiment was also conducted in small enclosures in 2004 to examine the impact of different predator densities on crustacean zooplankton prey. The combination of different experimental techniques allowed for the assessment of the effects of natural predator densities of *Chaoborus* and *Mysis* on the pelagic crustacean zooplankton community.

2 Methods

2.1 Site description

The study was conducted in Lake 239 at the Experimental Lakes Area (ELA). The ELA is located in the boreal forest ecoregion on the Precambrian Shield (Brunskill and Schindler 1971) between Kenora and Dryden, Ontario [93°30'-94°00'W, 49°30'-49°45'N].

Lake 239 is a first order, oligotrophic lake with a maximum depth of 30m, a surface area of 56ha, and an average depth of 10.5m (Brunskill and Schindler 1971). Details on long-term changes in nutrients, phytoplankton, and zooplankton of L239 can be found in Findlay et al. (2005). Abundant phytoplankton in Lake 239 include *Synedra*, *Ochromonas*, and *Botryococcus* (Schindler and Holmgren 1971). The pelagic zooplankton community includes rotifers (*Keratella cochlearis* (Gosse), *Kellicottia longispina* Kellicott, *Polyarthra vulgaris* Carlin, *Conochilus unicornis* Rousselet, *Polyarthra remata* Skorikov, and *Collotheca* spp.), copepods (*Leptodiaptomus minutus* (Lilljeborg), *Epischura lacustris* Forbes, *Mesocyclops edax* (Forbes), *Tropocyclops extensus* (Kiefer), and *Diacyclops thomasi* (Claus)) and cladocerans (*Daphnia* spp., *Bosmina longirostris* (Müller), *Diaphanosoma birgei* Korinek, and *Chydorus* cf. *sphaericus* (Müller)) (Malley and Chang 1994). *Mysis relicta* is also found in Lake 239 while *Chaoborus* spp. are rare (Hamilton 1971; Vanni 1988). The abundant fish species are *Perca flavescens* (Mitchill), *Esox lucius* Linnaeus, *Salvelinus namaycush* (Walbaum), *Coregonus artedii* Lesueur, and *Catostomus commersonii* (Lacepède) (Beamish et al. 1976).

2.2 Large enclosures

Experimental work was conducted in deep enclosures (>10m) during the summers of 2004 and 2005. Enclosures were sampled weekly to assess impacts of variations in natural densities of *Mysis* and *Chaoborus* on zooplankton abundance, length of individuals, biomass, and vertical migration. The experiment conducted in 2004 was replicated in 2005 because technical problems reduced the number of replicates in one treatment in 2004.

2.2.1 Experimental design

A 2 x 2 factorial design was applied with *Mysis* presence/absence crossed with *Chaoborus* presence/absence. Three replicates of each treatment were conducted in 2004 and four replicates of each treatment in 2005. In predator treatments, the same density of predators was added to all enclosures, following an additive design (Sih et al. 1998). Although this design confounds the multi-species treatment with total predator density, it allows for partitioning of the effects of different predator species (as in Cardinale et al. 2006). The potential importance of this assumption was examined using small enclosures (see section 2.3). An alternative to the additive design is a substitutive design, where total predator density is held constant resulting in fewer individuals of each predator species in multi-predator treatments (Griffen 2006). The number of treatments required to test both the multiplicative and substitutive designs (Griffen 2006) was too great to undertake in this study with the large enclosures.

2.2.2 Enclosure installation

Enclosure frames were constructed of wood with buoyancy supplied by extruded polystyrene. Each frame measured 2.3m by 1.74m and held a 1.58m

diameter polyethylene bag. Enclosures were open to the atmosphere with sides that extended approximately 0.2m above the water surface. The depth of the bags ranged from 10.5m to 12m and bottoms were sealed from the lake sediments. Enclosures were located in water 14 to 19m deep. The use of deep enclosures allowed zooplankton and predators to migrate vertically and allowed for the inclusion of *Mysis*, which can only tolerate water colder than approximately 17°C (Rudstam et al. 1999). Frames were joined together in units of four, with an anchor attached to each corner (Figure 1). A cinderblock, which rested on the lake bottom, was tied to the bottom of each bag to weight it.

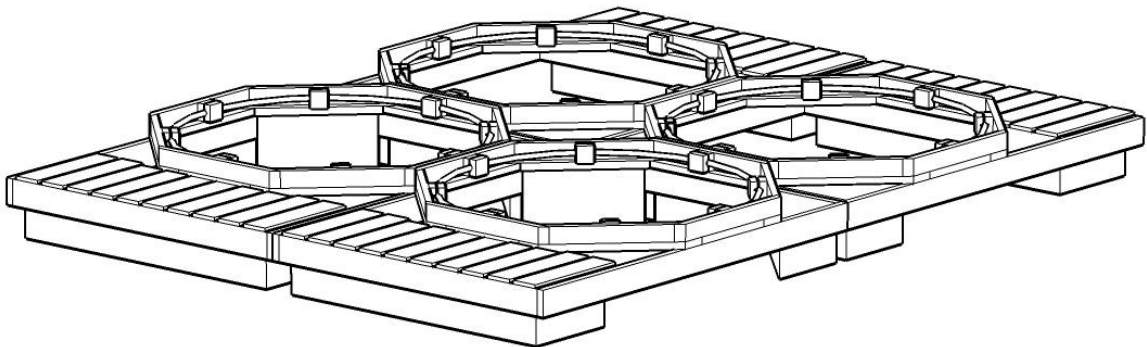


Figure 2.1: Supportive frames for four enclosure bags of large enclosures.

The four treatments (no predators, *Chaoborus*-only, *Mysis*-only, and both predators) were each randomly assigned to one enclosure in a group of four joined enclosures. Using gasoline-powered pumps, the bags were filled with water filtered through a 500µm mesh to ensure that no *Mysis* or *Chaoborus* were accidentally introduced. Zooplankton less than 500µm passed through the mesh with initial pumping and a further inoculum was subsequently added. Zooplankton for the inoculum were collected using repeated hauls of a 160µm

mesh net and filtered through an 864µm mesh to exclude predators. Zooplankton were added to all enclosures to obtain densities slightly higher than occurred naturally in the lake (dates of actions in both years in Table 2.1).

Zooplankton were allowed to adapt to the enclosures for approximately two weeks before predators were added. *Mysis relicta* from Lake 239 were collected and added to the enclosures at night. Because mortality of *Mysis* increases rapidly above 17°C (Rudstam et al. 1999), they were kept in cold water during the addition process. A Van Dorn sampler was modified to lower and release *Mysis* in each enclosure at a depth of 10m where temperatures were below 17°C. Care was taken not to expose *Mysis* to bright light to avoid damaging their eyes (Ramcharan and Sprules 1986).

Chaoborus, although present, are not abundant in Lake 239. *Chaoborus* larvae were collected from nearby Lake 227 at the ELA and transported to Lake 239 in large nalgene bottles. *Chaoborus* were rinsed with water from L239 to prevent introduction of non-native zooplankton and phytoplankton and added to each enclosure as required by the design. Greater than 95% of larvae added to the enclosures were later identified as *C. flavicans* (Sæther 1972) and were instars II to IV (Dumont and Balvay 1979).

Both *M. relicta* and *Chaoborus* spp. are common in ELA lakes and I attempted to stock enclosures at natural densities for the region. Natural abundances of *Mysis* range from 5 to 1050/m² (0.25 to 57/m³) and of *Chaoborus* from 0.2 to 5360/m² (0.03 to 482/m³) in ELA lakes (M.J. Paterson, unpublished data). The mean number of *Mysis* found in L239 from 1986 to 1992 was

127±24/m² (6.69±1.51/m³) (M.J. Paterson, unpublished data). Samples collected on 15 July, 2004 indicated a *Mysis* density of 122.5/m² (4.0/m³) in Lake 239. The target density of *Mysis* in the enclosures was 100/m² (or 8.74/m³). *Chaoborus* were added at a higher density, 600 individuals/m² (or 52.46/m³), a density close to the average measured in ELA lakes (M.J. Paterson, unpublished data).

Table 2.1: Dates of actions with large enclosures in 2004 and 2005.

Action	2004	2005
enclosure bags attached and filled	26-Jul	1-Jul
zooplankton added	21-Jul	1-Jul
<i>Mysis</i> added on night of	26&27-Jul	18-Jul
<i>Chaoborus</i> added	28-Jul	19-Jul
water chemistry and zooplankton sampled	31-Jul	20-Jul
chlorophyll and zooplankton sampled	9-Aug	26-Jul
water chemistry and zooplankton sampled	16-Aug	3-Aug
chlorophyll and zooplankton sampled	23-Aug	10-Aug
chlorophyll and zooplankton sampled	30-Aug	
water chemistry and zooplankton sampled	7-Sep	17-Aug
chlorophyll and zooplankton sampled		24-Aug
predators sampled	7-Sep	24-Aug
vertical migration sampling conducted	17-Aug	15&16-Aug

2.2.3 Enclosure sampling

In each enclosure, the epilimnion was sampled for major nutrients (dissolved and particulate nitrogen, phosphorus, and carbon) on three dates in 2004 and 2005 (Table 1) using an integrating water sampler (Shearer 1978) that collected water from the surface to 5m. pH was measured in only one enclosure of each treatment on two dates in each year (28 July and 7 September, 2004 and 20 July and 17 August, 2005). Epilimnetic water was analysed for total and <30µm chlorophyll a weekly. Phytoplankton less than 30µm are typically considered more edible by zooplankton (e.g. Gliwicz 1977; Vanderploeg 1981; Lehman and Sandgren 1985). To obtain water for <30µm analysis, samples were

sieved in the laboratory within four hours of collection. Samples were analysed for water chemistry at the ELA and Freshwater Institute chemistry laboratories according to the methods of Stainton et al. (1977).

Oxygen and temperature were measured with a YSI model 95D probe. The main concern was to determine whether oxygen concentrations ever fell below the 2mg/L minimum threshold for *Mysis*. As a result, oxygen concentrations were measured 0.1m above the bottom of every enclosure weekly in 2004. Because concentrations never fell below 2.8mg/L (section 3.1.1.1), more detailed measurements were deemed unnecessary. In 2004, oxygen and temperature profiles measured in different enclosures were essentially identical (section 3.1.1.1). Consequently, in 2005, oxygen and temperature were measured every metre in one enclosure of each treatment weekly. The deepest measurement was taken 0.25m above the bottom of each enclosure.

Zooplankton samples were collected weekly with two vertical hauls of a 0.2m diameter 53µm net from the maximum depth to the surface during the day (except for 31 July, 2004 when only one haul was taken). When predators were found in the zooplankton sample, they were not returned to the enclosure but this had minimal impact on predator populations. Few predators were caught in daytime collections because they were situated near the bottom of the enclosures. Each sample was narcotized in methanol, sieved into a vial in the laboratory, and preserved in 4% sugar-formalin (Haney and Hall 1973).

At the end of each experiment (7 September, 2004 and 24 August, 2005), predators were sampled at night with two vertical hauls of a 0.5m diameter,

150 μ m mesh net. Because of the large size of the net relative to the enclosures, predator density estimates had to be corrected for depletion in the second haul. Average depletion was determined in 2005, where each haul was counted separately. Based on these samples, mean densities from duplicate hauls were multiplied by 1.16 to estimate final predator densities in each enclosure.

2.2.4 Vertical migration sampling

Predators and prey typically undertake a vertical diurnal migration in the water column. To examine changes in diurnal vertical migration of crustacean zooplankton, samples were collected from one enclosure of each treatment (on 17 August, 2004 and 15 August, 2005) with a 26L Schindler-Patalas trap to obtain vertical profiles. The trap was deployed at 1m, 3m, 5m, 7m, 9m, and 11m (11m in 2005 only) during the day and again at least one hour after sunset. Temperature and oxygen were measured with a YSI model 95D probe concurrently with zooplankton sampling in 2005. The mean depths of different zooplankton taxa were calculated for day and night in each enclosure as $\Sigma(a \times d) / \Sigma a$, where a is the density (#/L) and d is the depth (e.g. Muluk and Beklioglu 2005). Since only one enclosure was sampled from each treatment, no statistical analysis was conducted on data from vertical migrations.

2.2.5 Zooplankton identification and measurement

In the laboratory, zooplankton samples were suspended in a known volume of water, subsampled with an auto-pipette and counted with a compound light microscope (Zeiss Photomicroscope) at 50 \times power. If possible, at least 200 microcrustacea were enumerated in each sample. If fewer than 200 animals

were encountered, all organisms were enumerated. Each sample was scanned for large, rare organisms (e.g. *Epischura lacustris*) using a dissecting microscope. Cladocerans and copepodid stage 4 (c4) and older copepods were identified to species. Copepodids younger than c4 were identified as calanoid or cyclopoid. For group calculations, nauplii were not included in Calanoida or Cyclopoida totals as they were not identified to Order but are included in Copepoda.

Zooplankton lengths in samples collected on three dates in 2005 (20 July , 3 August, and 17 August) were measured using a computerized calliper system (Allen et al. 1994). Zooplankton samples were projected with a Panasonic CCTV camera WV-BL204 from the microscope (Zeiss) onto a television screen (Panasonic WV-5410) and lengths were measured with automatic callipers (Mitutoyo Digimatic CD-8). Copepodid stages 4 and 5 identified to species were included with adults in calculations of mean lengths. An average of 141 ± 23 individuals were measured in each sample. Mean species lengths were computed for species in samples where five or more individuals were measured.

2.2.6 Biomass estimation

Biomass was calculated from lengths using regressions chosen from McCauley (1984), Lawrence et al. (1987), and Malley et al. (1989). Average zooplankton lengths for days where lengths were not measured were estimated by linear interpolation from dates with measurements. Where fewer than five individuals of a taxon were measured in a sample, the mean length of all individuals of that taxon in the treatment from all dates was used as an estimate.

If fewer than five individuals were measured in the treatment on all dates, the mean of all samples measured was used as an estimate.

Mean biomass for each taxon was calculated from all measured samples in 2005. This mean taxon biomass was used to estimate group biomass in 2004, as no lengths were measured from 2004 samples.

2.2.7 Predator identification and measurement

Predators were identified, sexed (where possible), measured, and counted with dissecting microscopes (Sæther 1972; Reynolds and DeGraeve 1972).

Variations in the size of *Mysis* and *Chaoborus* were estimated by using measurements of antennal scales (Nero 1981) and head capsules (Dumont and Balvay 1979), respectively. *Mysis* antennal scales are easier to measure than total length because individuals often bend and constrict between the thorax and abdomen (Grossnickle and Beeton 1979). *Chaoborus* head capsule length does not change over time when preserved (Lasenby et al. 1994).

Initial predator additions were subsampled for counting and measuring of both taxa. Samples from the final dates were counted and measured for *Mysis*; *Chaoborus* were counted and were subsampled for measurements.

2.2.8 Data analysis

On each sampling date, differences among treatments in species, group, and total abundances, species lengths, and group and total biomass were analysed using a 2 x 2 factorial ANOVA design that can be represented with the following model:

$$X_{ijk} = a + c_i + m_j + cm_{ij} + e_{ijk}$$

where c is an estimate of the *Chaoborus* effect (when it is alone), m the *Mysis* effect (when it is alone), cm the interaction (both species together), and e unexplained error. When using a log transformation (as in this study), this is equivalent to the multiplicative risk model used for multiple predators by Wilbur and Fauth (1990) and Sih et al. (1998).

The approach used in this study (multiple ANOVAs) follows that of Soto and Hurlbert (1991). Because of losses of several enclosures in 2004 and 2005 (see below), alternative approaches such as repeated measures ANOVA were not easily applicable to this dataset. For data from each sampling date, an experiment-wise significance level of 0.10, corrected for the number of tests within a table was used to determine differences (Rice 1989; Chandler 1995). Each table is determined as a set: date-taxa-variable-effect. For example, when six taxa are examined in a set, the comparison-wise error rate is 0.0167 ($=0.1/6$); when five taxa are examined in a set, the comparison-wise error rate is set at 0.02 ($=0.1/5$). (If the table was determined as a set of date-taxa-variable, the comparison-wise error rate would be a low value of $3.03 \times 10^{-4} = [0.01/33]$.) Additionally, p-values are shown in tables as recommended by Moran (2003).

Zooplankton data were \log_{10} transformed prior to applying analysis of variation (ANOVA) on each sampling date. Water chemistry variables were not transformed prior to by-date analysis as data were homogeneous with respect to variance. Where possible, Levene's test was used to assure homogeneity of variances (SYSTAT 11, Systat Software Inc, California). (Levene's test cannot be

conducted when a treatment has only one replicate and these occurrences are annotated in tables.)

In 2004 and 2005, some enclosures were dropped from analyses because of colonization by fish or because of the development of holes in enclosure walls. Additionally, one sample (no predator treatment, 26 July, 2005) could not be analysed, as formalin had mistakenly not been added. The removal of enclosures from analyses resulted in unequal replicates in several treatments in both years (Appendix: Table 2-a and Table 2-b) and the GLM procedure of SYSTAT 11 was used to analyse these data. In 2004, only one replicate remained in the *Chaoborus*-only treatment after 16 August, necessitating the removal of this treatment. After this date, among-treatment effects were assessed using a one-way ANOVA that excluded the *Chaoborus*-only treatment. Means are reported \pm one standard error of the mean (SEM). Tests with fewer than eight degrees of freedom (due to prey absence in all samples) were omitted.

In 2005, *Bosmina longirostris* densities statistically varied among treatments at the outset of the experiment. The cause of the initial variations is uncertain. As an alternative analysis, I examined rates of change of *Bosmina* densities with $r = \ln(n_t/n_{Jul20})/\Delta t$, where r is the rate of change, n_t is the abundance on day t , n_{Jul20} is the abundance on the first sampling day (20 July), and Δt is the number of days between 20 July and day t (Lehman and Sandgren 1985).

2.3 Small enclosures

2.3.1 Density impacts in small scale

An experiment was conducted in smaller enclosures (~20L) to examine the short-term impacts of different densities of *Mysis relicta* and *Chaoborus* spp. on pelagic crustacean zooplankton and to further characterize responses to multiple predators. The objectives of the experiment with small enclosures were 1) to assess whether changes in zooplankton prey densities associated with *Mysis* and *Chaoborus* in isolation could be used to predict prey risk when they occurred together; and 2) to compare the impacts of *Chaoborus* and *Mysis* at different densities. The small enclosures probably represent a worst-case scenario for zooplankton because prey refuges and habitat complexity were minimal due to the small size of the enclosures.

2.3.2 Experimental design

The experiment followed a 2³ factorial design (Box et al. 1978). The three factors were presence or absence of *Chaoborus*, presence or absence of *Mysis*, and high or low density of predator. This resulted in seven treatments: no predators, low *Mysis*, high *Mysis*, low *Chaoborus*, high *Chaoborus*, low *Mysis* and low *Chaoborus*, and high *Mysis* and high *Chaoborus* (Table 2.2). Each treatment had three replicates. The low *Mysis* treatments used one individual per enclosure and the high *Mysis* treatments used two *Mysis*. The low *Chaoborus* treatments used eight *Chaoborus* per enclosure and the high *Chaoborus* treatments used sixteen *Chaoborus*. These densities are approximately 10 to 30 times higher than those used in the large enclosures.

Table 2.2: Treatment combinations of 2³ factorial design used in the small-scale experiment. For *Chaoborus* and *Mysis* variables, - indicates absence and + indicates presence of organisms; for density variable, - is low density and + is high density.

	Variable		
	<i>Chaoborus</i>	<i>Mysis</i>	Density
OO	-	-	- / +
CO	+	-	-
OM	-	+	-
CM	+	+	-
CC	+	-	+
MM	-	+	+
CCMM	+	+	+

2.3.3 Enclosure setup and sampling

On 16 August, 2004, 21 - 20L cubitainers were filled with water sieved through 160µm mesh to remove large zooplankton. Zooplankton were then added to cubitainers in approximately natural densities. Zooplankton were collected from Lake 239 with a 0.5m diameter, 160µm mesh net, hauled to 20m and diluted in 60L of water. One litre of this zooplankton mix was added to each cubitainer. Cubitainers were hung in the lake for a day at 10m before predators were added to allow zooplankton to acclimate. *Chaoborus* were collected from L227 during the day and *Mysis* were collected at night from L239. Predators were stored in a refrigerator before introduction (~5°C). Aluminium flexi-forceps were used to gently separate the predators. *Mysis* were separated in a dark room under red light, since they are not sensitive to red spectrum light (Beeton 1959; Ramcharan and Sprules 1986). Larger individuals of both species were selected as they were predominant in the large enclosures.

Predators were added to the cubitainers on the morning of 17 August and the cubitainers were returned to 10m (~4°C). On the morning of 20 August,

enclosures were brought to the surface and the contents of the enclosures were sieved through a 53 μ m mesh. Organisms were preserved in 4% sugar-formalin. Zooplankton and predators were enumerated as previously described (sections 2.2.5 and 2.2.7).

2.3.4 Data analysis

Results for common zooplankton taxa were analysed using a 2³ factorial design with predator density and the presence or absence of *Chaoborus* or *Mysis* as the three factors (Box et al. 1978). To maintain a balanced design, the no predator treatment was used for the assessment of both high and low density effects because predator densities could not be manipulated in this treatment. Because density effects were minimal (section 3.2.2), assessment of results without inclusion of the density treatment (i.e. as a 2² factorial design) resulted in similar conclusions.

Analyses were conducted using Systat 11 (Systat Software Inc, California). An experiment-wise significance level of 0.10 was used, equivalent to significance levels of $0.10/9=0.011$ for species abundances and $0.1/5=0.02$ for group abundances and biomass). Zooplankton abundance data were log₁₀ transformed (consistent with the large enclosures) before analyses. Levene's test was used to test for homogeneity of variance on the seven treatments on each taxon (as in section 2.2.8) and was not significant for any taxon.

3 Results

3.1 Large enclosures

3.1.1 Enclosure environment: physical-chemical variables

3.1.1.1 2004

In 2004, enclosures were omitted from analyses because multiple holes were found in one enclosure and a fish was found in another enclosure (data from before the fish was seen were still considered in analyses). Both enclosures were in the *Chaoborus*-only treatment.

All enclosures were thermally stratified throughout the experiment with an epilimnion depth of approximately 5m. Oxygen concentrations measured 0.1m above the bottom of each enclosure ranged from 2.8 to 5.1mg/L. Epilimnion temperatures declined from 21°C at the start of the experiment to 16°C at the end of the experiment. Hypolimnion temperatures were stable at 6°C. Although complete temperature and oxygen profiles were only occasionally conducted in 2004, when measured, at least 40% of the enclosure volumes were colder than 15°C with minimum oxygen concentrations always above 3mg/L.

Based on temperature and oxygen, all enclosures contained considerable habitat suitable for both *Mysis* and *Chaoborus*. *Mysis* have a low tolerance to high temperature (upper temperature of 13°C to 17°C: Smith 1970; DeGraeve and Reynolds 1975; Rudstam et al. 1999) and low oxygen (lower oxygen limit of 2-3mg/L: Sandeman and Lasenby 1980). While *Mysis* are sensitive to high temperature and low oxygen, *Chaoborus* are known to withstand more severe temperature and oxygen conditions than *Mysis* and have been found in water

with less than 2mg/L of oxygen (Büns and Ratte 1991; Scholz and Zerbst-Boroffka 1998; Rine and Kesler 2001). While they survive a wide range of temperatures, high mortality is associated with emergence at temperatures greater than 20°C (Hanazato and Yasuno 1989) and less than 9°C (Ouimet 2001).

Concentrations of suspended and total nitrogen (N), phosphorus (P), and carbon (C) measured in the epilimnion of the enclosures were similar on all dates (Table 3.1), with the exception of suspended carbon on 7 September, 2004. Statistically significant differences among treatments were not detected on any date (Appendix: Table 3-a and Figure 3-a).

Table 3.1: 2004 mean concentrations \pm 1 standard error of the mean (SEM) of nutrients measured in large enclosures on three dates. Mean \pm 1 SEM in Lake 239 for four dates: 29-Jul-2004, 12-Aug-2004, 26-Aug-2004, 9-Sep-2004.

	31-Jul-2004	16-Aug-2004	7-Sep-2004	Lake 239
Suspended Nitrogen ($\mu\text{g/L}$)	59 \pm 3	12 \pm 1	31 \pm 4	57 \pm 6
Total Dissolved Nitrogen ($\mu\text{g/L}$)	234 \pm 4	283 \pm 12	242 \pm 6	239 \pm 7
Suspended Phosphorus ($\mu\text{g/L}$)	2.5 \pm 0.2	2.5 \pm 0.3	2.3 \pm 0.2	2.8 \pm 0.3
Total Dissolved Phosphorus ($\mu\text{g/L}$)	3.0 \pm 0.5	2.4 \pm 0.3	2.5 \pm 0.3	1.8 \pm 0.3
Dissolved Inorganic Carbon ($\mu\text{mol/L}$)	150 \pm 1	149 \pm 2	153 \pm 3	151 \pm 4
Dissolved Organic Carbon ($\mu\text{mol/L}$)	616 \pm 7	633 \pm 3	602 \pm 6	596 \pm 15
Suspended Carbon ($\mu\text{g/L}$)	473 \pm 19	301 \pm 17	431 \pm 24	595 \pm 32
pH	7.3 \pm 0.01	na	7.2 \pm 0.01	6.9 \pm 0.02

Lake 239 water chemistry data from 29 July, 12 August, 26 August, and 9 September, 2004 (M. Stainton, unpublished data) show the lake was chemically similar to enclosures. Overall, suspended nutrients were slightly lower in enclosures, whereas dissolved nitrogen was slightly higher in enclosures. Water

chemistry variables were similar among treatments indicating that enclosures did not diverge strongly from each other over time.

3.1.1.2 2005

In 2005, enclosures were omitted from analyses after fish were seen in enclosures and after an enclosure structurally failed. Two replicates from the both predators treatment and one replicate each from the no predators and *Mysis*-only treatments were removed from analyses.

In all measured enclosures, oxygen concentrations ranged from 9.3 to 6.0mg/L with a mean of 7.7 ± 0.03 mg/L between the surface and 11m (Appendix: Figures 3-b and 3-c). Below 11m, dissolved oxygen ranged from 4.9 to 7.4mg/L. In the enclosures, oxygen was less depleted in the metalimnion and was lower in the hypolimnion, compared to the lake but this difference was not greater than 1.5mg/L. Dissolved oxygen changed little over the course of the experiment. Temperature profiles in the enclosures closely resembled those of the nearby lake. Seasonally, the water temperatures in the epilimnion (~5m) increased towards 22°C by the first week of August and then declined to 18°C by the end of August.

With respect to temperature and oxygen, the enclosures were a suitable environment for both *Mysis* and *Chaoborus* during the experiment. On all dates, at least 40% of the volume of each enclosure consisted of water colder than 15°C and minimum oxygen concentrations were not measured below 5.0 mg/L.

Concentrations of suspended and total nitrogen (N), phosphorus (P), and carbon (C) measured in the epilimnion of enclosures in 2005 were similar on all

dates and no differences among treatments were detected (Appendix: Table 3-b, Figure 3-d).

Table 3.2: 2005 mean concentrations \pm 1 SEM of nutrients measured in large enclosures on three dates. Mean \pm 1 SEM in Lake 239 for four dates: 14-Jul-2005, 27-Jul-2005, 11-Aug-2005, 24-Aug-2005.

