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Invertebrate Predation and the Seasonal
Dynamics of Microcrustacea in the Littoral Zone
of Jack Lake, Nova Scotia

by

Michael J. Paterson

Submitted in partial fulfilment of the requirements
for the degree of Doctor of Philosophy

at

Dalhousie University
Halifax, Nova Scotia
October, 1991

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ABSTRACT

The influence of invertebrate predators on the seasonal dynamics of epiphytic and benthic microcrustacea was investigated in the littoral zone of a fishless lake called Jack Lake. Observational studies revealed that most cyclopoid copepods had two generations during the ice-free season, with maximum numbers of adults in June-July and October-November. The abundance of most species of Cladocera peaked in June-July or September-October. Numbers of all Cladocera were low in August. Changes in numbers of common cladoceran species did not follow changes in birth rates. This suggests that seasonal abundance was strongly affected by population losses, possibly from predation mortality.

Gut content analyses and abundance estimates indicated that copepods, tanypod chironomids, odonates, and water mites were the most important predators of littoral microcrustacea. With the exception of instar-4 Ablabesmyia sp., seasonal changes in the abundance of these predators were not correlated with microcrustacean abundance.

The influence of invertebrate predators was examined in a series of in situ enclosure experiments. Manipulations of large odonates, small odonates, tanypod chironomids, and adult water mites resulted in few statistically significant changes in microcrustacean numbers, species composition, or size structure.

Taken together, the observational and experimental data suggested that invertebrate predators did not strongly influence littoral microcrustacea in Jack Lake. The potential influence of other factors on littoral microcrustacean seasonal dynamics is discussed.

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Introduction

Meiofaunal invertebrates are those that pass through a 500 μm mesh and are retained on a fine screen (usually 40-100 μm) (Fenchel 1978). Macroinvertebrates are retained on large mesh screens (usually 500 μm or larger). In the littoral zone of freshwater lakes, meio- and macro-faunal invertebrates are abundant in the sediments (benthic invertebrates), on the surface of macrophytes (epiphytic invertebrates), and in the water column. Community interactions among littoral meio- and macrofaunal invertebrates have received little attention.

There are several indications that littoral meiofauna may be important components of the biota of freshwater lakes. A large proportion of the primary and secondary production of many lakes occurs in the shoreline regions, and interactions within the littoral zone may influence pelagic water chemistry, production and community structure (Howard-Williams and Lenton 1975; Wetzel 1983; Lodge et al. 1988). Meiofaunal invertebrates potentially influence littoral algal dynamics and are heavily preyed upon by fish and invertebrates. Although there are few quantitative estimates, total benthic meiofaunal production apparently equals or exceeds total benthic macrofaunal production in many lakes (Holopainen and Paasivirta 1977; Anderson and DeHenau 1980; Strayer and Likens 1986). In turn, total zoobenthic production may equal or exceed zooplanktonic

production in small lakes (Strayer and Likens 1986). There are no estimates of the contribution of epiphytic meiofaunal production, but it is likely to be considerable in small lakes with well developed littoral zones. Volumetric secondary production by zooplankton is typically much greater in the littoral zone than in the pelagic zone (Straškraba 1963; Lim and Fernando 1978).

Among the most abundant and diverse groups of littoral meiofauna are microcrustacea, including chydorid and macrothricid Cladocera and cyclopoid Copepoda. Most littoral Cladocera feed on detritus, bacteria, and periphyton, while cyclopoids may be detritivorous, herbivorous, or predaceous (Fryer 1957a,b; 1968; 1974; Downing 1981a; Meyers 1984a). The exuviae of littoral Cladocera preserve well in lake sediments and have been frequently used in paleolimnological studies. Unfortunately, the usefulness of Cladocera to paleolimnology has been severely hampered by inadequate information concerning their contemporary ecology.

In this study, I investigated the seasonal dynamics of microcrustacea in the littoral zone of Jack Lake, Nova Scotia, Canada. My primary objective was to examine the influence of predation by invertebrates on seasonal changes of microcrustacean community structure. A secondary objective was to identify other factors influencing seasonal fluctuations in littoral microcrustacean communities and to

generate hypotheses for future testing.

Large seasonal changes in the abundance and species composition of littoral microcrustacea have been observed in many lakes (Smyly 1957; Straškraba 1963; Goulden 1971; Keen 1973; Daggett and Davis 1974a; Whiteside 1974; Keen 1976; Phoenix 1976; Lim and Fernando 1978; Doolittle 1982; Fairchild 1983; Williams 1982; Sharma and Pant 1984). Several studies have concluded that shifts of vertebrate and invertebrate predation strongly affect these seasonal changes. The seasonal abundance of chydorid Cladocera often changes independently of birth rates, implying that variations in death rates (presumably related to predation) are responsible (Keen 1973; Williams and Whiteside 1978; Doolittle 1982; Robertson 1990). Summer declines of littoral cladoceran abundance frequently coincide with increased activity of fish (Phoenix 1976; Doolittle 1982; Fairchild 1982; Lehtovaara and Sarvala 1984; Robertson 1990). Exclosure of fish from littoral regions also results in changes in the abundance and species composition of Cladocera (Straškraba 1965; Phoenix 1976; Doolittle 1982; Fairchild 1982; Bohanan and Johnson 1983).

The effect of invertebrate predators on littoral microcrustacea is largely unknown. Microcrustacea are important components of the diets of many common littoral invertebrates including cyclopoid copepods, water mites,

odonates, tanypod midges, Notonecta, Chaetogaster, etc. (see references cited in Chapter 2). In Lake Lacawac, Pennsylvania, numbers of benthic chydorid Cladocera declined seasonally with increased abundance of late instar tanypod midges (Goulden 1971). In contrast, variation in profundal benthic microcrustacean abundance was not correlated with seasonal changes of tanypod abundance or biomass in Lake Sniardwy, Poland (Dusoge 1980). Williams and Whiteside (1978) and Williams (1983) reported that chydorids isolated in "biomonitors" achieved densities three times greater than maximum densities observed in natural weedbeds. Similar increases were not observed in fish enclosures and differences in biomonitors were ascribed to the absence of invertebrate predators. The potential roles of reduced competition, altered food supply, etc. in biomonitors were not addressed. Kajak et al. (1968) and Dusoge (1980) found that addition of water mites, Tanypodinae, or Ceratopogonidae to experimental chambers in the profundal zone resulted in decreased numbers of benthic Cladocera, copepods, and chironomids. The effects of natural variations of tanypod and mite densities were not explored experimentally. Johnson et al. (1987) and Van Buskirk (1988) reported that manipulation of densities of odonate larvae in enclosures did not cause large changes in the absolute or relative abundance of littoral microcrustacea. Notonecta sp. strongly

affected the abundance of planktonic invertebrates, but had no detectable impact on chydorid cladocerans or ostracods in experiments by Murdoch et al. (1984).

Although the effect of invertebrate predators on littoral microcrustacea is unclear, many studies in other freshwater systems have shown that invertebrate predation can strongly affect invertebrate communities. In the pelagic zone, interannual and seasonal changes of zooplankton numbers, species composition, and size structure have been associated with changes in the activity of various invertebrate predators including Chaoborus, Leptodora, Mysis, copepods, and water mites (Hall 1964; Cummins et al. 1969; McQueen 1969; Dodson 1972; Gliwicz and Biesiadka 1975; Threlkeld et al. 1980; Edmondson and Litt 1982; Yan et al. 1982; Elser et al. 1987; Luecke and Litt 1987; Black and Hairston 1988; Riessen et al. 1988; Varnhagen et al. 1988; Matveev et al. 1989). Many planktonic microcrustacea are apparently unable to coexist with certain invertebrate predators (Sprules 1972; Dodson 1974; Hebert and Loaring 1980; Luecke and O'Brien 1983) and estimates of feeding rates suggest that many invertebrate predators can crop substantial proportions of planktonic microcrustacean standing stocks (Cummins et al. 1969; McQueen 1969; Pastorok 1980; Dodson 1972; Federenko 1975; Lane 1978, 1979; Elser et al. 1987; Black and Hairston 1988). Manipulation of invertebrate predators in in situ

enclosures typically results in changes of zooplankton numbers, species composition, and size structure (Dodson 1974; Brandl and Fernando 1979; Hebert and Loaring 1980; Neill and Peacock 1980; Neill 1981; Murdoch et al. 1984; Riessen et al. 1988; Vanni 1988; Mackay et al. 1990). The presence of invertebrate predators may also stimulate changes in the behaviour and morphology of many zooplanktonic microcrustaceans (Krueger and Dodson 1981; O'Brien et al. 1979; O'Brien and Schmidt 1979; Sprules et al. 1984; Folt 1987; Kerfoot 1987; Luecke and Litt 1987; Stenson 1987).

Invertebrate predators have also been shown to affect macrobenthic invertebrate communities in streams. Townsend and Hildrew (1979) estimated that a trichopteran, Plectrocnemia conspersa, effected an 84% reduction in chironomid abundance within one month. Manipulation of stoneflies (Plecoptera) in enclosures by Oberndorfer et al. (1984) and Walde and Davies (1984) resulted in decreased prey numbers and changes in macroinvertebrate species composition. The presence of plecopteran predators also decreases colonization by many benthic macroinvertebrates (Peckarsky and Dodson 1980; Peckarsky 1985).

The influence of predation by invertebrates on littoral and profundal macrobenthic communities is uncertain. Benke (1976) estimated that anisopteran odonate larvae consumed close to 100% of the macrofaunal standing stock weekly in a

small pond in South Carolina. Experimental manipulations of anisopteran densities, however, usually fail to cause large changes in benthic community structure (Hall et al. 1970; Benke 1978; Benke et al. 1982; Thorp and Cothran 1982; Morin 1984; Johnson et al. 1987). The most frequently observed effects are shifts in odonate numbers and species composition that are apparently related to inter-odonate predation (Benke 1978; Benke et al. 1982; Morin 1984; Crowley et al. 1987; Anholt 1990; McPeck 1990). Addition of tanypod larvae to tubes containing natural benthic communities results in decreased invertebrate numbers and shifts in community composition (Kajak et al. 1968; Dusoge 1980; Hershey 1986). Manipulation of leeches in enclosures by Rasmussen and Downing (1988) affected only the spatial distribution of benthic chironomids.

In this thesis, I use a combination of observational and experimental approaches to examine the impact of invertebrate predation on the seasonal dynamics of littoral microcrustacea in a small fishless lake called Jack Lake. In Chapter 1, I examine the spatial distribution of microcrustacea and potential predators in Jack Lake. In Chapter 2, I discuss the seasonal dynamics of microcrustacea and invertebrate predators. I identify important predators of microcrustacea and assess how seasonal changes in their numbers and sizes may influence littoral microcrustacea. In Chapter 3, I

describe the effects of experimental manipulations of invertebrate predator densities on microcrustacean communities within in situ enclosures.

Observation of the littoral invertebrate community in Jack Lake provided important information about natural variations of food-web structure. No previous studies have examined the seasonal dynamics of a suite of invertebrate predators and their microcrustacean prey in the littoral zone. Basic descriptive information of this type is essential for the formulation of hypotheses concerning littoral food-web structure. Observational data are frequently difficult to interpret, because many factors affect communities simultaneously in space and time. Experimental approaches allow the precise manipulation of variables and the independent assessment of their effects. The use of replicated treatments and statistical analyses further strengthens inferences concerning the importance of various interactions.

Chapter 1

The distribution of invertebrates in Jack Lake

A. Introduction

The littoral zone of freshwater lakes typically supports an abundant and diverse community of microcrustacea and other invertebrates. As a first step in understanding littoral food webs, it is essential to determine which invertebrates co-exist in time and space. Organisms with overlapping temporal and spatial distributions are those most likely to interact on a regular basis. Non-overlapping distributions may reflect strong interactions that prevent co-existence.

The primary purpose of this chapter is to examine spatial and temporal variations in microcrustacean community structure in Jack Lake. In particular, I emphasize variations in the spatial distribution of microcrustacea and their invertebrate predators. Three aspects of spatial distribution are considered below: 1) The distribution of invertebrates in the water column, in the sediments, and among macrophyte species was examined in the shallow littoral zone (1-2m). 2) Several studies indicate that many benthic and epiphytic microcrustacea enter the water column at night to interact with planktonic organisms (Whiteside 1974; Whiteside et al. 1978; Kairesalo 1980; Fairchild 1981; Campbell et al. 1982; Bell et al. 1984; Meyers 1984a; Timms and Moss 1984). Day-night migrations of invertebrates were

assessed on two occasions using different sampling methodologies. 3) The distribution of epiphytic invertebrates with respect to water depth was examined in August, 1986.

A secondary objective of this chapter is to examine the usefulness of two common techniques for estimating the abundance of littoral microcrustacea: 1) funnel traps (Whiteside 1974; Whiteside and Williams 1975; Brakke 1976), and 2) ratio-regression methods (Cochran 1977; Downing 1986). These methods were used to collect invertebrates from Jack Lake and the results had implications for their application.

B. Study site

Jack Lake is an acidic, oligotrophic, headwater lake located near Bedford, Nova Scotia, Canada (Figure 1.1). Aside from hiking trails and a small access road, the watershed is forested and undeveloped. Some limnological characteristics of Jack Lake are listed in Table 1.1. Jack Lake was stratified from late May to September at a depth of 3.5 to 4.5 m. Oxygen levels in the littoral zone were always near saturation, even at the sediment-water interface. Low oxygen levels (less than $1 \text{ mg} \cdot \text{l}^{-1}$) were observed in the hypolimnion from July to September. The flushing of meltwater through peat deposits surrounding Jack Lake caused visible staining of lake water in May. With stratification, waters in the epilimnion rapidly cleared, while darker water

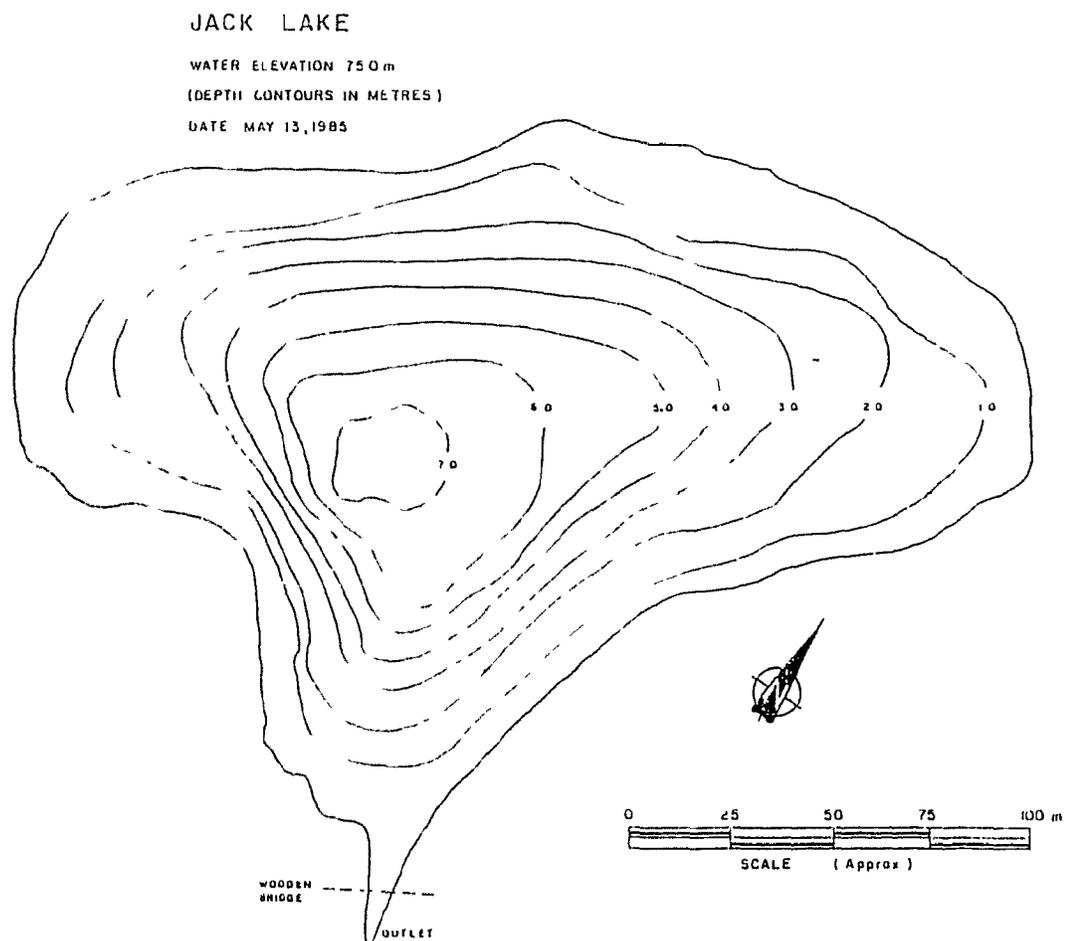


Figure 1.1. Morphometric map of Jack Lake, Nova Scotia.

Table 1.1. Some limnological characteristics of Jack Lake, Nova Scotia (44° 44' N, 63° 40' W).

Surface area	3.9	ha
Watershed area	32.8	ha
Maximum depth	7.0	m
pH	4.6	
Calcium ^a	1.18	mg·l ⁻¹
Sulfate ^a	5.56	mg·l ⁻¹
Chloride ^a	5.2	mg·l ⁻¹
Total Al ^a	0.27	mg·l ⁻¹
Ortho-phosphate ^a	0.02	mg·l ⁻¹
Sediment organic matter (littoral zone)	63.0	%

^a data from P. Lane & Associates Limited (1985)

remained trapped in the hypolimnion. A Secchi disk was always clearly visible to the depth of the thermocline, after which it rapidly disappeared.

