THE INFLUENCE OF VERTEBRATE AND INVERTEBRATE PLANKTIVORES ON ZOOPLANKTON COMMUNITIES IN LAKES ON THE AVALON PENINSULA OF NEWFOUNDLAND

CHRISTINE ELAINE CAMPBELL, B.Sc., M.Sc.

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By

© Christine Elaine Campbell, B.Sc., M.Sc.

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Abstract

Predation by vertebrate and invertebrate planktivores in freshwater lakes can lead to decreases in total biomass of the pelagic zooplankton community and can alter zooplankton community structure (defined by species and size-class frequencies). However, the relative influence of predation on the zooplankton community as compared with the influence of lake productivity and physicochemical characteristics is unclear. Planktivore impact should be greatest in lakes such as those on the Avalon Peninsula of Newfoundland that have low faunal diversity, which may strengthen the intensity of predator-prey interactions, and low habitat heterogeneity, which may elevate species encounter rates. Vertebrate and invertebrate predation was assessed in 15 oligotrophic Avalon lakes through determination of planktivore distributions, abundances and prey selectivities, along with total biomass and species and size composition of the zooplankton community. Phytoplankton biomass and lake physicochemical characteristics were monitored to evaluate their influence relative to that of the predators.

The major planktivores in the lakes are the vertebrate *Gasterosteus aculeatus*, the threespine stickleback, and the invertebrates *Chaoborus punctipennis*, *Chaoborus trivittatus* and *Leptodora kindtii*. Analysis of planktivore distribution patterns (presence/absence data) revealed that the distributions of both *Chaoborus* species were significantly and negatively related to the distribution of sticklebacks. There was no significant relationship between the distributions of *Leptodora* and sticklebacks or between *Leptodora* and *C. punctipennis*, however the distributions of *Leptodora* and *C. trivittatus* were significantly and negatively related. Examination of planktivore gut contents indicated that *G. aculeatus* selected mainly for large cladocerans (> 0.76 mm in length) while *Chaoborus* and *Leptodora* selected for rotifers and small cladocerans (< 0.50 mm in length). Total zooplankton biomass was significantly and negatively related to stickleback catch (linear regression: r^2 = 0.40), suggestive of predator control limiting zooplankton populations, but was not significantly related to total invertebrate planktivore density. Zooplankton biomass was further related to a physicochemical principal component identified as increasing ionic strength (multiple linear regression: cumulative R^2 = 0.65). Multivariate analyses revealed that zooplankton community structure was related to factors describing ionic strength, lake size, nutrient concentrations, and watershed characteristics, as well as to stickleback catch. Hence, even in these shallow and oligotrophic lakes in which predation would be expected to have a major impact on the zooplankton community, planktivore abundance is not the primary influence on zooplankton biomass and community structure.

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Chapter 1

General Introduction

> "If a local assemblage of organisms is to be regarded as a community with some degree of organization or structure, then it is in the interactions between the organisms that we must look to provide this structure"
>
> Connell (1975)

A community consists of organisms that coexist in the same time and place, with energy flowing through the various trophic levels in the community (Lindeman 1942) from primary producers through to top predators and detritivores. Characterizations of this energy flow, as described by feeding relations among organisms, are called food webs (Cohen 1989). Total biomass and species diversity (both the number of species present (species richness) and their relative abundances (equitability); Colinvaux 1986) at each trophic level in the food web can be a function of food limitation from lower trophic levels and predation pressure from higher trophic levels. Hairston *et al.* (1960) were among the first to argue for a strong relationship between measures of species abundances and the processes of food limitation and predation. The abundance of green plants in the world led Hairston *et al.* to hypothesize that this trophic level of primary producers is not being cropped down by herbivores and thus plant abundance reflects available nutrient (food) limitation. Herbivores are not able to limit plant numbers since herbivore numbers are held in check by predation from carnivores, while competition among carnivores for prey serves to limit predator numbers. The importance of food limitation and predator pressure thus alternates among trophic levels. However, lack of herbivore control of plant abundance in this model is strongly based on the assumption that all green plant material is edible (Murdoch 1966; Ehrlich and Birch 1976). Hence, the model is somewhat simplistic, since many plants are not wholly edible (e.g. certain gelatinous phytoplankton species; Porter 1973). Population densities of herbivores may be affected by interactions among edible and inedible food resources (Leibold 1989). The idea of alternation between food and predator limitation was extended by Fretwell (1977). Fretwell suggested that in food chains with odd numbers of links (e.g. 3-link chain of primary producer, herbivore and carnivore described by Hairston *et al.* 1960), primary producers are indeed nutrient limited, herbivores are predator limited, and carnivores are food limited. However, in food chains with even numbers of links, primary producers are predator limited and herbivores are food limited. Here, herbivore numbers are not limited by predators, either because there are no carnivores (2-link chain of primary producer and herbivore), or because carnivore numbers are held in check by a top predator which in turn is food limited (4-link chain of primary producer, herbivore, carnivore and top predator). In contrast, Menge and Sutherland (1976) and Cohen (1989) argued that both predation pressure and food limitation are important at all trophic levels. The relative importance of each factor depends on the trophic level being considered, with predation becoming more important than competition for food as trophic position goes from high to low within a community.

In aquatic communities, organisms in intermediate trophic levels, for example zooplankton in freshwater lakes, serve to transfer energy from food resources such as phytoplankton at low trophic levels to predators such as planktivorous fish and large invertebrates at higher trophic levels. Currently there is much debate as to what extent observed patterns in the zooplankton community, a subset of the whole lake community, might be attributable to biotic interactions operating at the level of the phytoplankton (resource limitation) or at the level of the predator (consumer control) (e.g. see Zaret 1980; Harris 1986; McQueen *et al.* 1986). In particular, there has been much debate on the relative strengths of vertebrate and invertebrate predation, as compared with lake productivity and physicochemical characteristics, as influences on patterns in the total biomass and structure of the zooplankton community. Patterns in zooplankton community structure have frequently been described by presence/absence and abundance of species (Pennak 1957; Patalas 1971; Roff *et al.* 1981; Zettler and Carter 1986), by abundances of various size classes (Sprules and Holtby 1979; Pace 1986; Martin and Pinel-Alloul 1988), and by abundances of size-related feeding ecology groups (i.e. herbivores and carnivores: Sprules and Holtby 1979; Sprules 1980). The physical uniformity of the pelagic habitat, which leaves few refugia for zooplankton to hide from predators, has suggested to various authors (Connell 1975; Sih *et al.* 1985) that the effects of predation on the zooplankton community in freshwater lakes could be quite marked. Rates of population generation times in pelagic food webs are also often relatively faster than those in terrestrial systems (Crowder *et al.* 1988), so that the effect of predators in lakes should be more readily observed.

Previous studies have shown that vertebrate and invertebrate predation can have strong and contrasting effects on both the species composition and size distribution of the pelagic zooplankton community in freshwater lakes. Planktivorous fish, such as threespine stickleback (*Gasterosteus aculeatus*), yellow perch (*Perca flavescens*), alewife (*Alosa psuedoharengus*) and juvenile salmonids, selectively feed on the larger, more visible zooplankton species (reviews by O'Brien 1979; Zaret 1980; Lazzaro 1987; Northcote 1988) such as *Daphnia* spp., large calanoid copepods and large invertebrate predators (e.g. *Leptodora kindtii*, *Chaoborus* larvae). This selective feeding shifts the zooplankton size spectrum towards smaller, less visible organisms such as *Bosmina* spp. and small cyclopoid copepods (Hrbáček *et al.* 1961; Brooks and Dodson 1965; Galbraith 1967; Hall *et al.* 1970; Wells 1970; Stenson 1972; Nilsson and Pejler 1973; Pope and Carter 1975; Sprules 1975; Lynch 1979; Anderson 1980; Hurlbert and Mulla 1981; Elliot *et al.* 1983; Gliwicz 1985; Vanni 1986; Carpenter *et al.* 1987; Ranta *et al.* 1987; Post and McQueen 1987; Stoddard 1987). Intense predation by fish can lead to decreases in total zooplankton biomass (Brooks and Dodson 1965; Brocksen *et al.* 1970; Hall *et al.* 1970; Wells 1970; Hurlbert and Mulla 1981; Gliwicz 1985; Post and McQueen 1987, Cryer 1988). In contrast, large invertebrate predators such as *Leptodora kindtii*, *Mysis relicta*, *Neomysis mercedis* and *Chaoborus* larvae selectively feed on the smaller and more easily handled zooplankton such as rotifers, copepodites and small cladocerans (Mordukhai-

Boltovskaia 1958; Roth 1971; Swüste *et al.* 1973; Swift and Fedorenko 1975; Pastorok 1980; Smyly 1980; Winner and Greber 1980; Zaret 1980; Havel 1985; Hare and Carter 1987; Jin and Sprules 1988) thereby shifting the zooplankton size spectrum towards larger grazers (Dodson 1974; Pope and Carter 1975; Smyly 1978; Kajak and Rybak 1979; Lynch 1979; Murtaugh 1981; Nero and Sprules 1986; Elser *et al.* 1987; Luecke and Litt 1987; Riessen *et al.* 1988; Vanni 1988). In some lakes, seasonal decreases in zooplankton biomass can be correlated with increases in populations of large invertebrate predators (Hall 1964; Wright 1965; Hillbricht-Ilkowska and Karabin 1970; Karabin 1974; de Bernardi and Guissani 1975; Smyly 1978; Gliwicz *et al.* 1978; Kajak and Rybak 1979; Lynch 1979; Hanazato and Yasuno 1985; Hovenkamp 1990).

The influence of vertebrate and invertebrate planktivores on the pelagic zooplankton community may be complicated by predator-prey or competitive interactions operating among the planktivore species themselves (Rogers 1968; Costa and Cummins 1972; Pope *et al.* 1973; Anderson 1980). Removal of large zooplankton by vertebrate predators may also allow for increases in the number of small zooplankton when the differently sized prey are competing for the same food resources. Increase in the numbers of small zooplankton can then lead to increases in the numbers of the invertebrate predators that prey upon these smaller species (Dodson 1970; Kerfoot and DeMott 1984). Besides having direct effects, predation may have indirect effects upon the zooplankton community. Fish can increase phytoplankton biomass, either by reducing zooplankton populations and consequent zooplankton grazing pressure on phytoplankton, or by increasing nutrient output through feces production and decomposition. Increased phytoplankton biomass in turn can result in elevated survivorship and/or reproduction of some zooplankton species (Vanni 1986; Threlkeld 1987*a*).

These studies that confirm the impact of vertebrate and invertebrate predation on the structure and total biomass of zooplankton communities can be placed into four distinct groups.

Group I - studies of oligotrophic, particularly alpine, lakes: Galbraith 1967;

Brocksen *et al.* 1970; Stenson 1972; Nilsson and Pejler 1973; Dodson 1974; Pope and Carter 1975; Sprules 1975; Anderson 1980; Gliwicz 1985; Nero and Sprules 1987; Stoddard 1987.

Group II - small pond or enclosure studies: Hrbáček *et al.* 1961; Hall *et al.* 1970; Smyly 1978; Kajak and Rybak 1979; Lynch 1979; Hurlbert and Mulla 1981; Elliot *et al.* 1983; Vanni 1986; Post and McQueen 1987; Cryer 1988; Riessen *et al.* 1988; Vanni 1988, Lancaster and Drenner 1990.

Group III - introduction of new predator to system: Brooks and Dodson 1965; Wells 1970; Murtaugh 1981; Carpenter *et al.* 1987; Elser *et al.* 1987; Luecke and Litt 1987; Ranta *et al.* 1987.

Group IV - predation effect noted only on short-term/seasonal basis: Hall 1964; Wright 1965; de Bernardi and Guissani 1975; Hillbricht-Ilkowska and Karabin 1970; Karabin 1974; Gliwicz *et al.* 1978; Hanazato and Yasuno 1985; Hovenkamp 1990.

Why might the effects of predation on the zooplankton community be strong in these types of systems? In oligotrophic lakes (Group I), faunal species diversity in the pelagic zone is often lower than is seen in eutrophic lakes (Hillbricht-Ilkowska 1977; Wetzel 1983). This low species diversity, by restricting the number of potential interactions (both direct and indirect) to a few species, could lead to species interactions that would be more intense than interactions spread out among a more complex species network. The more transparent waters of oligotrophic systems can also render zooplankton more susceptible to visual predation while the lower food concentration and generally lower temperatures in these lakes would result in slower zooplankton growth rates as compared with populations in eutrophic lakes (Gliwicz and Prejs 1977; Lammens 1988). Mortality due to predation losses should have a greater relative effect on such slow growing zooplankton populations (Neill and Peacock 1980). In their model of top-down (predator control) versus bottom-up (resource control) interactions in trophic levels in aquatic ecosystems, McQueen *et al.* (1989) suggested that as lake productivity decreases, top-down control at lower trophic levels strengthens and bottom-up control weakens Thus, top-down control of the zooplankton trophic level would be more important in oligotrophic systems. Both Brocksen *et al.* (1970: lakes in British Columbia) and Gliwicz and Prejs (1977: Polish lakes) found relationships between zooplankton biomass and vertebrate predator density to be stronger in lakes of lower productivity. Predation by invertebrates, however, may sometimes be stronger in mesotrophic lakes (Gliwicz *et al.* 1978) where early, less carnivorous life stages of the predators are not as food limited by low levels of algal and detrital biomass (Neill and Peacock 1980; Yan *et al.* 1985).

In enclosures or small ponds (Group II), predators and prey are often restricted to a small volume and thus have elevated encounter probabilities. As well, the shallowness of these systems often prevents zooplankton from avoiding predators through vertical migration. In enclosures especially, the number of prey and predator species is usually limited; this would increase the probable strength of the interactions between the species (see above). For these reasons, small enclosures tend to yield artificially high predation rates even with natural prey and predator densities (Melville and Maly 1981). Most frequently, however, predator densities in enclosures and manipulated pond systems are higher than those seen in natural, unmanipulated situations (e.g. Hrbáček *et al.* 1961; Kajak and Rybak 1979; Lynch 1979; Post and McQueen 1987), which in itself could lead to a high predation impact. Environmental variability among enclosures or shallow ponds is also generally small and hence differences in zooplankton biomass and community structure can be more easily related to differences in predation impact than to differences in lake morphometry or chemistry, especially where there is a voracious vertebrate planktivore present in some but not all enclosures or ponds (Dodson 1979). In a study of 696 lakes in eastern North America, Roff *et al.* (1981) found no clear relationships between size structure of zooplankton communities and predator abundance. They suggested that this was due to the large and heterogeneous study area and to less intense predatory interactions in large lakes that have greater habitat complexity. In large lakes, large-scale physical processes may be the dominant forces in structuring zooplankton communities (Harris 1986) as is the case in the North Sea (Koslow 1983).

In systems where new predators are introduced (Group III), there is often a noticeable, short-term impact on the prey community, but it is not clear if such effects persist once the predator has become integrated into the lake community (Thorp 1986). Zooplankton in these systems likely have no "experience" in evading predation by this new predator and thus mortality due to predation might initially be high. Long-term presence of predators in a system often induces the development of antipredator defences in the prey (e.g. patterns of vertical migration as protection from vertebrate predators that are mainly visual feeders: Zaret and Suffern 1976; and cyclomorphosis in daphnids as protection against capture by invertebrate predators: Krueger and Dodson 1981; Hebert and Grewe 1985) that would tend to reduce predation pressure on these prey. As well, while long-term predation can still influence the species composition and size distribution of the zooplankton community, trophic level production and biomass might be more influenced by resource-driven feedback loops, the result of competition among zooplankton species for food resources, that are less evident in short-term studies (Mills and Forney 1988).

Occasionally predation will dramatically increase on a short-term or seasonal basis (Group IV) with immediate effects on the zooplankton prey community. This situation holds true mainly for invertebrate predators that become highly predaceous only at certain stages in their life cycle, examples being the final instars of *Chaoborus* larvae (Swift and Fedorenko 1975; Moore 1988) and the larger adult stages of predatory cladocerans such as *Leptodora kindtii* and *Bythotrephes cederstroemi* (Mordukhai-Boltovskaia 1960). Long-term effects of this predation might be less noticeable, particularly if the invertebrates are unable to maintain high levels of predation pressure on the prey as a result of planktivore population decline due to pupation and emergence (*Chaoborus*) or to intolerance of water temperatures at certain seasons (*Leptodora* and *Bythotrephes*: Garton *et al.* 1990). The strength of the predation impact on the zooplankton community will depend to a great extent on whether zooplankton populations are food-limited during this period of high predation intensity (Hall *et al.* 1970) with resultant low reproduction rates inadequate to compensate for predation losses (Neill and Peacock 1980; Neill 1981). At low food concentrations, prey species such as *Daphnia pulex* might also grow more slowly, thereby prolonging the period of vulnerability to size-limited invertebrate predation (Lynch 1989). Predation on the smaller daphnid instars should have the greatest impact on the seasonal dynamics of the prey population (Hovenkamp 1990), since the 1st reproductive instar usually contributes the most to subsequent population growth rates (Threlkeld 1987*b*).

In view of the above analysis, the relative strength of the influence of vertebrate and invertebrate predation on zooplankton biomass and community structure in natural, unmanipulated systems should then be most readily evaluated in shallow and oligotrophic lakes that have low species diversity and low habitat heterogeneity, that do not differ greatly in physical and chemical characterization, and that also contain voracious planktivores that persist over several generations of zooplankton. Lakes on the Avalon Peninsula of Newfoundland, Canada, seem to fit these requirements. The lakes are oligotrophic and generally physically and chemically uniform (see Description of the Study Site). Both phytoplankton and zooplankton diversity are low compared to other temperate-zone lakes in Canada (Davis 1972, 1976; O'Connell and Andrews 1977; Chengalath *et al.* 1984). The fish communities are also simple (Scott and Crossman 1964; Wiseman 1973) with most fish species that are common on the mainland, in particular all cyprinid and centrachid fishes, absent as a probable result of the physical isolation of the island of Newfoundland. The vertebrate planktivore *Gasterosteus aculeatus* Linneaus (Teleostei), the threespine stickleback, and the invertebrates *Chaoborus* spp. (Diptera) and *Leptodora kindtii* Focke (Crustacea) have all been collected from Avalon lakes (Scott and Crossman 1964; Wiseman 1973; Davis 1976; O'Connell and Andrews 1977; Borkent 1979; Cooper 1985). Previous studies in other freshwater lakes have shown that pelagic zooplankton make up a large proportion of the diet of all these planktivores (Hynes 1950; Cummins *et al.* 1969; Karabin 1974; Fedorenko 1975b; Manzer 1976; Elser *et al.* 1987; Jakobsen *et al.* 1988; Moore 1988).

In the present study, a set of Avalon lakes was sampled in order to assess both vertebrate and invertebrate planktivory and to evaluate the impact of this planktivory on zooplankton community structure. The following questions were asked:

1. Are the distributions of *G. aculeatus*, *Chaoborus* spp. and *L. kindtii* random or are there distribution patterns which might reflect possible predator-prey or competitive interactions among these planktivores?

2. Do these planktivores feed non-selectively or do they exhibit significant and contrasting selectivities in their choice of zooplankton prey in terms of zooplankton species and size classes?

3. Are zooplankton biomass and community structure (species and size class

frequencies) significantly related to planktivore abundances, that is, does zooplankton biomass decrease with increasing planktivore abundance, suggestive of predator control limiting prey populations, and does community structure reflect predation pressure resulting from observed planktivore prey selectivities?

4. Are vertebrate and invertebrate predation dominant determinants of zooplankton biomass and community structure, or only minor factors among a suite of lake productivity and physicochemical factors that also influence the pelagic zooplankton community?

Assessment of the relative importance of vertebrate versus invertebrate planktivory in a group of lakes that are similar both in terms of fauna and environmental parameters can contribute to the understanding of the cumulative impact of predation in such ecosystems. The study of ecological interactions such as predation in these biologically and physically simple lake systems can be used to elucidate some of the mechanisms that determine zooplankton community biomass and structure in more complex aquatic systems where such interactions might be confounded by other variables.

Chapter 2

Description of Study Site

The study lakes (Figure 2.1) are all located between 47° 12' to 47° 45' N latitude and 52° 40' to 53° 05' W longitude on the Avalon Peninsula of Newfoundland, a region characterized by barrens of dwarf shrub heaths, bogs and shallow fens mixed with black spruce (*Picea mariana*) - balsam fir (*Abies balsamea*) forest (Damman 1983) and underlain by late Precambrian sedimentary and volcanic rocks (Rowe 1972). Newfoundland lakes are routinely named "ponds" regardless of depth and surface area. All the lakes are rocky-bottomed with little macrophyte growth. Water columns are generally well mixed as a result of strong winds in the region and show minimal thermal stratification over the open water season (Knoechel and Campbell 1988). The lakes are all oligotrophic with mean spring and summer phytoplankton and zooplankton biomass each less than 3.0 $mg \cdot l^{-1}$ (wet weight) (Knoechel and Campbell 1988). Over 50% of the phytoplankton biomass in the lakes is in the "edible" size fraction, defined as a cell size of less than 30 µm in maximum dimension. Dominant pelagic microcrustaceans are *Daphnia catawba* Coker, *Holopedium gibberum* Zaddach, *Eubosmina longispina* Leydig, *Leptodiaptomus minutus* Lilljeborg, *Epischura nordenskioldi* Lilljeborg and *Cyclops scutifer* Sars; the latter two copepods can be considered partially zooplanktivorous (Strickler and Twombly 1975). Dominant rotifers are *Kellicottia* spp., *Keratella* spp. and *Conochilus unicornis* Rousselet (Davis 1972, C. Campbell *pers. obs.*). Besides *Gasterosteus aculeatus*, the only common fish species are the American eel, *Anguilla rostrata* Lesueur, and salmonids: *Salvelinus fontinalis* Mitchill, *Salmo trutta* Linneaus and *Salmo salar* Linnaeus (Scott and Crossman 1964; Wiseman 1972, 1973). General physical, chemical, watershed and plankton characteristics of the study lakes have been previously described by Knoechel and Campbell (1988); Table 2.1 shows the ranges of selected physical, chemical and watershed variables.

Figure 2.1. Location of the 15 study lakes on the Avalon Peninsula. Lake labels refer to Bauline Long Pond (BA), Healeys Pond (HE), Hogans Pond (HO), Long Pond (LO), Middle Three Island Pond (MI), M.U.N. Long Pond (MU), Octagon Pond (OC), Paddys Pond (PA), Piccos Pond (PI), Quidi Vidi Lake (QU), Round Pond (RO), Second Pond (SE), Three Island Pond (TI), Tors Cove Pond (TO) and Whiteway Pond (WH). To distinguish among Long, Bauline Long and M.U.N. (Memorial University of Newfoundland) Long ponds, all officially named "Long Pond", the latter two lakes are referred to here by local names.

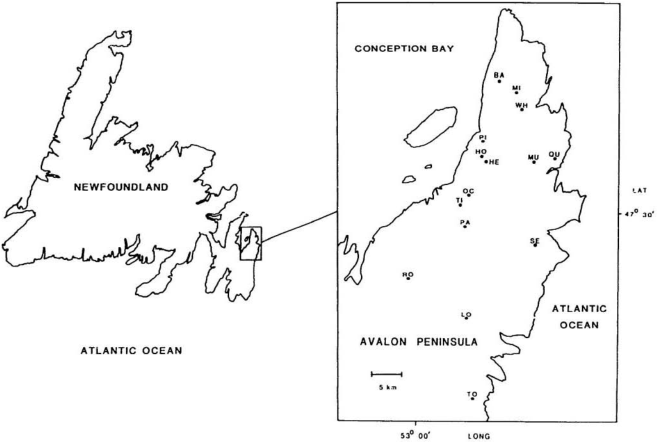

NEWFOUNDLAND
ATLANTIC OCEAN
CONCEPTION BAY
BA
MI
WH
PI
HO
HE
MU
QU
OC
TI
PA
SE
RO
LO
TO
AVALON PENINSULA
ATLANTIC OCEAN
5 km
LAT
47° 30'
53° 00'
LONG

Table 2.1. Range in selected environmental variables for the 15 Avalon lakes. Values are means for the individual lakes over the open-water season.

1. <u>Physical Variables</u>	
Surface area (ha)	13 - 234
Max. depth (m)	2.2 - 16.9
Secchi disk (m)	2.2 - 8.5
2. <u>Chemical Variables</u>	
Conductivity (μS-cm^{-1})	31 - 172
pH	6.0 - 6.2
Total nitrogen (μg-l^{-1})	180 - 650
Total phosphorus (μg-l^{-1})	6 - 16
3. <u>Watershed variables</u>	
Number of houses	0 - 5000

Chapter 3

Distribution patterns of vertebrate and invertebrate planktivores in Avalon Peninsula lakes

3.1. Introduction

Identification and analysis of patterns of species distributions is a challenging task in community ecology and an important preliminary step in the elucidation of the mechanisms responsible for such patterns. Patterns that are expected to result from biological interactions such as predation and competition may be difficult to detect because of community complexity and habitat heterogeneity. A complex community is one in which species diversity is high and where there is a diverse and highly interconnected web of species interactions (May 1984). In such complex communities (e.g. tropical island avifauna; Diamond 1975), distributional patterns may not be easy to distinguish from random distributions that can be derived from null models (Connor and Simberloff 1979). The applicability of null models to the testing of distributional data is controversial, however, since incorporation of original species abundances into a null model may unavoidably incorporate abundance and distribution patterns arising from biological interactions (Gilpin and Diamond 1984). Species distribution patterns in complex communities can often be more clearly detected through the use of multivariate ordination methods such as principal components analysis which reduce large and cumbersome data sets of species abundances down to a few composite components. However, because each component mathematically combines abundances of numerous species, some information about possible interactions operating among species may be lost. As well, large data sets collected from large sample areas might incorporate high habitat heterogeneity that, through the presence of prey refugia, etc., could confound the identification of biological interactions (Roff *et al.* 1981). Distributional patterns that arise from biological interactions therefore might be most easily detectable in more physically homogeneous areas and less biologically complex communities with lower species diversity and a resultant lower number of potential interactions (both direct and indirect) among species. Analysis of these simpler communities is statistically more manageable, while the less complicated network of species interactions allows for clearer interpretation of results. Even in simple communities, however, distributional patterns only suggest the presence of biological interactions which can then be directly evaluated through experimentation.

Pelagic animal communities of freshwater lakes on the Avalon Peninsula of insular Newfoundland appear to constitute an example of such simple communities. Compared with other freshwater temperate-zone lakes in mainland Canada (e.g. see studies by Scott and Crossman 1964; Carter *et al.* 1980; Sprules 1980 and Chengalath *et al.* 1984), lakes on the Avalon Peninsula are low in faunal diversity, especially with regards to zooplankton predators. The dominant predators of zooplankton in these Newfoundland lakes are here considered to be the vertebrate *Gasterosteus aculeatus*, the threespine stickleback (Teleostei), and the large invertebrates *Chaoborus* spp. (Diptera) and *Leptodora kindtii* (Crustacea) (see General Introduction). The omnivorous copepods, *Epischura nordenskioldi* and *Cyclops scutifer*, are generally not a major component of the zooplankton community in the Avalon lakes and hence are not considered as major zooplankton predators in these lakes (see Chapter 4). Habitat heterogeneity in the Avalon system is low: the lakes are all rocky-bottomed with few macrophytes and show minimal vertical thermal stratification over the open-water season (see Description of the Study Site). Analysis of factors that could potentially influence planktivore distributions should thus be relatively straightforward due to the faunal simplicity and habitat homogeneity of the lakes. Distributions of *Gasterosteus aculeatus*, *Chaoborus* spp., and *Leptodora kindtii* were described for a set of lakes on the Avalon Peninsula to determine if these distributions were random or if they showed strong patterns that might result from predator-prey or competitive interactions among the planktivores. Multivariate analyses were also used to evaluate the possible influence of various biotic and environmental factors on the distributions and abundances of the vertebrate and invertebrate planktivores.

A preliminary study of 11 Avalon lakes was undertaken during fall 1986. In 1987, the study was extended to 15 lakes that were sampled both in the spring and late summer to more thoroughly evaluate the distribution patterns of the planktivores. Laboratory experiments were conducted to examine predator-prey relationships between the vertebrate planktivore, the threespine stickleback, and the two invertebrate planktivores, *Chaoborus* larvae and *Leptodora*. The influence of environmental variability on the distributions of the 3 planktivores was assessed by examining the interrelationships between environmental factors and patterns of planktivore abundance.