	21-Jul-2005	3-Aug-2005	17-Aug-2005	Lake 239
Suspended Nitrogen ($\mu\text{g/L}$)	31 \pm 2	49 \pm 2	39 \pm 3	44 \pm 3
Total Dissolved Nitrogen ($\mu\text{g/L}$)	265 \pm 3	264 \pm 2	241 \pm 2	245 \pm 2
Suspended Phosphorus ($\mu\text{g/L}$)	4.0 \pm 0.2	3.7 \pm 0.2	3.6 \pm 0.2	3.3 \pm 0.6
Total Dissolved Phosphorus ($\mu\text{g/L}$)	2.6 \pm 0.3	2.2 \pm 0.3	2.5 \pm 0.2	3.8 \pm 1.6
Dissolved Inorganic Carbon ($\mu\text{mol/L}$)	164 \pm 2	143 \pm 2	140 \pm 1	168 \pm 25
Dissolved Organic Carbon ($\mu\text{mol/L}$)	664 \pm 4	654 \pm 4	662 \pm 2	733 \pm 72
Suspended Carbon ($\mu\text{g/L}$)	328 \pm 15	434 \pm 28	402 \pm 22	458 \pm 67
pH	7.2 \pm 0.01	na	7.3 \pm 0.08	7.3 \pm 0.02

Lake 239 water chemistry data from 14 July, 27 July, 11 August, and 24 August (M. Stainton, unpublished data) show the lake was chemically similar to enclosures. Water chemistry variables were similar among treatments indicating that enclosures did not diverge from each other. The conditions of the enclosures and lake in both years are considered oligotrophic (Wetzel 2001).

3.1.2 Predators

3.1.2.1 2004

Predators survived through the experiment in all enclosures to which they were added (Table 3.3). In enclosures with *Mysis*, densities on the final date were approximately half of target densities ($\sim 50/\text{m}^2$ compared to a target of $100/\text{m}^2$) while densities of *Chaoborus* were less than half ($\sim 250/\text{m}^2$ compared to a target of $600/\text{m}^2$). It is likely that some *Chaoborus* pupated and emerged from the enclosures during the experiment. Final densities of *Chaoborus* and *Mysis* in

enclosures were still well within the range of variation of natural densities in ELA lakes (M. Paterson, unpublished data).

The abundance of *Chaoborus* with and without *Mysis* could not be statistically compared on the final date, as only one enclosure remained in the *Chaoborus*-only treatment on the final date. Densities of *Chaoborus* in the remaining *Chaoborus*-only enclosure were within the range of densities observed in enclosures with *Mysis*. The abundance of *Mysis* was not significantly different in enclosures with and without *Chaoborus* (df = 4; t = -0.42; P = 0.69). Hence, there was little evidence of intraguild predation.

Table 3.3: 2004 mean abundance \pm 1 SEM of predators a) per square metre and b) per cubic metre in treatments in large enclosures.

Treatment	<i>Chaoborus</i> spp.	<i>Mysis relicta</i>
a) Areal		
<i>Chaoborus</i> -only	240	
<i>Mysis</i> -only		58 \pm 11
both predators	307 \pm 74	62 \pm 5
b) Volumetric		
<i>Chaoborus</i> -only	24.0	
<i>Mysis</i> -only		5.3 \pm 1.0
both predators	27.9 \pm 6.7	5.4 \pm 0.2

Chaoborus flavicans added to enclosures were primarily instar III and IV with a mean head capsule length of 1.3 \pm 0.06mm (head capsule length histograms in Appendix: Figure 3-e). Larvae increased in size during the experiment and those collected at the end of the experiment were primarily instar IV with a mean head capsule size of 1.5 \pm 0.01mm. Pupae were encountered in the final samples and made up 0.5% of *Chaoborus* collected. As is typical of most ELA lakes (Nero 1981), *Mysis* added to enclosures consisted of two cohorts: antennal scales for small mysids were 1.0 \pm 0.03mm and 2.0 \pm 0.02mm for

larger mysids (length histograms in Appendix: Figure 3-e). On the final sample date, mean *Mysis* antennal scale sizes were 1.2 ± 0.03 mm for immatures, 2.0 ± 0.02 mm for males, and 2.2 ± 0.02 mm for females. No statistically significant differences in *Mysis* antennal scale length were detected when *Mysis* was with or without *Chaoborus* ($df=2.0$, $t=0.90$, $P=0.46$).

3.1.2.2 2005

In 2005, densities of *Mysis* on the final date were similar to target densities ($100/m^2$) while densities of *Chaoborus* were approximately half ($300/m^2$) of target densities (Table 3.4). *Chaoborus* larvae likely pupated and emerged from the enclosures during the experiment in 2005. *Chaoborus* and *Mysis* were encountered in enclosures to which they were not added.

The abundance of *Chaoborus* was not significantly different in enclosures with or without *Mysis* ($df = 3.3$; $t = -0.77$; $P = 0.49$). Similarly, the abundance of *Mysis* was not significantly different in enclosures with or without *Chaoborus* ($df = 1.3$; $t = 1.06$; $P = 0.44$). Thus, there was no strong evidence of intraguild predation between *Mysis* and *Chaoborus*.

Table 3.4: 2005 mean abundance \pm 1 SEM of predators a) per square metre and b) per cubic metre in treatments in large enclosures.

Treatment	<i>Chaoborus</i> spp.	<i>Mysis relicta</i>
a) Areal		
no predators	6	
<i>Chaoborus</i> -only	393 \pm 87	16 \pm 10
<i>Mysis</i> -only	10 \pm 7	108 \pm 19
both predators	307 \pm 15	202 \pm 90
b) Volumetric		
no predators	0.6	
<i>Chaoborus</i> -only	35.1 \pm 6.6	1.7 \pm 1.2
<i>Mysis</i> -only	0.9 \pm 0.7	9.4 \pm 1.4
both predators	26.2 \pm 1.8	17.3 \pm 8.0

Chaoborus larvae added to enclosures were primarily *Chaoborus flavicans* instar III and IV with a mean head capsule size of 0.79 ± 0.04 mm (length histograms in Appendix: Figure 3-f). Most *Chaoborus flavicans* collected at the end of the experiment were instar IV with a mean head size of 1.5 ± 0.01 mm. No differences in *Chaoborus* head capsule size were detected between treatments when present with or without *Mysis* ($df=4$, $t=1.79$, $P=0.15$). In 2005, 0.6% of *Chaoborus* collected on the final date were pupae. As in 2004, there were two cohorts of *Mysis* with mean antennal scale sizes of 1.0 ± 0.03 mm and 2.0 ± 0.03 mm (length histograms in Appendix: Figure 3-f). *Mysis* antennal scale size was 1.2 ± 0.03 mm for immatures, 2.0 ± 0.02 mm for males, and 2.2 ± 0.02 mm for females. No differences in mean *Mysis* antennal scale length were detected in treatments with or without *Chaoborus* ($df=2$, $t=0.90$, $P=0.47$).

3.1.3 Zooplankton

In both 2004 and 2005, the most abundant crustacean zooplankton taxa in enclosures were *Bosmina longirostris*, *Chydorus* cf. *sphaericus*, *Diaphanosoma birgei*, *Daphnia* spp., *Tropocyclops extensus*, *Diacyclops thomasi*, and

Leptodiaptomus minutus (Figures 3.1 and 3.2). All are common in Lake 239 (Malley and Chang 1994). Rarer species included *Mesocyclops edax*, *Sida crystallina* (Müller), *Epischura lacustris*, *Polyphemus pediculus* (Linnaeus) and *Ceriodaphnia* spp. *Holopedium gibberum* Zaddach is generally rare in Lake 239 (Findlay et al. 2005) and this species was found in enclosures only in 2004.

3.1.3.1 Species composition

3.1.3.1.1 2004

At the experiment's start, mean total abundance of zooplankton in all enclosures was $6.0 \pm 0.4/L$. Total abundance in the lake was higher than in the enclosures ($15.1/L$). Overall seasonal changes in the enclosures were similar to the lake.

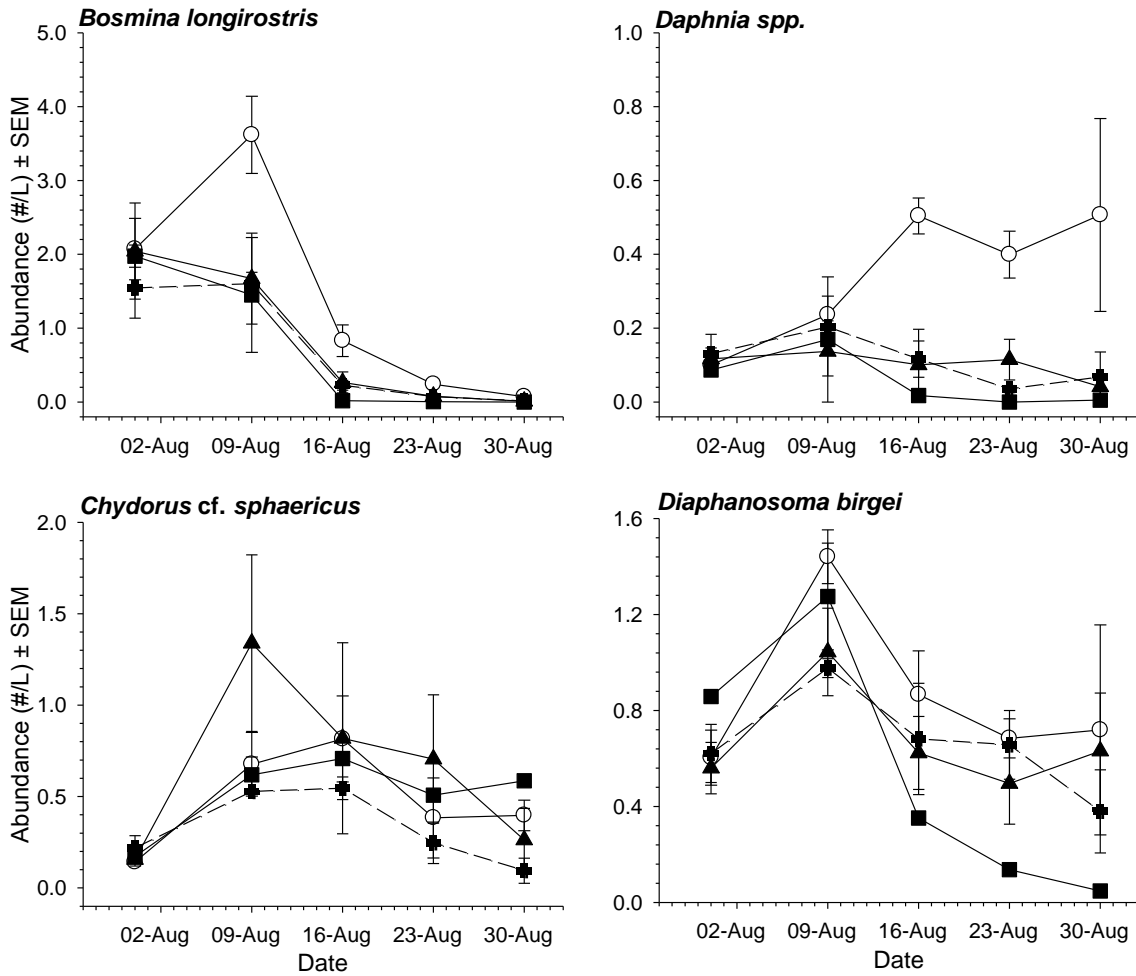


Figure 3.1: 2004 mean abundance (#/L) \pm 1 standard error of the mean (SEM) of zooplankton taxa over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

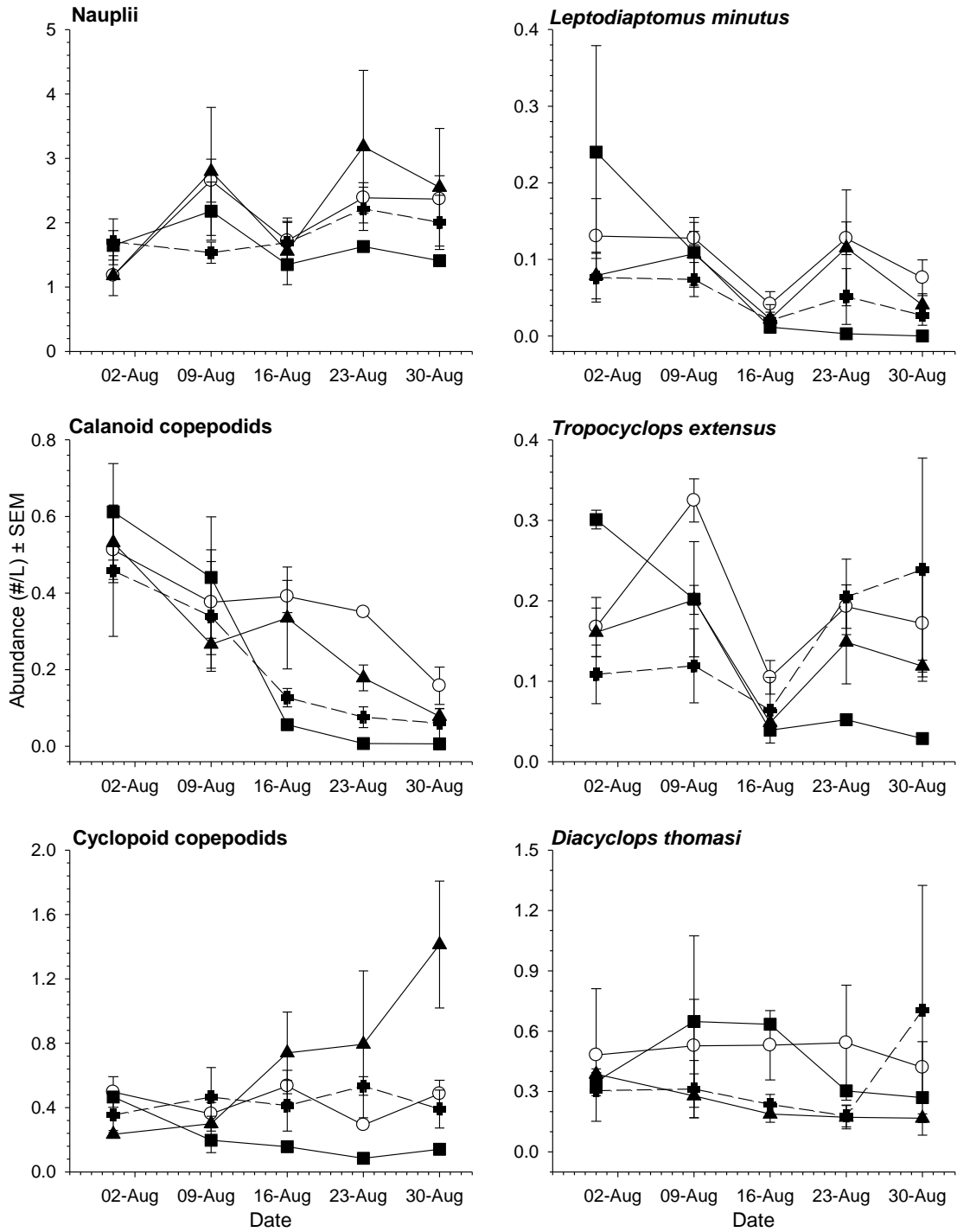


Figure 3.1 continued: 2004 mean abundance (#/L) \pm 1 SEM of zooplankton taxa over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

In 2004, statistically detectable effects of *Mysis* and *Chaoborus* on zooplankton densities in the enclosures were few. Because of the loss of enclosures, the effect of *Chaoborus* alone could not be tested after 16 August. Although total zooplankton abundance was usually greatest in enclosures without predators, it was not significantly different among treatments on any dates (Table 3.5). With one exception, the abundances of different zooplankton taxa in different predator treatments were also not statistically different on any dates (Table 3.5). A significant treatment effect was detected for *Daphnia* abundance on 16 August and 23 August, 2004. In part, the absence of treatment effects reflected high variability among enclosures and limited statistical power. For example, mean densities of *Bosmina* were frequently 50% lower in enclosures with predators but high variability among enclosures prevented the detection of statistically significant effects.

Table 3.5: 2004 P-values of ANOVAs on transformed abundance by Date and Species in large enclosures for *Chaoborus* (*Chaob*), *Mysis*, and interaction effects (C×M). ^a – Levene's variance testing not done. Starting on 16-August-2004, only one replicate was left in the *Chaoborus*-only treatment and results from a one-way ANOVA comparing remaining treatments are shown (1-way). Significance highlighted in BOLD for P<0.017 (experiment-wise error = 0.1).

Date	Species	Variable	Log ₁₀ Abundance (#/L)			
			<i>Chaob</i>	<i>Mysis</i>	C×M	1-way
31-Jul-04	<i>Tropocyclops extensus</i>		0.325	0.027	0.035	
	<i>Diacyclops thomasi</i>		0.658	0.823	0.961	
	<i>Bosmina longirostris</i>		0.675	0.569	0.721	
	<i>Chydorus cf. sphaericus</i>		0.328	0.538	0.743	
	<i>Diaphanosoma birgei</i>		0.217	0.264	0.436	
	<i>Daphnia</i> spp.		0.989	0.446	0.732 ^a	
9-Aug-04	<i>Tropocyclops extensus</i>		0.037	0.039	0.702	
	<i>Diacyclops thomasi</i>		0.775	0.241	0.886	
	<i>Bosmina longirostris</i>		0.110	0.226	0.094	
	<i>Chydorus cf. sphaericus</i>		0.156	0.369	0.206	
	<i>Diaphanosoma birgei</i>		0.469	0.044	0.730	
	<i>Daphnia</i> spp.		0.972	0.724	0.358	
16-Aug-04	<i>Tropocyclops extensus</i>					0.397
	<i>Diacyclops thomasi</i>					0.098
	<i>Bosmina longirostris</i>					0.061
	<i>Chydorus cf. sphaericus</i>					0.843
	<i>Diaphanosoma birgei</i>					0.664
	<i>Daphnia</i> spp.					0.014
23-Aug-04	<i>Tropocyclops extensus</i>					0.630
	<i>Diacyclops thomasi</i>					0.261
	<i>Bosmina longirostris</i>					0.020
	<i>Chydorus cf. sphaericus</i>					0.513
	<i>Diaphanosoma birgei</i>					0.582
	<i>Daphnia</i> spp.					0.004
30-Aug-04	<i>Tropocyclops extensus</i>					0.680
	<i>Diacyclops thomasi</i>					0.657
	<i>Bosmina longirostris</i>					0.222
	<i>Chydorus cf. sphaericus</i>					0.235
	<i>Diaphanosoma birgei</i>					0.787
	<i>Daphnia</i> spp.					0.103

3.1.3.1.2 2005

On the first sampling date in 2005, mean abundance of zooplankton in all enclosures was $18.7/L \pm 0.8$. Total abundance in the lake ($28.8/L$) was higher than in the enclosures. Over time, total zooplankton abundance in enclosures declined compared to the lake.

As in 2004, few statistically detectable differences in zooplankton densities were observed among treatments. Total zooplankton abundance was significantly lower in treatments with *Mysis* on one date (26 July) but was not different on other dates (Table 3.8). The abundances of most zooplankton taxa were also not statistically different among treatments (Table 3.6, Figure 3.2). The abundance of the most common taxon, *Bosmina*, was significantly lower in enclosures with *Mysis* on 20 July, 26 July, and 3 August. In late August, *Bosmina* densities were too low in all enclosures to detect statistical differences. *Chydorus* densities on 24 August were significantly greater in enclosures with *Mysis*. On 3 August, significantly lower densities of *Bosmina* were also detected in the presence of *Chaoborus* and a significant *Chaoborus*×*Mysis* effect was observed. On 26 July, a significant *Chaoborus*×*Mysis* effect was also detected for *Daphnia*.

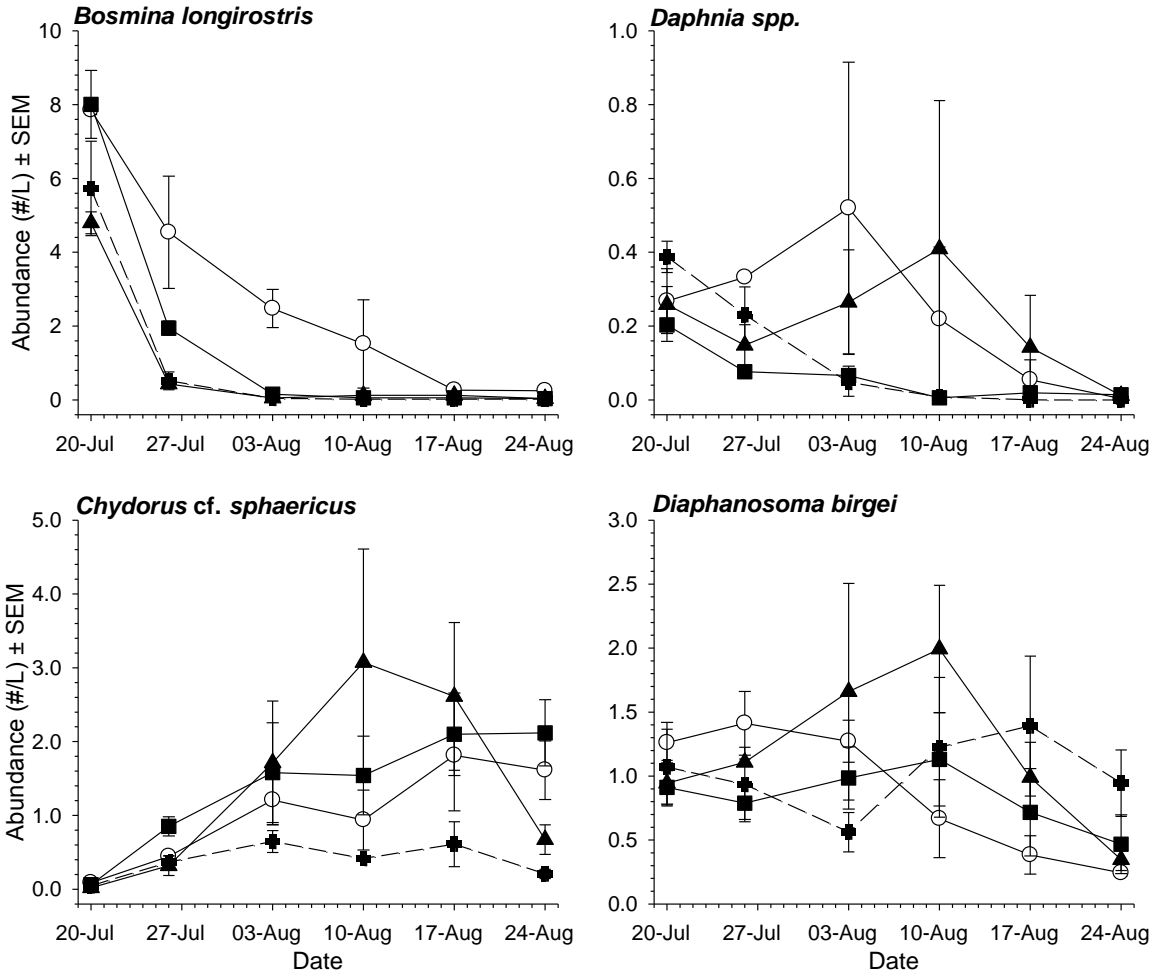


Figure 3.2: 2005 mean abundance (#/L) \pm 1 SEM of zooplankton taxa over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

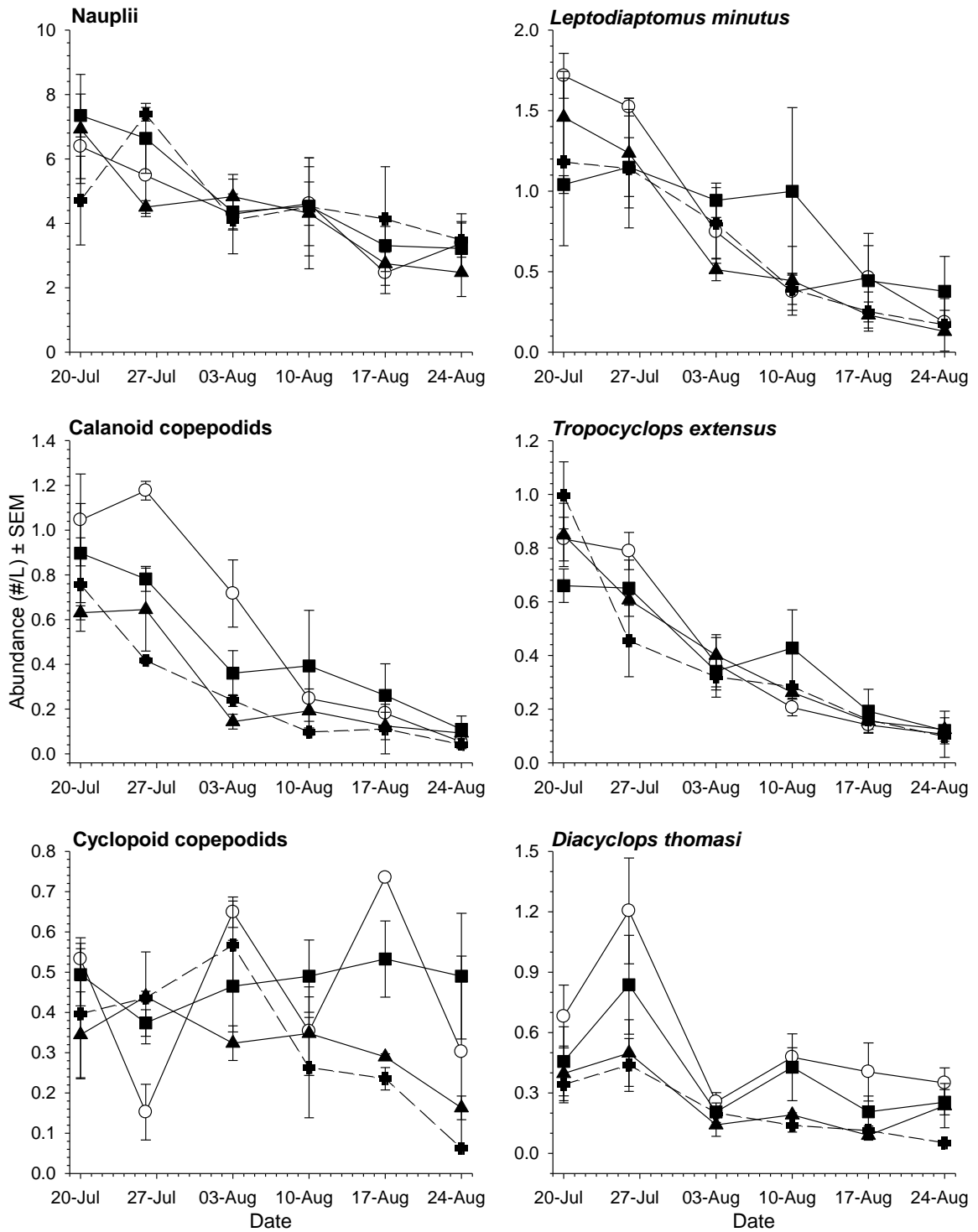


Figure 3.2 continued: 2005 mean abundance (#/L) \pm 1 SEM of zooplankton taxa over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

On the first sampling date (20 July), *Bosmina* abundances were already significantly lower in enclosures with *Mysis*. The reasons for these differing *Bosmina* abundances are unclear. Because all enclosures did not start with the same community, rates of change in *Bosmina* abundance were also compared among treatments using a 2-way ANOVA. This analysis resulted in similar conclusions (Appendix: Table 3-c): *Mysis* significantly affected *Bosmina* rates of change on 26 July and 3 August; *Chaoborus* and *Chaoborus*×*Mysis* impacts were also detected on 3 August.

Table 3.6: 2005 P-values of ANOVAs on transformed abundance and length/individual by Date and Species in large enclosures for *Chaoborus* (*Chaob*), *Mysis*, and interaction effects (C×M). ^a – Levene's variance testing not done. Where no values are shown, no test was conducted or test was omitted due to insufficient number of measurements. Significance highlighted in BOLD for P<0.017 (experiment-wise error = 0.1).