No fish were collected during extensive electrofishing surveys (P. Lane and Associates Limited 1985) or were observed during hundreds of hours of SCUBA diving for this study. Apparently, the low pH, high aluminum levels and limited access up the shallow outlet stream have prevented the establishment of fish populations. Waterfowl were rarely observed. Herbivorous tadpoles were seasonally abundant.

Unless stated otherwise, all samples were collected along the north shore of Jack Lake. The shoreline in this region consisted of peat bog that sharply dropped off to water depths of approximately 1 m. Chamaedaphne calyculata extended into the water along most of the shore. The lake bottom was covered by highly organic, flocculent sediments and dense submerged macrophyte growth.

The macrophyte community of Jack Lake was composed of thirteen species (Table 1.2). Biomass was dominated by Pallavicinia lyellii (a rootless liverwort), Eriocaulon septangulare, Scirpus subterminalis, Sphagnum sp. and Potamogeton confervoides. Emergent and floating leaved macrophytes (Pontederia cordata, Nymphaea odorata, Nuphar variegatum) were restricted to small areas of very shallow water (less than 0.5 m) and were rarely sampled. Submerged

Table 1.2. Mean annual biomass ($\text{g}\cdot\text{m}^{-2}$) of macrophytes in Jack Lake, 1987. Macrophytes not consistently sampled are indicated with +.

<u>Pallavicinia lyellii</u> (Hooker)	13.53
<u>Eriocaulon septangulare</u> Withering	5.27
<u>Scirpus subterminalis</u> Torrey	4.55
<u>Sphagnum</u> sp.	0.92
<u>Potamogeton confervoides</u> Reichenbach	0.78
<u>Isoetes muricata</u>	0.75
<u>Utricularia</u> sp.	0.17
<u>Utricularia purpurea</u> Walter	0.02
<u>Fontinalis</u> sp.	+
<u>Lobelia dortmanna</u> Linnaeus	+
<u>Nymphaea odorata</u> Aiton	+
<u>Nuphar variegatum</u> Engelmann	+
<u>Pontederia cordata</u> Linnaeus	+

macrophytes could be divided into two groups: 1) Pallavicinia lyellii, E. septangulare, and Sphagnum sp. formed a dense mat 5-10 cm deep at the sediment-water interface. Hereafter, these species will be referred to as "group A" macrophytes. Considerable quantities of sediment and detritus settled on this mat over the growing season. 2) Long, thin shoots of Scirpus subterminalis and Potamogeton confervoides grew through the mat of group A species and up to one meter into the water column. These species are called "group B" macrophytes below. By July-August, these macrophytes were surrounded by dense clouds of filamentous algae.

C. Methods

1) Distribution of invertebrates in the shallow littoral zone of Jack Lake: Invertebrates were collected from the water column, sediments, and macrophytes in water 1-2 m deep. Samples were collected at three-week intervals between August 22 and October 5, 1986 and at one-month intervals between June 11 and October 8, 1987. Samples collected in May, late October, and November were not used in the study because invertebrate numbers and species composition were strongly affected by cold water temperatures at these times (Chapter 2). Collection methods employed in each habitat are outlined below:

Water column: Integrated water-column samples were collected using a 10-cm diameter wire-reinforced plastic tube

(cf. Pennak 1962). The tube was lowered over the side of a boat to a position just above submerged macrophytes and a rope attached to the lower end was used to pull the tube to the surface. Enclosed water was poured through a 63- μ m sieve held over an empty bucket calibrated for volume. A minimum of ten tube samples was collected on each sampling date. Zooplankton samples were preserved in 5% formalin with sugar (Haney and Hall 1973) and each was counted without subsampling.

Benthos: Benthic invertebrates were collected from a boat using a 3.5-cm diameter corer attached to a metal pole (cf. Merritt and Cummins 1984, Figure 3.12). The relatively small size of the corer probably limited the collection of large invertebrates, such as odonates. The uppermost 4 cm of each core and 5 cm of overlying water were drawn off with a wide mouthed pipette and preserved in 5% sugar-formalin. Preliminary studies indicated that approximately 95% of benthic invertebrates occurred in the top 4 cm of sediment cores from Jack Lake. These findings were in accord with several other studies (Sarkka and Paasivirta 1972; Kirchner 1975; Holopainen and Paasivirta 1977; Dusoge 1980; Nalepa and Robertson 1981; Strayer 1985). The contents of each core were stained with rose bengal (Mason and Yevich 1967) and sieved with a 125- μ m screen. Examinations of filtrate through the sieve revealed only early instar chironomids and

nauplii. Attempts to retrieve animals using sugar flotation (Anderson 1959) resulted in unacceptable losses and insufficient removal of the highly organic sediment. Core samples were counted in their entirety under a dissecting microscope. At least five cores were collected haphazardly throughout the study area on each sampling date.

Epiphytic invertebrates: In 1986, epiphytic invertebrates and macrophytes were collected at randomly selected locations along a numbered rope transect placed parallel to shore in water approximately 1.5 m deep. In 1987, 3 permanent transects were established in water 1, 1.5, and 2 m deep, and sampling was randomly stratified along each transect.

The above-ground biomass of macrophytes was estimated by removing plants within randomly located 929 cm² (1986) or 232 cm² (1987) quadrats. Macrophytes were returned to the laboratory, washed, sorted to species, dried at 90° C, and weighed. All roots were removed before weight determinations were carried out. Biomass estimates for each sampling date were based on 12-20 replicates in 1986 and 19-30 replicates in 1987.

Epiphytic invertebrates were collected using the technique of Downing (1986). A SCUBA diver carefully closed a 5.5-i hinged plexiglass box around submerged macrophytes. The box effectively collected both sessile and mobile invertebrates, such as Notonecta. The box was brought to the surface,

unenclosed plant material trimmed away, and the contents drained through a 125- μ m sieve. As with sediment samples, only early instar chironomids and nauplii were encountered in the filtrate. The contents of box samples were returned to the lab, where the macrophytes were rinsed, sorted to species, dried at 90° C, and weighed. Epiphytic invertebrates were preserved in 5% sugar-formalin and stained with rose bengal.

Epiphytic invertebrates were counted in two steps. Samples were initially strained through a 600- μ m sieve, and all insects (except non-predatory Chironomidae) were counted. The 600- μ m fraction was then recombined with residue retained on the 125- μ m sieve and made up to a known volume. This volume was repeatedly subsampled with a wide-mouthed pipette until 300 microcrustaceans had been counted. A significant divergence of subsamples from a Poisson distribution was not observed, indicating that invertebrates were randomly subsampled. For abundant organisms, the standard error of subsamples was small (less than 10% of the mean) and was ignored in subsequent statistical analyses.

The surface area of macrophytes in box samples was indirectly estimated using a modification of the method of Harrod and Hall (1962) (cf. Pip and Stewart 1976; Lodge 1985). Surface area was estimated from the weight of detergent covering macrophytes. First, plants of simple

morphology were cut into fragments of known surface area, dipped in acetone and weighed. They were then dipped in a 50% aqueous solution of Liquinox detergent (Alconox, New York) and reweighed. The weight of detergent covering the plants was determined by subtraction and a regression equation relating surface area and detergent weight was calculated (Table 1.3, equation a). The weight of detergent covering plants of unknown surface area from Jack Lake was then determined and the regression equation was used to estimate surface area. Regressions between plant dry weight and surface area were calculated for each of the common macrophytes in Jack Lake. Because the y-intercept was not significantly different from zero in any case (t -tests, $p < .05$), regressions were recalculated with the intercept forced through zero (Table 1.3b). Finally, indirect estimates of macrophyte surface area were obtained from the biomass of different macrophytes in box samples.

The surface area of Spongilla lacustris could not be estimated using the above method, because it easily fragmented when dipped in detergent. Instead, the width and length of several of the fingerlike projections of S. lacustris were measured and surface area was estimated using the formula for a cylinder.

Mean densities of epiphytic invertebrates per m^2 of lake bottom (called lake bottom densities below) were estimated

Table 1.3. Regression equations used to estimate surface area of common macrophytes in box samples, where SA is surface area (cm²), Dt is weight (g) of detergent and DW is dry weight (g) of plants.

a. Calculated surface area vs. detergent weight (n=16, R²=.98):

$$SA = 2.589 + 254.3 * Dt$$

b. Surface area vs dry weight:

Eriocaulon septangulare (n=20, R²=.93):
SA = 794.4 * DW

Pallavicinia lyellii (n=17, R²=.99):
SA = 1619.9 * DW

Potamogeton confervoides (n=14, R²=.99).
SA = 1621.9 * DW

Scirpus subterminalis (n=18, R²=.98):
SA = 2373.3 * DW

Sphagnum sp. (n=20, R²=.99):
SA = 4960.3 * DW

Spongilla lacustris (n=5, R²=.92):
SA = 275 * DW

for 1987 using the following formula on each sampling date:

$$LBD_i = [SD_{Ai} * B_A] + [SD_{Bi} * B_B]$$

where LBD_i is the lake bottom density of invertebrate i , SD_{Ai} is the abundance of invertebrate i per cm^2 of leaf surface area on group A macrophytes, SD_{Bi} is the abundance of invertebrate i per cm^2 of leaf surface area on group B macrophytes, B_A is the above-ground surface area of group A macrophytes (cm^2 per m^2 of lake bottom) and B_B is the above-ground surface area of group B macrophytes. B_A and B_B were estimated from quadrat samples. To estimate SD_A and SD_B , box samples were divided into those containing greater than 75% group A or B macrophytes by surface area. Samples containing mixed assemblages were dropped from the analysis. At least 3 box samples containing greater than 75% group A and B macrophytes were available on all sampling dates in 1987. The surface area of S. lacustris was grouped with group A macrophytes. S. lacustris grew near the sediment-water interface and supported an invertebrate assemblage similar to that on Pallavicinia lyellii. Lake bottom densities on group A and B macrophytes were estimated separately, because the abundance of several invertebrates varied between these two groups of macrophytes (see results below). Lake bottom density estimates based on separate determinations of invertebrate numbers on group A and B macrophytes were always more easily interpreted than estimates determined without

regard for macrophyte type. Because the estimates of epiphytic invertebrate lake bottom densities rely on ratios, they should be regarded with caution (Atchely et al. 1976; Green 1979; Jackson et al. 1990). Unfortunately, alternative techniques for estimating epiphytic invertebrate abundance are also seriously flawed (Downing and Cyr 1985; Downing 1986). These problems are considered in detail later in the chapter.

Taxonomy: Microcrustacea and potential predators of microcrustacea were identified to species, whereas other invertebrates were identified with varying degrees of taxonomic precision. Detailed taxonomic analysis of water mites was not undertaken. Macrophytes were keyed out using Conrad (1956), Fassett (1957), and Roland and Smith (1969). Macroinvertebrates were identified using keys in Walker (1953), Saether (1972), Mason (1973), Walker and Corbet (1975), Pennak (1982), Oliver and Roussel (1983), and Merritt and Cummins (1984). Copepods were sorted using Yeatman (1959), Dussart (1969), Daggett and Davis (1974b), and Smith and Fernando (1978). All cyclopoid identifications were confirmed by Dr. H.C. Yeatman, University of the South, Sewanee, Tennessee. Different instars of copepods and macroinvertebrates were distinguished using criteria described in Chapter 2.

The taxonomy of littoral Cladocera is currently confused.

In recent years, it has become apparent that many North American species are taxonomically and ecologically unique from organisms bearing the same name in Europe (Frey 1982; 1986). In some cases, North American "species" have proved to be complexes of closely related species (Frey 1982; 1986). Cladocera were identified using literature cited in Paterson (1986). Pleuroxus straminus was identified using Frey (1988) and Camptocercus sp. closely matched the description of Hann (1981). Examination of headshells preserved in sediment samples from Jack Lake revealed the presence of both Alona cf. quadrangularis (three headpores) and Alona cf. affinis (two headpores). Almost all headshells were of the affinis type. Intact specimens of these species could not be separated reliably and have been lumped together as A. cf. affinis.

A unique form of Alonella was frequently encountered in Jack Lake. A drawing of exoskeletal remains of this chydorid is provided in Paterson (1985). I have frequently encountered this species in Nova Scotia and in the Adirondack Park, New York and it is probably common throughout eastern North America. Several other Cladocera from Jack Lake (Acroperus cf. harpae, Disparalona acutirostris, and Ilyocryptus sp.), differed from published descriptions and further taxonomic examination is probably warranted.

Data analysis: The relationship between the surface area

of all macrophytes in box samples and invertebrate abundance was examined using multiple linear regression (Neter et al. 1983). I examined two models: Model A considered only the effect of total macrophyte surface area on invertebrate abundance. Model B included two temporal variables - Julian date and year. Year was entered as an indicator variable (0=1986, 1=1987). A fourth-root transformation (Downing 1979) was the most effective for stabilizing variance and normalizing the distributions of abundance data (Appendix 1).

I sought relationships between invertebrate species associations and littoral microhabitats using Principal Components Analysis (PCA). PCA utilized information on the entire invertebrate community and summarized the data in a few dimensions of maximum variation. PCA ordered samples along orthogonal axes or components that were linear compounds of the transformed species' abundances. The first axis maximized the proportion of total explained variance of species abundances, with successive axes maximizing remaining variance. Components were obtained by eigenanalysis of the correlation matrix of taxa abundances (i.e. abundance data were centred and standardized) and this had the effect of making all taxa of equal importance (see Noy-Meir et al. 1975 for a discussion of the implications). With each axis, there is an associated eigenvalue that is proportional to the explained variance and an eigenvector that gives the weights

of each taxon in the linear compound. Mathematical descriptions of PCA are provided by Cooley and Lohnes (1971), Morrison (1976), Legendre and Legendre (1983), and Pielou (1984).

PCA has been criticized because of its reliance on an underlying linear model (Swan 1970; Gauch and Whittaker 1972; Gauch et al. 1977). If species have Gaussian distributions along an environmental gradient, higher axes may be quadratically related to the first (known as the "arch" effect). Although many alternative techniques have been proposed to circumvent this problem (non-metric multi-dimensional scaling, Detrended Correspondence Analysis, Canonical Correspondence Analysis), a clear resolution has not been found (Fasham 1977; Green 1979; Gauch et al. 1981; Pielou 1984; Austin 1985; Kenkel and Orloci 1986; Wartenburg et al. 1987). The arch effect in PCA becomes more severe as beta-diversity increases (Fasham 1977; Gauch et al. 1977). The data from Jack Lake, were derived from a short environmental gradient and most taxa occurred in a large percentage of samples. Because beta-diversity in the Jack Lake samples was apparently low, the application of PCA is probably acceptable. As a further check, the data matrices were also ordinated using Reciprocal Averaging (RA, also known as Correspondence Analysis) (Hill 1973). Although RA also relies on a linear model, it is less strongly affected

by the arch effect (Fasham 1977; Gauch et al. 1977). RA is related to PCA, but sample similarity is assessed using a X^2 distance matrix instead of a correlation matrix (Chardy et al. 1976; Legendre and Legendre 1983). The results using RA were almost always in agreement with those obtained with PCA. As a result, only the results of the PCAs are discussed below.

Several data matrices were analyzed with PCA and RA. First, the relative abundances of different species and life-stages of microcrustacea were used to ordinate 92 macrophyte box samples and 40 sediment samples. Proportions were arcsine square-root transformed before analysis (Sokal and Rohlf 1981) and taxa that occurred in less than 15% of samples were dropped. Although underlying species distributions were not multivariate normal, the ordinations were probably not severely affected (Cooley and Lohnes 1971; Legendre and Legendre 1983). To elucidate the influence of macrophyte species composition on invertebrate community structure, two separate ordinations were calculated using only the results from box samples. The first data matrix included the abundance per box sample of all common invertebrates. Data were fourth-root transformed before analysis. A second ordination of microcrustacean proportions was also performed using only data from the box samples. PCAs were completed using the SYSTAT statistical package

(Wilkinson 1988) and RAs with the ORDIFLEX package (Gauch 1977). All calculations were done on an IBM personal computer clone.

2) Day-night movement of microcrustacea into the water column: Nocturnal migration of benthic and epiphytic microcrustacea into the water column was assessed using two different approaches: 1) On May 27, 1986, numbers of microcrustacea captured using a 3.5-cm diameter sediment corer were compared with numbers moving upward into funnel traps (Whiteside 1974; Whiteside and Williams 1975; Brakke 1976). Funnel traps consisted of four 127-mm diameter funnels (Fisher #10-373A) attached to clear bottles filled with filtered lake water and held by a plexiglass frame. For invertebrates to become trapped inside the bottles, they had to move upwards 18 cm through a 10-mm internal diameter stem. Traps were placed mouth down on bare sediments and left for 24 h. 2) On August 18, 1988, I compared numbers of invertebrates captured in zooplankton tube samples collected during the day (sampling began at 1200 h) and at night (sampling began at 2400 h).

3) Depth distribution of macrophytes and epiphytic invertebrates: The depth distribution of macrophytes and epiphytic invertebrates was investigated on August 27, 1986. Two numbered transects were established from the study area to the deepest part of Jack Lake. Each transect was divided

into three sections of different water depths: 0 to 2 meters, 2 to 4 meters, 4 to 6 meters. Within each section, quadrat and box samples were collected at randomly selected locations. Box and quadrat samples were collected and processed as described above. To help separate the influence of macrophyte species composition and water depth on invertebrate associations, only Scirpus subterminalis and Potamogeton confervoides were collected in box samples taken between 0 and 4 m. Below 4 m, only an unidentified moss was encountered and all box samples contained this macrophyte. Moss surface areas were estimated using regressions calculated for Sphagnum sp..

The similarity of microcrustacean assemblages collected from each depth stratum was assessed using cluster analysis (see Pielou 1984 for a review). Input data were the arc-sine square-roots of the proportions of different microcrustacea in box samples. Euclidean distance was used as a distance measure and clusters were joined using average linkage.

