Trophic triangles and competition among vertebrate (*Oncorhynchus nerka, Gasterosteus aculeatus*) and macroinvertebrate (*Neomysis mercedis*) planktivores in Muriel Lake, British Columbia, Canada

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Trophic triangles and competition among vertebrate (*Oncorhynchus nerka*, *Gasterosteus aculeatus*) and macroinvertebrate (*Neomysis mercedis*) planktivores in Muriel Lake, British Columbia, Canada[1]

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Abstract: We investigated whether pelagic food web dynamics, expressed through a trophic triangle, could influence the potential success of whole-lake fertilization to enhance juvenile sockeye salmon growth. Muriel Lake (145 ha), located on Vancouver Island, was fertilized during 1984 with no apparent effect on juvenile sockeye growth. Unlike most sockeye nursery lakes, Muriel Lake contains a substantial population of the invertebrate zooplanktivore *Neomysis mercedis*. We hypothesized that competition for zooplankton prey between *Neomysis* and planktivorous fish (juvenile sockeye, threespine stickleback) could counteract beneficial effects of either natural or fertilizer-induced increases in food for fish. To test this, we assessed (1985-1986) biomass, production, and consumption of planktivorous mysids and fish and then used bioenergetics models to quantify potential competitive interactions. Our analysis suggested that *N. mercedis* consumed 7-8% of the zooplankton standing stock per day, while planktivorous fish consumed < 1.0% · d^{-1}. Although mysids were the main consumers of zooplankton, mysids were also consumed by fish. Late in 1986, an increase in mysid consumption by large, 1+ juvenile sockeye precipitated substantial declines in *Neomysis* biomass. Although this event came too late to reduce mysid competition with sockeye fry in Muriel Lake in 1986, it did highlight the potential importance of trophic triangles in pelagic food webs. We suggest that mysids may be held in check by juvenile sockeye when exogenous recruitment events result in high sockeye biomass. By contrast, recruitment failures and low sockeye biomass promote increases in *Neomysis* populations, which then control zooplankton communities such that sockeye gain little benefit from either natural or fertilizer-induced increases of zooplankton. For food web ecologists, the implication is that trophic triangles might produce alternate stable states that are mediated by external factors. For fisheries managers, the implication is that lakes containing mysids should only be fertilized when sockeye densities are high or mysid densities are low.
Keywords: competition, invertebrate planktivores, lake fertilization, pelagic food webs, sockeye salmon, trophic triangles.

Résumé : Nous avons tenté de vérifier si la dynamique de la chaîne alimentaire pélagique, exprimée sous la forme d'un triangle trophique, influence le succès de la fertilisation d'un lac et augmente la croissance de jeunes saumons rouges. Le lac Muriel (145 ha), qui est situé sur l'île de Vancouver, a été fertilisé en 1984, mais aucun effet apparent sur la croissance des jeunes saumons n'a été constaté. Contrairement à la plupart des lacs servant de pouponnières à saumons, le lac Muriel possède une grande population d'invertébrés qui se nourrissent de zooplancton, comme le *Neomysis mercedis*. Nous avons donc émis l'hypothèse que la compétition pour les proies zooplanctoniques qui existe entre les *N. mercedis* et les poissons planctonophages (jeunes saumons, épinoches à trois épines) annule les effets bénéfiques d'une plus grande quantité de nourriture disponible pour les poissons, qu'elle soit d'origine naturelle ou le résultat d'une fertilisation. Afin de tester cette hypothèse, nous avons d'abord évalué en 1985 et 1986 la biomasse, la production et l'ingestion de nourriture des mysis planctonophages et des poissons. Nous avons ensuite utilisé des modèles bioénergétiques pour quantifier les interactions de compétition potentielle. Selon notre analyse, les *N. mercedis* consomment de 7 à 8% du stock de zooplancton par jour, alors que les poissons planctonophages en consomment moins de 1,0%. Cela dit, bien que les mysis soient les principaux consommateurs de zooplancton, ils sont en retour mangés par les poissons. À la fin de 1986, une hausse de la consommation des mysis par de jeunes et gros saumons de la cohorte 1+ a engendré un déclin substantiel de la biomasse des *N. mercedis*. Cet événement est survenu trop tard pour entraîner une réduction de la compétition entre les mysis et les alevins du lac Muriel en 1986, mais il a toutefois mis en évidence l'importance potentielle des triangles trophiques dans les chaînes alimentaires pélagiques. En l'occurrence, nous croyons que les mysis puissent être mis en échec par les jeunes saumons lorsque des recrutements d'origine exogène se traduisent par une hausse de la biomasse des saumons. Au contraire, des problèmes de recrutement et une faible biomasse chez les saumons devraient favoriser un accroissement des populations de *N. mercedis* qui contrôlent pour leur part les communautés de zooplancton. Dans de telles circonstances, les saumons bénéficieraient peu d'une augmentation de la quantité de zooplancton, peu importe son origine. Pour les écologistes qui s'intéressent aux chaînes alimentaires, cela implique que les triangles trophiques peuvent produire des états de stabilité alternatifs, qui sont pour leur part modulés par des facteurs externes. Pour les gestionnaires des pêches, l'existence de ces triangles trophiques implique que les lacs contenant des mysis doivent être fertilisés uniquement lorsque les densités de saumons rouges sont élevées ou que les densités de mysis sont basses.
Mots-clés : chaînes alimentaires pélagiques, compétition, fertilisation lacustre, invertébrés planctonophages, saumon rouge, triangles trophiques.

Introduction

Traditional trophic cascade models (TCM) for freshwater pelagic food webs (Shapiro, Lamarra & Lynch, 1975; Shapiro & Wright, 1984; Carpenter, Kitchell & Hodgson, 1985; Carpenter *et al.*, 1987; 1996) imply that decreases in vertebrate-planktivore density will cascade down the food web, resulting in increased zooplankton biomass and decreased algal standing stocks (reviewed in DeMelo, France & McQueen, 1992; Brett & Goldman, 1997; Perrow *et al.*, 1997; Hansson *et al.*, 1998; McQueen, 1998). The TCM also implies that when nutrients (*i.e.*, fertilizers) are added to the bottom of a lake food web, there is an upward cascade featuring three competitive interactions. Among the primary producers, small edible algae with high surface to volume ratios are expected to out-compete large algae (Suttle *et al.*, 1988; Mazumder *et al.*, 1988). Among the grazers, large-bodied zooplankton with high grazing efficiencies are expected to out-compete small-bodied zooplankton (Brooks & Dodson, 1965). Near the top of the pelagic food web, the TCM assumes that planktivorous fish, such as juvenile sockeye salmon (Hyatt & Stockner, 1985; Stockner & MacIsaac, 1996), consume large-bodied zooplankton and that invertebrate planktivores such as *Mysis* consume small-bodied prey. This leads to the prediction that planktivorous fish benefit from increased nutrient supply because they are able to take advantage of the increased supply of large-bodied grazers and therefore out-compete macro-invertebrate planktivores.

The early major appeal of the TCM was its simplicity, and this has also proven to be its major weakness. Many studies (summarized in McQueen, Ramcharan & Yan, 2001) have shown that the dynamics of pelagic food webs are much too complex to be reliably described by the TCM. One of the major problems is that the TCM ignores or underestimates the role of invertebrate zooplanktivores. This has led to the suggestion that a more appropriate alternative model for pelagic food webs could be the intra-guild predation model (IGP) proposed by Holt and Polis (1997). The IGP is based on the proposition that fish and pelagic invertebrates compete through a trophic triangle (Hart, 2002). That is, fish can consume macro-invertebrates, and both fish and macro-invertebrates compete for a common prey (zooplankton). In contrast to the TCM, the underlying assumption is that both competitors have considerable diet overlap. Competitive outcomes are then dependent on the relative rates of production and consumption by the two competing planktivores, and on the extent of predator avoidance by the macro-invertebrates (usually through diel migration). A substantial literature supports the assertion that macro-invertebrates have important effects on zooplankton populations. *Leptodora* can consume 40-100% of annual zooplankton production (Herzig & Auer, 1990), *Chaoborus* can consume 30-120% (Ramcharan *et al.*, 2001), and introduced species such as *Bythotrephes* and *Cercopagis* can cause significant changes in the biomass and community structure of recipient lakes (Yan *et al.*, 2001).

This also applies to "mysids" (*e.g.*, *Mysis relicta* and *Neomysis mercedis*), which have been associated with the reduction or elimination of several cladoceran species in lakes where they have been introduced (Lasenby & Langford, 1973; Grossnickle, 1978; Morgan, Threlkeld & Goldman, 1978; Goldman *et al.*, 1979; Threlkeld *et al.*, 1980; Langeland, 1981; Rieman & Falter, 1981; Murtaugh, 1981a; Furst *et al.*, 1984; Furst, Hammar & Hill, 1986; Nero & Sprules, 1986). Estimates of consumption rates, based on either gut fullness or calculated from feeding experiments, have been used by several authors to conclude that mysid predation could explain the decline of several zooplankton species (Cooper & Goldman, 1980; Murtaugh, 1981a,b; Bowers & Vanderploeg, 1982). Fulton (1982b) combined estimates of mysid density, clearance rates, and prey density to predict that estuarine mysids could consume $4\text{-}16\% \cdot d^{-1}$ of the standing crop of several copepod species. Johnston and Lasenby (1982) estimated that *N. mercedis* predation could result in a 12% daily mortality rate on the meiofauna, particularly harpacticoid copepods, and they 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, where mysids significantly reduced the abundance of copepods and increased species diversity. 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 (Morgan, Threlkeld & Goldman, 1978; Rieman & Falter, 1981; Furst, Hammar & Hill, 1986; Nero & Sprules, 1986). Natural increases of the endemic species *N. mercedis* have also been correlated with the decline and near extinction of *Daphnia* in Lake Washington (Murtaugh, 1981a).