Date	Species	Variable	Log ₁₀ Abundance (#/L)			Log ₁₀ Length (mm)		
			<i>Chaob</i>	<i>Mysis</i>	C×M	<i>Chaob</i>	<i>Mysis</i>	C×M
20-Jul-05	<i>Tropocyclops extensus</i>		0.827	0.095	0.115	0.954	0.859	0.270
	<i>Diacyclops thomasi</i>		0.383	0.259	0.580	0.397	0.289	0.408
	<i>Bosmina longirostris</i>		0.624	0.010	0.641	0.053	0.273	0.501
	<i>Chydorus cf. sphaericus</i>		0.934	0.309	0.513			
	<i>Diaphanosoma birgei</i>		0.552	0.660	0.275	0.116	0.277	0.816
	<i>Daphnia</i> spp.		0.604	0.157	0.136	0.101	0.643	0.014
26-Jul-05	<i>Tropocyclops extensus</i>		0.194	0.124	0.878			
	<i>Diacyclops thomasi</i>		0.419	0.065	0.563			
	<i>Bosmina longirostris</i>		0.068	<0.001	0.041			
	<i>Chydorus cf. sphaericus</i>		0.112	0.034	0.235 ^a			
	<i>Diaphanosoma birgei</i>		0.086	0.753	0.394			
	<i>Daphnia</i> spp.		0.130	0.816	0.011^a			
3-Aug-05	<i>Tropocyclops extensus</i>		0.498	0.945	0.719	0.712	0.243	0.147
	<i>Diacyclops thomasi</i>		0.876	0.196	0.231	0.457	0.009	0.703
	<i>Bosmina longirostris</i>		<0.001	<0.001	<0.001	0.087	0.198	0.517 ^a
	<i>Chydorus cf. sphaericus</i>		0.493	0.673	0.353	0.323	0.037	0.175
	<i>Diaphanosoma birgei</i>		0.110	0.670	0.413	0.426	0.631	0.448
	<i>Daphnia</i> spp.		0.088	0.549	0.645	0.031	0.386	<0.001
10-Aug-05	<i>Tropocyclops extensus</i>		0.255	0.750	0.357			
	<i>Diacyclops thomasi</i>		0.589	0.042	0.961			
	<i>Bosmina longirostris</i>		0.137	0.198	0.253			
	<i>Chydorus cf. sphaericus</i>		0.305	0.844	0.097			
	<i>Diaphanosoma birgei</i>		0.871	0.152	0.237			
	<i>Daphnia</i> spp.		0.206	0.763	0.773			
17-Aug-05	<i>Tropocyclops extensus</i>		0.713	0.925	0.764	0.748	0.840	0.625
	<i>Diacyclops thomasi</i>		0.399	0.054	0.265	0.385	0.020	0.680
	<i>Bosmina longirostris</i>		0.080	0.298	0.550	0.049	0.079	0.956 ^a
	<i>Chydorus cf. sphaericus</i>		0.240	0.489	0.133	0.929	0.143	0.068
	<i>Diaphanosoma birgei</i>		0.375	0.084	0.985	0.121	0.292	0.610
	<i>Daphnia</i> spp.		0.293	0.716	0.536 ^a			
24-Aug-05	<i>Tropocyclops extensus</i>		0.965	0.997	0.672			
	<i>Diacyclops thomasi</i>		0.126	0.084	0.570			
	<i>Bosmina longirostris</i>		0.042	0.045	0.090			
	<i>Chydorus cf. sphaericus</i>		0.640	0.001	0.126			
	<i>Diaphanosoma birgei</i>		0.068	0.142	0.356			
	<i>Daphnia</i> spp.		0.946	0.833	0.352 ^a			

3.1.3.2 Zooplankton lengths

3.1.3.2.1 2005

Body lengths were measured for zooplankton in the enclosures in 2005 only. Analysis of variance of different species lengths revealed few significant differences among treatments (Table 3.6, Figure 3.3). *Diacyclops thomasi* lengths were lower in enclosures with *Mysis* and were significantly different on 3 August. For most taxa, mean lengths were similar among treatments on all dates and relatively constant during the experiment. *Chaoborus* × *Mysis* impacts were detected on *Daphnia* lengths on both 20 July and 3 August. Because the lengths were different at the beginning of the experiment, the differences cannot be attributed to the predators.

In addition to examining mean lengths of individual taxa, the mean size of group taxa in the zooplankton community was compared. Mean length of calanoids fluctuated over time with no consistent trend among treatments (Figure 3.4). The mean size of cyclopoids was statistically larger in the no predator treatment in the final portion of the experiment (Figure 3.4). When *Chaoborus* was present, cyclopoids tended to be smaller. Mean copepod size was influenced by the small size of nauplii, and mean size declined when both predators were present. While cladoceran mean size was lowest in no predator enclosures, it was highest in enclosures with both predators (Figure 3.4).

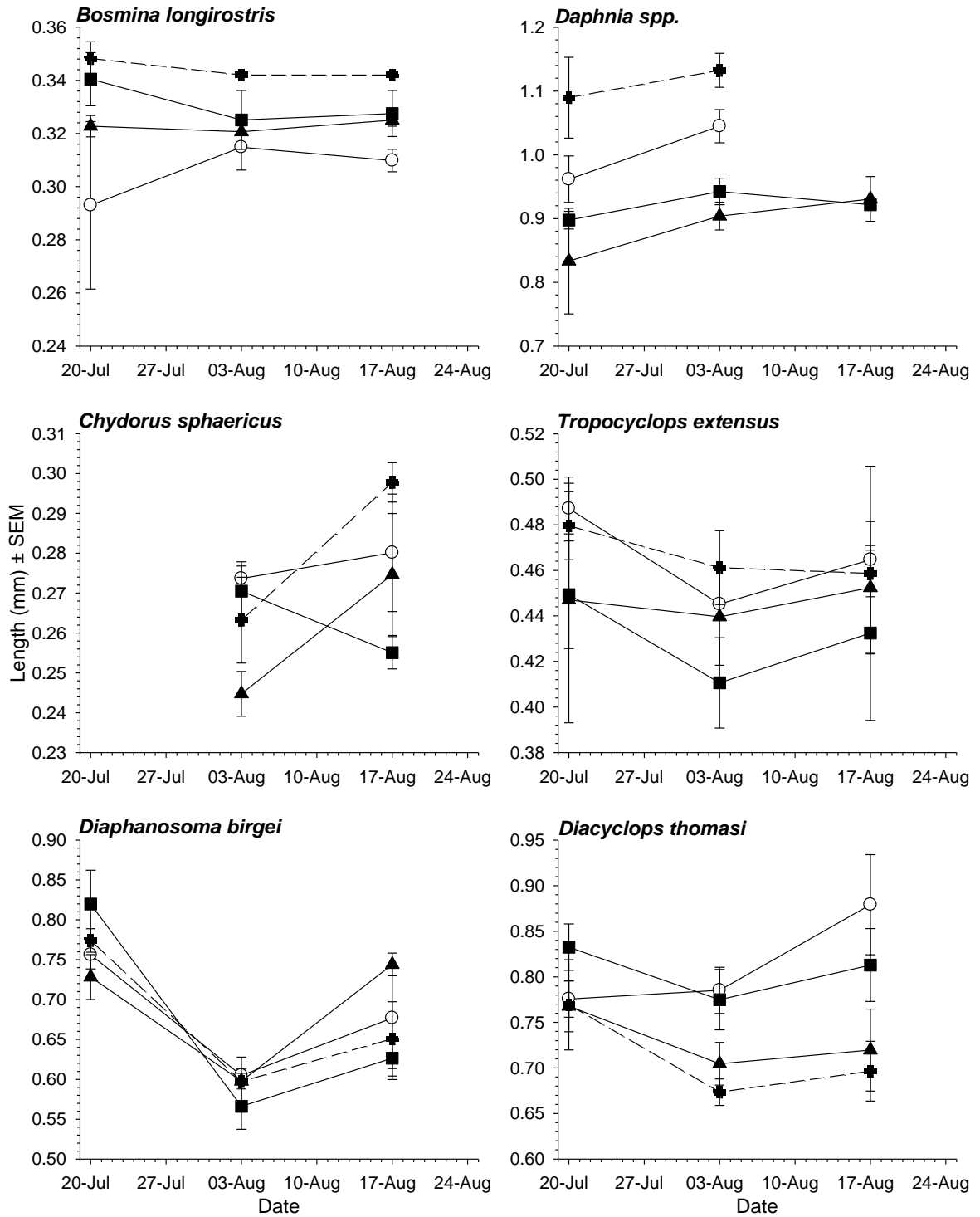


Figure 3.3: 2005 mean length (mm) \pm 1 SEM of zooplankton species over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

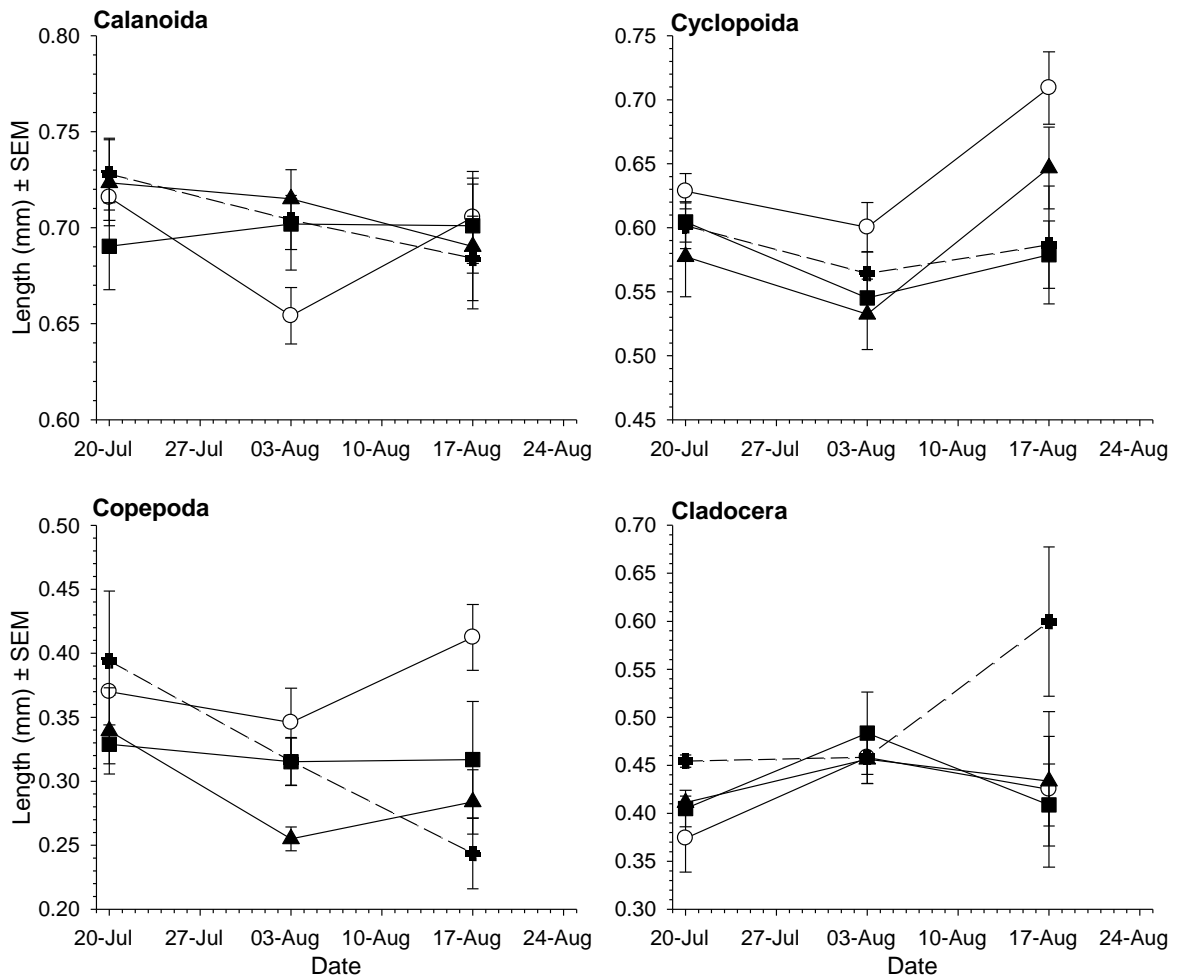


Figure 3.4: 2005 mean length (mm) ± 1 SEM of zooplankton groups over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

3.1.3.3 Crustacean biomass

3.1.3.3.1 2004

Strong statistically detectable effects of predators on the biomass of total zooplankton or major zooplankton groups were rarely observed (Figure 3.5). *Chaoborus* impacts were detected on 23 August, 2004 for Calanoida (Table 3.7). The biomass of different zooplankton groups was usually greatest in enclosures without predators and lowest with *Chaoborus* only (Figure 3.6). Despite reductions in mean zooplankton biomass of ~50% in treatments with predators, high variability frequently limited the statistical power of analyses.

3.1.3.3.2 2005

In 2005, few statistically significant impacts of predators on the biomass of total zooplankton or major zooplankton groups were detected (Figures 3.7 and 3.8). Biomass of Calanoida and Cyclopoida declined in all treatments during the experiment while Cladocera biomass fluctuated. An interactive effect of *Chaoborus* × *Mysis* was detected on 3 August, 2005 for Cyclopoida and *Mysis* impacts were detected on 17 August, 2005 for Cyclopoida and on 24 August, 2005 for total crustaceans (Table 3.8).

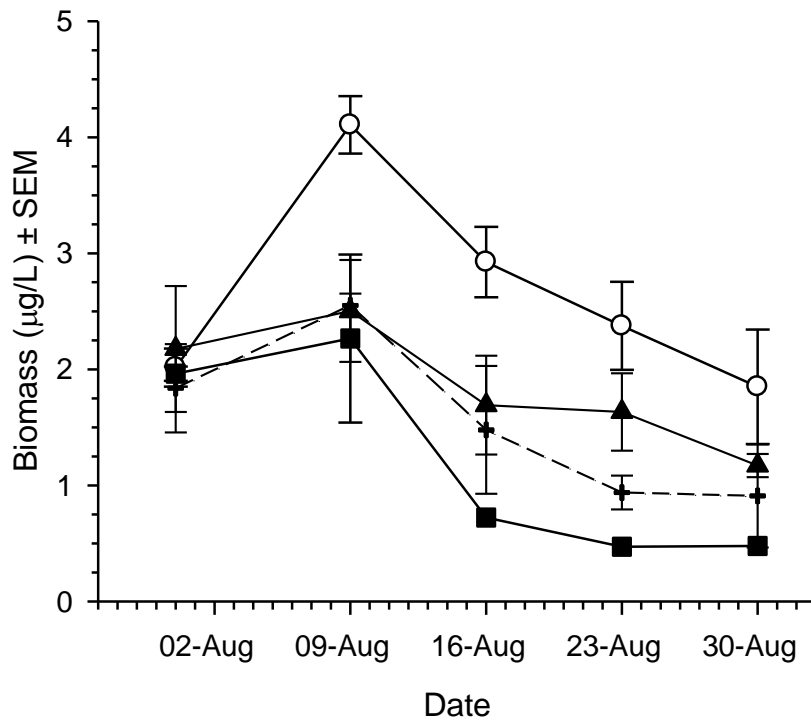


Figure 3.5: 2004 mean crustacean biomass ($\mu\text{g/L}$) \pm 1 SEM over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

Table 3.7: 2004 P-values of ANOVAs on transformed abundance and biomass by Date and Group in large enclosures for *Chaoborus* (*Chaob*), *Mysis*, and interaction effects (C×M) ^e – Levene’s variance test on four treatments significant (P<0.05). Starting on 16-August-2004, only one replicate was left in the *Chaoborus*-only treatment and results from a one-way ANOVA comparing remaining treatments are shown (1-way). Significance highlighted in BOLD for P<0.02 (experiment-wise error = 0.1).

Date	Variable Group	Log ₁₀ Abundance (#/L)				Log ₁₀ Biomass (µg/L)			
		<i>Chaob</i>	<i>Mysis</i>	C×M	1-way	<i>Chaob</i>	<i>Mysis</i>	C×M	1-way
31-Jul-04	Calanoida	0.795	0.306	0.426		0.918	0.300	0.596	
	Cyclopoida	0.834	0.231	0.987		0.827	0.474	0.588	
	Copepoda	0.109	0.204	0.866		0.780	0.315	0.921	
	Cladocera	0.902	0.525	0.670		0.853	0.971	0.632	
	Crustaceans	0.557	0.361	0.725		0.665	0.891	0.747	
9-Aug-04	Calanoida	0.824	0.390	0.989		0.999	0.270	0.816	
	Cyclopoida	0.891	0.258	0.386		0.735	0.295	0.266	
	Copepoda	0.440	0.356	0.885		0.834	0.212	0.631	
	Cladocera	0.067	0.334	0.415		0.235	0.596	0.683 ^e	
	Crustaceans	0.135	0.284	0.732		0.074	0.225	0.051	
16-Aug-04	Calanoida				0.085				0.179
	Cyclopoida				0.441				0.382
	Copepoda				0.600				0.197
	Cladocera				0.132				0.061
	Crustaceans				0.305				0.130
23-Aug-04	Calanoida				0.037				0.012
	Cyclopoida				0.902				0.289
	Copepoda				0.658				0.024
	Cladocera				0.145				0.076
	Crustaceans				0.381				0.028
30-Aug-04	Calanoida				0.143				0.149
	Cyclopoida				0.668				0.785
	Copepoda				0.742				0.609
	Cladocera				0.138				0.027
	Crustaceans				0.441				0.256

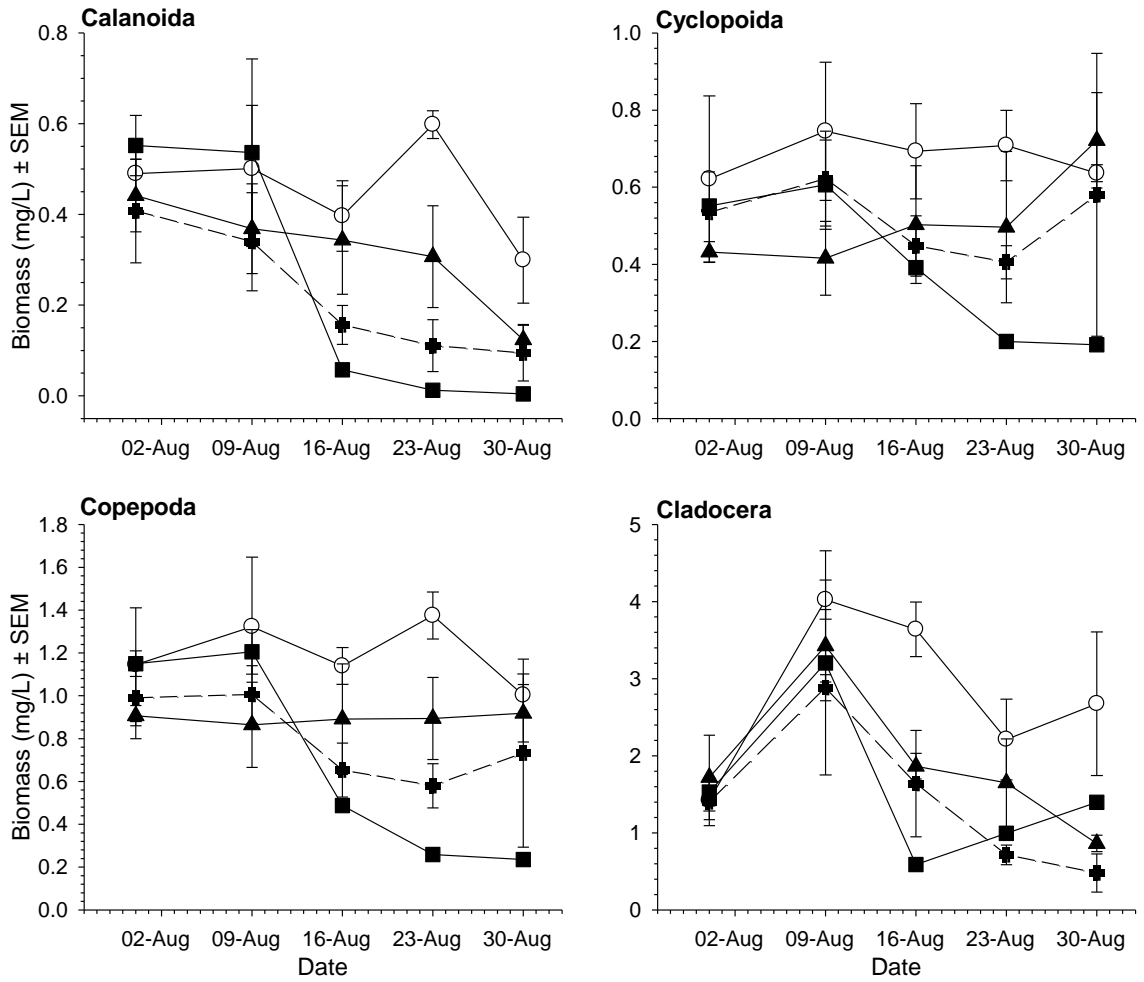


Figure 3.6: 2004 mean biomass ($\mu\text{g/L}$) \pm 1 SEM for crustacean groups over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

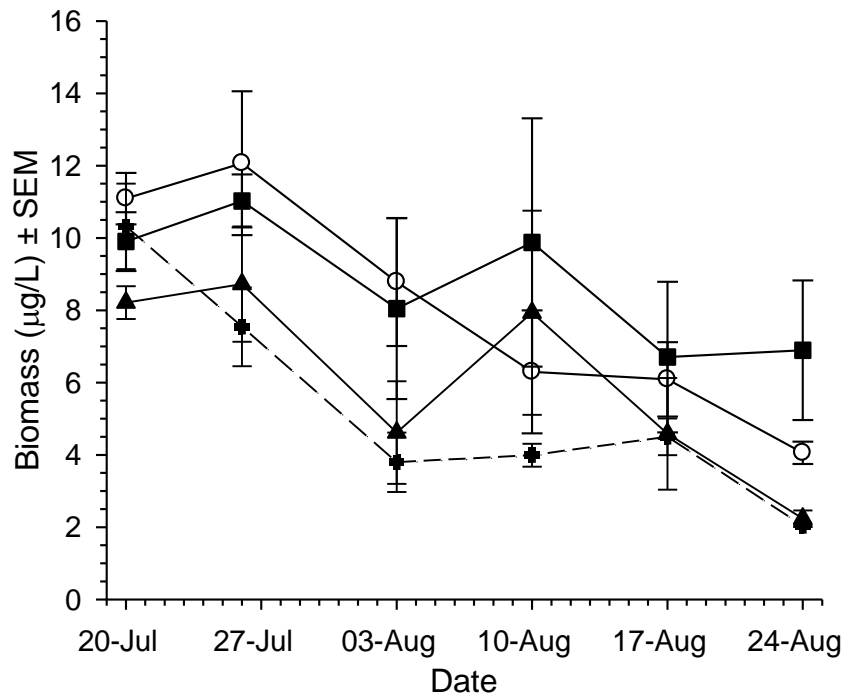


Figure 3.7: 2005 mean crustacean biomass ($\mu\text{g/L}$) \pm 1 SEM over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

Table 3.8: 2005 P-values of ANOVAs on transformed abundance, length, and biomass by Date and Group in large enclosures for *Chaoborus* (*Chaob*), *Mysis*, and interaction effects (C×M).^e – Levene’s variance test on four treatments significant (P<0.05). Significance highlighted in BOLD for P<0.02 (experiment-wise error = 0.1).

Date	Variable Group	Log ₁₀ Abundance (#/L)			Log ₁₀ Length (mm)			Log ₁₀ Biomass (µg/L)		
		<i>Chaob</i>	<i>Mysis</i>	C×M	<i>Chaob</i>	<i>Mysis</i>	C×M	<i>Chaob</i>	<i>Mysis</i>	C×M
20-Jul-05	Calanoida	0.162	0.292	0.461	0.614	0.299	0.475	0.079	0.504	0.232
	Cyclopoida	0.329	0.348	0.095	0.986	0.215	0.264	0.535	0.199	0.031
	Copepoda	0.350	0.196	0.452	0.857	0.621	0.159	0.080	0.157	0.041
	Cladocera	0.732	0.017	0.496	0.110	0.066	0.811	0.067	0.318	0.285
	Crustaceans	0.562	0.009	0.847	0.176	0.231	0.813	0.580	0.159	0.079
26-Jul-05	Calanoida	0.231	0.135	0.631				0.429	0.358	0.580
	Cyclopoida	0.196	0.068	0.932				0.165	0.068	0.863
	Copepoda	0.331	0.315	0.274				0.273	0.111	0.515
	Cladocera	0.100	0.001	0.192				0.684	0.038	0.560
	Crustaceans	0.974	0.003	0.041				0.478	0.034	0.883
3-Aug-05	Calanoida	0.379	0.011	0.145	0.283	0.083	0.100	0.199	0.064	0.399
	Cyclopoida	0.864	0.150	0.025	0.539	0.192	0.034	0.474	0.100	0.009
	Copepoda	0.849	0.577	0.936	0.439	0.045	0.043	0.448	0.035	0.074
	Cladocera	0.060	0.127	0.986	0.706	0.712	0.743	0.396	0.060	0.852
	Crustaceans	0.070	0.106	0.958	0.973	0.385	0.576	0.570	0.048	0.937
10-Aug-05	Calanoida	0.663	0.476	0.486				0.530	0.576	0.493
	Cyclopoida	0.979	0.088	0.400 ^e				0.219	0.093	0.676
	Copepoda	0.835	0.434	0.802				0.978	0.257	0.486
	Cladocera	0.218	0.998	0.370				0.793	0.708	0.282
	Crustaceans	0.150	0.494	0.081				0.780	0.544	0.295
17-Aug-05	Calanoida	0.974	0.427	0.974	0.861	0.585	0.983	0.962	0.411	0.929
	Cyclopoida	0.283	0.016	0.534	0.019	0.435	0.319	0.041	0.018	0.402
	Copepoda	0.372	0.617	0.716	0.122	0.035	0.525	0.296	0.038	0.520
	Cladocera	0.598	0.958	0.425	0.273	0.149	0.197	0.738	0.889	0.965
	Crustaceans	0.769	0.775	0.744	0.702	0.987	0.350	0.990	0.482	0.862
24-Aug-05	Calanoida	0.662	0.539	0.578				0.663	0.499	0.774
	Cyclopoida	0.657	0.110	0.284				0.366	0.107	0.222
	Copepoda	0.615	0.449	0.755				0.792	0.124	0.412
	Cladocera	0.390	0.003	0.572				0.331	0.020	0.520
	Crustaceans	0.333	0.039	0.977				0.460	0.009	0.307 ^e

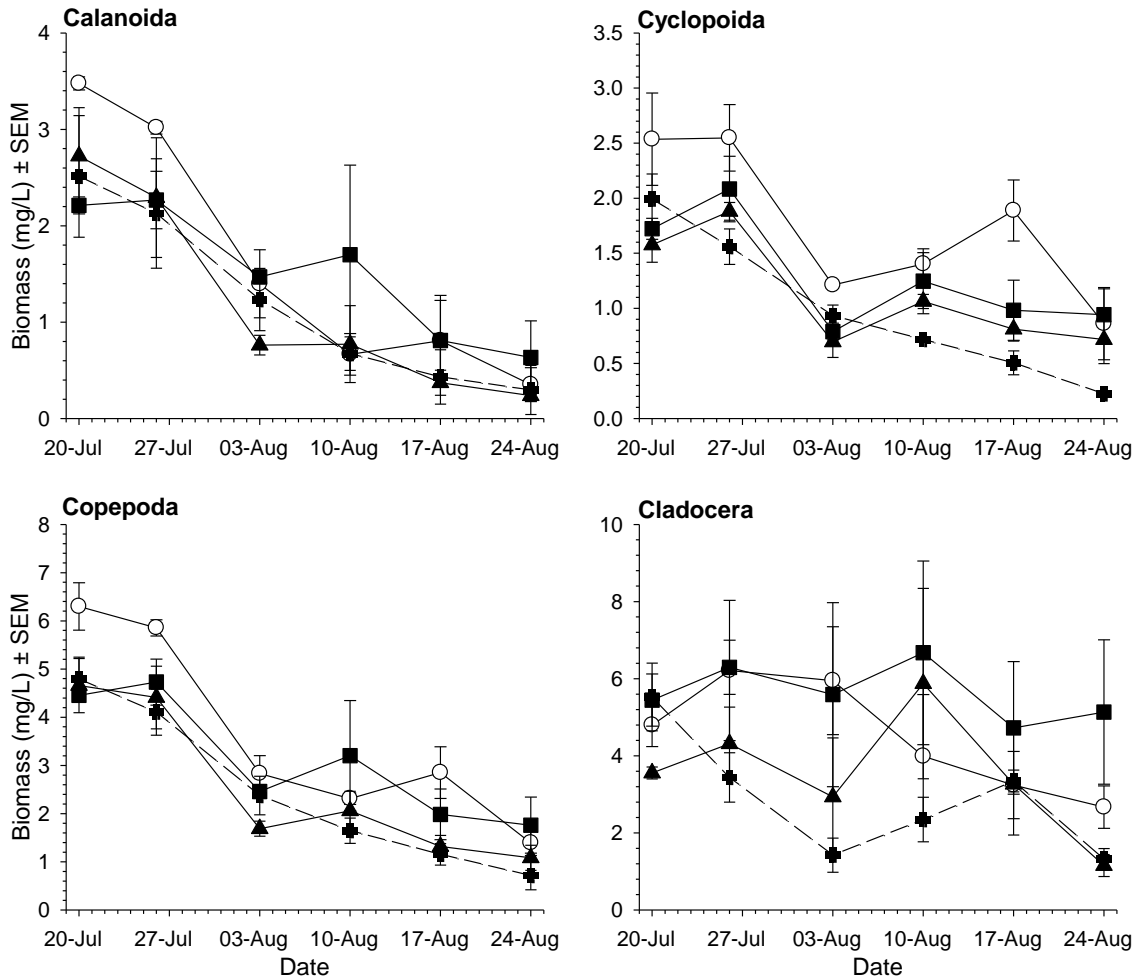


Figure 3.8: 2005 mean biomass ($\mu\text{g/L}$) \pm 1 SEM for crustacean groups over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

3.1.3.4 Interactive effects among predators

Following Sih et al. (1998), the emergent impacts of multiple predators and resulting risk reduction or enhancement for prey were determined by statistically significant interactive effects.