D. Results

1) Invertebrate distribution in the shallow littoral zone

The invertebrate community in the shallow littoral zone was dominated by Cladocera, copepods, and chironomids. The abundance of these groups in box samples was positively related to the total surface area of enclosed macrophytes (Table 1.4). Addition of temporal variables (Julian date, year) greatly improved the fit of regression equations. Separate consideration of the abundance of different macrophyte species in box samples using stepwise regression did not result in models that explained significantly more variance. This cannot be interpreted as evidence that macrophyte species composition did not affect invertebrate abundance because of multicollinearity among macrophytes in box samples (Table 1.5). Box samples tended to contain either group A or B macrophytes, causing the surface areas of group A macrophytes to be positively correlated with each other and negatively correlated with group B macrophytes. Overall, group A macrophytes dominated total macrophyte surface area in box samples. As a result, correlations of invertebrate numbers with total macrophyte surface area were also potentially affected by macrophyte species composition.

Seventy-four invertebrate taxa were identified from Jack Lake (Table 1.6). Mean lake bottom densities of Cladocera and cyclopoid copepods were within ranges reported from

Table 1.4 . Regression models relating the abundance of common epiphytic invertebrate groups and total macrophyte surface area. In Model A, only the influence of surface area was considered. In Model B, Julian date and year (1986, 1987) were also entered into the equations. Invertebrate groups are abbreviated as Cl (Cladocera), Cyc (Cyclopoida), and Chir (non-tanypod Chironomidae). All abundances and macrophyte surface areas were fourth-root transformed before analysis. All constants were significantly different from zero (t -tests, $p < .05$), except for the constant for Cladocera using Model B.

Variable	Model A			Model B		
	Cl	Cyc	Chir	Cl	Cyc	Chir
Constant	4.896	3.802	3.943	.110	4.547	1.897
Surface area	.283	.532	.563	.387	.577	.459
Julian date	-	-	-	.015	-.005	.013
Year	-	-	-	1.437	.390	-.863
R ²	.096	.468	.315	.468	.584	.714
p	.003	<.001	<.001	<.001	<.001	<.001

Table 1.5. Statistically significant ($p < .05$) Pearson correlation coefficients among the surface areas of different macrophytes and Spongilla lacustris in box samples. All surface areas were fourth-root transformed before analysis. Abbreviations are as follows: Es (Eriocaulon septangulare), Pl (Pallavicinia lyellii), S (Sphagnum sp.), Sl (Spongilla lacustris), Ss (Scirpus subterminalis), Pc (Potamogeton confervoides), M (total macrophytes).

	Es	Pl	S	Sl	Ss	Pc	M
Es							
Pl	-						
S	.360	.290					
Sl	.331	.498	.570				
Ss	-	-.597	-.277	-.411			
Pc	-.254	-	-	-	-		
M	-	.746	.453	.553	-.329	-	
Julian date	-	-	-	-	-	.322	-

Table 1.6. Mean lake bottom densities of invertebrates in the shallow littoral zone of Jack Lake, 1987. Potential predators were identified after consultation with literature sources and are indicated with *.

	Macrophytes (numbers·m ⁻²)	Sediments (numbers·m ⁻²)	Water Column (numbers·m ⁻³)
Porifera			
<u>Spongilla lacustris</u> (Linnaeus)	6.82 (g·m ⁻²)		
Tardigrada	694	-	-
Annelida			
Oligochaeta	24270	16053	-
Coelenterata			
* <u>Hydra</u> sp.	223	31	-
Mollusca			
<u>Ferrissia</u> sp.	344	-	-
<u>Pisidium</u> sp.	-	<1	-
Arthropoda			
Cladocera			
Bosminidae			
<u>Bosmina longirostris</u> (Müller)	-	-	11
Chydoridae			
<u>Acroperus</u> cf. <u>harpae</u> Baird	558	59	22
<u>Alona</u> cf. <u>affinis</u> Leydig	16040	4165	-
<u>Alona intermedia</u> Sars	45463	7061	14
<u>Alona guttata</u> Sars	81	-	2
<u>Alona rustica</u> Scott	2993	30	-
<u>Alonella</u> sp.	2212	-	18
<u>Anchistropus minor</u> Birge	<1	-	-
<u>Camptocercus</u> sp.	3352	-	-
<u>Chydorus brevilabris</u> Frey	2679	67	-
<u>Chydorus linguilabris</u> Frey	12062	304	4
<u>Chydorus piger</u> Sars	2848	89	1
<u>Disparalona acutirostris</u> (Birge)	4063	950	-
<u>Monospilus dispar</u> Sars	-	<1	-
<u>Pleuroxus straminius</u> Birge	<1	-	-
Daphniidae			
<u>Simocephalus</u> sp.	1467	245	-
Holopediidae			
<u>Holopedium gibberum</u> Zaddach	268	-	342

Table 1.6. (continued)

	Macrophytes (numbers·m ⁻²)	Sediments (numbers·m ⁻²)	Water Column (numbers·m ⁻³)
Macrothricidae			
<u>Acantholeberis curvirostris</u> (Müller)	1868	30	-
<u>Ilyocryptus</u> sp.	21675	2405	2
<u>Ophryoxus gracilis</u> Sars	2685	59	5
<u>Streblocerus serricaudatus</u> (Fisher)	21240	913	14
Polyphemidae			
* <u>Polyphemus pediculus</u> (Linnaeus)	-	-	10
Sididae			
<u>Diaphanosoma birgei</u> Korinek	1032	119	25
<u>Latona parviremis</u> Birge	3474	119	-
Copepoda			
Calanoida			
<u>Diaptomus minutus</u> Lilljeborg	10338	245	10289
* <u>Epischura nordenskioldi</u> Lilljeborg	551	-	1251
Cyclopoida			
* <u>Acanthocyclops vernalis</u> <u>robustus</u> (Fisher)	845	1626	-
<u>Diacyclops nanus</u> Sars	40708	15585	2
* <u>Diacyclops navus</u> Herrick	327	-	-
<u>Eucyclops agilis</u> (Koch)	13091	3044	5
<u>Eucyclops speratus</u> (Lilljeborg)	2792	208	7
* <u>Macrocyclops albidus</u> (Jurine)	29750	10751	4
* <u>Macrocyclops fuscus</u> (Jurine)	<1	-	-
<u>Microcyclops varicans</u> <u>rubellus</u> (Lilljeborg)	35	37	-
<u>Orthocyclops modestus</u> (Herrick)	339	423	-
<u>Paracyclops affinis</u> (Sars)	351	-	-
<u>Paracyclops yeatmani</u> Daggett & Davis	-	30	-
Harpacticoida	543	30	-
Ostracoda	82	59	-
Insecta			
Diptera			
Chironomidae			
non-Tanypodinae	112465	45181	29

Table 1.6. (continued)

	Macrophytes (numbers·m ⁻²)	Sediments (numbers·m ⁻²)	Water Column (numbers·m ⁻³)
Tanypodinae			
* <u>Ablabesmyia</u> sp.	10570	7284	-
* <u>Procladius</u> sp.	2919	5613	-
* Ceratopogonidae	284	297	-
Chaoboridae			
* <u>Chaoborus americanus</u> (Johannsen)	211	186	69
Ephemeroptera			
<u>Leptophlebia</u> sp.	46	-	-
Odonata			
Anisoptera			
* <u>Aeschna interrupta</u> Walker	14	-	-
* <u>Leucorrhinia glacialis</u> Hagen	142	31	-
* <u>Cordulia shurtleffi</u> Scudder	155	31	-
Zygoptera			
* <u>Enallagma borealis</u> Selys	10	-	-
* <u>Enallagma carunculatum</u> Morse	700	-	-
* <u>Lestes</u> sp.	2	-	-
Trichoptera			
* <u>Cernotina</u> sp.	297	-	-
<u>Oxyethira</u> sp.	292	149	-
<u>Phryganea</u> sp.	36	-	-
<u>Triaenodes</u> sp.	<1	-	-
<u>Orthotrichia</u> sp.	<1	-	-
Neuroptera	<1	-	-
Hemiptera			
Belostomidae			
* <u>Belostoma</u> sp.	<1	-	-
* Corixidae	<1	-	-
* Gerridae	<1	-	-
Nepidae			
* <u>Nepa</u> sp.	<1	-	-
Notonectidae			
* <u>Notonecta</u> sp.	8	-	8
Coleoptera			
Gyrinidae			
* <u>Dineutus</u> sp.	<1	-	-
Dytiscidae			
* <u>Graphoderus</u> sp.	-	-	<1
Lepidoptera			
<u>Parapyx</u> sp.	<1	-	-
<u>Lymnaecia</u> sp.	<1	-	-
Arachnida			
15136		750	-
* <u>Limnochares</u> sp.			
* <u>Limnesia</u> sp.			

studies in other lakes, whenever appropriate sampling techniques and sieve mesh sizes had been employed (for example Smyly 1957; Goulden 1971; Daggett and Davis 1974a; Evans 1984; Whiteside et al. 1978; Williams 1982; Whiteside and Lindegaard 1982; Strayer 1985). Numbers of many invertebrates (water mites, chironomids, zygopteran odonates) are among the highest reported in the literature (for example, compare with Macan 1964; Lawton 1970a; Hamilton 1971; Benke and Benke 1975; Pieczynski 1976; Walker et al. 1985; McPeck 1990). In part, this reflects the finer mesh sizes and improved sampling methods used in this study. Although Hummon (1981) found that 77% of diptera, 76% of oligochaetes and 96% of cyclopoid copepods passed through a 250- μ m sieve, the majority of benthic studies have used sieves of this size or larger (Downing 1984). Few studies have effectively sampled epiphytic invertebrates.

The densities of common invertebrate groups expressed per unit of surface area are presented in Table 1.7. Although care must be used in the interpretation of these ratios (see below), these data suggest that surface densities are similar on macrophytes and sediments. In spite of similar surface densities, lake bottom densities of epiphytic invertebrates usually greatly exceeded those of benthic invertebrates (Table 1.6). This reflected the greater surface area available on macrophytes compared with that of sediments.

Table 1.7. Mean surface densities (no. cm⁻²) of common invertebrate groups in different microhabitats in the shallow littoral zone of Jack Lake, 1987.

	Cladocera	Cyclopoida	Chironomidae
Sediments	2.19	3.98	5.23
Macrophytes	3.33	3.01	3.93

Many invertebrates in Jack Lake had the potential to feed upon littoral Cladocera and copepods (Table 1.6). Many of these were rare and unlikely to impact strongly on littoral microcrustacean community dynamics. These included Polyphemus pediculus, Diacyclops navus, Macrocyclus fuscus, Lestes sp., Belostoma sp., Corixidae, Gerridae, Nepa sp., Notonecta sp., Dineutus sp., and Graphoderus sp.. The carnivorous macrophyte Utricularia was also too rare to strongly affect microcrustacea. The most common predator groups were water mites, cyclopoid copepods (particularly Macrocyclus albidus), tanypod chironomid larvae (Procladius sp., Ablabesmyia sp.), and odonates (particularly Enallagma carunculatum, Leucorrhinia glacialis, and Cordulia shurtleffi). Potentially important secondary predators were Chaoborus americanus and Trichoptera. After consideration of macrophyte surface area and date, only late instar tanypod chironomids (Ablabesmyia sp., Procladius sp.) were significantly negatively correlated with numbers of total Cladocera or cyclopoids (Table 1.8).

The distribution of invertebrates varied among the water column, sediments, and different macrophyte species. Water column samples were dominated by Diaptomus minutus, Epischura nordenskioldi, Bosmina longirostris, and Holopedium gibberum. These planktonic species were not significantly correlated with macrophyte surface area in box samples.

Table 1.8. Statistically significant Pearson correlation coefficients ($p < .05$) between residuals from Model B regression equations (Table 1.4) and numbers of common predators in box samples.

<u>Predator</u>	<u>Cladocera</u>	<u>Cyclopoida</u>	<u>Chironomidae</u>
<u>Macrocyclops albidus</u> (c6)	-	-	-
Acari	-	.270	-
<u>Procladius</u> sp. (3-4)	-.287	-	-
<u>Ablabesmyia</u> sp. (3-4)	-.251	-	-
<u>Enallagma carunculatum</u>	.292	-	-
Anisoptera	-	-	-

Results of the PCA ordination of microcrustacean relative abundances in core and box samples are presented in Figure 1.2a and Table 1.9. Sediment samples generally had lower scores on axis 1 than macrophyte samples, indicating that microcrustacean community structure varied between the two habitats. Taxa strongly associated with sediments had negative loadings on axis 1 and included Diacyclops nanus, M. albidus, and Disparalona acutirostris.

The interpretation of PCAs of epiphytic invertebrates (box samples only) were confounded by strong intercorrelations among macrophytes in box samples. Only differences between invertebrate communities on group A and B macrophytes could be resolved clearly. PCA axis 1 of microcrustacean relative abundances was positively correlated with the relative abundance of group B macrophytes and negatively correlated with group A macrophytes, particularly Pallavicinia lyellii (Figure 1.2b, Table 1.10). Taxa associated with group B macrophytes had strong positive loadings on axis 1 and included Eucyclops agilis, Chydorus linguilabris, Ophryoxus gracilis, and Acroperus cf. harpae (Table 1.9). The relative abundance of Diacyclops nanus, Disparalona acutirostris, Camptocercus sp., Chydorus brevilabris, and c6 M. albidus increased in samples predominated by group A macrophytes. Axis 2 was most strongly correlated with Julian date. Taxa with positive loadings on axis 2 increased in abundance in

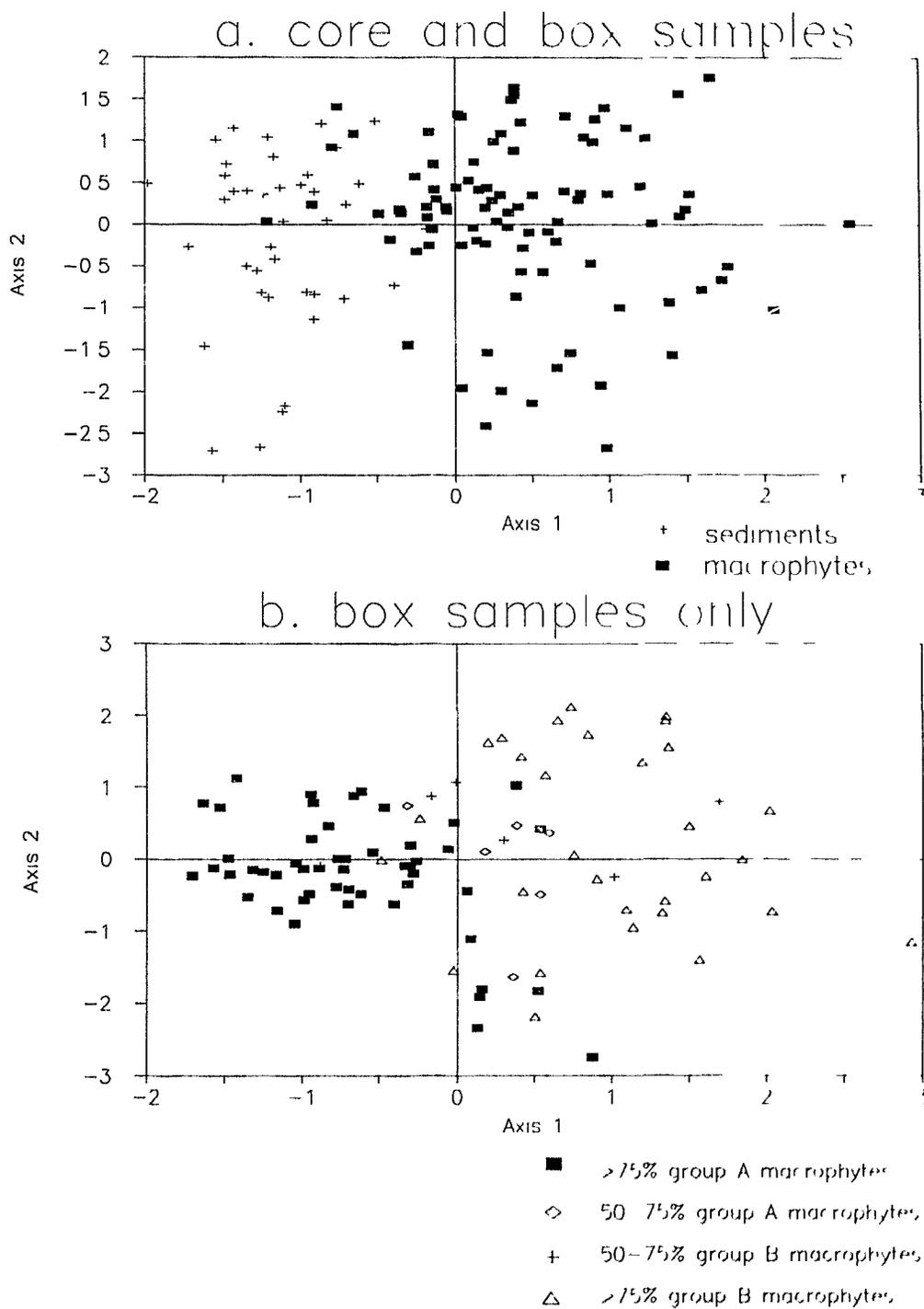


Figure 1.2 Axes 1 and 2 of PCA ordinations of microcrustacean proportions in a) sediment and box samples, and b) box samples only

Table 1.9. Scaled component loadings on axes 1 and 2 of the PCA ordinations. Taxa are ordered by axis 2 of the PCA of absolute densities.

