INTERACTIONS AMONG *NEOMYSIS MERCEDIS* POPULATIONS, ZOOPLANKTON COMMUNITY STRUCTURE, AND LAKE FERTILIZATION

by

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Interactions among Neomysis mercedis populations, zooplankton community structure, and lake fertilization

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ABSTRACT

Interactions among Neomysis mercedis populations, zooplankton communities and lake fertilization were examined through: (1) assessment of changes in mysid populations in two British Columbia coastal lakes subjected to controlled additions of inorganic nutrients; and (2) manipulation of mysid density and zooplankton communities in experimental enclosures.

Changes in mysid populations among lakes and through years supported the hypothesis that natural populations of mysids are food limited. Both numbers and biomass of mysids exhibited statistically significant increases in Kennedy Lake during years of treatment (fertilization). Untreated Muriel Lake and treated basins of Kennedy Lake exhibited similar densities and standing crops of mysids due to the more productive nature of Muriel Lake. Numerical responses of mysids may be influenced by changes in generation time, the proportion of females achieving maturity, female size at maturity, female clutch size and juvenile survival. I found no evidence for changes in generation time or clutch size of mysids under treated and untreated conditions. I did find evidence for increases in female size at maturity, proportion of females achieving maturity and juvenile survival under treated conditions. These results suggest that competition for food controls mysid populations under natural conditions. This conclusion is further supported by observations that

mortality and growth of mysids in experimental enclosures were highly density-dependent.

Experimental manipulations of mysid density in enclosures indicated that mysid predation had a variable effect on the structure of zooplankton communities in two summers of experimental trials. Enclosures treated with successively higher densities of mysids exhibited increasingly greater changes in species composition, density and biomass of zooplankton by comparison with mysid free controls in 1985, but not in 1986. Differences between results in 1985 and 1986 were attributable to lower starting densities of zooplankton in enclosures in 1985. Comparisons between the impacts of treatments involving either mysids or limnetic fish indicated that the latter are a more potent agent for control of zooplankton community structure. Interpretation of enclosure results relative to conditions observed in treated and untreated study lakes suggests that mysids do not have a major impact on the structure of the zooplankton communities under study.

ACKNOWLEDGEMENTS

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I. GENERAL INTRODUCTION

Predation by vertebrate and invertebrate predators has important, but different influences on the size and species-composition of freshwater zooplankton communities. Vertebrate predators such as fish are often size-selective and can virtually eliminate large prey species (Brooks and Dodson, 1965; Brooks, 1968; O'Neill and Hyatt, 1987; Werner and Hall, 1974; Zaret, 1980). Invertebrate predators, in contrast, consume small zooplankton and their influence on prey abundance is generally easily balanced by prey reproduction (Hall et al., 1976; Neill and Peacock, 1980). However, some invertebrate predators consume a substantial proportion of their zooplankton prey populations (Confer, 1971; Elser et al., 1987; Fedorenko, 1975; Kerfoot and Peterson, 1970; Lane, 1979; Johnson and Lasenby, 1982; McQueen, 1969), and could have a major role in lacustrine energy flow (Neill, 1981). One group of such invertebrate predators is the freshwater mysids, Mysidacea.

Introduction of the freshwater mysid, Mysis relicta into various lake systems to serve as prey for fish, has corresponded with changes in the abundance of certain zooplankton species. Cladocerans, in particular, have come close to extinction. These declines have been attributed to mysid predation (Furst et al., 1984; 1986; Grossnickle, 1978; Goldman et al., 1979; Langeford, 1981; Lasenby and Langeford, 1973; 1978; Nero and Sprules, 1986; Rieman and Falter, 1981; Threlkeld et al.,

1980; Zyblut, 1970). Others have concluded that predation on cladocerans by M. relicta has altered the trophic structure of lakes to the detriment of the fish species for which mysids were originally introduced as a forage item (Furst et al., 1986; Morgan et al., 1978; Rieman and Falter, 1981). The natural increase of the endemic species Neomysis mercedis has also been correlated with the decline and near extinction of Daphnia in Lake Washington (Murtaugh, 1981a). By removing resources important to pelagic fish diets, mysids may be responsible for the reduction in growth and abundance of certain fish species.

These considerations are important to the Lake Enrichment Program, conducted by the Department of Fisheries and Oceans (Canada), since one species of mysid, N. mercedis is present in several of the lakes within the enrichment program (Rankin et al., 1979). The objective of the Lake Enrichment Program is to increase juvenile sockeye salmon (Oncorhynchus nerka) growth and survival by increasing freshwater food resources (zooplankton). In an attempt to meet this objective inorganic nutrients have been added to several British Columbian coastal lakes during the growing season. This has resulted in increased autotrophic and heterotrophic production, larger standing stocks of zooplankton, increased in-lake growth of juvenile sockeye salmon, and larger outmigrant smolts (Hyatt and Stockner, 1985). It is not known how the presence of large invertebrate predators such as mysids may influence the zooplankton community, or sockeye salmon production.

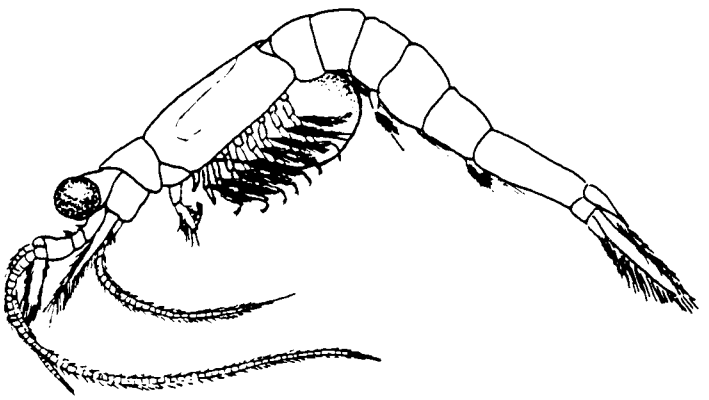
Based on evidence from other studies of mysids, N. mercedis is potentially capable of influencing the structure and production of the zooplankton community. N. mercedis and juvenile sockeye salmon prefer similar sizes and species of zooplankton (Foerster, 1968; Johnston and Lasenby, 1982; Murtaugh, 1981a; 1981b; O'Neill and Hyatt, 1987; Siegfried and Kopache, 1980). Thus, N. mercedis could influence the production of sockeye salmon by competing for zooplankton resources. The possibility exists that the increased production of zooplankton as a result of lake fertilization would not benefit sockeye salmon. It is therefore important to determine what influence mysids might have on the zooplankton community, and how this could affect juvenile sockeye salmon.

NATURAL HISTORY OF NEOMYSIS MERCEDIS

Habitat

Neomysis mercedis is a shrimp-like malacostracan crustacean (Figure 1). It is characterized by stalked eyes, a thin carapace covering most of the thoracic somites, through which respiration takes place, and poorly differentiated thoracic limbs that are used for swimming (Chace et al., 1959; Pennak, 1978). This species of mysid occurs in brackish bays and estuaries having a salinity of less than 20.0 ppt, and in the rivers and lakes along the coasts of British Columbia, Washington, Oregon, and California (Gosho, 1975; Holmquist,

Figure 1. Gravid adult female, Neomysis mercedis



1973). Congeneric species are found in Europe (N. integer), along the east coast of North America (N. americana), along the north Pacific coast of Asia and Alaska (N. intermedia), and along the central Pacific coast of Asia (N. awatschensis; Holmquist, 1973; Johnston, 1985; Tattersall and Tattersall, 1951; Wigley and Burns, 1971). N. mercedis tolerates a wide range in temperature during diel migrations from surface waters during darkness to depth or lake bottom during daylight hours.

Life history

Adult females are distinguished by the development of a brood pouch consisting of four ventral oostegites originating at the bases of the last two pair of legs. In the brood pouch the eggs are hatched, and the young are sheltered until development is complete. Mysids are known to "adopt" or capture embryos, which may have escaped from other females and place them in their own brood pouch (Wittmann, 1978). Embryos captured are usually close to the same age as their own brood. Females may produce as few as five or as many as 57 young per brood (Heubach, 1969), and usually reproduce only once although there is evidence for production of two broods by some females (Johnston, 1985; Mauchline, 1980; Morgan and Beeton, 1978; Morgan, 1980). All females in a population usually release their young at the same time, which results in a rapid increase in mysid population size. Males die soon after mating and

females die once the embryos have completed development and been released (Mauchline, 1980).

Most Neomysis species exhibit two distinct life history patterns and produce two or three generations per year. The overwintering generation has a life span of about eight months and matures and breeds in the early spring. The spring and summer generations have a life span of two to three months and reproduce in the summer and fall respectively. Summer mysids mature at a smaller size than mysids from the winter generation (Johnston, 1985; Toda et al., 1983), and the larger winter females produce almost twice as many young as the spring and summer generations (Johnston, 1985; Toda et al., 1983; Mauchline, 1980). As a result of the two life history patterns, there is a seasonal variation in population size-structure, and marked seasonality in abundance with a summer maximum (Johnston, 1985; Siegfied and Kopache, 1980; Murtaugh, 1983).

M. relicta exhibits a life span ranging from one to four years in different lakes, with continuous or seasonal periods of reproduction (Carpenter et al., 1974; Lasenby and Langeford, 1972; Morgan and Beeton, 1978; Morgan, 1980; 1981). Differences in growth rates and generation length between populations have been attributed to both temperature and food availability in various lake systems. Reduced growth rate and a longer time to maturity for mysids have been attributed to

colder temperatures and limited food resources (Berrill and Lasenby, 1983; Lasenby and Langeford, 1972; Morgan, 1980).

Feeding ecology

Like many species of mysids, N. mercedis exhibits two distinct methods of feeding. In raptorial feeding, large food masses or organisms are grasped by the thoracic endopodites and mandibular palps. As filter feeders, mysids filter suspended fine particles (small planktonic organisms and particles of organic detritus) from currents of water produced by the movement of the thoracic limbs (Tattersall and Tattersall, 1951). The diet of mysids appears to be quite varied, ranging from plant material and detritus to zooplankton (Grossnickle, 1982; Kost and Knight, 1975). Lasenby and Langford (1973) found that M. relicta feeds predominately on Daphnia and other cladocerans in eutrophic Stony Lake, Ontario, but primarily on diatoms and inorganic particles on the moss substrate of oligotrophic Char Lake, N.W.T. In many cases there is an ontogenetic shift in diet. Small mysids feed as herbivores while larger mysids feed increasingly as carnivores. Zooplankton accounted for greater than 90% of the energy represented by food material present in the guts of large N. mercedis (Siegfried and Kopache, 1980). This shift in diet could simply be a reflection of the ability to handle zooplankton prey as the mysids grow (Cooper and Goldman, 1980;

Johnston and Lasenby, 1982; Lasenby and Langeford, 1973; Siegfried and Kopache, 1980).

Prey preferences have been studied both in laboratory feeding experiments, and from lake mysid gut samples. Murtaugh (1981a) and Grossnickle (1978) found that Daphnia and Bosmina were consistently preferred to other prey while Diaptomus, cyclops copepodids and nauplii were always under-represented in the diet. In a number of studies the diet composition of mysids seemed to match the availability of food items reflecting the opportunistic nature of mysid feeding (Bowers and Grossnickle, 1978; Cooper and Goldman, 1980; Lasenby and Langeford, 1973).

There is evidence for size-selective predation by N. mercedis. Murtaugh (1981b) found that juvenile mysids (less than 7 mm) had a strong preference for Daphnia less than 1.0 mm, but larger mysids consistently preferred larger prey up to a maximum of 3.0 mm. This is well within the size range found attractive to vertebrate planktivores (Brooks, 1968) and also covers the size range of zooplankton found in the lakes I investigated.

Murtaugh (1981b) suggests that size is not the only factor determining prey selection. The vulnerability of prey items is also important. Based on studies by Drenner et al. (1978) cladoceran species seem vulnerable to planktonic-feeding currents produced by mysids. Ramcharan et al (1985)

demonstrated that slower moving zooplankton such as cladocerans were more likely to be consumed by M. relicta.

In summary, particular species of zooplankton may be susceptible to consumption by mysids. Their escape responses, size and availability, all contribute to their predation by mysids, and a combination of these factors interact to determine prey preferences in particular lake systems.

Predators

M. relicta is often an important item in the diets of many freshwater sport and commercial fish, particularly lake trout (Salvelinus namaycush), brown trout (Salmo trutta), kokanee (Oncorhynchus nerka) and rainbow trout (Salmo gairdneri), as well as many other fish species (Furst et al., 1986; Gosho, 1975; Janssen and Brandt , 1980; Langeland, 1981; Northcote, 1972; Morgan et al., 1978). The importance of mysids as a prey item was the premise for introducing M. relicta into lakes as a forage item. The following species included Neomysis spp. in their diets: several species of smelt, perch, sculpins, and salmon, as well as young striped bass (Morone saxatilis), American shad (Alosa sapidissima), threespine stickleback (Gasterosteus aculeatus), carp (Cyprinus carpio), eels (Anguilla anguilla) and several shrimp species (Bremer and Vijverberg, 1982; Egger et al., 1978; Johnston, 1985; Siegfried et al., 1979; Toda et al., 1982). However, the introduction of mysids may not always benefit the target fish species. Arctic char

(Salvelinus alpinus) and kokanee, for example, did not shift their diets to include mysids after introductions in several Swedish lakes and Pend Oreille Lake in the United States (Furst et al., 1986; Rieman and Falter, 1981).

Although many studies of mysids have compiled an extensive list of fish species that consume mysids and the contribution of mysids to the total fish diet, very few have actually looked at the impact of fish predation on mysid population structure or abundance. Bremer and Vijverberg (1982) and Toda et al. (1982) found that fish predation could significantly reduce the abundance of mysids. However, the impact of fish predation depended on prior winter conditions experienced by the mysids. When the mysid population was reduced due to adverse winter conditions, the effect of moderate fish predation during the spring and summer was enough to remove a large proportion of the mysid population (Bremer and Vijverberg, 1982).

THESIS OBJECTIVE

The objective of this thesis is to determine the impact of Neomysis mercedis on the zooplankton community, in order to evaluate what impact mysids as foragers may have on juvenile sockeye salmon. In Chapter 2, I present results from the study of N. mercedis populations under fertilized and unfertilized conditions in Kennedy and Muriel Lakes. The influence of lake enrichment on mysids is discussed in terms of life history, growth, and abundance. In Chapter 3, I look at the results of enclosure experiments in Muriel Lake in order to determine whether mysids significantly influence zooplankton abundance and community structure. Finally I examined the potential impact mysids could have on juvenile sockeye by considering: 1) mysid population characteristics; 2) mysid population responses to lake fertilization; and 3) the influence of mysids on the zooplankton communities of the study lakes.

II. EFFECT OF LAKE ENRICHMENT ON LIFE HISTORY AND ABUNDANCE OF *NEOMYSIS MERCEDIS* IN TWO COASTAL BRITISH COLUMBIA LAKES

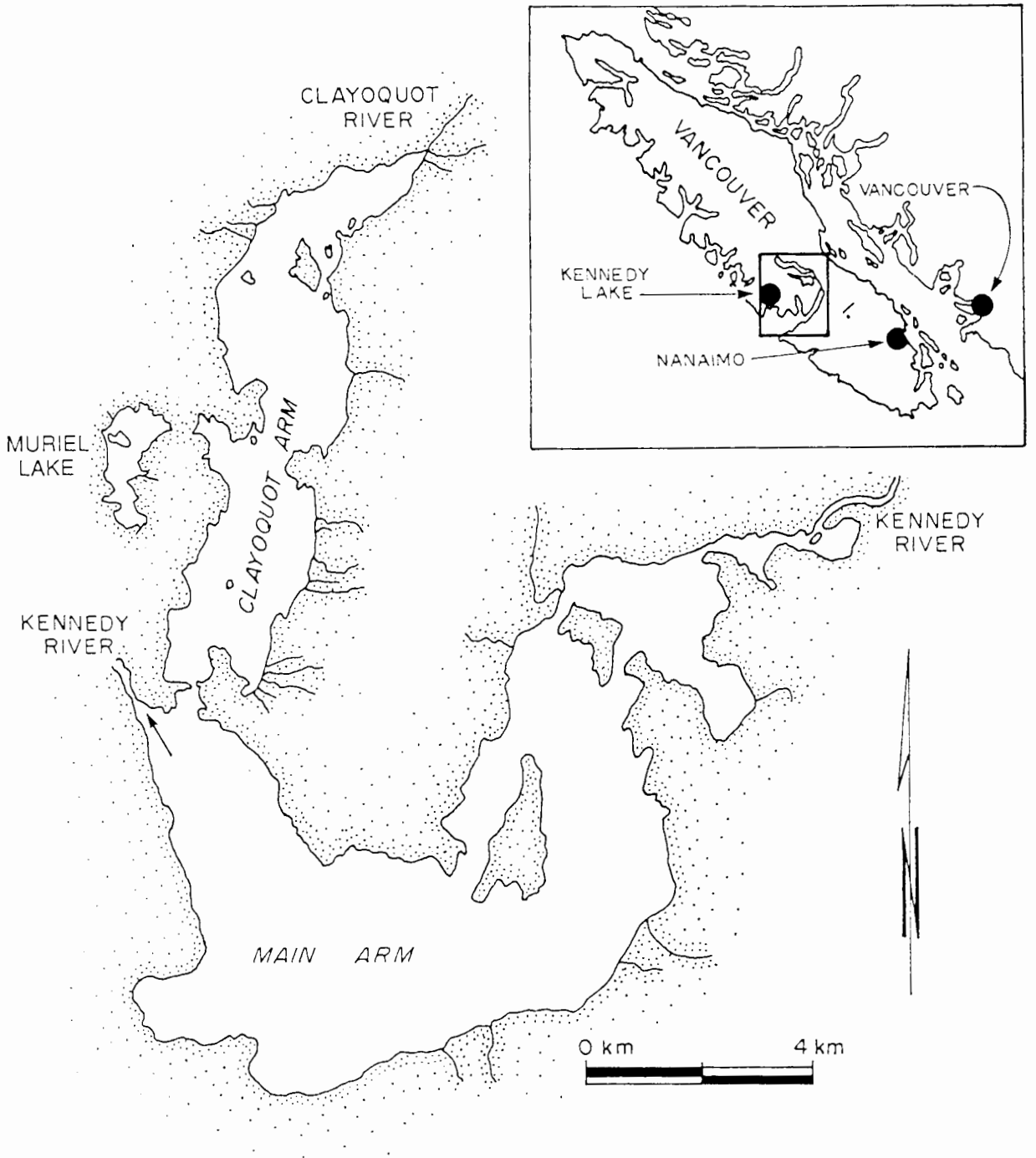
INTRODUCTION

Competition for limiting food resources may affect the growth rate of individuals, survivorship, fecundity, the rate of maturity, and the rate of population growth (Roughgarden, 1986; Schoener, 1974). Food supplementation has been one technique used to assess the effects of food limitation on communities or on particular species (Mason, 1976; Neill and Peacock, 1980).

If food is limiting, food additions should reduce competition and thereby increase productivity of organisms sharing the resources. The Lake Enrichment Program is based on this idea. The objective of the program is to increase the production of zooplankton for sockeye salmon consumption in several British Columbia coastal lakes in which sockeye are food limited (Hyatt and Stockner, 1985). In the untreated condition (no nutrient addition), lakes are ultraoligotrophic and are generally phosphorous limited (Stockner and Shortreed, 1985). By increasing inorganic nutrient supply to these lakes through whole lake fertilization, an increase in production at succeeding trophic levels has been accomplished, with positive effects on growth and survival of sockeye salmon (Hyatt and Stockner, 1985; Lebrasseur et al., 1978). Kennedy and Muriel (Figure 2) are two lakes in the program, and have been fertilized for various time periods during the last 10 years

Figure 2. Location of study sites.

KENNEDY LAKE



(Table 1). In Kennedy Lake, the addition of inorganic nutrients has resulted in a doubling of average chlorophyll levels and zooplankton biomass (Table 1). An increase in limnetic fish abundance, particularly sticklebacks, has been attributed to lake fertilization (Hyatt, pers. comm.; Rankin et al., 1979). Neomysis mercedis could also benefit from the increase in zooplankton biomass. N. mercedis has a generation time of less than one year, and consequently may exhibit a rapid numerical response to changes in lake productivity generated by lake enrichment (Murtaugh, 1983). Changes in juvenile survival and reproductive output of adult mysids could contribute to the numerical increase, as may changes in growth rate, and generation length. The objective of my study was to determine the responses of mysid populations to the increased food resources resulting from lake fertilization.

There is evidence from other studies that population parameters of mysids are affected by aquatic productivity. Morgan (1980) attributed differences in life history of several populations of M. relicta to differences in lake productivity. The more productive lake systems were characterized by mysids with a shorter time to maturity as a result of greater growth rates. Morgan (1980) also found that in the more productive lakes mysid populations were more likely to breed continuously throughout the year which he assumed was due to the availability of food resources sufficient for year round reproduction.

Table 1. History of lake fertilization, chlorophyll and zooplankton levels of Kennedy and Muriel Lakes. Zooplankton biomass estimates are based on dry weights.

Basin	Year	Phosphorous Added ($mg \cdot m^{-2} \cdot yr^{-1}$)	Nitrate Added ($mg \cdot m^{-2} \cdot yr^{-1}$)	Average Total Chlorophyll ($mg \cdot m^{-3}$)	Zooplankton Biomass** ($mg \cdot m^{-3}$)
Kennedy Clayoquot	1978	198	910	1.53	10.4
	1979	131	870	1.52	-
	1980	132	870	3.07	10.1
	1981	159	792	11.17	5.6
	1982	106	1241	5.68	5.6
	1983	76	1165	3.79	5.2
	*1984	54	853	2.11	9.2
	*1985	0	0	1.06	4.0
	*1986	0	0	-	-
Kennedy Main	1978	0	0	0.87	4.9
	1979	65	427	1.84	-
	1980	65	427	2.01	7.9
	1981	0	0	1.54	4.1
	1982	0	0	1.13	3.8
	1983	0	0	1.08	4.4
	*1984	0	0	1.13	5.2
	*1985	54	854	2.24	5.4
	*1986	-	-	-	-
Muriel	1983	0	0	0.93	12.5
	1984	(fertilized with slow-release pellets)			
	*1985	0	0	-	-
	*1986	0	0	-	-

(Costella et al., 1982; 1983a; 1983b; Nidle et al., 1984; Nidle and Shortreed, 1985; Rankin et al., 1979; Shortreed and Stockner, 1981; Stockner et al., 1980)

* years of this study

** excludes Neomysis mercedis since biomass estimates were based on 50 m vertical hauls during daylight hours.

Johnson (1985) found that the proportion of females reaching maturity within a population was directly related to food abundance.

The abundance of mysids may also be attributed to productivity of the habitat. Estuaries, which are very productive relative to lakes, are characterized by very dense populations of mysids. Hopkin (1965) found that estuarine N. americana reached densities up to $3300 \cdot m^{-3}$, while values ranged from 100 to 700 mysids$\cdot m^{-3}$ in the Sacramento San Joaquin estuary (Knutson and Orsi, 1983; Siegfried et al., 1979). In ultra-eutrophic Lake Kasumigaura, N. intermedia have reached maximum densities similar to estuary populations ($2500 \cdot m^{-3}$), but mesotrophic Lake Washington has supported a maximum population of only 1.5 N. mercedis$\cdot m^{-3}$ (Murtaugh, 1981c; Toda et al., 1982). The same trend is apparent for freshwater populations of M. relicta, with mysid densities lower in oligotrophic systems (Tahoe, Superior, and Huron lakes) than in mesotrophic lakes (Lakes Ontario and Michigan; Carpenter et al., 1974; Grossnickle and Morgan, 1979; Morgan et al., 1978).

In my study, the effect of lake fertilization (lake productivity) on N. mercedis populations is examined in two lakes, Kennedy and Muriel. The biomass and density of N. mercedis populations were measured, and particular attention was given to life history characteristics which would influence productivity and abundance of the mysid populations.

Specifically, I predicted that under fertilized conditions: 1) N. mercedis populations would be larger; 2) that more females would reproduce and produce larger clutches; 3) that juvenile survival would increase; 4) that size at maturity would increase; and 5) that the rate of maturation would increase, shortening the generation time.

MATERIALS AND METHODS

Study sites

Kennedy Lake is located on the west coast of Vancouver Island, British Columbia (49°06'N, 125°33'W; Figure 2). The lake is situated four m above sea level and covers an area of approximately 6475 ha with a maximum depth of 165 m and mean depth of 38 m (Rutherford et al., 1986). Littoral zone habitat is restricted to 3.2% of the total lake's surface area. The lake is divided into two major basins, Clayoquot Arm (CA) and Main Arm (MA) which are connected by a narrow channel, 100 m wide. Kennedy lake is a warm, monomictic lake with a short water residence time of 1.1 years, low phosphorous concentration (1.2-2.0 μg TP$\cdot l^{-1}$ in an untreated state) and extremely oligotrophic conditions (1.08-2.01 μg TChl$\cdot l^{-1}$ untreated state; Stockner and Shortreed, 1985). The lake is characterized by a low species diversity and low standing crops of both zooplankton and fish (Hyatt and Stockner, 1985). In order of decreasing numerical abundance, the fish species known to occupy the lake are sticklebacks (Gasterosteus aculeatus), sockeye salmon (Oncorhynchus nerka), prickly sculpin (Cottus asper), peamouth chub (Mylocheilus caurinus), cutthroat trout (Salmo clarki clarki), and coho salmon (O. kisutch; Hyatt and Ringler, 1988). The zooplankton community consists of abundant species such as Bosmina coregoni longispina, Diacyclops thomasi, Diaptomus oregonensis and two rotifers, Keratella sp. and Kelicottia sp.