3.1.3.4.1 2004

Significant interaction effects were not detected in 2004 and therefore there was no evidence for emergent impacts on crustacean prey when both predators were present.

3.1.3.4.2 2005

Significant interaction effects were detected for *Daphnia* spp. abundance on 20 July, 2005 and *Bosmina* abundance, *Daphnia* spp. length, and Cyclopoida biomass on 3 August, 2005. As interaction effects were rarely detected in 2005, there was no strong trend of emergent impacts on crustacean prey when both predators were present.

3.1.4 Vertical migrations of zooplankton and predators

The day and night vertical distributions of zooplankton were sampled on one date each in 2004 and 2005 in one enclosure for each treatment.

3.1.4.1 2004

Predators were rare in samples taken with the Schindler-Patalas trap; Abundances of *Mysis* and *Chaoborus* on the final sampling date in the enclosures sampled for vertical migration studies are presented in Table 3.9. The enclosure in the *Chaoborus*-only treatment was omitted because a fish was discovered in it. In 2004, no *Mysis* were captured during the day and it is

assumed that they were located close to the bottom of the enclosures. *Mysis* were also rarely captured in daytime sample of enclosures on other dates. At night, one individual was sampled at 7m, indicating upward migration. *Chaoborus* larvae were found near the bottom of the enclosure in day in the both predator treatment. At night, they migrated upwards in this enclosure and some were abundant in the epilimnion (surface to 5m) in the both predator enclosure. Thus, predators can be assumed to be close to the bottom during the day and to ascend at night, with *Chaoborus* getting closer to the surface than *Mysis*.

Table 3.9: 2004 Volumetric predator densities (#/m³) in the individual large enclosures sampled for vertical migrations (densities sampled on final date).

Treatment	<i>Chaoborus</i> spp.	<i>Mysis relicta</i>
no predators	0	0
<i>Mysis</i> -only	0	5
both predators	40	7

In 2004, cladocerans were distributed throughout the water column but were more abundant in the epilimnion (0-5m) in both day and night (Figure 3.9). Strong diurnal migrations were not observed (depth distributions of taxa presented in Appendix: Figures 3-g to 3-k).

Juvenile copepods (nauplii, calanoid and cyclopoid c1-3 copepodids) were found at all depths in the enclosures in 2004 and were more abundant in the epilimnion (Figure 3.9). Late instar *Leptodiaptomus* and *Tropocyclops* were also distributed throughout the water column in enclosures. *Diacyclops* was more abundant in the deeper half of enclosures and had a shallower mean depth during the day.

Most taxa had shallower mean depths in enclosures without predators (Figure 3.9). Mean depths in the both predator treatment were shallower than in the single predator treatments for many taxa.

3.1.4.2 2005

Predator abundances on the final sampling date for the enclosures sampled for vertical migration studies are presented in Table 3.10. Predator densities in these enclosures were similar to mean abundances for their respective treatments. Predators were more commonly encountered in samples taken with the Schindler-Patalas trap in 2005. *Chaoborus* were located below the epilimnion during the day in the *Chaoborus*-only enclosure and ascended into the epilimnion at night. In the both predator enclosure, *Chaoborus* larvae were found at 3 and 9m during the day and in the epilimnion at night. In the *Mysis*-only enclosure, one individual was found at 11m during the day and at night at both 9 and 11m. In the both predator enclosure, no *Mysis* were found in daytime samples, while at night, individuals were found at 9 and 11m.

Table 3.10: 2005 Volumetric predator densities (#/m³) in the individual large enclosures sampled for vertical migrations (densities sampled on final date).

Treatment	<i>Chaoborus</i> spp.	<i>Mysis relicta</i>
no predators	0.6	0
<i>Chaoborus</i> -only	24	0.6
<i>Mysis</i> -only	2	12
both predators	24	9

In 2005, *Chydorus* and *Diaphanosoma* were the most abundant cladocerans and were predominantly found in the epilimnion (depth distributions of taxa presented in Appendix: Figures 3-l to 3-p). Both taxa had similar distributions at day and night in the no predator enclosure. In enclosures with *Mysis*, these taxa moved upwards at night (Figure 3.9).

Juvenile copepods were distributed throughout the water column. Nauplii and cyclopoid copepodids had similar day and night mean depths (Figure 9). Their mean depths were shallower than those of older copepods. Calanoid copepodids were deeper during the day, particularly in the single-predator enclosures (Figure 9). *Leptodiaptomus* had deeper mean depths during the day in enclosures (Figure 9). *Tropocyclops* were evenly distributed and had similar day and night distributions (Appendix: Figure 3-p). *Diacyclops* was most abundant in the hypolimnion of the enclosures (Appendix: Figure 3-p).

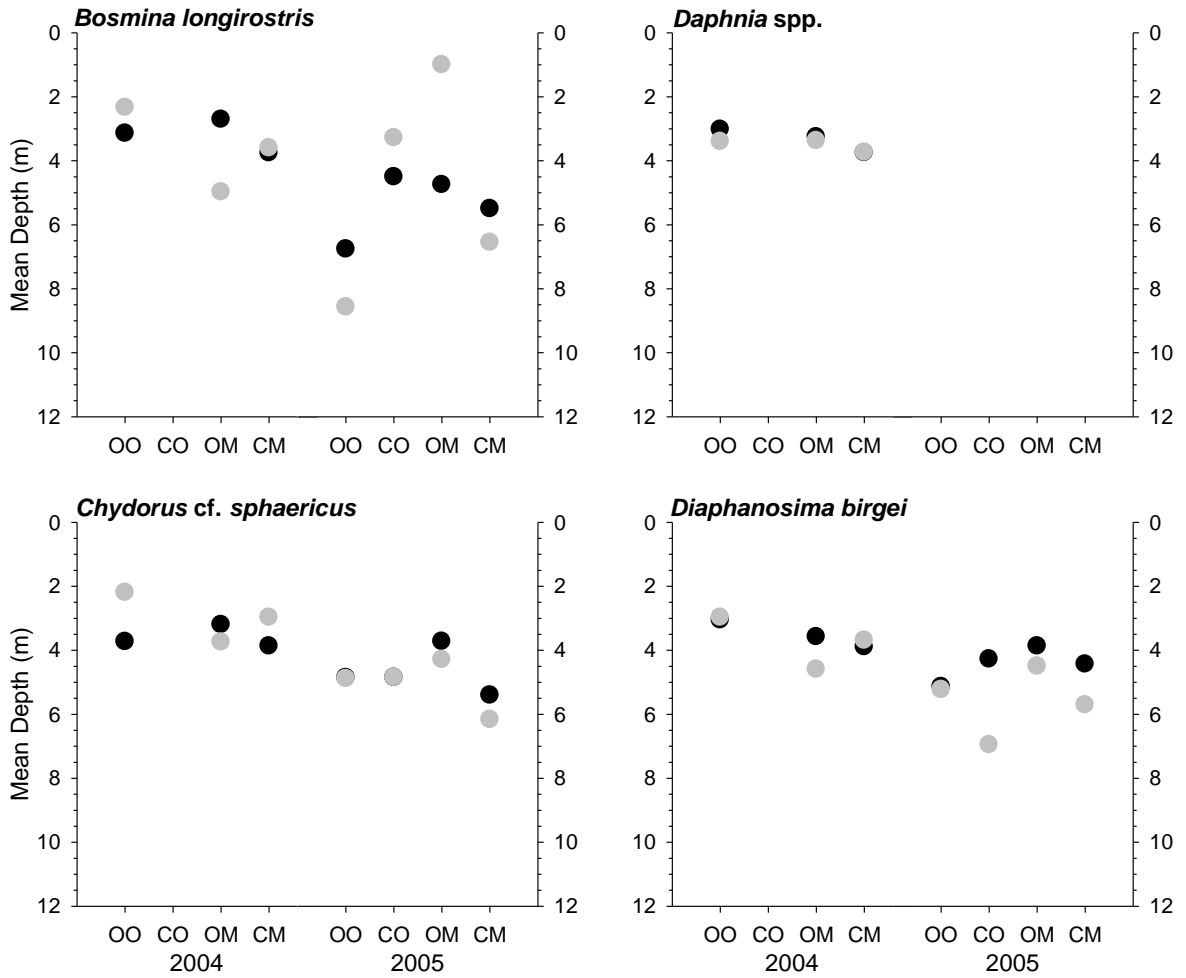


Figure 3.9: Mean day (light circles) and night (black circles) depths in large enclosures sampled in 2004 and 2005. Treatments on x-axis: no predators (OO), *Chaoborus*-only (CO), *Mysis*-only (OM), and both predators (CM). *Daphnia* omitted in 2005 due to low abundance in enclosures.

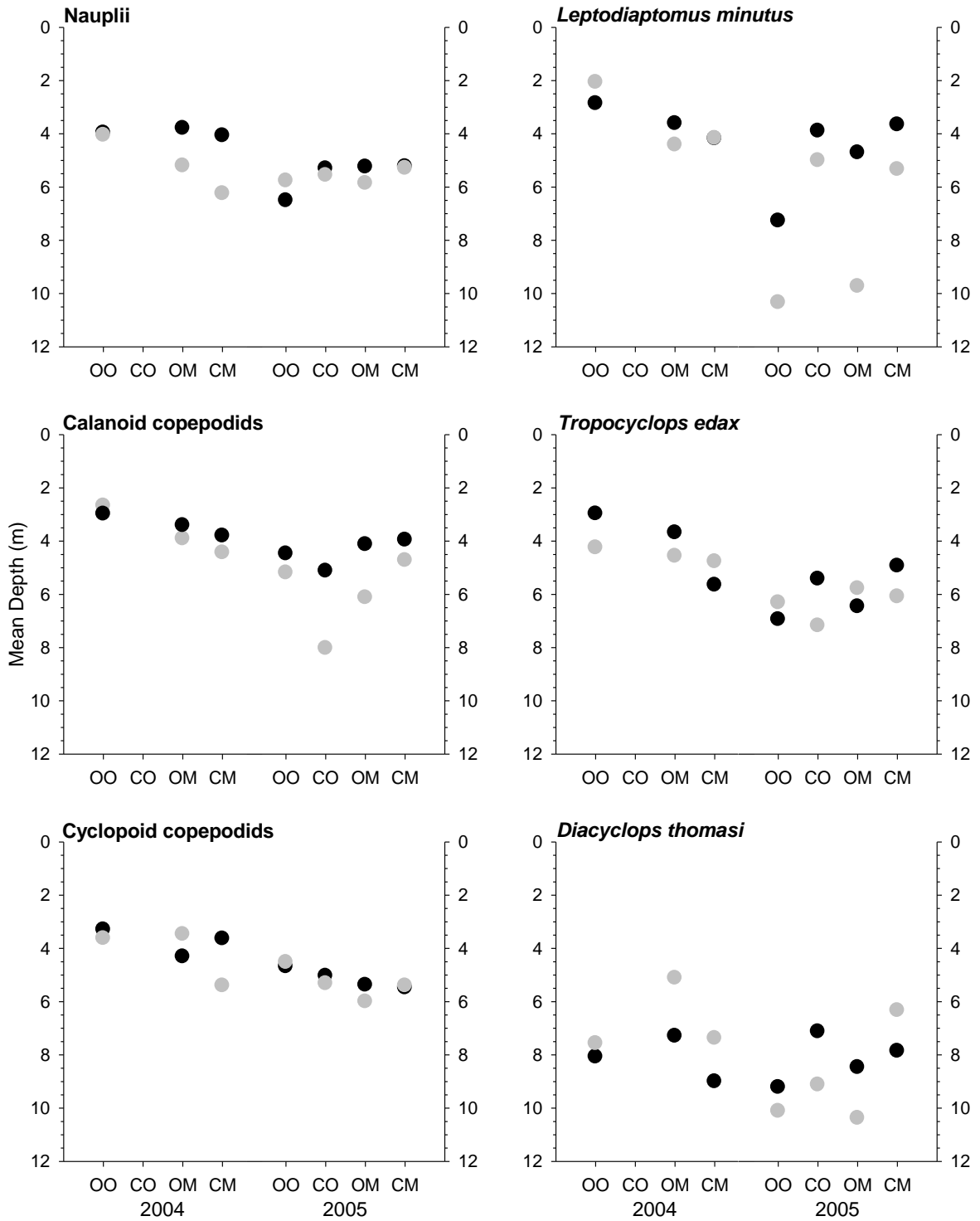


Figure 3.9 continued: Mean day (light circles) and night (black circles) depths in large enclosures sampled in 2004 and 2005. Treatments on x-axis: no predators (OO), *Chaoborus*-only (CO), *Mysis*-only (OM), and both predators (CM).

3.1.5 Chlorophyll

Because zooplankton consumers partially regulate algal primary production, differences in phytoplankton biomass may occur under different predatory regimes (Carpenter et al. 1985). Chlorophyll *a* was used as an estimate of changes in algal biomass during the experiments.

3.1.5.1 2004

In 2004, compared to Lake 239, chlorophyll *a* was lower in enclosures during the experiment (M.P. Stainton, unpublished data). Total chlorophyll was significantly greater when *Mysis* was present on 30 August, 2004 (Appendix: Table 3-a). For all other dates and effects, treatments were not significantly different. Results using testing data from the high performance liquid chromatography method were similar to those using the fluorescence method when both methods were utilized, but data were incomplete on two dates due to equipment failure during analysis. The percentage of phytoplankton in the edible <30 μ m fraction was high (approximately 80% on average). Chlorophyll *a* was similar in all enclosures at the beginning of the experiment and diverged over time.

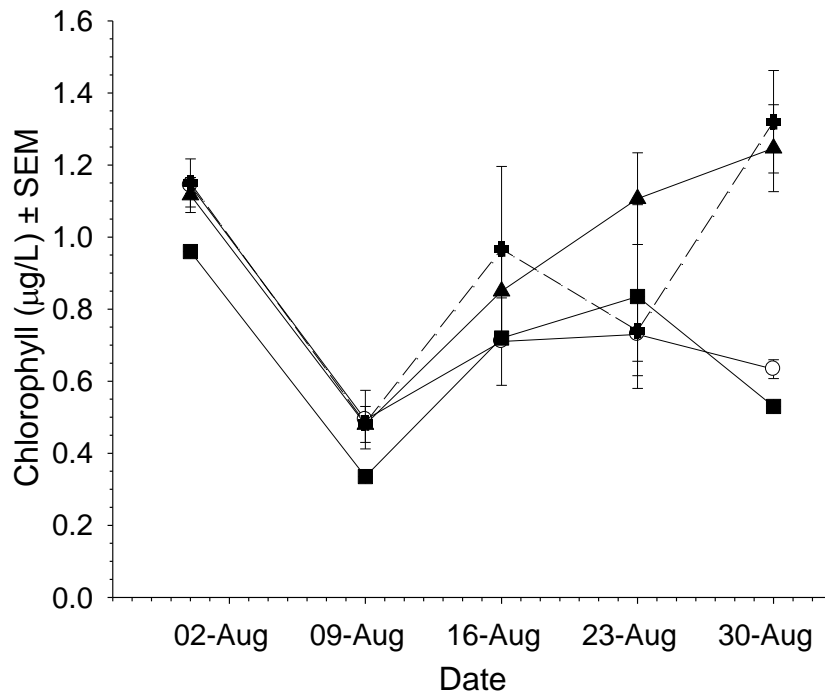


Figure 3.10: 2004 mean chlorophyll a, using HPLC (high performance liquid chromatography) \pm 1 SEM, over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

3.1.5.2 2005

Chlorophyll *a* in enclosures was also lower than the lake in 2005 (M.P. Stainton, unpublished data). No changes over time for chlorophyll *a* (high performance liquid chromatography method) of total or <30µm chlorophyll occurred in the enclosures (Figure 3.11). The proportion of phytoplankton in the edible <30µm fraction was high (approximately 80% on average). Chlorophyll *a* was similar in all enclosures at the beginning of the experiment but enclosures diverged over time.

Overall, there was little evidence that chlorophyll *a* varied among predator treatments. As effects of predators on zooplankton were weak, strong impacts on phytoplankton were not expected.

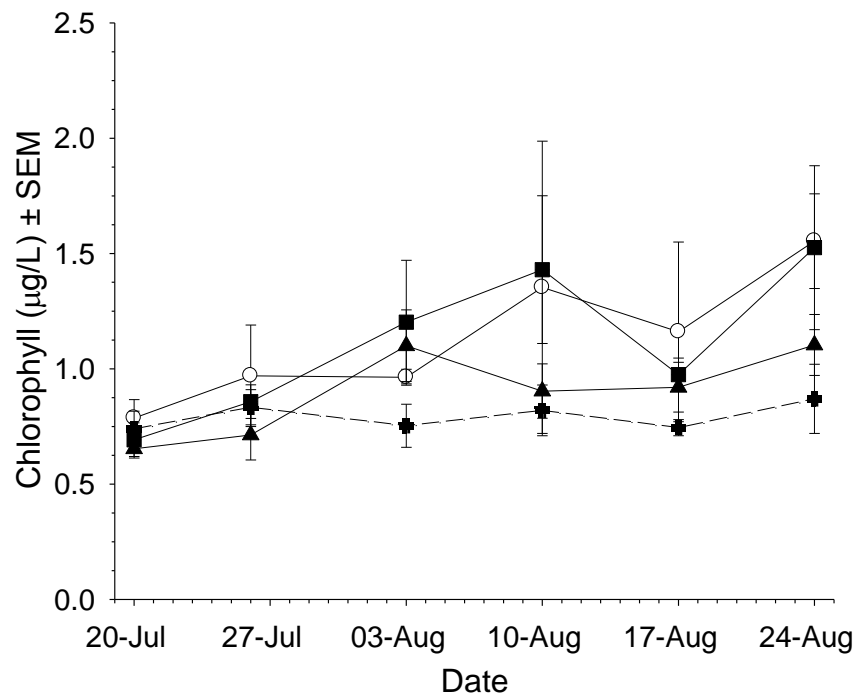


Figure 3.11: 2005 mean chlorophyll a, using HPLC (high performance liquid chromatography) \pm 1 SEM, over time in different treatments of large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

3.2 Small enclosures

3.2.1 Predators

Mysis suffered no mortality in any enclosures while some *Chaoborus* mortality occurred in all enclosures (Table 3.11) (average mortality = 25%). The mean number of *Chaoborus* in treatments with *Mysis* was lower than without *Mysis* [C > CM: df=4, t=2.00, P=0.0581; CC > CCMM: df=2, t=-3.88, P=0.0302].

Table 3.11: Abundance of predators (#/m³) ± 1 SEM in treatments (n=3) of small enclosures. Initial and final densities (mean ± 1 SEM) of *Chaoborus* spp.; *Mysis* densities did not change during the experiment.

Treatment	<i>Chaoborus</i> spp.		<i>Mysis relicta</i>
	initial	final	
low- <i>Chaoborus</i>	400	316.67 ± 16.67	0
low- <i>Mysis</i>		0	50
high- <i>Chaoborus</i>	800	750	0
high- <i>Mysis</i>		0	100
low predators	400	250.00 ± 28.87	50
high predators	800	516.67 ± 60.09	100

3.2.2 Zooplankton

Broadly, prey abundances were lower in treatments with predators than in the no predator enclosures (Figure 3.12).

With the exception of *Leptodiatomus*, the abundance of most zooplankton taxa was significantly reduced in the presence of *Mysis* especially nauplii, cyclopoid copepodids, and cladocerans *Bosmina*, *Chydorus*, and *Daphnia* (Table 3.12). Calanoid copepodids were significantly lower in abundance in enclosures with *Chaoborus*. In no case was a significant main effect of predator density detected. A significant effect of *Mysis* density (*Mysis* × density interaction) was observed for *Chydorus*. All other higher order interactions were not statistically significant.

Total crustacean abundance was significantly lower in treatments with *Chaoborus* and *Mysis*, as were cyclopoids and cladocerans. Interactions of *Mysis* and density were detected for cyclopoid, cladoceran, and total abundance as well. Interactions of *Chaoborus* and *Mysis* were detected for copepod abundance only. Calanoids were not significantly reduced by predators in these enclosures.

Table 3.12: P-values from results of ANOVA on transformed species abundances measured in small enclosures. Significance highlighted in BOLD; P<0.011 for species and P<0.02 for groups (experiment-wise error = 0.1). C – *Chaoborus* factor, M – *Mysis* factor, D – density factor.

Variable	Log ₁₀ Abundance (#/L)						
	C	M	D	CxM	CxD	MxD	CxMxD
<i>Tropocyclops extensus</i>	0.113	0.016	0.922	0.142	0.208	0.744	0.392
<i>Diacyclops thomasi</i>	0.059	0.003	0.115	0.070	0.652	0.014	0.527
<i>Leptodiaptomus minutus</i>	0.906	0.663	0.805	0.292	0.165	0.450	0.673
nauplii	0.026	0.001	0.837	0.046	0.510	0.592	0.936
calanoid copepodids	0.009	0.015	0.743	0.414	0.139	0.188	0.614
cyclopoid copepodids	0.064	<0.001	0.616	0.827	0.132	0.053	0.994
<i>Bosmina longirostris</i>	0.033	<0.001	0.421	0.134	0.468	0.352	0.550
<i>Chydorus cf. sphaericus</i>	0.021	<0.001	0.450	0.459	0.031	0.008	0.893
<i>Daphnia</i> spp.	0.343	<0.001	0.770	0.135	0.548	0.303	0.465
Groups							
Calanoida	0.116	0.101	0.802	0.236	0.150	0.357	0.424
Cyclopoida	0.011	<0.001	0.086	0.042	0.242	0.002	0.549
Copepoda	0.002	<0.001	0.108	0.007	0.105	0.003	0.959
Cladocera	0.015	<0.001	0.231	0.504	0.055	0.006	0.852
Crustacean taxa	0.002	<0.001	0.154	0.025	0.065	0.004	0.920

Overall, abundances in treatments with both predators were not significantly lower than abundances with predators alone and density impacts were rarely detected. Significant reductions of zooplankton were also not observed in high *Chaoborus* enclosures. Consequently, there was no evidence of a strong interaction between *Chaoborus* and *Mysis* in terms of their effect on the crustacean zooplankton community.

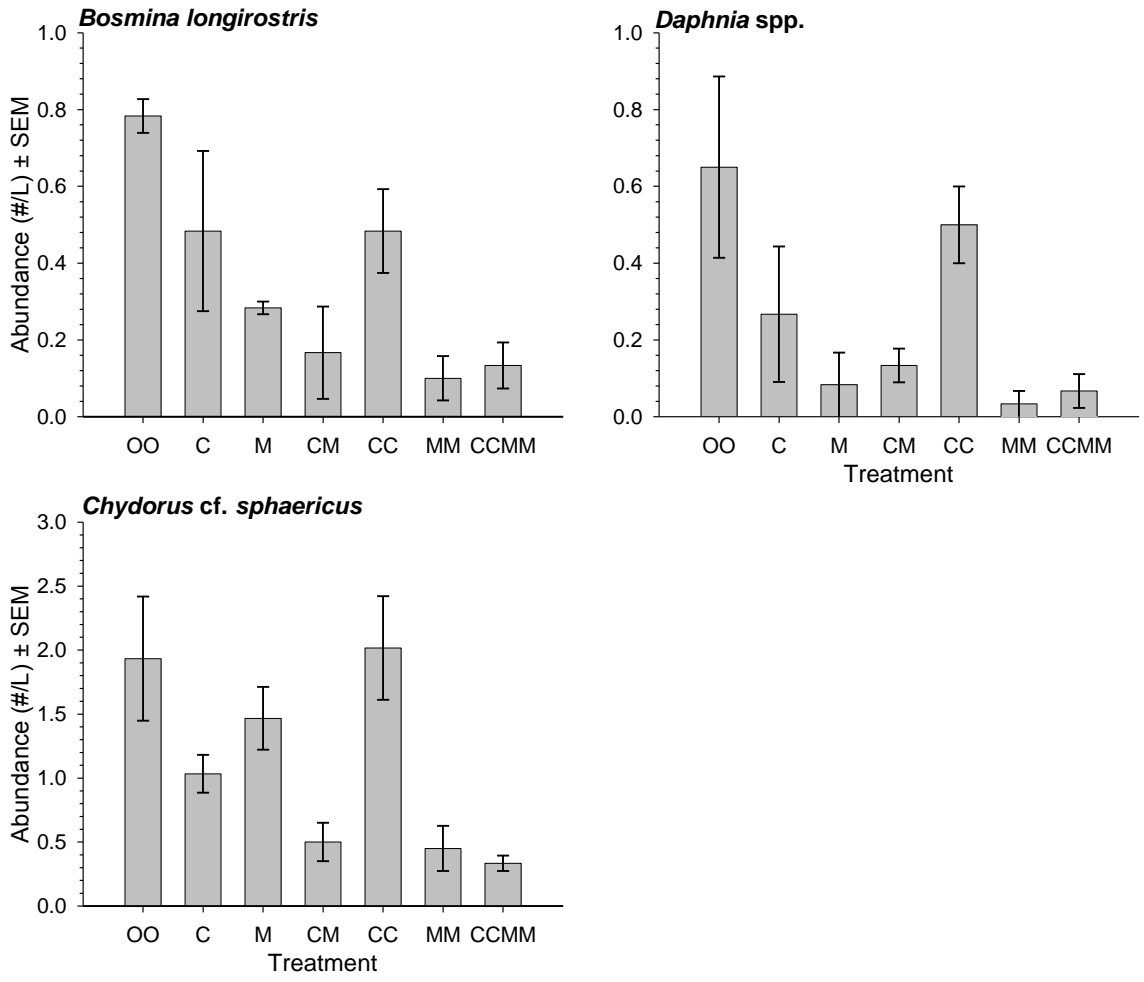


Figure 3.12: Mean abundance (#/L) ± 1 SEM of zooplankton taxa in treatments in small enclosures: OO – no predators; C – low-*Chaoborus*; M – low-*Mysis*; CM – low both predators; CCMM – high both predators; CC – high-*Chaoborus*; MM – high-*Mysis*.