3.2. Methods

Planktivore samples were taken in fall (late August to late October) 1986, and in spring (mid-May to mid-June) and late summer (mid-August to early September) 1987. These seasons were chosen so that, even though each lake was sampled only once per season, the presence of the planktivores should be detectable as their populations at this time would consist of abundant, easily collected individuals, that is: 1) *Chaoborus* populations would consist mainly of diurnally migrating 3rd and 4th larval instars, either as overwintering larvae from the previous year (spring sample) or as the present year's larvae (fall/late summer sample) (Carter and Kwik 1977; von Ende 1982; Yan *et al.* 1985), 2) *Leptodora* populations would be in a spring or late summer population pulse (Sebestyén 1960; Karabin 1974; Garton 1990; Hovenkamp 1990), and 3) threespine stickleback populations would be in pre-spawning or post-spawning stages so that sampling problems associated with spawning and consequent male territoriality (Wootton 1976) would be avoided; spawning has been noted to occur in mid-summer in other Atlantic temperate-zone populations (Coad and Power 1973, Jakobsen *et al.* 1988).

Chaoborus and *Leptodora* were sampled by means of two vertical tows taken to within 1.0 m of the sediments at the deepest spot in the lake, with a 1.0 m long tow net of 0.25 m mouth diameter fitted with 100-μm mesh. The tows were taken at one hour after sunset, a time when the diurnally migrating *Chaoborus* larvae are typically abundant in the water column (Goldspink and Scott 1971; Carter and Kwik 1977).

Leptodora, particularly the larger animals, are also more commonly found near the surface waters at night (Sebestyén 1933; Cummins *et al.* 1969); comparison of day and night samples in the Avalon lakes consistently showed more *Leptodora* in the night samples. Densities were routinely calculated assuming a tow net efficiency of 50%. Actual tow net efficiencies for *Chaoborus* and *Leptodora* were determined for the four lakes in which these species were most abundant - Bauline Long Pond and Piccos Pond for *Chaoborus* and Quidi Vidi Lake and Hogans Pond for *Leptodora*, and ranged from 44 to 64% (mean 51%) as determined by comparison of net samples with samples taken from the same depth range with a 1.0 m long Schindler-Patalas trap of 0.25 m width by 0.25 m breadth fitted with 100-μm mesh. Samples were preserved in 95% ethanol and the entire sample was examined under a Wild M5A dissecting microscope. *Chaoborus* species were identified following Saether (1972) and Borkent (1979). Instar determinations were made through measurements of head capsule length as in Fedorenko and Swift (1972) and Carter and Kwik (1977).

Stickleback populations were sampled with minnow traps baited with beef liver. Minnow traps are effective passive gear for the estimation of the relative abundance of populations of small fish species (He and Lodge 1990), particularly in lakes which are rocky-bottomed to enable fish to hide among the rocks and avoid seining, and are of low conductivity so that the effectiveness of electroshocking is reduced. In 1987, the traps were lined with dark nylon netting of 1.0-mm mesh that would retain small juvenile fish. Two strings of traps were set overnight on the same date as the night tow, with the traps placed along the lake bottom at metre depth intervals from 1.0 m deep (near-shore) to either the deepest point in the lake or the deepest point that could be reached with the length of the trap string (approx. 150 m). Previous studies have indicated that night sampling is more effective than day sampling; in a study of Alaskan lakes, Rogers (1968) caught more threespine stickleback in night versus day samples. The two trap strings were set out at opposite ends of the lake in order to minimize possible overlap in the fish "collection" area for each string. To standardize trapping effort between lakes of different volumes, traps were set out in numbers proportional to the maximum depth of the lakes (see Table 2.1). Number of traps (for two strings) per lake ranged from 4 (Middle Three Island Pond, maximum depth 2.2

m) to 25 (Tors Cove Pond, maximum depth 16.9 m) with a mean of 13 (median of 13) traps per lake. Distances between traps ranged from 6 to 24 m, depending on lake bottom topography. Catch replicability, assessed in Quidi Vidi Lake by consecutive sampling for three nights with two strings of mesh-lined traps, produced a variance (s^2) of 53% of the mean catch per trap. This level of variance in catch per trap, while high, allows for a qualitative ranking of stickleback abundance between the different lakes. Sticklebacks trapped overnight were counted and released. Up to 10 fish per lake were retained and preserved in 70% ethanol for later gut analysis. Gut (stomach and upper intestine) contents were transferred to 95% ethanol and examined for *Chaoborus* and *Leptodora* at 25 to 50X magnification under a Wild M5A dissecting microscope.

Laboratory feeding studies were conducted to investigate whether *Chaoborus* larvae and *Leptodora* were suitable prey items for sticklebacks. Ten sticklebacks, ranging in total length from 28 to 60 mm, were brought into the laboratory and allowed to acclimatize in a 90 L aquarium for 24 hours. *Chaoborus* (3rd and 4th instars) were then introduced into the aquarium and the behaviour of the planktivores was observed. As well, individual fish were placed in 2.0 L beakers and offered a size range of 10 *Chaoborus* individuals from 7.4 to 11.1 mm in length. Similar experiments were carried out with *Leptodora* that ranged in length from 3.2 to 8.8 mm.

The combined spring and summer distributional patterns of the planktivores were analysed with the Fisher exact probability test, a nonparametric test suited to analysis, by means of a 2 X 2 contingency table, of discrete data with small sample sizes (Siegel 1956, Snedecor and Cochran 1980). The test determines whether two groups (e.g., lakes with *Chaoborus* and lakes without *Chaoborus*) differ from random in the proportion with which they fall into a second classification (e.g. lakes with sticklebacks and lakes without sticklebacks). The result was evaluated against a one-tailed probability distribution; the hypothesis tested was that in lakes where species A and/or species B occurred, species A was found with species B less often than would be expected by chance (i.e., a pattern of exclusion). Absence of a planktivore from a lake sample does not preclude the possibility that the organism exists in the lake, but does indicate that the organism is below detectable sampling density and therefore of little probable influence on the other planktivores. Nonparametric Wilcoxon signed-rank tests (Siegel 1956; Sokal and Rohlf 1973) with two-tailed probabilities were used to compare total invertebrate planktivore densities and stickleback abundances between pairs of lakes in the different years. Nonparametric Mann-Whitney *U*-tests (Siegel 1956) were used to test for significant differences between selected lake groups in either *Chaoborus* or *Leptodora* densities; one-tailed probabilities were used to determine if *Chaoborus* or *Leptodora* densities were higher in the absence of stickleback predators.

Principal components analysis based on data correlation matrices (SPSS^x FACTOR programme, Norusis 1988) was used to summarize the 1987 density data of *Chaoborus* (both species together), *Leptodora* and stickleback into planktivore components which would account for most of the variation in the original data. Components were subjected to varimax rotation to minimize the number of variables that have high loadings on a component (Norusis 1988); this allowed for clearer interpretation of the components when compared with the non-rotated solution and solutions from other rotation methods. The data were $\log_{10}$ transformed ($\log_{10}(x + 1)$) prior to the analysis to correct for the observed dependence of the variance on the mean in the raw data. To determine the influence of environmental variability on planktivore density and distribution, the planktivore principal components were related in multiple linear regression models (SPSS^x REGRESSION programme, Noruŝis 1988) to chemical, morphometric, watershed and plankton principal components derived for the Avalon lakes. For the environmental components, raw data were normalized through $\log_{10}$ transformation and proportion or percentage data through arcsine square root transformation (Prepas 1984), with $\log_{10}(x + 1)$ and arcsine $(x + 0.05)$ used for variables which had zero values in the data. The final number of principal components was determined by the number of components with eigenvalues > 1.0 (Davies 1984). Subsequent components with eigenvalues < 1.0 would individually account for less variance than the average of all components and are therefore not considered to be interpretable (Legendre and Legendre 1983). All principal components were given names corresponding to the variables which explained the highest percentage of variance in each component as judged by inspection of the correlation coefficients of the raw data with the extracted component. As PCA assumes a linear relationship between the extracted components and associated variables, scatterplots of the components with the variables most strongly correlated with them were examined to ensure that the data distributions were not highly skewed

The chemical, morphometric and watershed components for the 15 lakes were derived from data in Knoechel and Campbell (1988). For lake chemical characterization, phosphorus (orthophosphate PO_4 and total phosphorus) and nitrogen (nitrate NO_3, ammonia NH_4 and organic = total Kjeldahl nitrogen) concentrations were determined from surface water samples collected shortly after ice-out between May 10 - 23, 1984 (defined by the authors as "spring") when surface water temperatures averaged 10 °C, and between June 12 - 16, 1986 (defined as "summer") when surface water temperatures averaged 13 °C. Concentrations of other chemical variables (Pb, Al, Ca, Mg, Fe, Si, Mn and SO_4) were determined from the spring samples. All chemistry samples were analyzed at the Water Analysis Facility at Memorial University of Newfoundland, by autoanalyzer techniques for phosphorus and nitrogen, by graphite furnace atomic absorption for Al, and by flame atomic absorption for the remaining variables. Morphometric characteristics included lake surface area and volume, mean and maximum depth, drainage area, water retention time and summer flushing rate. Lake volume was calculated from depth/area curves using a digitizer. For 10 lakes, lake depth was determined either from transects made with a recording echo sounder in 1982 or from bathymetric maps where available (E. Baggs, G. Cowan, C. Davis, *pers. comm.*; Wiseman 1972; O'Connell 1974). Mean depth was calculated as volume divided by surface area. For the remaining 5 lakes (Middle Three Island, Round, Second, Tors Cove, and Whiteway), maximum depth was determined from cursory echo sounding and mean depth was estimated from calculated ratios of mean to maximum depths of the surveyed lakes. Water retention was calculated on the basis of an average 100 cm annual excess of precipitation over evapotranspiration (Damman 1983) while flushing rate was calculated using the average measured water yield of 16.2 cm from June to August 1982 for two watersheds in the area (Northwest Pond River and Waterford river). Flushing rates of Second Pond and Tors Cove Pond were determined from monitored water yields from small hydroelectric plants that utilized the lake discharges. Watershed characteristics (proportions of total watershed area, excluding surface area of the study lake, that were forested, developed for housing, covered by barrens or covered by lakes) were determined from topographic maps (1:50,000) of the study site with areal measurements made using a digitizing tablet. Number of houses in the two urban watersheds of M.U.N. Long Pond and Quidi Vidi Lake was estimated from City of St. John's zoning plan census data.

Plankton components were derived from 1987 mean phytoplankton and zooplankton biomass data for the 15 lakes. The lakes were sampled once in spring (May 26 - June 20), midsummer (July 9 - 22) and late summer (August 10 - Sept 4). Phytoplankton was collected from two replicate water samples integrating the top 4.0 m at a main deep station using weighted plastic tubing of 1.3 cm diameter. A 100 ml subsample was preserved in acid Lugols solution. Zooplankton was collected with a 25 cm diameter net fitted with 100 µm mesh. Two vertical tows were made at a main deep station from within 1.0 m of the sediments to the surface and pooled samples were preserved in 95% ethanol. The tow net capture efficiency for the zooplankton community was set at 50% as compared with collections made with the Schindler-Patalas trap (range 35 - 61% in 8 lakes sampled). In the laboratory, 5.0 ml aliquots of the phytoplankton samples were settled onto slides from 2.54 cm tall settling chambers (Knoechel and Kalff 1976) and the slides were examined at 480X magnification under phase contrast. Phytoplankton were enumerated and cell sizes were determined with an eyepiece micrometer. Phytoplankton wet weight biomass was calculated using biovolume estimates based on simple geometric solids, assuming unit specific gravity. Total biomass was divided into three classes based on cell size: "small edible" cells < 10 µm in maximum dimension, "medium edible" cells between 10 and 30 µm in maximum dimension, and "large inedible" cells > 30 µm in maximum dimension. These classifications have previously proven useful in the functional analysis of trophic interactions (Sprules and Knoechel 1983). Subsamples of the zooplankton collections were enumerated (with a minimum of 50 organisms for each taxonomic group, if possible) and sized in a rotating circular plexiglas counting chamber with a Wild M3 dissecting microscope at 25 - 50X magnification. Zooplankton lengths were measured with electronic calipers from images magnified from the microscope onto a video screen (Sprules *et al.* 1981). Zooplankton wet weight biomass was calculated from recorded abundances using published length-dry weight relationships for the same or similar species (Bottrell *et al.* 1976, Dumont *et al.* 1975) and multiplying by 10 to estimate wet weight (Bottrell *et al.* 1976). Total biomass was divided into the broad taxonomic classes of Cladocera, Calanoida, Cyclopoida and Rotifers.

The strength of the relationships between the planktivore principal components and the environmental (chemical, morphometric, watershed and plankton) components was examined by Pearson product-moment correlation analysis, then stepwise multiple linear regression (MLR) was used to determine the amount of variation in the planktivore components which could be explained by these environmental components. Significant regression relationships, once identified, were then more closely inspected. Environmental components that were significantly related to the planktivore components were broken down into their respective constituent variables to determine the proportion of the variance in the planktivore data that could be explained by relating the original variables of the planktivore components to the variables of the specific environmental components. Multiple linear regressions were carried out to determine relationships between these component variables; the resulting multiple R^2 values were compared with those from the regression relationships between the planktivore and environmental components. For all regression models, assumptions of normal distributions of data and of linearity in the regressions were judged by examination of normal probability plots with standardized residuals, and by plots between predicted variables and residuals, respectively. Analysis was carried out on Memorial University's VAX 8800 operating under VMS 5.0. Except where noted, statistical significance (two-tailed) was set by the criterion level $\alpha = 0.05$.

3.3. Results

Specimens of the vertebrate and invertebrate planktivores are shown together in Figure 3.1. Two species of *Chaoborus* were identified: *C. punctipennis* Say, previously unreported from Newfoundland, and *C. trivittatus* Loew, previously reported from 2 lakes near St. John's (Borkent 1979). *Chaoborus* spp., *Leptodora* and sticklebacks all appear to be generally distributed throughout the geographic range of the Avalon lakes (1987 data: Figure 3.2), which suggests that all the lakes are available for colonization by any of these planktivores. Sticklebacks were found in traps at all depths in the lakes in which the fish were observed to be present.

Results from the preliminary study of 11 Avalon lakes sampled during fall 1986 (Table 3.1; see also Campbell and Knoechel 1988) revealed distributional patterns suggestive of interactions between the planktivores. *Chaoborus* larvae were found only in the three lakes that lacked sticklebacks and this pattern of exclusion was statistically significant (Fisher exact probability test: $p = 0.01$, $n = 11$). *Leptodora* was found only in four lakes which lacked *Chaoborus* and this exclusion pattern was also statistically significant ($p = 0.03$, $n = 7$). Sticklebacks were found in the four lakes that contained *Leptodora*. Population densities of the invertebrate planktivores (*Chaoborus* spp. + *Leptodora*) observed in the 11 lakes in fall 1986 were significantly different from those observed in the same lakes in late summer 1987 (paired comparison of total invertebrate densities with Wilcoxon signed-rank test: two-tailed $p = 0.05$, $n = 9$. Exact probability levels cannot be obtained with integral values of the rank sum in this test; Sokal and Rohlf 1973). Several lakes in which *Chaoborus* or *Leptodora* were present at low densities in 1987 lacked these species in the 1986 samples (e.g. *C. trivitattus* in Bauline Long Pond, *C. punctipennis* and *Leptodora* in Long Pond). In 1986, the lakes were only sampled once, in some cases in late October, and thus the presence of the invertebrate predators may have gone undetected; several *Chaoborus* species are known to undergo late summer pupation and emergence in temperate-zone lakes (Carter and Kwik 1977; von Ende 1982) while *Leptodora* often disappears from the open water by late fall (Sebestyen 1960; Cummins *et al.* 1969; Karabin 1974). Relative stickleback numbers may also have been slightly underestimated in 1986 compared with 1987 since few juveniles were

Figure 3.1. *Gasterosteus aculeatus* (top), *Chaoborus trivittatus* (left), *Chaoborus punctipennis* (right) and *Leptodora kindtii* (bottom): the major vertebrate and invertebrate planktivores in the Avalon lakes. (Specimens were preserved in ethanol).


10 mm

Figure 3.2. Geographic distribution (presence/absence) of *Chaoborus trivittatus* (◴), *Chaoborus punctipennis* (◷), *Leptodora kindtii* (◶) and *Gasterosteus aculeatus* (◵) in the 15 Avalon lakes in 1987; presence of each species indicated by solid shading of respective quadrant in circle symbol. Lakes are identified by a two-letter code as in Figure 2.1.

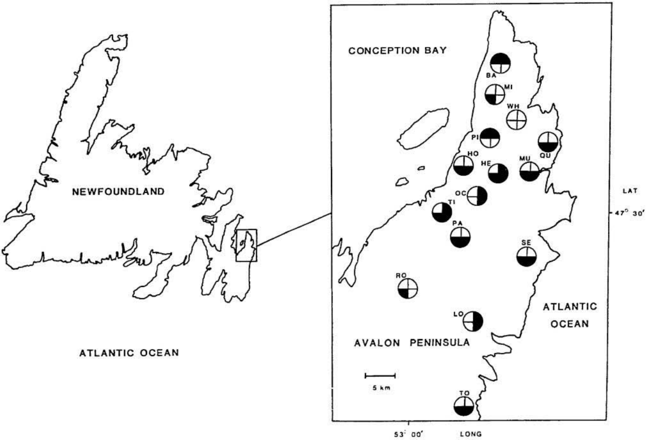

CONCEPTION BAY
NEWFOUNDLAND
ATLANTIC OCEAN
BA
MI
WH
PI
QU
HO
HE
MU
OC
TI
PA
SE
RO
LO
TO
ATLANTIC
OCEAN
AVALON PENINSULA
5 km
LAT
47° 30′
53° 00′
LONG

Table 3.1. Densities (animals-m^{-3}) of *Chaoborus* spp. (Chaob) and *Leptodora kindti* (Lepto) and relative abundances (animals-trap^{-1}) of *Gasterosteus aculeatus* (Gast) during fall 1986 for 11 Avalon lakes. All *Chaoborus* larvae are *C. punctipennis* except where marked * (= *C. trivittatus*).

Lake	Chaob	Lepto	Gast
Bauline Long	10*	0	0
Healeys	0	6	3.1
Hogans	0	4	40.3
Long	0	0	0.1
M.U.N. Long	0	0	2.9
Octagon	24	0	0
Piccos	129 37*	0	0
Quidi Vidi	0	71	0.9
Second	0	5	0.9
Three Island	0	0	46.2
Tors Cove	0	0	23.5

caught in the unlined traps in 1986 (see Chapter 4), although relative numbers did not differ significantly between fall 1986 and late summer 1987 samples (Wilcoxon signed-rank test, $p > 0.10$, $n = 8$). For these reasons, the distributions and densities of the planktivores are probably more accurately represented by the 1987 samples (Table 3.2). Further analyses will concentrate on the 1987 data.

Of the 15 Avalon lakes sampled in 1987, *C. trivittatus* was found in two lakes, *C. punctipennis* in 6, *Leptodora* in 10 and *G. aculeatus* in 10. The larger chaoborid, *C. trivittatus*, was found only in lakes in which no sticklebacks were trapped; these lakes lacked *Leptodora* as well but contained *C. punctipennis*. *C. punctipennis* and *G. aculeatus* were found together in only two lakes. *Leptodora* co-occurred with *C. punctipennis* in four lakes and with sticklebacks in 8 lakes. None of the planktivores was found in Whiteway Pond.

Where *C. punctipennis* co-occurred with *G. aculeatus* (in Healeys Pond and Three Island Pond), the density of the chaoborid was relatively low (5 and 9 animals-m^{-3}, respectively, Table 3.2). While stickleback density in Healeys Pond was also low (0.6 and 0.5 animals-trap^{-1} in spring and late summer), stickleback density in Three Island Pond was quite high (23.8 and 15.4 animals-trap^{-1} in spring and late summer). *Chaoborus* were collected in Three Island Pond only in the spring sample, and had not been found in the fall 1986 sample. Three Island Pond differed from the other lakes in the study in that a large proportion of the stickleback diet (as determined from gut contents) consisted of benthic organisms as opposed to the diet of mainly pelagic zooplankton observed for sticklebacks in the other Avalon lakes (Chapter 4; see also Campbell 1991 *in press*).

Densities of the planktivores in 1987 varied widely among lakes (Table 3.2). In lakes in which they were found, *C. trivittatus* ranged in late summer density from 14 to 311 animals-m^{-3}, *C. punctipennis* from 5 to 576 animals-m^{-3}, *Leptodora* from 5 to 127 animals-m^{-3}, and *G. aculeatus* from 0.5 to 75.8 animals-trap^{-1}. The overall highest densities of *Chaoborus* larvae were seen in Bauline Long and Piccos Ponds, the only lakes in which *C. trivittatus* was found. Spring populations of *Chaoborus*, found only in Piccos Pond and Three Island Pond, consisted wholely of 3rd and 4th

Table 3.2. Densities (animals.m^{-3}) of *Chaoborus* spp. (Chaob) and *Leptodora kindtii* (Lepto) and relative abundances (animals.trap^{-1}) of *Gasterosteus aculeatus* (Gast) during spring and late summer 1987 for 15 Avalon lakes. All *Chaoborus* larvae are *C. punctipennis* except where marked * (= *C. trivittatus*). Round Pond was not sampled in the summer.

	SPRING			SUMMER		
Lake	Chaob	Lepto	Gast	Chaob	Lepto	Gast
Bauline	0	0	0	207 14*	0	0
Healey's	0	5	0.6	5	0	0.5
Hogan's	0	19	30.5	0	24	46.4
Long	0	0	0	9	9	0
Middle 3 Is.	0	0	65.5	0	0	75.8
MUN Long	0	0	0.8	0	5	2.3
Octagon	0	0	0	7	11	0
Paddy's	0	0	40.4	0	15	20.8
Picco's	15 18*	0	0	576 311*	0	0
Quidi Vidi	0	6	14.7	0	127	11.9
Round	0	0	3.2	---	---	---
Second	0	0	0.5	0	18	1.0
Three Island	9	15	23.8	0	0	15.4
Tors Cove	0	3	23.0	0	0	33.5
Whiteway	0	0	0	0	0	0

instars of *C. punctipennis*, and of *C. trivittatus*. Late summer populations of *Chaoborus* in the Avalon lakes contained some 1st and 2nd instars although 3rd and 4th instars were most numerous: percentage abundance of 3rd + 4th instars in the lakes with *Chaoborus* ranged from 75 to 100% for *C. trivittatus* and from 54 to 75% for *C. punctipennis*. The densities of *Chaoborus* spp. and *Leptodora* in the Avalon lakes are comparable with those from other temperate-zone lakes (Cummins *et al.* 1969; Pope *et al.* 1973; Karabin 1974; Yan *et al.* 1985).

The distributions of both *C. trivittatus* and *C. punctipennis* were significantly and negatively related to the distribution of sticklebacks (Fisher exact probability test; Table 3.3). Densities of *C. punctipennis* in lakes lacking sticklebacks were significantly higher than densities in lakes with sticklebacks (averaged spring and summer densities, Mann-Whitney *U*-test, one-tailed, $p = 0.03$, $n = 15$). *C. trivittatus* was not present in stickleback lakes. While no identifiable *Chaoborus* spp. were found in the stickleback gut samples, pupal fragments that could have been *Chaoborus* were observed. Sticklebacks readily consumed both species of *Chaoborus* larvae in laboratory predator/prey experiments. In 5 trials of 10 mins duration, when a combination of 10 larvae of both species of lengths from 7.4 to 11.1 mm were available as prey for individual sticklebacks from 28 and 60 mm in length, the fish rapidly consumed all 10 larvae. *C. trivittatus*, being larger and more visible, was consumed first.

The distribution of *Leptodora* was not significantly related to the distributions of either *C. punctipennis* or sticklebacks, while the distributions of *Leptodora* and *C. trivittatus* were significantly and negatively related (Table 3.3). *Leptodora* densities in lakes without *C. punctipennis* did not differ significantly from densities in lakes with *C. punctipennis* (averaged spring and summer densities, Mann-Whitney, two-tailed, $p = 0.64$, $n = 15$), while *C. punctipennis* densities in lakes without *Leptodora* did not differ significantly from densities in lakes with *Leptodora* (averaged spring and summer densities, Mann-Whitney, two-tailed, $p = 0.67$, $n = 15$). *C. trivittatus* did not occur in *Leptodora* lakes. *Leptodora* densities in lakes without sticklebacks were not significantly higher than densities in lakes with sticklebacks (averaged spring and summer densities, Mann-Whitney, one-tailed, $p = 0.06$, $n = 15$) and no *Leptodora*

Table 3.3. Tests for exclusion patterns in the combined spring and summer distributions of *Gasterosteus aculeatus* (Gast), *Chaoborus punctipennis* (C.p.), *C. trivittatus* (C.t.) and *Leptodora kindtii* (Lepto) in the Avalon lakes. Data are presented in the form of a ratio (Obs/Exp) where Obs is the observed number of lakes in which Species A co-occurs with Species B and Exp is the number of lakes in which co-occurrence is expected. The probability (*p*) of a one-tailed test of the null hypothesis (no relationship) is based on the Fisher exact probability test; *n* is the number of lakes containing Species A and/or Species B, '-' (negative) or '+' (positive) refer to the direction of statistically significant interactions as they affect Species A. Species A is said to 'wholly co-occur' with Species B when the distribution of Species A is contained wholly within the distribution of Species B. Tests are based on data in Table 3.2.

	SPECIES A			
SPECIES B	Gast	C.p.	C.t.	Lepto
Gast		2/4.3 - *p*=0.015 *n*=14	0/1.7 - *p*=0.015 *n*=12	8/7.1 *p*=0.68 *n*=14
C.p.			wholly co-occur *n*=6	4/5 *p*=0.23 *n*=12
C.t.				0/1.7 - *p*=0.015 *n*=12
Lepto				

were seen in stickleback gut contents. In 5 laboratory trials of 10 mins duration in which individual sticklebacks from 30 to 50 mm in length were provided with 10 *Leptodora* of 3.2 to 8.8 mm in length as prey, the sticklebacks were observed to generally ignore the almost transparent *Leptodora* swimming around them. In one trial, the fish was left together with the *Leptodora* for 30 mins, at which time 4 of the 10 cladocerans had still not been eaten. When *Leptodora* and *Chaoborus* larvae were both placed in an aquarium with sticklebacks for qualitative observations of fish behaviour, the fish were observed to immediately eat the chaoborids and appeared not to see the cladocerans.

Only one common principal component could be extracted from the 1987 planktivore data; this 'planktivore' component accounted for only 57% of the variance in the data (Table 3.4). The component was based on 1987 mean (spring and summer) stickleback abundances and late summer *Chaoborus* and *Leptodora* densities, since the invertebrate planktivores were not present in many of the spring samples as a result of their life cycle patterns. Examination of scatterplots of the individual planktivore abundances against the extracted component suggested that there was some non-linearity due to *Chaoborus* or *Leptodora* being absent from a number of lakes. There was a total of four components derived from the lake chemical data, two components from the morphometric data, three components from the watershed data and three components from the plankton data. Pb was not included in the PCA of the chemical data as initial analysis indicated that distribution of this variable was highly skewed with respect to the extracted component. The environmental components, along with the percent of variance of the original data explained by the components, are shown in Tables 3.5 - 3.8. Pearson product-moment correlations of the 'planktivore' component with the plankton components and the environmental components are shown in Tables 3.9 and 5.5, respectively.

Results from multiple linear regressions with environmental principal components entered as independent variables showed 'planktivore' to be significantly related only to the plankton component 'copepods', with a negative regression of r^2 = 0.50 (p = 0.10, n = 15). This copepod component represented the biomasses of cyclopoid and calanoid copepod zooplankton and the decreases in biomass of "large

Table 3.4. Planktivore principal components analysis, with correlations of 1987 mean Gasterosteus aculeatus and 1987 late summer Chaoborus and Leptodora abundance data with the extracted component (PC). Only statistically significant ($p < 0.05$) correlation coefficients are shown.

Variable	PC 1 Planktivore
Chaoborus	- 0.878
Stickleback	0.818
Leptodora	0.524
Cumulative explained variance	0.571

Table 3.5. Chemical principal components analysis, with correlations of original data with the extracted components (PCs). For phosphorus (P; orthophosphate PO_4; total phosphorus TP) and nitrogen (nitrate NO_3; ammonia NH_4; total Kjedahl nitrogen TKN), spring refers to spring 1984, summer to summer 1986. Other water chemistry variables are spring 1984 samples. Only statistically significant ($p < 0.05$) correlation coefficients are shown.