	<u>Microcrustacean proportions</u>				<u>Absolute abundance</u>	
	(core and box samples)		(box samples)		(box samples)	
	Axis		Axis		Axis	
	1	2	1	2	1	2
<u>Diaicyclops nanus</u> (c3-c5)	-.290	-.008	-.791	-.190	.622	-.623
<u>Diaicyclops nanus</u> (c6)	-.544	-.212	-.699	-.300	.545	-.597
Anisoptera	-	-	-	-	.435	-.550
<u>Procladius</u> sp. (3-4)	-	-	-	-	.528	-.511
<u>Disparalona acutirostris</u>	-.230	.288	-.767	.057	.628	-.460
<u>Camptocercus</u> sp.	.165	.107	-.553	-.125	.446	-.408
<u>Macrocyclus albidus</u> (c1-c2)	-.056	-.671	.233	-.610	-.085	-.317
<u>Ablabesmyia</u> sp. (3-4)	-	-	-	-	.114	-.299
Acari	-	-	-	-	.711	-.207
cyclopoida (c1-c2)	.065	-.651	.251	-.557	.131	-.125
Ceratopogonidae	-	-	-	-	.463	-.109
<u>Chydorus brevilabris</u>	.369	.242	-.443	.005	.609	-.081
<u>Macrocyclus albidus</u> (c6)	-.278	.089	-.378	.156	.586	.012
<u>Alona intermedia</u>	.293	-.385	.209	-.500	.211	.044
<u>Acantholeberis curvirostris</u>	.207	-.100	-.200	.120	.469	.061
Oligochaeta	-	-	-	-	.722	.069
<u>Ferrissia</u> sp.	-	-	-	-	.533	.030
non-tanypod Chironomids	-	-	-	-	.733	.116
<u>Ablabesmyia</u> sp. (1-2)	-	-	-	-	.715	.169
<u>Macrocyclus albidus</u> (c3-c5)	-.110	.368	.019	.318	.641	.181
<u>Oxyetira</u> sp.	-	-	-	-	.490	.201
<u>Acroperus</u> cf. <u>harpae</u>	.617	-.095	.378	-.157	-.075	.210
<u>Alona</u> cf. <u>affinis</u>	-.161	.621	-.282	.652	.707	.244
<u>Ilyocryptus</u> sp.	.121	.595	-.083	.714	.493	.312
<u>Chydorus piger</u>	.348	.431	-.004	.487	.372	.330
<u>Eucyclops agilis</u> (c6)	.249	-.283	.487	-.063	.173	.359
<u>Enallagma carunculatum</u>	-	-	-	-	.531	.467
<u>Ophryoxus gracilis</u>	.644	.084	.560	.120	.149	.473
<u>Streblocerus serricaudatus</u>	.599	.271	.280	.544	.322	.510
<u>Ceratotina</u> sp.	-	-	-	-	.081	.581
<u>Alonella</u> sp.	.625	.204	.119	.079	.025	.597
<u>Eucyclops agilis</u> (c3-c5)	.239	-.007	.676	.166	.205	.647
<u>Chydorus linguilabris</u>	.592	.242	.568	.407	.203	.760
explained variance (%)	17.4	11.9	18.6	15.6	22.1	14.9

Table 1.10. Pearson correlation coefficients between habitat variables and first and second axes of PCAs for microcrustacean proportions (box samples only).

	Axis 1	Axis 2
% <u>Eriocaulon septangulare</u> ^a	-.16	-.13
% <u>Pallavicinia lyellii</u>	-.72***	-.13
% <u>Sphagnum</u> sp.	-.26*	-.34***
% <u>Scirpus subterminalis</u>	.61***	.16
% <u>Potamogeton confervoides</u>	.42***	.16
% group B	.77***	.24*
Temperature (°C)	-.01	-.07***
Julian date	-.07	.64***

Probability (p) of obtaining the estimated r^2 value if the true value is zero (two-tailed test) (df=90): * - P<.05, ** - p<.01, *** - p<.001. Probabilities have not been corrected for multiple comparisons.

^a - all percentages were arc-sine square-root transformed before analysis.

September and October, whereas taxa with negative loadings were most abundant in June and July.

The first axis of the PCA of absolute abundance data (numbers per box sample) was strongly correlated with both total macrophyte surface area and date (Table 1.11). Because group A macrophytes dominated total macrophyte surface area, axis 1 is also correlated with the surface area of these species. I interpret axis 1 as a reflection of two trends: 1) Epiphytic invertebrates are associated with macrophyte surfaces and their abundance increased with total macrophyte surface area. 2) Most epiphytic invertebrates increased in Jack Lake from spring to fall (Chapter 2). Most taxa had positive loadings on axis 1.

Differences in invertebrate communities on group A and B macrophytes were expressed most strongly on axis 2. This axis was positively correlated with the surface area of group B macrophytes and negatively correlated with the surface area of group A macrophytes. Axis 2 was also positively correlated with date. On all dates, box samples containing group B macrophytes had higher scores on axis 2 than samples with group A macrophytes. This suggests that invertebrate communities on group A macrophytes were always uniquely different from those on group B macrophytes.

Consideration of both axes 1 and 2 aided interpretation of species loadings (Table 1.8). Taxa with high loadings on

Table 1.11. Pearson correlation coefficients between macrophytes ($\text{cm}^2 \cdot \text{box}^{-1}$), other habitat variables and first and second axes of PCAs for numbers of invertebrates per box sample. All macrophyte biomasses were fourth-root transformed before analysis.

	Axis 1	Axis 2
<u>Eriocaulon septangulare</u>	.160	-.223*
<u>Pallavicinia lyellii</u>	.557***	-.452***
<u>Sphagnum</u> sp.	.104	-.042
<u>Scirpus subterminalis</u>	-.141	.349***
<u>Potamogeton confervoides</u>	.283**	.309**
group A	.596***	-.474***
group B	.003	.596***
Temperature ($^{\circ}\text{C}$)	-.161	-.192
Julian date	.533***	.532***

Probability (p) of obtaining the estimated r^2 value if the true value is zero (two-tailed test) (df=90): * - $p < .05$, ** - $p < .01$, *** - $p < .001$. Probabilities have not been corrected for multiple comparisons.

axis 1 and low loadings on axis 2 were most strongly associated with group A macrophytes and included Diacyclops nanus, anisoptera, Procladius, Disparalona acutirostris, and Camptocercus sp.. Taxa with low loadings on both axes 1 and 2 tended to have maximum abundances in spring (c1-c2 copepodids, instars 3 and 4 Ablabesmyia sp., Alona intermedia) and macrophyte associations for these groups are unclear. Species with strong positive loadings on axis 2 were associated with group B macrophytes (Chydorus linguilabris, Eucyclops agilis, Alonella sp., Ceratotina sp.) and most also increased in abundance in September-October. Several species of microcrustacea, including Alona cf. affinis, Streblocerus serricaudatus, Ilyocryptus sp., and M. albidus, were abundant in samples containing both group A and B macrophytes. Results of ordinations using microcrustacean proportions and absolute abundances were generally in close agreement.

Qualitative samples from water lilies (Nuphar variegatum) revealed the presence of a unique microcrustacean assemblage (Table 1.12). Alona guttata, Pleuroxus straminus, and Polyphemus pediculus were common on N. variegatum in August, 1986 but were always extremely rare on submerged macrophytes. The relative abundances of Alonella sp., Acroperus cf. harpa, and Eucyclops speratus were also much higher on water lilies than in other habitats.

Table 1.12. Mean abundance of invertebrates (numbers per box sample) on water lilies (N. variegatum), August 20, 1986.

<u>Taxon</u>	<u>Mean number per box sample (n=3)</u>
Cladocera	
<u>Alonella</u> sp.	30
<u>Acroperus</u> cf. <u>harpae</u>	50
<u>Alona</u> <u>guttata</u>	74
<u>Pleuroxus</u> <u>straminius</u>	9
<u>Polyphemus</u> <u>pediculus</u>	7
<u>Ophryoxus</u> <u>gracilis</u>	1
Copepoda	
<u>Eucyclops</u> <u>speratus</u> (c3-c6)	20
<u>Macrocyclops</u> <u>albidus</u>	1
calanoids (c1-c2)	6
Chironomidae	25
Arachnida	7
Oligochaeta	2
Ceratopogonidae	1

In summary, the absolute and relative abundance of many littoral microcrustacea varied among sediments, group A and B macrophytes, water lilies, and the water column. These differences are summarized in Figure 1.3. Unfortunately, strong intercorrelations among macrophyte species prevented the detection of finer differences in the spatial distribution of littoral invertebrates. Numbers of invertebrate predators also varied among habitats. Tanypod chironomids and M. albidus were predominant benthic predators; Ablabesmyia sp., M. albi.us, Enallagma carunculatum, and water mites were common on all macrophytes; anisopteran odonates were associated with group A macrophytes and Cerrotina sp. was most abundant on group B macrophytes. The predominant predators in the water column were Chaoborus americanus and Epischura nordenskioldi.

2) Vertical migration of littoral microcrustacea in the shallow littoral zone:

Estimates of lake bottom densities (numbers \cdot m⁻²) of Cladocera, copepods and chironomids obtained using funnel traps were approximately one-tenth of estimates from core samples (Table 1.13). All differences between core and funnel trap samples were statistically significant (t-tests, $p < .05$).

Numbers of cyclopoids and chydorid and macrothricid

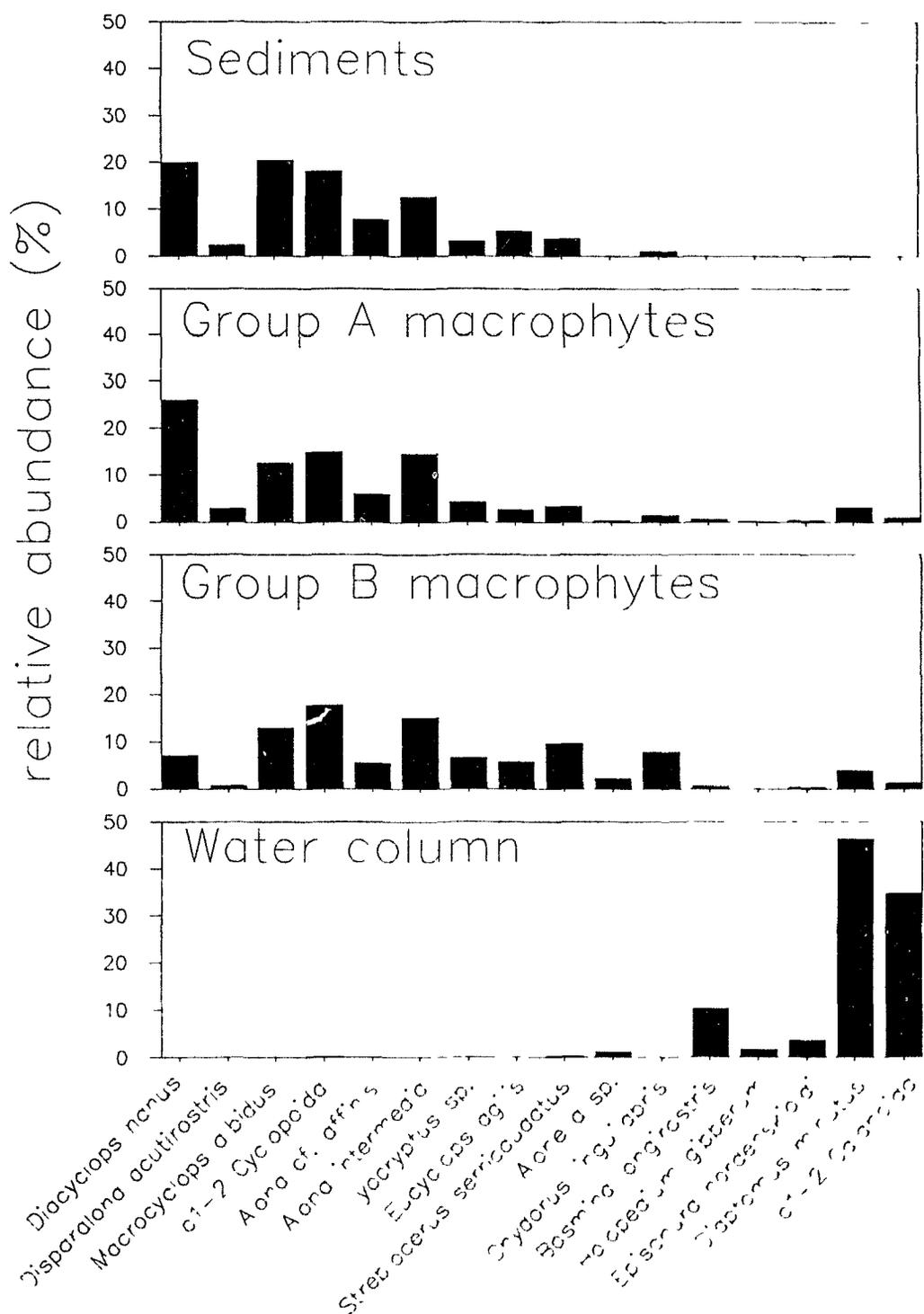


Figure 1.3. Mean percentages of common microcrustacea in different microhabitats in Jack Lake. Proportions on macrophytes were estimated from box samples containing greater than 75% group A or B macrophytes by surface area.

Table 1.13. Mean abundance (numbers · m⁻²) of common invertebrate groups in core and funnel trap samples, May 27, 1986. Numbers in brackets are one standard error.

	Cladocera	Copepoda	Chironomids
funnel traps (n=4)	443.4 (90.8)	2275.1 (812.0)	1478.3 (231.8)
cores (n=5)	3742.2 (957.4)	20582.1 (6101.9)	15592.5 (3389.8)

Cladocera increased only slightly in zooplankton samples collected at night versus day in August 1988 (Figure 1.4). The mean abundance of 3 planktonic species, Epischura nordenskioldi, Diaphanasoma birgei and H. gibberum, increased significantly in night samples. Numbers of Diaptomus minutus decreased at this time. Taken together, the funnel trap, core and zooplankton data suggest that few benthic or epiphytic animals moved into the water column at night.

3) Depth distribution of macrophytes and epiphytic invertebrates:

On August 27, 1986, the thermocline in Jack Lake occurred at a depth of 4.5 m. The biomass of macrophytes varied among depth strata (Table 1.14). Eriocaulon septangulare and Fallavicinia lyellii only occurred at depths less than 2 m and Scirpus subterminalis and Potamogeton confervoides dominated macrophyte biomass between 2 and 4 m. Below 4 m, large amounts of an unidentified moss were encountered. It is uncertain whether this moss was living at the time of collection.

Surface densities (numbers per cm² of macrophyte surface area) of common invertebrates in different depth strata are illustrated in Figure 1.5. Cluster analysis of microcrustacean proportions in box samples indicated that the invertebrate community below 4 m was different from that

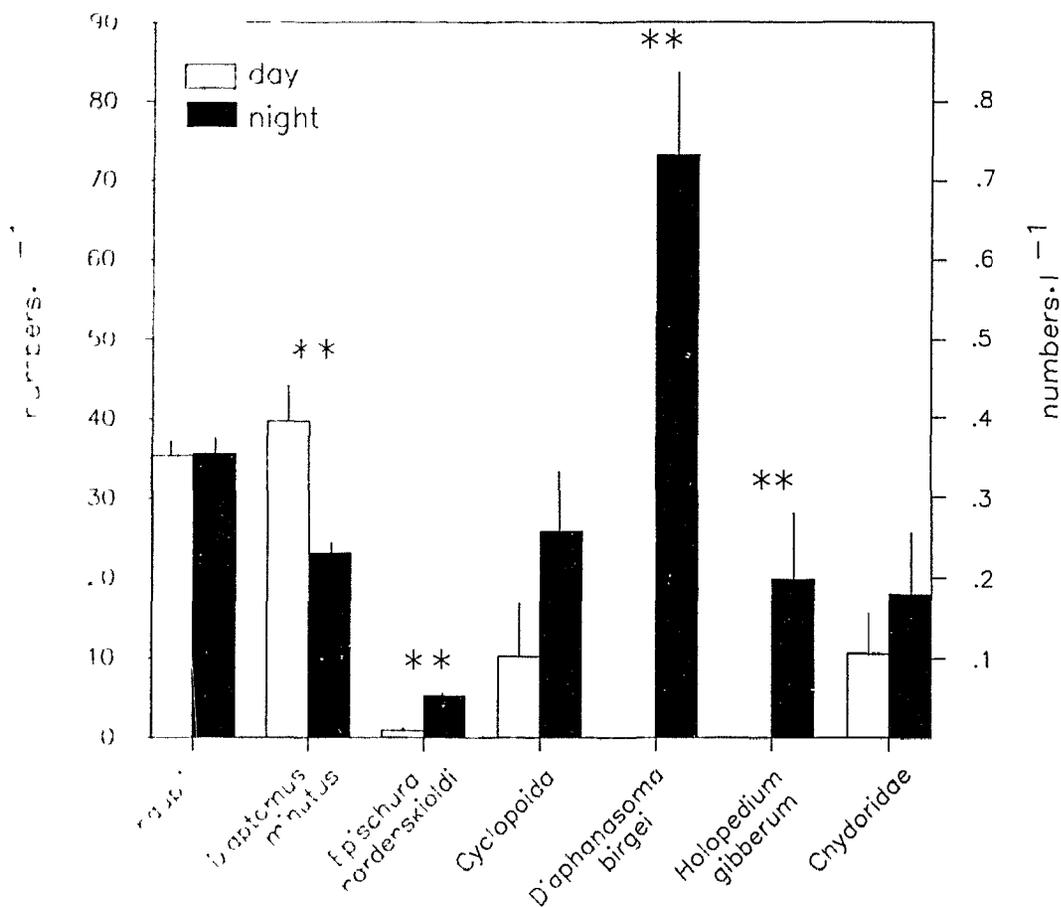


Figure 1.4. Densities of zooplankton collected during the day and night, 18 August 1988. Vertical lines represent + one standard error. Results of t-tests are indicated as * $p < 0.05$, ** $p < 0.01$. Probabilities have not been corrected for multiple comparisons. Note different scales on left and right halves of plot.