These results could be important to management programs that involve the fertilization of ultra-oligotrophic sockeye salmon nursery lakes containing mysids (Rankin, Ashton & Kennedy, 1979; Hyatt & Stockner, 1985; Stockner & Shortreed, 1985). Whole lake fertilization has been shown to increase biomass and production of phytoplankton and zooplankton (LeBrasseur *et al.*, 1978); planktivorous fish, including juvenile sockeye (Hyatt & Stockner, 1985); and macro-invertebrates such as *N. mercedis* (Cooper, Hyatt & Rankin, 1992). Since both sockeye and mysids include similar zooplankton prey in their diets (Foerster, 1968; Siegfried & Kopache; 1980, Murtaugh 1981a,b; O'Neill, 1986; O'Neill & Hyatt, 1987; Ashley *et al.*, 1997), it is important to determine whether mysid responses to lake fertilization events are, on balance, beneficial (a food resource) or detrimental (a competitor) to sockeye enhancement.

In the present context, Muriel Lake is known to have a substantial population of *N. mercedis* (Cooper, Hyatt & Rankin, 1992), and it is also known that when Muriel Lake was fertilized (1984), juvenile sockeye salmon failed to show increased growth rates. The question addressed here is to determine the extent to which *N. mercedis* might have been responsible for that outcome. To answer that question we used two data sets. First, we used the results of 1985 enclosure manipulations to assess the direct impacts of *N. mercedis* on zooplankton biomass. Second, we used 1985-1986 whole-lake data combined with bioenergetics analysis to estimate production and

consumption rates for all of the major zooplanktivores (*N. mercedis*, 0+ juvenile sockeye, 1+ sockeye, and threespine stickleback). We then used these data to model the resulting trophic triangle, and to draw conclusions about the relative competitive abilities of Muriel Lake macroinvertebrates and planktivorous fish.

Methods

SITE DESCRIPTION

Muriel Lake (40ϒ08' N, 125ϒ36' W) is situated 11 m above sea level and has an area of 145 ha (Figure 1), a maximum depth of 45 m, and a mean depth of 21 m (Rutherford *et al.,* 1986). It has a limited littoral zone, low epilimnetic nutrient levels (2.6 ∝g total phosphorous (TP)·L^{-1}, 0.93 ∝g chlorophyll *a* (chl *a*)·L^{-1} measured in 1983; 1.3 ∝g TP·L^{-1}, 1.0 ∝g chl *a*·L^{-1} measured in 1986), and a water residence time < 1 y. Fish species present in Muriel Lake include pelagic planktivores (three-spine stickleback, sockeye salmon), benthivores (peamouth chub [*Mylocheilus caurinus*]), and facultative benthivores (prickly sculpin [*Cottus asper*], cutthroat trout [*Salmo clarki clarki*], coho salmon [*Oncorhynchus kisutch*]) (Hyatt & Ringler, 1989). The zooplankton community consists of abundant species such as *Bosmina coregoni*, *Diacyclops bicuspidatus thomasi, Skistodiaptomus oregonensis, Diaphanosoma* sp., and two rotifers, *Keratella* sp. and *Kelicottia* sp. Rare species included *Sida* sp., *Polyphemus* sp., *Cyclops vernalis*, and *Hesperodiaptomus kenai* (O'Neill, 1986).

ENCLOSURE EXPERIMENTS

Enclosure experiments were conducted in Muriel Lake from July 15 through September 11, 1985. The
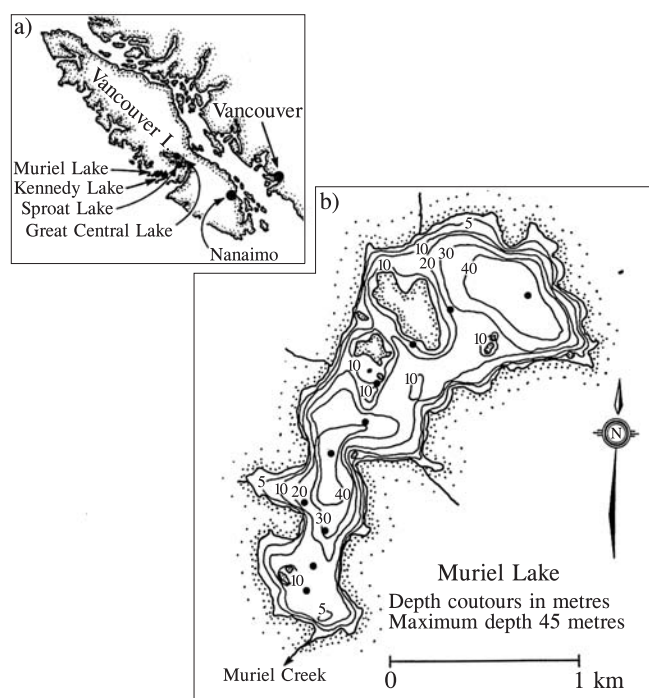

FIGURE 1. Muriel Lake bathymetric and location map showing depth features and the stations (solid circles) that were used for *Neomysis* sampling.

objective was to provide preliminary information about the relationship between mysid density and the survival of various zooplankton taxa. Twelve enclosures (2 m diameter, 14 m deep) made of a woven, impermeable, plastic were suspended from wooden and styrofoam floats that were anchored to the lake bottom. The enclosures were deployed with the assistance of scuba divers, who pulled them downwards from the surface, allowing water and plankton (excluding mysids and fish) to fill the enclosures from the bottom through 1,000 ∝m mesh. Once the enclosures were pulled to depth, the bottoms were tied securely and the tops attached to a float. Additional lake water from 0, 5, 10, and 15 m was added through 750 ∝m mesh using a gasoline-powered pump.

A randomized block design was used. Treatment levels included four different densities of mysids chosen to span the density range observed in Muriel Lake. Treatments 0, 1, 3, and 6 had 0, 1, 3, and 6 *N. mercedis*·m^{-3}. Each treatment was replicated three times, for a total of 12 enclosures. Mysids were collected at night using a 350-∝m net towed horizontally at 5, 10, and 15 m depths. They were mixed in one large bucket and randomly selected for addition to the enclosures. Mortality from collection and handling was less than 4% in controlled samples held for 72 h after mysid addition to the enclosures.

Neomysis mercedis density was estimated at the start of the experiment (July 15, 1985) and again at the end (September 11, 1985), when mysids were removed from the enclosures (after dark) using a 1,000-∝m mesh that spanned the diameter of the enclosures. All life stages of mysids—juveniles (no sexual development), immatures (sexually identifiable), and adults (females with pouch or males with 4th pleopod)—could be caught with a net of this mesh size. Mysid samples were enumerated by life stage, sex, and total length (from the rostrum to the end of the telson).

Zooplankton were sampled during daylight on July 15, 1985 (start date), August 13, and September 11, 1985 (end date). A plankton pump (pumping 33 L·min^{-1}) was used to collect 100-L integrated samples comprising subsamples of 10 L of water from the surface and 1-, 2-, 3-, 4-, 5-, 6-, 8-, 10-, and 12-m depths. The sample was filtered through a 100-∝m plankton net, and the zooplankton were preserved in 4% buffered formalin. Zooplankton were identified to genus (Pennak, 1978) and had their total length measured (excluding antennae, setae, and spines) with a computerized caliper system (Sprules, Holtby & Griggs, 1981). Zooplankton samples were processed in full or split using a Folsom splitter. Characteristics measured were species abundance and total length.

LAKE EXPERIMENTS

During 1985, four *N. mercedis* samples (June 15-17, July 18, August 1, August 14) were collected from 10 stations in Muriel Lake (Figure 1). During 1986, mysids were sampled on four dates (June 25, July 30, August 25, September 24) at 10 stations. For each station, vertical haul distances varied with station depth. Mysids were collected with a 350-∝m plankton net (mouth opening of 0.26 m^2). The net was hauled at a constant speed (1 m·sec^{-1}), and the 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. Additional sampling detail is given in Cooper, Hyatt, and Rankin (1992).

Immediately upon removal from the lake, mysid samples were preserved in 4% buffered formalin. Animals were later measured for total length and sex. Eggs and embryos from gravid females were counted, identified to developmental stage, and measured. Mysids were placed in three categories (described above). Total length was measured as the distance from the tip of the rostrum to the end of the telson. Mysids were measured with the aid of an electronic caliper–microcomputer arrangement (Sprules, Holtby & Griggs, 1981). The preserved wet weight of each animal was estimated from its length by using the regression equation $W = 0.0054 L^{3.19}$, where W is the preserved wet weight (mg) and L is the total length (mm) (details in Cooper, Hyatt & Rankin, 1992).

Mysid diets were assessed from direct inspection of gut contents of 23 adults and juveniles collected in the summer and fall of 1986. The foregut of each mysid was removed to a glass slide, dissected, compressed with a cover slip and examined under a light microscope. Each individual food item (4,320 in all) was identified and measured to estimate volume. Because zooplankton were frequently fragmented, identification was often based on body parts such as spines, mandibles, or post-abdominal claws. Phytoplankton were frequently present as intact cells, and identifications followed Prescott (1964).

Mysid production was estimated using two methods. New recruits were estimated using the egg ratio method (Downing & Rigler, 1984). Egg estimates were based on the densities and lengths of gravid females sampled on four sampling dates during both 1985 and 1986. Female lengths were required because egg number has been shown to increase with female body size according to the relationship egg number = 1.04*[female length] - 0.508 (Cooper, Hyatt & Rankin, 1992). Egg ratio production was estimated from the expression $P = \sum N_{ij} \beta_j$, where P is production of new recruits, N_{ij} is the density of gravid females with respect to sample date (i) and length (j), and β_j is the mean egg number for females of length j. The weight assigned to each new recruit was 0.047 mg wet weight, estimated from the weight of a 2-mm individual, and egg development time was estimated to be 4 d (Toda & Takahashi, 1985).