Rare species included Diaphanosoma sp., Sida sp., Polyphemus sp., Cyclops vernalis and Diaptomus kenai (O'Neill, 1986).

Both basins of the lake have been periodically treated with inorganic nutrients since 1978, as part of the Lake Enrichment Program. Treatment of the basins has generally alternated between arms with only one arm treated in a given year (Table 1). During the period of the study (1984-86) CA was treated during 1984, and treatment switched to MA for the remainder of the study (1985-86).

Muriel Lake ($40^{o}08'N$, $125^{o}36'W$) is situated 11 m above sea level and covers an area of 145 ha (Figure 2). It is much shallower than Kennedy with a maximum depth of 45 m and a mean depth of 22 m. Muriel is similar to Kennedy Lake in having a limited littoral zone, low nutrient levels (2.6 μg $TP \cdot l^{-1}$; 0.93 μg $TChl \cdot l^{-1}$), and a water residence time of less than 1.0 year. Fish species present in Muriel Lake are identical to those in Kennedy Lake, differing only in relative abundance. Peamouth chub are most abundant, followed by sockeye and coho salmon, sculpins, cutthroat trout, and sticklebacks respectively. Zooplankton species composition is similar to Kennedy Lake except that Diaphanosoma sp. occur commonly in Muriel Lake, but only sporadically in Kennedy Lake.

Muriel Lake was treated with inorganic nutrients in 1984. Rafts of slow release pellets were deployed in locations

scattered across the surface of the lake. During the present study no nutrient application took place.

Field sampling

In order to assess the relative abundance, distribution, and natural history of N. mercedis in Kennedy Lake, periodic surveys were conducted. Samples were collected at stations along seven transects in each of Clayoquot and Main Arms (Figure 3). Mysids were collected with a 350μm plankton net (mouth opening of 0.26 m^2). Vertical hauls were completed from 50 m to the surface, or from the lake bottom to the surface if the lake was less that 50 m deep. The net was hauled at a constant speed of 1 $m \cdot s^{-1}$. Filtering efficiency of the net was monitored by attaching a General Oceanics flow meter to the inside of the net opening. Sampling took place after civil twilight since mysids are rarely found in the upper water column during daylight hours. Surveys were conducted in spring (May), early summer (June), late summer (August, September) and fall (October, November) in 1984, 1985 and 1986, in order to determine seasonal changes in population structure and abundance.

Similar techniques were used to sample mysids in Muriel Lake. Ten stations representing most regions of the lake were sampled (Figure 4). Tow distance varied with station depth since Muriel Lake is less than 45 m deep. Surveys were

Figure 3. Contour map of Kennedy Lake and location of sampling transects (inset).

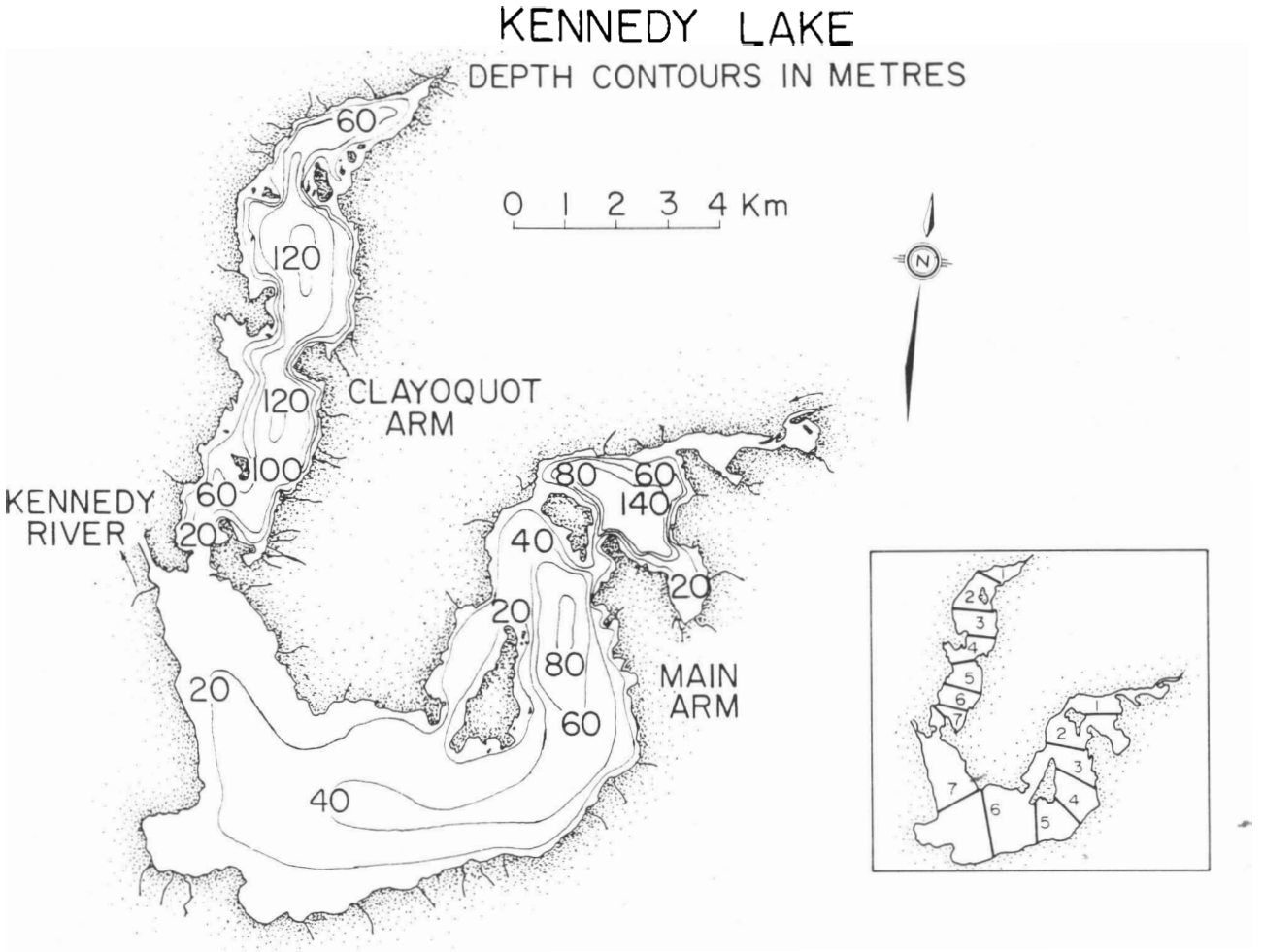
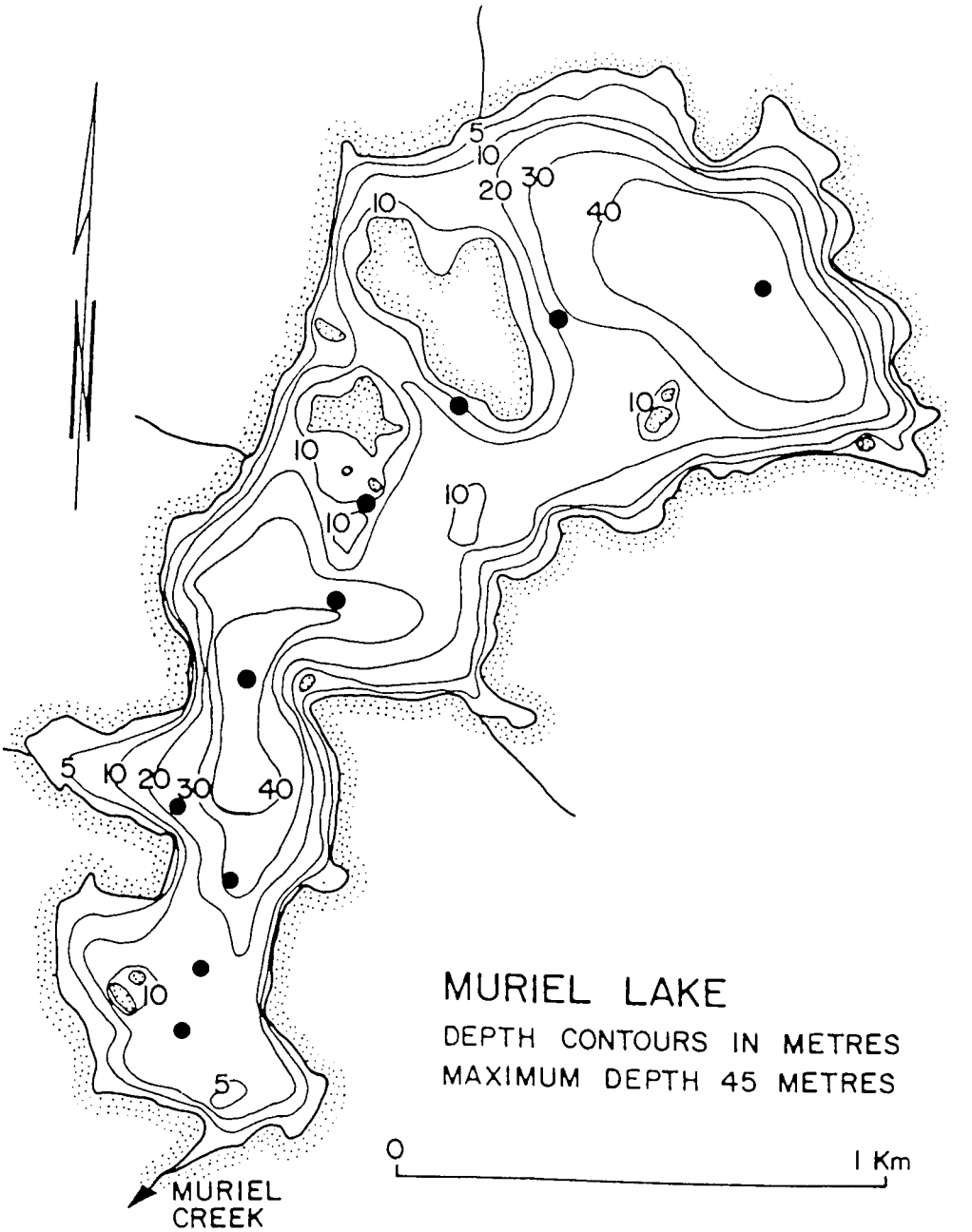

KENNEDY LAKE
DEPTH CONTOURS IN METRES
0 1 2 3 4 Km
N
60
120
120
CLAYOQUOT ARM
100
60
KENNEDY RIVER
20
80
60
140
40
20
20
80
MAIN ARM
20
60
40
1
2
3
4
5
6
1
2
3
7
6
5
4

Figure 4. Contour map of Muriel Lake and location of sampling stations (dots).


5
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10
5
MURIEL
CREEK
MURIEL LAKE
DEPTH CONTOURS IN METRES
MAXIMUM DEPTH 45 METRES
0
1 Km

conducted after civil twilight approximately every two weeks during the summers of 1985 and 1986.

Laboratory sample processing

Mysid samples were preserved in 4% buffered formalin immmediately upon removal from the lake. Animals were later measured for total length and sex. Gravid females' eggs and embryos were counted, staged and measured. Mysids were placed in three categories; juveniles (no sexual development), immatures (sexually identifiable), and adults (females with pouch or males with extended 4th pleopod). Embryos were divided into uneyed and eyed individuals. Total length was measured as the distance from the tip of the rostrum to the end of the telson (Figure 13). Mysids were measured with the aid of an electronic caliper-microcomputer arrangement (Sprules et al., 1981). The preserved wet weight of each animal was estimated from its length by using the regression equation $W=0.2482*[(L-0.74/3.479)^{2.7959}]$, where W is the preserved wet weight (mg) and L is the total length (mm) (Rankin, pers. comm., PBS, Nanaimo, B.C.).

Data analysis

In order to assess the impact of lake fertilization on mysids, observations in the fertilized basin of Kennedy Lake were compared to observations in the unfertilized basin of Kennedy Lake and in Muriel Lake, also untreated during the study

period. Comparisons of Muriel Lake to Kennedy Lake were restricted to the summer and early fall.

Density and biomass of mysids were calculated as the simple mean (no. or $mg \cdot m^{-3}$ respectively). To account for the heterogeneity in mysid abundance among transects, means were also weighted by the surface area represented by each transect (area of the lake surrounding each transect, extending one-half the distance between transects). To determine the effect of lake fertilization on the density and biomass of mysids, comparisons were made between treated and untreated basins of Kennedy Lake on each survey date. Also mysid populations within each basin were compared on fertilized and unfertilized dates. Comparisons were restricted to within seasons. A Mann-Whitney two sample comparison was used to test differences. Comparisons of the density and biomass of mysids during the summer in Muriel Lake were made to MA and CA.

Fecundity was measured as the number of eggs per female (clutch size). The number of gravid females with intact brood pouches in Muriel was small, so no comparisons were possible. However, by pooling females collected in all surveys, sufficient numbers of females were available to test fecundity differences between MA and CA. A Mann-Whitney two sample comparison was used to compare fecundity in MA against CA. Only females with at least five young in the marsupium were included in the test. This is the minimum number of embryos usually carried by this

species of mysid (Heubach, 1969). Although there were females with fewer young, this likely resulted from disruption of the brood pouch during collection and preservation. The proportion of gravid females present could also indicate the effect of resources on reproduction. The size of the smallest female found to be gravid was used as the lower limit to include in calculating the total number of females in the population capable of reproducing. The smallest gravid female in Kennedy Lake was 11.3 mm. A two-way contingency table (chi-square; Zar, 1974) was used to test for differences between the proportion of gravid females in MA and CA for each survey.

To determine if the size at maturity of mysids was influenced by lake fertilization, the body size of adults was compared between MA and CA. Adult body size in the spring would reflect the growing conditions of the previous winter and summer. Adult body size at the end of the summer would reflect conditions for growth during the summer. Males and females were compared separately since mean size of males and females can differ (Mauchline, 1980). A Mann-Whitney two-sample comparison was used to test for differences in adult size between treated and untreated basins for all surveys except November, 1984 when very few adults were sampled. Body size of adult mysids in Muriel Lake was compared to observations of adult body size in Kennedy Lake.

RESULTS

The statistical significance of the results presented here, for mysid density and biomass were unchanged with regard to the use of weighted versus unweighted observations. Unweighted means were therefore used to describe mysid density and biomass and to test for changes in these variables due to lake fertilization. The weighted means simply increased the magnitude of the differences between treated and untreated comparisons.

When CA was fertilized (1984), the density of mysids was greater than MA populations (Figure 5a; Table 2). When fertilization was switched to MA, populations of mysids were significantly larger, except the spring of May, 1985 (Table 2). The influence of lake fertilization on mysid density would have been minimal at this time, since fertilization of MA was initiated only two weeks prior to the May 1985 survey and juveniles had not yet been released. The abundance of mysids would more likely reflect environmental conditions experienced the previous reproductive year. Overall, fertilization produces a major and highly significant increase in mysid density. When biomass differences between arms were examined, the results followed the same pattern; the treated basins had a significantly larger biomass of mysids than the untreated basin (Figure 6a; Table 3).

Figure 5. Density ($no \cdot m^{-3}$) estimates of Neomysis mercedis in Kennedy (a) and Muriel (b) Lakes.; Error bars equal one standard error. (● = treated Clayoquot; ○ = untreated Clayoquot; ■ = treated Main; □ = untreated Main; ▲ = Muriel Lake)

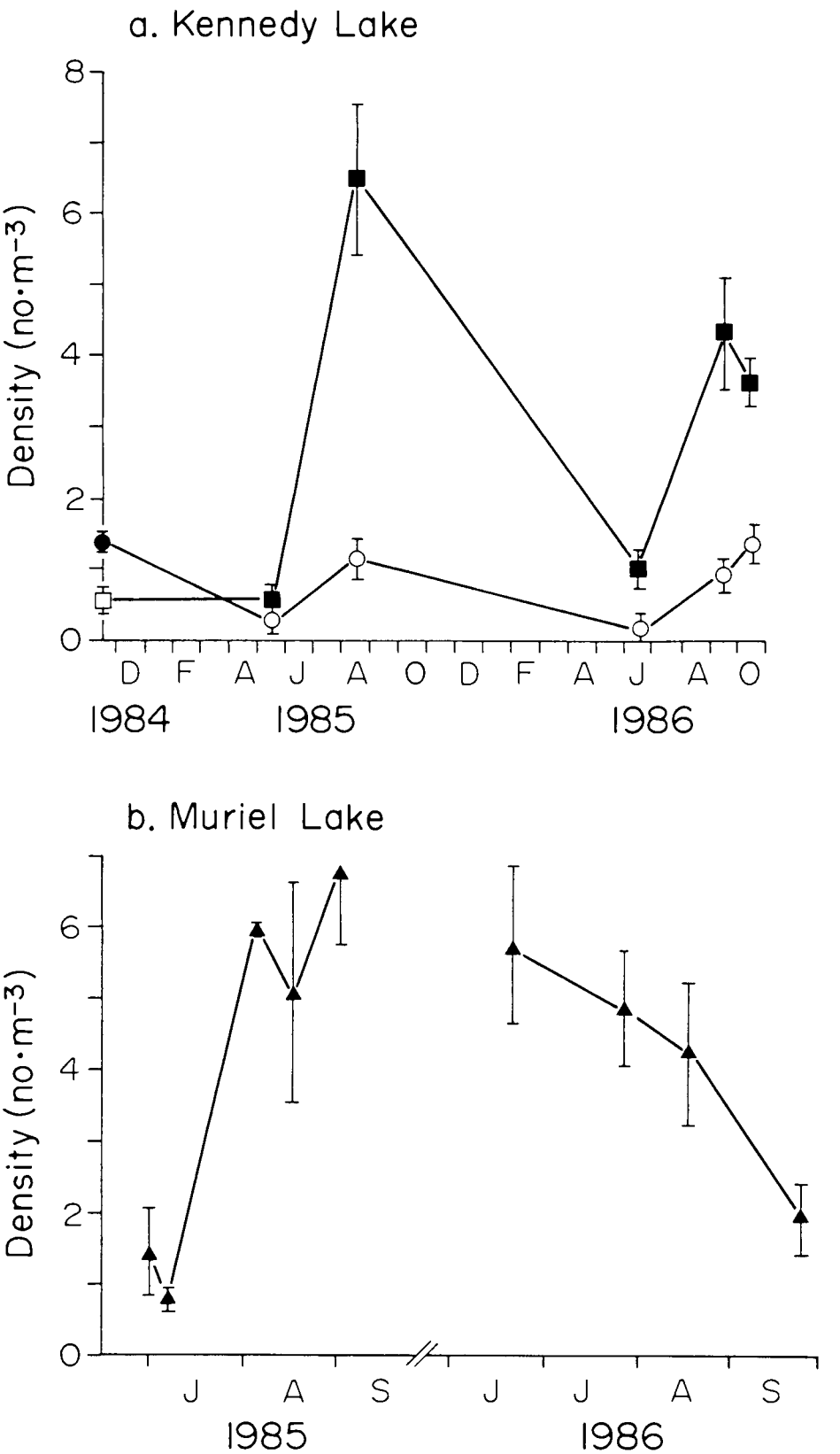

a. Kennedy Lake
Density (no·m⁻³)
8
6
4
2
0
D F A J A O D F A J A O
1984
1985
1986
b. Muriel Lake
Density (no·m⁻³)
6
4
2
0
J A S J J A S
1985
1986

Table 2. Density ($no \cdot m^{-3}$) of mysids in Kennedy Lake.

Survey	Main Mean Density (S.E.)	n	Clayoquot Mean Density (S.E)	n	P^{+}
Nov 14/84	0.55 (0.17)	19	*1.41 (0.20)	16	<0.001
May 16/85	*0.59 (0.14)	40	0.33 (0.04)	38	0.722
Aug 28/85	*6.57 (1.23)	40	1.26 (0.24)	38	<0.001
June 6/86	*0.98 (0.21)	40	0.27 (0.10)	38	<0.001
Sept 9/86	*4.28 (0.82)	40	0.90 (0.16)	38	<0.001
Oct 20/86	*3.61 (0.26)	40	1.36 (0.17)	38	<0.001

+ 1-tailed significance level of density between basins, Mann-Whitney U test
* years of nutrient addition

Figure 6. Biomass ($mg \cdot m^{-3}$) estimates of Neomysis mercedis in Kennedy (a) and Muriel (b) Lakes. Error bars equal one standard error. (● = treated Clayoquot; ○ = untreated Clayoquot; ■ = treated Main; □ = untreated Main; ▲ = Muriel Lake)

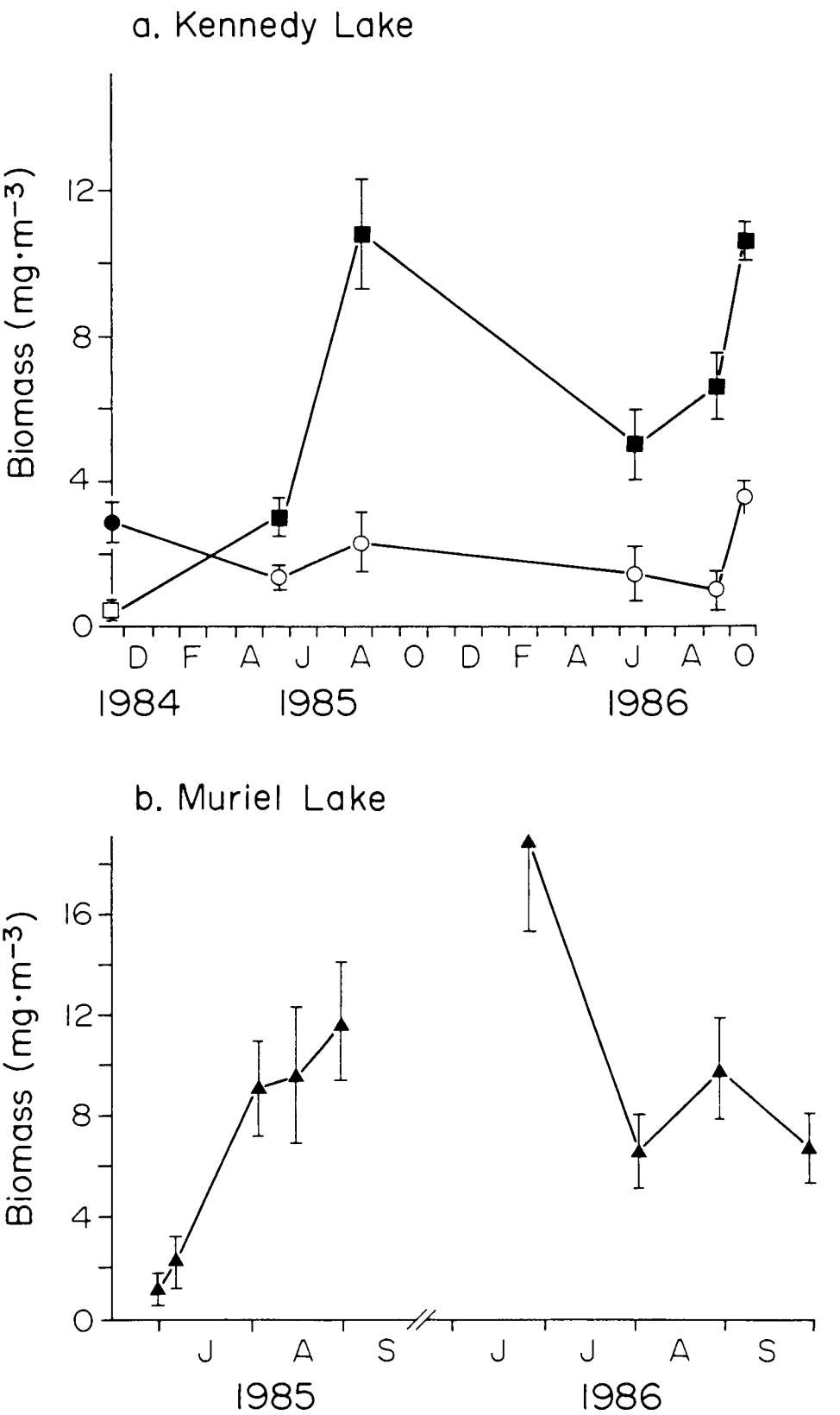

a. Kennedy Lake
Biomass (mg·m⁻³)
0
4
8
12
D F A J A O D F A J A O
1984
1985
1986
b. Muriel Lake
Biomass (mg·m⁻³)
0
4
8
12
16
J A S J J A S
1985
1986

Table 3. Biomass ($mg \cdot m^{-3}$) of mysids in Kennedy Lake.