Table 1.14. Common macrophytes ($\text{g}\cdot\text{m}^{-2}$) and physical-chemical variables at different depths in Jack Lake, August 27, 1986. Numbers in parentheses are one standard error. At depths shallower than 4 m, moss was Sphagnum sp.. Moss occurring below 4 m was not identified. Physical-chemical measurements are for the middle of each depth zone.

	0-2 m (n=6)	2-4 m (n=6)	4-6 m (n=5)
<u>Macrophytes</u>			
<u>Eriocaulon</u> <u>septangulare</u>	15.47 (9.76)	0.0	0.0
<u>Pallavicinia</u> <u>lyelli</u>	12.05 (10.89)	0.0	0.0
Moss	0.47 (0.20)	1.24 (0.91)	59.18 (30.17)
<u>Scirpus</u> <u>subterminalis</u>	9.63 (6.11)	12.16 (3.46)	0.36 (0.14)
<u>Potamogeton</u> <u>confervoides</u>	0.64 (0.52)	0.36 (0.14)	0.0

<u>Physical-chemical parameters</u>			
Temperature ($^{\circ}\text{C}$)	17.0	16.8	10.9
pH	4.6	4.6	4.6
Oxygen ($\text{mg}\cdot\text{l}^{-1}$)	11.6	11.2	7.1

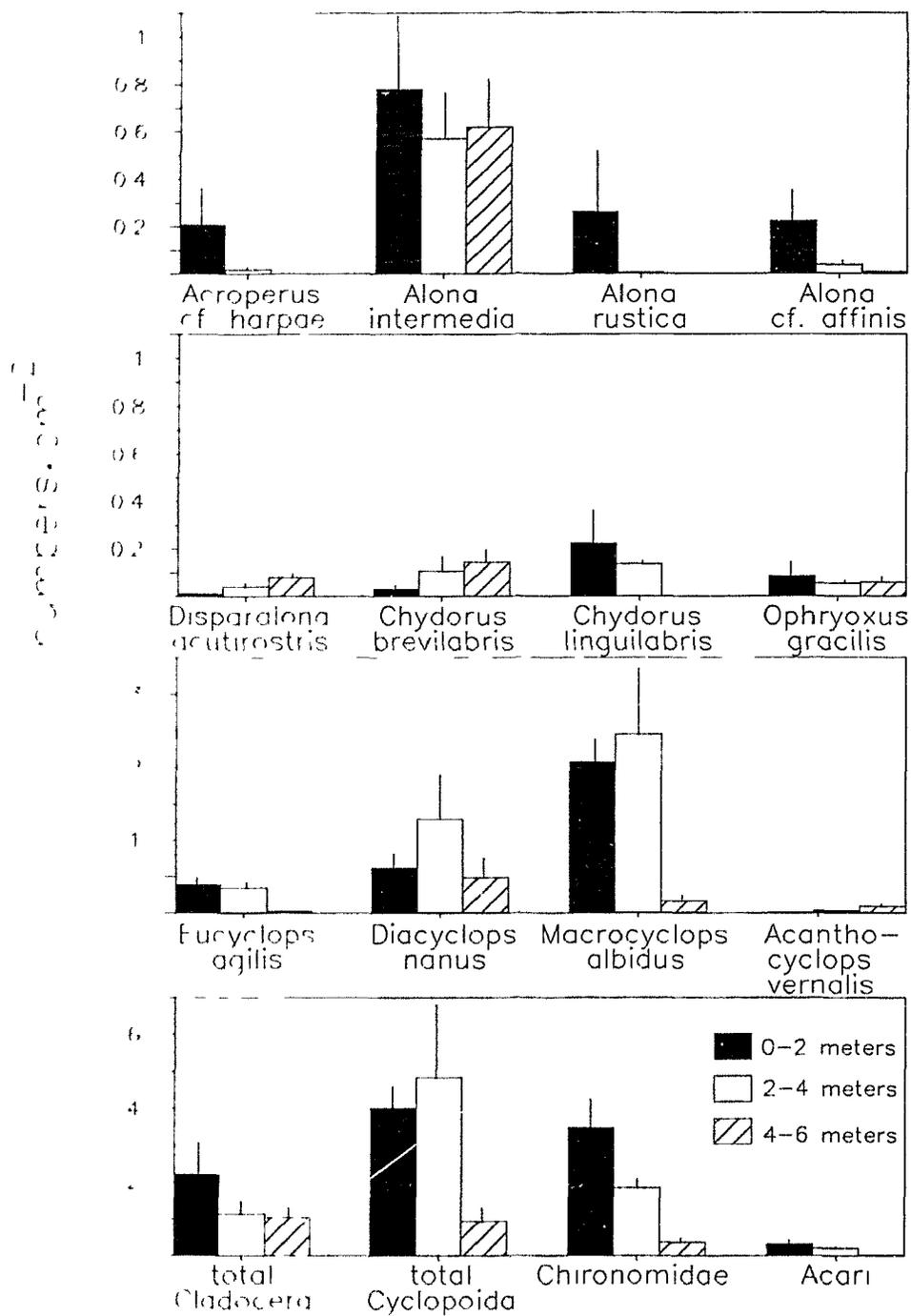


Figure 15. Surface densities of epiphytic invertebrates in different depth strata, 27 August 1986. Vertical lines represent + one standard error.

in the epilimnion (Figure 1.6). Samples below 4 m were characterized by increased densities of Disparalona acutirostris, Chydorus brevilabris, and Acanthocyclops vernalis and lower densities of Chydorus linguilabris, Alona rustica, Alona cf. affinis, M. albidus, and Eucyclops agilis. There was no indication that the invertebrate assemblage on group B macrophytes varied among depths in the epilimnion.

E. Discussion

1) Invertebrate distribution in the shallow littoral zone:

Large numbers of invertebrates were associated with macrophytes in the littoral zone of Jack Lake. This suggests that epiphytic organisms should be included in estimates of lake-wide invertebrate abundance, biomass, and production. This will be especially true for small lakes with well developed littoral zones.

A large number of studies have demonstrated that the distribution of littoral macroinvertebrates varies among different species of macrophytes, the sediments and the water column (Krecker 1939; Andrews and Hasler 1943; Rosine 1955; Krull 1970; Soszka 1975a; Voshell and Simmons 1977; Dvorak and Best 1982; Gilinski 1984; Keast 1984; Scheffer et al. 1984; Hershey 1985; Cyr and Downing 1988a,b; Hargeby 1990). Several studies have also demonstrated that microcrustacean distribution varies among littoral habitats (Smyly 1957; Quade 1969; Phoenix 1976; Whiteside et al. 1978; Frenzel 1982; Flössner 1985; DiFonzo and Campbell 1988; Benzie 1989). There are few records of the distributions of microcrustacean species encountered in this study. In Jack Lake, Diacyclops nanus and Disparalona acutirostris were most common in sediments and on macrophytes near the sediment-water interface. In other studies, these species have also been found primarily in sediments of the littoral and profundal

zones (Fryer 1953; 1968; Smirnov 1974; Daggett and Davis 1974a; Hare and Carter 1976; Holopainen and Paasivirta 1977; Strayer 1985). The distribution of other microcrustacea varied from distributions reported previously. Chydorus piger and members of the genus Ilyocryptus usually occur only in sediments (Cole 1955; Smyly 1958; Fryer 1968, 1974; Griffiths 1973; Fryer 1974; Chirkova and Romanenko 1973; Whiteside et al. 1978; Chengaleth 1982; Whiteside and Lindegaard 1982; Flössner 1985; Strayer 1985). In Jack Lake, these taxa were most common in macrophyte samples. Because cladoceran taxonomy is currently under revision (Frey 1982, 1986), it is possible that the species encountered in other lakes differ from those in Jack Lake. Most epiphytic and benthic microcrustacea in Jack Lake occurred frequently in samples from all habitats except the water column. In part, the failure to recognize distinct distributions in Jack Lake results because submerged macrophytes and sediments occurred in close proximity and samples did not retain animals from each habitat exclusively. Nonetheless, these results suggest that the microhabitat distributions of many littoral microcrustacea are highly flexible.

Because the results from Jack Lake are correlative, the causes of observed distributions cannot be ascertained absolutely. Some potentially important factors influencing spatial distributions include: 1) algal and detrital food

resources, 2) competition, 3) predation, 4) chemical conditions (cf. Pip and Stewart 1976) and 5) habitat permanence (Hargeby 1990).

Most of the microcrustaceans in Jack Lake are herbivores and detritivores (Fryer 1957b; 1968; 1974; Chirkova and Romanenko 1973; Sergeev 1973; Smirnov 1974; Downing 1981a; Meyers 1984a). Different species are apparently adapted to exploit different algal and detrital resources (Fryer 1957a; 1968; 1974) and their distributions may reflect local variations in food quality and availability. The upright stems of group B macrophytes grew closer to the water surface and probably supported different algal communities than group A macrophytes. Dense clouds of filamentous algae surrounded group B macrophytes and entrapped considerable amounts of fine detritus.

Diaptomus minutus, B. longirostris, H. gibberum, and Diaphanasoma birgei were dominant in water column samples and are adapted to feed on suspended algae. The occurrence of these zooplanktonic species in box samples probably reflects their presence in water near submerged macrophytes. Densities of planktonic invertebrates were similar in box and tube samples (Chapter 2) and were not correlated with macrophyte surface area. There was no evidence that planktonic microcrustacea are repelled by macrophytes as suggested by Gehrs (1974).

Microcrustacean densities and species composition may also have been affected by the presence of different predators in different habitats. Additionally, different microhabitats may provide varying degrees of protection from predator attack (cf. Stoner 1982; Coull and Wells 1983; Folsom and Collins 1984; Diehl 1988; Dionne and Folt 1991). Strong negative correlations between the densities of predators and prey were not found, once macrophyte surface area and date had been taken into account.

Many factors potentially affected the distribution of predators in Jack Lake. Large anisopterans were probably unable to climb on the thin blades of group B macrophytes. L. glacialis and Cordulia shurtleffi in samples containing only these macrophytes always had headwidths of less than 1.5 mm. Scirpus subterminalis and Potamogeton confervoides may have provided a refuge from predation by anisopterans for Cernotina sp. Remains of Cernotina were frequently encountered in anisopteran faecal pellets (Chapter 2). Competition among predators may also have influenced their distributions.

The influence on invertebrates of macrophyte exudates (Pip and Stewart 1976) or the persistence of different macrophyte species (Hargeby 1990) could not be assessed in this study.

2) Vertical migration of littoral microcrustacea: Although nightly vertical movements of littoral microcrustacea have

been observed in several studies (Whiteside 1974; Evans and Stewart 1977; Fairchild 1981; Campbell et al. 1982; Meyers 1984a; Timms and Moss 1984), few epiphytic and benthic microcrustacea migrated into the water column in Jack Lake. Meyers (1984a) suggested that many chydorid Cladocera are facultative planktivores that move upward at night to utilize phytoplankton. In Jack Lake low edible phytoplankton concentrations may have precluded vertical migration. Low phosphorus concentrations (Table 1.1), low zooplankton numbers, and low abundance of littoral filter-feeders (for example Simocephalus, Sida) suggest limited phytoplankton availability. Nightly decreases of oxygen concentrations in the littoral zone of Jack Lake may also have been less than in previously studied lakes. Many littoral crustacea show strong vertical movement with declining oxygen concentrations (Papinska and Prejs 1979; Meyers 1980; Tinson and Laybourn-Parry 1985).

Numbers of H. gibberum, Diaphanasoma birgei, and Epischura nordenskioldi increased in zooplankton samples taken at night. These increases were probably caused by vertical migration of zooplankters from water surrounding submerged macrophytes. Alternatively, transverse movement of animals between the pelagic and littoral zones cannot be ruled out (cf. Kairesalo 1980; Franke 1983; Davies 1985).

3) Depth distributions: Cluster analysis indicated that

the epiphytic microcrustacean community in the hypolimnion of Jack Lake differed from that in the epilimnion. Physical and chemical conditions in the hypolimnion, such as low water temperature and oxygen concentrations, may have directly and indirectly influenced distributions. For example, many microcrustacea are intolerant of low oxygen levels (Moore 1939; Cole 1955; Strayer 1985; Tinson and Laybourn-Parry 1985, 1986).

Microcrustacea may also have been affected by changes of macrophyte composition with depth. All samples collected in the epilimnion included Scirpus subterminalis and Potamogeton confervoides, while all hypolimnetic samples included only an unknown species of moss. Microcrustacean species that declined in the hypolimnion tended to be those that were most abundant on S. subterminalis and P. confervoides in the shallow littoral zone (Eucyclops agilis, Chydorus linguilabris). Species with increased densities in the hypolimnion were most common in sediments and on group A macrophytes in shallow water (Disparalona acutirostris, Chydorus brevilabris).

Food resources almost certainly changed with water depth. Light levels declined in the hypolimnion and probably led to an increased dependence of epiphytic and benthic food webs on detrital resources. Microcrustacean species that declined in abundance offshore may be most reliant on algae, whereas

those that increased may depend more on detritus. Because S. subterminalis and P. confervoides grow into the water column, microcrustacea that predominate on these species in the shallow littoral zone may also be those that depend most on algal food.

Inadequate numbers of most predators were collected to assess their depth distributions accurately. Densities of M. albidus and water mites decreased in the hypolimnion. Odonates, tanypod midges, and Cernotina sp. were found at all depths, with general decreases of abundance in the hypolimnion. Studies in other lakes suggest that odonate and trichopteran abundance usually decreases offshore (Benke and Benke 1975; Keast and Harker 1977; Thorp and Diggins 1982; Strayer 1985; Wissinger 1988).

4) Sampling of littoral invertebrates: The results of this chapter highlighted several problems with two common methods of sampling littoral invertebrates.

a) Funnel traps: Funnel traps have been employed in many studies to sample littoral microcrustaceans quantitatively (Whiteside 1974; Whiteside et al. 1978; Williams 1982; Bohanan and Johnson 1983; Meyers 1984a; Johnson et al. 1987). In Jack Lake, estimates of total microcrustacean abundance obtained using funnel traps were less than 20% of core sample estimates. Estimates of microcrustacean abundance obtained using funnel traps over macrophytes in July 1988 (unpublished

data) were also less than 10% of abundance estimates obtained using box samples in July-August 1986 and 1987. Although my results suggest that funnel traps grossly underestimate microcrustacean numbers, Whiteside and Williams (1978) and Meyers (1984a) found that funnel traps captured more than 90% of chydorid cladocerans on underlying macrophytes. Before funnel traps are used in other studies, care should be taken to compare results with alternative sampling techniques.

b) Ratios and the sampling of epiphytic invertebrates:

Most invertebrates in the littoral zone are poor swimmers and live in close association with the surfaces of macrophytes and sediments. Lake bottom densities of epiphytic invertebrates are a function of 1) numbers per unit of macrophyte (for example numbers per cm^2 of macrophyte surface area) and 2) the density of macrophytes per m^2 of lake bottom. Estimates of both bottom and surface densities are important to the assessment of interactions among epiphytic organisms. Encounter rates among epiphytic invertebrates and the strength of biotic interactions are probably strongly influenced by local surface densities. Because macrophyte surface area changes seasonally, changes in surface densities may only reflect increases or decreases of available habitat and not actual changes in population size. Hence, changes in population size, birth rates, and death rates need to be evaluated using lake bottom densities

or, preferably, total numbers of invertebrates in a lake. The latter approach is rarely practicable.

Although many samplers have been proposed to determine epiphytic lake bottom densities directly (reviewed by Downing 1984), most are highly destructive, difficult to employ, and result in unacceptable disturbance of macrophytes and loss of invertebrates (Downing and Cyr 1985; personal observations). As a result, many researchers independently assess numbers of epiphytic invertebrates per unit of macrophyte and the density of macrophytes per unit of lake bottom. These estimates are then combined to obtain estimates of epiphytic invertebrate lake bottom densities (Soszka 1975a; Menzie 1980; Fairchild 1981; Keast 1984; Iversen et al. 1985; Rasmussen 1988). This approach was used in this thesis.

With current sampling techniques, it is rarely possible to collect standard amounts of macrophyte surface area. Instead, numbers of invertebrates per sample are typically divided by the biomass or surface area of collected macrophytes. Unfortunately, the use of the resulting ratios has several important limitations:

- i) When epiphytic invertebrate abundance is expressed as a ratio, numbers are implicitly assumed to increase linearly with macrophyte surface area (or biomass) and to have an intercept of zero (Packard and Boardman 1988). Regression

equations relating macrophyte surface area and invertebrate abundance from Jack Lake (e.g. Table 1.4) frequently had large intercepts that were significantly greater than zero. These intercepts can be interpreted in different ways: 1) They may reflect numbers of animals not associated with macrophytes (for example, animals living in the water immediately surrounding macrophytes (Downing 1986)). 2) They may be statistical artifacts caused by variations of invertebrate surface densities among macrophyte species and the collinearity among macrophytes in box samples. 3) Because of the high variability of epiphytic invertebrate numbers, it was not possible to rule out nonlinear relations between invertebrate abundance and macrophyte surface area.

ii) Biotic interactions are often inferred from correlations between the temporal and spatial distributions of different organisms. The use of densities expressed as ratios with a common denominator (for example, numbers per unit of macrophyte) may lead to high, spurious correlations (Atchley et al. 1976; Jackson et al. 1990).