Variable	PC 1	PC 2	PC 3	PC 4
	Ionic strength	Summer P	Spring P	TKN
SO_4	0.944			
Ca	0.938			
Summer NO_3	0.910			
Mg	0.867			
Spring NO_3	0.861			
Si	0.850			
Summer NH_4	0.759			
Mn	0.713			
Spring NH_4	0.579		0.533	
Summer PO_4		0.858		
Al		0.817		
Fe		0.758		
Spring PO_4			0.896	
Spring TP			0.840	
Summer TP			0.567	
Summer TKN				0.878
Spring TKN				0.543
Cumulative explained variance	0.445	0.620	0.766	0.842

Table 3.6. Morphometric principal components analysis, with correlations of original data with the extracted components (PCs). Only statistically significant ($p < 0.05$) correlation coefficients are shown.

Variable	PC 1 Lake size	PC 2 Flushing rate
Lake volume	0.948	
Max. depth	0.903	
Mean depth	0.837	
Surface area	0.756	
Flushing rate		0.973
Water retention		− 0.961
Drainage area	0.521	0.853
Cumulative explained variance	0.488	0.874

Table 3.7. Watershed principal components analysis, with correlations of original data with the extracted components (PCs). Only statistically significant ($p < 0.05$) correlation coefficients are shown.

Variable	PC 1	PC 2	PC 3
	Development	% barrens	% upstream lakes
House density	0.903		
Cleared land	0.886		
# of houses	0.868		
% forested		- 0.940	
% barrens	- 0.607	0.667	
% upstream lakes			0.986
Cumulative explained variance	0.514	0.762	0.930

Table 3.8. Plankton principal components analysis, with correlations of mean 1987 biomass data with the extracted components (PCs). Only statistically significant ($p < 0.05$) correlation coefficients are shown.

Variable	PC 1 Edible phytoplankton	PC 2 Copepods	PC 3 Herbivores
Small edible phytoplankton	0.967		
Medium edible phytoplankton	0.932		
Cyclopoids		0.908	
Calanoids		0.779	
Large inedible phytoplankton	0.522	- 0.620	
Cladocerans			0.858
Rotifers			- 0.755
Cumulative explained variance	0.360	0.664	0.820

inedible" phytoplankton (Table 3.8). 'Copepods' showed a significant Pearson product-moment correlation with only one of the other environmental components, namely the morphometric component 'flushing rate' (r = - 0.605, p = 0.02, n = 15). Correlation coefficients among all the environmental principal components are listed in Appendix Table A.1. Aside from the significant correlation between 'planktivore' and 'copepods' (Table 3.9), 'flushing rate' was the only other environmental component to show a significant correlation with 'planktivore' (Table 5.5), although it did not enter as a significant variable in the MLR model. When 'copepods' was broken down into its constituent variables, only the log-transformed variable of cyclopoid biomass entered as a significant (p = 0.02) independent variable in the 'planktivore' model, with a (negative) r^2 of 0.35. When this relationship was broken down still further to the constituent variables in the 'planktivore' component, stickleback catch was found to be significantly and negatively related to cyclopoid biomass (r^2 = 0.41, p = 0.01, n = 15) alone, while *Chaoborus* density was significantly and positively related also to cyclopoid biomass (r^2 = 0.34, p = 0.02, n = 15) alone. When *Leptodora* density was the dependent variable, only the the biomass of "large inedible" phytoplankton entered the regression model, but this relationship was not statistically significant (r^2 = 0.18, p = 0.12, n = 15). For all significant MLR models, examinations of plots of residuals indicated that assumptions of linearity and normality were generally upheld.

3.4. Discussion

Analyses of the distributions of *C. punctipennis*, *C. trivittatus* and threespine stickleback in Avalon lakes suggest possible predatory exclusion by sticklebacks since both *Chaoborus* spp. are found in lakes with populations of sticklebacks significantly less often than would be expected if the distributions of the invertebrate and vertebrate planktivores were random and independent of each other. In addition, densities of the *Chaoborus* spp. were significantly higher in the lakes that lacked sticklebacks compared to lakes that contained sticklebacks. The pattern of predatory exclusion was most evident with the larger species, *C. trivittatus*, which was never found together with sticklebacks, while *C. punctipennis* co-occurred with sticklebacks

Table 3.9. Pearson product-moment correlations of 'planktivore' principal component, $\log_{10}$ stickleback catch (Gast), $\log_{10}$ *Chaoborus* density (Chaob), $\log_{10}$ *Leptodora* (Lepto) density and $\log_{10}$ total invertebrate planktivore density (Invert) with plankton principal components in the Avalon lakes. Significance levels of the correlation coefficients are indicated by * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) and *** ($p < 0.005$).

Plankton PCs	Planktivore PC	Gast	Chaob	Lepto	Invert
Edible phytoplankton	- 0.174	0.058	0.397	0.004	0.478 *
Copepods	- 0.708 ***	- 0.785 ***	0.596 *	- 0.092	0.365
Herbivores	- 0.054	- 0.233	0.024	0.229	0.255

in two lakes. *C. punctipennis* may be better adapted than *C. trivittatus* to avoid predation and thus to coexist with planktivorous fish, as suggested by Pope *et al.* (1973), since *C. punctipennis* is smaller and slimmer and therefore should be less visible to visually feeding fish, especially in highly coloured or turbid waters. *C. punctipennis* may also spend more time in the benthic habitat (Pope *et al.* 1973) thereby avoiding fish predation, in contrast with the more pronounced pelagic lifestyle of *C. trivittatus* (Nyberg 1984). In deep stratified lakes, the hypolimnion might serve *Chaoborus* as a refuge from predation (Lewis 1979), particularly if oxygen concentrations there are low. The well-mixed Avalon lakes lack any hypolimnetic refugia, however. Researchers have previously noted that both *Chaoborus* species undergo diurnal migration, reaching the lake surface at night; the larger *C. trivittatus* often stays deeper in the water column (Fedorenko and Swift 1972; Carter and Kwik 1977), perhaps as a predator avoidance mechanism. Vertical distribution patterns were not specifically examined in the present study since organisms were collected in vertically integrated tows. *Chaoborus* were rarely seen in day tows in the Avalon lakes, however, and hence I conclude that both species diurnally migrate.

In one of the two lakes in which *C. punctipennis* co-occurred with sticklebacks (Healeys Pond), stickleback density was low enough so that the predation impact on the distribution of the chaoborid might be minimal. In the other lake where they co-occurred (Three Island Pond), stickleback density was high but the fish were observed to feed mainly on benthic organisms as opposed to pelagic organisms such as *C. punctipennis* larvae, and thus the predation impact on the distribution of the chaoborid was probably reduced. In addition, *C. punctipennis* in Three Island Pond was present only in the spring with apparently no larvae surviving to reach the late summer sampling period. In the one other lake (Piccos Pond) where *C. punctipennis* was abundant enough to be noted in the spring, sticklebacks were absent; without this predation pressure, *C. punctipennis* subsequently displayed the highest late summer density that was recorded in any of the Avalon lakes.

While no identifiable chaoborid larvae were seen in the stomach contents of *G. aculeatus* in the Avalon lakes where the planktivores co-occured, possibly due to the fragility of the chaoborid body, stickleback diet items were mainly pelagic zooplankton (except in Three Island Pond) which indicates that the fish were feeding in the water column and thus should come into contact with *Chaoborus* larvae and pupae. Threespine stickleback are known to eat a wide range of food items, particularly those organisms of abundant biomass in the plankton (Hangelin and Vuorinen 1988), and they do take *Chaoborus* larvae in the field (Hynes 1950, Jakobsen *et al.* 1988). Sticklebacks experienced no difficulty in eating both *Chaoborus* species during the laboratory experiments, even though the invertebrate planktivore is transparent except for the hydrostatic organs and well-developed eyes. Possibly the fish are attracted by the sudden, erratic movements of the larvae. Hence, the consideration of *G. aculeatus* as a predator of *Chaoborus* spp. is justified. Other freshwater predators, such as the macroinvertebrates *Notonecta undulata* and *Anax junius*, are known to prey on *Chaoborus* larvae as well (Cooper 1983).

Studies elsewhere have provided conflicting evidence regarding exclusion patterns between the chaoborids, *C. punctipennis* and *C. trivittatus*, and planktivorous fish. Elser *et al.* (1987) experimentally reduced lake minnow numbers and noted a substantial increase in the population density of *C. punctipennis*. Nyberg (1984) found *C. trivittatus* to be absent from lakes with dense fish populations, while Vanni (1988) also reported populations of *C. trivittatus* (including the synonym *C. brunskilli*, Borkent 1979) to be restricted to fishless lakes. Conflicting or weak exclusion patterns found in other studies (e.g., Pope *et al.* 1973; von Ende 1979; Yan *et al.* 1985; Vanni 1988) may be due primarily to greater faunal complexity of the lake communities (both in terms of fish species and chaoborid species) combined with physical factors such as hypolimnetic refugia and highly coloured waters that would tend to moderate predation pressure.

Distribution patterns of *Chaoborus* spp., particularly *C. trivittatus*, that are suggestive of possible predatory exclusion by planktivorous fish such as threespine stickleback have been observed in the Matamek River system, Quebec (Pope *et al.* 1973). Of the 26 Matamek lakes studied by Pope *et al.* (1973) and Pope and Carter (1975), *C. trivittatus* occurred in 17 lakes, of which only 7 had fish (species included *Salvelinus fontinalis*, *S. alpinus*, *Pungitius pungitius*, *Osmerus mordax*, *Anguilla* *rostrata* and *G. aculeatus*) and only three had threespine stickleback, while *C. punctipennis* occurred in 7 lakes, all of which had threespine stickleback plus other fish species. My analysis (Table 3.10) of the distributions and abundances of *C. trivittatus* and *G. aculeatus* from the Matamek lakes shows that the distribution of *C. trivittatus* was significantly and negatively influenced by the distribution of the stickleback (Fisher exact probability test; $p = 0.002$, $n = 22$), although the relationship was weaker in this faunally more complex system than in the Avalon system. Maximum densities (per m^2) of *C. trivittatus* in Matamek lakes without threespine stickleback were significantly higher compared with lakes with stickleback (Mann-Whitney, one-tailed, $p = 0.03$, $n = 26$). Stickleback predation thus seems to influence the distribution and abundance of *C. trivittatus* in the Matamek lakes as well as in the Avalon lakes.

C. punctipennis co-occurs with sticklebacks in the Matamek lakes, in contrast to the Avalon lakes, perhaps by taking advantage of hypolimnetic refugia in the deeper Matamek waters. Maximum depths in the Matamek lakes ranged from 6 to 100 m and only three of the 26 lakes did not thermally stratify, as compared with the more shallow (see Table 2.1) and generally unstratified Avalon lakes. As well, there was greater species diversity of chaoborids and fish in the Matamek lakes, leading to interactions that could obscure chaoborid-stickleback patterns. *Chaoborus flavicans*, one unidentified chaoborid species and *Chaoborus americanus* also occurred in the Matamek system; the last, which did not diurnally migrate, was confined strictly to fishless lakes. Older instars of *C. americanus* can prey on early instars of other chaoborids such as *C. punctipennis* (von Ende 1979; Cooper 1983) which might contribute to the absence of *C. punctipennis* from fishless Matamek lakes. *C. americanus* has not yet been found in lakes on the Avalon Peninsula. Analyses of the gut contents of smelt and juvenile salmonids indicated that these species, more so than sticklebacks, were the major predators of *Chaoborus* larvae in the Matamek lakes (Pope and Carter 1975). Stickleback predation of *Chaoborus* larvae is relatively more important in the 15 Avalon lakes because smelt are absent (D. Copeman, *pers. comm.*). Examination of gut contents of juvenile and adult *Salvelinus fontinalis* from Octagon Pond also indicates that salmonids mainly consume benthic prey such as

Table 3.10. Tests for exclusion patterns in the distributions of *Gasterosteus aculeatus* (Gast), *Chaoborus punctipennis* (C.p.) and *C. trivittatus* (C.t.) in the Matamek lakes, based on data from Pope et al. (1973) and Pope and Carter (1975). Format as in Table 3.3.

		SPECIES A		
		Gast	C.p.	C.t.
SPECIES B	Gast		wholly co-occur n=8	3/6.2 - p=0.002 n=22
	C.p.			3/5.7 - p=0.006 n=21
	C.t.			

chironomid larvae and *Ephemeroptera* nymphs (Baggs 1989). Sticklebacks were found at all depths in the Avalon lakes. By contrast, in lakes with well-developed macrophyte beds, threespine stickleback were found mainly in the weedy, littoral areas (Kerfoot 1975; Ryan 1984) as a possible defense against piscivorous salmonids common in the limnetic zone (Jakobsen *et al.* 1988). In such lakes, the sticklebacks would have less predation impact on planktonic organisms such as *Chaoborus* larvae.

Of the 22 Michigan bog lakes studied by von Ende (1979), *C. trivittatus* occurred in three lakes, only one of which had fish (species included *Perca flavescens* and *Umbra limi*), while *C. punctipennis* occurred in 16 lakes, all of which had fish. Characteristic of bog lakes, the waters were stained and highly coloured; Secchi disk readings ranged from 0.7 to 2.2 m in the four lakes that were more intensively studied, as compared with the range from 2.2 to 8.5 m in the Avalon lakes (Table 2.1). *C. punctipennis* may commonly co-occur with fish in the Michigan lakes through avoidance of visual predation in these highly coloured waters. As in the Matamek lakes, *C. flavicans* and *C. americanus* also occurred in the Michigan lakes with *C. americanus* confined to fishless lakes and implicated in the absence of *C. punctipennis* from these lakes.

Yan *et al.* (1985) found no significant relationship between the distributions of two *Chaoborus* species (*C. punctipennis* and *C. flavicans*) and the presence of fish (13 planktivorous and non-planktivorous species) in 33 Ontario lakes. However, densities of the *Chaoborus* spp. were significantly and positively correlated with water colour (range from 0 to 60 Hazen units) and nutrient availability, suggesting an indirect visual predator (release) effect resulting from decreased water transparency. As well, maximum depths of these Ontario lakes ranged from 3 to 64 m which could allow for development of hypolimnetic refugia in some of the lakes. Nutrient availability, as related to food resources, might be crucial in determining *Chaoborus* abundance (Neill and Peacock 1980) as *Chaoborus* density may increase in the absence of fish only if the invertebrate planktivores are not initially restricted by low prey densities.

Stickleback predation seems to have little influence on the distribution and abundance of *Leptodora* in the Avalon lakes. The analyses found no significant relationship between the distributions of the two planktivores. In cases where *Leptodora* has been reported in fish stomach samples (Costa and Cummins 1972), lake densities of the cladoceran were much higher (late summer/early fall densities of 500 to 1000 animals-m^{-3}, determined from evening samples; Cummins *et al.* 1969) than were encountered in the Avalon lakes. Fish predation on *Leptodora* therefore is probably very low in these Avalon lakes, as is also indicated by the low numbers of *Leptodora* consumed by sticklebacks in the laboratory experiments. The fish were seemingly not attracted by the slow, paddling movements of this transparent cladoceran.

There was no significant relationship between the distributions of *Leptodora* and *C. punctipennis* in the Avalon lakes. In contrast, *C. trivittatus* was not found in lakes with *Leptodora* which might suggest a possible competitive interaction between these two invertebrate planktivores. However, *Leptodora* and *Chaoborus* species generally reach their most dense population levels at different times of the year - *Leptodora* in midsummer (Sebestyén 1960; Karabin 1974) and *Chaoborus* (3rd and 4th instars) in late summer/early autumn (Carter and Kwik 1977; von Ende 1982), and thus competition for shared prey organisms such as copepodites (Mordukhai-Boltovskaia 1958; Roth 1971; Karabin 1974; Fedorenko 1975; Chimney *et al.* 1981) would be minimized. It seems unlikely then that such competitive interactions could account for the observed distributions of *C. trivittatus* and *Leptodora*, especially since no significant pattern existed between the distributions of *Leptodora* and *C. punctipennis*, the chaoborid having a diet similar to that of *C. trivittatus* (Fedorenko 1975; Chimney *et al.* 1981). As well, while total *Chaoborus* density was positively related in the regression model to the biomass of cyclopoid copepod prey, *Leptodora* density was not significantly related to zooplankton biomass at all, and consequently there is little direct evidence that *Chaoborus* and *Leptodora* are competing for certain zooplankton species as a shared limiting food resource. Possible *Leptodora* predation on early instars of *C. trivittatus*, but not on the more transparent *C. punctipennis*, might also account for the distribution patterns of the cladoceran and the two chaoborids.

Environmental factors also appear to to have some influence on planktivore distributions in the Avalon lakes. The 'planktivore' component was most strongly related to 'copepods', although since 'planktivore' accounted for just 57% of the variance in the original vertebrate and invertebrate planktivore data, the relationship is not particularly interpretable. The low amount of variance explained by the 'planktivore' component is due largely to the non-normal distributions of the invertebrate planktivore data (both *Chaoborus* spp. and *Leptodora* were absent from a number of lakes) evidenced in plots of these data versus the extracted component, as well as being a function of the contrasting negative and positive loadings of *Chaoborus* and stickleback onto the 'planktivore' component. This contrast in loadings is a reflection of the negative relationship between the distributions of *Chaoborus* and stickleback in the lakes. Breakdown of the principal components indicated that stickleback abundance and density of *Chaoborus* spp. were most strongly related to cyclopoid biomass (negatively for stickleback, positively for *Chaoborus*). *Leptodora* density, however, was not significantly related to any of the variables that made up the 'copepod' component. In lake trophic systems, a strong "bottom-up" (producer or resource controlled) influence is expected to result in a positive relationship between producer and consumer abundance, while conversely, a strong "top-down" (consumer controlled) influence is expected to result in a negative relationship between the abundance of producers and consumers (McQueen *et al.* 1986). Hence, the negative relationship between stickleback abundance and cyclopoid biomass could indicate that sticklebacks (the consumer) are influencing the biomass level of the cyclopoid prey (the producer). In contrast, the positive relationship between *Chaoborus* density and cyclopoid biomass could indicate that the biomass of the cyclopoid prey is influencing the density of the invertebrate planktivore. However, only 41 and 34% of the total variance in stickleback abundance and *Chaoborus* density, respectively, could be related to cyclopoid biomass. High correlations of both the 'copepod' and 'planktivore' components with 'flushing rate' indicate that the relationship between planktivore abundance and copepod biomass might also reflect some underlying influence of lake morphometry on both of these variables (see also Chapter 5). Copepods, with relatively long generation times as compared with other zooplankton species, have been shown to be adversely affected by high flushing rates (O'Connell and Andrews 1977). None of the individual planktivore abundances, however, were signficantly correlated with 'flushing rate' in the present study.

Distributions of threespine stickleback have been related elsewhere to salinity (conductivity) and temperature (review by Wootton 1976). These parameters varied little among the 15 Avalon lakes and thus should not have markedly influenced stickleback distributions in this system. The influence of cyclopoid biomass on *Chaoborus* density cannot be divorced from the influence of stickleback predation, since the lakes with the highest cyclopoid wet weight biomasses (Bauline Long Pond, Long Pond, Octagon Pond, Whiteway Pond and Piccos Pond, in order of increasing biomass: Knoechel and Campbell 1988) also lacked stickleback predators. However, *Chaoborus* densities were very high only in Bauline Long and Piccos Ponds, so that other factors besides the distribution and abundance of the prey and predators of *Chaoborus* must affect the distribution of the invertebrate planktivore.

The low faunal diversity and low habitat heterogeneity of the Avalon lakes thus allows for the observation of patterns suggestive of biological interactions that are often obscured in more biologically or physically complex systems. Among the four major planktivores in Avalon lakes - *C. punctipennis*, *C. trivittatus*, *Leptodora* and threespine stickleback, the distribution pattern of the *Chaoborus* species would seem most influenced by predation ("top-down" control). While demonstration of distributional exclusion patterns between *Chaoborus* spp. and sticklebacks, and of stickleback consumption of *Chaoborus* larvae in laboratory situations, does not show conclusively that sticklebacks can eliminate chaoborids (particularly *C. trivittatus*) from Avalon lakes, when combined with the previous study of Pope *et al.* (1973) the results strongly suggest that fish predation plays a major role in determining the distribution of *Chaoborus* species. Interactions between invertebrate and vertebrate planktivores need to be considered when the effect of these predators on other links in the freshwater food chain, such as the zooplankton prey community, is evaluated.

Chapter 4

Prey selectivities of vertebrate and invertebrate planktivores in Avalon Peninsula lakes

4.1. Introduction

The threespine stickleback, *Gasterosteus aculeatus* Linnaeus (Teleostei), and the phantom midge larva, *Chaoborus* spp. (Diptera), are both predators of pelagic zooplankton in freshwater lakes, as noted in a number of studies (Hynes 1950; Rogers 1968; Fedorenko 1975*b*; Manzer 1976; Elser *et al.* 1987; Jakobsen *et al.* 1988; Moore 1988). While such studies have documented that these planktivores can demonstrate prey selectivity based on prey species and size, few studies have directly contrasted prey selectivities of the vertebrate and invertebrate planktivores in lakes that share similar pelagic zooplankton communities. Frequency distributions of species and size classes (both components of community structure) of the zooplankton community may, to some extent, reflect the cumulative impact of prey selectivities shown by vertebrate and invertebrate planktivores (Sprules 1972; Kerfoot 1975; Gliwicz *et al.* 1978). Assessment of such selectivities therefore is vital for the evaluation of planktivore influence on zooplankton community structure.

G. aculeatus and two species of *Chaoborus*, *C. punctipennis* Say and *C. trivittatus* Loew, are all commonly found in lakes on the Avalon Peninsula of Newfoundland (Figure 3.1; see also Campbell and Knoechel 1990). The Avalon lakes are well-suited to a comparative study of prey selectivities on vertebrate and invertebrate planktivores because the lakes, which show little among-lake variation in physicochemical characteristics, are all relatively shallow (< 6.6 m mean depth) with an undeveloped littoral zone and are well-mixed with no summer stratification (Knoechel and Campbell 1988). Consequently, pelagic zooplankton populations should be generally mixed throughout the water column and planktivores at different depths should encounter the same prey species. Comparison of the gut contents of *G. aculeatus* and the crop contents of *C. punctipennis* and *C. trivittatus* with lake plankton composition thus permits an analysis of the prey selectivities of these planktivores in the Avalon lakes.

Prey selectivity is defined as any difference in the relative proportions of prey species or prey of specific size classes in the planktivore diet as compared with the relative proportions of species or size classes in the zooplankton prey community (*sensu* Pastorok 1980). Such selectivity can be either positive (prey are selected for and thus are over-represented in the diet as compared with the lake community) or negative (prey are selected against and thus are under-represented in the diet). Selectivity may be active, as in cases in which certain prey types are actively sought out or avoided by the predator, and passive, as in cases in which certain prey are over- or under-represented in the diet due simply to their differential susceptibilities to encounter and capture (Pastorok 1980, 1981). Both active and passive selectivity can influence species composition and size distribution of the zooplankton community.

Previous studies in other freshwater systems have shown that *G. aculeatus*, which ranges in mean adult total length from 3.5 to 8.0 cm (Wootton 1976), generally consumes larger zooplankton when provided with a choice of prey: microcrustaceans are selected over large rotifers (Hangelin and Vuorinen 1988) and larger cladocerans are selected over smaller cladocerans (Kerfoot 1975; Gibson 1980; Jakobsen and Johnsen 1987), while long-featured bosminid morphs are selected over short-featured morphs (Kerfoot 1975). Cladocerans in general are consumed more frequently than are the faster swimming copepods (Coad and Power 1973; Kerfoot 1975; Manzer 1976; Ryan 1984) with their rapid predator-avoidance responses (Drenner *et al.* 1978). The smaller *Chaoborus* spp. are particularly predaceous during the 3rd and 4th instar stages (Fedorenko 1975*a*; Elser *et al.* 1987; Moore 1988); Yan *et al.* (1991) calculated that instar stages 1 through 4 contributed a seasonal average of 3, 7, 12 and

78%, respectively, of total prey consumption of *C. punctipennis* in Swan Lake, Ontario. These 3rd and 4th instar stages, which vary in length from 5 to 10 mm for *C. punctipennis* and from 6 to 13 mm for *C. trivittatus* (Carter and Kwik 1977), generally consume smaller zooplankton when provided with a choice of prey. These later instars have been observed to select small cladocerans over large cladocerans (Dodson 1970; Allan 1973; Winner and Greber 1980; Riessen *et al.* 1988) and generally select for copepods (particularly diaptomid species) over cladocerans (Roth 1971; Chimney *et al.* 1981; Elser *et al.* 1987). Copepodites between 0.4 to 0.8 mm may be the most consistently taken prey (Roth 1971; Swift and Fedorenko 1975). Handling of copepodid and adult copepod prey by *Chaoborus* larvae may be facilitated by the more stream-lined copepod shape as compared with the bulkier shape of cladocerans (Roth 1971; Swift and Fedorenko 1975; Pastorok 1980), although the more constant motion of cladocerans can result in higher encounter rates with the predator (Pastorok 1981; Riessen *et al.* 1984).

The cladoceran *Leptodora kindtii* Focke is also a common planktivore in the Avalon lakes (Chapter 3). However, since this predator feeds by sucking out the fluid contents of its prey and only occasionally retains recognizable prey body parts in the gut (Sebestyén 1931; Mordukhai-Boltovskaia 1958; Zaret 1980; but see Lunte and Luecke 1990), prey selectivities of this invertebrate planktivore could not be assessed in this study. Previous field and laboratory experiments have shown that *Leptodora kindtii* can exact heavy predatory mortality on zooplankton populations (Cummins *et al.* 1969; Hillbricht-Ilkowska and Karabin 1970; Karabin 1974; Gliwicz *et al.* 1978; Hovenkamp 1990). This predatory cladoceran becomes increasingly carnivorous at the larger adult sizes of 6 to 12 mm (Cummins *et al.* 1969; Browman *et al.* 1989) but can start taking small prey when only 3 mm in length (Mordukhai-Boltovskaia 1958). Maximum prey length taken is usually less than 1.5 mm, representing the maximum capture size of the *Leptodora* feeding apparatus (Sebestyén 1960, but see Lunte and Luecke 1990), and small organisms of up to 0.6 to 0.7 mm in length are preferentially consumed (Mordukhai-Boltovskaia 1958; Havel 1985; Hovenkamp 1990). Small immature daphnids are selected over larger adult individuals (de Bernardi and Guissani 1975) due to the slower escape response of the juveniles (Browman *et al.*

1989), while cladocerans in general are more susceptible to *Leptodora* predation than are the faster moving copepods (Mordukhai-Boltovskaia 1958; Hillbricht-Ilkowska and Karabin 1970; Karabin 1974; Browman *et al.* 1989; Lunte and Luecke 1990). Colonies of rotifers such as *Conochilus* spp. are also frequently consumed by *Leptodora* (Edmondson and Litt 1987; Lunte and Luecke 1990). *Leptodora* itself is seldom a prey item of threespine stickleback (see Chapter 3) or of *Chaoborus* larvae (Moore 1988).

The studies cited above lead to the following hypotheses with respect to contrasting prey selectivities of vertebrate and invertebrate planktivores in the Avalon lakes:

1. In terms of zooplankton species, threespine sticklebacks should show positive prey selectivity for cladocerans and negative selectivity for copepods and rotifers.

2. In terms of zooplankton size distribution, sticklebacks should show positive prey selectivity for the "larger" size classes.

3. *Chaoborus* larvae should show negative prey selectivity for cladocerans and positive selectivity for copepods and rotifer species.

4. *Chaoborus* larvae should show positive prey selectivity for the "smaller" size classes of zooplankton.

In this present study, these hypotheses were tested through comparison of predator diet with lake planktonic prey composition.

4.2. Methods

Analysis of planktivore diets was undertaken in conjunction with a study of planktivore distributions in 15 Avalon lakes (location of lakes is given in Figure 2.1). Sticklebacks were sampled from a subset of 11 lakes once from mid-August to late October 1986 (fall), with sticklebacks found in 8 lakes (Table 3.1), and from all 15 lakes once from mid-May to mid-June (spring) and from mid-August to early September 1987 (late summer) with sticklebacks found in 10 lakes (Table 3.2). Sampling times were chosen so as to avoid the mid-summer spawning season typical of stickleback populations in Atlantic-zone temperate lakes (Coad and Power 1973;

Jakobsen *et al.* 1988) when sticklebacks feed only intermittently (Allen and Wootton 1984; Jakobsen *et al.* 1988). Sticklebacks were sampled with liver-baited minnow traps (lined with dark, 1-mm mesh nylon netting in 1987 to catch small, juvenile fish) that were set out overnight along the lake bottom. Two strings of traps were set out at opposite ends of each lake: each string extended from near-shore waters (approx. 1 m deep) to the deepest waters of the lake or the deepest waters that could be reached with the trap string (approx. 150 m in length) with individual traps set at 1 m depth intervals. Total lengths (tip of snout to end of tail, measured to nearest mm) of the trapped fish were recorded and then the fish were released. Only fish from one trap string were measured in lakes such as Hogans Pond in which fish catch per trap (see Table 3.2) was high. A subset sample of sticklebacks, representative of the observed range in total fish lengths in the lake, were collected from each lake sample and preserved in 70% ethanol. Collections consisted of 7 to 9 fish per lake in 1986 and 10 fish per lake (unless fewer than 10 were caught) in 1987. Ten fish were collected from Hogans Pond in late summer 1987; however due to human error, only two fish were subsequently preserved.