Survey	Main Mean Density (S.E.)	n	Clayoquot Mean Density (S.E)	n	P+
Nov 14/84	0.46 (0.13)	19	*2.92 (0.45)	16	<0.001
May 16/85	*2.93 (0.62)	40	1.32 (0.20)	38	0.197
Aug 28/85	*10.74 (1.51)	40	2.21 (0.52)	38	<0.001
June 6/86	*4.95 (1.15)	40	1.62 (0.54)	38	<0.001
Sept 9/86	*6.61 (0.87)	40	1.04 (0.22)	38	<0.001
Oct 20/86	*10.48 (0.84)	40	3.54 (0.61)	38	<0.001

+ 1-tailed significance level of biomass comparisons between basins, Mann-Whitney U test.
* years of nutrient addition

The density of mysids within each basin, when treated and untreated were also compared. I predicted that the density of mysids would be lower in the unfertilized years within a basin. Within CA there were no differences in the density of mysids between treated (Nov. 1984) and untreated sampling dates (Aug. 1985, Oct. 1986; Table 4). This may be a weak test since fall estimates for treated CA (Nov. 1984) were based on samples collected approximately one month later in the year than samples for untreated CA (Oct. 1986). Mysid density declines over the fall period (see Figure 5). Further samples are needed to clarify the response of CA mysid populations to fertilization in terms of abundance. There was also no difference in mysid density between May, 1985 (the spring directly following fertilization) and June, 1986 (unfertilized survey; Table 4). Biomass of mysids exhibited a similar pattern, with no difference between fertilized and unfertilized years in CA (Table 5).

Density of mysids in MA was significantly greater under treated (Oct. 1986) as opposed to untreated conditions (Nov. 1984; Figure 5a; Table 4). I may have overestimated the difference in mysid density between the two fall surveys because of the month difference in timing of the surveys. However, it is very unlikely that a seasonal decline of mysids within a month would explain a difference of the magnitude observed in the density of mysids between treated and untreated fall surveys. The density of mysids was also higher in June, 1986

Table 4. A summary of the comparisons of the mysid density between sampling dates within each Kennedy Lake basin.

Clayoquot Comparison	P+	n	Main Comparison	P+	n
Nov 84* vs Aug 85	0.107	54	Nov 84 vs Oct 86*	<0.001	59
Nov 84* vs Oct 86	0.399	54	May 85* vs June 86*	0.013	80
May 85 vs June 86	0.053	76	Aug 85* vs Sept 86*	0.473	80

+ 1-tailed significance level of density comparison, Mann-Whitney U test
* years of nutrient addition

Table 5. A summary of the comparisons of mysid biomass between sampling dates within each Kennedy Lake basin.

Clayoquot Comparison	P+	n	Main Comparison	P+	n
Nov 84* vs Oct 86	0.970	54	Nov 84 vs Oct 86*	<0.001	59
May 85 vs June 86	0.313	54	May 85* vs June 86*	0.014	80
			Aug 85* vs Sept 86*	0.083	80

+ 1-tailed significance level of biomass comparison, Mann-Whitney U test
* years of nutrient addition

(following a year of fertilization in MA) than in May, 1985 (only two weeks after the initiation of treatment in MA; Figure 5a; Table 4). Mysid density was not significantly different for late summer surveys (August and September) in 1985 or 1986, both during years of treatment (Table 4). Biomass estimates of mysids were consistent with this pattern. Fall and early summer estimates of mysid biomass were significantly greater when MA was treated than when untreated, while summer biomass estimates were similar (Figure 6a; Table 5).

Changes in the density of mysids in Muriel Lake over the summer were similar to the trends shown in Kennedy Lake, with an increase in early summer with the release of juveniles, and a decline in late summer with adult mortality (Figure 5b). Density of mysids in Muriel Lake during the summer was similar to the density of mysids in MA when treated, and much higher than in untreated CA. Mysid density in early summer 1985 was as low as in CA, but once recruitment to the population had occurred in July, mysids increased to levels measured in MA. Biomass of mysids in Muriel Lake during the summer was at least as high as in MA. The biomass of mysids reached a maximum of 19 $mg \cdot m^{-3}$ during early summer, 1986 (Figure 6b). Biomass estimates for CA, in contrast, reached a maximum of 3 $mg \cdot m^{-3}$. The low biomass of mysids in Muriel Lake in June, 1985, was due to the low number of mysids in the population prior to the release of juveniles.

The density of mysids increased at most stations during any period of fertilization, however, the magnitude of increase does appear to be most pronounced on transects five to seven, in the shallow outlet region of MA (Figure 7). Size structure of the mysid population in the shallower region of MA was skewed towards smaller mysids, so that immature and juvenile mysids made up the greatest proportion of the population. This was most apparent in the August, 1985 and September, 1986 surveys. There were no similar consistent distributional trends in abundance within either CA (Figure 7) or Muriel Lake.

I predicted that fecundity would increase with fertilization. Comparisons of fecundity were made only between fertilized and unfertilized basins of Kennedy Lake, as there were very few females with intact brood pouches sampled in Muriel Lake. Since sample sizes were extremely small from the 1984 survey when CA was fertilized, I could not test for effects of treatment on fecundity. However sufficient numbers were collected to test for differences in clutch size in 1985-86, when MA was treated. The fecundities of MA females and CA females were not significantly different (number of embryos per female: Mann-Whitney U Test, $P=0.563$; Figure 8). Neither was the proportion of gravid females greater in treated MA than in untreated CA (Table 6), despite the trend for a larger proportion of gravid females in MA.

Figure 7. Density ($no \cdot m^{-3}$) of Neomysis mercedis by transects in Clayoquot and Main Basins of Kennedy Lake. Error bars equal one standard error.

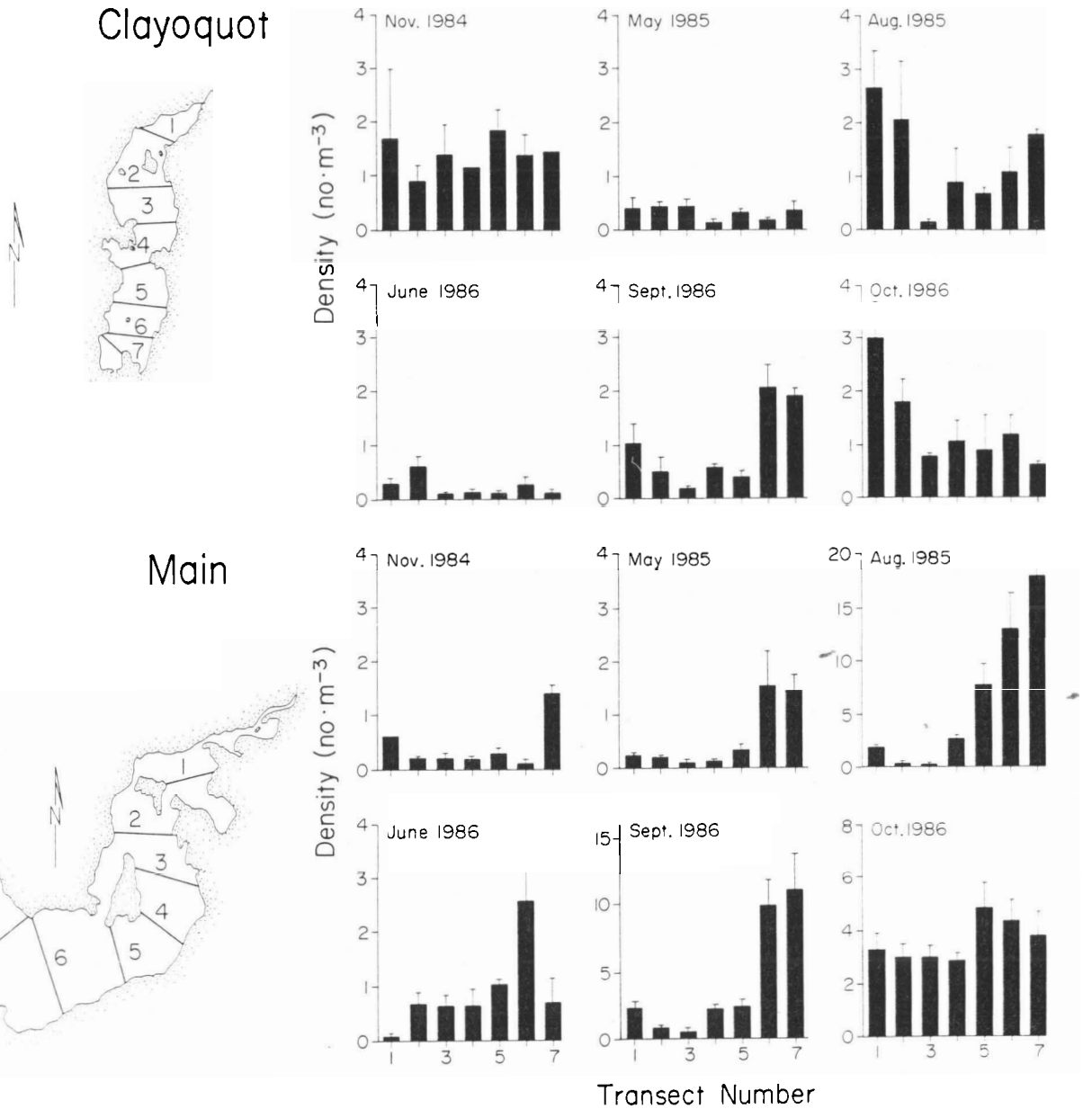

Clayoquot
Main
Nov. 1984
May 1985
Aug. 1985
June 1986
Sept. 1986
Oct. 1986
Density (no·m⁻³)
Transect Number

Figure 8. Frequency distributions of brood sizes among female mysids in Kennedy Lake($\bar{x}$= mean brood size $\pm$ one standard error).

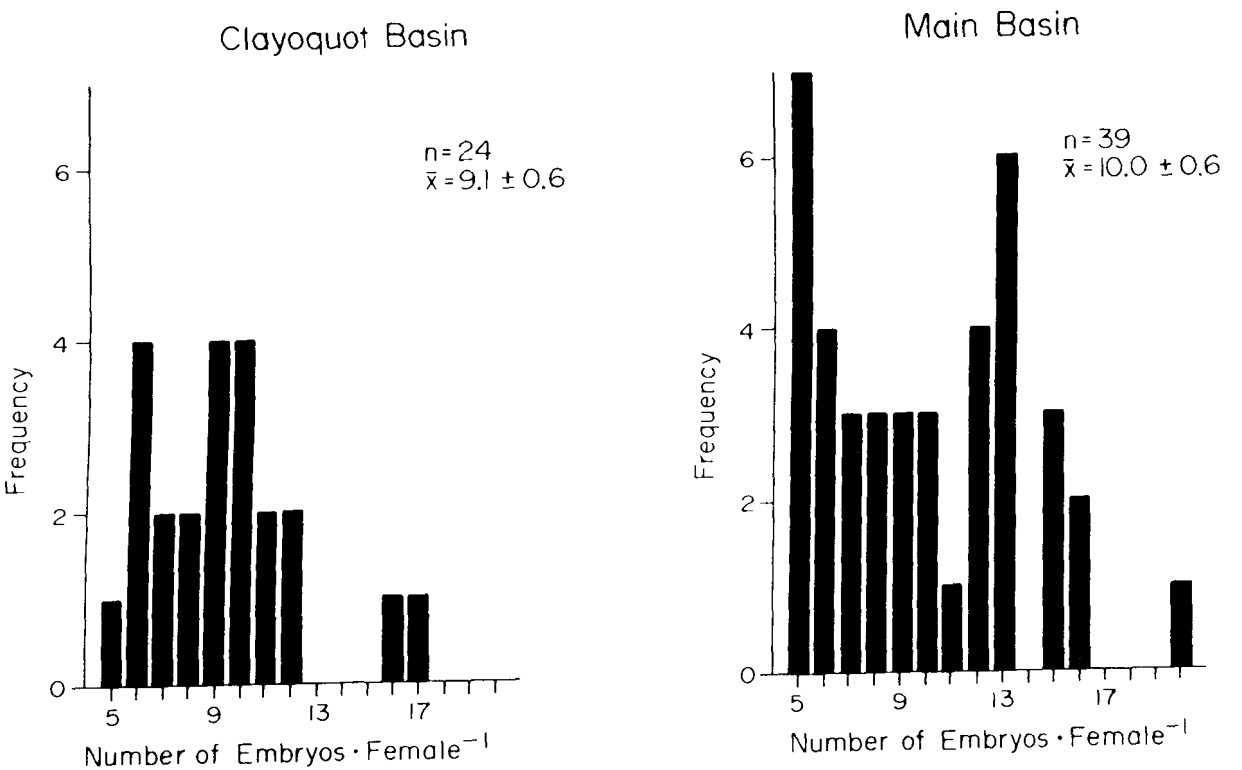

Clayoquot Basin
n = 24
x̄ = 9.1 ± 0.6
Frequency
0
2
4
6
5
9
13
17
Number of Embryos · Female⁻¹
Main Basin
n = 39
x̄ = 10.0 ± 0.6
Frequency
0
2
4
6
5
9
13
17
Number of Embryos · Female⁻¹

Table 6. Number of gravid and non-gravid females in Kennedy Lake surveys. Chi-square values are given for the comparison between treated and untreated basins of Kennedy Lake for each survey.

Survey	Clayoquot Basin		Main Basin		x^2
	Gravid	Not Gravid	Gravid	Not Gravid	Value
May 16/85	2	13	5	8	1.20 ns
Aug 28/85	14	16	20	19	0.02 ns
June 6/86	5	21	6	38	0.08 ns
Sept 9/86	2	7	9	22	0.01 ns
Oct 20/ 86	0	29	7	98	0.92 ns
Overall	23	86	47	185	0.07 ns

I predicted that with nutrient addition, size of adult mysids at the end of the growing season would increase. Since males were generally larger than females, and sex ratios were different in the two basins, I compared adult size within each sex. During the first summer of treatment in MA, the average female size was similar in CA and MA (Table 7). Also there was no significant difference in the size of adult females in MA and CA in June, 1986. However by the end of that same summer, females were significantly larger in treated MA (Sept. and Oct. 1986; Table 7).

If treatment were to affect mysids in a similar manner in CA one would expect CA females in May 1985 to be larger than MA females since CA females as juveniles would have experienced environmental conditions from the previous summer when CA was treated. There was however, no significant difference in the size of adult females between CA and MA (Table 7).

Male mysids were not significantly larger in MA when treated than in untreated CA (Table 8). In fact, in October (1986), males from untreated CA were larger than MA males even though MA was treated. In May, 1985, males from CA were not larger than males in MA. In summary there was a trend for larger females in treated MA relative to the untreated basin, CA. Males, in contrast, were not influenced by lake fertilization.

Table 7. Total length (mm ± 1 standard error) of adult female mysids.

Survey	Clayoquot n	Clayoquot Mean Size	Clayoquot Range	Main n	Main Mean Size	Main Range
Nov 14/84	1	12.74	-	0	-	-
May 16/85	26	11.90±0.29	9.61-15.74	28	11.52±0.20	9.64-13.38
Aug 28/85	29	13.43±0.18	11.51-15.65	33	13.23±0.22	10.01-15.07
June 6/86	32	12.02±0.21	9.83-15.13	42	12.59±0.20	9.16-16.02
Sept 9/86	8	12.65±0.35	11.39-14.24	*20	13.69±0.24	11.33-16.04
Oct 20/86	10	12.75±0.34	11.39-14.56	*15	13.85±0.26	12.39-15.96

*significantly larger, $p<0.05$, Mann-Whitney U test

Table 8. Total length (mm ± 1 standard error) of adult male mysids.

Survey	Clayoquot n	Clayoquot Mean Size	Clayoquot Range	Main n	Main Mean Size	Main Range
Nov 14/84	4	11.97±1.16	9.67-14.38	1	13.43	-
May 16/85	23	12.33±0.48	8.85-16.38	35	12.65±0.27	8.96-15.54
Aug 28/85	17	13.53±0.41	9.43-16.31	32	14.27±0.22	11.45-17.16
June 6/86	16	13.44±0.39	9.83-15.06	61	13.73±0.22	9.93-17.34
Sept 9/86	12	13.50±0.31	12.03-15.42	13	13.83±0.25	12.89-15.85
Oct 20/86	*13	14.50±0.26	13.03-15.68	41	13.73±0.16	11.19-16.67

*significantly larger, $p<0.05$, Mann-Whitney U test

Female mysids tended to be larger in Muriel Lake than in either basin of Kennedy Lake, even though Muriel Lake was untreated for the period of this study. Male mysids were only larger in Muriel Lake in early summer surveys, and were otherwise similar in size to males in CA (Table 9).

Mysid populations within the study lakes appear to produce only a single generation per year. Most females were gravid during the early summer (June) and released young during the summer period (Figures 9 to 12). Very few gravid females remained in the population by late summer or fall. As well, the number of adults declined in the population as summer progressed (Figures 9 to 12). By fall the population consisted of mainly immature mysids with a unimodal distribution of size. Although no fall samples were collected in Muriel Lake, based on the similarity of summer populations with Kennedy Lake and the presence of few gravid females in early fall samples (September 24) it is likely that both lakes produce only a single generation per year. There was no late summer or fall release of juveniles or a large number of gravid females during the same periods, characteristic of Neomysis spp. populations that produce two to three generations per year (Johnston, 1985; Murtaugh, 1983; Toda et al., 1983). There was no difference in generation time between treated and untreated basins, although MA females may have matured slightly earlier since there were a greater number of juveniles released in MA than in CA by the June, 1986 survey (Figure 10).

Table 9. Total length (mm) of adult mysids in Muriel Lake.

Survey	Females		Males	
	Mean Size	Range	Mean Size	Range
June 15/85	13.20	12.42-14.12	15.83	14.71-17.80
July 18/85	14.34	13.30-14.94	14.38	11.26-18.18
Aug 1/85	14.11	12.59-15.39	13.45	9.42-17.32
Aug 14/85	13.23	11.74-14.90	13.04	11.18-15.76
June 25/86	14.54	12.71-18.00	15.35	13.94-18.08
July 30/86	15.12	13.98-16.59	15.25	14.48-17.19
Aug 25/86	14.70	12.13-16.93	15.88	13.98-17.25
Sept 24/86	14.90	14.67-15.23	14.22	12.14-15.53

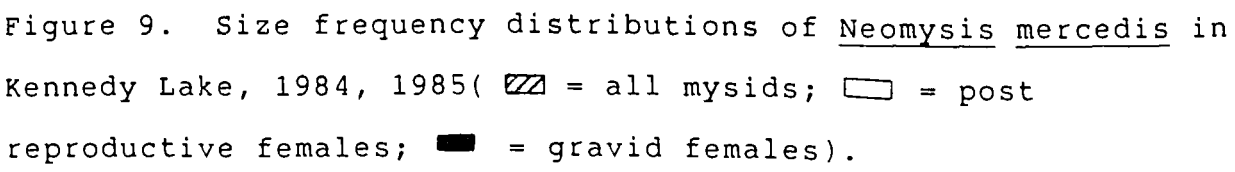


Figure 9. Size frequency distributions of Neomysis mercedis in
Kennedy Lake, 1984, 1985(= all mysids; = post
reproductive females; = gravid females).

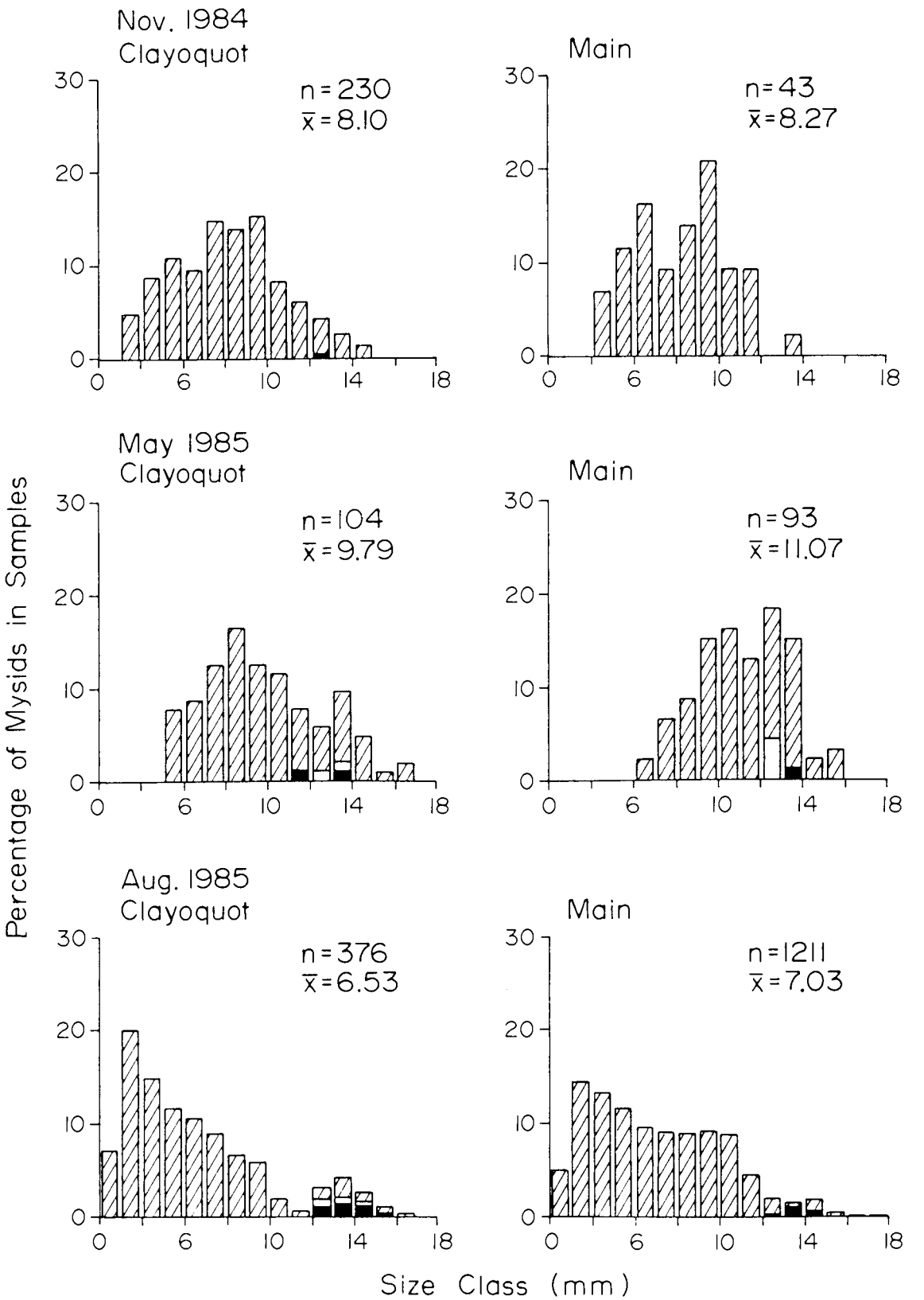

Nov. 1984
Clayoquot
n=230
x̄=8.10
Main
n=43
x̄=8.27
May 1985
Clayoquot
n=104
x̄=9.79
Main
n=93
x̄=11.07
Aug. 1985
Clayoquot
n=376
x̄=6.53
Main
n=1211
x̄=7.03
Percentage of Mysids in Samples
Size Class (mm)

Figure 10. Size frequency distributions of Neomysis mercedis in Kennedy Lake, 1986 (▨ = all mysids; ▭ = post reproductive females; ▬ = gravid females).