Ideally, the use of ratios can be avoided by using regression approaches (Cochran 1977; Downing 1986):

$$Y = a + b_1 X_1 + b_2 X_2 + \dots + b_j X_j$$

where Y is the number of invertebrates in each box, X_1 to X_j are the biomass of different macrophytes, b_1 to b_j are the fitted regression coefficients and a is the y -intercept. The

biomass of different species of macrophytes per m^2 can be inserted into the resulting equation to estimate epiphytic invertebrate lake bottom densities. Unfortunately, attempts to use this approach in Jack Lake were confounded by strong collinearity among macrophyte species in box samples. Patterns of collinearity among macrophytes were different in box and quadrat samples and varied from date to date. As a result, estimated regression coefficients were highly unstable and it was not valid to estimate lake bottom densities using this approach (Neter et al. 1983).

In summary, the results from Jack Lake emphasize some common problems plaguing epiphytic invertebrate sampling approaches. Unfortunately, I am not aware of superior methods that can be utilized in most lakes. Regression methods may work in monospecific macrophyte stands, but care must be used in their application to mixed vegetation. Strong intercorrelations among macrophyte species in littoral samples are probably common and will be difficult or impossible to break. The collection of larger numbers of samples and the inclusion of more predictive variables (for example, algal abundance, detrital quantity and quality, etc.) may improve the strength of regression equations. In most studies, however, larger investments of time are probably not justified. More than 200 hours were often required to process samples from one day from Jack Lake.

Clearly, there is a need for improved sampling methodologies.

Chapter 2

Seasonal dynamics of littoral microcrustacea and invertebrate predators in Jack Lake

A. Introduction

In this chapter, I describe the seasonal dynamics of littoral microcrustacea and macrofauna in Jack Lake. My objective is to assess the ability of different invertebrate predators to influence the seasonal dynamics of littoral microcrustacea. The following specific questions are addressed: 1) How does microcrustacean community structure (abundance, species composition, size structure) change seasonally in the littoral zone of Jack Lake? 2) What are the most important invertebrate predators of microcrustacea in Jack Lake? 3) Is there evidence that seasonal changes in microcrustacean community structure are affected by changes in invertebrate predation pressure? I use two approaches to address this latter question: a) I examine seasonal changes in birth rates of the 5 most common species of epiphytic and benthic Cladocera. Population sizes reflect a balance between gains (births and immigration) and losses (mortality and emigration). If seasonal changes in birth rates cannot account for observed changes in abundance, this suggests that seasonal changes in loss rates, possibly reflecting predation mortality, may be important. b) I compare the seasonal dynamics of littoral microcrustacea and invertebrate predators. I sought evidence that seasonal changes of

microcrustacean community structure were accompanied by changes in predator abundance. Seasonal changes in invertebrate predation rates were also considered qualitatively. To my knowledge, this study is the first simultaneous comparison of the seasonal dynamics of different species of epiphytic and benthic microcrustacea and a suite of invertebrate predators.

B. Methods

Estimation of invertebrate abundance: During the ice-free seasons of 1986 and 1987, samples were collected from sediments, macrophytes and the water column in the shallow littoral zone (1-2 m) of Jack Lake using methods described in Chapter 1. The abundance of invertebrates in the water column was estimated from 10-25 tube samples collected on each sampling date. Benthic invertebrate abundance was determined from 5-10 cores and epiphytic invertebrate abundance was estimated from 7-15 box samples collected on each date. The above-ground biomass of different macrophytes was estimated from 10-15 quadrat samples in 1986 and 19-30 samples in 1987.

A three-week sampling interval was used in 1986 and a one-month interval in 1987. Because of the large amount of time required to process samples, more frequent sampling could not be undertaken. Examination of results from studies employing shorter sampling intervals (for example Goulden 1971; Keen 1973; Whiteside 1974; Williams 1982; Robertson 1990) suggests

that large transient changes in littoral microcrustacean abundance are rare and that monthly sampling should provide evidence of general changes in population size. In 1986, sampling of the water column, sediments, and macrophytes began at different times. Benthic samples were first collected on May 21, zooplankton on June 16, macrophytes on July 30, and epiphytic invertebrates on August 20. No benthic samples were collected in November. In 1987, all samples were collected from May 5 to November 15. One set of core samples and qualitative sweep net samples were collected through the ice on February 18, 1988. All samples were collected between 1000 and 1600 hours.

I have expressed epiphytic and benthic invertebrate abundances in two ways: 1) surface densities (numbers per cm^2 of leaf or sediment surface area) and 2) lake bottom densities (numbers per m^2 of lake bottom). The determination of lake bottom densities in Jack Lake is described in Chapter 1.

Because surface densities of epiphytic invertebrates are ratios and lake bottom densities were derived from surface densities, they must be regarded with caution (see discussion in Chapter 1). In practice, expression of the results from Jack Lake as surface densities, lake bottom densities, or numbers per box sample led to similar conclusions. I have relied on surface densities and lake bottom densities in the discussion below because they facilitated direct comparisons

between sediments and macrophytes. Plots of seasonal changes in mean numbers per box sample for common invertebrates are presented in Appendix 2.

Invertebrate population parameters: Different instars of insect predators were distinguished by measuring head widths (Odonata) and head lengths (Tanypodinae, Trichoptera). Measurements were made with an ocular micrometer at magnifications of 12-63X. Histograms summarizing headwidth and headlength frequencies with instar designations are presented in Appendix 3. Odonates usually pass through 9 to 16 instars during their development (Corbet 1980). I have followed convention and labelled successive instars as F for the final instar, F1 for the penultimate instar, etc. Trichoptera and dipterans usually pass through 5 and 4 larval instars, respectively. I have again followed convention and labelled successive instars as instar-1 for the youngest instar and instar-4 or 5 for the final larval instar. Note that this numbering scheme is reversed from that used for odonates.

The biomass of odonates was estimated using the following regression equations developed for species of similar morphology:

<u>Enallagma carunculatum</u>	$DW = .0784HW^{2.9724}$
	(Pierce et al. 1985)
<u>Cordulia shurtleffi</u>	$DW = .823HW^{1.788}$
	(Johnson et al. 1985)

Leucorrhinia glacialis

$$DW = .109HW^{3.168}$$

(Johnson et al. 1985)

other odonates

$$DW = .63HW^{2.51} \quad (\text{Smock 1980})$$

where DW is dry weight (mg) and HW is head width (mm).

For 1987 samples, total body lengths of copepods (exclusive of caudal setae) and Cladocera (to the base of the caudal spine, when applicable) were measured with an ocular micrometer at 63X (+/- 0.02 mm). Copepods typically undergo 12 development stages, including 6 naupliar stages, 5 copepodid stages and an adult stage (c6). Copepodids were separated into three groups: c1-2, c3-5, and c6 (adults). The biomass of microcrustacea was estimated using length-weight regressions described in Dumont et al. (1975), Bottrell et al. (1976), and McCauley (1984). If no regression was available for a given species, regressions for morphologically similar species were used.

Clutch sizes and birth rates of Cladocera: In 1987, I recorded the clutch sizes of the 5 most common species of epiphytic and benthic Cladocera in Jack Lake (Alona intermedia, Alona cf. affinis, Chydorus linguilabris, Ilyocryptus sp., Streblocerus serricaudatus). Instantaneous birth rates were estimated from (Paloheimo 1974):

$$b = \ln(E+1)/D$$

where E is the average number of eggs per mature parthenogenetic female (clutch size) and D is the egg development time in days (Edmondson 1960). Egg development

times are a function of water temperature (Hall 1964; Weglenska 1971; Edmondson 1974; Bottrell 1975) and were estimated using results in Keen (1973). Birth rate estimates may be strongly influenced by the proportion of non-reproductive juveniles in a population (Edmondson 1965; 1968). As a result, I estimated clutch sizes only for mature, parthenogenetic females. Sizes at maturity were determined separately for each species using the minimum size found bearing eggs (Figure 2.1). Large changes in the minimum egg-bearing size were not observed among sampling dates. Mean clutch sizes of Cladocera in sediment and box samples were never significantly different (t -tests; $p < .05$).

Birth rate estimates were used only to follow qualitative seasonal trends. There are several important limitations to these data:

- 1) The sampling interval (3 weeks to one month) almost always exceeded the egg development times of Cladocera (as short as 2 days in midsummer (Keen 1973; Robertson 1988)). Consequently, transient changes in birth rates may have been missed.

- 2) Egg development times vary among species and even populations of Cladocera (Monro and White 1975; Bottrell 1975; Meyers 1984b; Robertson 1988). Because of the confused state of littoral cladoceran taxonomy (Frey 1982; 1986), it is uncertain that development times listed in the literature refer to the same species as those identified from Jack Lake.

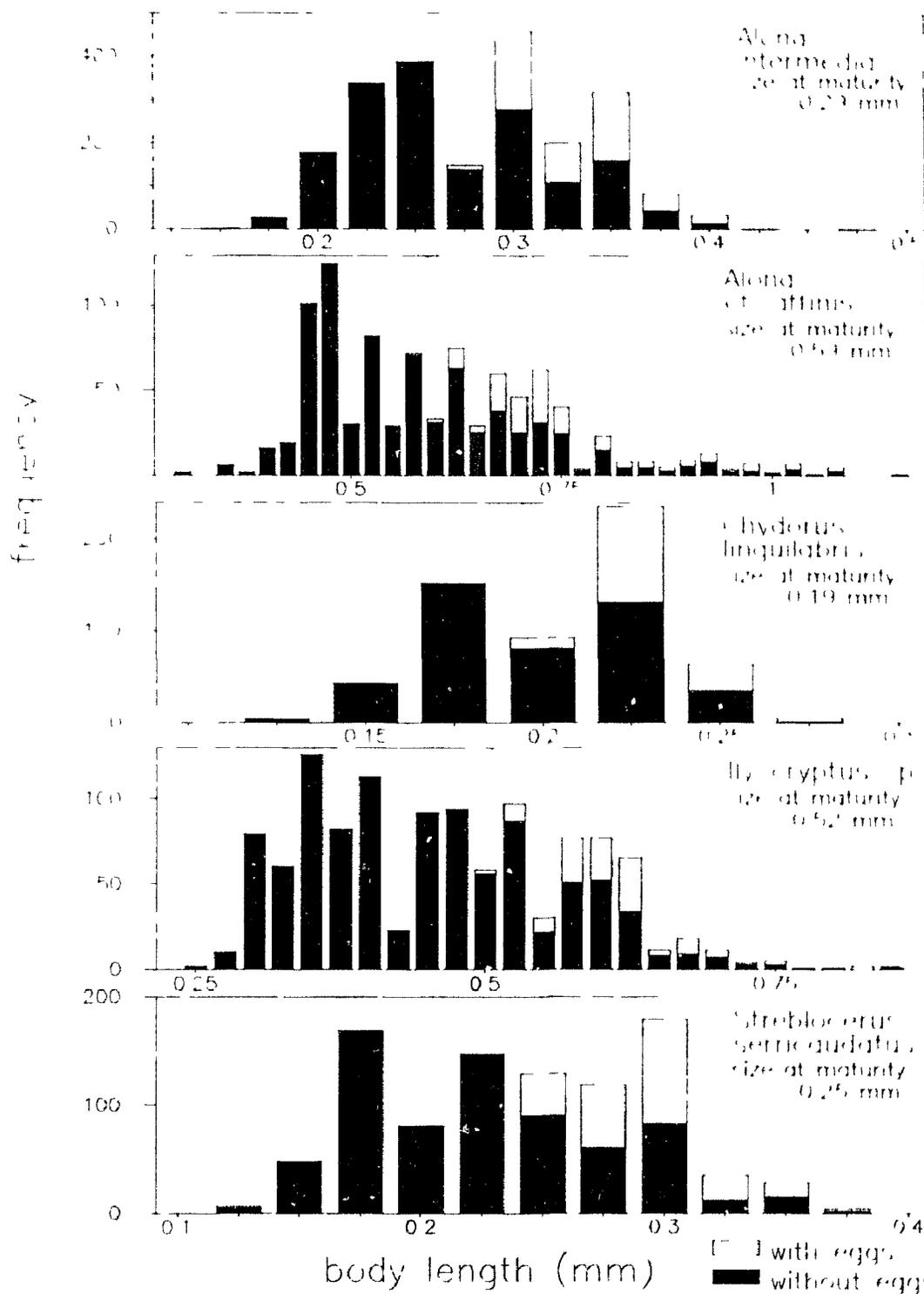


Figure 2.1. Overall size frequency distributions, and sizes at maturity for common Cladocera from Jack Lake, 1987. Open bars are ovigerous females. Males and ephippial females were omitted.

3) Eggs lost from brood pouches could not be identified amongst mud and detritus in samples and were not included in counts. Proportional losses of eggs were assumed to be constant across sampling dates.

Gut content analyses: Invertebrate predators were collected for gut analyses with a sweep net throughout the ice-free months of 1987. All invertebrates except odonates were immediately narcotized with carbonated water (Gannon and Gannon 1975). Individual animals were picked from samples and gut contents were isolated using a variety of techniques. For copepods, the urosome was separated from the cephalothorax using dissecting pins and gut contents were gently squeezed into a drop of glycerol and water under a coverslip. The head capsules of tanytoids and trichopteran larvae were pulled from the body, causing the gut to be dragged out behind. Gut contents were then teased out in a drop of glycerol and water. With odonates, live animals were placed for 48 hours in distilled water. During this time, they produced faecal pellets that were subsequently broken up under a coverslip.

For all guts and faecal pellets, recognizable prey fragments were tabulated separately using phase microscopy. The most abundant fragment, weighted by the number potentially contributed by one animal, was used to estimate numbers of prey consumed. If oligochaete setae were encountered, it was assumed that one animal was consumed.

Several factors potentially affected the interpretation of the gut content analyses: 1) Gut contents may vary according to the time of day when they were collected (Pearlstone 1973; Federenko 1975a; Lewis 1977; Johnson 1985). In this study, all invertebrates were collected between 1000 and 1400 hours. 2) Many organisms do not leave identifiable remains in the guts of predators. Furthermore, many predators only partially consume their prey, making identification of remains difficult. For example, cyclopoid copepods rarely ingest the shells of Cladocera (Fryer 1957a; Brandl and Fernando 1974; Kerfoot 1977; Li and Li 1979). As a result, Cladocera could be recognized only from small, easily overlooked parts such as post-abdominal claws, mandibles, and feeding appendages. 3) Many invertebrates may regurgitate or defecate during sampling (Davies and McCauley 1970). 4) Digestion times may vary among prey and leave the impression that more slowly digested items were preferentially selected (Lawton 1971a; Federenko 1975; Hildrew and Townsend 1982; Giguere 1986). 5) Frequently, it is difficult to separate the food of predators from food in the guts of their prey. 6) The presence of invertebrate remains may not reflect predation, but scavenging on dead carcasses (Thut 1969; Papinska 1985). As a result of these limitations, the results of the gut content analyses should be regarded as only crude indicators of predator diet in Jack Lake. Guts of water mites (Acari) could not be examined because they do

not ingest the hard parts of their prey (Pieczynski 1976; Paterson 1970; Riessen 1982).

Invertebrate predation rates: It was beyond the means of this study to estimate directly the predation rates of invertebrates in Jack Lake. As a result, seasonal changes in predation pressure were inferred primarily from changes in predator densities. Crude estimates of ranges of predation rates were made by reference to the literature and by combining results of gut content analyses and evaluations of gut passage times. To minimize the effects of variations of water temperature, these estimates were used only for data collected between June and September. Water temperatures in these months ranged from 16 to 22° C. Literature estimates of predation rates were invariably determined in the laboratory and probably varied considerably from natural predation rates. Physical-chemical conditions, prey densities, spatial heterogeneity, predator hunger levels, predator and prey sizes, and densities of alternate prey and predators were usually very different from those occurring in Jack Lake. The estimation of predation rates from gut contents and gut passage times is also fraught with difficulty (Lawton 1971a; Peckarsky 1984). Predation rate estimates were used only as rough guides of the potential impact of different predator groups.

Gut passage times for odonate larvae were measured in the laboratory at 14 and 22° C using an unidentified ostracod as

prey. Odonates were collected with a sweep net, returned to the lab, and allowed to feed on ostracods for 15 minutes. Odonates were then placed in vials of filtered water from Jack Lake and checked periodically for faecal pellet production. Ostracod remains were highly recognizable in faecal pellets and easily distinguished from remains of organisms from Jack Lake.

C. Results and Discussion

1) Physical-chemical parameters

Jack Lake froze over from early December to mid-April in both 1986 and 1987. Water temperatures rapidly rose after ice-out (Figure 2.2a), and stratification was established by late May at a depth of 3.5 to 4.5 m. Fall overturn occurred in September. Fluctuations of water level were small (less than 20 cm per year), with annual lows occurring in August (Figure 2.2b). Oxygen levels were always near saturation in the shallow littoral zone and seasonal pH fluctuations did not exceed 0.2 units.