Production for individuals ≥ 2 mm was estimated using the Hynes removal sum method, with modifications by Krueger and Martin (1980). Production was based on four sample dates in each year, and on individuals separated into 17 one-mm size categories (2-18 mm). The sample data were corrected for sampling interval as suggested by Krueger and Martin (1980). The expression used was $P = a \sum [(Y_j - Y_{j+1}) (W_j W_{j+1})]^{0.5}$, where P is production (mg wet weight·m^{-3}) over the time period for which data have been collected, Y is the weighted mean number of individuals in size category i and is defined in the expression listed below, a is the number of size cate-

gories, and W is the mean weight of individuals in each size category. $Y = [\sum (D_{i+1} - D_i) (y_{ij} + y_{(1+i)j})] / (D_n - D_1)$, where i = 1 through n and is the number of sampling intervals, $D_{i+1} - D_i$ is the number of days between sampling intervals, D_n is the number of days between the first and last sampling period, and y_{ij} is the density of individuals of category j sampled at time i.

For 1985, total production for *Neomysis* > 2 mm was estimated for the period 15 June through 14 August (59 d). For 1986, total production for *Neomysis* > 2 mm was estimated for the period 25 June through 24 September (90 d). Production for the time intervals between samples was then assigned based on mean interval biomass. Total interval production was calculated as the sum of interval production from eggs plus interval production by individuals > 2 mm in length. Losses due to mortality during each interval were calculated from $B_i - ([B_{i+1}] + [\text{total interval production}])$, where B_i is biomass at time i. The mean daily *Neomysis* biomass available to consume zooplanktonic prey was calculated as mean interval biomass + 1/2 interval loss due to mortality. This assumes that the average animal lost during each interval survived for 1/2 of the interval. Rudstam (1989) estimated conversion efficiencies for *Mysis mixta* to range from 10 to 15%, and other authors have reported mysid efficiencies ranging up to 29%. For *N. mercedis* at Muriel Lake, we assumed a constant conversion efficiency of 20%, so mean interval consumption rate is calculated as mean daily production $\times$ 5.

Muriel Lake zooplankton (excepting the mysids) were sampled on three dates during 1985 (July 15, August 13, September 11) and on four dates during 1986 (July 11, August 21, September 5, September 25). On each date, triplicate samples were taken using a plankton pump, which has been shown to outperform both nets and traps (Johannsson *et al.,* 1992), particularly for sampling rotifers and nauplii, which we expected would be an important food source for mysids. Samples were preserved in 4% buffered formalin and enumerated as described for enclosure samples.

Muriel Lake fish were sampled using three types of gear. 1) On four dates during 1985 (June 27-30, September 16-17, November 6-7, and January 22) and three dates during 1986 (July 24, August 20, October 27), fish densities were estimated from hydroacoustic surveys using a Furuno FM-22, 200-kHz echosounder with 100 W of power output (Furuno USA, Camas, Washington, USA). On all surveys, pulse width was maintained at 1.0 ms and a varied gain circuit controlled for signal attenuation losses due to increasing target depth. Surveys were conducted at night using whole-lake transects and as many as 12 depth strata. Details regarding transducer design and counting methods are provided in Hyatt *et al.* (1984), Gjernes, Hyatt, and Rankin (1986), and Hyatt and Stockner (1985). 2) On the same dates, a mid-water trawl net (2- $\times$ 2-m mouth opening, 7.5 m long, stretch mesh ranging from 5.0 cm at the mouth to 1.3 cm knotless nylon at the cod end) was used to collect samples of both juvenile sockeye and sticklebacks. These fish were used to estimate lengths, weights, and ages. The net was towed

only at night, and surveys were based on 11-15 trawls per sampling session. In Woss, Cheewat, Yakoun, and Skidegate lakes (located in southern British Columbia and the Queen Charlotte Islands), it has been determined that sockeye fry over 40 mm in length begin to swim at speeds that allow them to more easily avoid the trawl net. To correct for this size bias, the mean lengths of age 0+ and age 1+ sockeye captured on each date were corrected using the expression (corrected length = 0.5419 [length in the trawl]$^{1.1965}$). This expression was derived from comparisons of fish sizes sampled simultaneously with trawl nets and smolt traps (K. D. Hyatt, unpubl. data). In addition, a recent analysis (Hyatt, Rankin & Hanslett, 2000) has demonstrated that the size bias noted above also influences the relative capture efficiencies of juvenile sockeye and threespine sticklebacks. Acoustic techniques provide estimates of total fish density, but do not provide information about the relative densities of 0+ sockeye, 1+ sockeye, and sticklebacks. These relative estimates are based on probability of capture in the trawl net, and this is directly determined by species (sockeye *versus* stickleback) and body length. Therefore, the expression used to derive relative recruitment to the trawl net and therefore relative densities in the field is (relative catchability = 4464984 * [fork length]$^{-3.38}$) (Hyatt, Rankin & Hanslett, 2000). 3) All sockeye smolts migrating seaward from Muriel Lake between 1983 and 1990 were enumerated and sub-sampled from a trap and fence installation maintained at the lake outlet. The trap was emptied several times per day, and all fish were identified and counted. Smolts sampled for lengths (fork lengths), weights (wet weights), and scales were selected at random throughout the trapping interval. Proportions of 1+ and 2+ smolts were determined through scale aging, and these results were used in combination with in-lake acoustic counts to estimate relative summer densities of 0+ and 1+ juveniles in the water column.

Stomach content samples for juvenile sockeye and sticklebacks were derived from two sources. The first collection was made at Kennedy Lake, which is < 5 km downstream from Muriel and which shares a virtually identical species pool, including *Neomysis*, threespine stickleback, and juvenile sockeye. This collection was made during May, June, July, August, and September 1977 and included stomachs from both 0+ sockeye and sticklebacks. The second collection was also from Kennedy Lake. It was made during August, September, and October 1983 and included stomachs from 0+ sockeye.

Calculated rates of zooplankton consumption by 0+ sockeye and 1+ sockeye were based on bioenergetics models (Kitchell *et al.*, 1974; Kitchell, Stewart & Weininger, 1977). Two methods were used. 1) The Wisconsin Fish Bioenergetics 3.0 model (Hanson *et al.*, 1997) was used to estimate consumption rates for 0+ and 1+ cohorts sampled during both 1985 and 1986. For each year, the simulations were begun during June and ended near the end of September. Model inputs (water temperatures and fish lengths, weights) were measured *in situ* and are reported in the results that follow. Because the Wisconsin model lacks the capacity to simulate diel

migration, we approximated a 12h:12h migration pattern by alternating daily temperatures between epilimnetic and hypolimnetic values. 2) As we were concerned that this approach might cause bias in the output, we also used a "modified Wisconsin Model" (Stockwell & Johnson, 1997) to calculate consumption. Unlike the original, the modified version runs in 30-minute time steps and has the capacity to emulate diel and crepuscular migration. The modified version also independently calculates consumption rates based on a mechanistic feeding sub-model (Hyatt, 1980) and then compares calories consumed with calories required (based on a bioenergetics-based sub-model). Our version of the model was parameterized in the manner described by Stockwell and Johnson (1997).

To our knowledge, a bioenergetics model for three-spine sticklebacks has not been parameterized. In addition, threespine stickleback in Muriel Lake tend to remain onshore as juveniles and only venture into the pelagic zone as adults. This precludes the possibility of obtaining accurate estimates of growth rates from trawl samples. We therefore chose not to directly calculate consumption for threespine sticklebacks, but rather to estimate consumption based on comparisons with juvenile sockeye. Comparative data came from O'Neill and Hyatt (1987), who estimated consumption rates for both juvenile sockeye and threespine sticklebacks in a series of enclosure experiments conducted at Kennedy Lake (adjacent to Muriel Lake). Their experiment involved comparisons between 1) 0+ sockeye (3 months old) and juvenile sticklebacks, 2) 0+ sockeye (7 months old) and juvenile sticklebacks, and 3) 1+ sockeye (14 months old) and adult sticklebacks. In every case, the sticklebacks and their sockeye competitors had almost identical impacts on zooplankton stocks (with respect to both the type of prey consumed and the amounts consumed). With this in mind, we estimated stickleback production and consumption using the sockeye bioenergetic model parameterized with diet data collected for sticklebacks.

Results

ENCLOSURE CONSUMPTION BY *NEOMYSIS*

In order to gain some preliminary information about the potential impacts that various densities of *N. mercedis* could have on natural zooplankton communities, we treated 12 enclosures with four densities (replicated *n* = 3) of mysids. The resulting data revealed that throughout the experimental period, there was a general decline in total zooplankton biomass (Figure 2) (repeated-measures ANOVA "time effect" $P < 0.000$, df = 2). There was also a significant treatment*time interaction (R-ANOVA $P < 0.009$, df = 6), confirming that the largest declines in zooplankton prey were associated with the highest densities of *N. mercedis*. In addition, we found that mysid densities declined in all of the treatments (Table I) and that the declines were density dependent ($P < 0.000$ ANOVA on treatment differences df = 2, 6), being most extreme in the enclosures with the highest mysid densities. Mysid body sizes were also smaller at higher densities ($P < 0.05$ correlation, Table I), suggesting that mysid growth was negatively related to treatment density, reflecting a food resource shortage.