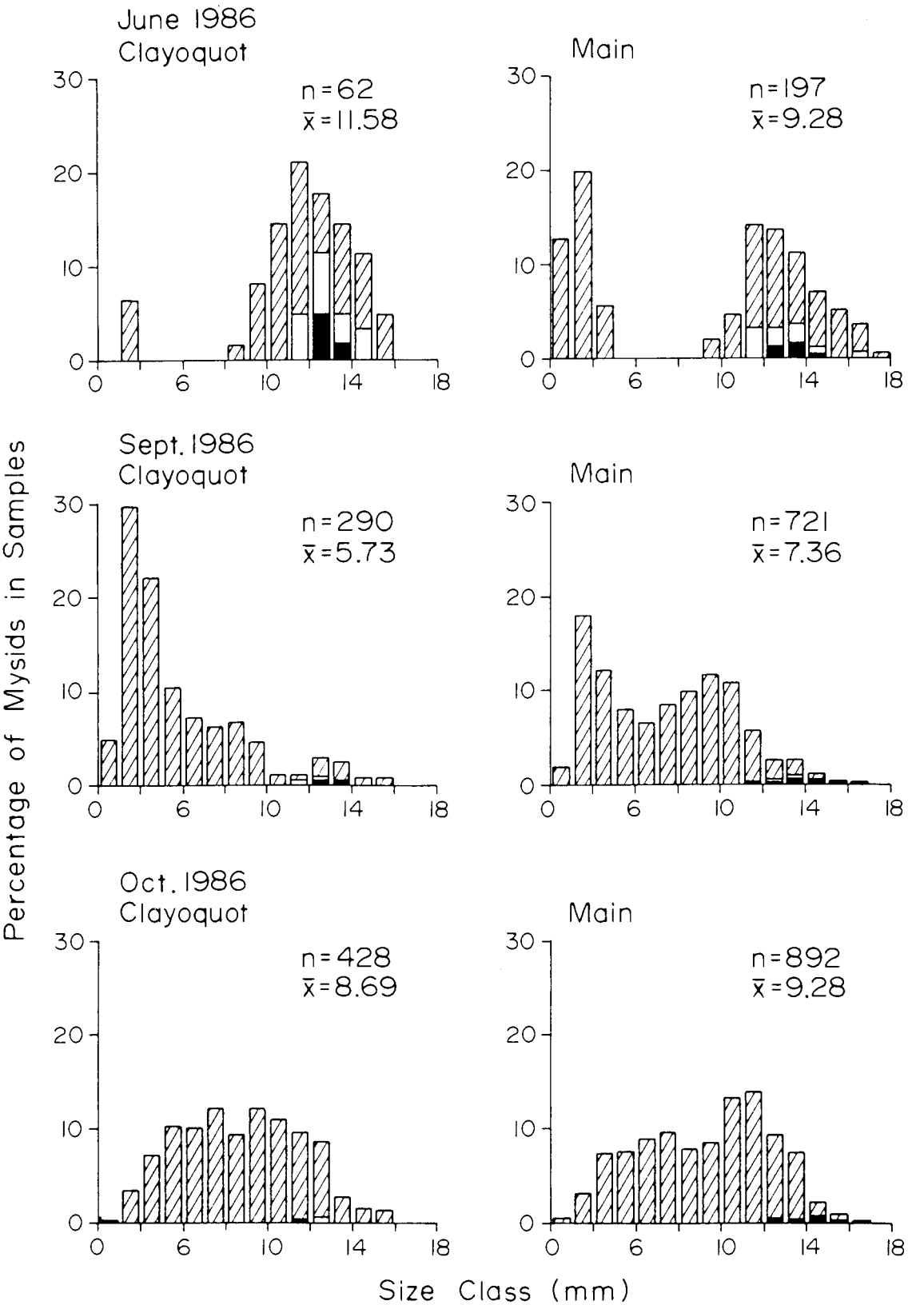

June 1986
Clayoquot
n=62
x̄=11.58
Main
n=197
x̄=9.28
Sept. 1986
Clayoquot
n=290
x̄=5.73
Main
n=721
x̄=7.36
Oct. 1986
Clayoquot
n=428
x̄=8.69
Main
n=892
x̄=9.28
Percentage of Mysids in Samples
Size Class (mm)
0
6
10
14
18
20
30

Figure 11. Size frequency distributions of Neomysis mercedis in Muriel Lake, 1985(▨ = all mysids; ▭ = post reproductive females; ■ = gravid females).

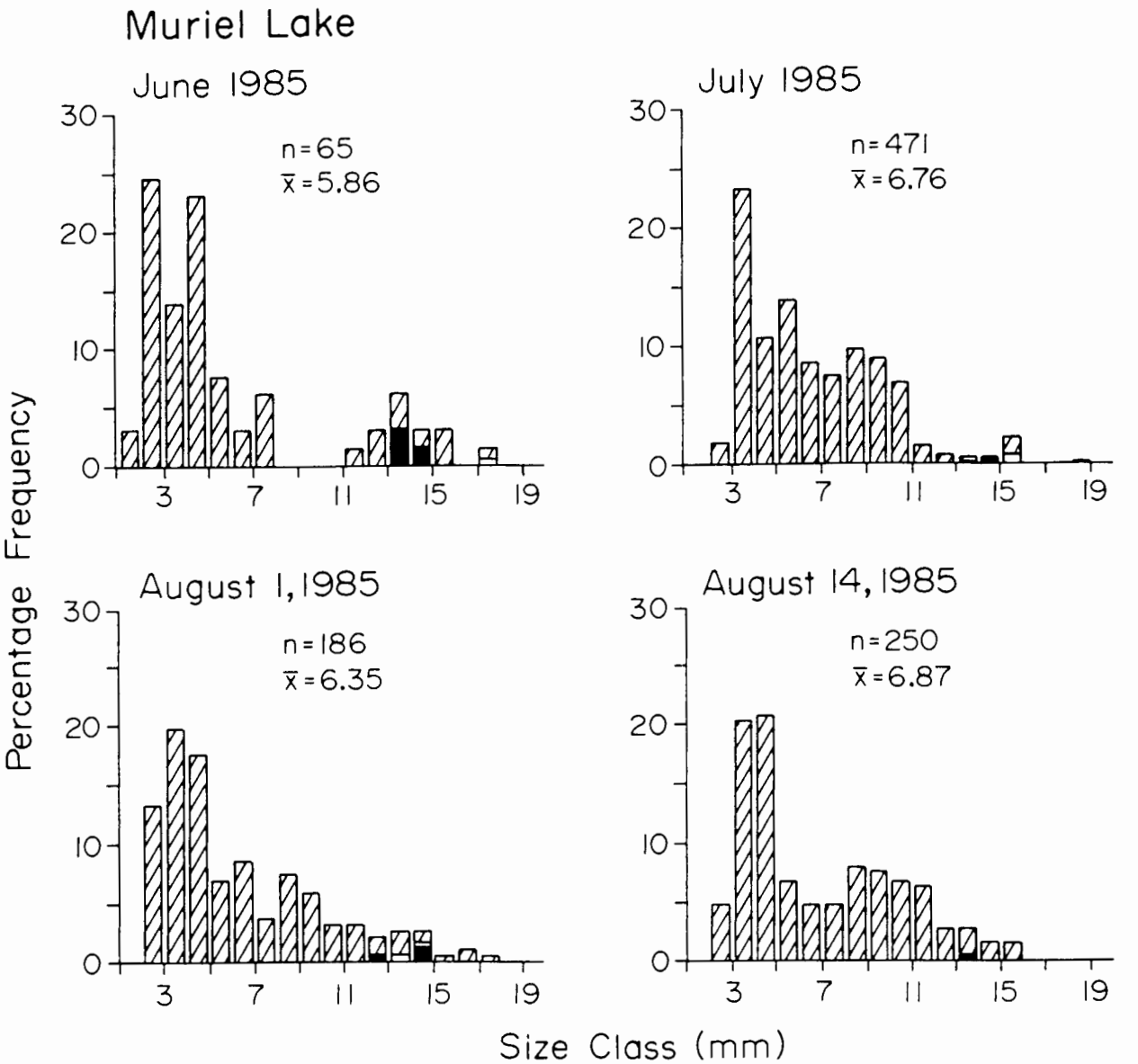
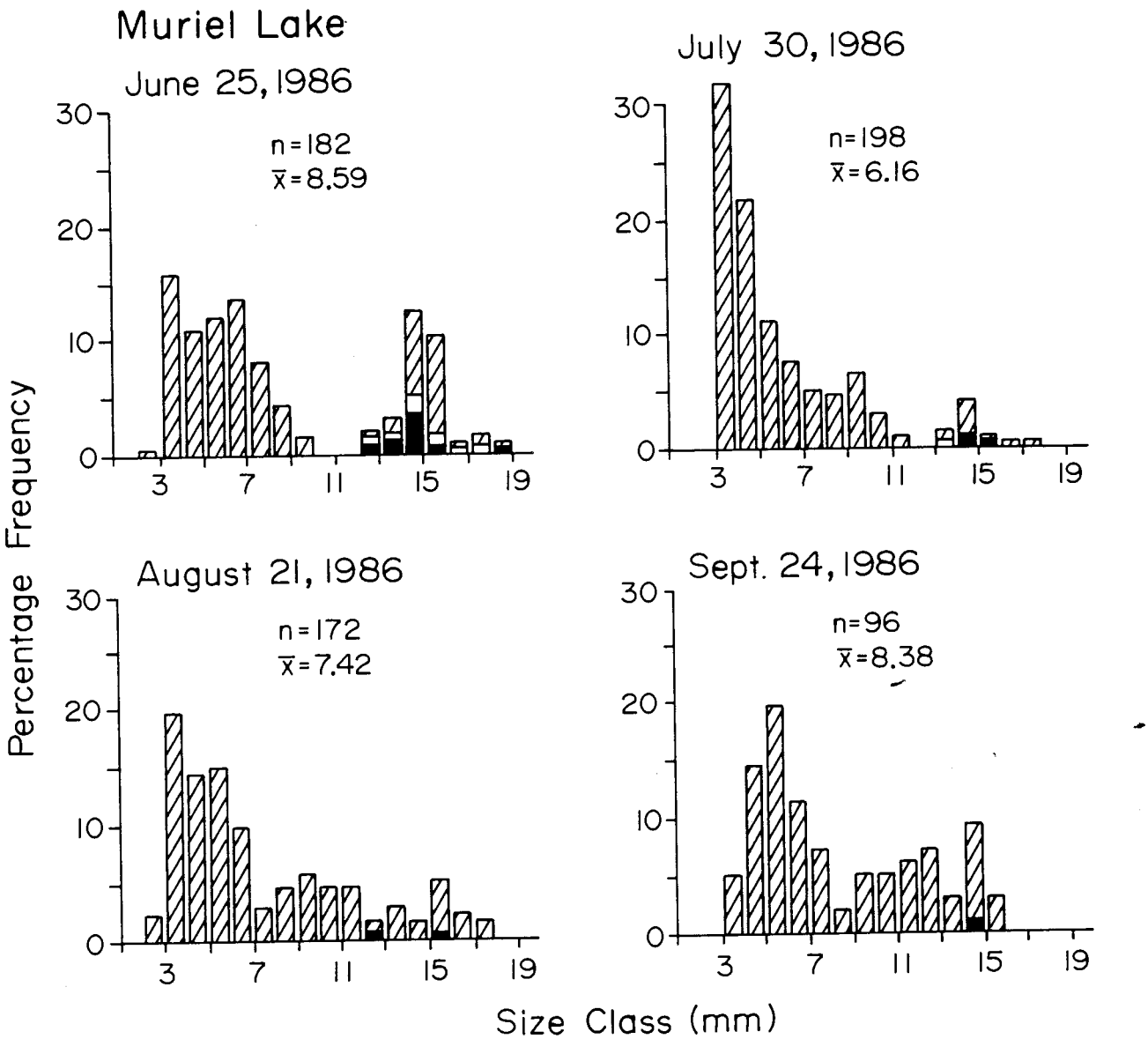

Muriel Lake
June 1985
n=65
x̄=5.86
July 1985
n=471
x̄=6.76
August 1, 1985
n=186
x̄=6.35
August 14, 1985
n=250
x̄=6.87
Percentage Frequency
Size Class (mm)
0
10
20
30
3
7
11
15
19

Figure 12. Size frequency distributions of Neomysis mercedis in Muriel Lake, 1986(▨ = all mysids; ▭ = post reproductive females; ▬ = gravid females).


Muriel Lake
June 25, 1986
n=182
x̄=8.59
July 30, 1986
n=198
x̄=6.16
August 21, 1986
n=172
x̄=7.42
Sept. 24, 1986
n=96
x̄=8.38
Percentage Frequency
Size Class (mm)
0
10
20
30
3
7
11
15
19

DISCUSSION

In my review of the literature I found that the productivity and life history parameters of mysids can be strongly influenced by food abundance. Changes in fecundity, survival, growth rates, and rate of maturity have all been attributed to increases in available food. Experimental manipulation of lake productivity through whole lake fertilization has provided further evidence that mysids are food limited.

In my study, the density and biomass of mysids was strongly related to lake fertilization. When MA was fertilized mysid density and biomass was significantly higher than in unfertilized CA. The significant increase in mysid density and biomass within MA between untreated and treated years provides further evidence that N. mercedis responded to increased production of food resources. Muriel Lake however, was not fertilized during the period of this study yet abundance of mysids was very similar to levels measured in MA when fertilized. Comparisons of natural productivity of phytoplankton and zooplankton have revealed that Muriel Lake is much more productive than Kennedy Lake when untreated. In fact, Muriel Lake is as productive untreated as CA is treated. For example, the biomass of zooplankton in Muriel Lake in 1983 was as high as CA, during years of treatment in CA. (Table 1). The response of mysids to treatment in MA, coupled with comparable

levels in naturally productive Muriel Lake provides convincing evidence that mysid population levels are dependent on lake productivity.

Two possible mechanisms which could result in an increase in population size of mysids are: 1) an increase in the reproductive output of the population; and 2) an increase in juvenile survivorship. These two mechanisms are not mutually exclusive. There was no evidence for an increase in female clutch size with treatment since clutch size did not differ between treated MA and untreated CA. However, resource limitation could affect the reproductive capacity of the population by changing the proportion of adult females breeding. Johnson (1985), in his study of a Fraser River N. mercedis population found that the proportion of gravid adult females depended on prior food availability. This would be expected if mysids, to produce eggs were largely dependent on the acquisition of energy over the molt preceding egg laying. In Kennedy lake I found that in four out of five surveys during which MA was fertilized, the proportion of gravid females was greater than found in CA, although not significant (Table 6). Since females appeared to release their young sooner in MA (June, 1986; Figure 10) relative to CA (June, 1986), the proportion of gravid females could have been underestimated in MA. It is therefore possible that the proportion of gravid females was greater in treated lake conditions. Based on these results, there is evidence that lake productivity affected the

proportion of reproductive females in the population. However, larger sample sizes are needed to assess this trend more conclusively.

A difference in juvenile survivorship with lake fertilization is another possible explanation for the numerical differences between treated and untreated basins. In experimental enclosure studies by Neill and Peacock (1980), the survival of juvenile Chaoborus spp. was increased significantly after additions of high levels of fertilizer. The increase in juvenile survivorship was attributed to an increase in rotifers, a major component of the diet of earlier life stages of Chaoborus. It may be that a similar bottleneck in juvenile survivorship controls mysid populations in Kennedy lake. The release of juvenile mysids is synchronous, with a large number of juveniles released over a short time span. Many individuals would therefore be competing for similar resources. If resources were limiting for juvenile mysids I would expect the abundance of mysids to be greater in the treated basin relative to the untreated basin following the release of juveniles. I observed that the density of mysids was higher in treated MA than in untreated CA following the release of juveniles in early summer (Figures 5a; 9; 10). The mysid population was comprised mainly of juveniles while adults made up a small proportion of the total population; thus the difference in abundance between treated and untreated basins was largely due to the number of juveniles. The larger population of mysids in

treated MA could therefore be the result of increased juvenile survivorship. A significantly larger population of mysids was present in the fall when CA was treated, also perhaps due to a greater survival of juveniles from the summer months.

Muriel appears to be as productive as fertilized Kennedy Lake, and the high densities of mysids could be due to a high survival of juveniles. Peak densities, which were similar to MA, coincided with a period when the population was composed mostly of juvenile or immature mysids (Figures 5b; 11; 12). More direct measures of the effects of resources on juvenile survivorship are needed to confirm this as the mechanism for the mysid population increase. In summary, an increase in the number of reproductive females due to an increase in lake productivity and an increase in juvenile survivorship seem to account for the larger population of mysids in MA and Muriel Lake, relative to untreated CA.

There also appears to be a relationship between lake productivity and mysid growth and/or size. Morgan (1980) found that in one bay of Lake Tahoe, Emerald Bay, mysids reached maturity after one year while in the main basin of Lake Tahoe mysid populations matured in two years. Emerald Bay was at least two times as productive as the main basin of Lake Tahoe, thus Morgan (1980) attributed the more rapid rate of maturity in Emerald Bay to the energetic benefits gained in Emerald Bay and the resultant faster growth rates of mysids. In the present

study, adult females were significantly larger in treated MA relative to untreated CA. Average body size of females in Muriel also tended to be larger than that of untreated CA. Size of males in contrast was not consistently associated with treatment of Kennedy Lake or the productivity of the system, in the case of Muriel Lake. The larger size at maturity of female mysids was associated with the productivity of the habitat in the present study, just as Morgan (1980) observed for the Emerald Bay population of mysids. In the case of Kennedy Lake, changes in productivity were the result of lake enrichment. However, size changes of mysids in my study may have been a consequence of either changes in the length of the growing season or growth rate of mysids under treated conditions. Circumstantial evidence that females released young earlier under treated conditions precluded ready determination of whether the increase in size of mature females was due to the growing season length or growth rate of mysids.

Differences in life history, specifically generation time have also been attributed to food abundance. Morgan (1980) found that M. relicata matured in one year in the more productive system of Emerald Bay, but matured in two years in the main basin of Lake Tahoe. Morgan (1980) compared M. relicata populations in a number of lakes and in general, found that eutrophic lake mysid populations matured in one year while mysid populations in less productive systems matured in two or more years. In my study, I found very little evidence for a

change in the time to maturity of mysids other than a slightly earlier release of juveniles by female mysids in the Main Arm of Kennedy Lake in spring of 1986 (June). Despite differences in productivity, whether natural or induced, mysids in the three basins studied had very similar life cycles with one generation produced per year and a life span of one year. It is possible that the additional food resources were not sufficient to have the effects on mysid life history that Morgan (1980) found in Lake Tahoe. It is also possible that the general life history exhibited by mysids is a local adaptation to conditions in these lakes. N. mercedis populations of Muriel and Kennedy Lakes are the only N. mercedis populations that I know of limited to one generation per year. All other Neomysis populations that have been studied, produce two to three generations per year with a life span less than eight months.

I have presented evidence that a numerical increase in abundance of mysids and an increase in size at maturity of female mysids were related to lake enrichment. I also presented evidence that mysid populations from the two Kennedy Lake basins did not respond to fertilization in exactly the same manner. Though similar in physical and chemical characteristics in their natural state, there are morphometric and biotic differences between the basins which might contribute to the dissimilarity in response to enrichment. While mysid abundance was significantly different between treated and untreated states in MA within a season, the change in CA was not as clear. Although

density of mysids was significantly larger in CA when treated (Nov. 1984) than in MA, there was no difference in the density of mysids between treated (Nov. 1984) and untreated years (Oct. 1986) within CA. Two characterististics of CA that could explain the difference in apparent response to enrichment include population levels of fish in each basin, and the depth of each basin.

Mysids are commonly found in the gut contents of several fish species, including salmon and sticklebacks (Johnston, 1985; Morgan, 1980; Toda et al., 1982; also see Chapter 1). It is possible that population levels of mysids in CA may be more affected by fish predation then those of MA, since lake populations of fish (mainly sticklebacks and sockeye salmon) are much larger in CA than in MA (Hyatt pers. comm.). This could result in a reduction of mysids through either consumption by fish or competition for shared resources. However, CA stickleback and sockeye gut contents rarely include mysids. It is possible that other fish species such as prickly sculpins (Cottus asper) consume mysids in the study lakes (Hyatt, unpublished data). Eggers et al.(1978) found that mysids constituted a significant portion of the diet of prickly sculpins. The importance of sculpin predation to mysid populations in Kennedy Lake is as yet undetermined since very little is known about sculpin populations and their diet within the lake. At present, fish do not appear to be a significant mortality factor for mysids. Under the competition hypothesis,

mysids must share zooplankton resources with a larger population of fish in CA than in MA. Therefore, equal increases in resources in MA and CA may result in different responses of mysids in each basin.

Differences in lake depth may also account for the different response of mysid populations to fertilization in CA compared to that observed in MA. Although both basins reach similar maximum depths, the mean depth of CA is 48 m while the mean depth of MA is 34 m. As well, where mysids are most abundant in MA, the depth is less than 40 m (Figure 7). According to Morgan (1980), in Emerald Bay M. relicta benefit from the shallower depth there relative to the Lake Tahoe population. In Lake Tahoe a majority of the population is wholly planktonic, while in Emerald Bay there is greater contact with the bottom and associated detritus. Mysids, which are omnivorous, would benefit from the added energy source of detrital material in Emerald Bay, a source not likely utilized by the Lake Tahoe mysids. The shallower depth of MA could also mean that mysids in MA would benefit from food resources found on the lake bottom while the majority of mysids in CA would be mainly planktonic.

In conclusion there is evidence that differences in the abundance of mysids in the two basins of Kennedy Lake may be partially attributed to lake fertilization. The similarity of mysid abundance in Muriel Lake and MA may be due to Muriel Lake

being naturally as productive as Kennedy Lake when fertilized. The numerical increase of mysids when MA was treated provides evidence that mysids are food limited given the natural production levels of Kennedy Lake. In CA, fish and physical conditions such as depth may have limited the numerical response of mysids when resources were increased. The larger size at maturity of female mysids observed in MA and Muriel may also be attributed to the abundance of food resources.

The increase in density of mysids with lake fertilization in Kennedy Lake could, however, reduce the benefits of increased resources via lake fertilization for juvenile sockeye salmon. Both are planktivorous and it appears from the literature that their prey species and preferred sizes of prey items overlap significantly (Brooks, 1968; Foerster, 1968; Johnston and Lasenby, 1982; Murtaugh, 1981a; 1981b; O'Neill, 1985; Siegfried and Kopache, 1980). O'Neill and Hyatt (1987) found that fish were also food limited in Kennedy Lake when the lake was untreated. By removing resources targeted for sockeye, mysids could reduce the benefit of a resource increase with lake fertilization for sockeye salmon. The purpose of the next section is to test the impact of N. mercedis predation on the zooplankton community. Densities of mysids were chosen to represent levels found in both untreated and treated basins of the study lakes. The impact of mysid predation was measured in

terms of changes in: 1) density and biomass of limnetic zooplankton; 2) size of limnetic zooplankton and; 3) species composition of the zooplankton community.

III. INFLUENCE OF NEOMYSIS MERCEDIS PREDATION ON THE ZOOPLANKTON COMMUNITY OF MURIEL LAKE, BRITISH COLUMBIA

INTRODUCTION

Several recent studies of zooplankton community ecology have focused attention on the role of invertebrate predators in the community (Dodson, 1974; Neill, 1981). Whereas fish are known to alter the size and species composition of zooplankton through the reduction of large-sized zooplankters, (O'Brien, 1979; O'Neill and Hyatt, 1987) the impact of invertebrate predators is not well understood. However, experimental studies are accumulating which provide evidence that invertebrate predators can reduce the number of their prey and therefore have strong effects on zooplankton species composition (Confer, 1971; Dodson, 1974; Elser et al., 1987; Fedorenko, 1975; Kerfoot and Peterson, 1980; Lane, 1979; Lynch, 1979; Neill and Peacock, 1980; McQueen, 1969; Neill, 1981). Such an organizing role has been suggested for mysids in freshwater communities.

Changes in the zooplankton community and concomitant reduction of several cladoceran species have been attributed to mysid predation both in lakes where mysids naturally occurred and in systems to which they were introduced (Furst et al., 1984; 1986; Grossnickle, 1978; Goldman et al., 1979; Langford, 1981; Lasenby and Langeford, 1973; Morgan et al., 1978; Murtaugh, 1981a; Nero and Sprules, 1986; Rieman and

Falter, 1981; Threlkeld et al., 1980; Zyblut, 1970). Concurrent changes in planktivorous fish populations (Morgan et al., 1978; Richards et al., 1975) and primary production (Goldman et al., 1979) however, complicate this interpretation. More direct measures of mysid predation through experimental manipulations are needed to assess the potential role of mysids in the aquatic community.

The potential for mysid predation to change the abundance of zooplankton or particular species depends on the relationship between removal rates by the predator and productivity of zooplankton prey. Based on calculations of consumption rates, either predicted from gut fullness or calculated in feeding experiments, and combined with prey selection, several studies have concluded that mysid predation could explain the decline of some zooplankton species (Cooper and Goldman, 1980; Bowers and Vanderploeg, 1982; Murtaugh, 1981a; 1981b). Fulton (1982b) combined estimates of mysid density, clearance rates, and prey density, and predicted that estuarine mysids could potentially consume four to 16% of the standing crop of several copepod species daily. Johnston and Lasenby (1982) estimated that N. mercedis predation could result in a 12% daily mortality rate on the meiofauna, particularly harpacticoid copepods. Based on this estimate, Johnston and Lasenby (1982) concluded that mysids could have a substantial effect on zooplankton abundance and species composition. Further evidence is provided by Fulton's (1982a) experiments in enclosures in which mysids significantly

reduced the abundance of copepods and increased species diversity.

The objective of this study was to investigate the influence of N. mercedis on the zooplankton communities of two British Columbia sockeye nursery lakes. I manipulated mysid density in experimental enclosures and investigated its impact on (a) zooplankton density; (b) total zooplankton biomass; (c) zooplankton species composition; and (d) zooplankton size composition. My predictions were that mysid predation would reduce zooplankton density, biomass and size. Information from these experimental manipulations was used to predict the potential impact that mysids, as competitors, could have on the growth and survival of juvenile sockeye.