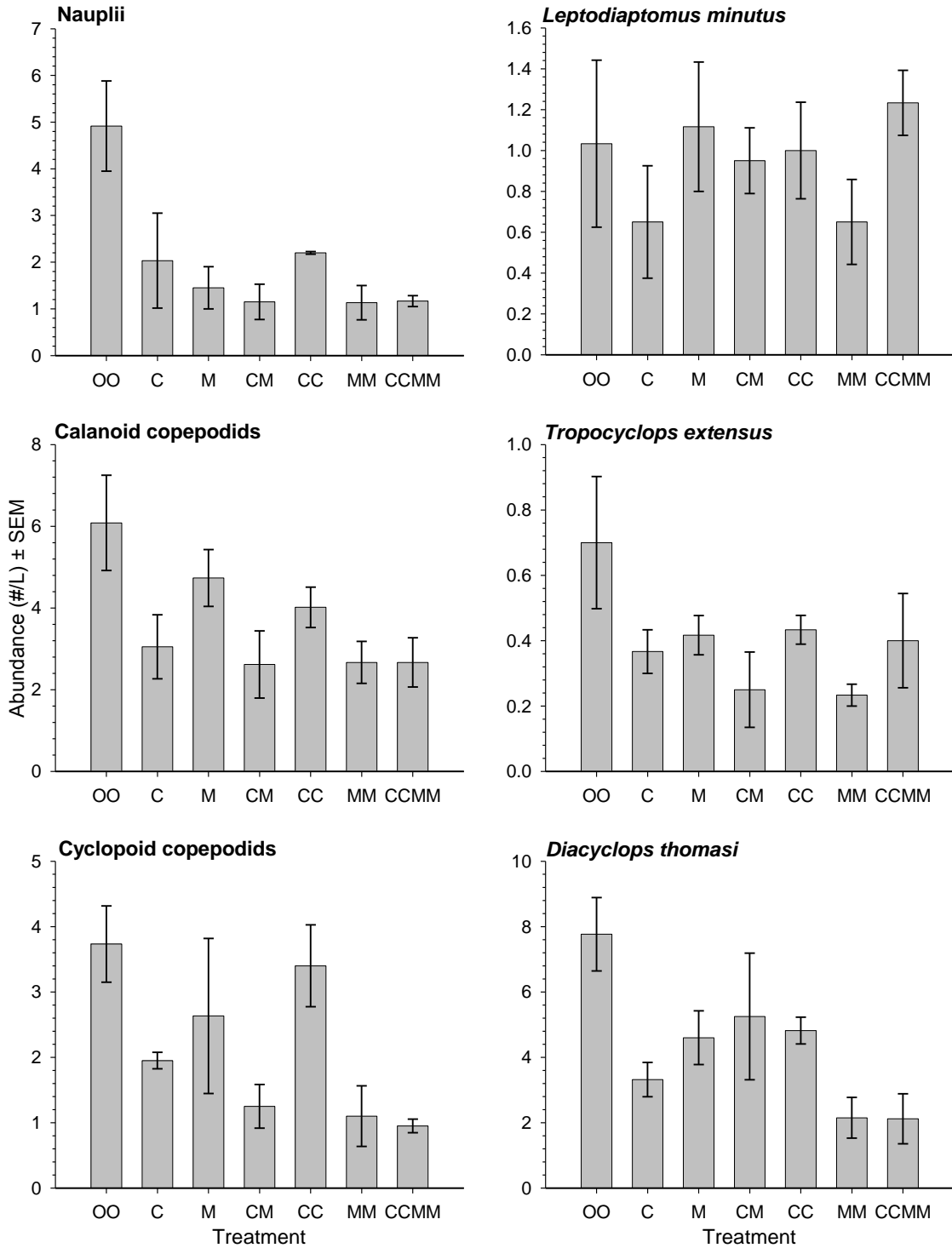


Figure 3.12 continued: Mean abundance (#/L) ± 1 SEM of zooplankton taxa in treatments in small enclosures: OO – no predators; C – low-*Chaoborus*; M – low-*Mysis*; CM – low both predators; CCMM – high both predators; CC – high-*Chaoborus*; MM – high-*Mysis*.

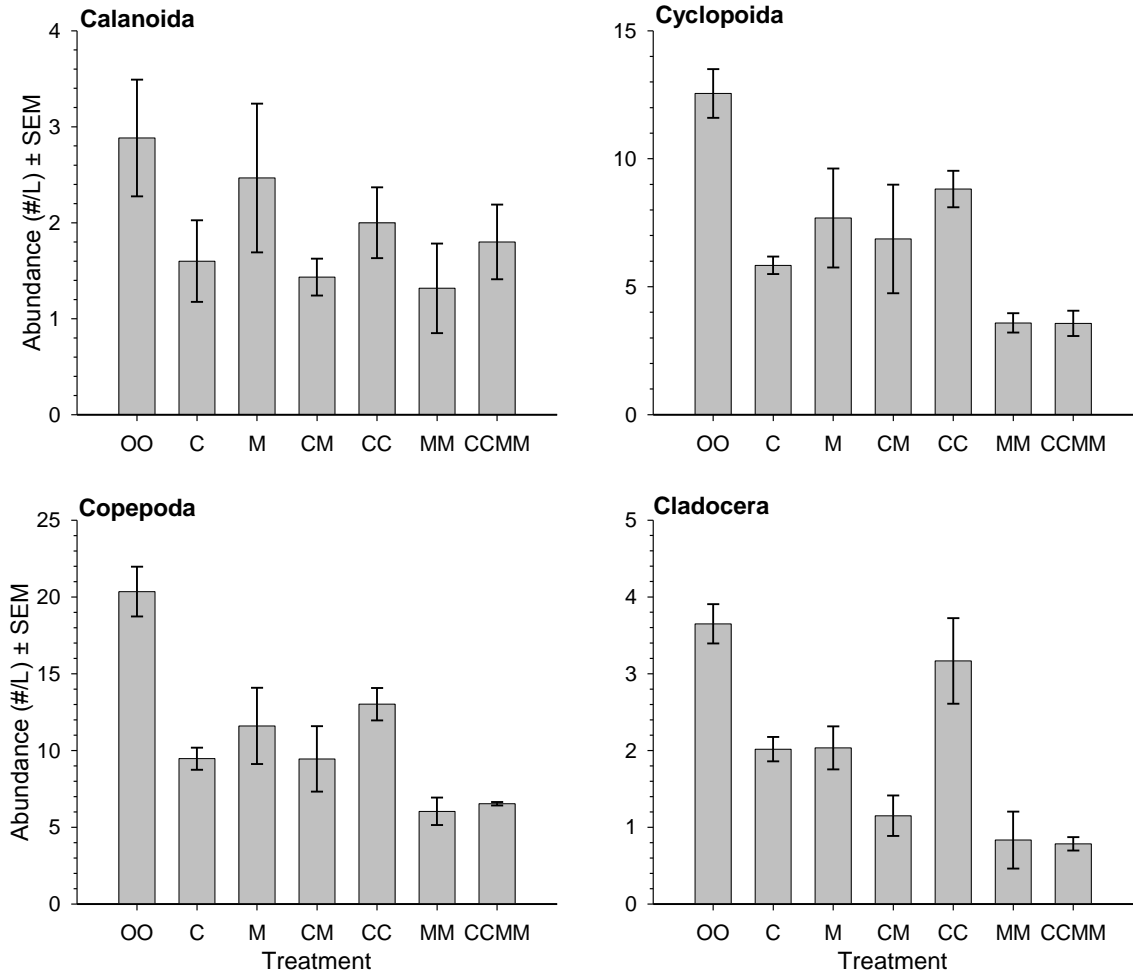


Figure 3.13: Mean abundance (#/L) ± 1 SEM of zooplankton groups in treatments in small enclosures: OO – no predators; C – low-*Chaoborus*; M – low-*Mysis*; CM – low both predators; CCMM – high both predators; CC – high-*Chaoborus*; MM – high-*Mysis*.

4 Discussion

The purpose of this study was to examine and compare the impacts of the common invertebrate predators, *Mysis relicta* and *Chaoborus* spp. on pelagic crustacean zooplankton at realistic densities and to determine whether the effects of the two predators together could be predicted from their impacts when they occurred alone.

In the large enclosures, the abundance of most species was stable in 2004 and declined regardless of treatment during 2005. In 2004, few significant predator impacts were observed and in 2005, only the most abundant taxon, *Bosmina longirostris* significantly declined when *Mysis* was present. Statistically significant effects of *Chaoborus* were detected only for *B. longirostris* on 3 August, 2005. Average species' lengths were not strongly affected by predator treatment in 2005, the only year they were measured. Large, consistent changes in zooplankton vertical migration were also not observed in the presence of *Chaoborus* or *Mysis*. *Chaoborus* and especially *Mysis* could reduce crustacean densities in short-term manipulations in the small enclosures. The strongest impacts in the small enclosures were on cladocerans.

Because neither predator strongly affected the overall community, strong interactive effects between *Chaoborus* and *Mysis* on zooplankton were not observed. I also did not find evidence for strong intraguild predation between these two species.

Below, I examine the impacts of *Chaoborus* and *Mysis* on zooplankton abundance, biomass, body length, and vertical migration and discuss the

possibility of interactions between the two predators. I first assess impacts of *Chaoborus* and *Mysis* on zooplankton in the large enclosures and then compare results from the small and large enclosures.

4.1 Predator impacts on zooplankton abundance and species composition

Overall, statistically detectable impacts of *Chaoborus* or *Mysis* were infrequently observed in the large enclosures. Although statistically significant results were primarily seen only in 2005, the no predators treatment had higher abundance of *Bosmina*, *Daphnia*, and calanoid copepodids during part of the large enclosure experiments in both years. *Chaoborus* and especially *Mysis* may have had an effect on these zooplankton taxa. Abundances of other taxa were not strongly affected by predator treatment.

In the small enclosure experiments, significant declines in the abundance of many zooplankton taxa were observed in enclosures with *Mysis*. The taxa most strongly affected included nauplii, cyclopoid copepodids and the cladocerans *Bosmina*, *Daphnia*, and *Chydorus*. *Leptodiptomus*, calanoid copepodids, and *Tropocyclops* were unaffected by invertebrate predator treatments in this short-term experiment. A significant effect of *Chaoborus* was detected for calanoid copepodids and for copepod and cladoceran groups.

While the small and large enclosures were designed to examine impacts of invertebrate predation on pelagic crustacean zooplankton, the experiments had different volumes, durations, and predator densities (Table 4.1). The small enclosures were very small compared to the large enclosures, the experimental

time frame used was shorter, and predator densities were much higher (Table 4.1).

Table 4.1: Comparison of size, duration, and densities used in small and large enclosure experiments.

scale	small	large
size (L)	20	~22800
duration (days)	3	31 to 35
predator <i>Chaoborus</i>	0.25-0.75	0.02-0.03
density (#/L) <i>Mysis</i>	0.05-0.1	0.004-0.015

Results from the small enclosures confirm that *Mysis* is a predator of many pelagic crustacean zooplankton. Due to the higher predator densities in the small enclosures and reduced opportunities for behavioural responses, it is reasonable to expect a less dramatic impact of *Mysis* on zooplankton in the large enclosures. Given that few strong impacts of *Chaoborus* were detected in the small enclosures, even less dramatic effects would be expected in the large enclosures. Impacts attributable to *Chaoborus* were rarely detected in large enclosures.

The higher predator densities were not the only factor expected to result in greater predation on zooplankton prey in the small enclosures. Enhanced predation could also result from confinement of predators and prey in the small volume of water. As well, prey were unable to seek refuges and no taxa were able to migrate vertically. Reproduction in the small enclosures would be minimal because of the short time span of the experiment, while density-dependent numerical responses of prey were more possible in the large enclosures.

Chaoborus did not have a large impact on zooplankton prey in the small enclosure experiment and this may be partly attributable to reduced consumption

at the low temperatures (~4°C) experienced at the 10m depth at which the enclosures were held. Fedorenko (1975b) found that consumption by *C. trivittatus* and *C. americanus* decreased at lower temperatures. Swift (1976) also found digestion of fourth instar *C. trivittatus* to be slow at low temperatures (5°C). *Chaoborus* ordinarily vertically migrate into the warm epilimnion to feed at night (Luecke 1986) but migration was prevented in the small enclosures. As a result, the small enclosure experiments may underestimate the potential impact of higher densities of *Chaoborus* on the zooplankton community.

In keeping with the results from my enclosure experiments, in several other studies, *Bosmina* and *Daphnia* were among the most sensitive crustacean taxa to *Mysis* predation. In Lake Granby, Colorado, *Bosmina* was preferred prey and was found in *Mysis* stomachs even when other prey were more abundant (Martinez and Bergersen 1991). In Lake Tahoe, *Bosmina* abundance declined following *Mysis* introduction (Threlkeld et al. 1980). In Lake Granby, *Mysis* consumed *Bosmina*, *Daphnia galeata mendotae*, *Diacyclops*, and rotifers (Martinez and Bergersen 1991). When offered a natural prey assemblage in Lake Michigan, *Mysis* consumed nauplii, copepodids, and cladocerans (Bowers and Vanderploeg 1982).

In the large and small enclosure experiments, adult calanoid copepods were not strongly affected by *Mysis*. This is consistent with other studies in which *Mysis* did not consume many *Diaptomus* adults when feeding in multi-species assemblages (Cooper and Goldman 1980; Folt et al. 1982).

Small cladocerans have been affected by *Chaoborus* predation in many studies. *Bosmina* is considered susceptible because of its small size (making it easy to handle) and lack of evasive response following contact with the predator (von Ende and Dempsey 1981; Lüning-Krizan 1997). *Chaoborus* crop contents frequently contain remains of *Bosmina*, *Daphnia*, and *Diaphanosoma* (Moore 1988; Lüning-Krizan 1997; Sutor et al. 2001). When *C. americanus* (Johannsen), a large, non-migrating species of *Chaoborus*, was added to enclosures, *Bosmina*, *D. galeata mendotae*, *Diaphanosoma*, and *Diaptomus* declined, relative to controls without *Chaoborus* (Vanni 1988). Cladocerans in Paul Lake, MI, declined following increases in the abundance of *C. flavicans* (Elser et al. 1987).

In my experiments, large impacts of *Chaoborus* on copepods were not observed, contrary to the results in several other studies. In enclosure studies in bog lakes in Wisconsin and Michigan, *Chaoborus* caused declines of nauplii and cyclopoids (Arnott and Vanni 1993). Crops of *C. punctipennis* in Tuesday Lake, MI, were dominated by copepods, mainly *Tropocyclops prasinus* (Fischer) (Elser et al. 1987). Copepod biomass made up the majority (60-70%) of prey consumed by fourth instar *C. americanus* and *C. trivittatus* in Eunice Lake, BC (Fedorenko 1975a).

While *Bosmina* abundance declined in the large enclosures in 2005, another small species, *Chydorus*, increased in abundance in some predator treatments (Figure 3.2). *Chydorus* ($0.26\text{mm}\pm 0.002$) was smaller than *Bosmina* ($0.32\text{mm}\pm 0.003$) ($df=1195.9$, $t=15.62$, $P<0.001$) but its small size is unlikely to

have inhibited consumption. Possibly *Chydorus* had a greater rate of increase than *Bosmina* in enclosures. While *Chydorus* has a maximum clutch size of only two (reviewed in Lynch 1980), its egg development time is rapid at various temperatures, pH's, and food sources (de Eyto and Irvine 2001). *Bosmina* can have a larger clutch size (reviewed in Lynch 1980) but is more affected by poor food quality than *Chydorus* (Lundstedt and Brett 1991). Lundstedt and Brett (1991) surmised that the generalist nature of *Chydorus* enables it to increase in abundance when selective predation affects large cladocerans and poor food quality affects *Bosmina*. Additionally, the enclosures may have improved *Chydorus* habitat by decreasing lateral water movement within the enclosures (Bloesch et al. 1988) and by providing wall habitat similar to macrophytes found in the littoral, where *Chydorus* is frequently abundant.

4.2 Predator impacts on zooplankton lengths in 2005

Large impacts of *Chaoborus* and *Mysis* on mean zooplankton sizes were not observed in the 2005 large enclosure experiment. This was probably because the overall impact of the predators on the zooplankton community was small, which limited the statistical power of analyses. In addition, most of the Crustacea in the enclosures may have been in the size range that was potentially susceptible to predation by both *Mysis* and *Chaoborus*.

Impacts of predation on zooplankton lengths were first suggested by Hrbáček (1962) and Brooks and Dodson (1965). Fish tend to consume large zooplankton because most are visual predators, while invertebrate predators often are assumed to crop smaller zooplankton (Zaret 1980). Invertebrate

predators are typically limited to smaller items by their smaller gapes and abilities to capture and manipulate their prey (Zaret 1980). On the other hand, small prey may be inconspicuous to larger predators (Cooper et al. 1985).

Both *Mysis* and *Chaoborus* in the enclosures should have been able to consume most of the available crustacean zooplankton prey (mean prey size was 0.45mm). Consistent differences in mean sizes among predator treatments were not observed. Swift and Fedorenko (1975) pointed out that prey size is only influential after contact has been made, while behaviours (e.g. swimming patterns) and distributions also affect prey encounter rates. This may partly explain the minimal impact of predators on prey length in my study.

As *Mysis* and *Chaoborus* age and increase in size, they prefer larger prey (Cooper and Goldman 1980; Moore 1988; Swift 1992). Approximately 80% of *Mysis* sampled on the last date of the large enclosure experiments were adults and would have had comparatively large gapes and the ability to consume larger prey (Cooper and Goldman 1980). Even so, ultimate attack success usually decreases with increasing prey size (Ramcharan et al. 1985), so that very large zooplankton may escape consumption by *Mysis*. However, even the large *E. lacustris* was susceptible to *Mysis* predation in several studies (Beeton and Bowers 1982; Folt 1985; Nero and Sprules 1986a).

Older and larger *Chaoborus* also usually consume larger prey (Moore 1988; Swift 1992). Maximum size of prey ingested is correlated with the head capsule size of the larvae, which increases with instar and varies among *Chaoborus* species (Swift and Fedorenko 1975; Irvine 1997). Prey width and

predator gape size are better predictors of whether a prey item can be ingested but texture and shape also influence the ability of larvae to ingest the prey (Swift 1992). *Chaoborus* easily consumes copepods head first (Luecke and Litt 1987; Jin and Sprules 1988). While Swift and Fedorenko (1975) suggest there is a limit of 0.6mm for the smallest size of prey ingested by instar IV *C. americanus* larvae, Swift (1992) later reported, “there was no decrease in prey capture ability by fourth-instar larvae feeding on the smallest prey” (p21). An enclosure experiment with *Chaoborus* in central Ontario resulted in decreased average lengths of zooplankton (Sutor et al. 2001).

4.3 Vertical migrations of zooplankton and predators

Both *Chaoborus* spp. and *Mysis relicta* typically occur near the bottom of the water column during the day and move upward at night (Bowers 1988). *Chaoborus flavicans* instar III and IV larvae are also located near the sediments during the day (Luecke 1986). They rise through the water column into the epilimnion in the evening and descend in the early morning (Teraguchi and Northcote 1966; Sardella and Carter 1983). *Mysis* are usually located near sediments during the day and ascend into the water column in the evening, descending again in the early morning (Lasenby and Langford 1972; Beeton and Bowers 1982; Bowers 1988). Studies have demonstrated that *Mysis* rarely enter the warm waters of the epilimnion (e.g. Lehman et al. 1990). Although predator densities were too low to determine accurately their vertical distribution in the enclosures without affecting their abundance, *Chaoborus* typically migrate into the warm waters of the epilimnion at night (Teraguchi and Northcote 1966),

whereas *Mysis* remain in the colder waters of the hypolimnion (Nero 1981; Beeton and Bowers 1982). *Mysis* have an upper temperature threshold of 13 to 17°C (Smith 1970; DeGraeve and Reynolds 1975; Rudstam et al. 1999; Boscarino et al. 2007), which is colder than the epilimnetic temperatures in the enclosures during the 2004 and 2005 large enclosure experiments. Zooplankton species that decline most following introductions of *Mysis* to lakes are those that inhabit the hypolimnion (Threlkeld et al. 1980; Rieman and Falter 1981; Bowles et al. 1991). Impacts of *Mysis* on zooplankton that inhabit the epilimnion are typically greatest in the spring, when epilimnetic water temperatures are lowest (Rieman and Falter 1981; Bowles et al. 1991).

Zooplankton typically maintain vertical distributions that avoid ultraviolet radiation and predation (Kerfoot 1985; Lampert 1993; Boeing et al. 2004; Fischer et al. 2006). After Neill (1990) added *C. trivittatus* larvae to enclosures with non-migrating *Diaptomus kenai*, *Diaptomus* started to migrate down at night when *Chaoborus* were located in surface waters. In acrylic enclosures sampled during the day, *Chaoborus* were located near the bottom while *Daphnia catawba* Coker, *Diaphanosoma* spp., nauplii, and calanoid copepodids were located near the top (Boeing et al. 2004). *Daphnia* were more abundant in surface waters of 4m deep enclosures with *C. americanus*, which occupied the bottom of enclosures, than in enclosures without the predator (Nesbitt et al. 1996). *Daphnia pulex* Leydig with overlapping distributions with *C. americanus* were more susceptible to predation (Young and Riessen 2005). *Mysis* were found in the meta- and hypolimnia of Lake Michigan at night while *Daphnia* spp. were usually abundant close to the

surface (Lehman et al. 1990). Maintaining distributions that do not overlap with invertebrate predators can be used to reduce interactions with predators.

Alternately, overlapping zooplankton and predator vertical distributions have also been reported. Both *Mysis* and their prey, *Diaptomus sicilis* Forbes, were more abundant in the surface waters of Waterton Lake at night (Chess and Stanford 1998). Three *Daphnia* species continued to migrate towards the surface at night, despite the high abundance of *Chaoborus* larvae at 2m in enclosures (González and Tessier 1997). In Lake Kärnsjön, Sweden, day and night vertical distributions of many taxa and *Chaoborus* overlapped in July (Lagergren et al. 2008). Thus, while vertical migration can sometimes reduce the possibility of predation by invertebrate predators, its occurrence is not universal.

As with other variables examined in the large enclosures, consistent effects of *Mysis* and *Chaoborus* on vertical migration were not observed. Unfortunately, the taxon whose abundance was most strongly affected in 2005, *Bosmina*, were too scarce to accurately determine changes in vertical migration on the day of vertical sampling in that year.

In 2004, the no predator enclosure was characterized by similar diurnal and nocturnal distributions for most species. Most species were more abundant closer to the surface, except for *Diacyclops* which was most abundant deeper depths in the enclosures. This may partially explain the low impact of *Mysis* on the abundance of many species; extensive overlap of predator and prey distributions did not occur. In 2005, day and night distributions of most taxa were more evenly distributed throughout the water column and mean depths at day

and night within enclosures were not as similar as in 2004. In 2005, mean depths of species were commonly lower in the day compared to 2004. Mean depths of many taxa were not similar in enclosures of the same treatment between years.

Low densities of *Mysis* were found on the final date in *Chaoborus*-only enclosures in both 2004 and 2005 and low densities of *Chaoborus* were also found in the no predator enclosure and *Mysis*-only enclosure in 2005. Studies of vertical distributions have found *Daphnia* respond to kairomones produced by invertebrate predators, so it is possible that these low predator densities influenced the vertical distributions of zooplankton (e.g. Black 1993; Weber and Van Noordwijk 2002).

4.4 Chlorophyll

Because crustacean zooplankton are important phytoplankton grazers, changes in their abundance or behaviour in the presence of invertebrate predators may result in changes in phytoplankton abundance. In both years, statistically demonstrable differences of chlorophyll *a*, an indicator for phytoplankton biomass, were rare among treatments. This could be anticipated because responses of zooplankton densities and biomass to predators were weak. In addition, both *Chaoborus* and *Mysis* may consume phytoplankton some of the time (*Mysis*: Grossnickle 1982; *Chaoborus*: Moore 1988), which would make the impact of zooplankton on phytoplankton even harder to detect.

Particularly in biomanipulation studies, phytoplankton biomass can be affected by changing the abundances of upper trophic level predators. For example, after *Mysis* was introduced to Lake Jonsvatn, Norway, phytoplankton

biomass increased (Koksvik et al. 1991). Lasenby et al. (1986) explained that this frequently occurs following *Mysis* introductions because their predation on zooplankton reduces grazing. Following removal of roach (*Rutilus rutilus* (Linnaeus)) from Lake Lilla Stockelidsvatten, *Chaoborus* abundance increased, the dominant zooplankton changed from *Bosmina* and other small cladocerans to large copepods, and the biomass of net phytoplankton increased (particularly the more grazer-insensitive species) (Stenson et al. 1978).

While changes may occur when predator abundances are modified or are different, other researchers have found that even with changes in zooplankton abundance or biomass, no phytoplankton response was detected. In an enclosure experiment at the ELA, there were no differences in phytoplankton biomass in enclosures with and without *Chaoborus* (Vanni 1988; Vanni and Findlay 1990). An increase in *Chaoborus* abundance in the former quarry Gräfenhain was followed by low zooplankton biomass but this had no effect on total phytoplankton biomass, although the proportion of edible phytoplankton decreased (Benndorf 1990). Following establishment of *C. flavicans* in Lake Lenore, Washington, *Diaptomus nevadensis* Light was extirpated, the abundance of *D. sicilis* was reduced, and many *Daphnia pulicaria* Forbes grew neckteeth (Luecke and Litt 1987). However, the number and type of phytoplankton before and after *Chaoborus* establishment was not different. In Peter Lake, Michigan, introductions of *C. americanus* to enclosures caused declines in *Daphnia* and *Skistodiaptomus oregonensis* Lilljeborg but chlorophyll *a* was not different between treatments (Mackay et al. 1990).

4.5 Reasons for lack of prey response

Strong effects on crustacean zooplankton have been observed by invertebrate predators in enclosures, whole lakes, and the laboratory (*Chaoborus*: Pastorok 1980; Pastorok 1981; Ramcharan and Sprules 1986; Swift 1992; *Mysis*: Cooper and Goldman 1980). Crustacean zooplankton are also common in invertebrate predator stomachs and crops (*Chaoborus*: Fedorenko 1975a; Chimney et al. 1981; Lüning-Krizan 1997; Sutor et al. 2001; *Mysis*: Chess and Stanford 1998; Johannsson et al. 2001; Nordin et al. 2008). In my experiments, *Chaoborus* and *Mysis* did not have detectable impacts on zooplankton in the large enclosures. This raises the question as to why I did not detect predator effects similar to published studies. Contributing factors include the pre-adapted zooplankton community of the study lake and the low but realistic predator densities used in this experiment. The potential importance of these factors and their implications are discussed further below.

4.5.1 Predator-prey coexistence

Prey species coexisting with predators are the “least likely to be strongly affected” compared to prey with predators not native to the system (Neill and Peacock 1980). Arnott and Vanni (1993) surmised that when experiments with coexisting predators and prey are conducted, fewer impacts will be determined because susceptible prey will have been driven to extinction prior to the experiment’s initiation. They suggest the use of “naive” prey to demonstrate immediate predation effects (Arnott and Vanni 1993). When added to a lake where zooplankton are not potentially as adapted to its predation, Lake 239, few impacts of *Chaoborus* were determined. However, taxa in Lake 239 are also

abundant in lakes with *Chaoborus* at the ELA and could be considered to be pre-adapted to both predators.

4.5.2 Predator densities

The most probable reason for the small changes in zooplankton abundances observed in this study as compared with previous studies was the comparatively low predator densities used in my experiment.

A number of previous studies have manipulated *Chaoborus* densities in deep enclosures similar to those used in this study. Almost all that found strong effects of *Chaoborus* have used densities far greater than in my experiments (Table 4.2). In addition, many used *C. americanus*, a large, non-migrating species, that is known to be a more voracious predator of crustacean zooplankton than *C. flavicans*, used in my research (MacKay et al. 1990). I am aware of at least three experiments that included treatments with lower numbers of *Chaoborus* (0.09/L – Neill 1981; 0.05 /L – Mackay et al. 1990; 0.05-0.5/L – Sutor et al. 2001). In each case, no significant effects of low *Chaoborus* densities on zooplankton were detected.

Table 4.2: *Chaoborus* densities and enclosure sizes used in enclosure experiments.