Chaoborus larvae were collected from two lakes (Bauline Long and Piccos ponds) in August 1988, with sample size increased to four lakes (Bauline Long, Long, Octagon and Piccos ponds) in August 1989, previous samplings having shown that *Chaoborus* were abundant in these lakes with populations made up mainly of the more predatory large 3rd and 4th instars at this late summer season (Chapter 3). While *Chaoborus*, specifically *C. punctipennis*, co-occurred with sticklebacks in some of the study lakes (Figure 3.2), the fish were generally absent from these particular four lakes. Population densities of the invertebrate planktivore were much higher in the four lakes, however, so that larvae for diet analysis could be most conveniently obtained from these lakes, while species composition of the pelagic zooplankton community did not noticeably differ from those of the other study lakes. *Chaoborus* samples were taken one hour after sunset with a 25-cm diameter net fitted with 100-μm mesh, with two net tows taken from 1 m above the lake bottom at the deepest part of the lake. *Chaoborus* were immediately narcotized with a chloroform - ethanol solution, prior to preservation with 100% Formalin, in order to prevent crop eversion upon preservation (Swift and Fedorenko 1973). Samples were transferred to 70% ethanol in the laboratory. *Chaoborus* species were identified following Saether (1972) and Borkent (1979) with instar stage determined from head capsule length as in Carter and Kwik (1977).

Samples of the lake zooplankton communities were taken in conjunction with the collection of sticklebacks and *Chaoborus* larvae. Two vertical net hauls were taken from approximately 1.0 m above the lake bottom at the deepest part of the lake. The tow net was the same as for the *Chaoborus* sample. Tow net capture efficiency for the zooplankton community was set at 50% (see Chapter 3). In 1986, the zooplankton samples were taken at night after the minnow traps had been set out. In 1987, the plankton samples were taken in the morning when the traps were picked up. A comparison of night and day samples for a set of lakes in 1986 had shown no significant difference in total zooplankton density or percent species composition (Wilcoxon signed-rank tests, $p > 0.05$, $n = 10$). In 1988 and 1989, zooplankton samples were taken at the same time as the *Chaoborus* samples. All zooplankton samples were preserved in 95% ethanol.

In the laboratory, contents of the planktivore guts (stomach and upper intestine for stickleback, crop for *Chaoborus* larvae) were dissected and examined under 25 to 50X magnification with a Wild M5A dissecting microscope with both dark-field and light-field illumination. All prey species were enumerated and total body lengths of species of pelagic zooplankton were measured with an eyepiece micrometer. Total lengths for cladocerans were measured from the top of the head to the point of insertion of the tail spine, while total lengths for copepods were measured from the top of the cephalothorax to the end of the caudal rami. In cases where the zooplankton body was not intact, total length was estimated from the remaining body parts (primarily cladoceran helmets and postabdominal claws and copepod metasomes) through empirical linear regression equations relating species total length to lengths of the body parts (Appendix Table A.2). Subsamples of the lake zooplankton collections were enumerated and sized in a rotating, plexiglas counting chamber with a Wild M3 dissecting microscope. In 1987 and 1988, zooplankton lengths, determined from images magnified from the microscope onto a video screen, were measured and recorded with a microcomputer-based electronic caliper system (Sprules *et al.* 1981). In 1989, zooplankton lengths were measured with an eyepiece micrometer; species lengths were not recorded in 1986. Zooplankton species and other prey organisms were identified following Edmondson (1959) and Pennak (1978). Based on total lengths in mm, pelagic zooplankton in the diet and in the lake samples were placed in the following 7 size classes: 0.00 - 0.25, 0.26 - 0.50, 0.51 - 0.75, 0.76 - 1.00, 1.01 - 1.25, 1.26 - 1.50, and 1.51 - 3.00 mm. As zooplankton prey greater than 1.26 mm in length were rare, the last two size classes were combined prior to statistical analyses.

The comparison of planktivore gut contents with lake zooplankton communities for the estimation of prey selectivity assumes that prey are not regurgitated and are recognizable in gut contents, and that lake zooplankton densities represent prey densities encountered by the predator. Sticklebacks and *Chaoborus* larvae showed little evidence of prey regurgitation in this study; none of the stickleback guts examined were empty and only two of the *Chaoborus* examined were observed to have everted crops. Prey items in the guts were readily identifiable under either light-field or dark-field illumination. Pelagic zooplankton populations were assumed to be generally present throughout the water column of the shallow and well-mixed Avalon lakes (Knoechel and Campbell 1988) to allow planktivores at different depths access to prey of similar prey species composition. Small rotifers may have been underestimated by sampling with a tow net of 100-μm mesh size; however, such rotifers are not common prey items for *G. aculeatus* (Hynes 1950; Jakobsen *et al.* 1988) or for 3rd and 4th instars of *C. punctipennis* and *C. trivittatus* (Fedorenko 1975*a*; Moore 1988).

Prey selectivities were quantified by means of the selectivity index α_i, an index which has been variously described by a number of authors (Chesson 1978; Paloheimo 1979; Vanderploeg and Scavia 1979; Lazzaro 1987). For each prey type i, the index was calculated by the forage ratio (the ratio of the proportion (r_i) of prey type i in the diet to the proportion (p_i) of prey type i in the environment) normalized by the sum of forage ratios for all prey types:

$$\text{Selectivity Index } \alpha_i = r_i/p_i \Big/ \sum_{i=1}^{m} r_i/p_i$$

where m = total number of prey types. The index varies from 0 to 1; neutral selectivity corresponds to $1/m$. This index is approximately multivariate normally distributed and is not influenced by the relative abundance of prey types in the environment as are some other common selectivity indices (Paloheimo 1979; Lazzaro 1987). Since the index is based on relative proportions of prey types, with the sum of the indices or standardized forage ratios for all prey types equal to unity, an increase in the index for one prey results in decreases in the indices for the other prey and vice versa. Consequently, the index alone cannot determine whether over-representation of a particular prey in the planktivore diet is due to preference for that prey or to avoidance or escape of other prey. Similarly, by itself the index cannot determine if under-representation of a prey item is due to avoidance or escape of that prey or to selection of alternate prey items.

For the calculations of proportion of prey types in the planktivore diets, individual gut and crop contents collected on a particular sampling date were pooled for the sticklebacks and *Chaoborus*, respectively. Lakes sampled at different dates therefore were considered as separate samples. Seasonal influences on planktivore diet could thus not be statistically examined. Combining the data allows for comparison between the average diet of the planktivores and the average zooplankton community among a set of lakes at times when sticklebacks and *Chaoborus* larvae would be at the most predaceous stages of their life cycles. Predator size distributions were not taken into account in this analysis. However, size distributions of the collected predators were taken so as to be representative of the size distributions of the predators in the lakes. Thus, the analysis should generate an overall mean estimate of prey selectivities of the lake planktivore populations. Mean species or size selectivites averaged over all lake and date samples for the vertebrate and invertebrate planktivores were calculated, and 95% confidence limits about these means, based on the Central Limit Theorem, were determined. Selectivity indices were determined for each prey type only when this prey type was found in the lake zooplankton samples. All calculations were carried out with the Minitab 6.1 (Minitab 1985) statistical package on Memorial University's Vax 8800 operating under VMS 5.0. Except where noted, statistical significance (two-tailed) was set by the criterion level $\alpha = 0.05$.

4.3. Results

Total zooplankton density, the density of the potential planktivore prey community, ranged from 0.6 to 182.3 animals·l^{-1} in the Avalon lakes (Table 4.1). Pelagic zooplankton species were identified as *Daphnia catawba* Coker, *Holopedium gibberum* Zaddach, *Eubosmina longispina* Leydig, *Leptodiaptomus minutus* Lilljeborg, *Epischura nordenskioldi* Lilljeborg, *Cyclops scutifer* Sars and rotifers (*Conochilus unicornis* Rousselet and *Keratella* and *Kellicottia* spp.). Copepod nauplii and rotifers were not classified to the species level. Most of the lake samples contained at least six of the prey types (Table 4.1); *C. scutifer* and *E. nordenskioldi* were the least commonly encountered species. Sizes of pelagic zooplankton in the Avalon lakes (Table 4.2) varied from a mean length of 0.12 mm (range 0.05 - 0.15) for rotifers to a mean length of 1.06 mm (range 0.87 - 1.23) for *E. nordenskioldi*. Mean lengths of pelagic zooplankton species in the individual lakes are given in Appendix Tables A.6 and A.8.

The potential importance of threespine stickleback as a predator of pelagic zooplankton in the Avalon lakes is illustrated in Table 4.3. Diet items were characterized as pelagic microcrustaceans (pelagic zooplankton without rotifers; rotifers were never observed in stickleback gut contents), littoral cladocerans (*Latona setifera* O.F. Muller, *Chydorus bicornutus* Doolittle, *Acantholebris curvirostris* O.F. Muller, *Eurycercus lamellatus* O.F. Muller and *Alona* spp.), amphipods, chironomid larvae, and other (adult insects, molluscs, ostracods, *Trichoptera* larvae, etc.). Further breakdown of the diet into specific species of pelagic microcrustaceans is given in Appendix Table A.3, while Table A.4 shows the percent abundance of pelagic microcrustaceans in the lakes. Relative frequency of occurrence of pelagic microcrustaceans ranged from 6 to 97% (mean 50%) of the total abundance of diet items across all lakes and seasons (Table 4.3). Neither percent occurrence nor

Table 4.1. Total zooplankton density and relative percent abundance of zooplankton species in the Avalon lakes from which *Gasterosteus aculeatus* were collected for analysis of gut contents during fall (f) 1986 and spring (s) and late summer (ls) 1987 and from which *Chaoborus* larvae (*C. punctipennis* + *C. trivittatus*) were collected for analysis of crop contents during late summer (ls) 1988 and 1989. Daph refers to *Daphnia catawba*. Holo to *Holopedium gibberum*, Bosm to *Eubosmina longispina*, Diap to *Leptodiaptomus minutus*, Epi to *Epischura nordenskioldi*, naup to copepod nauplii, Cyc to *Cyclops scutifer*, and Rot to rotifer spp. Lakes are labelled as in Figure 2.1. Rows of % abundance may not add up exactly to 100% due to numerical rounding.

			% Abundance in Lake							
Lake	Year	Density $(\#\cdot l^{-1})$	Daph	Holo	Bosm	Diap	Epi	naup	Cyc	Rot
G. aculeatus lakes										
He	1986 f	15.9	13	2	5	36	15	2		26
	1987 s	31.2	2	17	9	47	1	2		23
	1987 ls	16.5	51	13	7	18	1	2		7
Ho	1986 f	37.3	2	5	46	24	3	4		16
	1987 s	53.3		4	49	42	1	1	1	4
	1987 ls	33.2	1	30	11	35		12		12
Mi	1987 s	43.4	1	1	8	37	1	46		7
	1987 ls	41.8	1	1	8	44	1	28		18
Mu	1986 f	111.4	20		60	3	10	1	3	3
	1987 s	0.6	6		5	10		63	9	7
	1987 ls	33.6	85			4	9	2		
Pa	1987 s	16.5	4	11	32	11		2		41
	1987 ls	31.4	7	5	6	12	1	1	1	68
Qu	1986 f	28.0	63		2	33	1	1		
	1987 s	19.0	12	1	1	10	3	4	18	52
	1987 ls	20.3	43		1	46	1	7		1
Ro	1987 s	75.1	1	58	15	14		3		9
Se	1986 f	15.8	17	16		40	11			16
	1987 s	24.3	8	3	3	10	5	1	1	68
Ti	1986 f	15.6	17	2	2	37	3	5		33
	1987 s	9.2	6	16	18	32	4	6		17
	1987 ls	14.5	53	14	7	20	3			3
To	1986 f	8.6	7		21	44	3	2	1	22
	1987 s	14.2	9	5	52	30	1	2	1	1
	1987 ls	14.4	13	2	5	62	1	6	2	10
Chaoborus lakes										
Ba	1988 ls	30.3	10	1	9	31		7		42
	1989 ls	23.8	12		3	50		21	1	13
Lo	1989 ls	11.9	14	30	3	17	3	22		11
Oc	1989 ls	22.2	22	1	1	26	1	37	12	1
Pi	1988 ls	68.3	9	2	4	16		52		17
	1989 ls	182.3	1	13	2	4		30	1	50

Table 4.2. Mean lengths of pelagic zooplankton averaged over all Avalon lake and date samples. Range values refer to ranges in individual sample means. Species measurements encompass preadult and adult cladocerans and copepodite and adult copepods. Zooplankton are listed in order of increasing mean lengths.

Species	Mean Length (mm)	Range (mm)
Rotifer spp.	0.12	0.05 - 0.15
Copepod nauplii	0.19	0.13 - 0.25
Eubosmina longispina	0.33	0.19 - 0.53
Cyclops scutifer	0.43	0.25 - 0.94
Leptodiaptomus minutus	0.47	0.29 - 0.68
Holopedium gibberum	0.76	0.41 - 1.16
Daphnia catawba	0.87	0.60 - 1.09
Epischura nordenskioldi	1.06	0.87 - 1.23

Table 4.3. Number of *Gasterosteus aculeatus* (Gast) collected from the Avalon lakes during fall (f) 1986, spring (s) 1987, and late summer (ls) 1987 for analysis of gut contents, with total number of diet items found in all the guts and the relative percent occurrence of pelagic microcrustaceans (Pel Micr), littoral cladocerans (Lit Clad), amphipods (Amph), chironomids (Chir) and Others (adult insects, molluscs, ostracods, *Trichoptera* larvae, etc.) found in the guts. All stickleback guts contained at least one diet item. Lakes are labelled as in Figure 2.1.

				% Occurrence in Diet				
Lake	Year	Gast (#)	Diet Items (#)	Pel Micr	Lit Clad	Amph	Chir	Other
He	1986 f	9	399	97	1		2	1
	1987 s	8	104	48	5	2	42	3
	1987 ls	4	34	24	29	32	15	
Ho	1986 f	8	118	14	81		2	3
	1987 s	10	311	10	60	1	13	16
	1987 ls	2	14	14		64	7	14
Mi	1987 s	10	140	41	1	9	34	14
	1987 ls	10	356	6	82	1	4	6
Mu	1986 f	8	178	87	7		3	2
	1987 s	10	79	15	30	3	33	19
	1987 ls	10	522	95	1	1	2	2
Pa	1987 s	10	93	74	3	1	20	1
	1987 ls	10	56	18	16	9	50	6
Qu	1986 f	9	92	68	6	12	10	3
	1987 s	10	100	28	21		9	42
	1987 ls	10	90	70		2	7	13
Ro	1987 s	10	77	16	34	3	38	9
Se	1986 f	7	151	80		11	9	
	1987 s	10	114	56	3	14	24	3
Ti	1986 f	7	292	32		62	3	3
	1987 s	10	190	19	6	6	64	6
	1987 ls	10	130	88		5	6	2
To	1986 f	9	218	88		6	6	1
	1987 s	10	200	93	1	1	4	1
	1987 ls	10	379	81	3		1	15

number of pelagic microcrustaceans in the stickleback guts were linearly related to pelagic microcrustacean density in the lakes (regressions with density $\log_{10}$ transformed, $n = 25$, $p > 0.50$ in both cases), and there was no density threshold of pelagic microcrustaceans at which stickleback consumption of these prey suddenly dropped as if sticklebacks had switched to other, more abundant prey (Figure 4.1). Densities of pelagic microcrustaceans in the Avalon lakes (Table 4.1) are already lower, however, than those in lakes in which this switching in diet of planktivorous fish has been observed (e.g., 40 prey individuals·l^{-1} for European roach *Rutilus rutilus*: Townsend *et al.* 1986). Nonetheless, the percent mean seasonal abundance of pelagic microcrustaceans for all Avalon lakes was lowest in the spring (means of 70, 40 and 50% for fall 1986, spring 1987 and late summer 1987, respectively), which could result from the increased availability of chironomid larvae and newly emergent insects as alternate prey at this time. Insect pupae made up a large proportion of the stickleback diet in the spring samples from Quidi Vidi Lake (Qu), while chironomids were abundant in the diet of fish from spring samples in Three Island Pond (Ti). Only Hogans Pond (Ho) consistently showed a low percent occurrence of pelagic microcrustaceans across all three sampling dates. Littoral cladocerans (mainly *Acantholebris curvirostris*) made up the major proportion of diet items in fall 1986 and spring 1987 in Hogans Pond, with amphipods most abundant in late summer 1987. Another littoral cladoceran, *Chydorus bicornutus*, was quite abundant in the diet of sticklebacks in Middle Three Island Pond (Mi) in late summer 1987. Amphipods also figured prominently in the diet of sticklebacks in Three Island Pond in fall 1986.

The sticklebacks examined for diet analysis ranged in length from 2.9 to 7.6 cm, approximating the range in total lengths of all measured fish which ranged from 1.8 to 9.7 cm (Figure 4.2). Very few fish less than 3.0 cm were trapped, particularly in 1986 when the traps were not lined with the 1-mm nylon mesh. Fish under 4.0 cm in length are most probably 0+ years old, while fish between 4.0 and 6.0 cm are likely to be 1+ years old and fish over 6.0 cm are 2+ years old, consistent with length-age relationships determined for stickleback populations in other Newfoundland lakes (Ryan 1984).

Figure 4.1. Percent occurrence of pelagic microcrustaceans in the stickleback diet related to density (#-l^{-1}) of pelagic microcrustaceans in the Avalon lakes for the combined years 1986 and 1987.

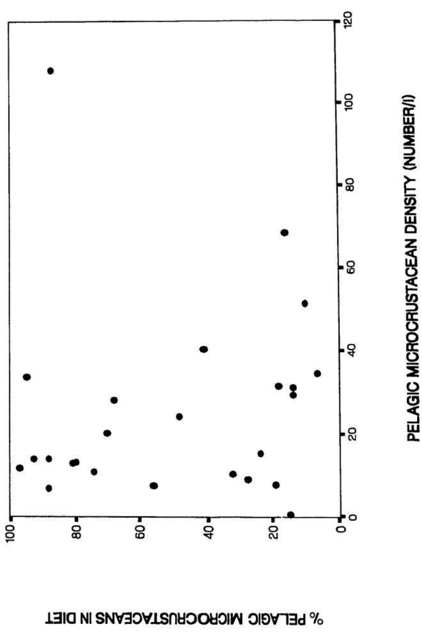
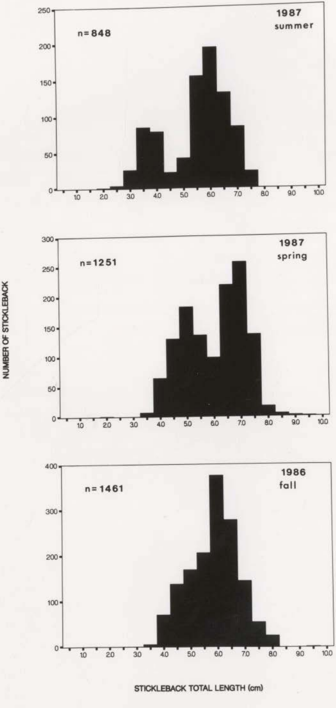

PELAGIC MICROCRUSTACEAN DENSITY (NUMBER/l)
0
20
40
60
80
100
120
% PELAGIC MICROCRUSTACEANS IN DIET
0
20
40
60
80
100

Figure 4.2. Total length-frequency histograms of *Gasterosteus aculeatus* measured in fall 1986 and spring and late summer 1987 from the Avalon lakes. n = number of fish measured, a subset of the total number of fish trapped.


1987
summer
n=848
250
200
150
100
50
0
1987
spring
n=1251
300
250
200
150
100
50
0
1986
fall
n=1461
400
300
200
100
0
10
20
30
40
50
60
70
80
90
100
NUMBER OF STICKLEBACK
STICKLEBACK TOTAL LENGTH (cm)

Examination of stickleback predation on the species of pelagic zooplankton in the Avalon lakes (Figure 4.3) revealed positive selectivity only for the cladoceran *D. catawba*. *E. longispina*, *C. scutifer* and *E. nordenskioldi* were all neutrally selected (as indicated by the extent of their respective 95% confidence limits), while the sticklebacks showed increasingly strong negative selectivity for *H. gibberum*, *L. minutus* and copepod nauplii. Since rotifers were never found in the stickleback guts, yet were generally abundant in the lakes (Table 4.1), these zooplankters were not considered as potential stickleback prey and were excluded from the calculations of stickleback prey selectivities. Inclusion of rotifers in the analysis would not affect the relative prey selectivities shown in Figure 4.3 but would simply decrease the mean value for neutral selectivity (*1/m*) from 0.18 to 0.15 by increasing the number of prey types *m*.

Chaoborus larvae collected for crop examination ranged in length from only 3.3 to 10.0 mm for *C. punctipennis*, with a mean of 97% (range 80 - 100%) of the larvae in the 3rd and 4th instar stage, and from 5.7 to 13.1 mm for *C. trivittatus*, with a mean of 61% (range 0 - 100%) of the larvae in the 3rd and 4th instar. Remaining larvae were in the 2nd instar. Due to observed similarities in the prey species consumed and to the few numbers of *C. trivittatus* collected, the diets of *C. punctipennis* and *C. trivittatus* were pooled and analyzed together (Table 4.4). Prey items in the crops of both *Chaoborus* species were restricted almost completely to pelagic zooplankton. Phytoplankters *Ceratium* and *Dinobryon* spp. were also encountered but too rarely to be recorded as a significant percentage of the diet, although previous researchers (Sardella and Carter 1983; Moore 1988) have found these algal species to be quite abundant in crop contents, particularly in the earlier instars of *C. punctipennis*.

Examination of *Chaoborus* diet in the Avalon lakes (Figure 4.4) revealed signficant positive selectivity only for the cladoceran *E. longispina*. Rotifers and *L. minutus* were neutrally selected while the chaoborids exhibited significant negative selectivity for copepod nauplii, *D. catawba*, *C. scutifer*, *H. gibberum* and *E. nordenskioldi*. *C. scutifer* was found in only three of the six lakes that were sampled for *Chaoborus* (see Table 4.1) with the resultant large variance in selectivities among lakes making it difficult to draw a firm conclusion regarding *Chaoborus* selectivity

Figure 4.3. Mean species selectivities with 95% confidence limits about the mean (vertical bar, only upper half of range shown for clarity) for *Gasterosteus aculeatus* in the Avalon lakes. Numbers above confidence intervals refer to sample size, the number of lake and date samples in which each prey taxon is found. Dashed line represents neutral selectivity averaged for all lake and date samples. Values above this line indicate a positive selectivity trend while those below the line indicate a negative selectivity trend. Prey taxa are labelled as in Table 4.1.

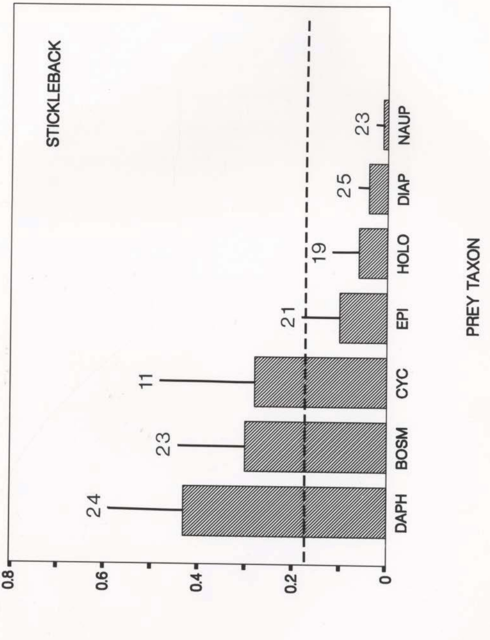
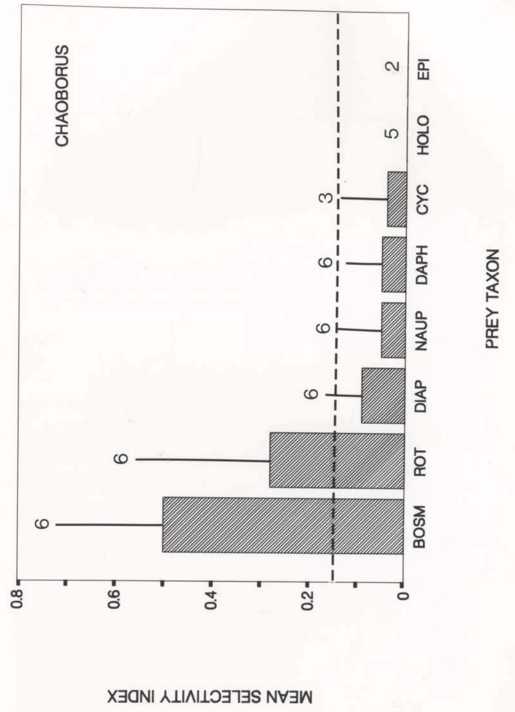

STICKLEBACK
MEAN SELECTIVITY INDEX
0
0.2
0.4
0.6
0.8
24
23
11
21
19
25
23
DAPH
BOSM
CYC
EPI
HOLO
DIAP
NAUP
PREY TAXON

Table 4.4. Number of Chaoborus larvae (C. punctipennis + C. trivittatus) collected from the Avalon lakes during late summer 1988 and 1989 for analysis of crop contents, with total number of diet items found in all the chaoborid crops and the percentage of crops which contained at least one diet item. Pelagic zooplankton comprised 100% of the chaoborid diet.

Lake	Year	Chaoborus (#)	Diet Items (#)	% Crops with ≥ 1 item
Bauline Long	1988	20	20	70
	1989	30	17	57
Long	1989	28	17	64
Octagon	1989	19	21	68
Piccos	1988	42	74	71
	1989	43	47	77

Figure 4.4. Mean species selectivities with 95% confidence limits about the mean for *Chaoborus* (*C. punctipennis* + *C. trivittatus*) larvae in the Avalon lakes. See Figure 4.3 for key to symbols. Prey taxa are labelled as in Table 4.1.


CHAOBORUS
MEAN SELECTIVITY INDEX
0
0.2
0.4
0.6
0.8
6
6
6
6
6
3
5
2
BOSM
ROT
DIAP
NAUP
DAPH
CYC
HOLO
EPI
PREY TAXON

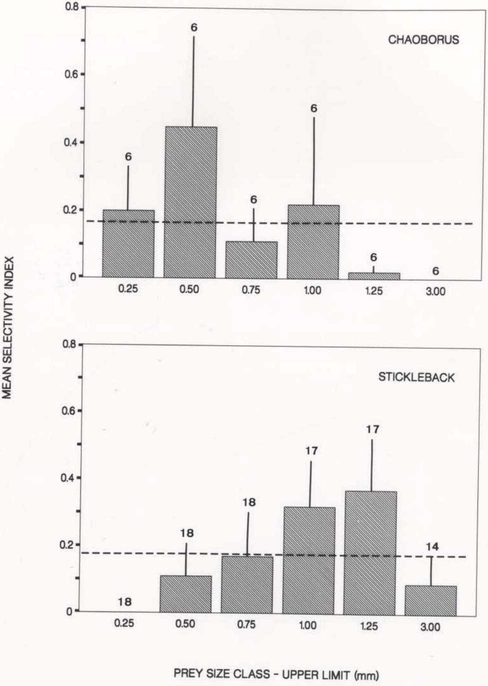
for the cyclopoid copepod. Neither *H. gibberum* nor *E. nordenskioldi* were encountered in any of the *Chaoborus* crops examined.

The vertebrate and invertebrate planktivores showed distinctly contrasting size selectivities in their choice of zooplankton prey (Figure 4.5). Sticklebacks showed positive selectivity for the larger size classes of zooplankton, between 0.76 and 1.25 mm in length, and neutral selectivity for the smaller size classes as well as for the largest size class. *Chaoborus*, on the other hand, showed positive selectivity only for the small size class of 0.26 to 0.50 mm, and showed negative selectivity for the two largest size classes, with all other size classes selected neutrally. Large 95% confidence limits around the mean selectivity shown for the 0.76 to 1.00 mm size class (Figure 4.5) are a consequence of the large range in the relative percent abundance (0 to 68%) of this size class observed in the chaoborid diet in the different lake samples. Zooplankters in the largest size class (1.26 to 3.00 mm) were never found in the *Chaoborus* crops. The relative rarity of such large zooplankters in the lake communities results in a high variance in selectivities among lakes, making it difficult to draw conclusions with respect to selectivity for this size class by either of the planktivores.