MATERIALS AND METHODS

Experimental design and procedures

Experiments were conducted in enclosures (two meter diameter) made of a woven, impermeable, fabrine^{R} plastic, that were located in Muriel Lake. Enclosures were suspended vertically in the water column to 14 m depth from wooden and styrofoam floats. Three floats were constructed, each supporting four enclosures. The floats were anchored to the lake bottom and each enclosure was weighted at the bottom. The basic experimental design involved adding differing densities of N. mercedis to the natural zooplankton community in each of these enclosures.

Techniques for water and zooplankton addition to the enclosures differed in 1985 and 1986. In 1985, with the assistance of scuba divers, enclosures were pulled downwards from the surface. The bottoms of the enclosures were covered with a 1000 μm screen to prevent entry of mysids or fish while allowing water and zooplankton to enter each enclosure as it was put in place. Once the enclosures were pulled to depth, the bottoms were tied securely and the tops attached to the float. Additional water was added by using a gasoline-powered pump. Equal quantities of water were pumped from 15, 10, 5 m, and the surface and screened through a 750 μm mesh to prevent inclusion of fish and mysids.

In 1986, in an attempt to equalize the initial zooplankton abundance and composition, a different technique was used to prepare the enclosures for the experiments. Enclosures were first emptied, cleaned and repaired. Each enclosure was then filled with filtered water from 15, 10, 5 m and the surface, as in 1985. All water was filtered through a 54 μm mesh net which excluded all zooplankton, but allowed grazable seston through. Zooplankton were collected from Muriel Lake with a 100 μm mesh SCOR net (mouth diameter 0.50 m) which was repeatedly hauled from 14 m depth to the surface. Zooplankton collected were then pooled in one large bucket, mixed and randomly distributed to each of the 12 enclosures. Filtered water (54 μm mesh) was added periodically to the enclosures during both years.

The experiment followed a randomized block design. Treatment levels included five different densities of mysids, $0 \cdot m^{-3}$, $1 \cdot m^{-3}$, $3 \cdot m^{-3}$, and $6 \cdot m^{-3}$ in 1985, and $0 \cdot m^{-3}$, $6 \cdot m^{-3}$, $6 \cdot m^{-3}$ with sticklebacks, and $12 \cdot m^{-3}$ in 1986 (Table 10). Each treatment was replicated three times, with three replicates processed in 1985 and two replicates in 1986. Densities were selected to span the range of mysid density observed in the study lakes under both treated and untreated conditions (Figure 5a). Mysids were collected from Muriel Lake after civil twilight with a 350 μm SCOR net towed horizontally at 15, 10 and 5 m depths. Mysids were mixed in one large bucket and randomly selected for addition to the enclosures. Mortality from

Table 10. Treatment conditions in experimental enclosures in 1985 and 1986, where: DC = the control enclosure lacking *Neomysis*; D1 = enclosures containing one *Neomysis*·m^{-3}; D3 = enclosures containing three *Neomysis*·m^{-3}; D6 = enclosures containing six *Neomysis*·m^{-3}; D12 = enclosures containing 12 *Neomysis*·m^{-3}; DF = enclosures containing six *Neomysis*·m^{-3}, plus sticklebacks. Stickleback density given in Table 11.

Treatment	Replicates	Mysid Density	Date
1985			
DC	3	$0 \cdot m^{-3}$	July 15-Sept 11
D1	3	$1 \cdot m^{-3}$	July 15-Sept 11
D3	3	$3 \cdot m^{-3}$	July 15-Sept 11
D6	3	$6 \cdot m^{-3}$	July 15-Sept 11
1986			
DC	2	$0 \cdot m^{-3}$	July 11-Sept 25
D6	2	$6 \cdot m^{-3}$	July 11-Sept 25
D12	2	$12 \cdot m^{-3}$	July 11-Sept 25
DF	2	$6 \cdot m^{-3}$+Fish	July 11-Sept 25

collection and handling was less than 4% in controls held for 72 h after mysid addition to the enclosures.

In 1986, sticklebacks (Gasterosteus aculeatus) were added to three enclosures which contained six mysids·m^{-3}. Sticklebacks were collected from Muriel or Kennedy Lakes (Table 11). The purpose of this treatment was to test the effect mysids would have on the zooplankton community in the presence of limnetic fish. Since sticklebacks consume similar sizes and species of zooplankton as juvenile sockeye salmon (O'Neill and Hyatt, 1987) and are more numerous, I chose to use sticklebacks in the experiments rather than sockeye.

Differences between natural lake interactions and those that occur in enclosures are often a result of enclosing the water column communities for extended periods (Stephenson et al., 1984; Smyly, 1976). To investigate whether the zooplankton community of enclosures differed from the lake, three samples were collected from the lake on each of the dates the enclosures were sampled.

Hereafter, enclosures containing 0, 1, 3, 6, and 12 mysids·m^{-3} will be referred to as DC, D1, D3, D6, and D12 respectively. Enclosures containing fish will be referred to as DF, and sample observations external to the enclosures from Muriel Lake, as DL.

Table 11. Number and body length of sticklebacks in experimental enclosures (caudal length in mm ± 1 standard deviation). Except where noted, enclosures were stocked with sticklebacks from Kennedy Lake.

Date	Replicate 1		Replicate 2	
	# Added	Mean Length	# Added	Mean Length
July 11	5	49.0±0.2	5	48.6±2.7
July 25	5	49.6±1.6	5	51.0±2.2
July 31	5	49.8±2.2	5	50.0±1.1
Aug 21	5	50.4±1.6	5	50.6±1.1
Sept 4	*6	40.2±9.1	*5	43.2±9.4
Sept 18	**8	37.4±2.6	**8	36.3±1.7

* Kennedy and Muriel Lake sticklebacks added.
** Muriel Lake sticklebacks added

Zooplankton were sampled weekly between July 15 and September 11 in 1985, and biweekly in 1986 between July 15 and September 25. From each enclosure in 1985, a 100 liter integrated zooplankton sample was obtained by collecting 10 liters of water from the surface, 1, 2, 3, 4, 5, 6, 8, 10, and 12 m depths. In 1986, a 130 liter integrated sample was obtained from each enclosure by collecting 10 liters at one meter intervals from the surface to 12 meters. Lake samples (DL) for each year were collected outside each of the three floats in the same manner enclosures were sampled for zooplankton. Mysids were not sampled with the water pump since they are not in the water column during daylight hours. Mysids are generally on or close to the bottom during the daytime. This was determined from periodic daytime vertical hauls with a 350 μm net in Muriel Lake.

Mysids were removed from the enclosures at the end of the experimental period. A net, which spanned the diameter of the enclosures (1000 μm mesh size) was used to collect mysids from the enclosures. All life stages of mysids could be caught with a net of this mesh size. Mysids were removed after civil twilight and immediately preserved in a 4% buffered formalin solution. Sticklebacks were sampled with replacement from the enclosures at biweekly intervals for gut analysis. Sticklebacks were routinely sampled and removed from the enclosures by hauling the 1000 μm net from 12 meters to the water surface, five times. To determine if mysid numbers were affected in the

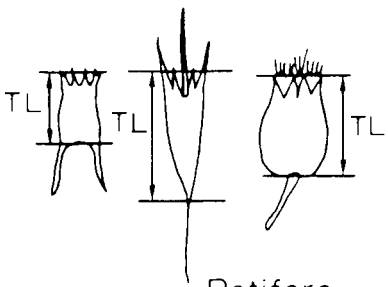
process of fish removal, the net was also hauled through one replicate of each of the mysid treatments. Replicate three from D6 and replicate two from D12 were selected randomly, and the net hauled through the enclosures in the same manner as in the fish treatments.

To investigate the nutrient status of the enclosures and lake, a water chemistry analysis was conducted in 1986. Water samples were collected on two occasions (September 11 and October 1) and tested for total phosphorous (excluded zooplankton) and chlorophyll, nitrate, and ammonia using the methods of Stephens and Brandstaetter (1983). Total phosphorous was determined using unfiltered water samples. Samples for chlorophyll a determination were collected by filtering 0.5 L of water from each depth through a 0.8 μm, 47 mm diameter Millipore AA filter.

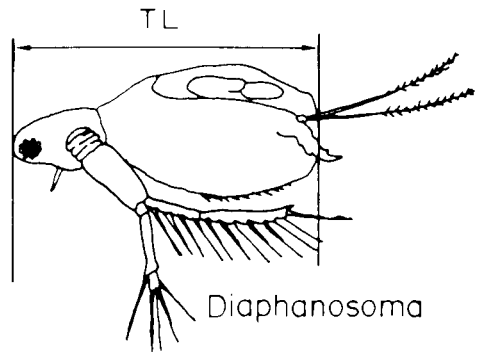
Sample processing

Mysids from the enclosures were enumerated by life stage and sex, and total length (from the rostrum to the end of the telson) measured (Figure 13). Zooplankton were identified to genus (Pennak, 1978) and total length measured (excluding antennae, setae and spines; Figure 13) with a computerized caliper system (Sprules et al., 1981). Mysids from enclosures were processed in full while zooplankton were processed in full, or split by using a Folsam splitter. If split, zooplankton in 1/4 or 1/2 of the sample were counted and measured. Zooplankton

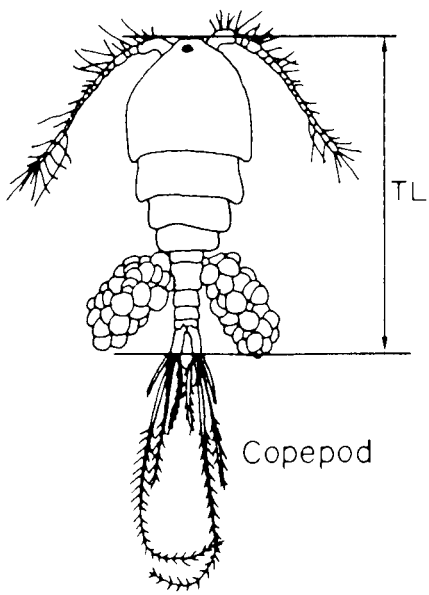
Figure 13. Dimensions measured for total body length (TL) of zooplankton species.



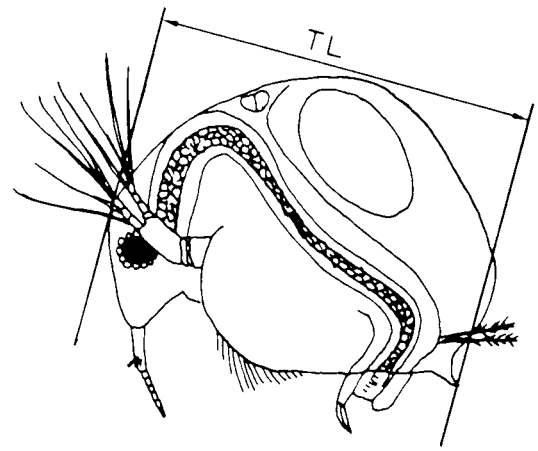
Rotifers



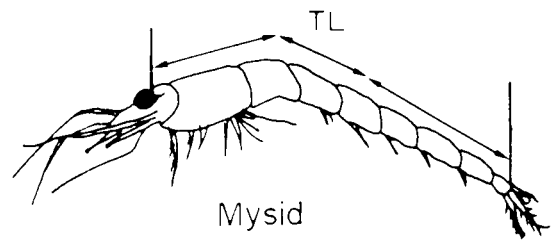
Diaphanosoma



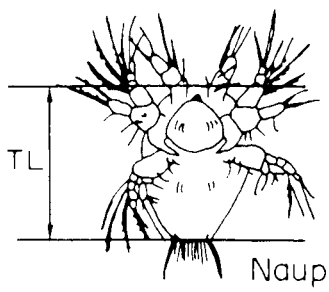
Copepod



Bosmina



Mysid



Nauplii

characteristics measured were density, biomass, species abundance and size (total length). Measures for each of these characteristics were determined at the experiment's start (July), it's midpoint (August) and endpoint (September). Zooplankton biomass was determined on the basis of published wet weight to total length regressions (Edmondson, 1971).

Data analysis

The analysis was focused to identify differences between the treatments in zooplankton density, biomass, abundance within taxa and size. I examined the mean size for all limnetic zooplankton as well as the mean size of zooplankton larger than 0.30 mm. O'Neill and Hyatt (1987) found that the majority of zooplankton in the diets of juvenile sockeye salmon or limnetic sticklebacks consisted of organisms greater than 0.30 mm in size. In order to determine if mysids had a significant impact on resources of juvenile sockeye salmon, I examined the changes within these size classes.

To test for initial similarity of these characteristics between treatments, means for each were compared at the start of each experiment (July) with a one-way analysis of variance (ANOVA). I then tested for differences between the treatments by comparing means with a repeated measures ANOVA on the August and September estimates (SPSSX, 1983). My expectation was that zooplankton density, biomass, taxa abundance and mean size would all decline as mysid abundance was experimentally increased.

Differences between the lake zooplankton community and the enclosure treatments were determined by comparing means. Zooplankton density, biomass, taxa abundance and size were measured in the lake. To test for initial similarity of enclosures and lake samples, means for each were compared with a one-way ANOVA, while conditions of the zooplankton community during the experimental period were compared by applying a repeated measures ANOVA on August and September samples. I predicted that the predators (two to six mysids$\cdot m^{-3}$ in 1985 and 1986; Figures 5b; 6b; limnetic fish: 1320 fish$\cdot ha^{-1}$(1985); 829 fish$\cdot ha^{-1}$ (1986); Kim Hyatt, pers. comm.) in Muriel Lake would reduce the density, biomass and mean size of the zooplankton population below that observed in the predator free control enclosure (DC), which excluded all large planktivores such as mysids or limnetic fish.

Repeated measures ANOVAs present a difficulty in that the significance testing procedure is unclear when there is a significant interaction term (Sokal and Rohlf, 1981). When this occurred I analyzed the August and September dates separately with a one-way ANOVA. These results are presented along with those from the repeated measures ANOVA.

RESULTS

Changes in mysid populations in enclosures

In most mysid treatments, the initial density of mysids stocked in the enclosures was not maintained for the full two months of the experiment in both 1985 and 1986 (Table 12). Mysid density also declined in Muriel Lake over the experiment period in 1986 which would indicate that mortality of mysids was not limited to enclosure treatments. The decline of mysids in both the lake and enclosures may be attributed partly to mortality of post-reproductive adults (Figure 5b). Early fall estimates of mysid density were not available for Muriel Lake in 1985, but it is apparent from the 1986 pattern in Muriel Lake and the decline of mysids in Kennedy Lake that mysid populations generally decline during the fall period.

Ignoring enclosures used as net controls and those of treatment DF for now, it would appear that growth and mortality of mysids within enclosures was density-dependent. The higher the initial density of mysids in enclosures the greater the change in mysid density by the experiment end (Table 12). Over the course of the two month experiment in 1985, there was little change in the density of mysids in treatment D1, but in D3, mysid density declined by approximately one mysid$\cdot m^{-3}$ (30 to 36% lower by September; Table 12). The reduction of mysid density was even larger in treatment D6 with mysid density 55, 52 and 75% lower in replicates one, two and three respectively. A

Table 12. Density ($no \cdot m^{-3}$) and body size (mm ± 1 standard error) of *Neomysis mercedis* in experimental enclosures for 1985 and 1986 experiments.

Treat	Rep	Density July	Density Sept	Juveniles n	Juveniles Length	Mean Length Immatures n	Immatures Length	Adults n	Adults Length
1985									
D1	1	1.0	0.6	0	-	12	14.7±0.3	12	15.9±0.2
D1	2	1.0	1.0	0	-	25	12.6±0.5	16	14.7±0.3
D1	3	1.0	1.2	0	-	31	11.7±0.4	19	15.1±0.2
D3	1	3.0	2.1	9	6.2±0.2	56	12.7±0.2	27	14.1±0.1
D3	2	3.0	1.9	12	6.8±0.2	48	11.9±0.3	22	13.9±0.2
D3	3	3.0	1.9	3	7.2±0.6	55	11.4±0.2	24	13.3±0.2
D6	1	6.0	2.7	3	6.5±0.2	96	11.3±0.2	11	13.3±0.3
D6	2	6.0	2.9	5	6.0±0.2	103	11.4±0.1	16	13.8±0.2
D6	3	6.0	1.5	0	-	53	11.0±0.2	7	12.7±0.1
1986									
D6	1	6.0	2.4	18	6.3±0.1	46	11.3±0.4	24	15.1±0.2
D6	2	6.0	2.6	14	5.9±0.8	62	10.9±0.3	18	15.3±0.2
D6	*3	6.0	1.2	-	-	-	-	-	-
D12	1	12.0	5.1	31	4.9±0.3	88	10.7±0.2	46	14.7±0.2
D12	*2	12.0	1.9	6	6.0±0.3	30	11.5±0.3	30	14.0±0.2
D12	**3	12.0	-	-	-	-	-	-	-
DF	1	6.0	0.1	-	-	-	-	-	-
DF	2	6.0	0.1	-	-	2	9.4±0.3	2	14.6±0.5
DF	3	6.0	0.0	-	-	-	-	-	-

* net control enclosures
** enclosure torn during experiment

similar pattern of mortality for mysids existed in 1986 (Table 12). In D6, mysid density was 56 to 60% lower in September relative to the initial treatment density, a similar change as in treatment D6 in 1985. Mysid density was 58% lower in D12 by the experiment end. Growth of mysids also appeared to be dependent on the density of mysids within enclosures. The higher the initial density of mysids, the smaller the mean size of individual mysids within a life stage by September (Table 12). This trend was fairly consistent for immature and adult life stages of mysids for both experimental years. Juveniles were not present in D1 treatments by the experiment endpoint in 1985. The absence of juveniles in D1 could mean that growth conditions were better when mysid density was low, so that individuals matured at a faster rate in D1 than in the D3, D6 or D12 treatments.

In 1986, the decline in mysid density was much higher within net control enclosures, over the course of the two month experiment than in other replicates of the same treatment. Mysid density was 48 to 50% lower in the net control (replicate three) than in replicates one and two of treatment D6, and 63% lower in the net control of D12 (replicate two) relative to replicate one of the same treatment (Table 12). The net was obviously detrimental to the mysid population as indicated by the decline of mysids in net control enclosures. Net control enclosures were excluded from any further comparisons. Treatment D12 was also excluded from the statistical analysis

because of the large decline in mysid density and uncertainty of treatment status of D12 over the experiment period.

The decline in mysid density was also high in enclosures of treatment DF in 1986. Less than 2% of the initial mysid density remained by the experiment end (Table 12). Stickleback predation and net mortality combined were likely responsible for the reduction of mysids in DF. High mortality of mysids within DF made it unlikely that the changes in the zooplankton community were due to mysids. Subsequent changes in the zooplankton community in August and September were therefore attributed to stickleback predation.

The influence of mysid predation on the zooplankton community

Zooplankton communities established in enclosures at the start of experiments in 1985 and 1986 were very similar. Comparisons of zooplankton community characteristics (e.g. total density, total biomass, species composition, mean size of all zooplankton; Table 13) in the mysid-free control enclosures versus those of treatment enclosures exhibiting the greatest differences revealed that no statistically significant differences existed among enclosure zooplankton communities upon initiation of experiments in either 1985 or 1986. However, subsequent comparisons between mysid-free controls and mysid treatments indicated a variable but statistically significant impact of mysids on zooplankton community structure by the

Table 13. Oneway ANOVAs and t-tests on starting conditions (July) of the zooplankton community for experimental enclosures.

Characteristics	1985			1986					
				DC vs D6			DC vs DF		
	F	df	P	F	df	P	t	df	P
Total Density	0.56	3,8	0.655	0.10	1,2	0.907	0.26	2	0.822
Diaphanosoma	0.78	3,8	0.536	0.54	1,2	0.623	-0.26	2	0.818
Bosmina	0.03	3,8	0.093	0.56	1,2	0.623	2.34	2	0.144
Diacyclops	0.24	3,8	0.868	2.74	1,2	0.210	0.70	2	0.556
Diaptomus	2.11	3,8	0.177	0.38	1,2	0.712	0.06	2	0.593
Nauplii	0.71	3,8	0.481	0.09	1.2	0.918	0.65	2	0.585
Rotifers	0.21	3,8	0.887	0.54	1,2	0.632	-0.72	2	0.548
Total Biomass	0.41	3,8	0.749	0.97	1,2	0.473	-0.57	2	0.624
Size (all)	0.92	3,8	0.476	1.80	1,2	0.306	-0.59	2	0.612
Size(>0.30mm)	1.70	3,8	0.244	0.10	1,2	0.909	0.40	2	0.726

mid-point or experiment's end in both 1985 and 1986.

In 1985, mysid predation had a major impact on the total density of zooplankton with a successive reduction of zooplankton density as mysid density increased within treatments (DC>D1>D3>D6; Figures 14b; c). This relationship was significant as revealed by a repeated measures ANOVA on August and September samples (Table 14). Zooplankton density was approximately three times higher in DC relative to D6, and twice as high in D1 as in D6 (Figures 14b,c). Zooplankton density was also reduced by mysid predation in 1986, however, the differences between DC and D6 were smaller than in 1985 (14% lower in D6 in August; Figure 15b; and 51% lower in D6 in September; Figure 15c) and a repeated measures ANOVA on August and September samples revealed that the differences were not significant (Table 14). The impact of mysid predation on the density of zooplankton in treatment D12 was not much larger than in D6. The density of zooplankton was only 37% lower in D12 than in D6 in August (Figure 15b), and 14% lower in September samples (Figure 15c).

Mysid predation also influenced the biomass of zooplankton, but again the influence was significant only in the 1985 experiment (Table 14). In August, 1985 there was a successive reduction of the biomass of zooplankton as mysid density increased across treatments (DC>D1>D3>D6). Biomass of zooplankton was two to 2.5 times higher in DC than in D3 and D6,

Figure 14. Density (a,b,c) and biomass (d,e,f) of zooplankton in Muriel Lake (DL) and experimental treatments(DC = control enclosure lacking Neomysis; D1 = enclosures containing 1 Neomysis$\cdot m^{-3}$; D3 = enclosures containing 3 Neomysis$\cdot m^{-3}$; D6 = enclosures containing 6 Neomysis$\cdot m^{-3}$) for July, August, and September, 1985 samples. Error bars equal one standard error.