Muriel Lake *Neomysis* biomass and gut analysis

At Muriel Lake, mysid density (Figure 3) and biomass increased significantly through the summer of 1985 and then decreased through the summer of 1986. During both years, the population was univoltine, with most egg production observed during the summer months (June–August) and growth from immatures to adults taking place during the fall and winter. This was especially clear during June 1986, when carry-over from the large 1985
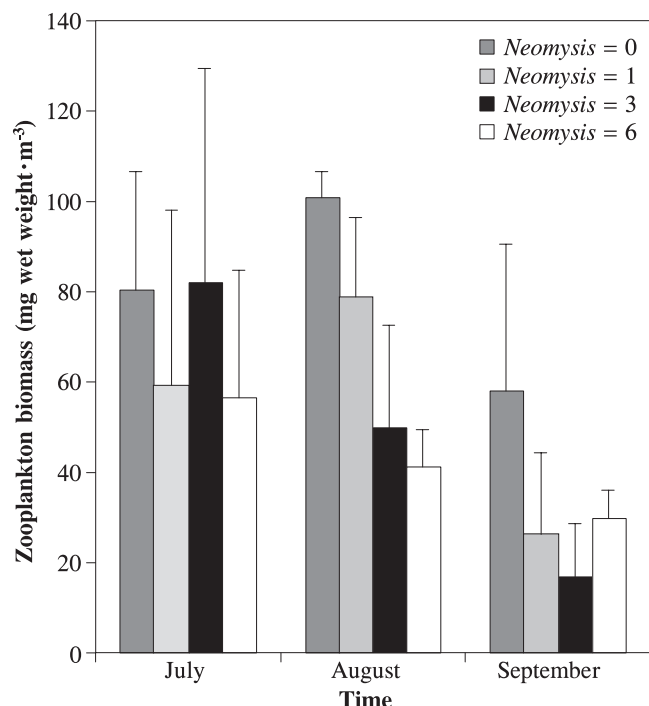
cohort was represented by a significant length–frequency peak at 14-15 mm.

To investigate the possibility that zooplankton taxa may not all have been equally vulnerable to *Neomysis* predation, stomach contents were analyzed for both immature and adult mysids (Table II). Phytoplankton were by far the most numerically dominant component of the gut contents of both groups, but when prey items were weighted with respect to measured volume (Table II), zooplankton were much more important food items, comprising 92.5% and 83.0% of the gut contents by volume for adult and immatures, respectively. Among the zooplankton, *Diaphanosoma* and *Bosmina* were the most numerous prey items. Rotifers were also consumed in significant quantities, especially by the juveniles. Copepods were not strongly represented in terms of either numbers or volumes.

Sockeye and stickleback biomass and gut analysis

During 1983-1990, traps and a weir were used to sample 1+ and 2+ sockeye smolts as they exited the lake (Table III). These data are of interest because they were used to test the hypothesis that fertilization of Muriel Lake resulted in increased juvenile sockeye growth rates and larger smolt weights. Fertilizer was added to Muriel Lake during 1984, so the expectation was that 1+ and 2+ smolts caught in 1985 and 2+ smolts caught in 1986 would be larger than normal. Clearly, this was not the case (Figure 4). Smolt weights varied from year to year and, for unknown reasons, were higher than normal during 1989-90, but they were not higher in 1985-1986.

Muriel Lake pelagic fish (0+, 1+ sockeye, and threespine sticklebacks) were monitored through 1985-1986, using acoustic and mid-water trawl techniques. The acoustic samples were used to estimate total limnetic fish abundance, and the trawls were used to gather data pertaining to species, length, weight, and age composition. Relative densities of sockeye and threespine sticklebacks
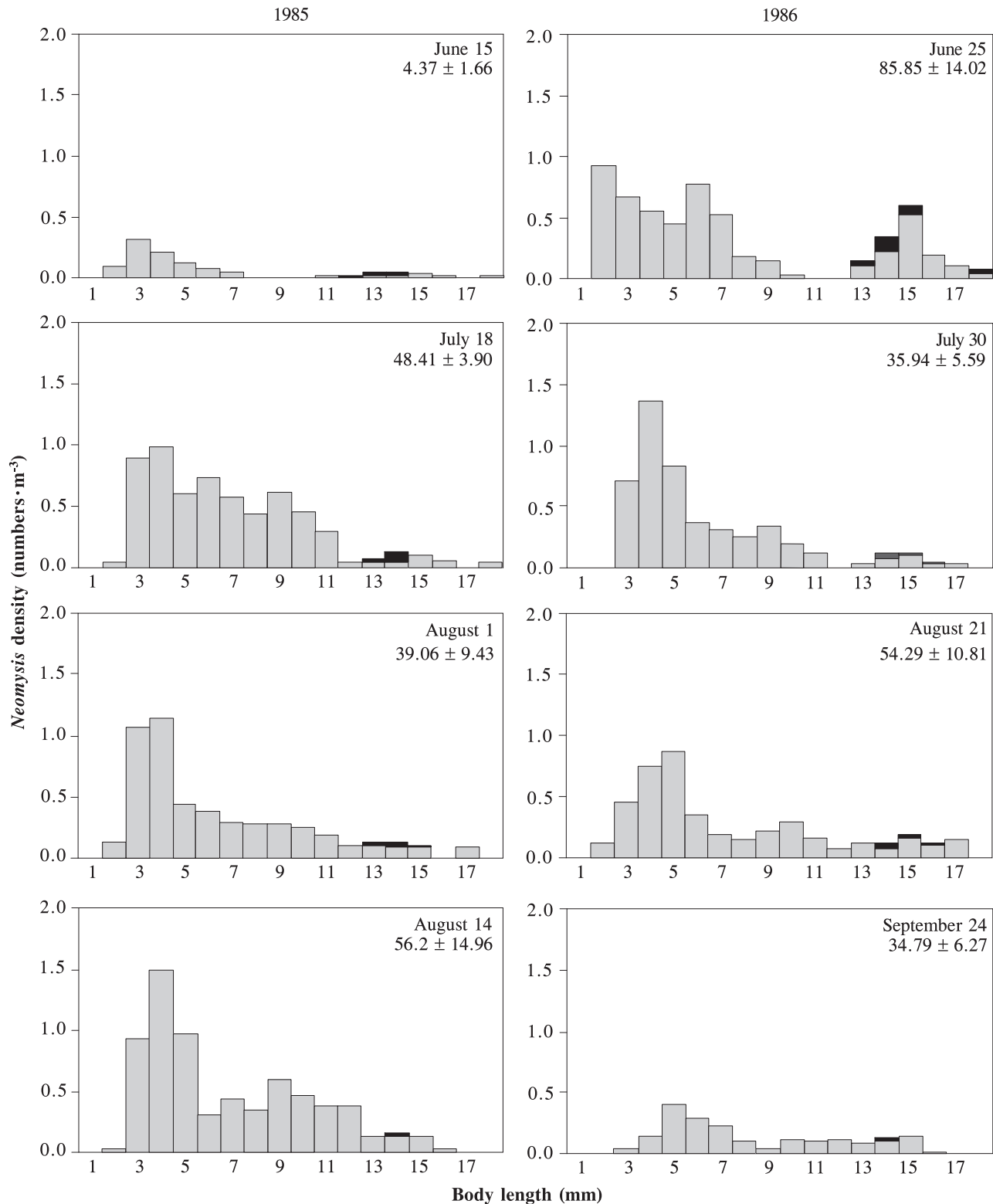

FIGURE 2. Biomass of enclosure zooplankton (± 1 SD) sampled on July 15, August 13, and September 11, 1985. Enclosures were replicated $n = 3$. Mysid density treatments included 0, 1, 3, or 6 *Neomysis mercedis*·m^{-3}.

TABLE I. Density and body length (mm ± SE) of *Neomysis mercedis* in the experimental enclosures. Each of the four treatments was replicated three times. Treatment 0 = control (no *Neomysis*). Treatments 1, 3, 6 = *Neomysis* densities (numbers·m^{-3}) placed into the enclosures at the start of the experiment (July 15, 1985). Lengths were measured at the end of the experiment (11 September, 1985). n is the number in each size class counted.

Treatment: *Neomysis* density (numbers·m^{-3})	Replicate	Starting density July 15 (numbers·m^{-3})	Ending density September 11 (numbers·m^{-3})	Difference	Juvenile length (mm) September 11 (± SE)	n	Immature length (mm) September 11 (± SE)	n	Adult length mm September 11 (± SE)	n
0	1	0	0	0.0						
0	2	0	0	0.0						
0	3	0	0	0.0						
1	1	1	0.6	-0.4			14.7 ± 0.3	12	15.9 ± 0.2	12
1	2	1	1.0	0.0			12.6 ± 0.5	25	14.7 ± 0.3	16
1	3	1	1.2	+0.2			11.7 ± 0.4	31	15.1 ± 0.2	19
3	1	3	2.1	-0.9	6.2 ± 0.2	9	12.7 ± 0.2	56	14.1 ± 0.1	27
3	2	3	1.9	-1.2	6.8 ± 0.2	12	11.9 ± 0.3	48	13.9 ± 0.2	22
3	3	3	1.9	-1.2	7.2 ± 0.6	3	11.4 ± 0.2	55	13.3 ± 0.2	24
6	1	6	2.7	-3.3	6.5 ± 0.2	3	11.3 ± 0.2	96	13.3 ± 0.3	11
6	2	6	2.9	-3.1	6.0 ± 0.2	5	11.4 ± 0.1	103	13.8 ± 0.2	16
6	3	6	1.5	-4.5			11.0 ± 0.2	53	12.7 ± 0.1	7

FIGURE 3. Muriel Lake *Neomysis mercedis* length–frequency distributions expressed as density (numbers·m⁻³) for each sampling date during 1985 and 1986. Densities for each date are based on 10 samples stratified with respect to lake depth (Figure 1). The black bars represent females with eggs. Total biomass (mg wet weight·m⁻³ ± SE) is shown on each panel.

caught in the trawls were combined with the echosounding data to apportion fish densities among the two species. Numbers of 1+ and 2+ smolts caught at the weir (Table IV) were used to back-calculate relative densities

of 0+ and 1+ sockeye juveniles. Together, these data show that smolt densities during sampling years 1986 and 1987 were among the lowest recorded (Table IV), suggesting that in-lake sockeye densities during spring-sum-
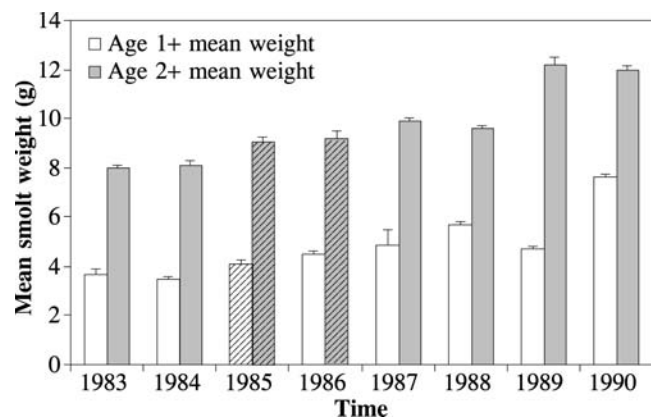
TABLE II. Summary of gut contents of *N. mercedis* collected in Muriel and Kennedy lakes during the fall of 1986. Mysids were divided into small (length ″ 7 mm) and large (length > 7 mm) size categories.