4.4. Discussion

G. aculeatus, *C. punctipennis* and *C. trivittatus* can all be considered as primarily planktivorous in the Avalon lakes since a large proportion of their diets is made up of pelagic zooplankton, in accordance with other studies in freshwater lakes (Hynes 1950; Rogers 1968; Fedorenko 1975*b*; Manzer 1976; Elser *et al.* 1987; Jakobsen *et al.* 1988; Moore 1988). These planktivores also demonstrated contrasting species and size selectivities in their choice of zooplankton prey. The selectivity index used does not evaluate prey preference by the planktivores and only indicates whether certain zooplankton species and size classes are found relatively more often in the planktivore diets, given the frequencies of the prey species and size classes in the Avalon lakes. Active and passive selectivity are not distinguished. Distinct selectivities shown by the vertebrate and invertebrate planktivores were, in the main, consistent between lakes (as witnessed by confidence intervals around mean

Figure 4.5. Mean size selectivities with 95% confidence limits about the mean for *Gasterosteus aculeatus* and *Chaoborus* (*C. punctipennis* + *C. trivittatus*) larvae in the Avalon lakes. See Figure 4.3 for key to symbols.


CHAOBORUS
STICKLEBACK
MEAN SELECTIVITY INDEX
PREY SIZE CLASS - UPPER LIMIT (mm)
0
0.2
0.4
0.6
0.8
0.25
0.50
0.75
1.00
1.25
3.00
6
6
6
6
6
6
18
18
18
17
17
14

selectivity values), suggesting that these results could be extrapolated to other shallow and well-mixed oligotrophic lakes.

The vertebrate planktivore *G. aculeatus* exhibited strong, positive species selectivity for *D. catawba*, and negative selectivities for *L. minutus* and copepod nauplii. This selectivity of the slower moving daphnids over copepods is consistent with the observed dominance of cladocerans in stickleback diets in other lakes (Coad and Power 1973; Kerfoot 1975; Manzer 1976; Ryan 1984). Sticklebacks are seemingly more attracted by the continuous erratic movement (Gibson 1980) that is typical of cladoceran locomotion as contrasted with the slow cruising movement of calanoid copepods and the "hop and sink" movement of cyclopoid copepods (Zaret 1980). Positive stickleback selectivity for the larger daphnid over the smaller bosminid *E. longispina* (which was neutrally selected) in the Avalon lakes also concurs with results from other studies of threespine stickleback predation (Kerfoot 1975; Jakobsen and Johnsen 1987). Sticklebacks in the Avalon lakes exhibited negative selectivity for *H. gibberum*, as noted also by Cooper (1985) who found that *G. aculeatus* selected *Daphnia* species over *H. gibberum* of comparable body size; the latter species is presumably avoided due to its gelatinous sheath. *Holopedium* may become a more important diet item for sticklebacks when other prey species are not abundant in the water column. Such was not the case for the Avalon lakes where mean percent abundance of *Holopedium* in the lakes in which sticklebacks were found was only 8% (n = 25, Table 4.1) of total pelagic microcrustacean abundance. Manzer (1976) found *Holopedium* to be a dominant item in the diet of threespine stickleback in Great Central Lake, B.C., but the cladoceran was one of the most abundant pelagic microcrustaceans in the lake and other large cladocerans were rare.

G. aculeatus in the Avalon lakes also seemed to prey selectively on zooplankton of the larger size classes. The size class of 0.76 to 1.25 mm, for which sticklebacks showed positive selectivity, roughly encompasses the range of 0.60 to 1.10 mm in mean lengths for *D. catawba*, the prey species for which sticklebacks also showed positive selectivity. Selectivity for size thus cannot be divorced from selectivity for species. Negative selectivity by stickleback for small zooplankton also correspords to observed species selectivities; copepod nauplii, never larger than 0.25 mm, were rarely seen in the stickleback gut contents. Rotifers were never seen in the gut contents of sticklebacks in the Avalon lakes; these zooplankton are also never a major component of the diet of threespine stickleback in other freshwater lakes (e.g., Hynes 1950; Coad and Power 1973; Manzer 1976; Ryan 1984; Jakobsen *et al.* 1988).

Prey choice by sticklebacks may be affected by predation from piscivorous fish that can, by confining sticklebacks to the littoral zone of lakes, restrict stickleback diet to littoral zooplankton (Jakobsen *et al.* 1988). Such predation risk did not noticeably influence stickleback diet in the present study. Although piscivores (*Salmo salar*, *Salmo trutta*, *Salvelinus fontinalis* and *Anguilla rostrata*) are found in the Avalon lakes (Scott and Crossman 1964), sticklebacks in the study lakes were caught in traps at all depths (Chapter 3) and hence were demonstrably not confined to near-shore areas. Low macrophyte densities in the littoral zone of the study lakes (Knoechel and Campbell 1988) minimizes the importance of the littoral zone as a weedy refuge from piscivores. In other lakes in which threespine stickleback also are not greatly restricted to the littoral zone, such as in Alaskan lakes that lack large populations of piscivores, stickleback diet consists mainly of pelagic microcrustaceans (Rogers 1968) as in the Avalon lakes. Stickleback diet is also influenced by age, size, sex, and parasite (*Schistocephalus solidus*) load of the fish (Hynes 1950; Rogers 1968; Coad and Power 1973; Jakobsen *et al.* 1988) but none of these factors were examined in this study.

As expected, prey selectivities of *Chaoborus* larvae in the Avalon lakes differ from those of the much larger sticklebacks. The larvae exhibit positive selectivity and neutral selectivity for *E. longispina* and rotifers, respectively. Both Moore (1988) and Yan *et al.* 1991 (*in press*) likewise found a bosminid, *Bosmina longirostris*, to be a major component of the diet of 3rd and 4th instars of *C. punctipennis*, although Moore (1988) found that a large soft-bodied rotifer, *Asplanchna priodonta*, made up the bulk of the chaoborid diet. Later instar larvae of both *C. trivittatus* and *C. punctipennis* show a preference for soft-bodied over hard-bodied rotifer species (Fedorenko 1975*a*; Moore and Gilbert 1987). The classification of all rotifers as one prey type in the present study consequently might have masked a strong positive selectivity by *Chaoborus* for a particular rotifer species, such as the large, soft-bodied and colonial *Conochilus unicornis*. Selection by *Chaoborus* for rotifer prey is also a function of predator size, in that rotifers are a more important diet item for the smaller 1st and 2nd instar stages (Fedorenko 1975*a*; Moore 1988).

The negative selectivity demonstrated by *Chaoborus* for the copepod *L. minutus* in the Avalon lakes contrasts with other studies (Roth 1971; Elser *et al.* 1987) in which chaoborids have been observed to select for copepods (particularly diaptomids) over cladocerans. Selection by *Chaoborus* for copepods over cladocerans, however, is often a function of prey densities and predator hunger levels, in that when prey are not abundant, *Chaoborus* tend not to be satiated and are less selective for copepods in their prey choice (Pastorok 1980). Thus, while *Chaoborus* larvae may find the bulkier cladoceran prey more difficult to manipulate once caught (Swift and Fedorenko 1975; Roth 1971), the faster swimming speeds (and hence higher predator encounter rates) and slower escape response of cladocerans as compared with that of copepods (Pastorok 1980; Riessen *et al.* 1984) could lead to a higher proportion of cladocerans in the chaoborid diet when prey are not abundant. Such would seem to be the case for *E. longispina* in the oligotrophic Avalon lakes. The larger size of *D. catawba* presumably renders this cladoceran less vulnerable than the smaller bosminid to capture by *Chaoborus* and explains the observed negative selectivity evinced by *Chaoborus* for the daphnid. *D. catawba* did not appear to produce the spines or crests that are often manifested by other *Daphnia* species as defenses against *Chaoborus* predation (Krueger and Dodson 1981; Hebert and Grewe 1985; Luecke and Litt 1987). *H. gibberum* was never encountered in the *Chaoborus* crops in the Avalon lakes. This cladoceran is only rarely ingested by *Chaoborus* larvae (Allan 1973; Neill 1981; Moore 1988), probably due to difficulties in prey handling occasioned by its gelatinous sheath. *Chaoborus* also showed negative selectivity for copepod nauplii; rarity of copepod nauplii in the chaoborid crops has been similarily noted in other studies (Fedorenko 1975*b*; Moore 1988).

Chaoborus larvae seemed to prey selectively on zooplankton in the smaller size classes. The size range of 0.26 to 0.50 mm, for which the larvae showed positive selectivity, accords well with the observed range of 0.17 to 0.53 mm in mean lengths for *E. longispina*, the preferred prey species, illustrating the correspondence between species and size selectivities. Prey larger than 1.01 mm were rarely taken by the invertebrate planktivore. The largest size observed for prey in the *Chaoborus* crops was *D. catawba* at 1.05 mm in length, which is smaller than the maximum prey sizes of 1.8 and 2.6 mm recorded for *C. punctipennis* and *C. trivittatus* by Roth (1971) and Swift and Fedorenko (1975), respectively.

While vertical distributions and subsequent spatial segregation of predator and prey can be an important influence on the prey choice of *Chaoborus* larvae (Fedorenko 1975*b*), this factor can probably be discounted in the well-mixed Avalon lakes. *Chaoborus* diet can also show instar- and species-specific selectivities (Fedorenko 1975*a*; Pastorok 1980; Moore and Gilbert 1987; Moore 1988), but these were not considered in the present study.

Distinct prey species and size selectivities demonstrated by the vertebrate and invertebrate planktivores in the Avalon lakes suggests that predation by such planktivores may have contrasting influences on species composition and size distribution of the zooplankton communities in these shallow and well-mixed oligotrophic lakes. The positive selectivity evinced by *Chaoborus* in the Avalon lakes for small zooplankton prey such as *E. longispina* is also fairly similar to prey selectivies estimated by various authors (see Introduction) for *Leptodora* - i.e. generally rotifers and small cladocerans of up to 0.7 mm in length. Hence, the major invertebrate predators in the Avalon lakes are expected to have similar impacts on the lake zooplankton communities. Interactions between the planktivores themselves, such as predator-prey interactions between sticklebacks and *Chaoborus* (Chapter 3), might also lead to differential predation impacts on the pelagic zooplankton communities of different lakes. These contrasting influences of vertebrate and invertebrate planktivores must be taken into account in any study of predation effects on the zooplankton community. Such effects will be evaluated in Chapter 5.

4.5. Other Invertebrate Planktivores

Aside from the invertebrate planktivores *Chaoborus* spp. and *Leptodora kindtii*, the partially zooplanktivorous *Epischura nordenskioldi* and *Cyclops scutifer* (Strickler and Twombly 1975; Wetzel 1983) also occur in the Avalon lakes (Table 4.1). *E. nordenskioldi* may consume a significant number of nauplii of *Leptodiaptomus minutus* in some Newfoundland lakes (Strickler and Twombly 1975). However, the potential predatory impact of *E. nordenskioldi* and *C. scutifer* on the zooplankton community of the Avalon lakes was not considered to be as great as that of the much larger *Chaoborus* and *Leptodora*. Rough estimates of the daily prey consumption of each planktivore averaged over all the lakes in which each predator species was found could be calculated (Table 4.5) from 1987 densities of *Chaoborus* larvae (*C. punctipennis* and *C. trivittatus* together), *L. kindtii*, *E. nordenskioldi* and *C. scutifer* and from literature values of predation rates for these or comparable species. As mentioned previously (Chapter 3), densities determined for *Chaoborus* and *Leptodora* populations in the Avalon lakes refer to late summer populations of the larger, more predominantly predaceous stages that migrate to the lake surface waters at night - that is, the 3rd and 4th (with some 2nd) instar stages of *Chaoborus* larvae (Fedorenko 1975*a*; Elser *et al.* 1987; Moore 1988) of about 5 to 13 mm in total length (measured from the anterior tip of the head capsule to the base of the anal tubules) in the Avalon lakes, and *Leptodora* that are > 5 to 6 mm (Cummins *et al.* 1969; Browman *et al.* 1989), ranging from 5 to 9 mm in total length (measured from the anterior tip of the head to the base of the tail spines) in the Avalon lakes. Both *Epischura* and *Cyclops* species are also known to be predaceous only in their later developmental stages, as are most predatory copepods (Anderson 1970). Kerfoot (1975) found that *Epischura nevadensis* in Lake Washington had a strong influence on *Bosmina* prey populations when the planktivore had reached its adult stage, while McQueen (1969) found *Cyclops bicuspidatus thomasi* in Marion Lake to be predaceous only in copepodite IV + V and adult stages. To determine prey consumption by *Epischura* and *Cyclops* species in the Avalon lakes then, population densities (mean of spring and summer samples) of the two copepods were restricted to densities of individuals in the later copepodite and adult stages, of total lengths

Table 4.5. Calculated daily prey consumptions (prey-l^{-1}-day^{-1}) of pelagic zooplankton by zooplanktivorous Chaoborus spp. (C. punctipennis + C. trivittatus), Leptodora kindtii, Epischura nordenskioldi and Cyclops scutifer in the Avalon lakes during 1987. Predation rates are median values of recorded rates (prey-$predator^{-1}$-day^{-1}) from the literature. All planktivore densities (#-l^{-1}) are averaged over all the lakes in which the species was found. Chaoborus and Leptodora densities were determined from late summer samples, i.e. mainly 3rd + 4th (some 2nd) instar chaoborid larvae, and Leptodora > 5 mm in length. Epischura and Cyclops densities were determined from means of spring, summer and late summer samples of later copepodite (stages IV + V) and adult stages only (lengths: Epischura > 1.0 mm, Cyclops > 0.95 mm), with total copepod (adults + all copepodid stages) densities shown in brackets. Bracketed prey consumptions for the two copepods refer to consumptions based on the total copepod densities.

Planktivore Species	Predation Rates[A] with range from literature	Planktivore Density	Daily Prey Consumption
Chaoborus	14.8 1.5 - 28.0	0.224	3.31
Leptodora	18 6 - 30	0.030	0.54
Epischura	1.2 0.10 - 2.2	0.380 (0.541)	0.44 (0.65)
Cyclops	0.57 0.29 - 0.85	0.171 (0.750)	0.10 (0.43)

[A] = Median predation rates (prey-$predator^{-1}$-day^{-1}) determined from the ranges of rates recorded in the literature for the same or comparable predator species with a number of different zooplankton prey and differing predator/prey densities: Chaoborus = 3.9 (C. trivittatus, Dodson 1970), 2.2 to 28.0 (C. trivittatus, Fedorenko 1975b), 4.1 (C. trivittatus, Riessen et al. 1988), 1.5 to 2.1 (C. punctipennis, Allan 1973), 12 to 22 (C. punctipennis, Winner and Greber 1980); Leptodora = 10 to 30 (Mordukhai-Boltovskaia 1958), 6 (Havel 1985), 14 (Browman et al. 1989); Epischura = 0.10 to 2.2 (E. lacustris, Confer and Blades 1975), 0.12 to 0.87 (E. lacustris, Confer and Applegate 1979); Cyclops = 0.36 and 0.39 (C. bicuspidatus thomasi, Anderson 1970), 0.29 to 0.85 (C. vernalis, Confer and Applegate 1979).

(measured from the base of the caudal ramus to the anterior tip of the cephalothorax) > 1.00 mm for *E. nordenskioldi* and > 0.95 mm for *C. scutifer* (based on Davis 1976 and *pers. obs.*). Typical adult lengths for these species are 1.1 mm for *E. nordenskioldi* and 1.0 mm for *C. scutifer* (Pennak 1978). The overall mean lengths of these species in the Avalon lakes were 1.06 mm for *E. nordenskioldi* and 0.43 mm for *C. scutifer* (see Tables A.6 and A.8), indicating that adult calanoids were well represented but that many of the cyclopoids were present in small and nonpredatory stages. Based on the predator densities in Table 4.5, prey consumptions of pelagic zooplankton by *Chaoborus* spp., *L. kindtii*, *E. nordenskioldi* and *C. scutifer* populations were calculated to be 3.31, 0.54, 0.44 and 0.10 prey-l^{-1}-d^{-1}, respectively. The prey consumption of the two copepods was therefore lower than that of the larger planktivores, with *Chaoborus* having by far the greatest potential impact on the prey community, at least during the late summer period. *E. nordenskioldi* seems to have a potential predatory impact only slightly less than that of *Leptodora*. However, this copepod is abundant in only a few of the Avalon lakes (Table 4.1). Adults of *C. scutifer* were generally only present in spring samples, as noted by Davis (1976) as well, which could lessen the impact of this copepod on mean (spring + summer) zooplankton populations. Abundances of the two copepods did not seem to show any patterns consistent with the abundances of the other invertebrate planktivores and threespine sticklebacks (see Chapter 5). Thus, while *E. nordenskioldi* and *C. scutifer* undoubtedly have some potential predatory impact on the pelagic zooplankton community, this present study will be restricted to the impact of the major invertebrate planktivores, that is, *Chaoborus* spp. and *Leptodora*.

Chapter 5

Relative influence of vertebrate and invertebrate planktivores on the pelagic zooplankton community

5.1. Introduction

The effects of vertebrate and invertebrate planktivores on total biomass and community structure (species composition and size-class distribution) of the pelagic zooplankton community have been noted in a number of studies of freshwater lakes (see General Introduction), most particularly in studies involving the experimental or fortuitous manipulations of predators and/or prey (e.g. Hrbáček *et al.* 1961; Brooks and Dodson 1965; Hall *et al.* 1970; Kajak and Rybak 1979; Lynch 1979; Carpenter *et al.* 1987; Elser *et al.* 1987; Post and McQueen 1987; Vanni 1988). Such studies have demonstrated that increased planktivory can lead to decreases in total zooplankton biomass and can alter zooplankton community structure through selective predation (via both direct and indirect effects). Food concentrations and lake physicochemical characteristics, however, can also influence zooplankton biomass and community structure (Patalas 1971; Sprules and Holtby 1979; Pinel-Alloul *et al.* 1990; Tessier 1990). Predator influence on zooplankton communities should be most noticeable in lakes that are oligotrophic with low faunal diversity and low habitat heterogeneity given that this influence is generally believed to increase with decreasing lake trophy (Brocksen *et al.* 1970, Gliwicz and Prejs 1977; McQueen *et al.* 1989, but see Neill 1981) and with decreasing lake biological diversity and physical heterogeneity (Dodson 1979; Roff *et al.* 1981; Sih *et al.* 1985). Few studies, however, have evaluated the relative influence of both vertebrate and invertebrate predation in such lakes as compared with the entire suite of food concentration and lake chemical, physical and watershed factors.

Natural abundances of both vertebrate and invertebrate planktivores (the threespine stickleback, *Gasterosteus aculeatus*; the phantom midge larvae, *Chaoborus punctipennis* and *C. trivittatus*; and the predatory cladoceran, *Leptodora kindtii*) have been observed to vary over two to three orders of magnitude in a set of 15 lakes on the Avalon Peninsula of Newfoundland (see Tables 3.1 and 3.2). These marked differences in both vertebrate and invertebrate predator abundances offer the opportunity to observe possible resultant among-lake differences in zooplankton biomass and community structure. Definite, contrasting species and size selectivities evinced by the planktivores in their choice of zooplankton prey (i.e. selection by *G. aculeatus* mainly for cladocerans > 0.76 mm in length and selection by *Chaoborus* (and possibly also *Leptodora*) for rotifers and small cladocerans < 0.50 mm in length; Chapter 4 and see also Campbell 1991 *in press*) render these predators potentially capable of exerting strong and contrasting influences on zooplankton community structure. As well, because the study lakes are restricted to one physiographic region (Damman 1983), environmental variation among the water bodies should be low enough so as not to confound interpretation of biological interactions within the lakes (Roff *et al.* 1981). The Avalon lakes are all oligotrophic with depauperate zooplankton and planktivore fauna and low habitat heterogeneity (see Description of Study Site) and hence predator influence on the zooplankton community should be relatively easy to detect, as mentioned above. Common piscivores in the Avalon lakes are the American eel, *Anguilla rostrata*, and the salmonids *Salvelinus fontinalis*, *Salmo trutta* and *Salmo salar*.

If predator control by planktivores is important in structuring the zooplankton communities of the oligotrophic Avalon lakes, then the effect of planktivores on these zooplankton communities should be noticeably strong relative to the effects from other limnological factors such as resource supply (phytoplankton biomass) and lake physiochemical characteristics. Observed patterns in total zooplankton biomass and in species composition and size distributions of the zooplankton communities should relate significantly to patterns in the abundances of the vertebrate and invertebrate planktivores. Specifically, total zooplankton biomass should decrease with increasing planktivore abundance, while absolute and relative biomass of large cladocerans should decrease with increasing stickleback abundance and absolute and relative biomass of small zooplankton such as rotifers should decrease with increasing *Chaoborus* and *Leptodora* abundance. To evaluate the effect of predator control as compared with other limnological factors, measures of zooplankton biomass and community structure were related through multivariate analyses to variables of planktivore abundance, phytoplankton biomass, and lake chemical, physical and watershed characteristics to determine which combination of these variables could explain the greatest proportion of the variance observed in the Avalon lake zooplankton communities.

5.2. Methods

All sampling methods were as previously outlined in Chapter 3 (for planktivores and phytoplankton) and Chapter 4 (for zooplankton). Planktivores were sampled once from a set of 11 lakes in 1986 (fall: late August to late September) and twice from the original 11 lakes plus an additional 4 lakes in 1987 (spring: mid-May to mid-June, and late summer: mid-August to early September). In each lake, mean zooplankton biomass and community structure and mean phytoplankton biomass were estimated from samples taken twice over the open-water season in 1986 (spring and mid-summer), and three times in 1987 (spring, mid- and late summer). For each date, approximately 50 females of each cladoceran species (*Daphnia catawba*, *Holopedium gibberum* and *Eubosmina longispina*) were examined to determine the percentage of females with eggs and the mean number of eggs per ovigerous female per lake. This examination was restricted to cladocerans as many of the copepods did not retain their egg sacs upon preservation. Chemical, morphometric and watershed data for the Avalon lakes were collected as described in Chapter 3. 'Spring' water chemistry samples refers to surface water samples taken shortly after ice-out between May 10 - 23, 1984 when surface water temperatures averaged 10 °C, while 'summer' chemistry samples refer to samples collected between June 12 - 16, 1986 when surface water temperatures averaged 13 °C. Nonparametric Wilcoxon signed-rank tests (Siegel 1956; Sokal and Rohlf 1973) with two-tailed probabilities were used to compare stickleback catch, zooplankton biomass and invertebrate planktivore densities between years across lakes.

The data in each separate group of variables (planktivore, zooplankton, phytoplankton, chemical, morphometric and watershed variables) were condensed with principal components analysis (PCA) with varimax rotation (SPSS^x FACTOR programme, Noruŝis 1988). This analysis mathematically summarizes large sets of multivariate data into smaller numbers of orthogonal components which account for most of the variance in the original data. Varimax rotation, by minimizing the number of variables that have high loadings on a component (Norusis 1988), allowed for clearer interpretation of components over non-rotated solutions. For all analyses, the final number of components was determined by the number with eigenvalues > 1.0 (Davies 1984); the remaining components are judged to individually account for less variance than the average of all components and are therefore not considered to be interpretable (Legendre and Legendre 1983). Extracted components were given names corresponding to the variable(s) that contributed most strongly to the variance in each component as judged by inspection of the variable loadings; scatterplots of these variables versus the components were examined to ensure that distributions of the data were not highly skewed. Principal components relating to zooplankton community structure were derived both from measures of % species composition and from % size distribution measures. For % species composition, total zooplankton wet weight biomass per lake was divided up into 8 species classes: *Daphnia catawba*, *Eubosmina longispina*, *Holopedium gibberum*, *Leptodiaptomus minutus*, *Epischura nordenskioldi*, *Cyclops scutifer*, copepod nauplii and all rotifers (mainly *Keratella* spp., *Kellicottia* spp. and *Conochilus unicornis*). For % size distribution, zooplankton wet weight biomass was divided up into 7 size classes based on organism length in mm: 0 - 0.25, 0.26 - 0.50, 0.51 - 0.75, 0.76 - 1.00, 1.01 - 1.25, 1.26 - 1.75 and 1.76 - 3.00. Prior to principal components analysis, raw data were normalized through logarithmic ($\log_{10}$) transformation and percentage data through arcsin square root transformation (Prepas 1984). Where the raw data contained values of zero, $\log_{10}$ (x + 1) and arcsine (x + 0.05) transformations were used. The transformations helped correct for the dependence of the variance on the mean in the original data and also improved the fit of the data to the normal distribution (confirmed by graphical comparisons).

To evaluate the relative importance of planktivore influence on zooplankton biomass and community structure, total zooplankton biomass and principal components of community structure were related in stepwise multiple linear regression (MLR) models to all the other principal components as independent variables. In a series of separate linear regressions, planktivore abundances were entered separately as independent variables to determine how much variance in the zooplankton community could be accounted for by planktivore influences alone. Total phytoplankton biomass was also entered individually as an independent variable in single linear regressions to determine the influence of food resource supply on the zooplankton community. Correlations of the planktivore factors with the other independent components were evaluated through inspection of Pearson product-moment correlation coefficients. Significant correlations were examined further through inspection of correlations between separate planktivore abundances and the appropriate lake physicochemical principal components. For all regression models, assumptions of normal distributions of data and of linearity in the regressions were judged by examination of normal probability plots with standardized residuals, and plots between predicted variables and residuals, respectively.

The PCA and MLR procedures outlined above assume that planktivore abundances show some continuous variation among the lakes and that patterns in total zooplankton biomass and community structure may be related to this continuous variation. However, if planktivore abundances exhibit a strong grouped variation, that is, if the Avalon lakes fall into distinct groups or clusters in terms of their vertebrate and invertebrate planktivore abundances, then patterns in total zooplankton biomass and community structure might be related more to such predator groups than to a continuum of predator abundances. To determine if results from PCA and MLR procedures might be biased by this assumption of continuous variation in predator abundances, cluster analysis was used to see if the Avalon lakes fell into distinct predator abundance clusters based on stickleback catch and total invertebrate planktivore density. Results from two clustering methods based on similarity matrices were compared: unweighted pair-groups method using arithmetic averages (UPGMA), and complete-linkage clustering. Euclidean distance measures were used with both clustering methods. Analyses were run on NTSYS-pc, version 1.40 (Rohlf 1988). UPGMA with Euclidean distance measures is the clustering technique recommended when there is no specific reason for choosing any other technique (Gauch 1986), while comparison of the two methods strengthens conclusion regarding the number of clusters derived from the data (Rohlf 1988). One-way Analysis of Variance (ANOVA) was used to determine if total zooplankton biomass alone differed among the predator groups. Multiple analysis of variance (MANOVA), an extension of ANOVA which evaluates the influence of several dependent variables simultaneously, was used to determine if measures of community structure (% species composition and % size distribution) differed significantly among the clustered predator groups. Both % species composition and % size distribution were calculated in terms of zooplankton biomass of the species and size classes outlined previously. For MANOVA, Pillai's trace was used to test for significant differences between groups, as this multivariate test of significance is the most robust among commonly used tests; significance levels in this test are reasonably correct even when assumptions about the data (normality, homogeneity of variance) are not exactly met (Norušis 1988).

As a comparison with results obtained from the aforementioned PCA and MLR procedures, the latter which assumes a linear relationship between the dependent (zooplankton) and independent (planktivore and environment) variables, cluster analysis and discriminant analysis were also used to evaluate the relative impact of planktivore abundance on zooplankton biomass and community structure. Descriptive discriminant analysis provides a powerful technique for assessing the significance of separation between two or more groups or clusters (dependent variables) as related to several independent variables simultaneously (Green and Vascotto 1978; Klecka 1981; Williams 1983) and only assumes a linear relationship among the independent variables rather than between the dependent and independent variables. The distribution of dependent variables (i.e. clusters) on environmental variables is assumed to be roughly multivariate normal but discriminant analysis is generally robust enough to overcome violations of this assumption (Green and Vascotto 1978). Mean total zooplankton biomass, % species composition and % size distribution (the percentage data previously calculated in terms of biomass) were each subjected to separate cluster analyses in the manner previously mentioned, then discriminant analysis was used to determine if the resulting clustered groups were significantly differentiated by the independent variables of stickleback catch, total invertebrate planktivore (*Chaoborus* + *Leptodora*) density, and lake physicochemical and phytoplankton variables. Since, for valid discriminant analysis, the number of independent discriminating variables should be less than the number of cases - 2 (Klecka 1981), no more than 13 independent variables could be included (15 cases or lakes - 2). All redundant variables, or variables that were linear combinations of other variables, were eliminated prior to the analysis. Of the remaining variables, a total of twelve was selected as representative of planktivore abundance and lake chemical, physical, watershed and phytoplankton parameters, with roughly an equal number of variables in each parameter group. The twelve variables were mean stickleback catch, total late summer invertebrate planktivore density, mean total nitrogen concentrations, mean total phosphorus concentrations, conductivity, lake surface area, maximum depth, flushing rate, % development in the watershed, % upstream lakes in the watershed, mean biomass of "total edible" phytoplankton (algal cells < 30 μm in maximum dimension, see Chapter 3) and mean biomass of "inedible" phytoplankton (cells > 30 μm in maximum dimension). Variables were restricted to the same years as noted for the principal components.