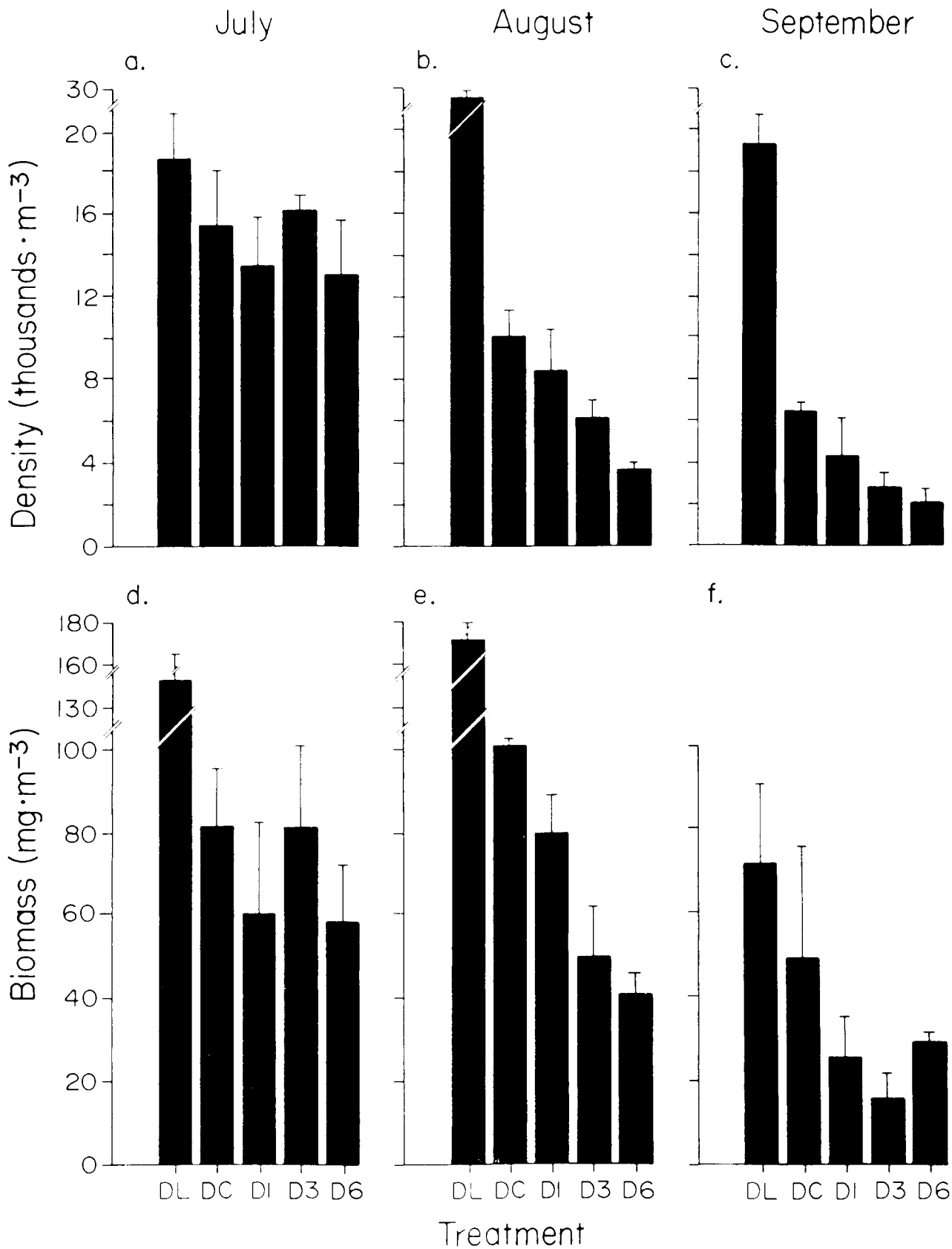

July
August
September
a.
b.
c.
d.
e.
f.
Density (thousands·m-3)
Biomass (mg·m-3)
30
20
16
12
8
4
0
180
160
130
100
80
60
40
20
0
DL DC DI D3 D6
Treatment

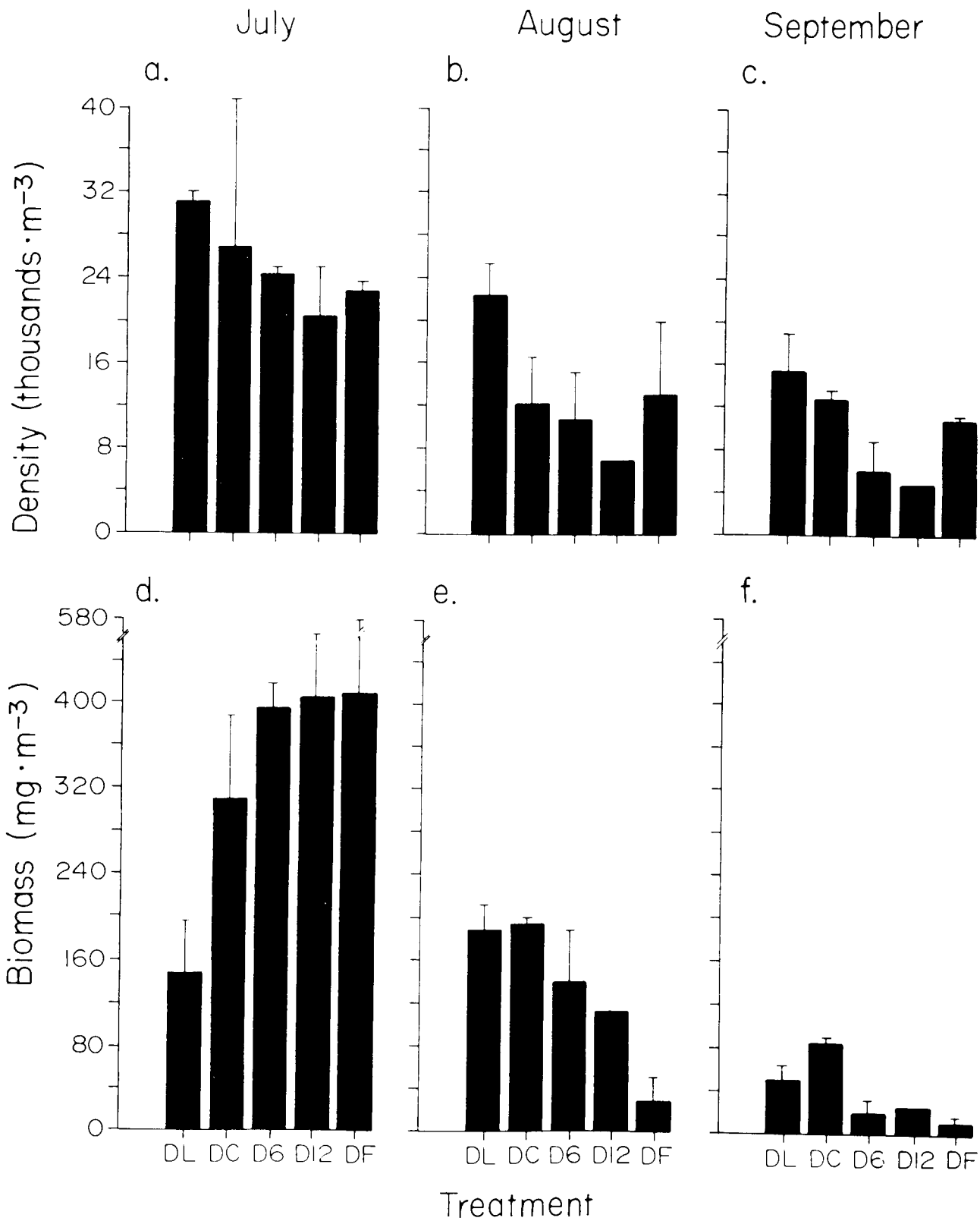
Table 14. Repeated measures ANOVAs testing for the effect of mysid predation on characteristics of the zooplankton community. Where interaction terms were significant oneway ANOVA results were used.

Characteristic	1985			1986		
	F	df	P	F	df	P
Zooplankton density						
Main Effects						
Predation	5.47	3,8	0.024	0.97	1,2	0.429
Time	63.51	1,8	<0.001	1.17	1,2	0.392
Interaction	1.88	3.8	0.211	1.58	1,2	0.336
Diaphanosoma						
Predation	15.05	3,8	0.001	1.88	1,2	0.304
Time	21.08	1,8	0.002	15.24	1,2	0.060
Interaction	2.17	3,8	0.170	1.65	1,2	0.328
Bosmina						
Predation	5.53	3,8	0.024	46.90	1,2	0.021
Time	2.15	1,8	0.181	0.66	1,2	0.502
Interaction	0.16	3,8	0.921	0.35	1,2	0.614
Diacylops						
Predation	1.59	3,8	0.267	0.96	1,2	0.431
Time	35.15	1,8	<0.001	3.60	1,2	0.198
Interaction	0.85	3,8	0.503	0.99	1,2	0.425
Diaptomus						
Predation	0.94	3,8	0.467	1.12	1,2	0.401
Time	14.69	1,8	0.005	2.96	1,2	0.227
Interaction	0.86	3,8	0.499	1.46	1,2	0.350
Nauplii						
Predation	2.49	3,8	0.135	0.83	1,2	0.458
Time	11.68	1,8	0.009	0.32	1,2	0.628
Interaction	0.71	3,8	0.571	4.46	1,2	0.169
Rotifers						
Predation	3.51	3,8	0.069	5.26	1,2	0.149
Time	24.19	1,8	0.001	0.24	1,2	0.675
Interaction	0.38	3,8	0.767	0.70	1,2	0.492

(Table 14 continued)

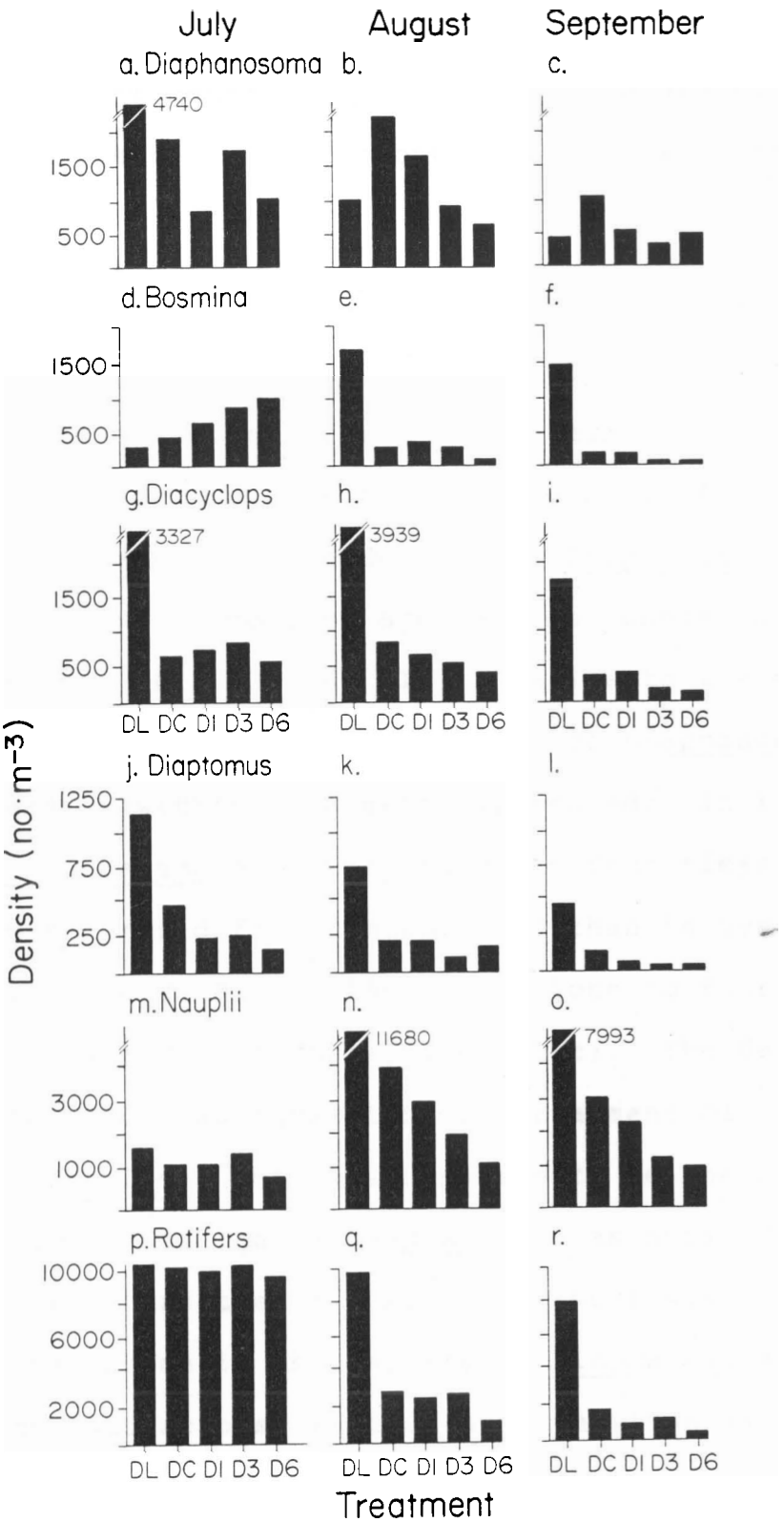
Characteristic	1985			1986		
	F	df	P	F	df	P
Zooplankton biomass						
Main Effects						
Predation	6.69	3,8	0.014	4.52	1,2	0.167
Time	34.23	1,8	<0.001	46.37	1,2	0.021
Interaction	2.19	3,8	0.168	0.05	1,2	0.840
Zooplankton Size (total community)						
Main Effects						
Predation	8.19	3,8	0.008	0.45	1,2	0.572
Time	0.00	1,8	0.977	26.18	1,2	0.036
Interaction	7.03	3,8	0.012	0.07	1,2	0.812
Oneway Aug	1.75	3,8	0.234			
Oneway Sept	11.90	3,8	0.003			
Zooplankton Size (>0.30 mm)						
Main Effects						
Predation	2.40	3,8	0.143	1.04	1,2	0.415
Time	5.59	1,8	0.046	2.61	1,2	0.247
Interaction	1.36	3,8	0.322	1.57	1,2	0.337

Figure 15. Density (a,b,c) and biomass (d,e,f) of zooplankton in Muriel Lake (DL) and experimental treatments(DC = control enclosure lacking *Neomysis*; D6 = enclosures containing 6 *Neomysis*$\cdot m^{-3}$; D12 = enclosures containing 12 *Neomysis*$\cdot m^{-3}$; DF = enclosure containing 6 *Neomysis*$\cdot m^{-3}$ and sticklebacks) for July, August, and September, 1986 samples. Error bars equal one standard error.


July
August
September
a.
b.
c.
d.
e.
f.
Density (thousands · m⁻³)
Biomass (mg · m⁻³)
40
32
24
16
8
0
580
400
320
240
160
80
0
DL DC D6 D12 DF
Treatment

respectively (Figure 14e). A similar pattern was observed across treatments in September with the exception of treatment D6 (DC>D6>D1>D3). The biomass of zooplankton in treatment D6 was similar to D1 (Figure 14f). The density of Diaphanosoma in D6 was not much lower than in treatment D1 (Figure 16c) which may explain the larger than expected biomass of zooplankton in D6 in September samples. Changes in the density of this large (generally larger than 0.3 mm) cladoceran would alter the total biomass of the zooplankton community. Within the first month of the 1986 experiment, the biomass of zooplankton had declined only slightly in D6 relative to DC (biomass of zooplankton in D6 was 28% lower; Figure 15f). By the same point in time in 1985, zooplankton biomass in D6 was over 50% lower than DC (Figure 14e). Mysid predation appeared to have a larger influence on zooplankton biomass by September since biomass in D6 was 73% lower than in DC (Figure 15f), however, the relationship was not significant as revealed by a repeated measures ANOVA on August and September sampling dates (Table 14). Doubling the density of mysids in enclosures in 1986 appeared to have little further impact on the total biomass of zooplankton since zooplankton biomass in D12 was only marginally lower than D6 in August (Figure 15e) and higher than D6 by September (Figure 15f). Mysids had declined dramatically in the D12 treatment over the course of the experiment, thus the difference in mysid density between treatments D6 and D12 was smaller than initially established (Table 12). The more similar treatment density of

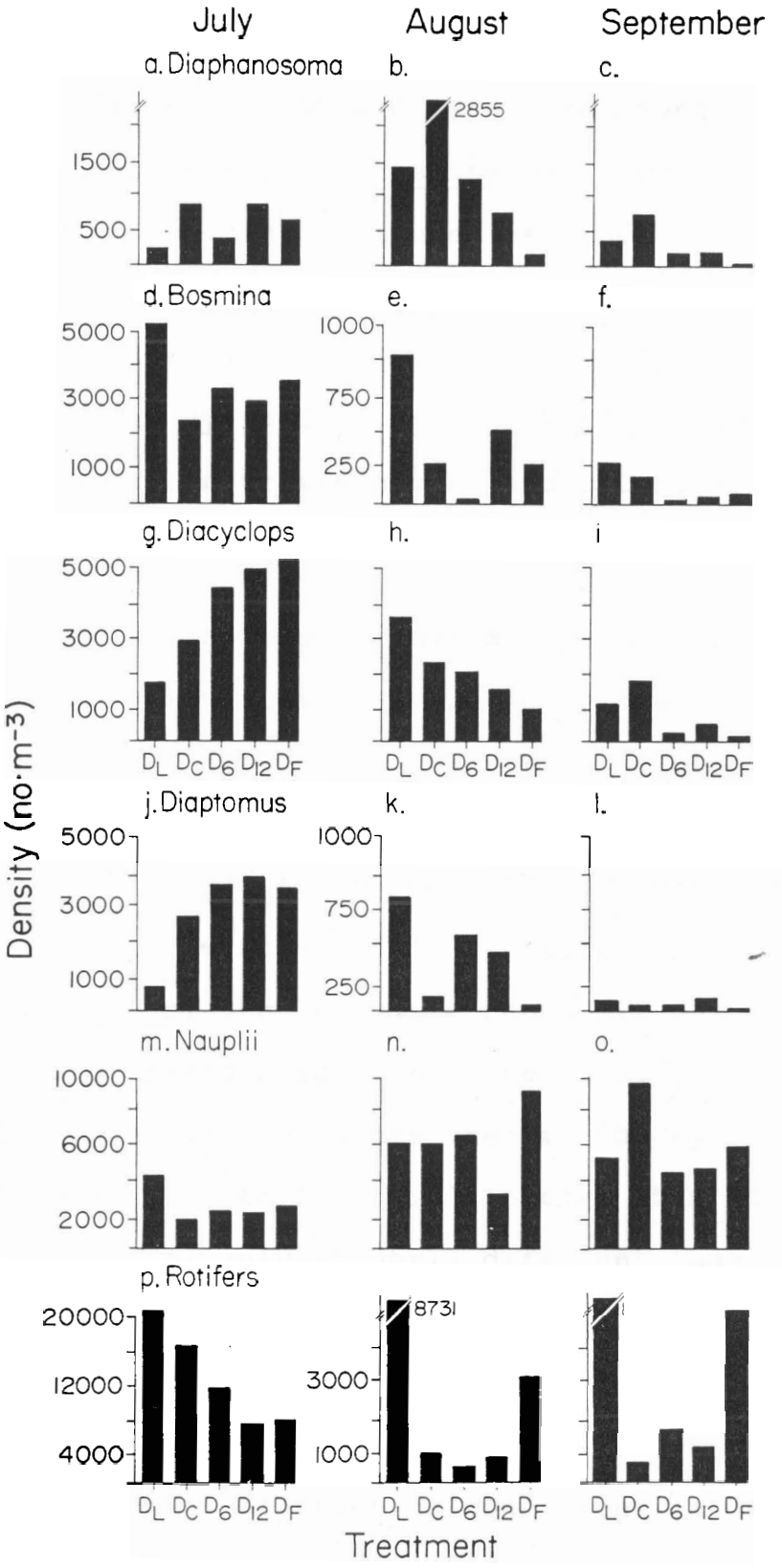
Figure 16. Density of zooplankton by species in Muriel Lake (DL) and experimental treatments (DC, D1, D3, D6) for July, August, and September, 1985 samples.


July
August
September
a. Diaphanosoma
b.
c.
4740
1500
500
d. Bosmina
e.
f.
1500
500
g. Diacyclops
h.
i.
3327
3939
1500
500
DL DC DI D3 D6
DL DC DI D3 D6
DL DC DI D3 D6
j. Diaptomus
k.
l.
1250
750
250
m. Nauplii
n.
o.
11680
7993
3000
1000
p. Rotifers
q.
r.
10000
6000
2000
DL DC DI D3 D6
DL DC DI D3 D6
DL DC DI D3 D6
Density (no·m⁻³)
Treatment

mysids in D6 and D12 by the experiment's end, may explain why the changes in the density and biomass of zooplankton within the two treatments were so similar over the course of the experiment.

The impact of mysid predation on the zooplankton community was species specific with the largest influence on the density of cladocerans, a smaller effect on the number of Diacyclops and copepod nauplii, and no effect on the density of the remaining species of zooplankton. The density of Diaphanosoma, the largest of the two cladoceran species was consistently lower in mysid treatments (D1, D3, D6, D12) relative to the mysid free control (DC) and in general the density of Diaphanosoma declined as mysid density within treatments increased. In 1985, Diaphanosoma were approximately three to four times more abundant in the mysid free control (DC) than in mysid treatments D3 and D6 in August (Figure 16b), and close to four times higher in DC than in D3 in September (Figure 16c). The density of Diaphanosoma in D6 was equivalent to treatment D1 in September samples (Figure 16c), but this appeared to be the only departure from the general decline of Diaphanosoma as mysid density increased across treatments. Although there was also a successive reduction in the density of Diaphanosoma as mysid density increased across treatments in the 1986 experiment (DC>D6>D12; Figures 17b; c), the differences were not significant (Table 14).

Figure 17. Density of zooplankton by species in Muriel Lake (DL) and experimental treatments (DC, D6, D12, DF) for July, August, and September, 1986 samples.


July
August
September
a. Diaphanosoma
b.
c.
2855
1500
500
d. Bosmina
e.
f.
5000
3000
1000
1000
750
250
g. Diacyclops
h.
i
5000
3000
1000
j. Diaptomus
k.
l.
5000
3000
1000
1000
750
250
m. Nauplii
n.
o.
10000
6000
2000
p. Rotifers
8731
20000
12000
4000
3000
1000
D_L D_C D_6 D_{12} D_F
Density (no·m⁻³)
Treatment

Mysid predation had an significant impact on Bosmina population size in both 1985 and 1986 experiments (Table 14). Relative to DC the density of Bosmina was lower in treatment D6 in August (about 69% lower; Figure 16e) and in D3 and D6 in September (88% lower; Figure 16f) in the 1985 experiment. In 1986, Bosmina density was approximately 85% lower in D6 (Figure 17e; f) than in the mysid free control (DC). The density of Bosmina was similar in treatments D6 and D12 by September samples (Figure 17f).

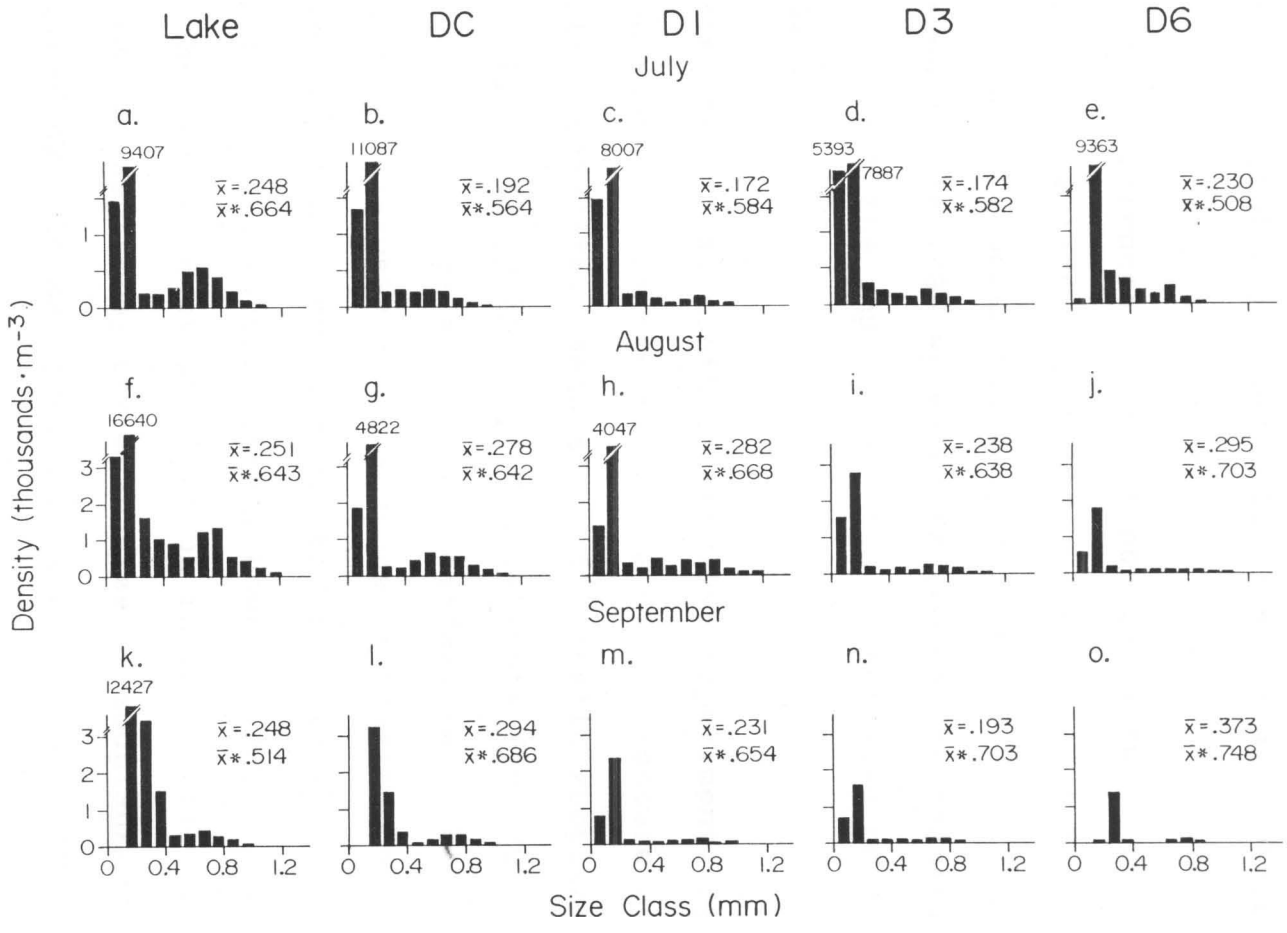
In contrast to the impact that mysids had on cladocerans, copepods were not significantly reduced by mysid predation. Although there was a progressive reduction of Diacyclops density with an increase in mysid density in both 1985 (DC>D1>D3>D6; Figures 16h; i) and 1986 (DC>D6 and D12; Figures 17h; i) the differences were not statistically significant (Table 14). Density of Diaptomus, the largest copepod present was clearly not influenced by mysid predation. The density of Diaptomus was either higher in mysid treatments than in the mysid free control (D6 and D12 were three to four times higher than DC in August, 1986; Figure 17k) or only slightly different than DC (Figures 16k; 17 l). The minimal differences in Diaptomus density between the mysid treatments (D1, D3, D6) and the mysid free control (DC) by September of the 1985 experiment (Figure 16 l) were likely a function of starting conditions rather than treatment experienced since density of Diaptomus was roughly two times higher in DC than in mysid treatments in July (Figure

16j). Although copepod nauplii generally declined with a successive increase in mysid density (DC>D1>D3>D6 and D12), this was likely due to the decline of reproductively active copepod adults in enclosure treatments rather than mysid predation. The pattern of abundance of nauplii across mysid treatments by September (Figures 16o; 17o) was generally consistent with the abundance of adult copepods, particularly Diacyclops (Figures 16i; 17i).