Taxa in gut	Large mysids $n = 11$			Small mysids $n = 12$		
	Number prey counted	Volume (∞m^3)	% by volume	Number prey counted	Volume (∞m^3)	% by volume
Cladocera	236	179.0	85.2	26	19.7	59.7
Rotifer	189	4.6	2.2	77	1.9	5.7
Copepod	11	10.6	5.1	6	5.8	17.6
Total			92.5			83.0
Dinoflagellates	928	9.3	4.4	322	3.2	9.8
Diatoms	1,575	1.1	0.5	217	0.2	0.5
Desmids	135	0.8	0.4	62	0.4	1.1
Cyanobacteria	173	1.3	0.6	99	0.7	2.2
Total			5.9			13.6
Unidentified	1,073	3.3	1.6	865	1.1	3.4

TABLE III. Sampling effort and numbers of smolts sampled at the Muriel Lake outlet during the 1980s. In all years smolts were trapped at a fence located at the lake outlet.

Year	Sampling days	Age 1+ number of smolts examined	Age 2+ number of smolts examined
1983	31	56	983
1984	7	231	117
1985	5	55	79
1986	5	65	38
1987	22	88	256
1988	33	177	555
1989	7	158	97
1990	13	354	425

TABLE IV. Sockeye smolt counts at the weir located at the outlet of Muriel Lake.

Year	Total smolts counted	Percent age 1+	Percent age 2+	Percent age 3+
1983	12,930	19.3	80.6	0.1
1984	22,286	66.38	33.61	0.0
1985	4,064	41.04	58.96	0.0
1986	587	61.9	36.19	1.9
1987	2,416	35.35	64.65	0.0
1988	2,258	11.62	86.03	2.36
1989	6,471	38.25	58.33	3.41

FIGURE 4. Mean weights (± 1 SD) of 1+ and 2+ smolts captured at the Muriel Lake outlet weir from 1983-1990. Sample sizes are shown in Table III. Hatched bars are for year classes that were in the lake when fertilizer was added during 1984.

mer 1985 and especially 1986 were low. Repeated acoustic measures of limnetic fish abundance in 1985 and 1986 (Table V) indicated total densities below 1,000 fish·ha^{-1} and confirmed that 1985 densities exceeded those observed in 1986 throughout the year. Despite these differences, the length–weight relationships (Figure 5), growth trajectories, and condition factors of juvenile sockeye for both years were very similar, suggesting that densities were so low that food shortage was likely not an issue.

Gut analysis for stickleback and sockeye suggested that the diets of both groups were almost entirely composed of zooplankton, with bosminids, cyclopoids, and diaptomids being important throughout the summer and fall (Figure 6). In the case of sticklebacks, *Neomysis* was also a common prey item throughout the late summer and fall. For 0+ sockeye, *Neomysis* was not an important diet component during the spring, but became more important during the late summer and fall (Figure 6).

ZOOPLANKTON BIOMASS AND TAXONOMIC COMPOSITION

During 1985 and 1986, zooplankton biomass (Figure 7) changed significantly through time (repeated-measures ANOVA $P < 0.02$), but there were no significant between-year effects. Given the importance of rotifers and bosminids as potential prey for mysids, we investigated density trends for these and other zooplankton taxa (Figure 8). During both years, nauplii and rotifers were numerically dominant on almost all sampling dates. Other larger taxa tended to be more abundant during the summer, then to decline into the fall. Again there were no obvious between-year differences, suggesting that during 1985 and 1986, zooplankton prey were about equally available to all of the major predators (0+ sockeye, 1+ sockeye, stickle-backs, and *Neomysis*).

NEOMYSIS PRODUCTION AND CONSUMPTION

Mysid production was calculated for the summer months of both 1985 and 1986 (59 days during 1985 and 90 days during 1986). Two sets of calculations were involved. Biomass from new recruits was estimated using the egg ratio method (Downing & Rigler, 1984). Egg density (Table VI) during the spring of 1986 was much higher than during 1985, and these high egg numbers were reflected in the high densities of juveniles observed during the spring of 1986. However, as the summer pro-

TABLE V. Densities (based on echogram samples) of total juvenile sockeye and sticklebacks (± 95% confidence interval). Mean weights (corrected for gear bias) are based on the fish captured in the trawl nets. Numbers in parentheses are sample sizes. Mean weights of fish captured in smolt traps are in italics. Sample sizes are in parentheses. Densities of juvenile sockeye aged 0+ and 1+ are based on the relative densities found in the smolt samples. The designation ns = no sample.

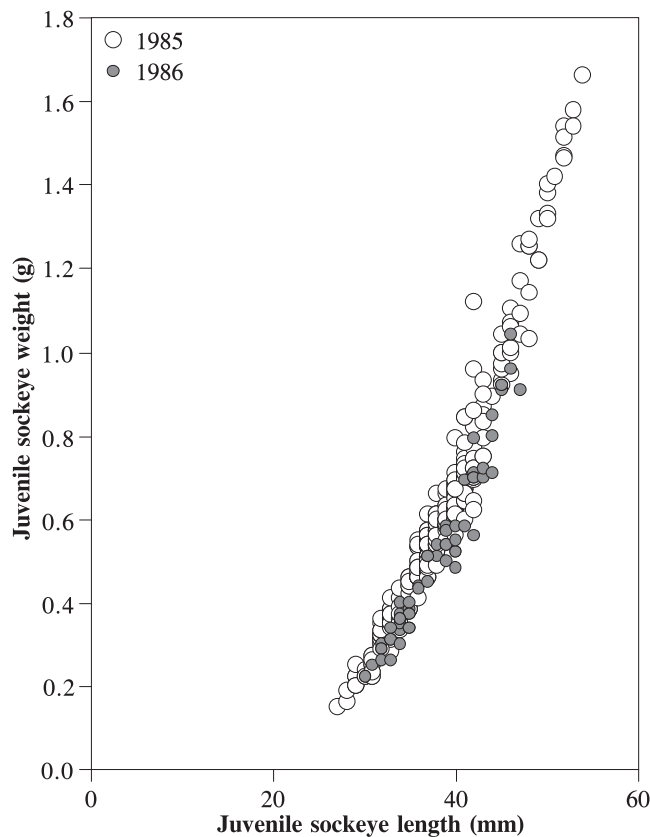| Date	Total sockeye density (numbers·ha⁻¹)	Stickleback density (numbers·ha⁻¹)	Stickleback mean weight (g)	0+ sockeye density (numbers·ha⁻¹)	0+ sockeye mean length (mm) [weight (g)]	1+ sockeye density (numbers·ha⁻¹)	1+ sockeye mean length (mm) [weight (g)]
1985							
26 June	707 (133)	333 (56)	0.56 (23)	667	33.3 [0.35] (35)	40	64.7 [2.73] (4)
16 September	1,077 (101)	242 (55)	0.62 (12)	1,016	43.1 [0.74] (202)	61	87.0 [7.43] (12)
16 November	850 (176)	98 (20)	0.52 (32)	812	54.3 [1.62] (44)	38	99.5 [10.60] (2)
22 January	691 (121)	195 (32)	0.55 (14)	651	57.1 [1.79] (34)	40	100.2 [10.75] (2)
May 1986					*4.50 (65)*		*9.20 (38)*
1986							
24 July	681 (80)	46 (8)	0.30 (8)	510	36.9 [0.45] (20)	171	81.1 [6.14] (7)
20 August	749 (145)	63 (38)	0.30 (3)	749	38.4 [0.53] (15)	ns	ns
27 October	472 (104)	356 (60)	ns	409	46.9 [0.99] (28)	63	93.8 [9.62] (4)
May 1987					*4.90 (88)*		*9.88 (256)*

FIGURE 5. Weight-length relationships for juvenile sockeye sampled during 1985 (open circles) and 1986 (solid circles).

gressed, high mortalities among juveniles and immatures resulted in a three-fold decline in total population densities, and the early spring production potential of mysids in 1986 was never realized.

Production for individuals ≥ 2 mm (Table VII) was calculated using the Hynes size-frequency method (Krueger & Martin, 1980). Total production for *Neomysis* > 2 mm over 59 d in 1985 was 115.1 mg·m⁻³, and total production for *Neomysis* > 2 mm over 90 d in 1986 was 179.6 mg·m⁻³. When converted to daily rates, this translated into about equal daily production during each of the two
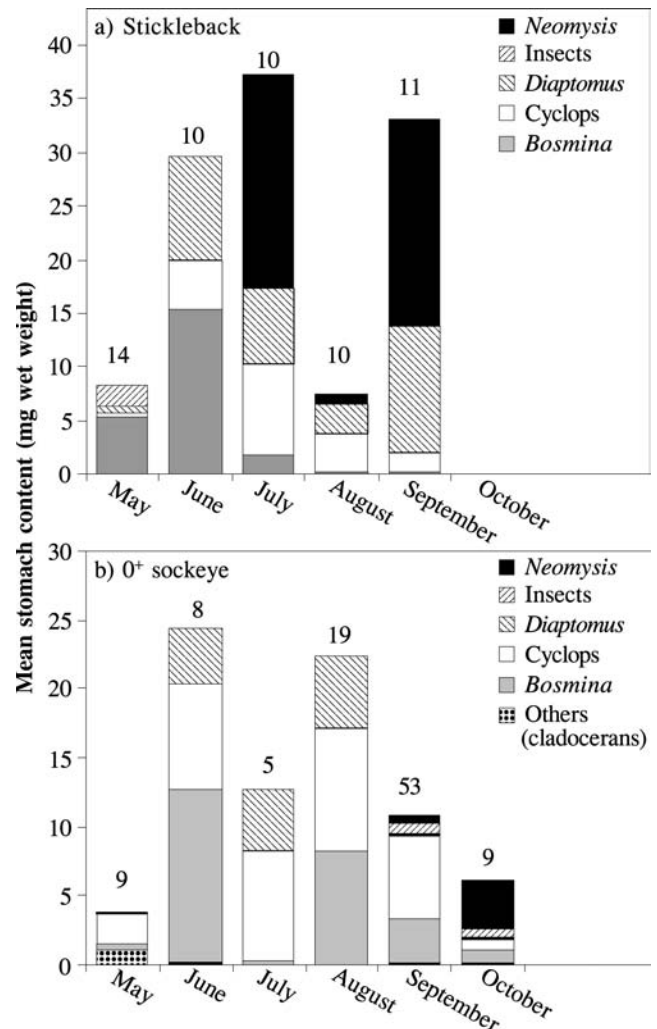