Unless otherwise indicated, all statistical analyses were carried out with the SPSS^x (Norušis 1988) statistical package on Memorial University's Vax 8800 operating under VMS 5.0. Statistical significance (two-tailed) was determined by the criterion level $\alpha = 0.05$, except where otherwise mentioned.

5.3. Results

The relationship between vertebrate planktivore abundance and zooplankton biomass in the Avalon lakes was consistent with the hypothesis that zooplankton biomass should decrease with increasing planktivore abundance. Total zooplankton wet weight biomass was significantly and negatively related to mean stickleback catch per trap (Figure 5.1, $\log_{10}$ transformed variables: $r^2 = 0.40, p = 0.001, n = 25$). Data from 1986 and 1987 were combined since year had no significant influence on either stickleback catch (Chapter 3) or zooplankton biomass (Wilcoxon signed-rank test, $p > 0.10, n= 11$; only data from lakes sampled in both years were used). Year as a binary variable also did not enter into the regression model. The negative relationship between zooplankton biomass and stickleback abundance for the 2 years combined was consistent with negative relationships seen for the 2 years separately: for 1986, $r^2 = 0.58, p = 0.01, n = 11$; and for 1987, $r^2 = 0.43, p = 0.01, n = 15$.

Zooplankton biomass showed no corresponding decrease with increasing abundance of invertebrate planktivores. The influences of *C. punctipennis*, *C. trivittatus* and *L. kindtii* on the zooplankton community were evaluated together, rather than by the individual predator species, due to observed similarities in diet among the invertebrate planktivores (see Chapter 4) and to minimize the number of zero density data points resulting from the patchy distribution of these planktivores among the lakes (see Figure 3.2). There was no significant relationship between total zooplankton biomass and total invertebrate planktivore density in 1986, with a positive relationship observed in 1987 (Figure 5.2, $\log_{10}$ transformed variables: $r^2 = 0.28, p = 0.05, n = 15$.) The effect of the invertebrate planktivores was analyzed separately for 1986 and 1987 since sample year proved to have a significant effect on total invertebrate density (see Chapter 3). Samples in 1986 were taken later in the year than in 1987 (fall vs late summer) and the invertebrate planktivores seemed to have greatly declined in abundance or disappeared altogether from the water column of several of the lakes by this date. This fall disappearance has been noted in other studies of temperate-zone lakes for both *Chaoborus* larvae (Carter and Kwik 1977; von Ende 1982) and *Leptodora* (Sebestyén 1960; Cummins *et al.* 1969; Karabin 1974). For 1987, only the late summer data were used to evaluate invertebrate

Figure 5.1. Mean $\log_{10}$ total zooplankton wet weight biomass ($\mu g \cdot l^{-1}$) related to mean $\log_{10}$ stickleback catch ($animals \cdot trap^{-1} + 1$) for the combined years 1986 and 1987. The solid line represents the calculated regression equation: $\log_{10}zooplankton = -0.286\log_{10}stickleback + 2.900$.

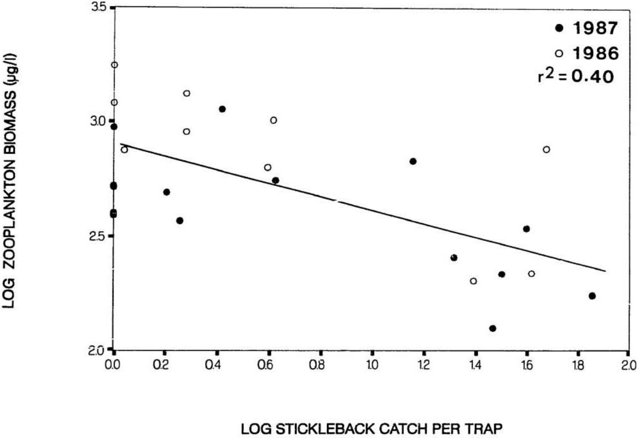
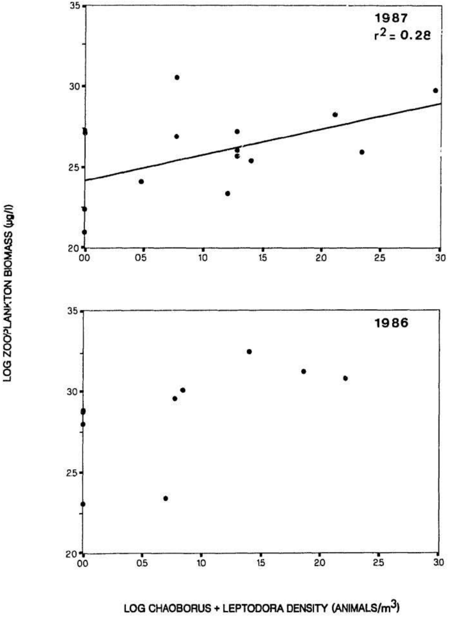

● 1987
○ 1986
$r^2 = 0.40$
LOG ZOOPLANKTON BIOMASS (µg/l)
3.5
3.0
2.5
2.0
0.0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
1.6
1.8
2.0
LOG STICKLEBACK CATCH PER TRAP

Figure 5.2. Mean $\log_{10}$ total zooplankton wet weight biomass ($\mu g \cdot l^{-1}$) related to $\log_{10}$ total invertebrate planktivore density (*Chaoborus* + *Leptodora*, animals-m^{-3} + 1) for the separate years 1986 and 1987 (fall and late summer, respectively). For 1986, $r^2 = 0.26$. For 1987, the solid line represents the calculated regression equation: $\log_{10}$zooplankton = $0.158\log_{10}$total invertebrate planktivores + 2.417.

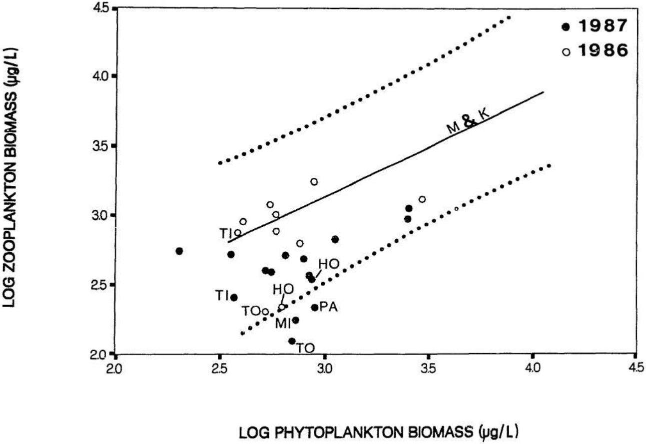

1987
r^2 = 0.28
1986
35
30
25
20
00
05
10
15
20
25
30
LOG ZOOPLANKTON BIOMASS (µg/l)
LOG CHAOBORUS + LEPTODORA DENSITY (ANIMALS/m^3)

planktivore influence, as *Chaoborus* and *Leptodora* were absent from many of the spring samples (see Table 3.2) due to the seasonality of the life cycles of these species. *Chaoborus* and *Leptodora* densities individually were not significantly correlated with zooplankton biomass but the large number of zero values in the planktivore density data reduced the ability to detect any such effects.

Total zooplankton biomass was also not significantly linearly related to total phytoplankton biomass, either for 1986 and 1987 combined (Figure 5.3, $\log_{10}$ transformed variables: $r^2 = 0.09$, $p = 0.15$, $n = 25$), or for the two years considered separately (1986: $r^2 = 0.11$, $p = 0.35$, $n = 11$, and 1987: $r^2 = 0.15$, $p = 0.16$, $n = 15$), indicating that the influence of food supply was relatively weak. There were also no significant relationships observed between total zooplankton biomass and the biomass of "edible" phytoplankton. Sample year did not have a significant effect on total phytoplankton biomass (Wilcoxon signed-rank test: $p > 0.10$, n = 11). The majority of the Avalon lakes fell below the regression line predicted by the empirical model of McCauley and Kalff (1981) based on zooplankton and phytoplankton biomass data for 17 freshwater lakes (Figure 5.3), while some of the Avalon lakes fell completely outside calculated 95% confidence limits for the regression line. The Avalon lakes are all clustered towards the low end of the biomass range covered by McCauley and Kalff's model; this alone would tend to result in a decreased r^2 value as compared with the r^2 value derived by McCauley and Kalff. The predicted slope of the McCauley and Kalff regression (0.719) did fall within the rather large 95% confidence interval of the slope of total zooplankton versus total phytoplankton in the Avalon lakes (slope = 0.346, 95% confidence interval = - 0.149 to 0.841). The Avalon lakes that showed the greatest deviation from the predicted line were generally those with the highest catches of fish per trap: Hogans Pond, Middle Three Island Pond, Paddys Pond, Three Island Pond and Tors Cove Pond (see Tables 3.1 and 3.2).

Due to the effects of year and season on invertebrate planktivore abundances, principal components analysis of the planktivore variables was restricted to 1987 mean stickleback catches and late summer *Chaoborus* and *Leptodora* densities. Although year had no significant effect on stickleback catch, estimates of fish catch

Figure 5.3. Mean $\log_{10}$ total zooplankton wet weight biomass ($\mu g \cdot l^{-1}$) related to mean $\log_{10}$ phytoplankton wet weight biomass ($\mu g \cdot l^{-1}$) for the combined years 1986 and 1987, $r^2 = 0.09$. The solid line represents the regression equation of McCauley & Kalff (1981): $\log_{10}\text{zooplankton} = 0.719\log_{10}\text{phytoplankton} + 1.015$, $r^2 = 0.74$. The dotted lines are 95% confidence limits about predicted values outside the regression model, calculated from Prepas (1984). HO = Hogans Pond, MI = Middle Three Island Pond, PA = Paddys Pond, TI = Three Island Pond, and TO = Tors Cove Pond.


● 1987
○ 1986
M & K
TI
TI
HO
HO
TO
TO
PA
MI
LOG ZOOPLANKTON BIOMASS (μg/L)
LOG PHYTOPLANKTON BIOMASS (μg/L)
2.0
2.5
3.0
3.5
4.0
4.5
2.0
2.5
3.0
3.5
4.0
4.5

per trap may have been underestimated in 1986 as few juvenile fish were caught as compared with 1987 (Figure 4.1) when the traps were lined with 1 mm-mesh nylon netting to retain smaller fish. The principal components that resulted from the analyses of planktivore abundances and lake chemical, morphometric, and watershed variables are as described in Chapter 3. Only one component could be extracted from the planktivore data (Table 3.4); this 'planktivore' component accounted for just 57% of the variance in the original data. *Chaoborus* loaded negatively on to the component while both stickleback and *Leptodora* loaded positively. Due to the low amount of variance explained by this component (a reflection of lack of normality in the invertebrate planktivore data and the negative relationship between the distributions of *Chaoborus* and stickleback, see Chapter 3), 'planktivore' was not thought to be a useful variable in subsequent MLR models and the constituent variables of stickleback catch and total invertebrate planktivore density were used instead.

Lake chemical variables were condensed into 4 components (Table 3.5), labelled as 'ionic strength', 'summer phosphorus', 'spring phosphorus', and 'total Kjeldahl (organic) nitrogen (TKN)'. Together these components accounted for 84% of the variance in the original data. Complete chemical data were unavailable for Middle Three Island Pond and Tors Cove Pond, so the components were based only on 13 lakes. Lake morphometric variables were condensed into 2 components (Table 3.6), labelled 'lake size' and 'flushing rate', which together accounted for 87% of the variance in the original data. For the watershed data, 93% of the variance was explained by the 3 extracted components of 'development' (extent of housing development in the watershed), '% barrens' (proportion of dwarf shrub heath barrens in the watershed), and '% upstream lakes' (proportion of watershed occupied by upstream lakes) (Table 3.7).

Only data from 1987 were used for the principal components analyses of phytoplankton biomass and zooplankton community structure to correspond with the restriction of planktivore abundances to 1987 data. (Lake physical, chemical and watershed characteristics were assumed to show less yearly variation than did these biotic variables). Only one component could be derived from the phytoplankton biomass data (Table 5.1). This 'phytoplankton' component accounted for 72% of the original data variance.

Five components were derived from the measures of zooplankton community structure. The % species composition data was condensed into 3 components which accounted for 65% of the original data variance (Table 5.2). The components were labelled 'lack of small herbivores' (*E. longispina* and rotifers loaded negatively), '*Diaptomus* vs *Daphnia*' (*L. minutus* and copepod nauplii loaded positively while *D. catawba* loaded negatively), and 'large copepods vs *Holopedium*' (*E. nordenskioldi* and *C. scutifer* loaded positively while *H. gibberum* loaded negatively). Two components, accounting for 77% of the variance in the original data, were extracted from the % size distribution data (Table 5.3). Due to the rarity of large zooplankters > 1.51 mm in length, the two largest size classes were combined to increase class sample size prior to statistical analysis. The first component 'medium size', included most of the size classes less than 1.25 mm in length with the 2 smallest size classes loading negatively, while the second component, 'large > 1.26', included the 2 largest size classes and the negatively loading size class of 0.51 - 0.75 mm.

Table 5.4 shows the results of the series of stepwise MLR models evaluating the influence of planktivore abundance (stickleback catch and total invertebrate planktivore density) compared with the environmental principal components, on zooplankton biomass and community structure. In these MLR models, increasing total zooplankton biomass was significantly related to decreasing stickleback catch and increasing ionic strength which together explained 65% of the biomass variance. The % species composition and % size distribution components were significantly related to such environmental components as 'ionic strength', 'summer phosphorus', 'lake size', 'development', 'TKN' and '% barrens'. Planktivore abundance entered only once as a significant independent variable with respect to community structure; the component 'medium size' was significantly related to 'TKN', stickleback catch and 'lake size', which together explained 93% of the variance in this component. Total invertebrate planktivore density did not enter as a signficant independent variable in any of the biomass or community structure models. Examination of plots of residuals showed no violations of linearity in any of the significant regressions.

Table 5.1. Phytoplankton principal components analysis, with correlations of mean 1987 data with the extracted component (PC). Only statistically significant ($p < 0.05$) correlation coefficients are shown.

Variable	PC 1 Phytoplankton
Small edible phytoplankton	0.966
Medium edible phytoplankton	0.922
Inedible phytoplankton	0.606
Cumulative explained variance	0.717

Table 5.2. Principal components analysis of % species composition of total zooplankton biomass, with correlations of mean 1987 data with the extracted factors (PCs). Only statistically significant ($p < 0.05$) correlation coefficients are shown except where no significant correlations were found, in which case the largest correlation is shown in brackets. *Diap* = *Leptodiaptomus minutus*, *Daph* = *Daphnia catawba*, *Holo* = *Holopedium gibberum*.

Variable	PC 1	PC 2	PC 3
	Lack small herbivores	*Diap* vs *Daph*	Large copepods vs *Holo*
E. longispina	- 0.909		
rotifers	(- 0.344)		
L. minutus		0.907	
nauplii		0.640	
D. catawba		- 0.678	
E. nordenskioldi			0.746
C. scutifer			(0.406)
H. gibberum			- 0.844
Cumulative explained variance	0.263	0.489	0.649

Table 5.3. Principal components analysis of % size distribution of total zooplankton biomass, with correlations of mean 1987 data with the extracted components (PCs). Only statistically significant ($p < 0.05$) correlation coefficients are shown. Size class ranges in mm are ranked in each component in order of increasing size.

Variable	PC 1 Medium size	PC 2 Large > 1.26
0.00 - 0.25	- 0.809	
0.26 - 0.50	- 0.833	
0.76 - 1.00	0.807	
1.01 - 1.25	0.843	
0.51 - 0.75		- 0.791
1.26 - 1.50	0.537	0.803
1.51 - 3.00		0.856
Cumulative explained variance	0.523	0.768

Table 5.4. Multiple linear regression models of zooplankton biomass and principal components of zooplankton community structure related to stickleback catch, total invertebrate planktivore (*Chaoborus* + *Leptodora*) density and chemical, morphometric, watershed and phytoplankton principal components for the Avalon lakes. The '+' or '-' sign indicates whether the relationship is positive or negative. Significance levels of the cumulative R^2 values are indicated by * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) and *** ($p < 0.005$).

Dependent Variable	Significant Independent Variables	Cumulative R^2
Zooplankton biomass	- stickleback	0.43 *
	+ ionic strength	0.65 **
Lack small herbivores	+ ionic strength	0.36 *
Diap vs *Daph*	- summer P	0.54 **
	- lake size	0.75 **
	- development	0.86 ***
Large copepods vs *Holo*	ns	
Medium size	+ TKN	0.40 *
	- stickleback	0.65 **
	+ lake size	0.93 ***
Large > 1.26	+ summer P	0.38 *
	- % barrens	0.61 **

Distribution of data in models with community structure measures, however, showed some slight deviation from normality, even with transformed data.

Inspection of correlation coefficients (Table 5.5) between planktivore abundance and other independent variables in the MLR models showed a strong, albeit not significant, correlation of stickleback catch per trap with 'flushing rate' (the 'planktivore' component was significantly correlated only with 'flushing rate'). Stickleback catch per trap showed no significant correlations with any of the other independent components. Hence, the significance of stickleback catch in the models was not confounded by correlations with other independent variables in these models. Total invertebrate planktivore density was significantly correlated only with 'phytoplankton' and 'spring phosphorus'. Correlation coefficients among all environmental principal components are listed in Appendix Table A.1.

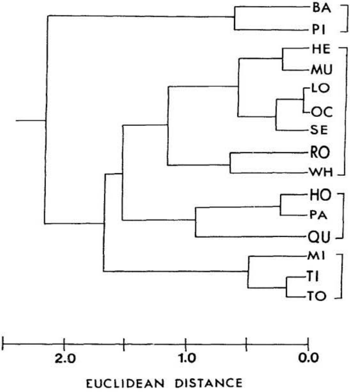
The observation that planktivore abundance was not the predominant influence on zooplankton community structure, as demonstrated by the MLR analyses, was mirrored in results from separate single linear regressions which showed none of the community structure components to be significantly related to any of the separate planktivore abundances alone, i.e., stickleback catch, invertebrate planktivore density, *Chaoborus* or *Leptodora* densities. By itself in single linear regression models, 'planktivore' was also unable to explain a significant proportion of the variance in either total zooplankton biomass or in any of the measures of zooplankton community structure. In addition, 'lack of small herbivores' was the only community structure component to be significantly influenced by food supply in the lakes, showing significant positive relationships in linear regressions with the 'phytoplankton' component ($r^2 = 0.32, p = 0.03, n = 15$) and with total phytoplankton biomass ($r^2 = 0.51, p = 0.01, n = 15$).

The alternate analytical approach using cluster analysis to evaluate planktivore influence resulted in division of 15 Avalon lakes into four observed groups in terms of stickleback catch and total invertebrate planktivore density (Figure 5.4). To coincide with the PCA and MLR procedures, only the 1987 mean stickleback catch per trap and the 1987 late summer *Chaoborus* and *Leptodora* densities (Table 3.2)

Table 5.5. Pearson product-moment correlations of 'planktivore' principal component, $\log_{10}$ stickleback catch (Gast), $\log_{10}$ Chaoborus density (Chaob), $\log_{10}$ Leptodora density (Lepto) and $\log_{10}$ total invertebrate planktivore density (Invert) with chemical, morphometric, watershed and phytoplankton principal components (PCs) for the Avalon lakes. Complete chemical principal components were available only for 13 lakes; otherwise sample size = 15. Significance levels of the correlation coefficents are indicated by * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) and *** ($p < 0.005$).

Lake PCs	Planktivore PC	Gast	Chaob	Lepto	Invert
Chemical					
Ionic strength	0.262	0.111	- 0.079	0.584 *	0.352
Summer P	0.172	0.192	- 0.099	0.140	0.103
Spring P	- 0.031	0.098	0.304	0.290	0.627 *
TKN	- 0.320	- 0.278	0.146	- 0.433	- 0.100
Morphometric					
Lake size	0.249	0.124	- 0.245	0.209	- 0.054
Flushing rate	0.527 *	0.461	- 0.484	0.194	- 0.268
Watershed					
Development	0.135	- 0.190	- 0.087	0.591 *	0.289
% barrens	0.186	0.077	- 0.244	0.079	- 0.140
% upstream lake	0.043	0.072	- 0.078	- 0.103	- 0.218
Phytoplankton					
Phytoplankton	- 0.186	0.020	0.408	0.044	0.532 *

Figure 5.4. Predator groups derived from cluster analysis of the 15 Avalon lakes based on 1987 $\log_{10}$ late summer total invertebrate planktivore (*Chaoborus* spp. + *Leptodora*) densities (INVERT) and 1987 $\log_{10}$ mean stickleback catch per trap (STICKLE). Relative planktivore abundance in the 4 predator groups is indicated by '++' (high), '+' (low) and 0 (planktivores absent). Lakes are identified by a two-letter code as in Figure 2.1. Cluster groups were derived by the UPGMA method with Euclidean Distance as a measure of similarity.

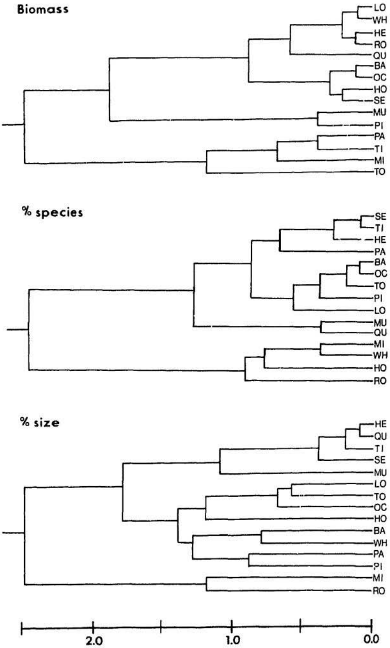


GROUP	INVERT	STICKLE
1	++	0
2	+	+
3	++	++
4	0	++

were used in the cluster analysis, with 1987 mean zooplankton biomasses used in subsequent analyses of variance. The predator groups were labelled as 1) lakes with high invertebrate planktivore density and no stickleback (Bauline Long and Piccos), 2) lakes with low invertebrate planktivore density and low stickleback catch (Healeys, M.U.N. Long, Long, Octagon, Second, Round and Whiteway), 3) lakes with high invertebrate planktivore density and high stickleback catch (Hogans, Paddys and Quidi Vidi) and 4) lakes with no invertebrate planktivores and high stickleback catch (Middle Three Island, Three Island and Tors Cove). Only the UPGMA solution is shown; the complete-linkage method produced the same clusters. Total zooplankton biomass differed significantly among the four groups (one-way ANOVA: $F_{3,14}$ = 5.63, $p = 0.01$). Multiple comparison of means by the *a posteriori* Scheffe's test with MS_{error} from the one-way ANOVA (Snedecor and Cochran 1980) indicated that this significant difference was primarily a function of the significantly lower zooplankton biomass in the three lakes with no invertebrate planktivores and high stickleback catch (Group 4 above) as compared with the other lakes ($t = 3.44$, $0.025 < p < 0.05$). Results of the MANOVA indicated that neither % species composition nor % size distribution differed significantly among the four predator groups (Pillai's trace: p levels = 0.909 and 0.929 for % species and % size, respectively). The possibility existed that the distribution of other invertebrate planktivores might influence the division of the predator cluster groups. However, ANOVA tests demonstrated that the abundances of neither *Epischura nordenskioldi* nor *Cyclops scutifer* were significantly related to the four predator groups from Figure 5.4 (p levels = 0.243 and 204 for *E. nordenskioldi* and *C. scutifer*, respectively).

Results of the separate cluster analyses performed on the total zooplankton biomass, % species composition and % size distribution data suggested that three clusters were present in each of these variable groupings (Figure 5.5, note that clusters with only one case cannot be used in discriminant analysis; Klecka 1981). Only the UPGMA solutions are shown since clusters produced by the complete-linkage method were similar. Both M.U.N. Long and Piccos Ponds can be classified as lakes with high zooplankton biomass, while Middle Three Island, Paddys, Three Island and Tors Cove Ponds can be classified as lakes with low zooplankton biomass,

Figure 5.5. Groups derived from cluster analyses of the 15 Avalon lakes based on 1987 $\log_{10}$ total zooplankton wet weight biomass, % species composition and % size distribution. Lakes are identified by a two-letter code as in Figure 2.1. Cluster groups were derived by the UPGMA method. Similarity (on x axis) is measured by Euclidean distance as in Figure 5.4.


Biomass
LO
WH
HE
RO
QU
BA
OC
HO
SE
MU
PI
PA
TI
MI
TO
% species
SE
TI
HE
PA
BA
OC
TO
PI
LO
MU
QU
MI
WH
HO
RO
% size
HE
QU
TI
SE
MU
LO
TO
OC
HO
BA
WH
PA
PI
MI
RO
2.0
1.0
0.0

the other Avalon lakes having intermediate zooplankton biomass levels with respect to these six lakes (see Appendix B). As determined by discriminant analysis, clusters based on total zooplankton biomass were most strongly differentiated by flushing rate, "inedible" phytoplankton biomass, total nitrogen concentrations and maximum depth (as shown by pooled within-group correlations of these variables with the significant canonical discriminant function, Table 5.6). The strengths of the pooled within-group correlations of the discriminating variables with the canonical discriminant function are considered to be more ecologically interpretable than are the strengths and signs of the standardized canonical discriminant coefficients themselves (Williams 1983). Only one significant canonical discriminant function could be derived from this analysis; this first function maximizes the differences between cluster group means (Klecka 1981), with significance of group separation ascertained by Wilk's λ and associated χ-square (Norušis 1988). A total of two discriminant functions (number of groups or clusters - 1, Klecka 1981) could potentially be derived from the analysis. The single significant discriminant function was able to explain 73% of the separation between the biomass groups. When the influence of the planktivore and environmental variables on zooplankton biomass were assessed individually, only the variables of stickleback catch, lake surface area and edible phytoplankton biomass were observed to be significant separators of the zooplankton biomass groups, based on univariate F tests (*p* levels of 0.01, 0.02 and 0.04, respectively). Cluster groups derived from the % species composition data were most strongly differentiated by the chemical variables of total nitrogen concentration, total phosphorus concentration and conductivity, and by flushing rate, development in the watershed and "inedible" phytoplankton biomass, based on the correlations between these variables and the first discriminant function (Table 5.7). Only this function was significant and explained 83% of the separation between % species groups. Development in the watershed, conductivity, total nitrogen concentration and flushing rate were also observed to be significant separators of the % species groups in univariate models (univariate F test: $p = 0.001, 0.002, 0.03$ and 0.04, respectively). In the case of the % size distribution groups, the discriminating variables of total phosphorus, conductivity and lake area were most highly correlated with the one significant discriminant function (Table 5.8). This function accounted for 82% of the

Table 5.6. Discriminant analysis of total zooplankton biomass groups related to planktivore and environmental (chemical, physical, watershed and phytoplankton) variables. Only significant ($p < 0.05$) canonical discriminant functions are shown, along with the associated standardized canonical discriminant coefficients and the pooled within-group correlations between the discriminating variables and the discriminant functions. An asterix (*) refers to discriminating variables that are more highly correlated with the first discriminant function than with any subsequent functions.