2) Submerged macrophytes

All common species of submerged macrophytes in Jack Lake, except Potamogeton confervoides, retained viable tissue throughout the year. The above-ground biomass of macrophytes that grew near the sediment-water interface (Pallavicinia lyellii, Eriocaulon septangulare, Sphagnum sp.) increased from May to a peak in June-July and slowly declined thereafter (Figure 2.3a-c). These macrophytes were designated as group A macrophytes in Chapter 1. Two species of taller, grass-like macrophytes (Scirpus subterminalis, Potamogeton confervoides; designated as group B macrophytes in Chapter 1) increased from May to September and collapsed in October-November (Figure 2.3d-e). These collapsed shoots decayed over winter and new ramets grew through the mat of group A species the following spring. Group A macrophytes

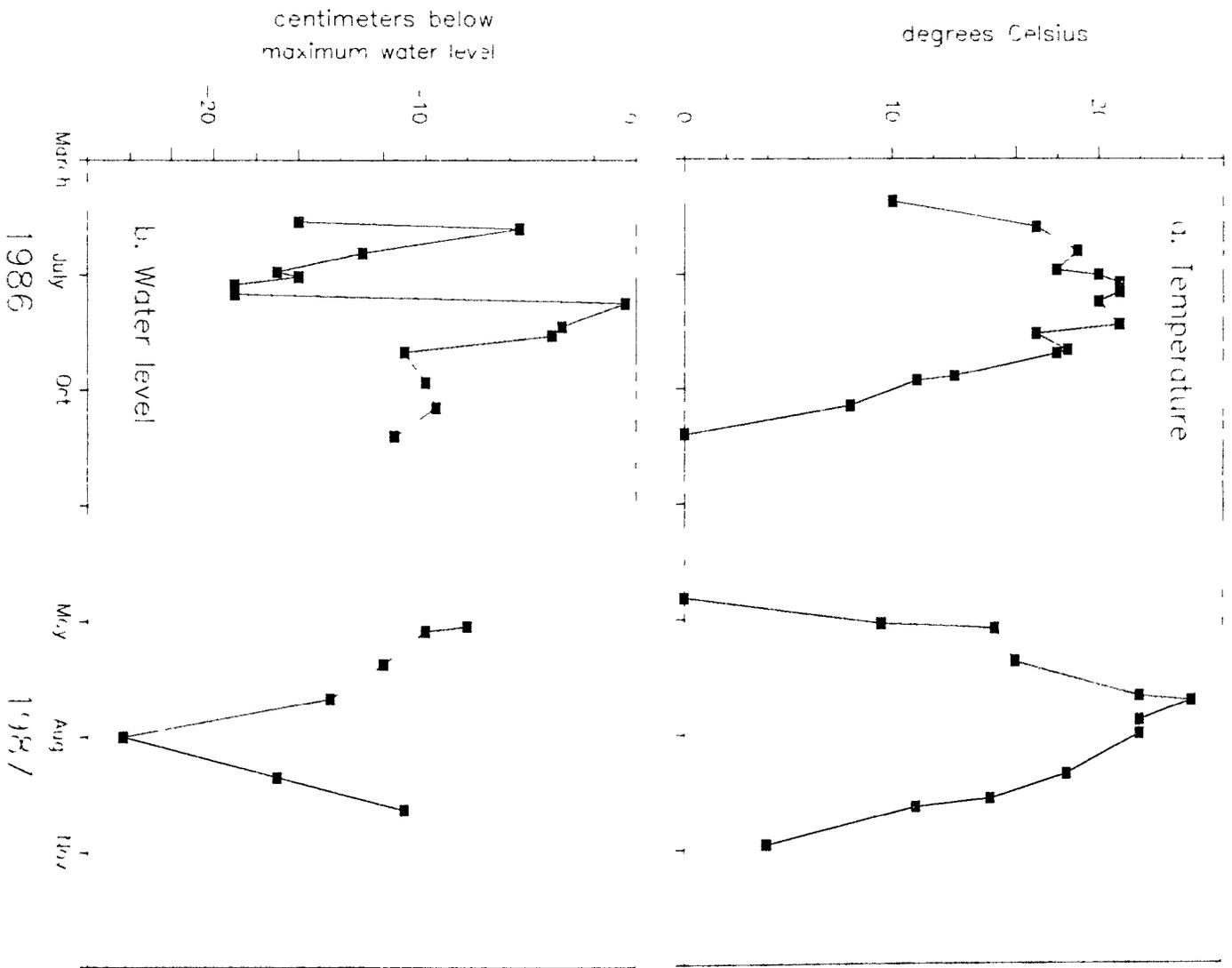


Figure 2.2. Seasonal changes of a) surface water temperature and b) water level in Jack Lake.

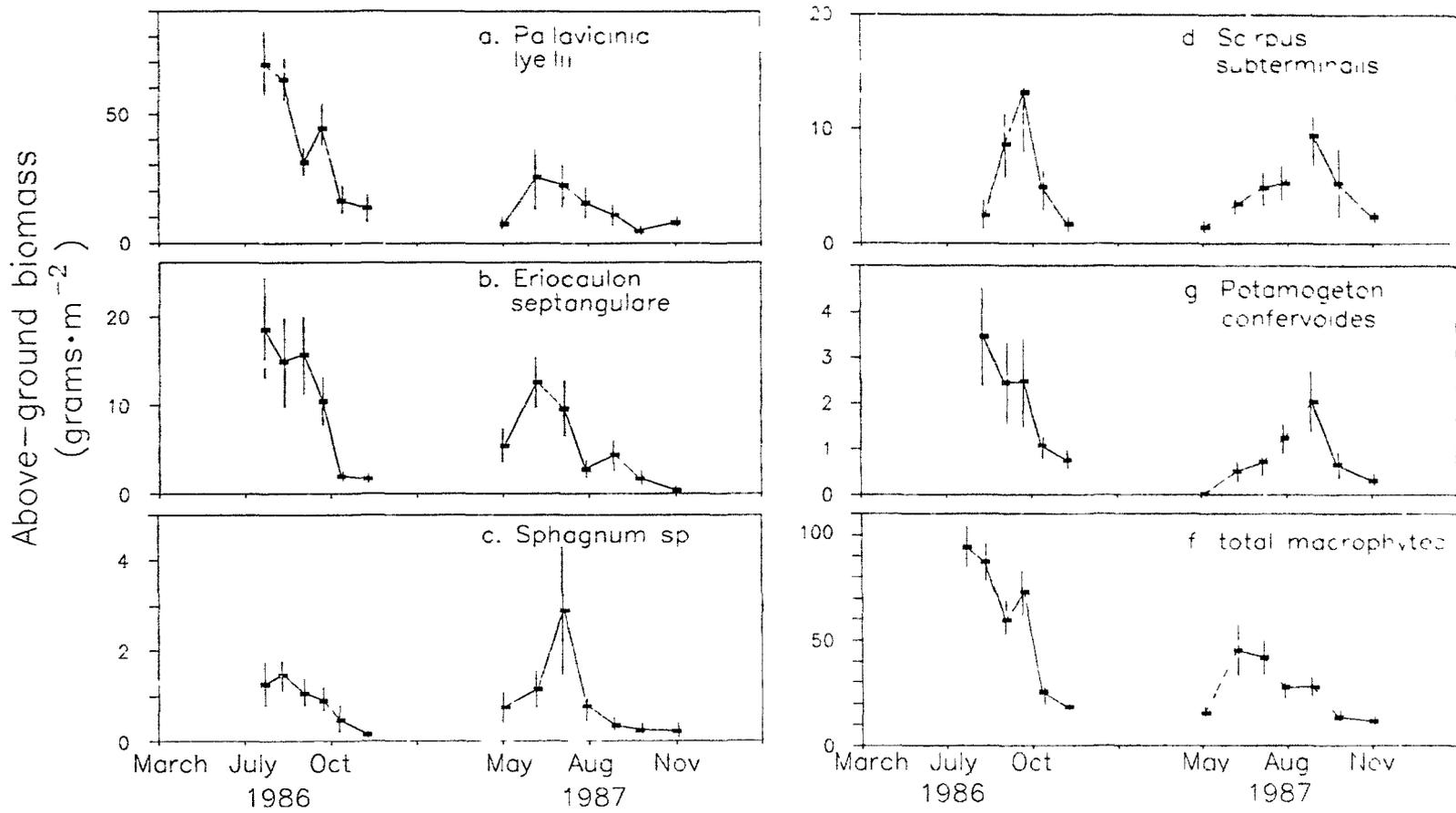


Figure 2.3 Above-ground biomass of common macrophytes in Juel Lake. Data for *Scirpus subterminalis* and *Potamogeton confervoides* are not available for samples collected in July 1986. Vertical lines represent \pm one standard error. Note that Y-axis scales vary among graphs.

dominated total macrophyte biomass, which peaked in June-July and declined thereafter (Figure 2.3f). Seasonal changes in total macrophyte surface area per m² of lake bottom closely paralleled biomass dynamics.

3) Microcrustacea

a) Zooplankton: The invertebrate community of the water column was dominated by a calanoid copepod, Diaptomus minutus (Figure 2.4a,b). Similar densities of this species were found in water surrounding macrophytes (box samples) and in the water column over macrophytes (tube samples). D. minutus apparently overwintered as adults. Although c1-c2 calanoid copepodids were not identified to species, most were probably D. minutus, and large numbers were encountered in May (Figure 2.4c). These developed to c3-c5 copepodids by June and adults by June-July. A second generation of D. minutus was evident from September to November in 1986. The only other calanoid copepod encountered in Jack Lake was Epischura nordenskioldi (Figure 2.4d,e). Numbers of this species peaked in August-September of both 1986 and 1987.

The species composition of planktonic Cladocera changed considerably between 1986 and 1987. Bosmina longirostris was abundant in June and September 1986, but was rarely encountered in 1987 (Figure 2.4f). Holopedium gibberum was more common in 1987 than in 1986 and numbers peaked in August-September (Figure 2.4g).

b) Epiphytic and benthic Cyclopoida: In 1987, surface

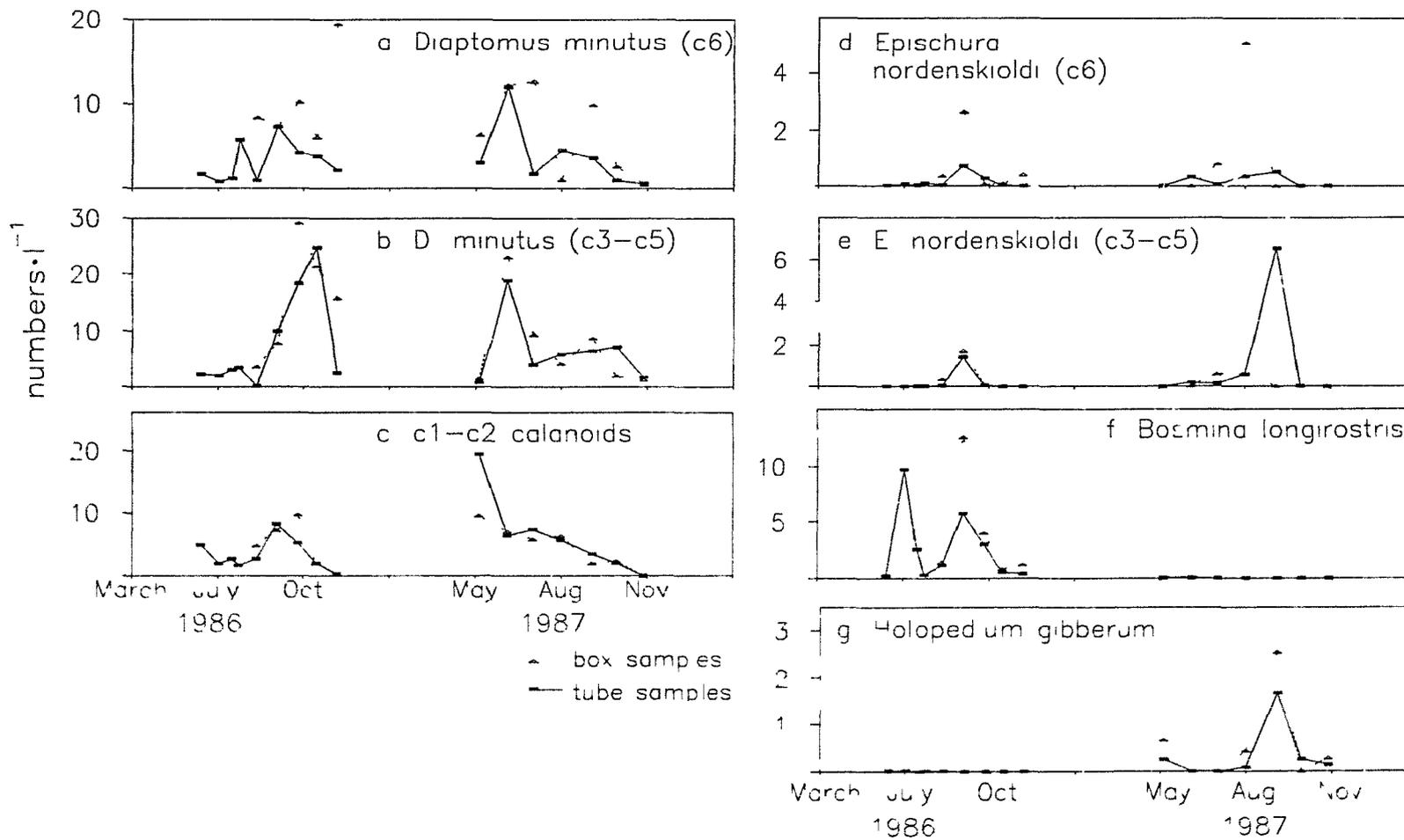


Figure 2.4 Seasonal abundance of zooplankton in Jack Lake. Note different density scales.

densities of epiphytic cyclopoids increased from May to June and were relatively stable thereafter (Figure 2.5a). Lake bottom densities of epiphytic cyclopoid copepods also increased from May to June in 1987 and then declined to November (Figure 2.5c). A similar pattern was evident in 1986. Changes in densities of benthic cyclopoids were different from those on macrophytes (Figure 2.5b). In both 1986 and 1987, benthic densities increased from May to July, decreased in August, and increased again in September-October. In 1987, both epiphytic and benthic cyclopoid biomass followed a bimodal pattern on macrophytes and in sediments, with peak biomasses in June-July and September (Figure 2.5d). The mean size of the cyclopoid community was high in May 1987, declined between June and August, and increased in September-October (Figure 2.5e).

Three cyclopoid species, Diacyclops nanus, Eucyclops agilis, and Macrocyclus albidus, dominated the benthic and epiphytic copepod community of Jack Lake. These species had similar seasonal dynamics (Figure 2.6, Figure 2.7). Each species overwintered in late copepodid and adult stages (Table 2.1) and had a strong burst of reproduction shortly after ice-out. Early instar copepodids were abundant in June and these developed to adults by July. A second generation of c1-c2 copepodids occurred in August-September and developed to adults by October-November. M. albidus had the most highly synchronized seasonal cycle while D. nanus

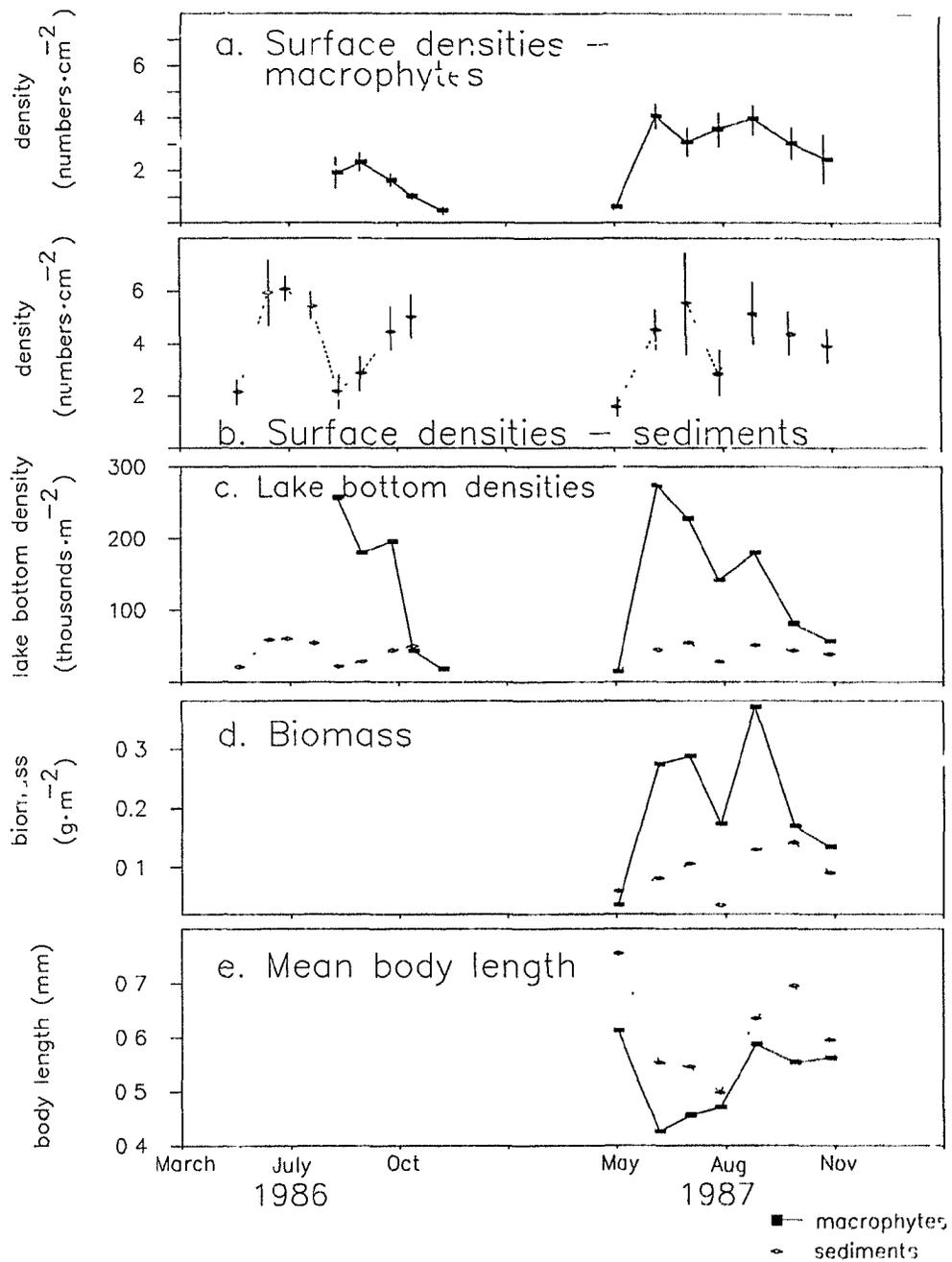


Figure 2.5. Seasonal dynamics of total cyclopoid copepods on macrophytes and in sediments in Jack Lake. a. Mean surface densities of total Cyclopoida on macrophytes (+/- one standard error). b. Mean surface densities of total Cyclopoida in sediments (+/- one standard error). c. Mean lake bottom densities of total Cyclopoida. d. Biomass of total Cyclopoida, 1987. e. Mean body lengths of cyclopoid copepods, 1987.