Density (#/L)		Diameter	Depth	Reference
Lower range	Upper range	(m)	(m)	
0.600	1.750	1.13	10	González and Tessier 1997
0.050	0.800	1	10	Mackay et al. 1990
0.090	0.170	1.55	9, 14	Neill 1981
0.050	0.500	2	7.5	Sutor et al. 2001
0.020	0.200	1	7	Wissel et al. 2003b
	1.200	1	7	Young and Riessen 2005a
0.017	0.053	1.58	11.6	this study

Despite the higher densities of *Chaoborus* used in many previous enclosure studies, densities of *Chaoborus* used in my large enclosure experiments (200-500 animals/m²) are typical for lakes on the Canadian Shield. For example, Pope et al. (1973) found *Chaoborus* spp. densities from 7/m² to 1200/m² in various lakes (mean number in lakes without fish equal to 634/m² and 86/m² in lakes with fish) in the Matamek River System in Quebec (Table 1 in Pope et al. 1973). In unimpacted Ontario lakes, Yan et al. (1985) found a mean *Chaoborus* abundance of 83/m². In a survey of 47 unimpacted lakes near Dorset, Ontario by Persaud and Yan (2001), 21 had *Chaoborus* densities of 0-50/m², 8 had 50-100/m², and only one had densities greater than 350/m².

Since *Mysis* have not been manipulated previously in large *in situ* enclosures, densities used in this experiment cannot be compared to published studies. Published estimates of *Mysis* abundance in lakes (Table 4.3), however, suggest that the densities used in my large enclosures (50-200/m²) were realistic. In Lake Tahoe, aerial densities ranged from 27/m² in 1978 to 250-300/m² in 1971 (Threlkeld et al. 1980). At a station in Lake Ontario sampled in 1984, densities were 110/m² in September and 860/m² in July (Shea and Makarewicz 1989). My

target density of 100/m² in the enclosures is in the lower range of published *Mysis* densities in lakes but are appropriate for smaller, shallower oligotrophic lakes similar to those at the ELA. Many of the lakes listed in Table 4.3 are extremely deep and volumetric densities of *Mysis* would be far lower than in the large enclosure studies.

Table 4.3: Densities of *Mysis relicta* in Holarctic lakes.

Location	Description, Date	Density		Reference
		(#/m ²)	(#/m ³)	
Bob Lake, ON	oligotrophic, 1982-1983	284		Nero and Sprules 1986b
Char Lake, NU	oligotrophic, 1970		0.97	Lasenby 1971 in Nero 1981
Gull Lake, ON	oligotrophic, 1982-1983	602		Nero and Sprules 1986b
White Partridge Lake, ON	oligotrophic?, 1987	61	2.00	Langland et al. 1991
L161, ELA	oligotrophic, benthic, 1969	4		Hamilton 1971
L224, ELA	oligotrophic, 1981	595		Nero and Schindler 1983
L239, ELA	oligotrophic, 1979-1980	149	15.92	Nero 1981, Nero and Schindler 1983
L239, ELA	oligotrophic, benthic, 1969	18		Hamilton 1971
L305, ELA	oligotrophic, 1980	313	16.30	Nero 1981, Nero and Schindler 1983
L305, ELA	oligotrophic, benthic, 1969	9		Hamilton 1971
L465, ELA	oligotrophic, benthic, 1969	13		Hamilton 1971
Lake Huron	1971	40	1.91	Carpenter et al. 1974
Lake Michigan	1970-1971	14		Reynolds and DeGraeve 1972
Lake Michigan	1974	466		Grossnickle and Morgan 1979
Lake Michigan	1975-1976	188		Morgan and Beeton 1978
Lake Michigan	1986-1989	107		Lehman et al. 1990
Lake Michigan	1998-1999	35		Pothoven et al. 2000
Lake Ontario	1971	53	1.79	Carpenter et al. 1974
Lake Ontario	1984-1987	475		Johannsson 1992
Lake Ontario	1995-1996	267		Gal et al. 2006
Lake Superior	1971	154	2.33	Carpenter et al. 1974
Lake Pend Orielle*, US	oligotrophic, 1978	1980		Rieman and Falter 1981
Lake Pend Orielle*, US	oligotrophic, 1995-1996	500		Chipps and Bennett 2000

Location	Description, Date	Density		Reference
		(#/m ²)	(#/m ³)	
Flathead Lake*, US	oligomesotrophic, 1986	130		Beattie and Clancey 1991
Flathead Lake*, US	oligomesotrophic, 1989	27		Spencer et al. 1991
Lake Tahoe*, US	oligotrophic, 1978	27		Threlkeld et al. 1980
Lake Jonsvatn*, Norway	oligotrophic, 1986-1987		0.67	Næsje et al. 1991
Selbusjøen*, Norway	oligotrophic?, 1981-1984	101		Langeland et al. 1986 in Langeland et al. 1991
Lake Mjøsa, Norway	oligotrophic, 1976-1980	200		Kjellberg et al. 1991
Lake Hiidenvesi, Finland	eutrophic, June-1999	186		Horppila et al. 2003
Pääjärvi, Finland	oligotrophic, 1974		9.08	Hakala 1978
Lake Breiter Luzin, Germany	mesotrophic, 2001-2002	113		Scharf and Koschel 2004
Lough Neagh, Ireland	1999-2000	84		Griffiths 2007
Lough Neagh, Ireland	eutrophying, 2005-2006	39		Griffiths 2007

* denotes introduction of *Mysis*

In a previous study of *Mysis* predation on zooplankton in cubitainers, ten mysids were used in six-hour predation experiments in 20L cubitainers in central Ontario (Nero and Sprules 1986a). The authors mentioned unpublished experiments in which densities of 0.1 to 1.0 mysids/L had no effect on clearance rates of *Mysis* on *Daphnia* (Ramcharan, unpublished, data in Nero and Sprules 1986a). These researchers suggested higher predator densities may be needed to detect prey declines. Prey declines were detected in my experiment but cubitainers were left *in situ* twelve times longer. Clearance rates estimated from small enclosures (D. Seckar, unpublished data) following Vanderploeg et al. (Vanderploeg et al. 1982) are similar but lower than those reported by Nero and Sprules (1986a) and Vanderploeg et al. (1982). Clearance rates can be variable in different lakes, when conducted on different dates, and when different ages of

mysids are used, suggesting outcomes of this type of predation experiment are variable (Nero and Sprules 1986a).

While the low impact of predators in this experiment compared to other studies can probably be explained by the low predator densities, densities used in this experiment were appropriate for the ecozone and for the area and volume of the enclosures. I suggest that the impacts of *Chaoborus* and *Mysis* in oligotrophic Canadian Shield lakes may frequently be overstated.

4.6 Interactive effects among predators

Generally, few statistically significant interaction effects occurred in my experiments and prey risk reduction or enhancement was not detected. This outcome is rare in published studies on multiple predators (reviewed in Sih et al. 1998). For example, Cardinale et al. (2006) found that one predator of aphids interfered with the other predators so that fewer aphids were consumed when predators occurred together. Soluk (1993) found that predaceous stoneflies changed their behaviours in the presence of sculpins and did not consume as many mayfly larvae (*Baetis tricaudatus* Dodds). When two crab species foraged together on mussels, fewer mussels were consumed than when the predators foraged alone (Griffen 2006). In these studies, interactive effects occurred when multiple predators were present, effects varied with prey density (Griffen 2006) and prey type (Soluk 1993).

The small enclosure experiment encouraged interactions between *Chaoborus* and *Mysis* and between predators and prey because animals were

confined in a small volume. Lower *Chaoborus* abundances in small enclosures with *Mysis* may be due to intraguild predation by *Mysis*.

In my study, strong effects of predators when alone were rarely detected and this influenced my ability to detect interaction effects. My results suggest that impacts of multiple predators at low densities may be effectively predicted from estimates derived from predators in isolation. Under higher predator pressure in small enclosures, declines with *Chaoborus* were not detected, while declines with *Mysis* were occasional. As well, final prey abundances in the high-both predators treatment was similar to the high *Mysis* treatment, indicating that prey declines could mainly be attributed to *Mysis*.

4.7 Challenges

Challenges and limitations of the study include the use of mesocosms, the temporal scale, and the enumeration of only crustacean zooplankton.

Many researchers have pointed out the shortcomings of using enclosures or mesocosms (e.g. Carpenter 1996; Schindler 1998a). To summarize, enclosures in aquatic systems can alter physical states (filter light wavelengths), change physical processes (prevent mixing, decrease air-water gas exchange rates), have an increased ratio of surface to water (providing more sites colonisable by periphyton), and are useful for only one season (Schindler 1998a). Over the medium term (a month), enclosures diverge from the lake; external nutrient sources are prevented and immigration and recruitment from resting eggs are prevented (Lampert et al. 1986).

While these criticisms can be applied to many aquatic enclosure studies, including mine, this study would be extremely difficult if undertaken with whole-lakes. Returning the lake to its previous community would prove very challenging (Martinez and Bergersen 1989). Additionally, finding lakes with similar conditions to apply treatments is very difficult. Wilhelm et al. (2000) include advantages of “speed, replication, statistical power, affordability, and insights into mechanistic processes” (p1720) associated with the use of mesocosms. The enclosures used in this experiment were a good compromise: they were located in the same system with comparable water chemistry, phytoplankton and zooplankton communities; reached into the hypolimnion and allowed predator survival and migration; and experienced similar climatic conditions so that the comparison of impacts on the zooplankton community could be examined without other confounding factors such as lake size, depth, residence time, and fish predators.

The temporal scale used in the experiment is an important limitation. The five week study period does not encompass the complete life cycle of the predators: a year for *Chaoborus* and two or three years for *Mysis*. Because only larger individuals were placed in the enclosures, intraguild feeding may have been reduced. Fischer and Moore (1993) found that the cyclopoid *Mesocyclops edax* fed on instar I *Chaoborus* in the laboratory (instar I larvae moulted in 3 to 5 days thus reducing their exposure to the cyclopoid predator). It is quite likely that the larger *Mysis* could consume early instar *Chaoborus* at the ELA. In support of this, Nordin et al. (2008) found remains of *Chaoborus* in the stomachs of *Mysis* from central Ontario lakes. The reverse may also be true but *Mysis* are retained

in the egg sac and are released at a larger size that may help them avoid predation by *Chaoborus*. The seasonality of predator-prey and predator-predator interactions that change throughout the year were not examined. *Mysis* impacts on zooplankton are greatest in spring and fall when lakes are not thermally stratified (Rieman and Falter 1981; Bowles et al. 1991).

I saw little response of crustacean zooplankton or phytoplankton to predators was seen but the complete zooplankton community was not enumerated. Both invertebrate predators could have been preying on alternate food sources, such as rotifers, protozoa, and phytoplankton that were available in the enclosures. Rotifers are consumed by *Chaoborus* (Kajak and Rybak 1979; Neill 1985; Moore 1988; Havens 1990) and *Mysis* (Lasenby and Langford 1973; Cooper and Goldman 1980; Nero and Sprules 1986a). As well, more of the diet of *Mysis* is composed of phytoplankton when zooplankton prey densities are low (<20/L) (Grossnickle 2001). While both predators may consume rotifers and phytoplankton, these food options were not examined in the present study. Rotifers could be counted and gut and crop content analysis could be conducted in future studies to further evaluate this aspect of omnivorous feeding.

5 Conclusion

The impact of invertebrate predators, *Mysis relicta* and *Chaoborus* spp., on pelagic crustacean zooplankton was examined using deep enclosures at the Experimental Lakes Area. Notably, in the first medium duration enclosure experiment with *Mysis relicta*, I found these organisms were able to survive in deep enclosures. A natural multi-species prey assemblage was used and abundances of predators and prey reflected those found in the region. Deep enclosures allowed vertical migration of predators and prey.

Impacts on the natural zooplankton assemblage in the large enclosures were weak. In 2004, *Daphnia* abundances were higher in the no predators treatment on two dates. In 2005, *Mysis* impacts were detected on *Bosmina* abundance in the first half of the experiment. *Chaoborus* impacts were rarely detected. Species lengths were generally unaffected by predators. Biomass of cyclopoids and cladocerans tended to be lower in the both predators treatment compared to the no predators treatment but significant differences of group biomasses were rarely detected. Vertical migrations of zooplankton were variable in enclosures of the same treatment between years. Prey distributions overlapped with predators at night. With low predator densities used in the experiment, impacts due to both predators together were rarely detected.

In small enclosures, *Mysis* density was not affected over the three day experiment, while the abundance of *Chaoborus* larvae was lower than introduced in all enclosures. Prey abundances in enclosures with predators were lower than enclosures with no predators. *Bosmina* abundances were significantly lower in

treatments with low *Mysis* abundances and *Daphnia*, *Chydorus*, *Diacyclops*, nauplii and cyclopoid copepodid abundances were reduced in high *Mysis* treatments. *Chydorus* and calanoid copepodid abundances were significantly reduced with low *Chaoborus* density while high *Chaoborus* densities did not cause significant prey declines. Impacts in small enclosures could mainly be attributed to *Mysis*.

At low predator densities, impacts of predators alone could be used to predict zooplankton abundances when predators are together. Predator impacts in small enclosures were more readily detected than impacts in large enclosures due to higher densities of predators and smaller volumes of enclosures.

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Table 2-a: Number of replicates in treatments on each date in 2004 in large enclosures.

Date	no predators	<i>Chaoborus</i> -only	<i>Mysis</i> -only	both predators
31-Jul-04	3	2	3	3
9-Aug-04	3	2	3	3
16-Aug-04	3	1	3	3
23-Aug-04	3	1	3	3
30-Aug-04	3	1	3	3

Table 2-b: Number of replicates in treatments on each date in 2005 in large enclosures.

Date	no predators	<i>Chaoborus</i> -only	<i>Mysis</i> -only	both predators
20-Jul-05	3	4	3	3
26-Jul-05	2	4	3	3
3-Aug-05	3	4	3	3
10-Aug-05	3	4	3	2
17-Aug-05	3	4	3	2
24-Aug-05	3	4	3	2

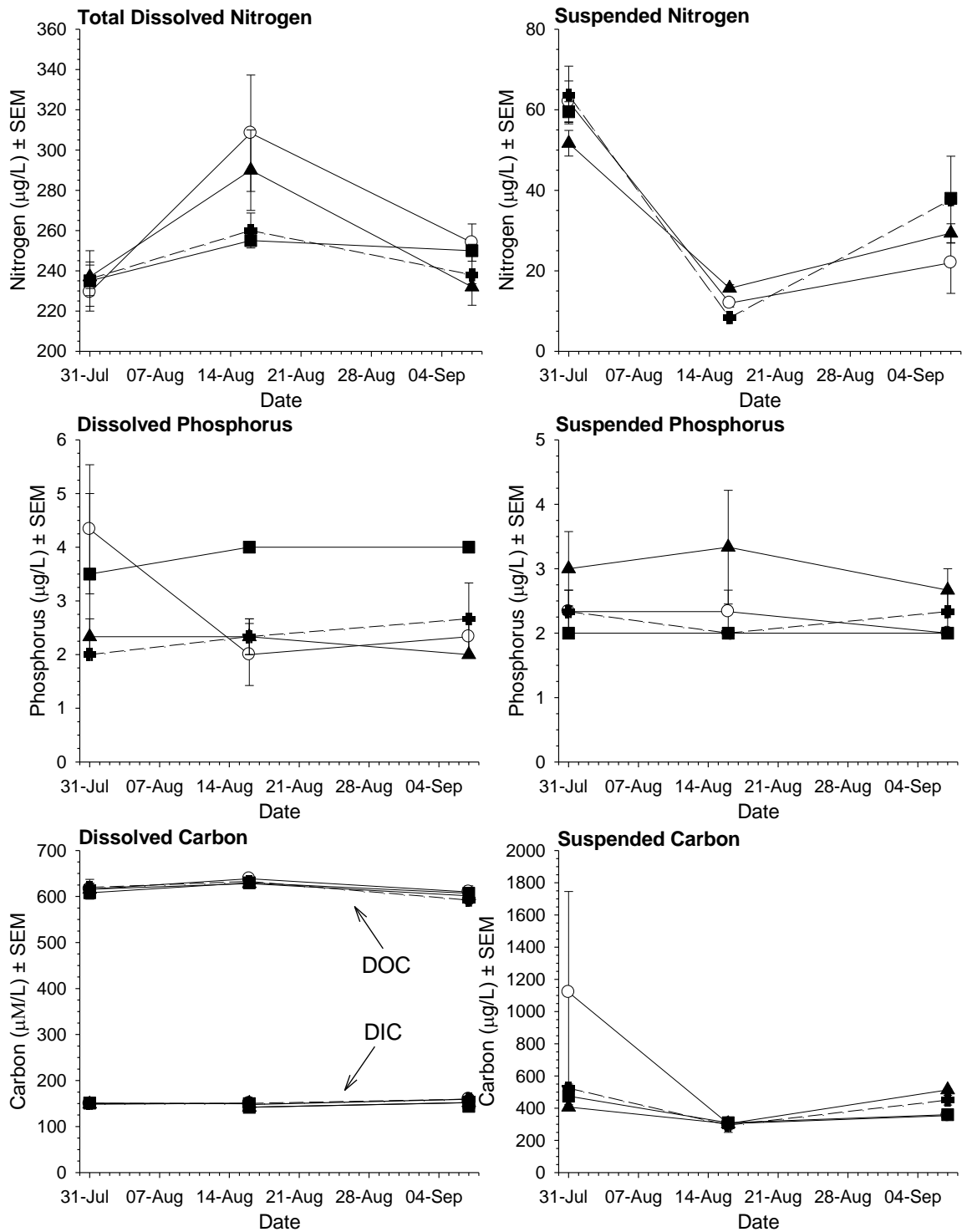


Figure 3-a: 2004 Nutrients measured over time in treatments in large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

Table 3-a: 2004 P-values from results of 2-way and 1-way ANOVAs on chemistry variables measured in large enclosures for *Chaoborus* (*Chaob*), *Mysis*, and interaction effects (C×M). Data are untransformed. ^a – Levene’s variance testing not done, ^e – Levene’s variance test significant (P<0.05). Where no values are shown, no test was conducted or test was omitted due to low numbers of replicates. Starting on 16-August-2004, only one replicate was left in the *Chaoborus*-only treatment and results from a one-way ANOVA comparing remaining treatments are shown (1-way). Significance highlighted in BOLD of nutrients (N, P, C) for P<0.014 and of chlorophyll for P<0.025.

Date	Chemistry Variable	<i>Chaob</i>	<i>Mysis</i>	C×M	1-way
31-Jul-04	Suspended Nitrogen (µg/L)	0.406	0.584	0.220	
	Total Dissolved Nitrogen	0.793	0.628	0.708	
	Suspended Phosphorus	0.275	0.275	0.705 ^a	
	Total Dissolved Phosphorus	0.520	0.082	0.780 ^a	
	Dissolved Inorganic Carbon	0.501	0.820	0.939	
	Dissolved Organic Carbon	0.894	0.721	0.721	
	Suspended Carbon (µg/L)	0.126	0.490	0.046	
	Chlorophyll <i>a</i> (infl)	0.457	0.130	0.109	
	Chlorophyll <i>a</i> <30µm (infl)				
	Chlorophyll <i>a</i> (HPLC)	0.165	0.135	0.060	
	Chlorophyll <i>a</i> <30µm (HPLC)				
9-Aug-04	Chlorophyll <i>a</i> (infl)	0.150	0.106	0.052 ^e	
	Chlorophyll <i>a</i> <30µm (infl)	0.374	0.209	0.059	
	Chlorophyll <i>a</i> (HPLC)	0.215	0.273	0.198	
	Chlorophyll <i>a</i> <30µm (HPLC)				0.726 ^a
16-Aug-04	Suspended Nitrogen (µg/L)				0.004
	Total Dissolved Nitrogen				0.325
	Suspended Phosphorus				0.273 ^a
	Total Dissolved Phosphorus				0.824
	Dissolved Inorganic Carbon				0.915
	Dissolved Organic Carbon				0.339
	Suspended Carbon (µg/L)				0.976
	Chlorophyll <i>a</i> (infl)				0.572
	Chlorophyll <i>a</i> <30µm (infl)				0.500
	Chlorophyll <i>a</i> (HPLC)				0.572
Chlorophyll <i>a</i> <30µm (HPLC)				0.596	
23-Aug-04	Chlorophyll <i>a</i> (infl)				0.134
	Chlorophyll <i>a</i> <30µm (infl)				0.134
	Chlorophyll <i>a</i> (HPLC)				0.087
	Chlorophyll <i>a</i> <30µm (HPLC)				0.064
30-Aug-04	Chlorophyll <i>a</i> (infl)				0.006
	Chlorophyll <i>a</i> <30µm (infl)				0.806
	Chlorophyll <i>a</i> (HPLC)				0.008
	Chlorophyll <i>a</i> <30µm (HPLC)				0.745
7-Sep-04	Suspended Nitrogen (µg/L)				0.415
	Total Dissolved Nitrogen				0.359
	Suspended Phosphorus				0.296 ^a
	Total Dissolved Phosphorus				0.579 ^a
	Dissolved Inorganic Carbon				0.691
	Dissolved Organic Carbon				0.572
	Suspended Carbon (µg/L)				0.002
	Chlorophyll <i>a</i> (infl)				0.003
	Chlorophyll <i>a</i> <30µm (infl)				0.006
	Chlorophyll <i>a</i> (HPLC)				
Chlorophyll <i>a</i> <30µm (HPLC)				0.006	

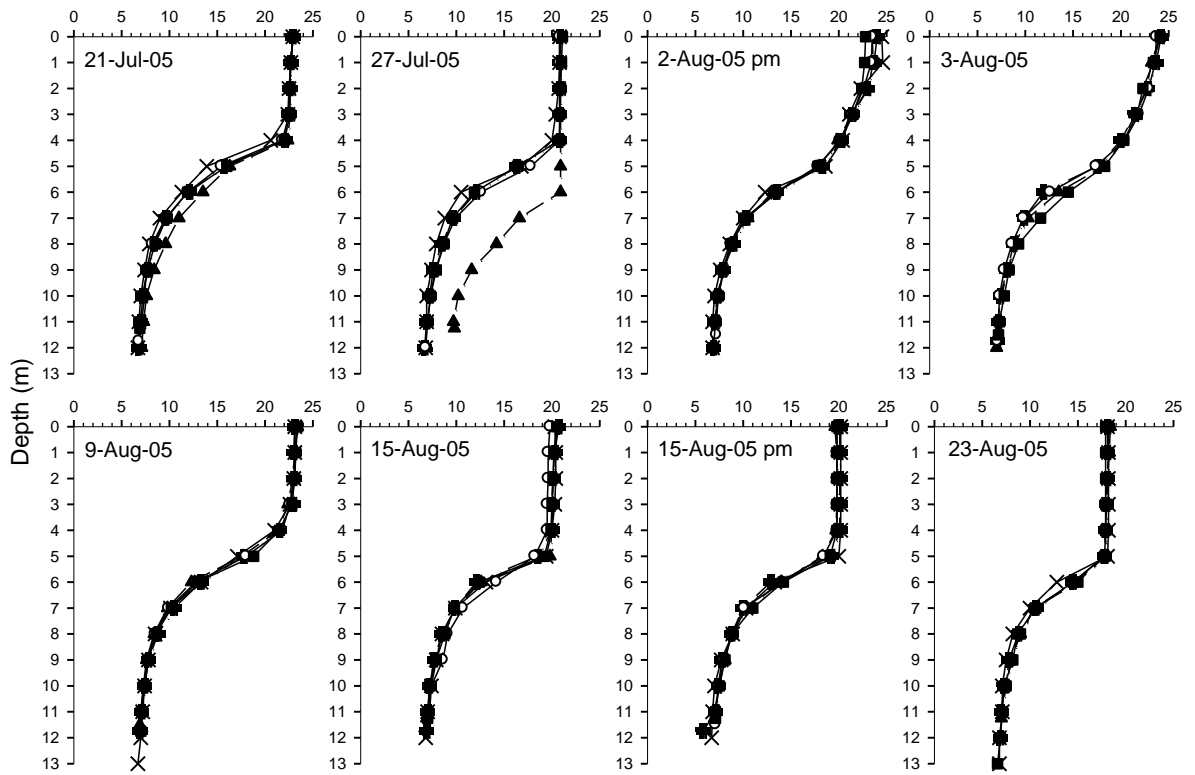


Figure 3-b: Temperature ($^{\circ}\text{C}$) profiles over time (2005) in large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross – both predators; X – lake. Only one replicate measured per date.

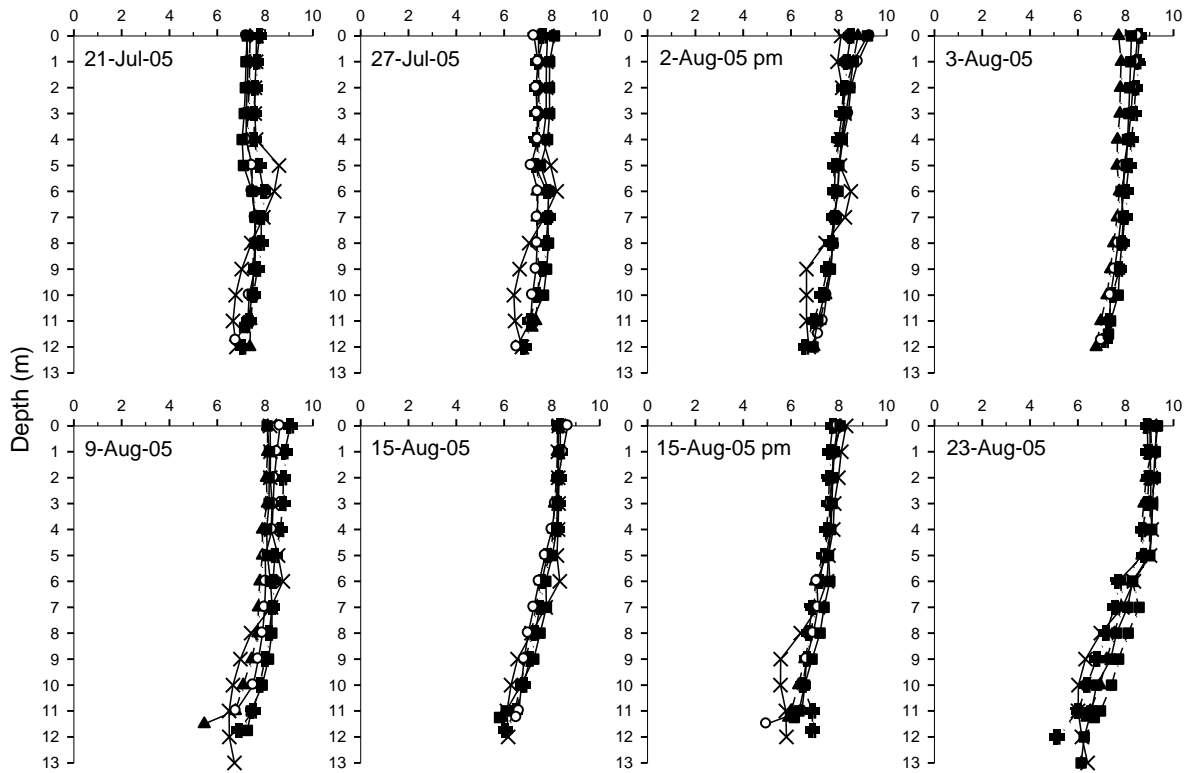


Figure 3-c: Oxygen (mg/L) profiles over time (2005) in large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross – both predators; X – lake. Only one replicate measured per date.

Table 3-b: 2005 P-values from results of 2-way ANOVAs on chemistry variables measured in large enclosures for *Chaoborus* (*Chaob*), *Mysis*, and interaction effects (C×M). Data are untransformed. ^a – Levene's variance testing not done. Significance highlighted in BOLD of nutrients (N, P, C) for P<0.014 and of chlorophyll for P<0.025.