Discriminating Variables	Function 1	
	Coefficients	Correlations
Planktivore		
stickleback catch	- 2.369	+ 0.074
invertebrate planktivore density	- 0.497	+ 0.003
Chemical		
total nitrogen *	- 2.637	+ 0.097
total phosphorus	- 2.639	+ 0.048
conductivity	+ 0.832	+ 0.017
Physical		
lake surface area	+ 4.024	- 0.005
maximum depth *	- 2.884	- 0.039
flushing rate *	+ 4.282	+ 0.135
Watershed		
% development	+ 0.341	+ 0.024
% upstream lakes	- 3.866	- 0.016
Phytoplankton		
total edible phytoplankton biomass	+ 1.689	+ 0.146
inedible phytoplankton biomass *	+ 4.192	+ 0.114
Cumulative Explained Separation between groups:		
Function 1	0.732	

Table 5.7. Discriminant analysis of % species composition groups related to planktivore and environmental (chemical, physical, watershed and phytoplankton) variables. Only significant ($p < 0.05$) canonical discriminant functions are shown, along with the associated standardized canonical discriminant coefficients and the pooled within-group correlations between the discriminating variables and the discriminant functions. An asterix (*) refers to discriminating variables that are more highly correlated with the first discriminant function than with any subsequent functions.

Discriminating Variables	Function 1	
	Coefficients	Correlations
<u>Planktivore</u>		
stickleback catch	+ 0.945	- 0.004
invertebrate planktivore density	+ 2.134	+ 0.039
<u>Chemical</u>		
total nitrogen *	- 0.397	+ 0.107
total phosphorus *	+ 1.814	+ 0.080
conductivity *	- 1.430	+ 0.166
<u>Physical</u>		
lake surface area	- 2.504	- 0.041
maximum depth	+ 2.888	+ 0.027
flushing rate *	+ 3.232	+ 0.103
<u>Watershed</u>		
% development *	+ 2.463	+ 0.196
% upstream lakes	+ 0.525	- 0.040
<u>Phytoplankton</u>		
total edible phytoplankton biomass	+ 0.892	+ 0.011
inedible phytoplankton biomass *	- 1.180	+ 0.100
Cumulative Explained Separation between groups:		
Function 1	0.927	

Table 5.8. Discriminant analysis of % size distribution groups related to planktivore and environmental (chemical, physical, watershed and phytoplankton) variables. Only significant ($p < 0.05$) canonical discriminant functions are shown, along with the associated standardized canonical discriminant coefficients and the pooled within-group correlations between the discriminating variables and the discriminant functions. An asterix (*) refers to discriminating variables that are more highly correlated with the first discriminant function than with any subsequent functions.

Discriminating Variables	Function 1	
	Coefficients	Correlations
<u>Planktivore</u>		
stickleback catch	- 7.890	- 0.051
invertebrate planktivore density	- 2.195	+ 0.071
<u>Chemical</u>		
total nitrogen	- 6.132	+ 0.012
total phosphorus *	- 0.887	+ 0.101
conductivity *	+ 10.163	+ 0.092
<u>Physical</u>		
lake surface area *	+ 7.395	- 0.016
maximum depth	- 0.581	+ 0.119
flushing rate	+ 2.256	+ 0.004
<u>Watershed</u>		
% development	- 4.648	+ 0.084
% upstream lakes	- 1.714	- 0.030
<u>Phytoplankton</u>		
total edible phytoplankton biomass	+ 2.534	+ 0.037
inedible phytoplankton biomass	+ 2.109	+ 0.093
Cumulative Explained Separation between groups:		
Function 1	0.822	

separation between the % size groups. None of the independent discriminating variables alone were significantly related to the % size distribution groups as evaluated by univariate F tests.

The lack of a relationship between stickleback abundance and patterns in zooplankton size structure, despite the evidence for a relationship between stickleback catch and total zooplankton biomass, is also shown by the distribution of mean % density per size class of the zooplankton community in lakes with no sticklebacks (Bauline Long Pond and Piccos Pond; Group 1 in Figure 5.4) and lakes with high stickleback catch (Middle Three Island Pond, Three Island Pond and Tors Cove Pond; Group 4 in Figure 5.4). There was no consistent and significant difference in the distribution of size classes between the "No Stickle" and "High Stickle" lakes (Figure 5.6). Examination of the mean number of eggs per ovigerous female (cladocerans only) in the "No Stickle" and "High Stickle" lakes (Figure 5.7) indicated that the mean number of eggs per female for both *D. catawba* and *E. longispina* did not differ significantly between the two lake groups, while *H. gibberum* had significantly more eggs per ovigerous female in the lakes with sticklebacks than in the lakes without sticklebacks (Mann-Whitney *U* test; $p < 0.05$).

5.4. Discussion

Only total biomass of the pelagic zooplankton communities in the oligotrophic Avalon lakes seems to be clearly influenced by predator abundance. Decreases in total zooplankton biomass are associated with increases in abundance of the vertebrate planktivore, *G. aculeatus*, as shown both by MLR analysis and by clustering and MANOVA procedures. In contrast, the invertebrate planktivores, *Chaoborus* spp. and *Leptodora*, seem to exert little predator control since regression relationships between invertebrate planktivore density and zooplankton biomass are either not significant or weakly positive, but never negative as would be the case if planktivory were limiting overall prey abundance. As well, neither the vertebrate nor invertebrate planktivores appear to be major influences on zooplankton community structure. Patterns in the species composition of the zooplankton communities showed no significant relationship with patterns in the abundances of any of the

Figure 5.6. Mean % density of zooplankton in size classes in lakes with no stickleback (NO STICKLE = Bauline and Piccos Ponds) and in lakes with high stickleback catch (HIGH STICKLE = Middle Three Island, Three Island and Tors Cove Ponds) in 1987.

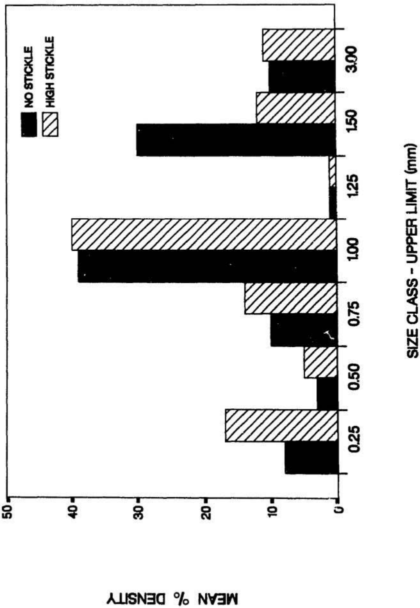
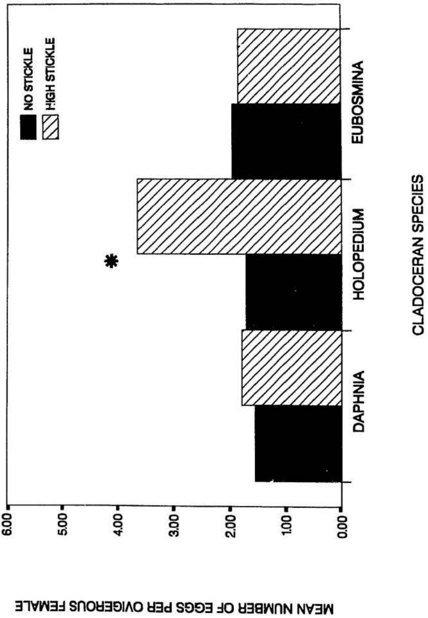

NO STICKLE
HIGH STICKLE
MEAN % DENSITY
0
10
20
30
40
50
0.25
0.50
0.75
1.00
1.25
1.50
3.00
SIZE CLASS - UPPER LIMIT (mm)

Figure 5.7. Mean number of eggs per ovigerous female for the cladocerans *Daphnia catawba*, *Holopedium gibberum* and *Eubosmina longispina* in lakes with no stickleback (NO STICKLE = Bauline and Piccos Ponds) and in lakes with high stickleback catch (HIGH STICKLE = Middle Three Island, Three Island and Tors Cove Ponds) in 1987. An * indicates a significant difference ($p < 0.05$, Mann-Whitney U test) for a species in mean egg number between the two lake groups.


NO STICKLE
HIGH STICKLE
*
DAPHNIA
HOLOPEDIUM
EUBOSMINA
CLADOCERAN SPECIES
0.00
1.00
2.00
3.00
4.00
5.00
6.00
MEAN NUMBER OF EGGS PER OVIGEROUS FEMALE

planktivores, as analyzed either by PCA and MLR procedures or by clustering and MANOVA procedures. While patterns in size distribution, specifically the 'medium size' component, were significantly related in a stepwise MLR model to stickleback abundances, planktivore abundance was not the primary significant independent variable in the model. Mean % densities per size class of zooplankton also did not noticeably differ between lakes with no sticklebacks and lakes with high stickleback catches. Size distribution patterns showed no significant relationships with patterns in abundances of stickleback or total invertebrate planktivore density in subsequent linear regression models.

Despite the possible influence of stickleback abundance on total zooplankton biomass, stickleback catch did not appear to influence zooplankton egg production, at least in cladoceran prey. Species-specific clutch size can vary greatly in cladocerans in probable response to differing environmental conditions and predation pressures (Lynch 1980), with higher reproduction rates possibly compensating for mortality losses due to predation. However, only *H. gibberum* in the Avalon lakes had significantly higher number of mean eggs per ovigerous females in the lakes with high stickleback abundance compared to the lakes in which sticklebacks were absent. Both *D. catawba* and *E. longispina* were preyed upon by sticklebacks, while *H. gibberum* was not a common component of the stickleback diet in the Avalon lakes (Chapter 4). Consequently, a factor other than direct stickleback predation, such as decreased competition from other cladocerans due to the removal of these species by sticklebacks, would seem to be related to the difference in *H. gibberum* egg production between the two lake groups.

Seasonal variation in the ability of the invertebrate planktivores to prey upon zooplankton may explain why invertebrate planktivore density had no negative influence on zooplankton biomass, while stickleback abundance did have such an influence. Both *C. punctipennis* and *C. trivittatus* become primarily predaceous only in the 3rd and 4th instar (Pastorok 1980; Elser *et al.* 1987) while *Leptodora* is predominantly predaceous only in the larger adult body sizes (Cummins *et al.* 1969; Browman *et al.* 1989). Hence, predation effects of the seasonally predaceous invertebrate planktivores might be less easily detected than those of the more consistently predaceous stickleback, particularly given the present zooplankton community data which are composed of seasonal means. The positive relationship observed between total invertebrate planktivore density and zooplankton biomass suggests that *Chaoborus* and *Leptodora* populations are limited by the abundance of their prey, and that their predation rates are too low to markedly reduce the growth rates of the prey populations.

The negative regression relationship between 'medium size' and stickleback catch, together with the lack of a significant relationship between the component 'large > 1.26' and stickleback catch, indicates that the impact of stickleback predation on zooplankton biomass is concentrated mainly on zooplankton less than 1.26 mm in length. This concurs with the analysis of stickleback diet that showed that sticklebacks preyed mainly on zooplankters from 0.76 to 1.25 mm in length (Figure 4.4), specifically the cladoceran *D. catawba* (Figure 4.2). The relationship between 'medium size' and stickleback catch is strengthened further by the negative loadings of size classes of less than 0.50 mm in length onto the % size class component and hence the positive relationship between increasing biomass of small zooplankton and increasing stickleback catch. Analysis of stickleback diet indicated that the fish showed negative selection for such small prey, which consisted mainly of copepod nauplii and rotifers. Increased biomass of small zooplankton with increasing stickleback abundance might result from competitive release, there being little stickleback predation on such zooplankton while larger, potentially competing zooplankton species, such as *E. longispina* and *D. catawba*, are being removed through predation. The lack of a significant regression relationship between 'large > 1.26' and stickleback abundance is consistent with the observation that sticklebacks showed no selectivity for very large zooplankton (Figure 4.2) such as *E. nordenskioldi* and *H. gibberum*, as a probable result of the overall rarity and escape capabilities of the former species and the protective gelatinous sheath of the latter species.

Results from the MLR models show increasing zooplankton biomass to be related to increasing 'ionic strength' in the lakes (a probable correlate of lake productivity; see Rawson 1951) as well as to decreasing stickleback abundances. In addition, 'medium size', while significantly related to decreases in stickleback abundance, was primarily related to increasing concentrations of organic nitrogen (TKN) in the lakes. The appearance of 'ionic strength' and 'TKN' as significant independent variables in the MLR models can be construed as evidence for nutrient and resource level ("bottom-up") control, as opposed to predator ("top-down") control (*sensu* McQueen *et al.* 1986) of the zooplankton communities. Even though 'phytoplankton' itself did not enter the MLR models, possibly due to confounding effects from correlations with the other independent variables of invertebrate planktivore density and phosphorus concentrations (see below), many of the factors that do relate to zooplankton community structure in the Avalon lakes can also be described in terms of nutrient and resource control, e.g. 'summer phosphorus', 'development' and '% barrens'. Phosphorus is a well-known correlate of phytoplankton abundance in lakes (Dillon and Rigler 1974; Prepas and Trew 1983) and the 'phytoplankton' component correlated significantly with 'spring phosphorus' in the Avalon lakes (Pearson product-moment correlation: $r = 0.647, p = 0.02, n = 13$). Extent of watershed development reflects the number of persons living in the watershed and hence the levels of nutrient loadings to the lake through increased use of septic tanks, agricultural and lawn fertilizers, etc. The proportion of barrens in the watershed also reflects nutrient levels in the drainage basin since heath barrens are ecologically restricted to nutrient-poor soils (Meades 1983).

The community structure component 'large > 1.26' was positively related to 'summer phosphorus' and negatively related to '% barrens', while 'lack of small herbivores' and 'medium size' (on to which the biomass of small zooplankton such as *E. longispina* and rotifers loaded negatively) were positively related to 'ionic strength' and 'TKN', respectively. 'Lack of small herbivores' was also positively related to phytoplankton biomass in a single linear regression. Taken together, these regression relationships suggest that within the narrow productivity range of the oligotrophic Avalon lakes, the biomass of large zooplankton increases and the biomass of small zooplankton decreases with increasing lake productivity. Total invertebrate planktivore density was significantly and positively correlated with 'phytoplankton' biomass and 'spring phosphorus' levels, both measures of lake productivity as well. Consequently, the decrease of small zooplankton with increasing lake productivity might partially reflect increases in invertebrate planktivory, even though none of the components that described small zooplankton biomass were significantly related to invertebrate planktivore density (Table 5.4). In contrast, the biomass of small herbivores in more eutrophic lakes may increase, rather than decrease, with increasing lake productivity, mainly as a function of increases in biomass of large inedible algae (Watson and Kalff 1981) and of detritus upon which the small zooplankters feed most efficiently (Hillbricht-Ilkowska 1977). Increasing lake productivity can also lead to a shift in zooplankton species composition from dominance by calanoids to dominance by cladocerans (McNaught 1975); this is in accordance with the observed negative relationship between the components '*Diaptomus* vs *Daphnia*' and 'summer phosphorus' and 'development' in the Avalon lakes.

Just as variation among zooplankton communities cannot be ascribed solely to planktivore control, such variation also may not be ascribed solely to resource control. Zooplankton biomass in the Avalon lakes was not linearly related to phytoplankton biomass alone (Figure 5.3), as it should be if resource control was dominant (McQueen *et al.* 1986), although the weak relationship may be partially attributed to the low range in phytoplankton biomass observed in the Avalon lakes as compared with other phytoplankton - zooplankton models (McCauley and Kalff 1981; McQueen *et al.* 1986). "Total edible" phytoplankton biomass in the Avalon lakes did appear as a significant univariate influence of total zooplankton biomass groups in the cluster procedure and discriminant analysis, however, indicating that a significant non-linear impact of resource control is probable. 'Lack of small herbivores' was the only community structure component to be linearly related to phytoplankton biomass. The lakes that showed the most deviation from the predicted linear zooplankton-phytoplankton relationship were generally those with the highest catches of fish per trap, demonstrating again the influence of planktivores, most particularly vertebrate planktivores, on zooplankton biomass.

Lake morphometry also has some influence on the zooplankton community in the Avalon lakes. The community structure component '*Diaptomus* vs *Daphnia*' was negatively related to 'lake size' (the proportion of *Daphnia* in terms of species composition thus increasing with increasing lake size), while 'medium size' zooplankton was positively related to 'lake size'. Similarily, Sprules (1980) found zooplankton communities to be dominated by larger zooplankton species as lake size increased in Ontario lakes. Vertebrate predation pressure may be higher in small, shallow lakes than in larger, deeper lakes since predators and prey have elevated chances of encountering one another when restricted to shallower lakes. As mentioned above, analyses of stickleback diet in the Avalon lakes showed the medium-sized cladoceran *D. catawba* to be the preferred stickleback prey item. Hence, the observed relationships between zooplankton community structure and lake morphometry might reflect increased predation pressure on such medium-sized zooplankters in the smaller, shallower lakes.

The observed influences of vertebrate and invertebrate planktivores on the zooplankton community in the Avalon lakes, as evaluated by the PCA and MLR procedures, are generally confirmed by results obtained with the alternative procedure of clustering and discriminant analyses. Following these analyses, stickleback catch was noted to have some influence on total zooplankton biomass based on univariate models, although vertebrate planktivore abundance did not enter as a significant discriminating variable and was not a major influence on zooplankton community structure. Total invertebrate planktivore density did not significantly influence either total zooplankton biomass or community structure. Since only a subset of the environmental variables were employed in the discriminant analysis method as opposed to the multiple linear regression method, there are differences observed in the specific environmental factors that are seen as significant by each method. Measures of ionic strength, nutrient concentrations and development in the watershed were found by both methods to be significant influences on % species composition. Measures of nutrient concentrations and lake size and area were found by both methods to be significant influences on % size distribution.

The slightly different results obtained by the different multivariate procedures (PCA and MLR versus clustering and discriminant analysis) reflect some of the problems associated with these multivariate analyses. Both principal components and clustering methods, by mathematically "forcing" a number of variables into a smaller number of components or groups, will necessarily tend to account for less than 100% of the variance explained by the original uncombined data. Subsequent multivariate analyses will only compound this problem of decreased explained variance. Differences in assumptions of multiple regression and discriminant analysis may lead to some contrasts in final results between these procedures. MLR assumes a linear relationship between the dependent (zooplankton) and independent (planktivore and environment) variables, which seems roughly to hold true in this study as evidenced by observed plots between predicted variables and residuals. Small deviations from linearity based on only a few independent variables, however, could be compounded in the overall multivariate model, and lead to decreases in explained variance. Discriminant analysis assumes a linear relationship only among the independent variables themselves, but is heavily influenced by the initial choice of the number of clusters; this choice cannot be judged statistically (Davies 1984). Hence, such multivariate procedures may end up explaining only a small proportion of the variance associated with the original data, although results from such procedures, by taking data collinearity into account, are often more clearly indicative of trends in the data structure than are more complex results derived straight from the original data. In this sense, the multivariate analyses in this study have been used as exploratory tools to determine the relative influence of vertebrate and invertebrate predation on the zooplankton community, rather than as predictive models demonstrating the exact strengths of the predator influence. Such analyses illuminate structure in the data and serve to confirm or refute patterns that are expected based on results from previous experiments or manipulations. Confirmatory results observed between the separate multivariate procedures strengthen the conclusion of this study that, despite expectations of the importance of planktivory in these shallow, oligotrophic and depauperate Avalon lakes, vertebrate and invertebrate planktivores are not dominant influences on pelagic zooplankton community structure, although stickleback abundance may have an influence on total zooplankton biomass.

The relative importance of planktivore abundances and various environmental and limnological variables as influences on zooplankton communities of oligotrophic and mesotrophic lakes in physiographically homogeneous regions has also been examined in a small number of other studies. In a set of 8 small subalpine lakes in Colorado, Sprules (1972) observed two distinct zooplankton communities, differentiated by both species composition and size distribution. Large herbivores such as *Daphnia pulex*, *Diaptomus shoshone* and *Branchinecta shantzi* (adult lengths of 2.28, 2.47 and 1.0 - 16.0 mm, respectively) were found only in shallow lakes or ponds which lacked the two major planktivores, a *Chaoborus* sp. and the planktivorous axolotl (neotenic *Ambystoma tigrinum*). Small herbivores such as *Diaptomus coloradensis* and *Daphnia rosea* (mean adult lengths 1.35 and 1.61 mm, respectively) co-existed in deep lakes with the two planktivores. Only the distribution of the large *D. pulex* seemed to be influenced by lake physicochemical variables. In contrast, both Anderson (1971), working on 146 alpine and subalpine lakes in the Canadian Rockies, and Dodson (1979), working on 36 tundra ponds in Alaska, concluded that presence and absence of zooplankton species was limited mainly by lake temperature, morphometry and chemistry. Anderson also found that the distributions of certain large zooplankton species were negatively influenced by the presence of large vertebrate planktivores, particularly salmonids, while Dodson suggested that avian planktivores might be important as well. In none of these studies, however, was the relative influence of planktivore abundances more stringently examined through multivariate analyses.

Sprules (1975) used MLR analysis to relate numbers of zooplankton species to a number of vertebrate planktivore and limnological variables in 47 acidic to neutral (pH 3.8 - 7.0) lakes in Ontario. Increased zooplankton species diversity was significantly related to increases in the combined number of planktivorous and piscivorous fish, increasing lake pH, increasing lake perimeter, and decreasing lake mean breadth, the latter two being measures of increasing littoral zone influence. Sprules postulated that zooplankton species diversity was higher in lakes with high pH due to the presence of numerous acid-intolerant zooplankters and also due to the reduced interspecific competition between the zooplankton that might result from increased selective predation (fish diversity also increased with increasing pH) leading to more diverse prey associations. Increased proportion of littoral habitat in the lakes might also lead to higher zooplankton species diversity through increased diversity of planktivorous fish, many of which are littoral (e.g. centrarchids and cyprinids), and hence increased selective predation. When the effect of pH was factored out through partial correlation, the number of planktivorous fish species by itself was seen to account for a significant proportion of the variance in zooplankton species number. Sprules cautioned, however, that the unusually large pH gradient observed in his study might obscure observation of other factors that could also influence zooplankton community structure.

Using similar data from 23 non-acidic Ontario lakes, Holtby (1981) constructed models relating measures of zooplankton community size structure to various limnological and fish species factors. The abundance of zooplankton was negatively influenced by abundance of planktivorous fish (mainly the yellow perch, *Perca flavescens*), although this was not the primary influence. Increased abundance of large zooplankton > 1.2 mm in length, described by a principal component similar to the Avalon lake component 'large > 1.26', was significantly related in a MLR model to increasing lake pH, increasing metalimnion thickness, decreasing abundance of planktivorous fish, decreasing density of large seston, and decreasing temperature of the epilimnion. Average zooplankton size was also significantly smaller in the presence of abundant planktivorous fish. Increased abundance of zooplankton up to 1.2 mm in length, described by a principal component similar to the Avalon lake component 'medium size', was significantly related to decreasing width of the metalimnion, decreasing nitrogen/phosphorus ratio, increasing lake depth, decreasing particle loss rates from the epilimnion, decreasing abundance of planktivorous fish, and increasing lake size. With the exception of planktivorous fish abundance, all the independent variables in the MLR models could be related to lake productivity: small, shallow, high pH lakes with large littoral areas were generally more productive than deeper and larger lakes and had higher epilimnetic temperatures and particle loss rates in the epilimnion, higher nitrogen/phosphorus ratios, greater abundance of large seston, and narrower metalimnia. Width of the metalimnion, a measure of lake thermal structure, might also relate to planktivory since a wide metalimnion that extends beyond the photic zone can be used by large zooplankters as a refugium from visual planktivores (O'Brien 1979).

Holtby concluded that the relative importance of planktivores in his models was less than the importance of general lake productivity and thermal structure. Nonetheless, as in the Avalon study, neither measures of planktivore abundance nor resource levels by themselves could convey as much information about the zooplankton community as could a combination of such "top-down" and "bottom-up" controls. Increased lake productivity and metalimnion size, combined with decreasing numbers of planktivorous fish, together led to increases in abundance of large zooplankton and were the major factors affecting zooplankton size structure. Stoddard (1987), working on 75 high elevation lakes in California, also found that zooplankton communites (based on species composition) could be best distinguished through cluster analysis and MLR by a combination of "top-down" and "bottom-up" variables, as well as morphometric variables. While fish (predominantly salmonid) presence was the single best predictor of community type, with a strong negative effect on the distribution of large zooplankton species, the other variables of lake phosphate concentrations, % volcanic bedrock in the lake basin, lake elevation and lake depth also significantly affected the distribution of various zooplankton species.

Results from the Avalon lakes then are in accordance with these studies in demonstrating that planktivores, particularly vertebrates, can have a impact on zooplankton communities of oligotrophic lakes, by generally reducing the biomass of medium and large zooplankton species. Predation exerted by threespine stickleback populations in the Avalon lakes, however, may not be as strong as that exerted by yellow perch (Holtby 1981) or salmonid (Anderson 1971; Stoddard 1987) populations in other lakes since most of the measures of community structure in the Avalon lakes were not strongly related to stickleback catch. Perhaps stickleback densities in the Avalon lakes are simply too low to markedly affect zooplankton species composition or size distribution. Absolute fish densities could not be determined from the studies of Anderson (1971), Holtby (1981) or Stoddard (1987). Estimates of stickleback densities in the Avalon lakes through catch per unit effort data (Appendix B) indicated that densities ranged from 0 to 4423 fish per hectare, with Middle Three Island Pond having the highest densities. Calculated stickleback biomass in each lake was < 10% of the combined planktivore plus plankton biomass except for Hogans

Pond (11%) and Middle Three Island Pond (57%). Zooplankton species- and size-specific responses to predation stress may show greater variability than do responses shown by entire trophic levels (e.g. total zooplankton biomass) and hence, higher predation intensities may be required to effect changes in community structure (see Carpenter 1989). The impact of selective predation may be negated by differential reproduction rates of zooplankton species, as well as by size-specific growth and reproduction rates within each species (Lynch 1983). In the Avalon lakes, only *Holopedium* was observed to have reproduction rates (number of eggs per ovigerous female) that differed among lakes with different predator abundances. Although salmonids *Salvelinus fontinalis*, *Salmo trutta* and *Salmo salar* were also present in the Avalon lakes (Scott and Crossman 1964), they appear to be mainly benthivorous rather than planktivorous (Baggs 1989).

The present Avalon study also indicates that the negative influence of invertebrate planktivores on zooplankton communities of oligotrophic lakes is much less than the negative influence of vertebrate planktivores. Seasonality in invertebrate planktivory may render invertebrate predation generally insufficient to cause significant changes in either the timing or magnitude of seasonal peaks in abundance of many zooplankters, e.g. *Daphnia* spp. (Threlkeld 1987*b*). Predation avoidance behaviour (vertical migration) of *Daphnia galeata mendotae* may also be manifested more strongly in the presence of fish than of *Chaoborus* (Leibold 1990). Cases in which invertebrate planktivory has been observed to be an especially strong negative influence on zooplankton communities appear to be restricted to nutrient-rich systems, in which early life stages of the planktivores are not food-limited (Neill and Peacock 1980), or to systems in which fish predation on the invertebrate planktivores is minimized due to acidic lake conditions (Nyberg 1984; Sprules 1975; Yan *et al.* 1991) or winter-kill of fish (especially prominent in high altitude lakes which may freeze to the bottom, Sprules 1972) limiting fish populations. Invertebrate planktivory may also be strong in lakes with high turbidity levels that impede visual predation of the invertebrates by vertebrate predators (Costa and Cummins 1965; Cummins *et al.* 1969). The positive correlation of invertebrate planktivore density with nutrient and resource levels in the Avalon lakes, and the significant relationship between decreasing small zooplankton biomass and increasing lake productivity, seems to accord with the importance of nutrient and phytoplankton availability as limits to the production of early life stages of the invertebrate planktivores and the consequent number of planktivorous adults that survive to prey on small zooplankton. The negative relationship between stickleback distributions and the distributions of the invertebrate planktivores, particularly *Chaoborus*, agrees with the importance of fish predation as an influence on invertebrate density and consequent invertebrate planktivory.

Finally, this Avalon study indicates that, even in shallow and oligotrophic lakes in which predation would be expected to have a major impact on the zooplankton community due to low faunal diversity and low habitat heterogeneity of the lakes, planktivore abundance is not the primary influence on zooplankton biomass and community structure. Reports that stress the importance of planktivores as major control agents for zooplankton communities often have either not evaluated such control against these other limnological factors (e.g. Nilsson and Pejler 1973; Pope and Carter 1975), have used manipulative experiments with often unrealistically high predator densities (e.g. Hrbáček *et al.* 1961; Hall *et al.* 1970; Kajak and Rybak 1979; Lynch 1979; Post and McQueen 1987; Vanni 1988), or have looked at newly introduced predators over short time periods (e.g. Brooks and Dodson 1965; Carpenter *et al.* 1987; Elser *et al.* 1987). Such studies ignore the complex interactions between various limnological conditions and trophic levels (demonstrated in factorial experiments by Vanni 1987; Mazumder *et al.* 1988; Threlkeld 1988; Drenner *et al.* 1989; Lancaster and Drenner 1990) that can arise when a predator has become incorporated over a long time period into a lake system (Neill 1981; Thorp 1986; Mills and Forney 1988; Leibold 1989). Over these longer periods, the impact of strong "top-down" forces on the zooplankton community may be balanced by the development of producer-driven feedback loops which involve competition among the zooplankton prey for available food and the consequent regulation of trophic level production by "bottom-up" forces (Mills and Forney 1988). For example, removal of one prey species by predation may result in an increase in abundance of another prey species, given that the two prey species are competing for a shared food resource.