FIGURE 6. Average stomach content (mg wet weight per fish) for stickleback and juvenile sockeye. Sample sizes are shown next to each bar.

years (1.95 mg·m⁻³·d⁻¹ during 1985 and 1.99 mg·m⁻³·d⁻¹ during 1986). During 1985, the production-to-bimass ratio (P/B) was 0.05·d⁻¹, which extrapolates to an annual P/B of
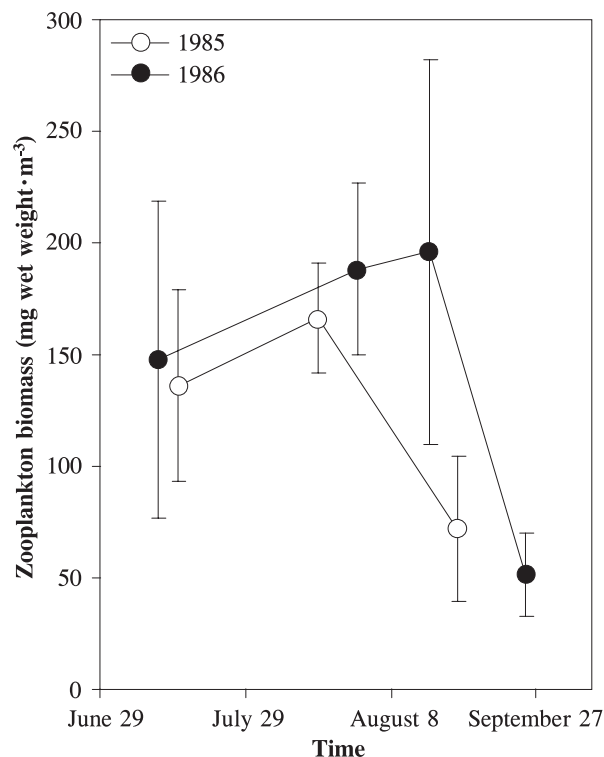
FIGURE 7. Muriel Lake zooplankton biomass (mg wet weight $\cdot$ m^{-3} ± 1 SD) for 1985 and 1986.

20.2, and during 1986 P/B was 0.04 $\cdot$ d^{-1}, which extrapolates to an annual P/B of 14.3.

SOCKEYE AND STICKLEBACK PRODUCTION AND CONSUMPTION

To calculate production and consumption rates for 0+ sockeye and 1+ sockeye, we used the Wisconsin model developed by Kitchell *et al.* (1974) and Kitchell, Stewart, and Weininger (1977) and summarized in Hanson *et al.* (1997) (see details in Methods). In order to parameterize the model we required sockeye biomass and growth rates recorded in the field (Table V), diet composition (Figure 6), and continuous recordings of water temperatures (Figure 9). Sockeye production (Table VIII) showed the same general pattern for both age classes (0+ and 1+) and both years. Through the growing season, production was roughly inversely proportional to epilimnetic water temperature (*i.e.,* high during the spring, lowest during July and August, and higher again in the fall). For example, model results indicated that during July 1986, 1+ sockeye began the month at 3.14 g and ended the month at 5.56 g. However, during August 1986, when the water temperatures were higher (Figure 9), 1+ sockeye began the month at 5.63 g and ended the month at 5.57 g.

Consumption rates (Table VIII, Figure 10) for 0+ and 1+ sockeye and sticklebacks were estimated using the Wisconsin bioenergetics model. The main prey of all fish were diaptomid copepods (primarily *Skistodiaphomus oregonensis*), cyclopoid copepods, and bosminids. Substantial numbers of *Neomysis* were also consumed during the late summer. In all cases, consumption rates were directly related to predator biomass, such that as the sockeye grew through the season, overall consumption rates roughly doubled.
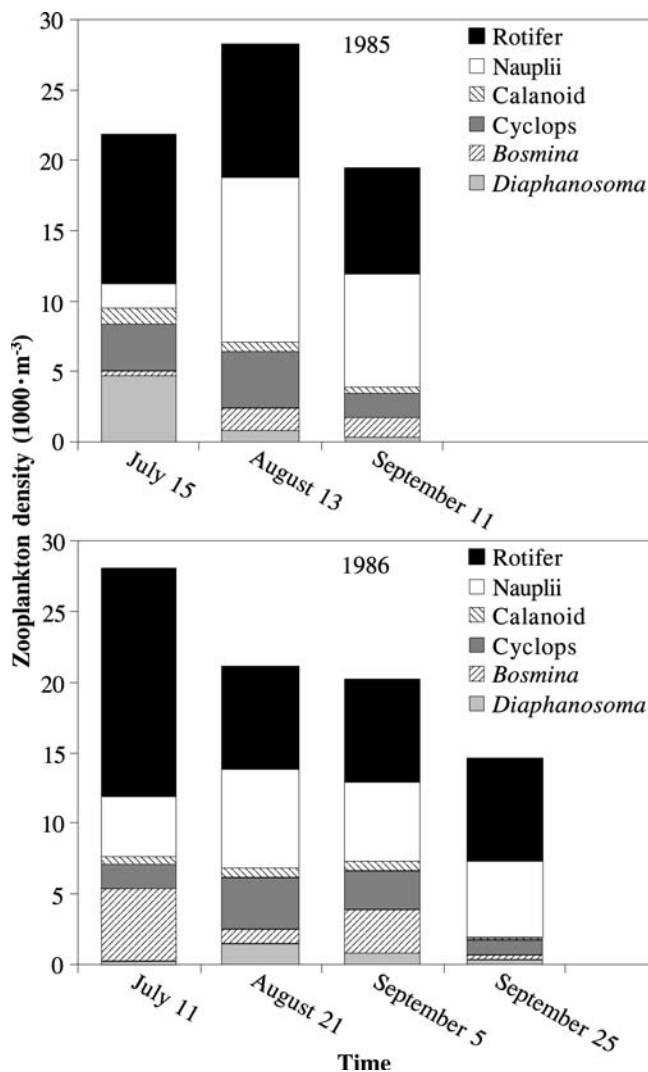

FIGURE 8. Muriel Lake zooplankton densities (1000 $\cdot$ m^{-3}) with respect to taxonomic group.

TABLE VI. Muriel Lake 1985, 1986, *Neomysis* egg production.

	Density of gravid females (numbers $\cdot$ m^{-3})	Number of eggs per gravid female	Egg density (numbers $\cdot$ m^{-3})	Production of new eggs (numbers $\cdot$ d^{-1} $\cdot$ m^{-3})
Date 1985				
15 June	0.0860	13.22	1.14	0.28
18 July	0.1166	13.71	1.60	0.40
1 August	0.1084	14.05	1.52	0.38
14 August	0.0269	14.05	0.38	0.09
Date 1986				
25 June	0.248	15.97	3.97	0.99
30 July	0.098	14.82	1.45	0.36
21 August	0.048	13.53	0.65	0.16
24 September	0.024	14.05	0.34	0.08

During both years, 0+ and 1+ sockeye seldom consumed more that 0.5% $\cdot$ d^{-1} of the zooplankton standing stock (Figure 10, Table IX), the exception being during the fall, when zooplankton standing stocks fell and consumption increased to > 1.0% $\cdot$ d^{-1}. Consumption estimates

TABLE VII. Summary calculation of daily *Neomysis* production from eggs and from new biomass resulting from growth. Interval egg production is based on data provided in Table VI. Interval production for *Neomysis* > 2 mm is based on calculations developed by Krueger and Martin (1980) – details in the Methods section.

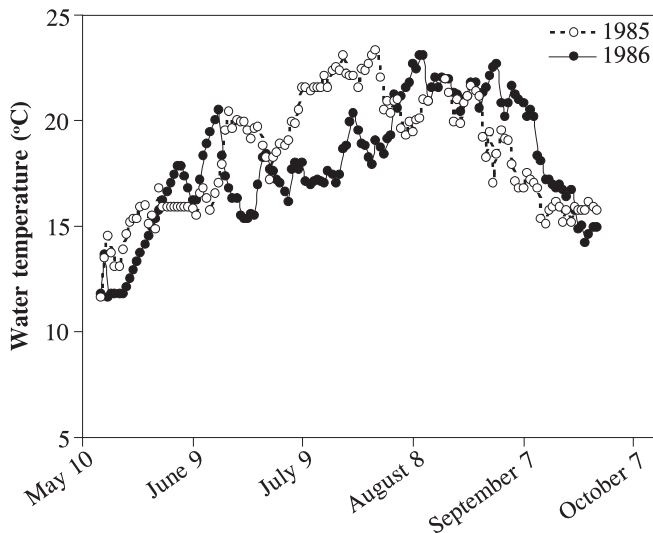| Sample date	$\varnothing$ t days	*Neomysis* biomass (mg·m⁻³ ± SD)	Mean interval *Neomysis* biomass (mg·m⁻³)	Mean interval production from hatched eggs (mg·m⁻³·d⁻¹)	Mean interval production from *Neomysis* > 2 mm (mg·m⁻³·d⁻¹)	Mean combined daily interval production (mg·m⁻³·d⁻¹)	Daily interval consumption by *Neomysis* (mg·m⁻³·d⁻¹)
15 June 1985		4.4 ± 1.66					
	32		26.4	0.016	0.8	0.8	4.2
18 July 1985		48.4 ± 3.90					
	14		43.7	0.018	3.1	3.1	15.3
1 August 1985		39.1 ± 9.43					
	13		47.6	0.011	3.6	3.6	17.9
14 August 1985		56.2 ± 14.96					
25 June 1986		85.9 ± 14.02					
	34		60.9	0.032	2.1	2.2	10.8
30 July 1986		35.9 ± 5.59					
	22		45.1	0.012	2.4	2.5	12.3
21 August 1986		54.3 ± 10.81					
	34		44.5	0.006	1.5	1.6	7.8
24 September 1986		34.8 ± 6.27					

FIGURE 9. Muriel Lake epilimnetic water temperatures for 1985 and 1986.

for stickleback were even smaller, seldom exceeding 0.2% of the zooplankton standing stock·d⁻¹. Both fish species consumed *Neomysis*, especially in the fall, when consumption rates exceeded 40% of daily mysid production (Figure 11).