The presence of mysids clearly had no influence on the density of rotifers in the zooplankton community. The density of rotifers was not significantly reduced by mysid predation in 1985 (Table 14), in fact rotifers in all treatments including the mysid free control (DC) declined by roughly 80% within the first month of the experiment (Figure 16p; q). In 1986, a similar pattern emerged with small differences in rotifer density between treatments in August (Figure 17q), and the density of rotifers slightly higher in mysid treatments (D6, D12) than in DC by September (Figure 17r).

Mysid predation had no influence on the size structure of the zooplankton community in the 1985 study. Size frequency distributions were similar in pattern between the mysid free control enclosure (DC; Figures 18g; l) and mysid treatments (D1, D3, D6; Figures 18h; i; j; m; n; o) for both August and September samples. The mean size of all zooplankton was

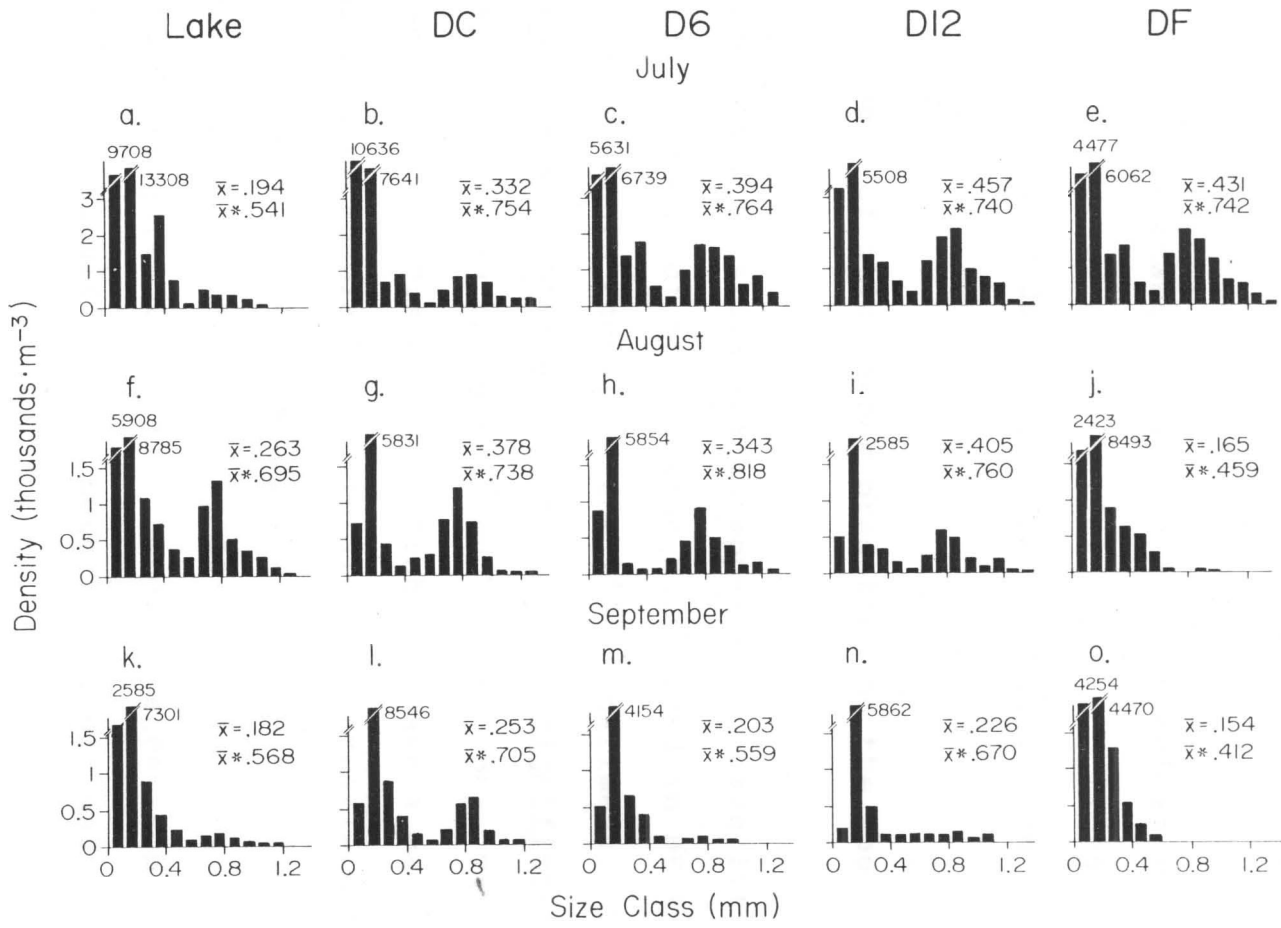
Figure 18. Size frequency distributions of zooplankton in Muriel Lake (DL) and experimental treatments (DC, D1, D3, D6) in July, August, and September, 1985. ($\bar{x}$ = mean size of total zooplankton population; $\bar{x}^*$ = mean size of zooplankton >0.30 mm).


Lake
DC
D1
D3
D6
July
August
September
a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
k.
l.
m.
n.
o.
9407
11087
8007
5393
7887
9363
16640
4822
4047
12427
x̄ =.248
x̄*.664
x̄=.192
x̄*.564
x̄=.172
x̄*.584
x̄=.174
x̄*.582
x̄=.230
x̄*.508
x̄=.251
x̄*.643
x̄=.278
x̄*.642
x̄=.282
x̄*.668
x̄=.238
x̄*.638
x̄=.295
x̄*.703
x̄=.248
x̄*.514
x̄=.294
x̄*.686
x̄=.231
x̄*.654
x̄=.193
x̄*.703
x̄=.373
x̄*.748
Density (thousands·m-3)
Size Class (mm)
0
0.4
0.8
1.2
1
2
3

significantly different between treatments by September of 1985 (Table 14) but, mean size did not decline with mysid density as predicted (D6>DC>D1>D3; Figures 18 1; m; n; o). Differences in the mean size of zooplankton between treatments were largely a function of differences in the abundance of small zooplankton rather than large zooplankton since there was no difference in the mean size of zooplankton larger than 0.3 mm (Table 14). Mysid predation in 1985 appeared to reduce the density of zooplankton, but the impact was not concentrated on large individuals.

During the first month of the 1986 experiment, mysid predation again had no impact on the size structure of the zooplankton community. Mean size of limnetic zooplankton changed very little within mysid treatments from July to August (Figures 19b; c; d; g; h; i). Any difference in mean size of zooplankton was largely a consequence of starting differences in mean size rather than changes due to treatments. Within the next month of the 1986 experiment, however, mysid predation had reduced the abundance of zooplankton in large size classes. From August to September the mean size of zooplankton (>0.30 mm) had declined by 0.26 mm in treatment D6 (Figures 19h; m), 0.09 mm in treatment D12 (Figures 19i; n) and in contrast, by only 0.03 mm in DC (Figures 19g; l). In September samples the mean size of zooplankton (>0.3 mm) was highest in DC (0.705 mm), followed by D12 (0.670 mm) and D6 (0.559 mm) respectively.

Figure 19. Size frequency distributions of zooplankton in Muriel Lake (DL) and experimental treatments (DC, D6, D12, DF) in July, August, and September, 1986. ($\bar{x}$ = mean size of total zooplankton population; $\bar{x}^*$ = mean size of zooplankton >0.30 mm).


Lake
DC
D6
D12
DF
July
August
September
a.
b.
c.
d.
e.
f.
g.
h.
i.
j.
k.
l.
m.
n.
o.
9708
13308
x̄=.194
x̄*.541
10636
7641
x̄=.332
x̄*.754
5631
6739
x̄=.394
x̄*.764
5508
x̄=.457
x̄*.740
4477
6062
x̄=.431
x̄*.742
5908
8785
x̄=.263
x̄*.695
5831
x̄=.378
x̄*.738
5854
x̄=.343
x̄*.818
2585
x̄=.405
x̄*.760
2423
8493
x̄=.165
x̄*.459
2585
7301
x̄=.182
x̄*.568
8546
x̄=.253
x̄*.705
4154
x̄=.203
x̄*.559
5862
x̄=.226
x̄*.670
4254
4470
x̄=.154
x̄*.412
Density (thousands·m⁻³)
Size Class (mm)
0
0.4
0.8
1.2
0.5
1
1.5
2
3

There was not a statistically significant difference between the mean size of zooplankton in treatments DC and D6 (Table 14), but the decline of both density of zooplankton larger than 0.3 mm and total zooplankton biomass in mysid treatments (D6,D12) relative to the changes observed in DC provides evidence that mysid predation had a substantial impact on limnetic zooplankton larger than 0.3 mm during the final month of the 1986 experiment.

The influence of stickleback predation on the zooplankton community

Predation by sticklebacks appeared to have little impact on the total numbers of zooplankton maintained in DF treatments over the two month course of the 1986 experiment. Total numbers of zooplankton in DF treatments were not significantly different from those observed in control enclosures (DC; Table 15; Figures 15b; c). Predation by fish did have a major impact on the biomass of zooplankton maintained in experimental enclosures since in August and September, DC treatments contained approximately six times the biomass of zooplankton present in DF enclosures (Figures 15e; f). The difference in biomass between DF and DC was significant on both the August and September sampling dates (Table 15).

The effects of predation by fish on the zooplankton community exhibited some similarities and some differences

Table 15. Repeated measures ANOVAs and t-tests testing for the effects of fish predation on characteristics of the zooplankton community for the 1986 experiment. Fish treatments were compared to DC (controls).

Characteristic	F	df	P
Zooplankton Density			
Main Effects			
Predation	0.01	1,2	0.923
Time	0.11	1,2	0.771
Interaction	0.18	1,2	0.711
Diaphanosoma			
Predation	8.20	1,2	0.103
Time	34.89	1,2	0.027
Interaction	29.37	1,2	0.032
T-test Aug	-3.46	2	0.074
T-test Sept	-1.75	2	0.223
Bosmina			
Predation	0.23	1,2	0.676
Time	1.71	1,2	0.321
Interaction	0.10	1,2	0.783
Diacyclops			
Predation	5.13	1,2	0.152
Time	3.62	1,2	0.197
Interaction	0.17	1,2	0.718
Diaptomus			
Predation	2.95	1,2	0.228
Time	10.13	1,2	0.086
Interaction	5.75	1,2	0.139
Nauplii			
Predation	0.01	1,2	0.948
Time	0.00	1,2	0.963
Interaction	2.06	1,2	0.288
Rotifers			
Predation	5.02	1,2	0.154
Time	2.06	1,2	0.288
Interaction	3.66	1,2	0.196

(Table 15 continued)

Characteristic	1986		
	F	df	P
Zooplankton Biomass			
Main Effects			
Predation	216.02	1,2	0.005
Time	40.18	1,2	0.024
Interaction	21.46	1,2	0.040
T-test Aug	9.15	2	0.012
T-test Sept	23.88	2	0.012
Zooplankton Size (Total Community)			
Main Effects			
Predation	6.85	1,2	0.120
Time	7.24	1,2	0.115
Interaction	5.01	1,2	0.155
Zooplankton Size (>0.30mm)			
Main Effects			
Predation	173.70	1,2	0.006
Time	4.44	1,2	0.170
Interaction	0.14	1,2	0.748

relative to the effects of mysids. Both mysids and fish reduced the biomass of all zooplankton present in treatment enclosures relative to control enclosures. However, biomass reductions produced by fish predation were considerably greater than those associated with mysid predation (Figures 15e; f). Predation by mysids appears to have depressed total numbers of zooplankton present in mysid treatments relative to control enclosures while predation by fish had a major impact on zooplankton biomass, but little effect on total numbers.

Stickleback predation had a large impact on all medium to large-sized zooplankton species, since almost all species larger than 0.30 mm were eliminated in DF. Although the difference in abundance between DF and DC was not significant for individual species (Table 15), it was obvious that densities of all medium to large (>0.3 mm) zooplankton observed in DF were much lower than in DC. The densities of Diacyclops, Diaptomus and Diaphanosoma in DC were respectively two, six, and 25-fold greater than those same species present in treatment DF in August samples (Figures 17b; h; k). By September, the densities of Diacylops, Diaptomus and Diaphanosoma in DC were respectively 12, five, and 33-fold greater than those in DF (Figures 17c; i; l). Fish predation did not appear to reduce Bosmina density within the first month of the experiment (Figure 17e), however, by September the density of Bosmina present in treatment DC was two times higher than in DF (Figure 17f). By August, copepod nauplii were more abundant in DF than in DC (Figure 17n). The

increase in copepod nauplii was not surprising considering that sticklebacks generally consume prey larger than nauplii (>0.3mm; Hyatt and O'Neill, 1987). By September, the density of nauplii was lower in DF than in DC which was likely due to the decline of adult copepods as a result of stickleback predation (Figure 17o).

Rotifer populations appeared to do better in the presence of sticklebacks, since rotifers were four times more abundant in DF than in DC in August (Figure 17q) and about nine times more numerous in DF in September (Figure 17r). In Muriel Lake, which also contains populations of limnetic fish, rotifers were three to four times more abundant than in DC in 1985 (Figures 16q; r), and up to 16 times more abundant than in DC in 1986 (Figures 17q; r).

Relative to mysid predation, predation by sticklebacks had a larger influence on the number of medium to large-sized zooplankton, with the possible exception of Bosmina which were found in comparable numbers in DF, D6 and D12 in September samples (Figure 17f). Densities of Diaphanosoma and Diacyclops were consistently lower in DF than in either D6 or D12 in the 1986 study (Figures 17b; c; h; i). Sticklebacks also reduced the abundance of Diaptomus while mysids had no influence on their abundance. Rotifers were also present in much higher densities in DF treatments than in mysid treatments.

Stickleback predation had a major impact on the size structure of the zooplankton community. The size frequency distribution of zooplankton in DF changed considerably within a month, with zooplankton larger than 0.5 mm virtually eliminated from the community by August (Figure 19j). The mean size of zooplankton (>0.3 mm) in DF had declined by over 0.3 mm by September, while in DC the mean size of zooplankton (>0.3 mm) remained relatively unchanged (Figures 19 l; o). In both August and September samples, the mean size of zooplankton (>0.3mm) was close to 0.3 mm larger in DC (Figures 19g; l) than in DF (Figures 19j; o). These differences were statistically significant (Table 15).

The influence of predators on the zooplankton community of Muriel Lake

Enclosing the zooplankton community and the stocking procedures for these enclosures resulted in differences between the communities of the lake (DL) and the enclosure control (DC) which were maintained throughout the 1985 experiment and for a portion of the 1986 experiment. Total biomass (Figure 14d), mean size of zooplankton (Figures 18a; b) and densities of Diacyclops, Diaptomus and Diaphanosoma (Figures 16a; g; j; Table 16) in 1985 were all initially lower in the control enclosure (DC) relative to the lake (DL). Total biomass (Figures 14e; f), total density (Figures 14b; c), and densities of Bosmina, rotifers (Figures 16 q; r), and copepods (Figures

Table 16. Oneway ANOVAs testing for differences in starting conditions of the zooplankton community between enclosure treatments and lake samples.

Characteristic	1985			1986		
	F	df	P	F	df	P
Total Density	1.06	4,10	0.426	0.31	4,5	0.861
Diaphanosoma	0.66	4,10	0.637	0.92	4,5	0.519
Bosmina	4.29	4,10	0.280	0.53	4,5	0.719
Diacyclops	7.26	4,10	0.005	1.05	4,5	0.465
Diaptomus	7.26	4,10	0.005	1.05	4,5	0.465
Nauplii	0.58	4,10	0.684	0.77	4,5	0.610
Rotifers	0.20	4,10	0.935	0.98	4,5	0.494
Total Biomass	2.16	4,10	0.148	1.75	4,5	0.275
Size (all)	1.41	4,10	0.299	1.88	4,5	0.252
Size (>0.30mm)	3.25	4,10	0.059	7.77	4,5	0.023

16e; f; h; i; k; l) were lower in DC in August and September samples in that year. In contrast, in 1986 total biomass (Figure 15d), mean size (Figures 19a; b; Table 16), and densities of copepods (Figures 17g; j) were initially higher in DC relative to the lake (DL) and densities of Bosmina, nauplii and rotifers were slightly lower in DC than in the lake (Figures 17d; m; p). Bosmina and rotifer densities remained lower in DC for the remainder of the experiment in 1986 (Figures 17e; f; q; r).

Techniques used to stock enclosures in 1985 (see Methods) would account for most differences between the zooplankton communities of the lake and control enclosures (DC). Large zooplankton such as copepods, which are rapid swimmers may have escaped inclusion in the enclosures when enclosures were pulled down through the water column. The densities of Diacyclops, Diaptomus and Diaphanosoma (Figures 16a; g; h; Table 16) were lower in DC which also resulted in a lower total biomass of zooplankton (41% lower in DC; Figure 14d), and mean size of zooplankton (Figures 18a; b) in DC relative to the lake (DL). Differences in total zooplankton biomass (39% lower in DC in August, Figure 14e; 19% lower in DC in September, Figure 14f), and copepod densities (Figures 16h; i; k; l; Table 17) were maintained for the two months of the experiment. Total zooplankton density was also two to three-fold higher in DL relative to DC in August and September samples (Figures 14b; c; Table 17). This could be attributed to a combination of factors

Table 17. Repeated measures ANOVAs testing for differences in lake and enclosure zooplankton communities during the experimental period in 1985 and 1986. Where interaction terms were significant, oneway ANOVA results were used.

Characteristic	1985			1986		
	F	df	P	F	df	P
Zooplankton density						
Main Effects						
Predation	56.18	4,10	<0.001	2.05	3,4	0.249
Time	171.78	1,10	<0.001	3.35	1,4	0.141
Interaction	13.05	4,10	0.001	0.64	3,4	0.627
Oneway Aug	57.64	4,10	<0.001			
Oneway Sept	43.98	4,10	<0.001			
Diaphanosoma						
Predation	14.09	4,10	<0.001	2.92	3,4	0.164
Time	28.85	1,10	<0.001	27.61	1,4	0.006
Interaction	2.14	4,10	0.150	3.98	3,4	0.108
Bosmina						
Predation	7.77	4,10	0.004	5.03	3,4	0.076
Time	1.23	1,10	0.294	7.44	1,4	0.053
Interaction	0.05	4,10	0.994	2.99	3,4	0.232
Diacylops						
Predation	84.28	4,10	<0.001	2.31	3,4	0.218
Time	22.71	1,10	0.001	14.97	1,4	0.018
Interaction	6.43	4,10	0.008	1.66	3,4	0.311
Oneway Aug	48.90	4,10	<0.001			
Oneway Sept	11.13	4,10	0.001			
Diaptomus						
Predation	10.33	4,10	0.001	2.70	3,4	0.181
Time	9.89	1,10	0.010	6.28	1,4	0.066
Interaction	1.07	4,10	0.423	1.46	3,4	0.351
Nauplii						
Predation	28.01	4,10	<0.001	0.22	3,4	0.881
Time	11.31	1,10	0.007	0.38	1,4	0.570
Interaction	2.97	4,10	0.074	1.31	3,4	0.338

(Table 17 continued)

Characteristic	1985			1986		
	F	df	P	F	df	P
Rotifers						
Predation	71.75	4,10	<0.001	12.65	3,4	0.016
Time	19.87	1,10	0.001	1.71	1,4	0.261
Interaction	0.32	4,10	0.857	1.27	3,4	0.397
Zooplankton biomass						
Main Effects						
Predation	13.91	4,10	<0.001	8.61	3,4	0.032
Time	60.48	1,10	<0.001	84.25	1,4	0.001
Interaction	5.23	4,10	0.015	6.52	3,4	0.051
Oneway Aug	24.29	4,10	<0.001	7.50	3,4	0.041
Oneway Sept	3.11	4,10	0.066	13.78	3,4	0.014
Zooplankton Size (total community)						
Main Effects						
Predation	8.09	4,10	0.004	4.21	3,4	0.099
Time	0.01	1,10	0.942	47.29	1,4	0.002
Interaction	5.59	4,10	0.013	4.66	3,4	0.086
Oneway Aug	1.87	4,10	0.192			
Oneway Sept	10.93	4,10	0.001			
Zooplankton Size (>0.30 mm)						
Main Effects						
Predation	7.06	4,10	0.006	56.40	3,4	0.001
Time	0.03	1,10	0.864	6.19	1,4	0.068
Interaction	1.20	4,10	0.369	1.22	3,4	0.410

which influenced the densities of Bosmina, rotifers, and copepod nauplii within enclosures. Bosmina populations appeared to be limited within enclosures. The density of Bosmina was slightly higher in enclosures to start (Figure 16d), but within a month Bosmina were more abundant in the lake than in the predator-free enclosure control (DC; Figures 16e; f; Table 17). The large decline of rotifers within enclosure treatments, including DC (Figure 16q; r) appeared at first due to some effect of enclosing the water column. However, as I will discuss in following sections, the reduction of rotifers was likely due to interactions among zooplankton species rather than the influence of the enclosures. The introduction of a smaller population of adult copepods within DC and thus a relatively smaller reproductive population would likely account for the smaller population of nauplii in DC than in the lake (DL) during the experiment period (Table 17; Figures 16n; o).

Stocking procedures used for the introduction of zooplankton to enclosures in 1986 would account for the higher biomass (Figure 15a) and mean size of zooplankton (Figures 19a; b; c; d; e; Table 16), and densities of large zooplankton (density of copepods was 44 to 76% lower in DL; Figures 17g; j) in enclosures in July relative to that observed in the lake (DL). The 100 μm SCOR net used to collect zooplankton for enclosures in 1986 would undersample animals such as rotifers and nauplii, which are generally smaller than 100 μm. By using this net I introduced an equivalent total density of zooplankton

to enclosures as found naturally in the lake (Figure 15a; Table 16), but large zooplankton made up the greatest proportion of the total density. Small to medium-sized zooplankton such as Bosmina, nauplii and rotifers were generally found in lower densities in enclosures, than in the lake (Figures 17d; m; p). Differences in the zooplankton communities in enclosures, as a result of stocking biases did not, however, generally extend beyond the first month of the experiment in 1986 since total zooplankton biomass, densities of Diacyclops and nauplii, and the size structure of zooplankton were quite similar in DC and DL samples by August. Bosmina populations did not recover from the initial low densities stocked in enclosures since the density of Bosmina remained lower in DC relative to the lake (DL) throughout the course of the experiment (Figures 17e; f). The lower density of rotifers in DC relative to lake samples (DL) in August and September was likely due to interactions among zooplankton species rather than an enclosure effect. The density of rotifers increased within enclosures of treatment DF (Figures 17q; r) which would indicate that enclosure environments were themselves not limiting for rotifer populations.

Nutrients and total chlorophyll levels in enclosures and in the lake were examined to determine if nutrient limitation may have contributed to differences in the density of zooplankton in enclosures. It is possible that enclosures altered the exchange patterns between the epilimnetic and hypolimnetic water so that

enclosures were less productive than the lake. Comparisons of nutrients and total chlorophyll levels in the epilimnion (two meters) of the lake and enclosures on two separate occasions during 1986 revealed no significant differences (Tables 18; 19; 20). Nitrates and total chlorophyll concentrations in the hypolimnion (seven meters) were higher in the lake than in DC in September samples (Tables 18; 20), and nitrate concentrations were significantly higher in the lake than in all treatments for October samples (Tables 19; 20). It is possible that the lower nitrate and chlorophyll concentrations within the hypolimnion may have influenced Bosmina populations. However, stocking procedures appear to account for most differences in the zooplankton communities between the lake (DL) and the enclosure control (DC). The same enclosures were used for the 1985 study, thus it is unlikely that nutrient conditions would have been any different within enclosures during the 1985 experiment.

Although the stocking procedures and the enclosures resulted in variations in the zooplankton communities within enclosures relative to the lake, some variations within the lake zooplankton community could also be attributed to the influence of predation. The density of predators (mysids and limnetic fish) in Muriel Lake did not appear to have a major influence on the total density or biomass of zooplankton in the lake throughout the study. Zooplankton density in Muriel Lake (DL) in 1986 did not differ significantly from that in the predator-free control enclosure (DC; Table 17; Figures 15b; c).

Table 18. Experimental enclosure nutrient and chlorophyll concentrations for September 11, 1986 ($\mu g \cdot l^{-1}$). Ammonia concentrations were not measured.

2 Meters Depth

Treat	Rep	Total Phosphorous	Nitrate	Ammonia	Total Chlorophyll
DC	1	1	3	-	1.00
DC	2	1	2	-	1.51
DC	2	1	5	-	1.24
DF	1	1	3	-	1.48
D12	1	3	2	-	1.22
Lake	1	3	1	-	1.07
Lake	2	1	1	-	1.00
Lake	3	*	1	-	1.05

7 Meters Depth

Treat	Rep	Total Phosphorous	Nitrate	Ammonia	Total Chlorophyll
DC	1	1	5	-	0.80
DC	2	1	1	-	0.62
DC	3	1	8	-	0.52
DF	1	1	5	-	0.62
D12	1	1	9	-	0.82
Lake	1	1	27	-	1.04
Lake	2	2	26	-	1.17
Lake	3	2	18	-	1.36

* negligable amount

Table 19. Experimental enclosure nutrient and chlorophyll concentrations for October 1, 1986 ($\mu g \cdot l^{-1}$).