Date	Chemistry Variable	<i>Chaob</i>	<i>Mysis</i>	C×M
20-Jul-05	Suspended Nitrogen (µg/L)	0.283	0.441	0.134
	Total Dissolved Nitrogen	0.924	0.652	0.776
	Suspended Phosphorus	0.158	0.921	0.921
	Total Dissolved Phosphorus	0.645	0.555	0.276
	Dissolved Inorganic Carbon	0.226	0.464	0.927
	Dissolved Organic Carbon	0.077	0.135	0.100
	Suspended Carbon (µg/L)	0.783	0.621	0.093
	Chlorophyll <i>a</i> (infl)	0.839	0.505	0.317
	Chlorophyll <i>a</i> <30µm (infl)	0.959	0.563	0.238
	Chlorophyll <i>a</i> (HPLC)	0.897	0.807	0.930
	Chlorophyll <i>a</i> <30µm (HPLC)	0.452	0.479	0.908
26-Jul-05	Chlorophyll <i>a</i> (infl)	0.861	0.211	0.273
	Chlorophyll <i>a</i> <30µm (infl)	0.973	0.232	0.316
	Chlorophyll <i>a</i> (HPLC)	0.269	0.898	0.551
	Chlorophyll <i>a</i> <30µm (HPLC)	0.267	0.767	0.869
3-Aug-05	Suspended Nitrogen (µg/L)	0.481	0.577	0.141
	Total Dissolved Nitrogen	0.194	0.728	0.447
	Suspended Phosphorus	0.543	1.000	0.543
	Total Dissolved Phosphorus	0.262	0.318	0.140
	Dissolved Inorganic Carbon	0.336	0.511	0.871
	Dissolved Organic Carbon	0.869	0.972	0.195
	Suspended Carbon (µg/L)	0.977	0.512	0.165
	Chlorophyll <i>a</i> (infl)	0.778	0.365	0.177
	Chlorophyll <i>a</i> <30µm (infl)	0.786	0.438	0.163
	Chlorophyll <i>a</i> (HPLC)	0.771	0.991	0.817
Chlorophyll <i>a</i> <30µm (HPLC)	0.748	0.904	0.936	
10-Aug-05	Chlorophyll <i>a</i> (infl)	0.898	0.241	0.805
	Chlorophyll <i>a</i> <30µm (infl)	0.994	0.230	0.849
	Chlorophyll <i>a</i> (HPLC)	0.883	0.285	0.991
	Chlorophyll <i>a</i> <30µm (HPLC)	0.874	0.310	0.962
17-Aug-05	Suspended Nitrogen (µg/L)	0.812	0.559	0.698
	Total Dissolved Nitrogen	0.227	0.765	0.289
	Suspended Phosphorus	0.512	0.404	0.404 ^a
	Total Dissolved Phosphorus	0.414	0.721	0.721
	Dissolved Inorganic Carbon	0.433	0.605	0.605
	Dissolved Organic Carbon	0.750	0.183	0.130
	Suspended Carbon (µg/L)	0.708	0.334	0.935
	Chlorophyll <i>a</i> (infl)	0.149	0.127	0.336
	Chlorophyll <i>a</i> <30µm (infl)	0.427	0.306	0.982
	Chlorophyll <i>a</i> (HPLC)	0.502	0.283	0.828
	Chlorophyll <i>a</i> <30µm (HPLC)	0.404	0.303	0.824
24-Aug-05	Chlorophyll <i>a</i> (infl)	0.734	0.029	0.537
	Chlorophyll <i>a</i> <30µm (infl)	0.665	0.094	0.734
	Chlorophyll <i>a</i> (HPLC)	0.496	0.284	0.924
	Chlorophyll <i>a</i> <30µm (HPLC)	0.708	0.514	0.748

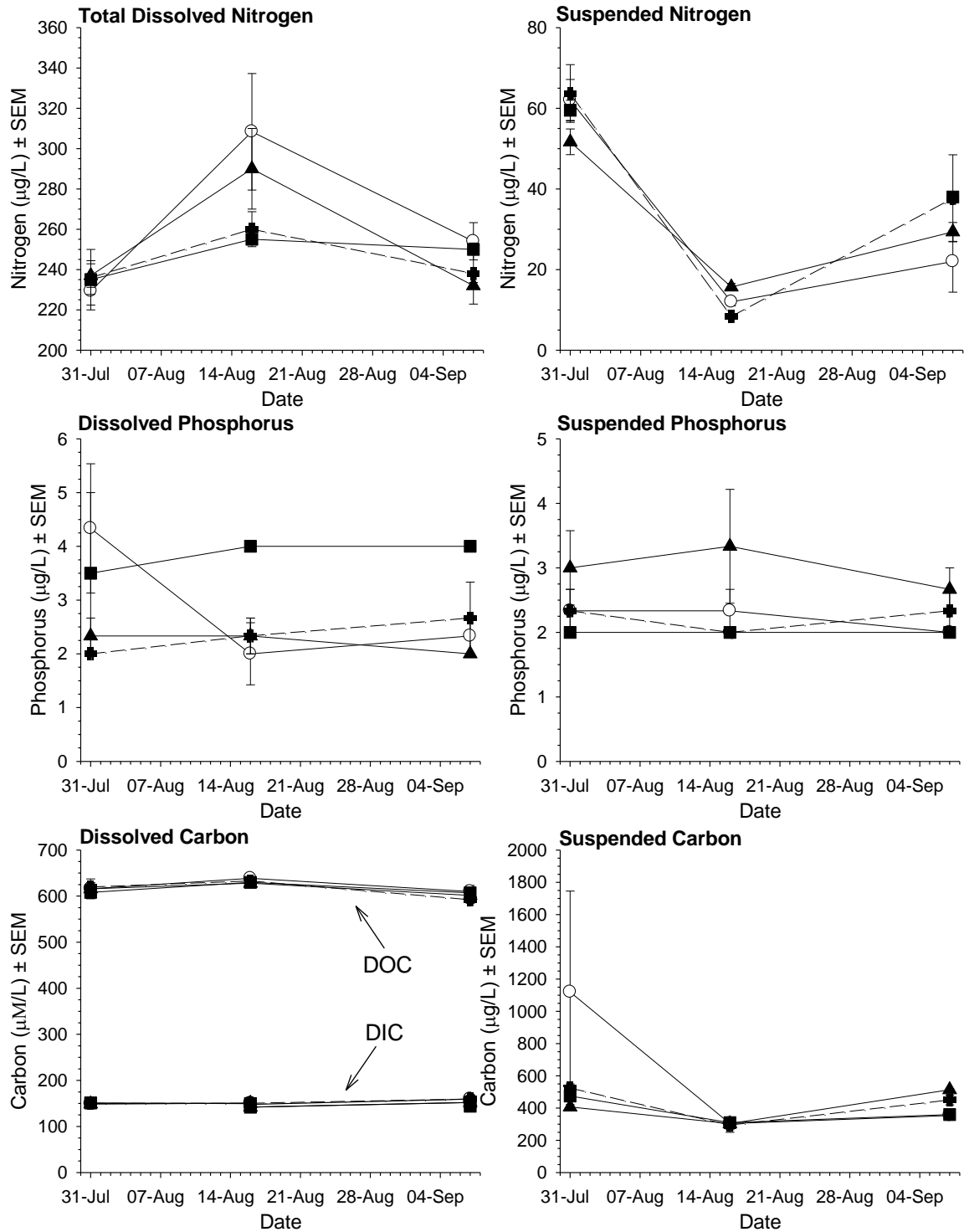


Figure 3-d: 2005 Nutrients measured over time in treatments in large enclosures: open circle – no predators; filled square – *Chaoborus*-only; filled triangle – *Mysis*-only; filled cross, dashed line – both predators.

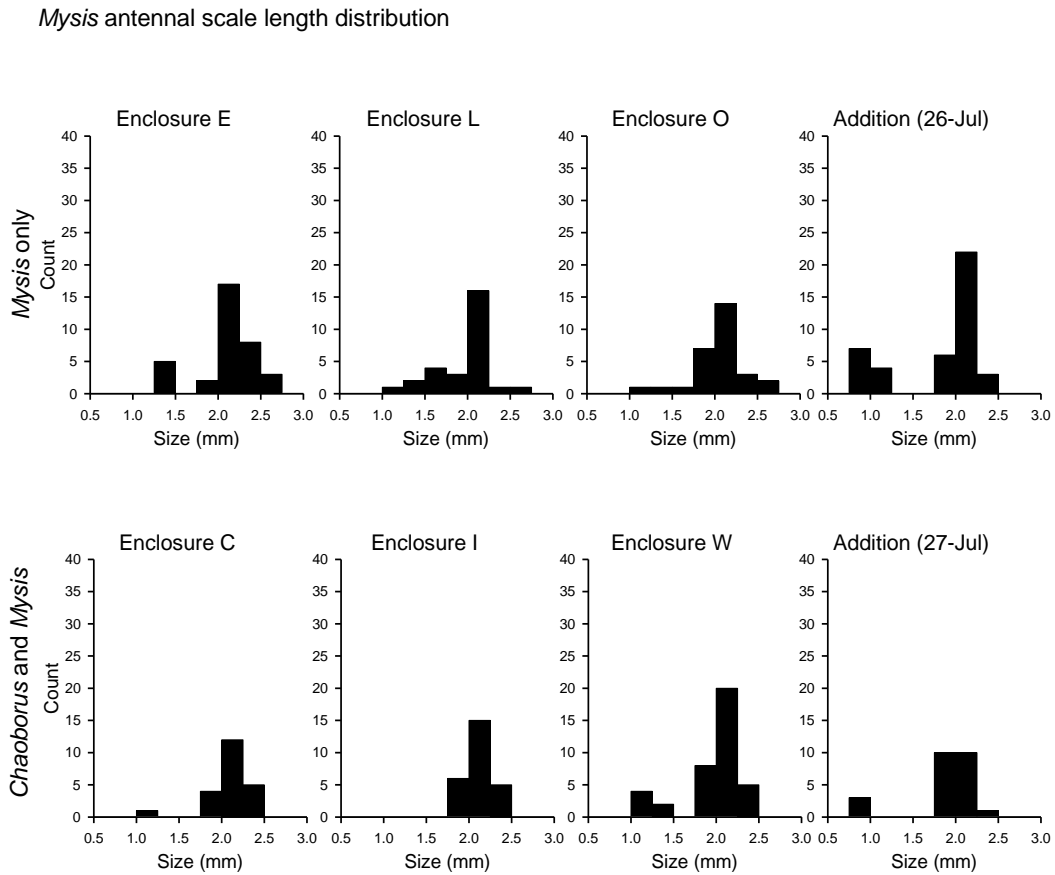
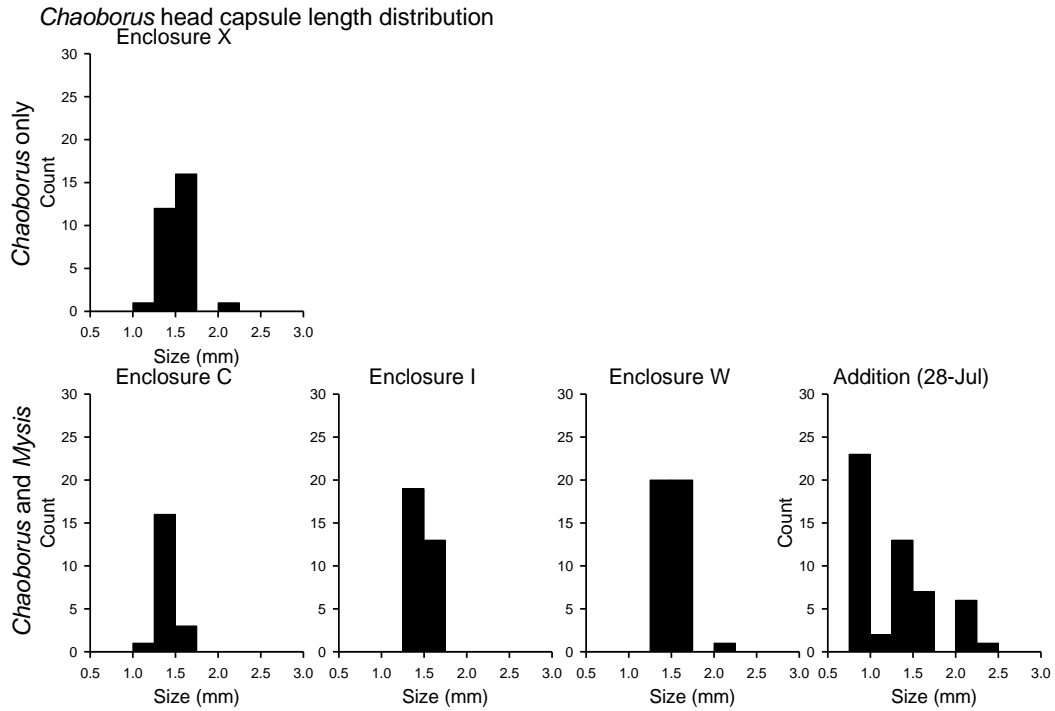


Figure 3-e: 2004 Predator body part size (mm) histograms based on raw measurements in large enclosures. Histograms are organized by treatment (shown on left).

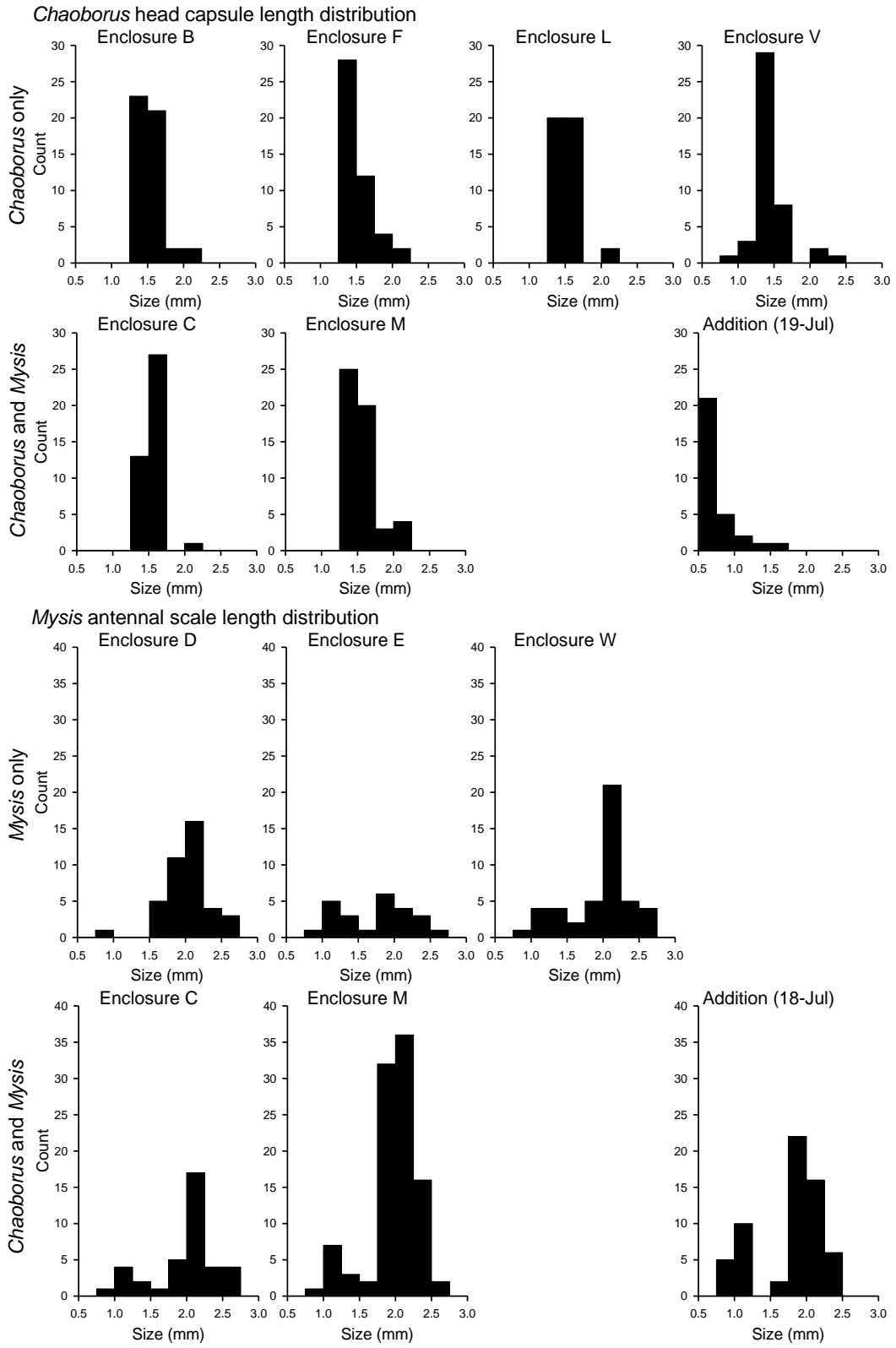


Figure 3-f: 2005 Predator body part size (mm) histograms based on raw measurements in large enclosures. Histograms are organized by treatment (shown on left).

Table 3-c: 2005 Rate of change of *Bosmina* in large enclosures for *Chaoborus* (*Chaob*), *Mysis*, and interaction effects (C×M). P-values of ANOVAs on rate of change ($r = \ln(n_t/n_{Jul20})/\Delta t$). Number of replicates in test given in last column.

Date	Rate of Change			n of test
	<i>Chaob</i>	<i>Mysis</i>	C×M	
26-Jul-05	0.118	<0.001	0.157	12
3-Aug-05	0.002	<0.001	0.005	13
10-Aug-05	0.073	0.702	0.528	9
17-Aug-05	0.460	0.862	0.557	10
24-Aug-05	0.065	0.061	0.909	10

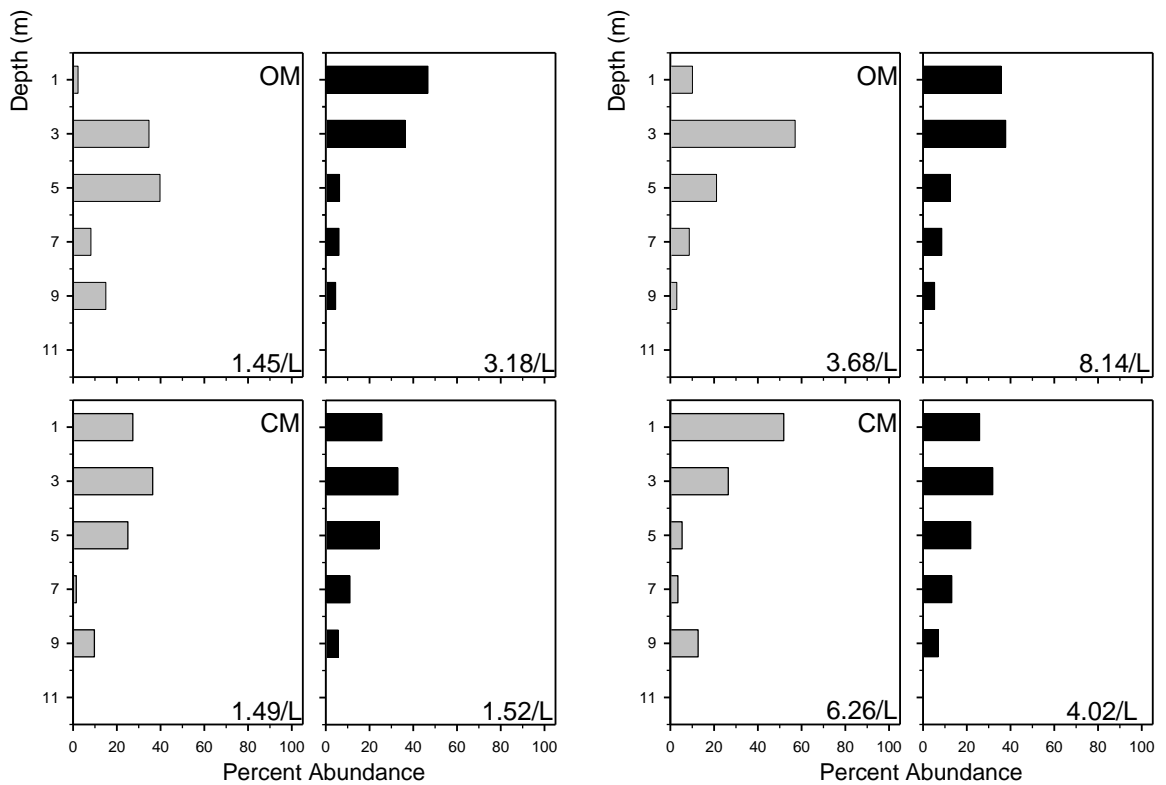
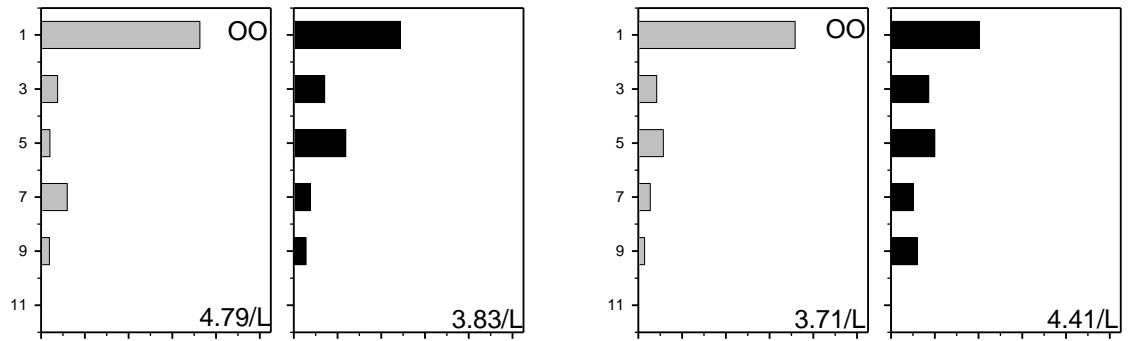


Figure 3-g: 2004 vertical distributions in large enclosures of *Bosmina longirostris* (left) and *Chydorus cf. sphaericus* (right) in no predators (OO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each species in each enclosure in lower right corner.

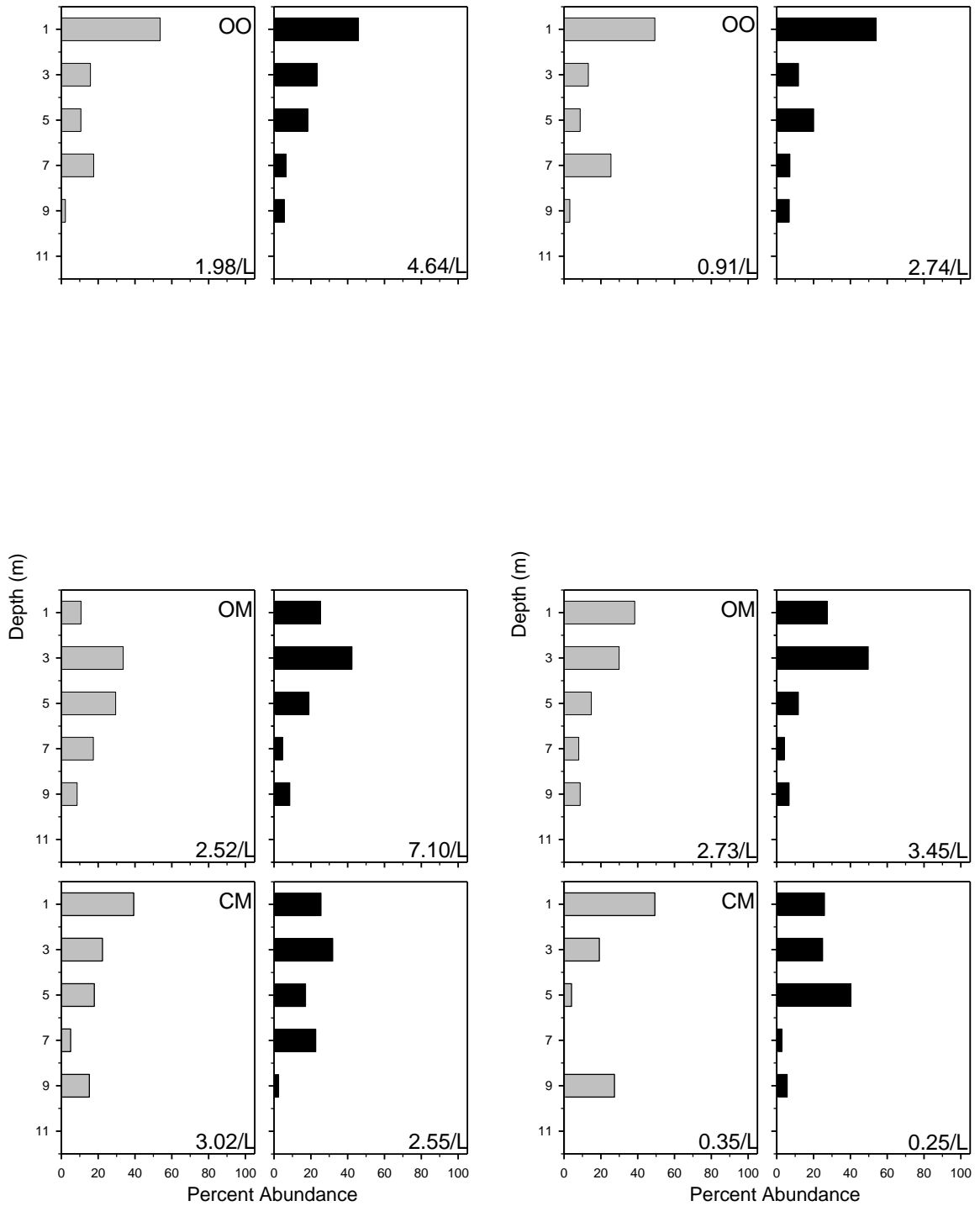


Figure 3-h: 2004 vertical distributions in large enclosures of *Diaphanosoma birgei* (left) and *Daphnia* spp. (right) in no predators (OO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each species in each enclosure in lower right corner.

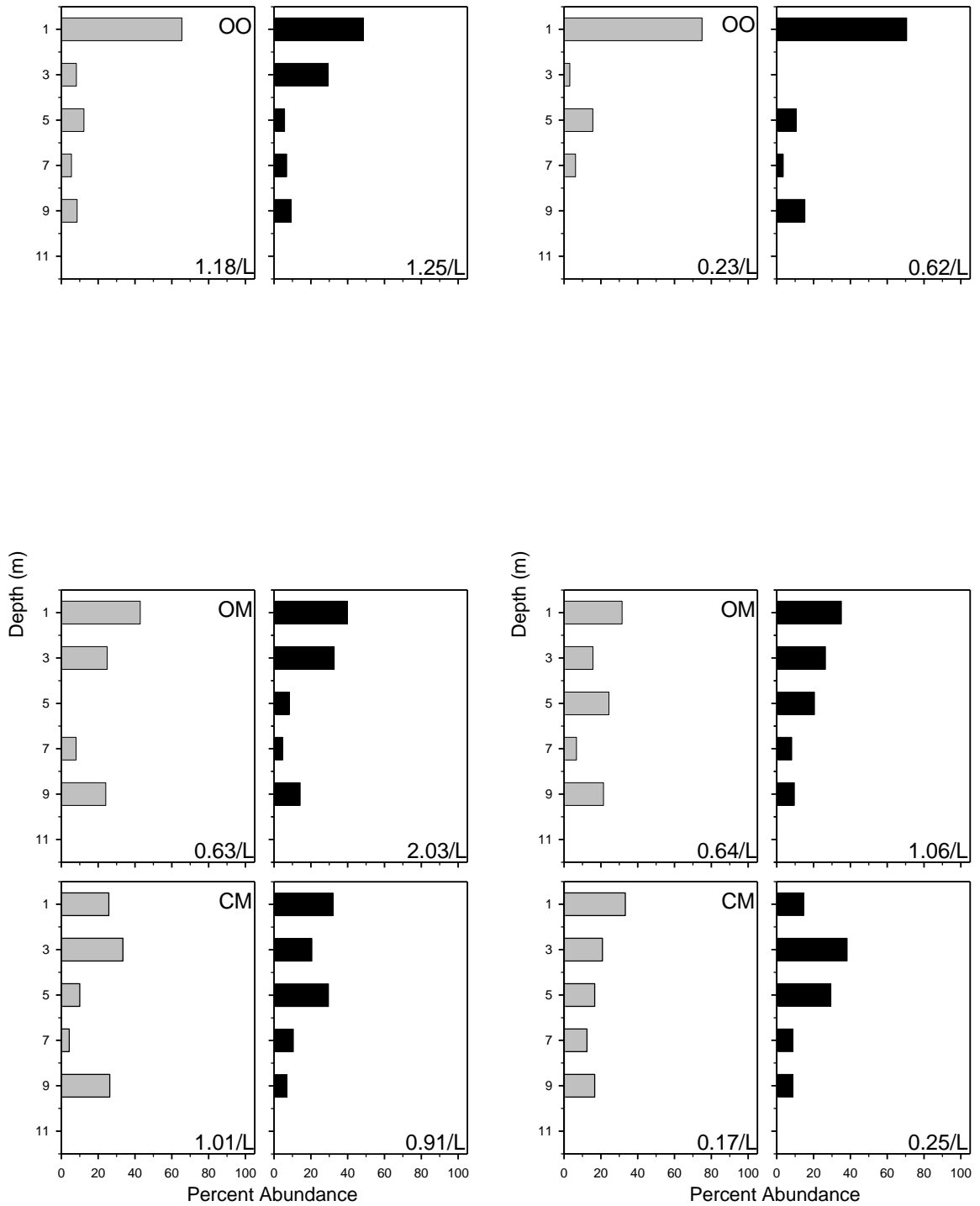


Figure 3-i: 2004 vertical distributions in large enclosures of calanoid copepodids (left) and *Leptodiaptomus minutus* (right) in no predators (OO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each taxon in each enclosure in lower right corner.