Relative proportions of competing edible and inedible algal species may also vary, depending on herbivore pressure, and these changes in food resources may in turn influence the herbivore community (Leibold 1989). Ultimately, the strength of these "top-down" and "bottom-up" forces is a function of lake trophy - i.e. the impact of fish planktivory seems to be more important in oligotrophic lakes (Gliwicz and Prejs 1977). Wide fluctuations in annual population abundances occasioned by climatic and other short-term disturbances need also to be taken into account (Harris 1986; Carpenter 1989).

This study's use of comparative multivariate analyses in a holistic examination of community patterns in aquatic systems thus definitely indicates that the importance of vertebrate and invertebrate predation cannot be taken out of context from the other factors that also influence the biomass and community structure of the pelagic zooplankton community.

Chapter 6

General Summary

"... one of the things most evidently designed is that a large proportion of all animals should pass their existence in tormenting and devouring other animals."

Mill (1874)

1. The major planktivores in 15 lakes on the Avalon Peninsula of Newfoundland are the vertebrate *Gasterosteus aculeatus* (the threespine stickleback) and the invertebrates *Chaoborus punctipennis*, *C. trivittatus* and *Leptodora kindtii*. Noticeably absent, as a probable result of the physical isolation of the island of Newfoundland, are other planktivores such as cyprinids and centrarchids and some predatory copepods that are common in lakes in mainland Canada.

2. The pelagic zooplankton fauna of the Avalon lakes is also depauperate; species commonly found are *Daphnia catawba*, *Eubosmina longispina*, *Holopedium gibberum*, *Leptodiaptomus minutus*, *Epischura nordenskioldi*, *Cyclops scutifer* and the rotifers *Keratella* and *Kellicottia* spp. and *Conochilus unicornis*. Low species diversity of zooplankton and zooplankton predators suggests that predatory interactions should be strong and direct and not confounded by a interconnected web of species interactions. Low habitat heterogeneity of the lakes also suggests that predatory interactions should not be confounded by the presence of prey refugia. These Avalon lakes are therefore excellent systems for the study of planktivore influence on the zooplankton community.

3. *G. aculeatus* was found in 10 of the 15 lakes, *C. punctipennis* in 6, *C.*

trivittatus in 2 and *L. kindtii* in 10 (1987 data). Mean 1987 spring + late summer stickleback catch per trap ranged from 0.0 (undetectable) to 70.6 over the 15 lakes. Late summer densities of *C. punctipennis*, *C. trivittatus* and *L. kindtii* ranged from 0 to 576, 0 to 311, and from 0 to 127 animals-m^{-3}, respectively, over the 15 lakes.

4. The planktivores were not distributed independently of each other. Distribution patterns of *Chaoborus*, particularly *C. trivittatus*, in the Avalon lakes were suggestive of predatory exclusion by sticklebacks. Sticklebacks were observed to eat *Chaoborus* larvae in laboratory experiments. There was no relationship between the distribution patterns of stickleback and *Leptodora*, and sticklebacks did not readily take *Leptodora* in laboratory experiments. *Leptodora* and *C. punctipennis* were distributed independently of each other. However, *C. trivittatus* was never found in lakes with *Leptodora*. Predation by the predatory cladoceran on early instars of *C. trivittatus*, but not on the more transparent *C. punctipennis*, might account for this pattern.

5. Distribution of the planktivores was also influenced by environmental variables. One principal component could be derived from the combined planktivore data. Environmental data for the lakes were condensed into 4 chemical components, 2 morphometric components, 3 watershed components and 3 plankton (phytoplankton + zooplankton) components. With the environmental components as independent variables in multiple linear regression (MLR) models, the 'planktivore' component was found to be significantly related to the plankton component 'copepods'. Breakdown of this relationship revealed that stickleback catch per trap was significantly and negatively related to cyclopoid biomass, an indication of possible "top-down" control, while *Chaoborus* density was significantly but positively related to cyclopoid biomass, an indication of possible "bottom-up" control. *Leptodora* density was most related to the biomass of large 'inedible' phytoplankton, although the relationship was not significant.

6. Examination of the gut and crop contents of sticklebacks and *Chaoborus* larvae indicated that these planktivores can all be considered to be major predators of zooplankton in the Avalon lakes since a major proportion of the diets of these species

are made up of pelagic zooplankton. *G. aculeatus* and *Chaoborus* showed definite and contrasting prey selectivity in their choice of zooplankton prey and hence have the potential to exert strong and contrasting influences on the species composition and size distribution of the zooplankton community. The sticklebacks seemed to select for zooplankton > 0.76 mm in length, predominantly the cladoceran *D. catawba*. *Chaoborus* seemed to select for smaller zooplankton < 0.50 mm in length, predominantly the cladoceran *E. longispina*. Based on the literature, the fluid-sucking *Leptodora* has a diet similar to that of *Chaoborus*.

7. The abundance of the vertebrate planktivore, *G. aculeatus*, had a significant negative relationship with total zooplankton biomass, while the density of the invertebrate planktivores, *Chaoborus* and *Leptodora*, did not. Relationships between total invertebrate planktivore density and zooplankton biomass were either not significant or were weakly positive, never negative as would be indicative of predator control limiting prey abundance. Stickleback abundance explained more of the variance in zooplankton biomass than did the composite 'planktivore' component, most likely due to interactions between sticklebacks and *Chaoborus* which led to 'planktivore' accounting for only 57% of the variance in the combined planktivore data, while the contrasting diets of stickleback and invertebrate planktivores would also lessen the amount of overall variance in the biomass relationship explained by 'planktivore'.

8. Total zooplankton biomass was not significantly related to total phytoplankton biomass in the Avalon lakes. Of the community structure measures, only the biomass of rotifers and small cladocerans (described by the principal component 'lack of small herbivores') was related to phytoplankton biomass, with a significant positive relationship in a single regression model.

9. In a MLR model with stickleback catch, total invertebrate planktivore (*Chaoborus* + *Leptodora*) density, and environmental principal components (3 plankton components replaced by one phytoplankton component) as independent variables, increasing total zooplankton biomass was significantly related to decreasing stickleback density and increasing ionic strength. Total invertebrate planktivore density did not enter as a significant variable.

10. Stickleback catch entered only once as a significant influence on zooplankton community structure, with increasing 'medium size' significantly related to increasing 'TKN', decreasing stickleback catch and increasing 'lake size'. Invertebrate planktivore density again did not enter as a significant variable. Principal components describing lake productivity (development in the watershed, number of upstream lakes, lake flushing rate, and summer phosphorus levels) could explain a large proportion of the variance in the community structure measures.

11. The biomass of large zooplankton increased, and the biomass of small zooplankton decreased, with increasing lake productivity (development in the watershed and lake summer phosphorus levels). However, the density of invertebrate planktivores was significantly and positively correlated with lake productivity (spring phosphorus levels and phytoplankton biomass) indicating that the decreases in biomass of small zooplankton might be partially attributable to increasing invertebrate planktivory with the increasing lake productivity. Lack of a significant relationship between total zooplankton biomass and total phytoplankton biomass also indicates that lake productivity is not the only factor influencing the zooplankton community.

12. Clustering procedures and discriminant analysis generally concurred with the PCA and MLR procedures in demonstrating that neither stickleback catch nor total invertebrate planktivore density are predominant influences on zooplankton biomass and community structure, although stickleback catch did influence total zooplankton biomass in a univariate analysis of variance. Patterns in mean size class frequencies of the zooplankton community also showed no distinct differences between lakes with no sticklebacks (Bauline and Piccos Ponds) and lakes with high stickleback catch (Middle Three Island, Three Island and Tors Cove Ponds). Of the three cladocerans (*D. catawba*, *Eubosmina longispina* and *H. gibberum*), only *H. gibberum* showed significantly higher mean egg number per ovigerous female in the lakes with high stickleback catch compared with the lakes without sticklebacks. However, the low prey selectivity shown by stickleback for *Holopedium* indicates that the difference in egg production is due to causes other than predation.

13. The influence of vertebrate planktivores on the zooplankton community of the Avalon lakes is thus more noticeable than that of invertebrate planktivores. Interactions between the vertebrate and invertebrate planktivores, reflected in distribution patterns of the species, coupled with the observed contrast in prey selectivities, weakens the cumulative impact of the predators.

14. The correlations between planktivore abundances and lake productivity components demonstrate that the zooplankton community is not influenced solely by "top-down" or "bottom-up" control, but by a combination of the two. The impact of vertebrate planktivory may be relatively more important in oligotrophic lakes than in eutrophic lakes, but still the impact cannot be said to be paramount, even in the shallow, oligotrophic Avalon lakes with their low faunal diversity and habitat heterogeneity.

Chapter 7

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Appendix A

Appendix Tables

Table A.1. Pearson product-moment correlations among all environmental principal components for the Avalon lakes. Complete chemical principal components were available for only 13 lakes; otherwise sample size = 15. Significance levels of the correlation coefficients are indicated by * ($0.01 < p < 0.05$), ** ($0.005 < p < 0.01$) and *** ($p < 0.005$).

	Ionic strength	Summer P	Spring P	TKN	Lake size	Flushing rate	Develop-ment	% barren	% upstream lakes	edible phyt.	cope-pods	herb-vores	phyto-plank
Ionic strength	1.000	0.062	0.012	-0.045	-0.150	0.134	0.848 ***	0.282	-0.198	0.246	0.029	0.505	0.283
Summer P		1.000	-0.009	-0.004	0.206	0.785 ***	-0.042	0.745 ***	0.224	0.048	-0.505	0.599 **	0.178
Spring P			1.000	-0.028	0.080	0.035	0.049	-0.456	-0.129	0.668 *	0.120	-0.106	0.647
TKN				1.000	0.017	-0.311	-0.156	0.127	-0.463	0.235	0.207	0.112	0.229
Lake size					1.000	0.000	-0.228	-0.343	-0.034	-0.224	-0.231	0.085	-0.147
Flushing rate						1.000	0.126	0.441	0.531 *	0.010	-0.605	0.176	0.066
Develop-ment							1.000	0.000	0.000	0.290	0.171	0.379	0.317
% barrens								1.000	0.000	-0.280	-0.313	-0.639 **	-0.143
% upstream lakes									1.000	0.005	-0.250	-0.409	-0.025
edible phyt.										1.000	0.000	0.000	0.981 ***
Cope-pods											1.000	0.000	-0.026
Herbi-vores												1.000	0.169
Phyto-plankton													1.000

Table A.2. Linear regression equations relating total lengths of some zooplankton species in the Avalon lakes to lengths of body parts. Sample size = 15 for all regressions. Magnification refers to level of magnification at which body parts were measured. Lengths are in mm.

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1) Daphnia catawba:

Body length = 6.70(length postabdominal claw) + 7.00
$r^2 = 0.89$, 50X magnification

2) Eubosmina longispina:

Body length = 4.00(length postabdominal claw) + 17.67
$r^2 = 0.81$, 50X magnification

Body length = 1.54(length helmet) + 1.95
$r^2 = 0.67$, 25X magnification

3) Diaptomus minutus:

Body length = 1.12(length cephalothorax) - 0.24
$r^2 = 0.97$, 25X magnification

Table A.3. % occurrence of pelagic microcrustacean species found in gut contents of *Gasterosteus aculeatus* sampled in fall (f) 1986, spring (s) 1987 and late summer (ls) 1987 from the Avalon lakes. Daph refers to *Daphnia catawba*, Holo to *Holopedium gibberum*, Bosm to *Eubosmina longispina*, Diap to *Leptodiaptomus minutus*, Epi to *Epischura nordenskioldi*, naup to copepod nauplii and Cyc to *Cyclops scutifer*. Lakes are labelled by a two letter code as in Figure 2.1.

Lake	Yr	Daph	Holo	Bosm	Diap	Epi	naup	Cyc
He	1986f	68	1	24	1	5		
	1987s	4		92	4			
	1987ls	75		25				
Ho	1986f	12	19	69				
	1987s			77	13			10
	1987ls	100						
Mi	1987s	15		49	29	3		3
	1987ls	73		14	14			
Mu	1986f	13		47	7	28	1	3
	1987s	8						92
	1987ls	97			1	2		
Pa	1987s	13	77		9	1		
	1987ls	91						9
Qu	1986f	62		20	13	1		3
	1987s	11		14	18	4	1	53
	1987ls	63			6	23		9
Ro	1987s	8	62	23	8			
Se	1986f	83	7		1	7		2
	1987s	55			33	9		3
Ti	1986f	91		5		3		
	1987s	26		63	3	9		
	1987ls	97		3				
To	1986f	31		47	8	13		1
	1987s			100				
	1987ls	5	1	93		1		

Table A.4. % abundance of pelagic microcrustacean species in zooplankton communities sampled in fall (f) 1986, spring (s) 1987 and late summer (ls) 1987 from the Avalon lakes. Species labels are as Table A.3, lake labels are as in Figure 2.1.

Lake	Yr	Daph	Holo	Bosm	Diap	Epi	Naup	Cyc
He	1986f	17	3	6	49	20	3	
	1987s	2	22	11	60	1	3	
	1987ls	55	14	7	20	1	2	
Ho	1986f	2	6	55	28	4	5	
	1987s		4	51	42	1	1	1
	1987ls		35	12	40		13	
Mi	1987s	1	1	9	40		49	1
	1987ls	1	1	10	54	1	33	
Mu	1986f	20		62	3	10	1	3
	1987s	6		5	11		68	10
	1987ls	85			4	9	2	
Pa	1987s	6	19	53	19		3	
	1987ls	22	15	19	37	2	4	1
Qu	1986f	63		2	33	1	1	
	1987s	24	1	1	21	7	9	38
	1987ls	43		1	48	1	7	
Ro	1987s	1	63	17	16		3	
Se	1986f	20	19		48	13		
	1987s	25	10	9	33	16	4	2
Ti	1986f	26	3	3	56	4	8	
	1987s	8	19	22	39	5	8	
	1987ls	32	15	45	7	1		
To	1986f	9		27	56	4	2	1
	1987s	9	5	53	30	1	2	1
	1987ls	14	2	6	69	1	6	2

Table A.5. Mean lengths (mm) of pelagic microcrustacean species found in gut contents of Gasterosteus aculeatus sampled in spring (s) and late summer (ls) 1987 from the Avalon lakes. Zooplankton measurements encompass preadult and adult cladocerans and copepodite and adult copepods. Species labels are as in Table A.3, lake labels are as in Figure 2.1.

Lake	Yr	Daph	Holo	Bosm	Diap	Epi	naup	Cyc
He	1987s	0.808		0.470	0.808			
	1987ls	1.110		0.636				
Ho	1987s			0.533	0.520			0.539
	1987ls	1.155						
Mi	1987s	1.142		0.430	0.732	1.174		0.713
	1987ls	1.143		0.360	0.642			
Mu	1987s	1.155						0.833
	1987ls	1.223			0.578	1.040		
Pa	1987s	1.204	0.956		0.712	1.078		
	1987ls	0.859						0.655
Qu	1987s	0.655		0.356	0.447	1.040		0.606
	1987ls	0.963			0.462	1.112		0.539
Ro	1987s	0.655	0.818	0.347	0.616			
Se	1987s	0.966			0.710	1.040		0.617
Ti	1987s	1.241		0.539	0.578	1.219		
	1987ls	0.963		0.385				
To	1987s			0.485				
	1987ls	0.770	0.578	0.462		0.905		

Table A.6. Mean lengths (mm) of pelagic microcrustacean species in zooplankton communities sampled in spring (s) and late summer (ls) 1987 from the Avalon lakes. Species measurements encompass preadult and adult cladocerans and copepodite and adult copepods. Species labels are as in Table A.3, lake labels are as in Figure 2.1.

Lake	Yr	Daph	Holo	Bosm	Diap	Epi	naup	Cyc
He	1987s	0.810	0.833	0.300	0.480	1.113	0.190	
	1987ls	0.910	0.921	0.359	0.527	1.215	0.184	
Ho	1987s		0.448	0.256	0.522	1.150	0.142	
	1987ls		0.501	0.326	0.405		0.184	
Mi	1987s	0.680	0.440	0.211	0.291		0.183	0.250
	1987ls	0.600	0.630	0.198	0.421	1.100	0.148	
Mu	1987s	0.960		0.338	0.317		0.173	0.355
	1987ls	0.910			0.525	1.032	0.130	
Pa	1987s	1.029	0.990	0.274	0.507		0.134	
	1987ls	0.997	0.944	0.283	0.559	1.063	0.195	
Qu	1987s	0.696	0.830	0.285	0.546	1.095	0.189	0.247
	1987ls	0.926		0.530	0.376	1.165	0.154	
Ro	1987s		0.411	0.185	0.310		0.183	
Se	1987s	0.891	0.664	0.380	0.677	1.015	0.230	0.360
Ti	1987s	0.791	0.509	0.239	0.445	0.947	0.201	
	1987ls	0.837	0.902	0.290	0.501	1.026		
To	1987s	0.692	0.755	0.290	0.355	0.870	0.248	0.600
	1987ls	0.709	0.844	0.326	0.465	0.880	0.175	0.940

Table A.7. % occurrence of zooplankton species found in crop contents of *Chaoborus* larvae (*C. punctipennis* + *C. trivittatus*) with % abundance of zooplankton in zooplankton communities sampled in August 1988 and 1989 from the Avalon lakes. Species labels are as in Table A.3, 'rot' refers to rotifer spp. Lake labels are as in Figure 2.1.

Lake	Yr	Daph	Holo	Bosm	Diap	Epi	naup	Cyc	rot
1. Crop contents									
Ba	1988			22	22		11		44
	1989	23		23	31				23
Lo	1989	27		36	18				18
Oc	1989	33		7	13				47
Pi	1988			21	7		10		62
	1989			17	5		2	2	72
2. Zooplankton communities									
Ba	1988	10	1	9	31		7		42
	1989	12		3	50		21	1	13
Lo	1989	14	30	3	17	3	22		11
Oc	1989	22	1	1	26	1	37	12	1
Pi	1988	9	2	4	16		52		17
	1989	1	13	2	4		30	1	49

Table A.8. Mean lengths (mm) of zooplankton species found in crop contents of *Chaoborus* larvae (*C. punctipennis* + *C. trivittatus*) and in zooplankton communities sampled in August 1988 and 1989 from the Avalon lakes. Zooplankton measurements encompass preadult and adult cladocerans and copepodite and adult copepods. Species labels are as Tables A.3 and A.7, lake labels are as in Figure 2.1.

Lake	Yr	Daph	Holo	Bosm	Diap	Epi	naup	Cyc	rot
1. Crop contents									
Ba	1988			0.342	0.390		0.117		0.112
	1989	0.812		0.527	0.429				0.104
Lo	1989	0.871		0.408	0.458				0.108
Oc	1989	0.642		0.577	0.332				0.133
Pi	1988			0.413	0.390		0.143		0.103
	1989			0.429	0.371		0.195	0.468	0.119
2. Zooplankton communities									
Ba	1988	1.021	0.924	0.462	0.491		0.193		0.157
	1989	1.087		0.440	0.531		0.193	0.308	0.154
Lo	1989	1.032	1.163	0.411	0.514	0.992	0.231		0.154
Oc	1989	0.870	1.079		0.592	1.232	0.193	0.361	0.193
Pi	1988	0.953	0.704	0.412	0.456		0.194		0.154
	1989	0.789	0.948	0.380	0.544		0.231	0.408	0.117

Appendix B

Estimation of planktivore biomass in the Avalon lakes

1. Stickleback

In August 1988, a two-week programme of fish catch and removal was undertaken to estimate the biomass of a population of threespine stickleback in a small (5.1 ha) and shallow (approx. 2 m maximum depth) Avalon pond, with biomass calculations extrapolated to give estimates of stickleback biomass in the 15 larger Avalon study lakes. The pond under investigation, Topsail Round Pond, has no visible inflow and drains out only intermittently (i.e. during periods of heavy rain) through a culvert into Three Island Pond. Consequently, sticklebacks in Topsail Round Pond were restricted to the pond; hence, a method of population estimation such as catch and removal (Leslie's method; Ricker 1975) that assumes no migration of individuals can validly be used.

A total of 56 liver-baited minnow traps, of which 6 were later discarded as they were found to be ineffectual in catching fish, were used to sample the pond for threespine stickleback from August 17 to August 30. Five trap strings were employed around the pond, with 9, 14, 13, 9 and 8 traps per string (3 traps were set out individually). The traps were set out at roughly equal intervals along the trap strings, from the shore to the deepest part of the pond that could be reached based on trap string length. All the traps were examined during the morning and evening every day for the first week, then on the morning of every second day for the next week. Fish found in the traps were enumerated, then placed in large buckets filled with pond water and transferred to Three Island Pond. Once in Three Island Pond, the sticklebacks were unable to return to Topsail Round Pond.

Through this constant removal of sticklebacks from Topsail Round Pond, the size of the total population of stickleback in the pond can be estimated by the principle of diminishing returns. When catch per unit effort (CPUE) drops to zero, all the stickleback in the pond are assumed to have been trapped. Extrapolation to the x axis of the slope of the linear regression of CPUE (number of fish caught per trap per hours fished) versus cumulative catch (Figure B.1.) thus gives an estimate of the total number of stickleback caught when CPUE drops to zero. For Topsail Round Pond, the total number of stickleback in the pond was calculated to be 4981 fish or 976.73 fish-ha^{-1}. The initial catch of 773 fish (Figure B.1) per 50 traps (15.46 fish-trap^{-1}) therefore is associated with a per hectare catch of 976.73 sticklebacks. From these data, a conversion factor of 63.18 (976.73 divided by 15.46) can be generated to convert initial stickleback catch per trap in the 15 Avalon lakes to stickleback abundance per hectare.

To determine stickleback wet weight biomass per hectare, the number of fish per hectare was multiplied by the approximate mean wet weight for threespine stickleback in each lake. These mean weights were based on the weights of a subset of the sticklebacks that were trapped in each lake. Total lengths (tip of snout to end of tail) of these fish had been measured (see Chapter 3) and these lengths (mm) were converted to wet weight biomass (g) by the length-weight regression:

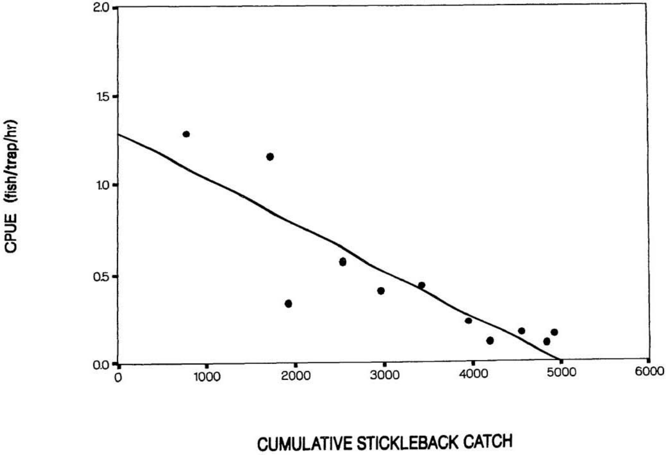
$$\text{Wet weight} = 8.22 \times 10^{-6}(\text{Length})^{3.01}$$

for *Gasterosteus aculeatus* as calculated by Wootton (1976). Given lake depths and surface areas previously determined (Knoechel and Campbell 1988), an overall estimate of mean stickleback biomass per m^3 (mean of spring and late summer samples) could then be generated (Table B.1).

2. *Chaoborus* spp. and *Leptodora*

Estimates of the wet weight biomass per m^3 of *Chaoborus* larvae and *Leptodora* were determined from length-dry weight regressions, with dry weight multiplied by 10 to give wet weight (Bottrell *et al.* 1976). In 1987, total lengths of *Chaoborus*

Figure B.1. Cumulative stickleback catch versus catch per unit effort ($CPUE$ in fish-trap^{-1}-hr^{-1}) for Topsail Round Pond. The solid line represents the calculated regression equation: $CPUE = -2.592 \times 10^{-4} Catch + 1.292$, $r^2 = 0.77$, with the x intercept of 4981 stickleback.


2.0
1.5
1.0
0.5
0.0
CPUE (fish/trap/hr)
0
1000
2000
3000
4000
5000
6000
CUMULATIVE STICKLEBACK CATCH

(from anterior tip of head to base of anal tubules) and *Leptodora* (from anterior tip of head to base of tail spines) were measured in all samples, except for Piccos Pond in late summer where only a subset of the chaoborids were measured with the biomass of this subset extrapolated to the whole sample.

Chaoborus dry weight biomass (μg) for both *C. punctipennis* and *C. trivittatus* were determined from lengths (mm) with the equations of Pawson and McEachern (1987):

$$\text{Weight} = 0.148(\text{Length})^{3.31}$$
$$\text{Weight} = 0.372(\text{Length})^{2.97}$$

for 3rd and 4th instars of *C. punctipennis*, respectively. These instars of *C. punctipennis* made up the majority of the chaoborids sampled in both spring and later summer samples (see Chapter 3).

Leptodora dry weight biomass (μg) was determined from lengths (mm) with the equation of Rosen (1981):

$$\text{Weight} = 0.44(\text{Length})^{2.67}$$

Mean (spring and late summer) wet weight biomass for *Chaoborus* spp. and *Leptodora* combined are compared to stickleback biomass in the Avalon lakes in Table B.1.

3. Total lake biomass

Summing together mean phytoplankton biomass, mean zooplankton biomass, mean threespine stickleback biomass and mean invertebrate planktivore (*Chaoborus* spp. + *Leptodora*) biomass gives estimates of total lake biomass that range from 703 mg-m^{-3} in Three Island Pond to over 4500 mg-m^{-3} in M.U.N. Long and Piccos Ponds (Table B.1). These estimates do not take into account biomass potentially contributed

Table B.1. Mean (spring and summer) 1987 wet weight biomass (mg-m^{-3}) estimates of phytoplankton (Phyt), zooplankton (Zoop), threespine stickleback (Stick) and total invertebrate planktivores (*Chaoborus* spp. + *Leptodora*, = Invert) in the 15 Avalon lakes, with the total sum of these biomass components (Total) for each lake.

Lake	Phyt	Zoop	Stick	Invert	Total
Bauline	553.67	390.53	0	83.47	1027.67
Healeys	788.33	487.74	1.00	9.53	1286.60
Hogans	862.50	345.57	145.73	12.42	1366.22
Long	354.50	523.52	0	10.19	888.21
Middle 3 Island	723.67	175.03	1190.50	0	2089.20
MUN Long	3528.17	1127.06	2.08	2.50	4659.81
Octagon	518.50	400.16	0	8.16	926.82
Paddys	893.17	217.03	56.06	4.87	1171.13
Piccos	2427.00	941.40	0	1154.70	4523.10
Quidi Vidi	1120.83	670.42	15.81	30.54	1837.60
Round	201.00	552.60	8.91	0	762.54
Second	838.50	369.26	1.11	3.11	1211.98
Three Island	367.67	256.68	51.02	27.86	703.23
Tors Cove	697.67	125.30	50.44	0.62	874.03
Whiteway	645.83	514.79	0	0	1160.62

by the benthos or by piscivorous fish in the lakes. The fact that Three Island Pond shows the lowest total biomass of the Avalon lakes may indicate that there is a large benthic component in this lake (as also suggested by the large proportion of benthic items in the diet of sticklebacks from Three Island Pond; see Chapter 4) which could account for a large biomass component in this system. A few fourspine sticklebacks, *Apeltes quadracus* Mitchill, were also trapped in Paddys Pond (6 fish in the spring and 6 fish in the late summer); their biomass and subsequent impact on the zooplankton community was considered negligible compared to that of threespine stickleback in the lake (525 threespine sticklebacks were trapped in the spring and 291 were trapped in the late summer).

Total biomass in a system presumably is limited by the amount of nutrients entering the system. The total biomass calculated for the Avalon lakes is significantly related to nutrient concentrations such as mean (spring + summer) total phosphorus levels. However, total phosphorus explains only a small proportion of the variance in total lake biomass (linear regression model: $r^2 = 0.32, p = 0.03, n = 15$). Again, this indicates that other biomass components such as the benthos and piscivores need to be taken into account in such a mass balance approach.