Because diel migration is not easily accommodated by the Wisconsin model, we verified these results using a modified bioenergetics formulation developed by Stockwell and Johnson (1997). We parameterized the Stockwell and Johnson model by assuming that feeding was crepuscular and that during the day the fish moved to cold hypolimnetic water, while at night they remained in the metalimnion. We also simulated a variety of prey handling times and prey sizes and found that for all cases where prey consumption matched the quantity of prey required to balance the growth rates of fish sampled in the field, the Stockwell and Johnson model produced results that were very similar to those generated from the Wisconsin model.

Discussion

Our study was based on the idea that the dynamics of a pelagic trophic triangle (Holt & Polis, 1997) involving macroinvertebrate planktivores (*N. mercedis*), vertebrate planktivores (0+ sockeye, 1+ sockeye, and threespine stickleback), and their common zooplankton prey might explain the lack of a response by juvenile sockeye to the 1984 Muriel Lake fertilization event. Specifically, it was hypothesized that if *N. mercedis* could out-compete fishes for zooplankton prey, the benefits of lake fertilization would accrue to this macroinvertebrate rather than to the vertebrate planktivores. We tested this hypothesis with two different approaches. 1) We assessed the effects of various densities of *N. mercedis* on zooplankton populations in enclosures. 2) We used field data to calculate rates of production and consumption for *N. mercedis* and the pelagic fishes (0+ and 1+ sockeye and threespine stickleback) and then estimated the impacts of all four on zooplankton and also the impacts of the fish on *Neomysis*.

The enclosure work suggested that *N. mercedis* growth and mortality (Table I) were dependent on the number of *N. mercedis* in each treatment. The enclosure studies also showed that zooplankton biomass (Figure 2) decreased most rapidly in the enclosures with the highest *N. mercedis* treatment densities. Overall, *N. mercedis* was as much affected by food shortage as the zooplankton were by *N. mercedis* predation.

Muriel Lake field work showed that during the summer of 1985, *N. mercedis* population density increased seven-fold and during the summer of 1986, density decreased three-fold (Figure 3). During both summers, maximum abundances of gravid females and eggs were observed early in the season and growth from the juvenile to immature stages proceeded throughout the summer. Growth from immatures was observed during the winter–spring with egg production commencing again during the late spring and summer. From this we conclude that *N. mercedis* in Muriel Lake is univoltine, which is in

TABLE VIII. Sockeye production summary based on simulations using the Wisconsin bioenergetics model.

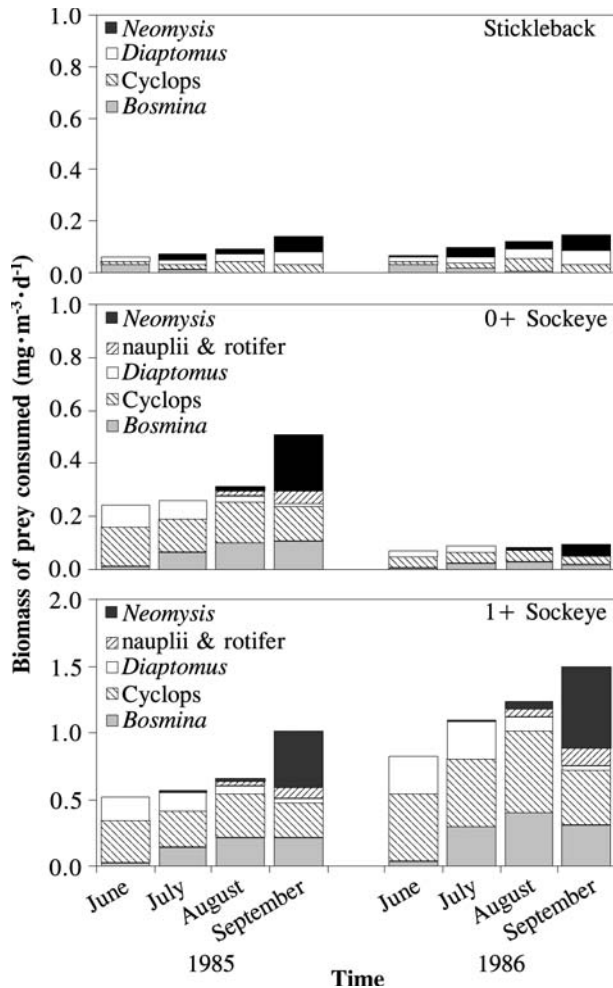|		Fish density (numbers·ha⁻¹)	Mean fish weight per individual (g)	Net production (mg·m⁻³)	Consumption (mg·m⁻³·d⁻¹)	% body weight consumed per day
1985 0+ sockeye	June	700	0.37	0.024	0.242	11.16
	July	700	0.45	0.004	0.263	9.90
	August	700	0.57	0.027	0.316	9.50
	September	700	1.09	0.099	0.516	8.08
1985 1+ sockeye	June	250	2.88	0.057	0.521	8.68
	July	250	3.48	0.015	0.559	7.72
	August	250	4.34	0.063	0.672	7.43
	September	250	7.56	0.206	1.025	6.50
1986 0+ sockeye	June	200	0.47	0.006	0.072	9.18
	July	200	0.63	0.007	0.087	8.34
	August	200	0.65	-0.004	0.087	7.94
	September	200	0.71	0.013	0.095	8.00
1986 1+ sockeye	June	400	2.92	0.109	0.829	8.50
	July	400	4.36	0.131	1.090	7.49
	August	400	5.55	0.001	1.249	6.75
	September	400	6.99	0.255	1.524	6.54

FIGURE 10. Monthly mean daily consumption rates for sticklebacks and 0+ and 1+ sockeye calculated using the Wisconsin bioenergetics model.

TABLE IX. Summary estimates of biomass and consumption rates of zooplankton, mysids, and fish in Muriel Lake during 1985 and 1986.

	1985	1986
Mean zooplankton biomass (mg wet weight·m⁻³)	124.7	145.8
Mean *Neomysis* biomass (mg wet weight·m⁻³)	35.2	50.9
Mean fish biomass (mg wet weight·m⁻³)	13.64	17.85
Mean daily consumption of zooplankton by *Neomysis* (mg·m⁻³·d⁻¹)	9.82	10.07
Zooplankton standing stock consumed by *Neomysis* (%·d⁻¹)	**7.9**	**6.9**
Mean daily consumption of zooplankton by stickleback (mg·m⁻³·d⁻¹)	0.065	0.075
Mean daily consumption of zooplankton by 0+ sockeye (mg·m⁻³·d⁻¹)	0.277	0.075
Mean daily consumption of zooplankton by 1+ sockeye (mg·m⁻³·d⁻¹)	0.582	1.005
Mean daily consumption of zooplankton by all fish (mg·m⁻³·d⁻¹)	0.92	1.16
Zooplankton standing stock consumed by fish (%·d⁻¹)	**0.7**	**0.8**
Mean daily consumption of *Neomysis* by stickleback (mg·m⁻³·d⁻¹)	0.028	0.034
Mean daily consumption of *Neomysis* by 0+ sockeye (mg·m⁻³·d⁻¹)	0.057	0.011
Mean daily consumption of *Neomysis* by 1+ sockeye (mg·m⁻³·d⁻¹)	0.112	0.168
Mean daily consumption of *Neomysis* by all fish (mg·m⁻³·d⁻¹)	0.20	0.21
Neomysis standing stock consumed by fish (%·d⁻¹)	**0.6**	**0.4**
Daily production of *Neomysis* (mg·m⁻³·d⁻¹)	1.949	1.996
Neomysis production consumed by fish (%·d⁻¹)	**28.7**	**21.0**