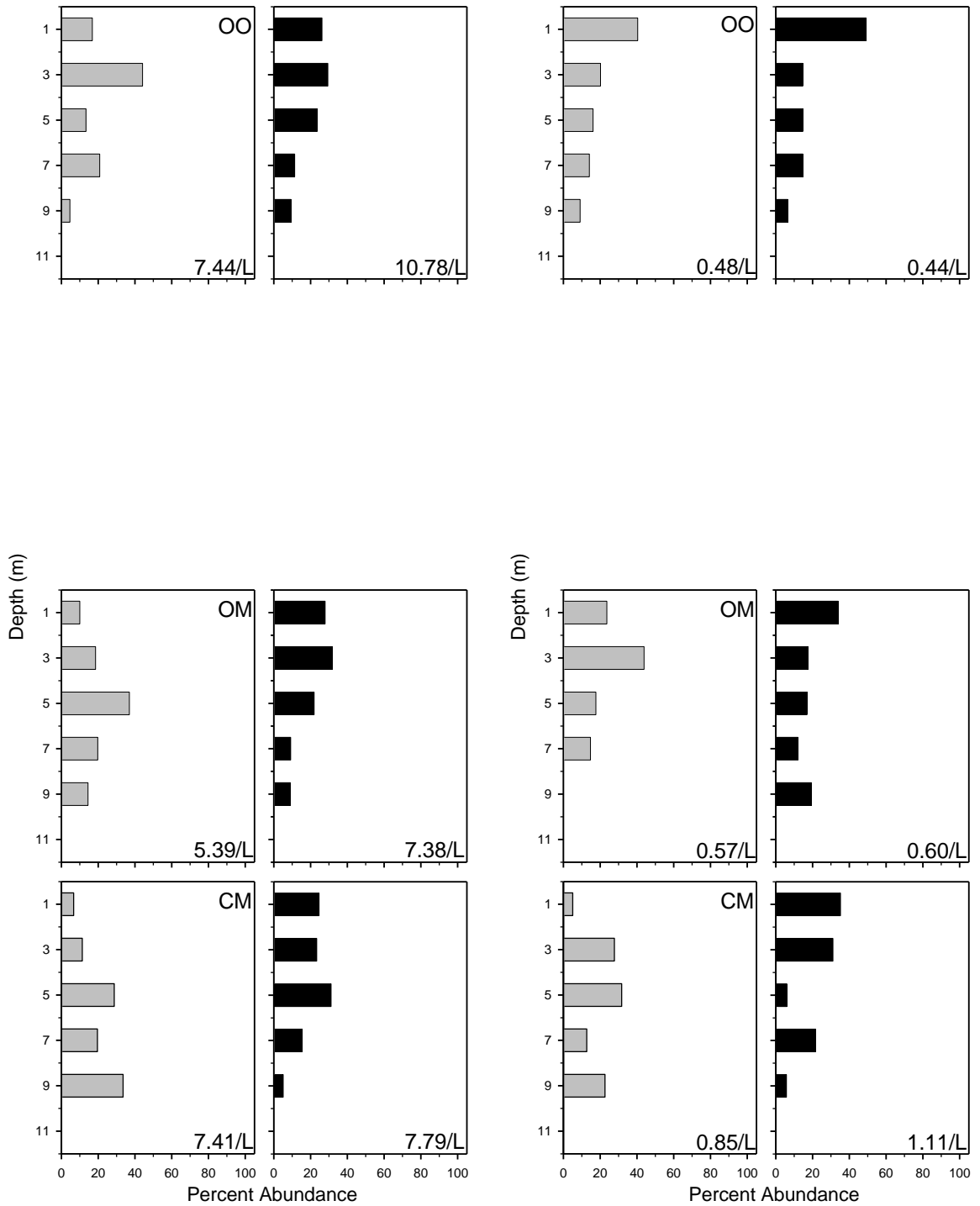


Figure 3-j: 2004 vertical distributions in large enclosures of nauplii (left) and cyclopoid copepodids (right) in no predators (OO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each taxon in each enclosure in lower right corner.

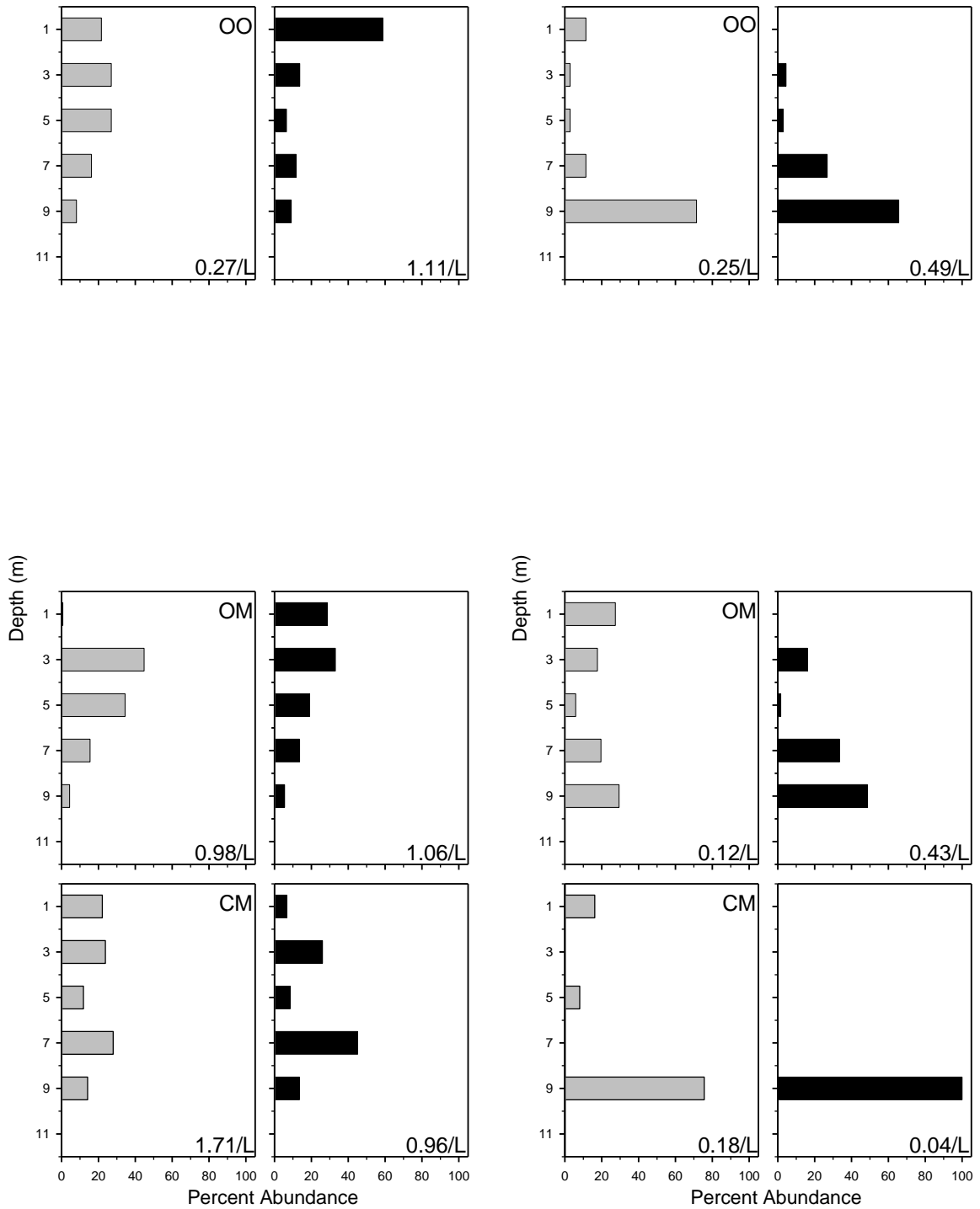


Figure 3-k: 2004 vertical distributions in large enclosures of *Tropocyclops extensus* (left) and *Diacyclops thomasi* (right) in no predators (OO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each species in each enclosure in lower right corner.

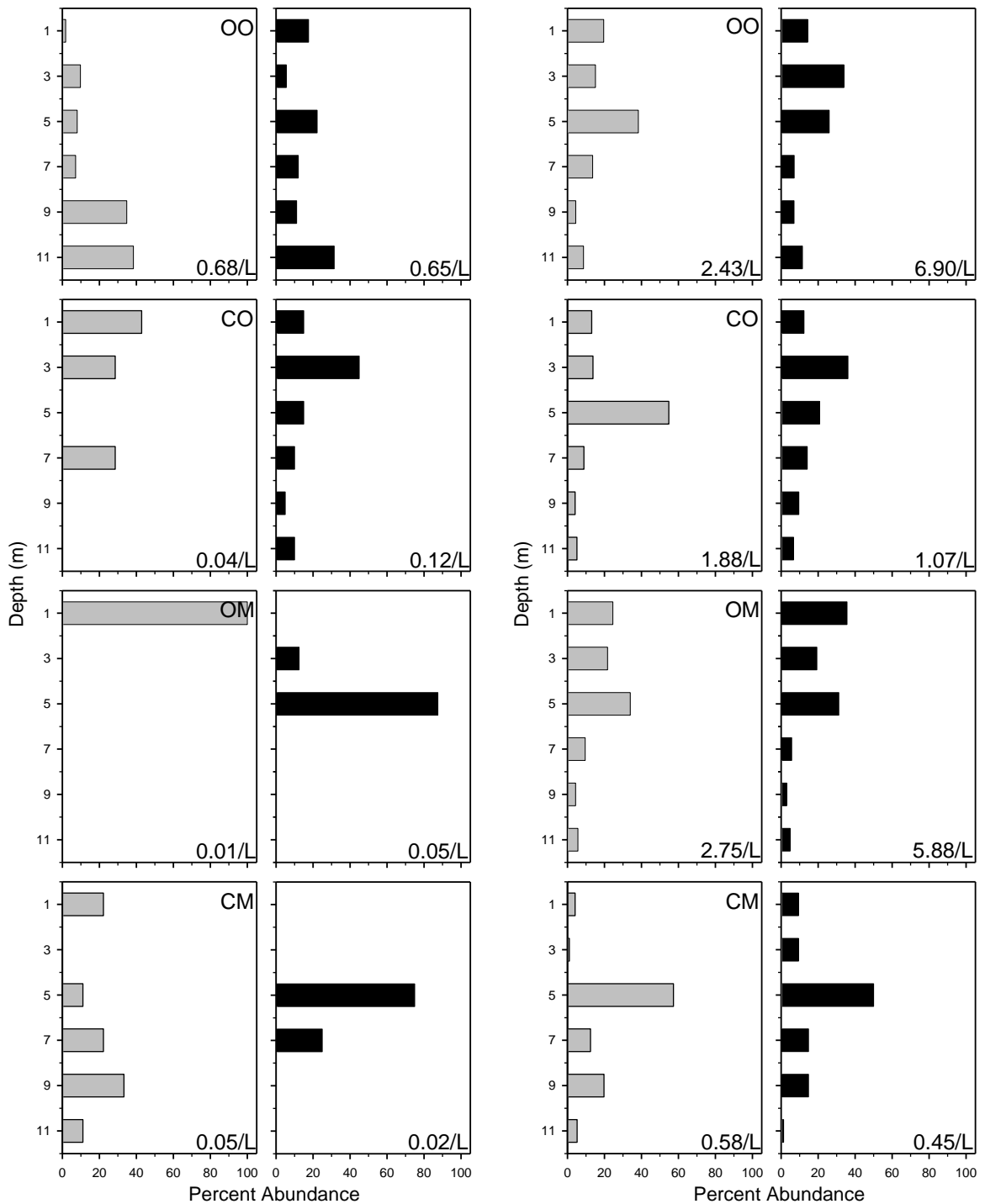


Figure 3-I: 2005 vertical distributions in large enclosures of *Bosmina longirostris* (left) and *Chydorus cf. sphaericus* (right) in no predators (OO), *Chaoborus*-only (CO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each species in each enclosure in lower right corner.

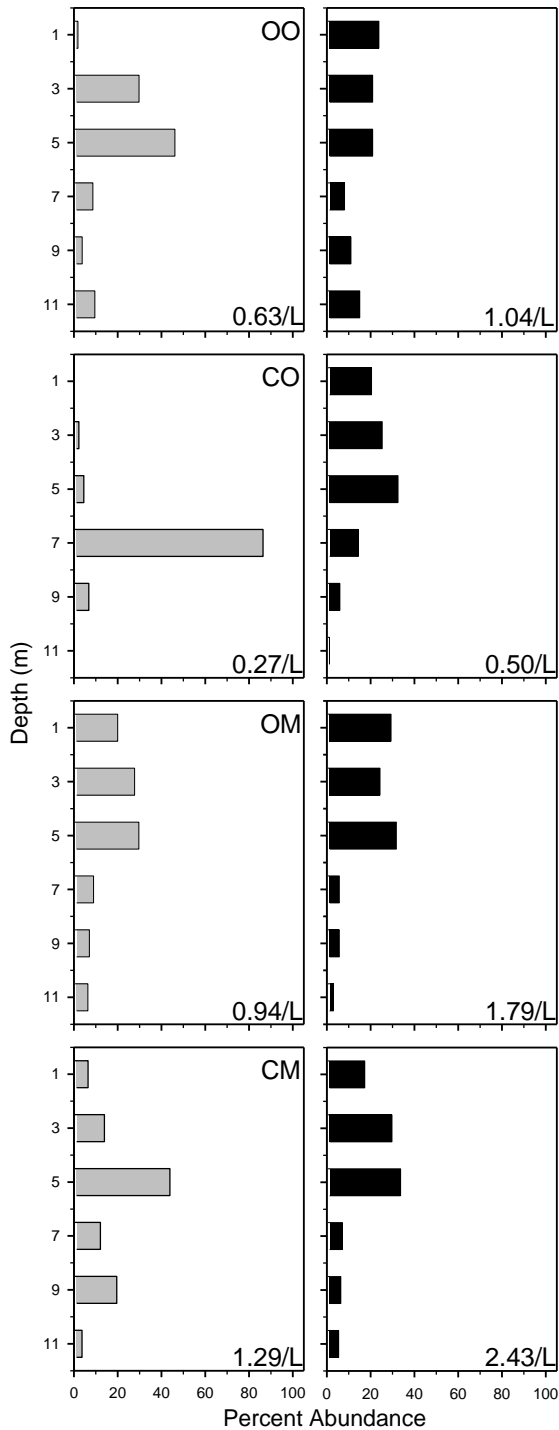


Figure 3-m: 2005 vertical distributions in large enclosures of *Diaphanosoma birgei* in no predators (OO), *Chaoborus*-only (CO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of species in each enclosure in lower right corner. *Daphnia* omitted due to low abundance in all enclosures.

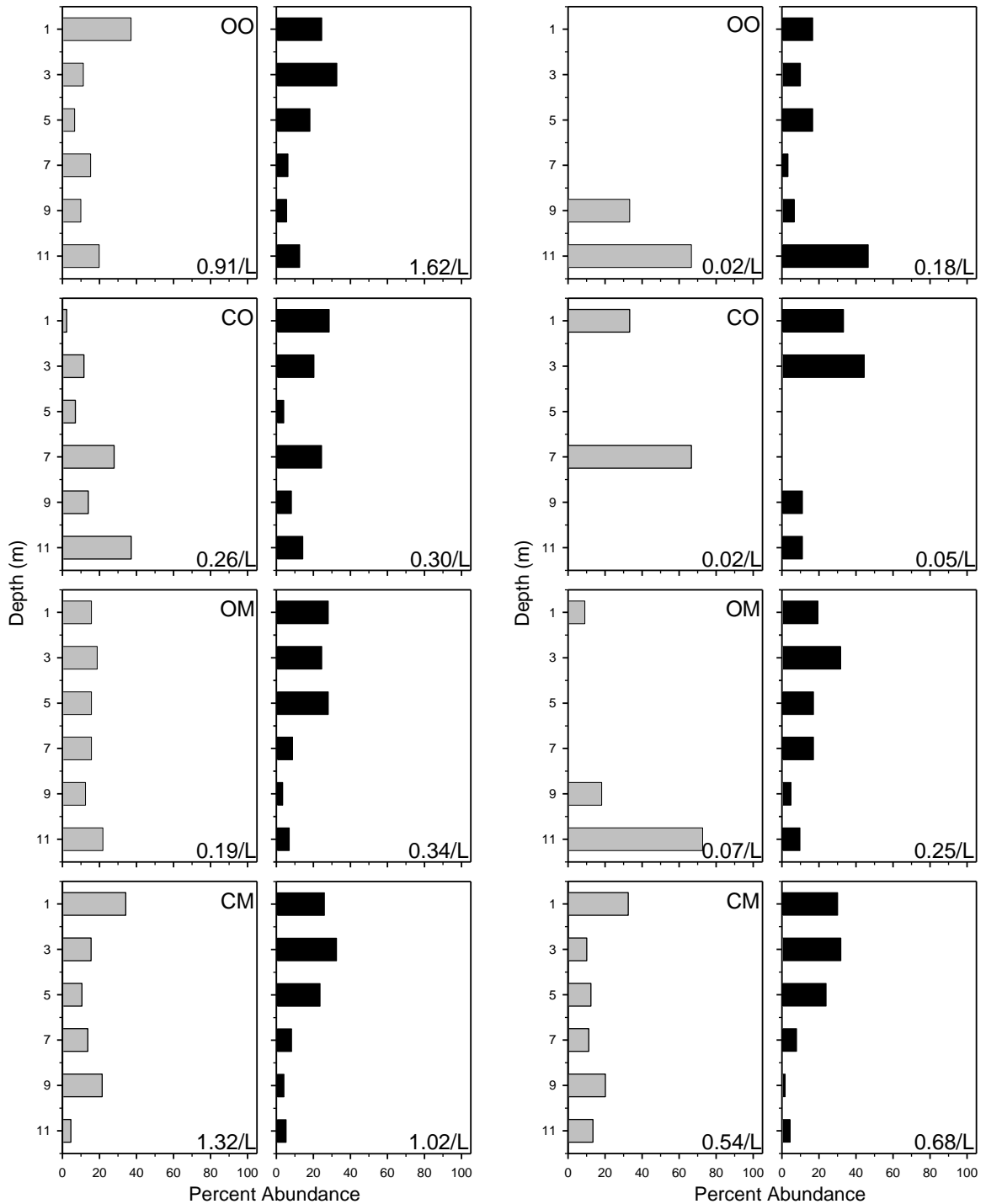


Figure 3-n: 2005 vertical distributions in large enclosures of calanoid copepodids (left) and *Leptodiaptomus minutus* (right) in no predators (OO), *Chaoborus*-only (CO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each taxon in each enclosure in lower right corner.

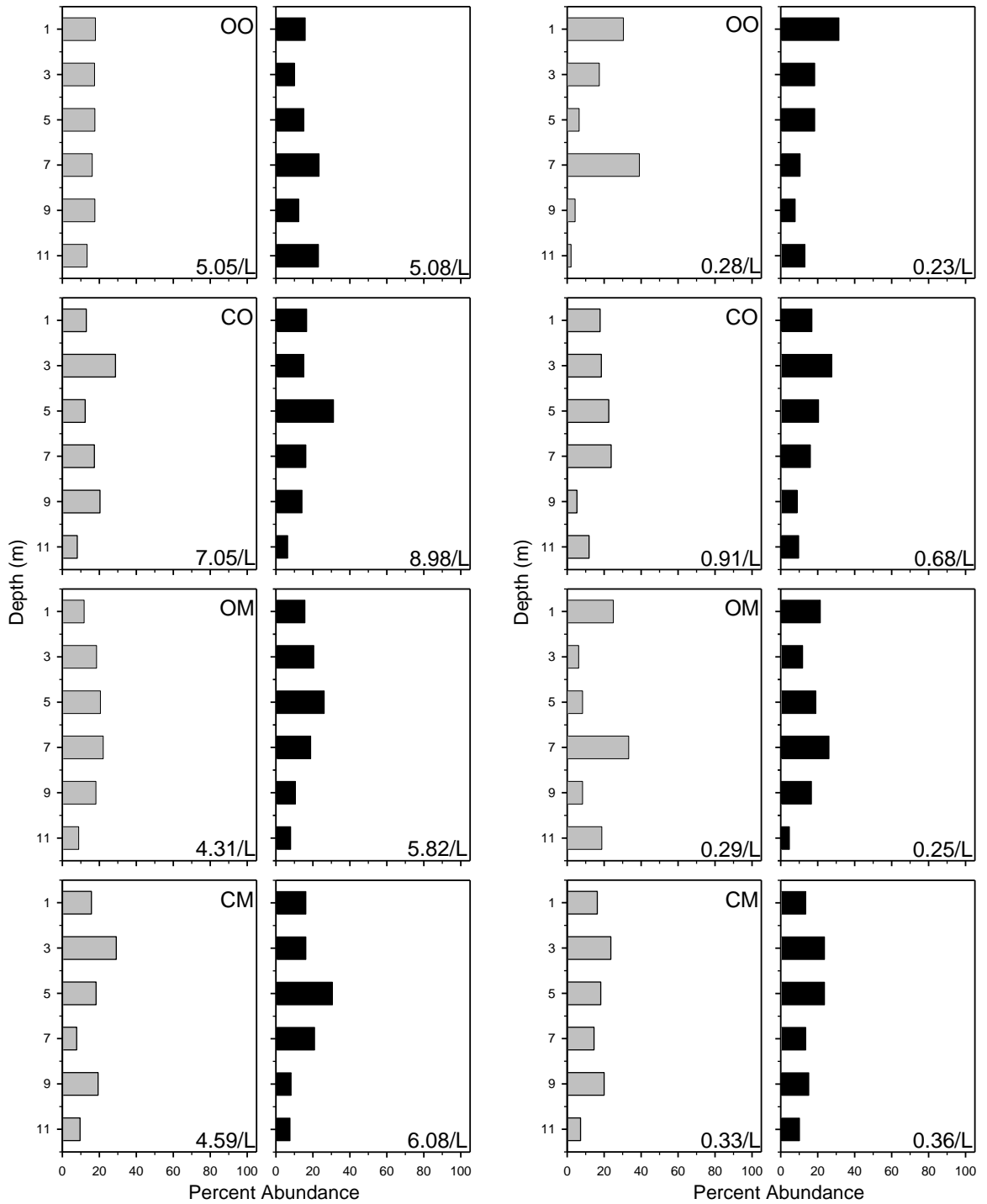


Figure 3-o: 2005 vertical distributions in large enclosures of nauplii (left) and cyclopoid copepodids (right) in no predators (OO), *Chaoborus*-only (CO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each taxon in each enclosure in lower right corner.

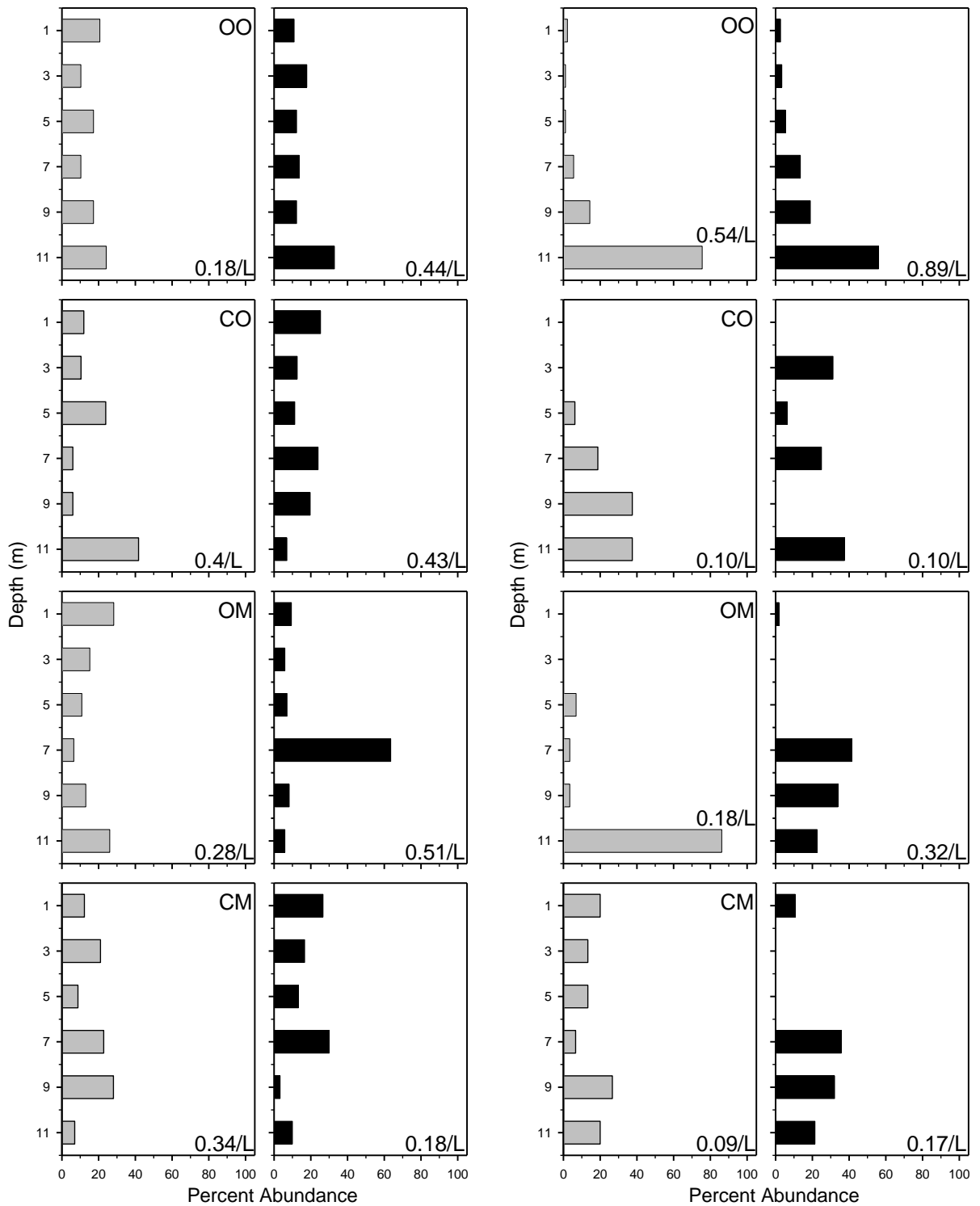


Figure 3-p: 2005 vertical distributions in large enclosures of *Tropocyclops extensus* (left) and *Diacyclops thomasi* (right) in no predators (OO), *Chaoborus*-only (CO), *Mysis*-only (OM), and both predators (CM) treatments. Mean abundance of each species in each enclosure in lower right corner.