2 Meters Depth

Treat	Rep	Total Phosphorous	Nitrate	Ammonia	Total Chlorophyll
DC	1	2	7	13	0.66
DC	2	3	6	5	0.71
DC	3	2	6	11	0.86
DF	1	5	7	7	0.61
DF	2	2	6	9	0.81
DF	3	5	6	15	1.70
D6	1	2	7	21	0.66
D6	2	2	6	8	0.86
D6	3	2	6	10	0.80
D12	1	2	7	13	0.68
D12	2	3	3	17	0.64
D12	3	2	5	13	1.00
Lake	1	2	7	9	1.23
Lake	2	3	6	8	1.31
Lake	3	6	6	11	1.44

7 Meters Depth

DC	1	6	6	11	0.36
DC	2	2	7	12	0.48
DC	3	2	7	8	0.80
DF	1	3	8	15	0.63
DF	2	2	7	7	0.69
DF	3	2	7	14	0.51
D6	1	2	9	18	0.32
D6	2	3	8	12	1.92
D6	3	2	7	7	0.54
D12	1	2	9	13	0.43
D12	2	4	7	5	0.59
D12	3	2	11	10	0.71
Lake	1	3	13	12	1.25
Lake	2	5	18	12	1.01
Lake	3	3	21	8	0.96

Table 20. Results of t-tests and oneway ANOVAs for the comparison of water chemistry parameters between the lake and DC in September, 1986, and the lake and all treatments in October, 1986.

September 11, 1986	t	df	P
2 Meters			
Total phosphorous	-0.38	4	0.725
Nitrate	2.65	4	0.057
Ammonia	-	-	-
Total chlorophyll	1.41	4	0.231
7 Meters			
Total phosphorous	-2.00	4	0.116
Nitrate	-5.43	4	0.006
Ammonia	-	-	-
Total chlorophyll	-4.39	4	0.012

October 1, 1986	F	df	P
2 Meters			
Total phosphorous	1.52	4	0.269
Nitrate	1.00	4	0.452
Ammonia	0.80	4	0.550
Total chlorophyll	2.33	4	0.127
7 Meters			
Total phosphorous	0.64	4	0.649
Nitrate	13.03	4	0.001
Ammonia	0.30	4	0.869
Total chlorophyll	0.77	4	0.567

Additionally, there was little difference between the biomass of zooplankton observed in DL and DC (Figures 15e; f) over the course of the two month experiment. Although there was a significant difference between the biomass of zooplankton in the lake and enclosure treatments in August and September (Table 17), this differential was due mainly to the large decline of biomass in DF rather than any major difference between treatments DC and DL (Figures 15e; f). There was also little variation in decline of zooplankton biomass in the predator free control (DC) and the lake (DL) over the course of the 1985 experiment (Figures 14d; e; f).

Predator populations in Muriel Lake (DL) did have a major influence on the density of Diaphanosoma within the lake. The density of Diaphanosoma was consistently lower in the lake (DL) than in the predator-free enclosure control (DC; approximately 65%; Figures 16b; c; 17b; c) for both the 1985 and 1986 experiments. Predators in Muriel Lake appeared to have a similar impact on Diaphanosoma as mysids did in enclosure treatments as indicated by the similarity of Diaphanosoma density in the lake (DL) and mysid treatments (Figures 16b; c; 17b; c). Sticklebacks in DF had a larger influence on the density of Diaphanosoma than lake predators (DL) since Diaphanosoma were about sixteen times more abundant in DL than in DF (Figure 17b; c). The smaller population of Diaphanosoma in DF, relative to the lake (DL) was likely due to the higher predation pressure of sticklebacks in treatment DF. The density

of fish in Muriel Lake had declined from previous years so that the biomass of sticklebacks in treatment DF was about three times higher than the natural biomass of limnetic fish in the lake during the experimental period (Hyatt pers. comm.). Predation by limnetic fish and mysids did not however, have a large influence on the abundance of copepods within the lake since changes in copepod populations were similar to those observed in the predator-free control enclosure (DC). From July to September in 1985, the percent change in the density of Diaptomus was similar in the lake (DL) and predator free control (DC; 68% lower by September in both DL and DC samples, Figures 16j; k; l) while the decline of Diacylops populations was only slightly higher in DL than in DC (39% and 49% lower by September in DC and DF respectively, Figures 16g; h; i). In 1986, Diacyclops were either found in higher densities in the lake or were present in only slightly lower numbers in the lake relative to the predator-free control enclosure (DC; Figures 17h; i). The influence of predation on Diaptomus populations in the lake during 1986 is not clear since Diaptomus density declined even in the absence of predators (DC) during the first month of the experiment (Figures 17k). Lake predators also had no clear influence on Bosmina populations since the density of Bosmina increased in the lake during the study period in 1985 (Figures 16d; e; f), but declined at a rapid rate (about 80% per month) over the two month study period in 1986 (Figures 17d; e; f).

Predation by mysids and fish in Muriel Lake did not result in any major shifts in the size structure of the zooplankton community in 1985, nor during the first month of the 1986 experiment. In 1985 the mean size of zooplankton (>0.3 mm) was about 0.2 mm smaller in DL than in DC by September, but this was largely due to the presence of a greater number of medium-sized (0.3 to 0.4 mm) zooplankton in DL (likely Bosmina) rather than the reduction of large zooplankton by predators in the lake (Figures 18k; l). From July to August in 1986, the abundance of large zooplankton and mean size of zooplankton increased within the lake (Figures 19a; f). The abundance of zooplankton within larger size classes (>0.4 mm) in the lake was quite similar to that of the predator-free control (DC) in August samples (Figure19g). Between August and September, however, predators in the lake appeared to have some influence on the density of large zooplankton which resulted in a 0.13 mm decline in the mean size of zooplankton (>0.3 m; Figures 19f; k). The mean size of zooplankton (>0.3 mm) and the density of zooplankton in size classes larger than 0.4 mm also declined slightly within the predator-free control (DC) so some differences in the size structure of the zooplankton community within the lake may have been due to seasonal changes. The influence of predation on size structure in the lake appeared to be similar to the influence of mysids, but much less than the effect of sticklebacks in enclosure treatments.

DISCUSSION

Experimental manipulation of N. mercedis density revealed that mysid predation had a significant impact on the density and biomass of zooplankton, with the largest effect on cladocerans. The influence of mysid predation on the zooplankton community was however, limited to times when zooplankton prey densities were low.

In 1985, total density and biomass of zooplankton, and the density of both cladoceran species, Diaphanosoma and Bosmina were reduced by mysid predation. Mysids had a small, but insignificant effect on Diacyclops and copepod nauplii, but no effect on Diaptomus, a larger calanoid copepod, or on rotifers. These findings are consistent with a number of studies of mysid feeding in which cladocerans were commonly selected, and copepods and nauplii under-represented in the diets of mysids (Cooper and Goldman, 1980; Grossnickle, 1978; Murtaugh, 1981a; Siegfried and Kopache, 1980). Rotifers have rarely been reported in the diets of mysids (Siegfried and Kopache, 1980). In 1986, when I repeated the experiments, total density and biomass of zooplankton were not significantly influenced by mysid predation. Bosmina was the only species significantly reduced by mysid predation. The density of Diaphanosoma and Diacyclops also declined with the experimental increase of mysids, but the relationship between mysid density and zooplankton abundance was not significant. These results are

similar to those reported by Neill (1981) working with Chaoborus trivittatus. He found that predation by Chaoborus reduced zooplankton numbers in one year (1976), but not for the remainder of the study. In 1976, a cool, low productive year, Chaoborus appeared to produce clearly detectable changes in the zooplankton community of Gwendoline Lake. Diaphanosoma, Bosmina and two species of Diaptomus declined significantly in the presence of Chaoborus. Neill (1981) established that low temperatures in spring and small initial population densities of zooplankton slowed population growth and tended to increase the proportion of each zooplankton prey species lost to the Chaoborus population. However, in a warmer summer (1977), rapid juvenile development and compensating increases in adult zooplankton fertility generally permitted most prey species to escape regulation by Chaoborus. In 1985 of my study, the densities of cladocerans and copepods were lower in enclosures relative to populations observed in Muriel Lake. This was due to either low stocking densities of species (Diacyclops, Diaptomus and Diaphanosoma) or a reduction in abundance due to some effect of enclosing the zooplankton species in the enclosures (Bosmina). These "enclosure effects" created a situation of low population abundance similar to that produced by low spring temperatures and low lake productivity. Predators, such as mysids which behave as Type II predators (Holling, 1965) and maintain relatively high clearance rates even at low prey densities (Bowers and Vanderploeg, 1982;

Cooper and Goldman, 1980; Folt et al., 1982; Murtaugh, 1981a; Neill, 1981) are a greater threat to zooplankton when prey are present in low numbers. Thus, despite the characteristic large broods and short generation time of cladocerans, mysids were able to reduce their abundance in the zooplankton community. Copepods were not significantly influenced by mysid predation. In 1986, the density of zooplankton in enclosures was at least as high as in the lake initially, i.e. Diaphanosoma, Diacyclops and Diaptomus were present in slightly higher densities in enclosures. In this situation, with prey present at higher densities, mysid predation did not produce significant reductions in the zooplankton populations. The exception to this general trend was Bosmina, which mysids reduced significantly in both years of the study. However, populations of Bosmina were generally greater in Muriel Lake than in enclosures, including the predator-free control (DC) in both 1985 and 1986. The enclosures somehow influenced the rate of population growth of Bosmina and reduced the density of Bosmina relative to that naturally maintained in Muriel Lake. The control of zooplankton prey by mysids was limited to a time when the rate of population growth of prey was restricted, in this case by some "enclosure effect". Mysid predation appeared to have a larger, although not significant influence on densities of Diaphanosoma and Diacyclops by September of 1986. However, both species declined in the predator-free control (DC) and in the lake (DL) by the September sampling date so that the

influence of mysid predation appeared to be limited to periods when prey species were perhaps limited by seasonal changes in the lake environment.

Goldman et al. (1979) and Johnston and Lasenby (1982) also concluded that temperature and productivity of the lake would be important determinants of the extent to which freshwater mysids would influence zooplankton populations. For example, cladocerans were severely limited by resources in oligotrophic Lake Tahoe (Goldman et al., 1979). Low birth rates due to limited resources, compounded with increased death rates caused by M. relicta apparently resulted in a major decline in cladoceran numbers. In more productive Emerald Bay of Lake Tahoe, and Donner and Fallen Leaf Lakes the influence of mysids on cladoceran populations was not as large presumably due to higher birth rates among the cladocerans with the increase in food resources (Goldman et al., 1979; Morgan et al., 1981).

Only cladoceran species were significantly reduced by mysid predation, while copepods were not. The susceptibility of cladocerans to mysid predation has been attributed to their relatively slow escape response. Several workers have tested the ability of different species of zooplankton to escape currents produced by suction intake tubes simulating currents produced by filter-feeding predators. Drenner et al. (1978), for example found that Diaptomus and Cyclops were entrained significantly less often than Daphnia. The large body size and

faster escape speed of copepods may be a good "precontact" defense against mysids (Ramcharan et al., 1985). These "defenses" appeared to be sufficient in my study since mysids did not have a significant effect on copepod abundance even when copepods were present in low number in enclosures in 1985. Several studies have found that mysid predation significantly reduced the density of copepods (Johnston and Lasenby, 1982; Fulton, 1982a). However, the abundance of alternative prey items may have contributed to this pattern since alternative prey such as cladocerans were either rare (Johnston and Lasenby, 1982) or absent (Fulton, 1982a). In my study, differences in the ability of prey to escape mysid feeding currents would likely explain the "selection" and decline of cladocerans rather than the relative availability of prey since the densities of copepods and cladocerans were quite similar within enclosures.

Mysid predation appeared to have no influence on the size composition of the zooplankton community during the 1985 experiment nor during the first month of the 1986 experiment. A major reduction of zooplankton mean size (>0.3mm) and the biomass of zooplankton in mysid treatments (D6, D12) relative to the changes in DC, by September of the 1986 experiment provides some evidence that mysid predation influenced the abundance of large zooplankton. The low density of large zooplankton in enclosures at the experiment start in 1985 (i.e. there was little scope for an overall reduction in mean size to occur; Figures 18a; b; c; d; e) compared with the large number of

zooplankton within size classes greater than 0.5 mm in enclosures in 1986 at the experiment start (Figures 19b; c; d; e) may be one possible explanation for the absence of a change in mean size of zooplankton with mysid predation in 1985. It would appear however, that the influence of mysids on the size structure of the zooplankton community may be limited to a period when zooplankton populations are already affected by seasonal changes in the environment, such as a decline in food resources and temperature. The decline of large zooplankton in the mysid treatments in 1986 corresponded with a period when numbers of Diacylops, Diaphanosoma, and Bosmina, and total zooplankton biomass had also declined in the mysid free enclosure (DC). It would appear that mysid predation had no influence on larger zooplankton species during the mid-summer period, when temperature and food would be less likely to limit zooplankton populations.

In contrast to the small influence mysids had on the zooplankton community, sticklebacks had a pronounced effect on zooplankton size and species composition. Sticklebacks reduced both the biomass of the zooplankton community and the mean size of all zooplankton by virtually eliminating medium to large-sized species which included Diaphanosoma, Bosmina, Diacyclops and Diaptomus. The zooplankton community which remained was largely limited to zooplankton such as nauplii and rotifers, generally smaller than 0.3 mm in size. Physical constraints such as gill raker spacing and visual perception generally limit

planktivorous fish to zooplankton larger than 0.3 mm (O'Brien, 1979). O'Neill and Hyatt (1987) observed a similar effect of stickleback predation in enclosure experiments on the zooplankton community of Kennedy Lake. Within a short period of less than three weeks, the mean size of zooplankton decreased in enclosures containing adult sticklebacks. This size shift was associated with a decline in absolute numbers of adult copepods and an increase in the number of nauplii and rotifers. Similar results were produced by sockeye yearlings and sympatric treatments of underyearling sockeye and sticklebacks.

The influence of sticklebacks on the zooplankton community also appeared to have affected densities of rotifers. In this study, large populations of rotifers were restricted to treatments which included sticklebacks. The density of rotifers declined substantially during the course of the experiment in the predator free control (DC; 97% lower in September) and in mysid treatments (D6, D12; from 86 to 99% lower in September), but in comparison, declined only slightly in the fish treatment (DF; 37% lower in September; Figures 17p; q; r). Vanni (1987) observed a similar trend in his study, with larger populations of rotifers present when bluegills were included in treatments. Although it was not surprising to find a high density of rotifers in the presence of sticklebacks, since sticklebacks rarely consume prey in the size range encompassed by rotifers (O'Neill and Hyatt, 1987) the large difference in rotifer abundance between DC and DF was unexpected since predators of

rotifers were also rare in DC. The presence of fish appeared to contribute to the maintenance of high number of rotifers. Neill (1984) found that when large herbivorous zooplankton were removed from the fishless community he studied, rotifers increased in number. He attributed this to the removal of competition (herbivorous zooplankton) for limiting phytoplankton resources consumed by both rotifers and large herbivorous zooplankton such as Daphnia. The increase in rotifer abundance in fish treatments in this study, relative to the decline of rotifers in DC could also be explained by the change in abundance of herbivorous zooplankton (Bosmina, Diaphanosoma, Diacyclops, and smaller sizes of Diaptomus). The densities of these zooplankton species declined dramatically in fish treatments due to fish consumption, but herbivorous zooplankton were still present in large numbers by September in DC. The reduction of herbivorous zooplankton in mysid treatments appeared to be insufficient to increase resources for rotifers since the densities of rotifers in mysid treatments were not significantly different from rotifer populations in the predator-free control (DC).

In summary, stickleback predation reduced zooplankton biomass, and reduced the abundance of medium to large zooplankton to shift the size structure of the zooplankton population towards smaller size classes. In contrast, mysid predation produced significant reductions in total zooplankton density and biomass, densities of Diaphanosoma and Bosmina, and

mean size of limnetic zooplankton only when zooplankton were present in low densities. Smaller populations of rotifers in mysid treatments provides further evidence of the limited effect of mysid predation on the abundance of large herbivorous zooplankton. Stickleback control of the zooplankton community was not limited to low density zooplankton communities as were mysids.

Comparisons of the zooplankton communities in the lake and predator-free control during both years of the study provides further evidence of the limited influence of mysid predation. Densities of mysids, which ranged from a low of two mysid$\cdot m^{-3}$ in spring and late fall samples, up to a summer maximum of six mysids$\cdot m^{-3}$, and limnetic fish (ranged from 1230 fish.ha-1 in 1985 to 829 fish.ha-1; Hyatt, pers. comm) appeared to have little influence on either total density or biomass of zooplankton. The size structure of the zooplankton community, other than by September of the 1986 study was also similar in both the lake and predator-free control. Diaphanosoma, however, appeared to be clearly influenced by predator populations in the lake. Although the change in the mean size of zooplankton in 1986 and the abundance of Diaphanosoma in the lake could be attributed to mysid predation given similar trends in mysid enclosure treatments, limnetic fish populations may have contributed to this pattern. It is evident from my study of stickleback predation and from a separate study of juvenile sockeye and sticklebacks (O'Neill and Hyatt, 1987) that limnetic

fish populations produce considerable changes in the size structure, species compositions and total density of zooplankton.

Impact of mysids on juvenile sockeye salmon

Considering the limited influence of mysids on the zooplankton community of Muriel Lake, and the impact of mysid predation in experimental enclosures, it appears that mysid predation would potentially have little impact on resources for juvenile sockeye salmon during the summer months. Mysid predation did not have a significant effect on total zooplankton biomass, nor was there a strong and consistent influence on zooplankton prey "preferred" by juvenile sockeye salmon (copepods and zooplankton species larger than 0.3 mm) when zooplankton were present in densities observed naturally within Muriel Lake during the summer months. Mysid predation would likely have a similar impact on resources of juvenile sockeye salmon in Kennedy Lake. The production of zooplankton in Kennedy Lake, when fertilized was similar to the situation in untreated Muriel Lake (Table 1). The abundance of mysids in Kennedy Lake, when treated, also approximated populations in Muriel Lake (Figures 5a; b). As well, the life history and seasonal changes in the structure of mysid populations were equivalent in the two lakes. Given these similarities, the potential role and impact of mysids on the zooplankton

commmunity in Kennedy Lake, during the summer months would not likely differ significantly from observations in Muriel Lake.

The influence of mysids on the zooplankton community in both lakes could however, change seasonally. As demonstrated in the enclosure experiments in 1985 and in the late summer (September) of 1986, mysids were capable of removing a significant proportion of the biomass of zooplankton when the density of zooplankton was low or declining. During periods of low productivity such as early spring or late fall and winter when lake temperatures are generally low and zooplankton populations small (spring zooplankton biomass is approximately 66 to 80% lower than summer maximums; Kim Hyatt, pers. comm.) mysids could potentially remove a large proportion of the standing crop of zooplankton. Examination of the seasonal changes in mysid populations, however, demonstrated that total mysid biomass declined over the winter, to much lower levels by spring. By early June (spring), mysid biomass in Kennedy Lake had declined by at least 50% from summer and fall maximums (Figure 6a). Mysid biomass in Muriel Lake was also substantially lower (approximately 80% lower) in the spring than in the summer in 1985 (Figure 6b). Given the magnitude of the change of mysid biomass it is unlikely that the ratio of mysids to zooplankton during the winter period would differ much from the summer. Thus, it is probable that total zooplankton biomass consumed by the mysid population would not be any greater than observed in the summer months in Muriel Lake.

It would appear then that the increase in mysid numbers with lake fertilization would result in little impact on resources for juvenile sockeye salmon. Larger populations of mysids would be required for mysid predation to account for a significant proportion of the total zooplankton biomass. However, the apparent decline of the mysid population over the winter months indicates that conditions during this period may limit the rate of increase of the mysid population even with lake fertilization and increase of resources over the summer months.

Adult mortality following breeding would account for a portion of the decline of mysids, but juvenile and immature mortality would have to be invoked to account for the large drop in total mysid biomass over the winter months. Predation by fish, although apparent during the fall months would not likely contribute significantly to the total population decline (Kim Hyatt, pers. comm) nor would cannibalism. Experiments designed to test for cannibalism during this study did not reveal a single incident of cannibalism by mysids. A severe shortage of resources for mysids during the winter months would be the most likely explanation for the seasonal declines in the Muriel and Kennedy Lake mysid populations. Density-dependent mortality of mysids, and the relationship of individual mysid growth with population density in experimental enclosures (Table 17) makes competition for resources a plausible mechanism for population control of mysids in Kennedy and Muriel lakes. In lake systems

such as Kennedy and Muriel Lakes with such large seasonal changes in nutrient input and fluctuations in zooplankton populations, mysids would have a limited scope for increase. In conclusion, it would appear that alteration of nutrients, primary production of the lake, and changes in fish density would have more significant effects on the structure and biomass of the zooplankton community.

IV. SUMMARY AND CONCLUSIONS

Changes in Neomysis mercedis populations among treated (fertilized) lakes and years supported the hypothesis that natural populations of N. mercedis are food limited. The density and biomass of mysid populations in treated basins of Kennedy Lake increased significantly relative to populations in untreated controls. A comparison of treated and untreated years within Main basin provides further evidence that populations are food limited since both density and biomass of mysids increased significantly in treated years. The response of mysid populations to lake fertilization in Clayoquot basin was not as clear since there were no statistically significant differences in density or biomass of mysids between treated and untreated surveys. Predation by fish or competition with the large populations of limnetic sticklebacks or juvenile sockeye salmon present in Clayoquot basin, may explain why mysid populations did not respond to fertilization of this basin. The similarity of density and biomass of mysids in untreated Muriel Lake and treated Main was attributed to the naturally productive state of Muriel Lake. An increase in juvenile survivorship, and in the proportion of reproductive females could both account for the numerical increase of mysid populations in Kennedy Main following lake fertilization. I found no evidence for changes in either generation time (it remained at one generation per year) or female clutch size under treated or untreated conditions. Size at maturity of female mysids was influenced by

lake fertilization since the size of mature females was significantly greater in treated versus untreated basins in Kennedy Lake. Male mysids, in contrast did not exhibit any change in body size with lake fertilization. These results suggest that competition for food resources control N. mercedis populations under natural conditions. Density-dependent mortality and growth of mysids in experimental enclosures provides further support that competition for resources regulate mysid populations within the study lakes.

Manipulation of population density of mysids in experimental enclosures led to the general conclusion that mysid predation on zooplankton would have potentially little impact on zooplankton communities in study lakes. In 1985, enclosures treated with one, three and six mysids$\cdot m^{-3}$ had successively greater impacts on density, biomass, and species composition of zooplankton by comparison with mysid free controls. Both density and biomass of zooplankton were significantly reduced by mysid predation, however, the impact appeared to be largely limited to cladocerans. Mysid predation reduced the density of Bosmina and Diaphanosoma, but did not significantly influence densities of copepods or rotifers. Mysids did not produce a change in the mean size of zooplankton. In 1986, mysid predation had a less pronounced influence on the density, biomass and species composition of zooplankton despite the presence of mysids at six and 12 mysids$\cdot m^{-3}$ in experimental treatments. The density, biomass and mean size of zooplankton

was not significantly different in enclosures treated with mysids than in treatments lacking mysids. Bosmina was the only species significantly reduced by mysid predation. Differences between results in 1985 and 1986 were attributable to the lower zooplankton densities present in 1985 trials. Stocking techniques in 1985, and the influence of enclosing the water column resulted in a lower abundance of zooplankton within enclosures than naturally found in Muriel Lake. When zooplankton were limited in number, in this case due to "enclosure effects", mysid predation produced significant changes in the abundance of zooplankton, particularly of cladocerans. When zooplankton abundance in enclosures approached densities naturally observed in the study lake, mysid predation had a small and insignificant influence on the zooplankton community, as in 1986. The seasonal decline in density of zooplankton (density of zooplankton declined in the mysid free enclosure as well) likely due to a combination of temperature and production changes in the lake could explain why mysid predation had a larger impact on total zooplankton biomass and the abundance of zooplankton larger than 0.3 mm by September in the 1986 study, but not in the mid-summer period of the study. Observations of mysid populations within Kennedy and Muriel Lakes during periods when environmental conditions would limit zooplankton communities to low densities (fall and winter seasons) demonstrated that mysid predation would potentially have little impact on the community given the low population

levels of mysids themselves. Comparison between the impacts of treatments involving either mysids or limnetic fish indicated that planktivorous fish such as sticklebacks or juvenile sockeye salmon would be more potent agents for control of zooplankton community structure in the study lakes.

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