agreement with results from another ultra-oligotrophic lake (Kennedy Lake) situated on the west coast of Vancouver Island near Muriel Lake (Cooper, Hyatt & Rankin, 1992).
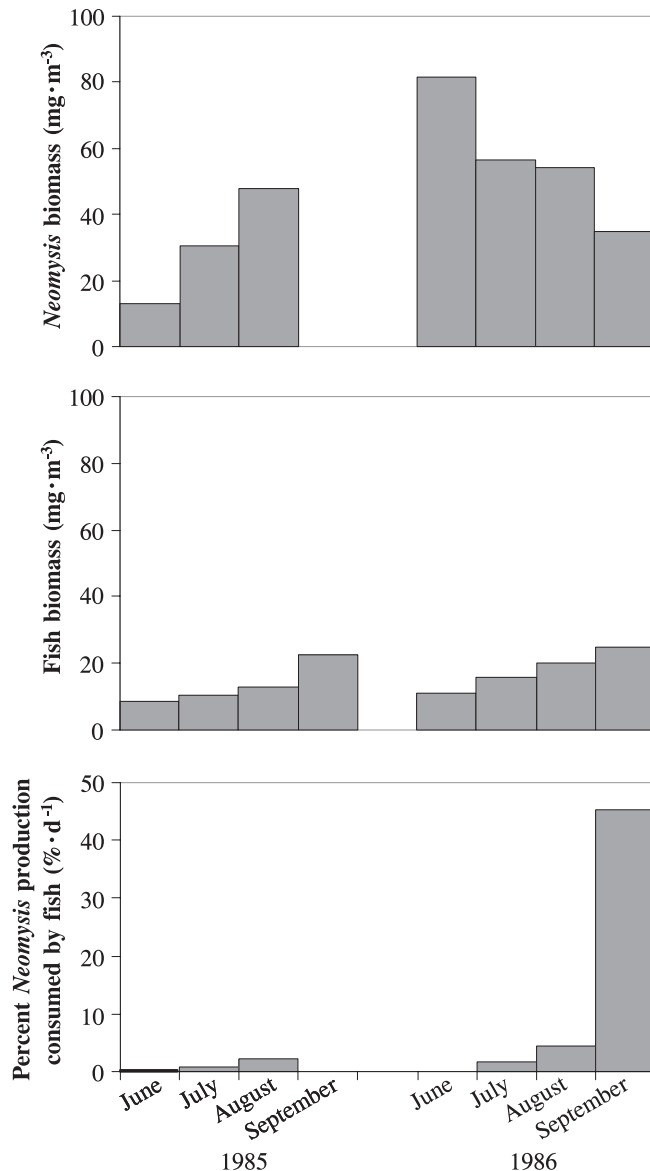
FIGURE 11. Monthly mean biomass for *Neomysis* (top panel) and planktivorous fish (middle panel). Monthly mean daily consumption expressed as percent of *Neomysis* production consumed by fish during 1985-1986 (bottom panel).

Consumption analysis (Table IX) suggested that *N. mercedis* ate about $7.9\% \cdot d^{-1}$ of the available zooplankton standing stock during the first summer and $6.9\% \cdot d^{-1}$ during the second summer. Given the significant impact that mysid predation has had on zooplankton in other lakes (Lasenby & Langford, 1973; Morgan, Threlkeld & Goldman, 1978; Threlkeld *et al.,* 1980; Murtaugh, 1981a,b; Lasenby, Northcote & Furst, 1986; Rudstam, Hansson & Larsson, 1986; Hanazato & Yasuno, 1988; Rudstam, 1989; Rudstam *et al.,* 1989), our results might at first appear to be underestimates. However, two factors are of note here: 1) mysid densities in Muriel Lake ($1-6 \cdot m^{-3}$ or $20-120 \cdot m^{-2}$) and in the enclosures ($1-6 \cdot m^{-3}$) were at the lower end of densities recorded by others (Morgan, Threlkeld & Goldman, 1978, recorded densities of $10-300 \cdot m^{-2}$ in Lake Tahoe; Rudstam, Hansson & Larsson, 1986, $10-200 \cdot m^{-2}$ in the Baltic Sea; Nero & Sprules, 1986, $200-1,500 \cdot m^{-2}$

in Gull Lake; Hanazato & Yasuno, 1988, $10-10,000 \cdot m^{-2}$ in Lake Kasumigaura; Johnston & Northcote, 1989, $30-1,500 \cdot m^{-2}$ in the Fraser River; Kinsten & Olsen, 1982, up to $600 \cdot m^{-3}$ in enclosures; Murtaugh, 1981a, $0-3.5 \cdot m^{-3}$ in Lake Washington), so it might be expected that impacts on zooplankton in our study lake and enclosures would be weaker than the impacts recorded by many others. Also, 2) magnitudes of predation impact must be calibrated against zooplankton production. Muriel Lake, like most coastal British Columbia lakes (Stockner & MacIsaac, 1996) is ultra-oligotrophic (TP about $2 \propto g \cdot L^{-1}$), and while mysid densities are low, so too are the biomass and production rates of the zooplankton. For example, LeBrasseur *et al.* (1978) measured zooplankton production and biomass at Great Central Lake (near Muriel Lake) before, during, and after whole lake fertilization. They found that during non-fertilized years zooplankton biomass during the growing season (200 d) averaged about 21.8 mg $\cdot m^{-3}$ in the top 40 m of the lake and daily zooplankton production was 0.63 mg $\cdot m^{-3}$, such that the daily P/B ratio was only 2.9%. During 4 y of lake fertilization, growing season zooplankton biomass averaged 183.7 mg $\cdot m^{-3}$ and daily production was 5.85 mg $\cdot m^{-3}$, giving a daily P/B ratio of 3.2%. These values bracket the zooplankton biomass measured at Muriel Lake during the summers of 1985 and 1986 (124.7 and 145.8 mg $\cdot m^{-3}$); thus, it might be assumed that daily production during those years averaged about 3% of the zooplankton standing stock. From this we conclude that over the summer growth season, mysid consumption was slightly greater than zooplankton production, and should have caused a gradual decline in zooplankton biomass. In enclosures containing mysids and for both years in Muriel Lake, this was the case (Figures 2 and 7). In addition, during early summer of 1986, when *N. mercedis* densities were high, there was a notable decline in rotifer numbers (Figure 8). Similarly, throughout the summers of both years, bosminids, a preferred prey, declined throughout the season (Figure 8), recovering only during the fall of 1986 when mysid numbers fell to very low levels. Overall, given the relative balance of mysids and their prey, the expectation is that at Muriel Lake considerable time (weeks) would be required for *N. mercedis* to perceptibly influence zooplankton standing stocks.

Our bioenergetic calculations for the Muriel Lake pelagic fish community (Table IX) suggested that consumption rates were seldom higher than $0.7-0.8\%$ of the zooplankton standing stock $\cdot d^{-1}$. These low consumption rates appear to be at odds with the results of earlier enclosure experiments in both Kennedy Lake (O'Neill & Hyatt, 1987) and Muriel Lake (Cooper, 1988). In both cases, sticklebacks and/or juvenile sockeye reduced zooplankton biomass and mean body size by virtually eliminating medium to large-sized species (including *Diaphanosoma, Eubosmina, Diacyclops,* and *Diaptomus*). The effects were quite spectacular. Within a few weeks, the zooplankton surviving in enclosures stocked with fish were largely limited to nauplii and rotifers, all generally smaller than the 0.4-mm size limit that is known to represent the lower limit for prey consumed by juvenile sockeye and sticklebacks (O'Neill, 1986; O'Neill & Hyatt, 1987). However, the fish densities used by O'Neill and Hyatt

(1987) (4,000-9,600·ha⁻¹) and Cooper (1988) (15,900·ha⁻¹) were much higher than the fish densities observed in Muriel Lake during 1984-1986 (*ca* 1,000·ha⁻¹). While it is certain that pelagic fish can have some impact on zooplankton biomass and community structure (reviewed in McQueen, 1990), enclosure data reflecting high fish densities will overestimate impacts for coastal British Columbia lakes exhibiting lower densities of limnetic fish.

Although the 1985-1986 Muriel Lake sockeye population did not have much effect on zooplankton, it is not surprising that many other investigations of British Columbia lakes (summarized in Hyatt & Stockner, 1985) have concluded that sockeye are capable of altering zooplankton biomass and species composition. Using Muriel Lake as an example, zooplankton production averaged 3-4 mg·m⁻³·d⁻¹, and bioenergetic calculations suggest that the population density required to exceed this threshold was only 2,000-3,000 juvenile sockeye·ha⁻¹ (probably closer to 2,000·ha⁻¹ given that juvenile sockeye feed only on food items > 0.4 mm in length). Sockeye densities of this magnitude are common in British Columbia nursery lakes; thus, it is not surprising that sockeye growth rates have long been characterized as being food limited and density dependent. In the case of Muriel Lake, it should be noted that although the 1985-1986 sockeye densities did not exceed the density threshold required to deplete zooplankton, they were relatively close (*ca* 1,000·ha⁻¹). Available smolt data (Table IV) indicate that in-lake densities were much higher in other years (*i.e.,* 1982-1983), such that during some years zooplankton consumption by Muriel Lake fish could exceed zooplankton production and in other years such as 1985-1986 it could not.

The same type of inter-annual variability is likely for the effects of sockeye on *Neomysis*. On average, fish consumed only 0.5%·d⁻¹ of *Neomysis* standing stock and 20 to 30%·d⁻¹ of *Neomysis* production (Tables VIII, IX). However, as the sockeye grew, their intake and relative impacts on *Neomysis* increased (Figures 10 and 11). This was especially true in 1986, when the 1+ juvenile sockeye were relatively more abundant (Table V) and consumption rates exceeded 40% of daily *Neomysis* production (Figure 11). Given that 1987 smolt abundance (reflecting in-lake abundance of sockeye during fall 1986) was only 20 to 50% of the densities recorded in other years (Table III), it is likely that negative effects of sockeye on *Neomysis* are quite substantial in some years.

Our observations highlight the inherent interannual unpredictability resulting from a strong pelagic trophic triangle (Holt & Polis, 1997). At Muriel Lake, when successive years of high spawner abundance and fry recruitment yields high juvenile sockeye biomass, it seems likely that *Neomysis* populations could be held in check by 0+ and especially 1+ sockeye, such that benefits of lake fertilization could accrue to sockeye rather than to *Neomysis*. By contrast, during years of low sockeye fry recruitment and biomass (*e.g.,* 1984-1987), zooplankton consumption rates by *Neomysis* may be so high that sockeye gain little immediate benefit from either fertilizer-induced or even natural increases to the zooplankton food base. For food web ecologists, the implication is that trophic triangles may produce alternate stable states in pelagic communities (*i.e.,* mysid-dominated *versus* fish-dominated) that are mediated by the effects of external factors (*e.g.,* climate-induced changes in marine survival, fishing pressure, etc.) on spawning fish abundance. For salmon managers, the implication is that fertilizer additions to lakes containing mysids will have a greater chance of success when sockeye densities are high and when mysid densities are low.

Acknowledgements

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