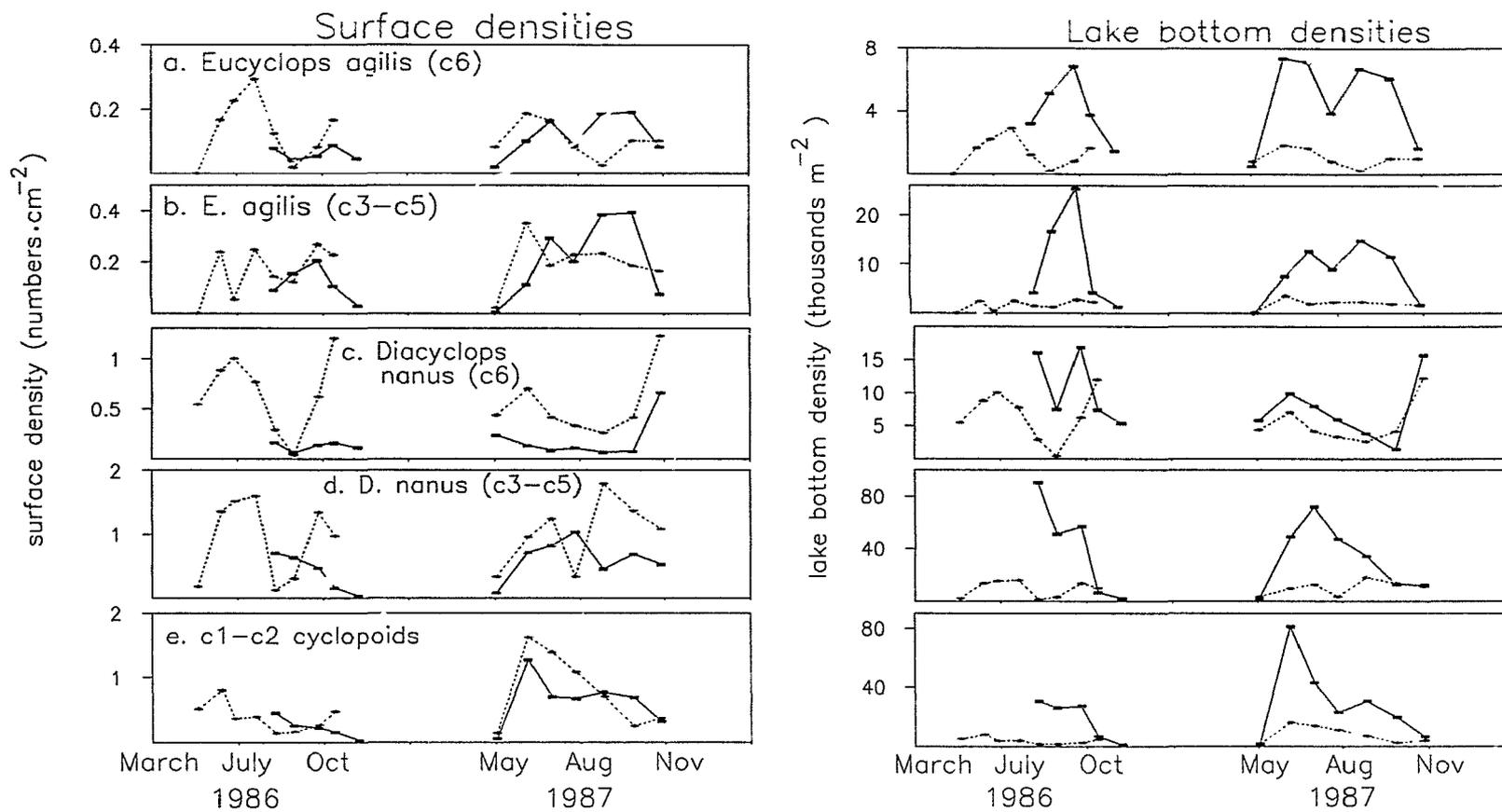


Figure 2.6. Seasonal changes of surface and bottom densities of *Diacyclops nanus*, *Eucyclops agilis*, and small c1-c2 copepodids. Although c1-c2 copepodids were not identified to species, most were probably *D. nanus* and *E. agilis*. Note that density scales vary among graphs.

Table 2.1. Invertebrates collected under ice on February 18, 1988. Total collected numbers were determined from combined results of sweep net and core samples. Benthic densities were estimated from core samples alone (n=3).

	total collected	benthic density (numbers·m ⁻²)
Oligochaeta	15	3465
Cladocera		693
<u>Alona</u> cf. <u>affinis</u>	2	
<u>Alona</u> <u>rustica</u>	1	
<u>Disparalona</u> <u>acutirostris</u>	1	
<u>Ilyocryptus</u> sp.	3	
<u>Simocephalus</u> sp.	1	
Copepoda		4505
<u>Acanthocyclops</u> <u>vernalis</u> (c6)	2	
<u>Diacyclops</u> <u>nanus</u> (c6)	26	
(c3-c5)	3	
<u>Eucyclops</u> <u>agilis</u> (c6)	2	
small copepodids (c1-c2)	3	
<u>Macrocyclus</u> <u>albidus</u> (c6)	15	
(c3-c5)	1	
harpacticoida	1	
Chironomidae		13654
<u>Procladius</u> sp. (instar-4)	5	
(instar-3)	2	
<u>Ablabesmyia</u> sp. (instar-3)	2	
(instar-1)	18	
non-tanypods	80	
<u>Chaborus</u> <u>americanus</u>	9	
<u>Acaei</u> i	1	

and E. agilis had more continuous reproduction between June and October. Encysted cyclopoids were never encountered in Jack Lake and there was no evidence that any species had a diapause stage.

The mean size of adult cyclopoids of all species decreased from May to July-August and increased again to November (Figure 2.8). Mean sizes were negatively correlated with temperature, as has been frequently observed for both planktonic and benthic copepods (McLaren 1963; Vijverberg 1977; Abdullahi and Laybourn-Parry 1985).

c) Epiphytic and benthic Cladocera: Seasonal changes of total cladoceran surface densities, bottom densities, and biomass followed a bimodal pattern on macrophytes and in sediments (Figure 2.9a-d). Abundance peaked in June-July and September-October. Although the surface densities of Cladocera in September-October were higher in 1987 than in 1986, lake bottom densities were similar in both years. The mean body length of Cladocera increased slowly from May to November (Figure 2.9e).

Most populations of Cladocera had peaks of abundance either in spring (June-July), autumn (September-early October) or both seasons (Figure 2.10, 2.11, 2.12). In June 1987, Alona intermedia dominated the epiphytic and benthic cladoceran communities. In 1986, however, numbers of A. intermedia in core samples were low until September. All species had low densities in August and increasing densities in September-

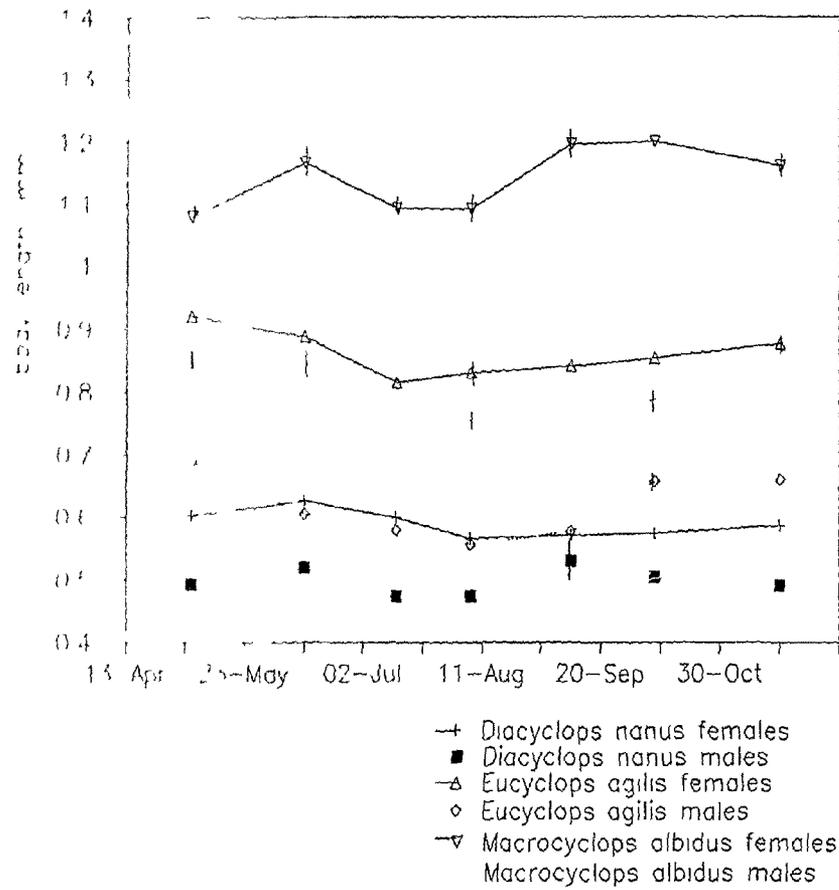


Figure 28. Seasonal changes of mean body lengths of adult male and female cyclopoid copepods. Vertical lines represent \pm one standard error. Standard errors less than 0.01 mm are not shown.

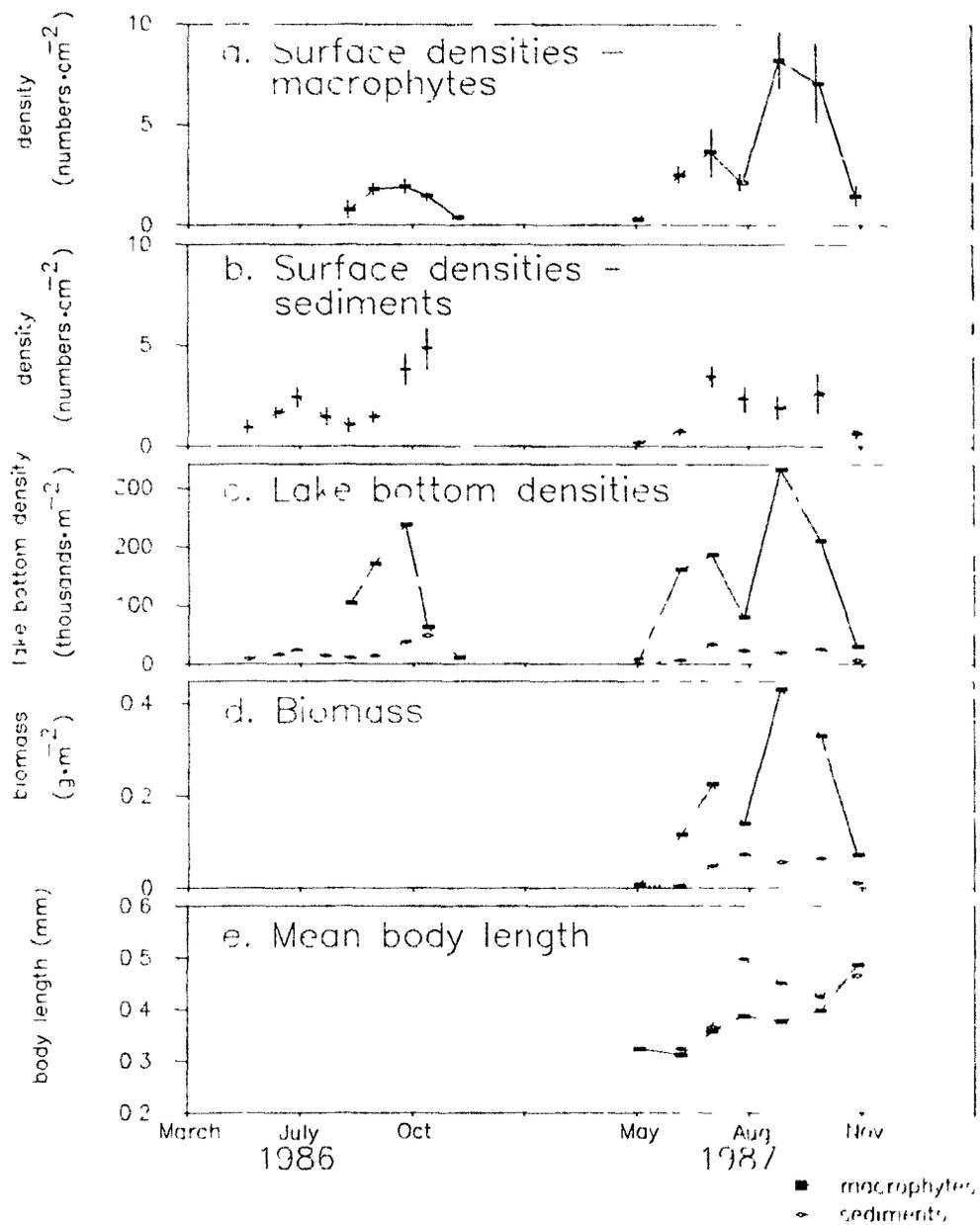


Figure 2.9. Seasonal dynamics of total Cladocera on macrophytes and in sediments. a. Mean surface densities on macrophytes (+/- one standard error) b. Mean surface densities in sediments (+/- one standard error) c. Mean bottom densities on macrophytes and in sediments. d. Biomass of total Cladocera, 1987. e. Mean body lengths of Cladocera, 1987. Mean body length was not estimated for sediment samples collected in May.

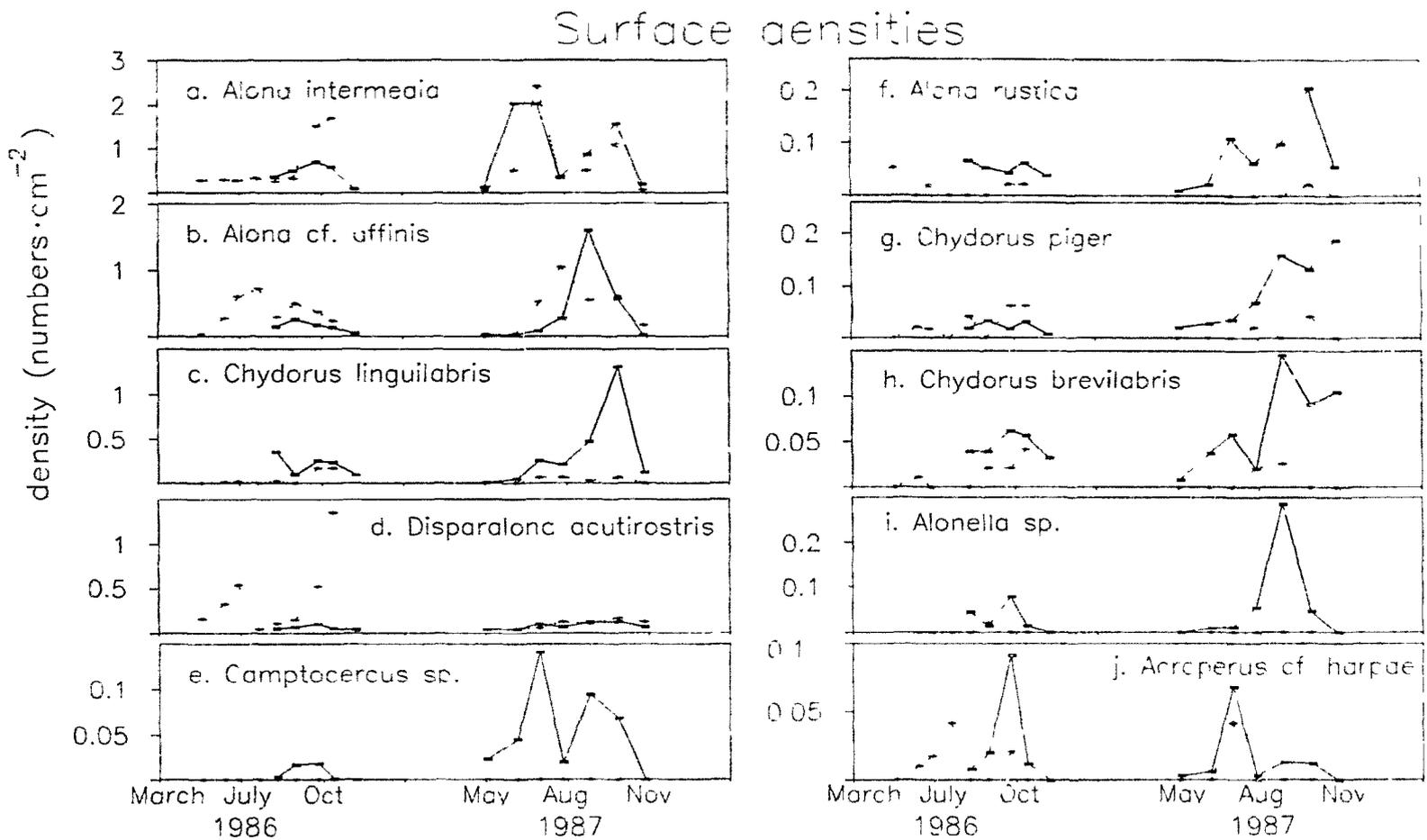


Figure 2.10. Seasonal changes of surface densities for different species of chydorid Cladocera. Note different density scales

Lake bottom densities

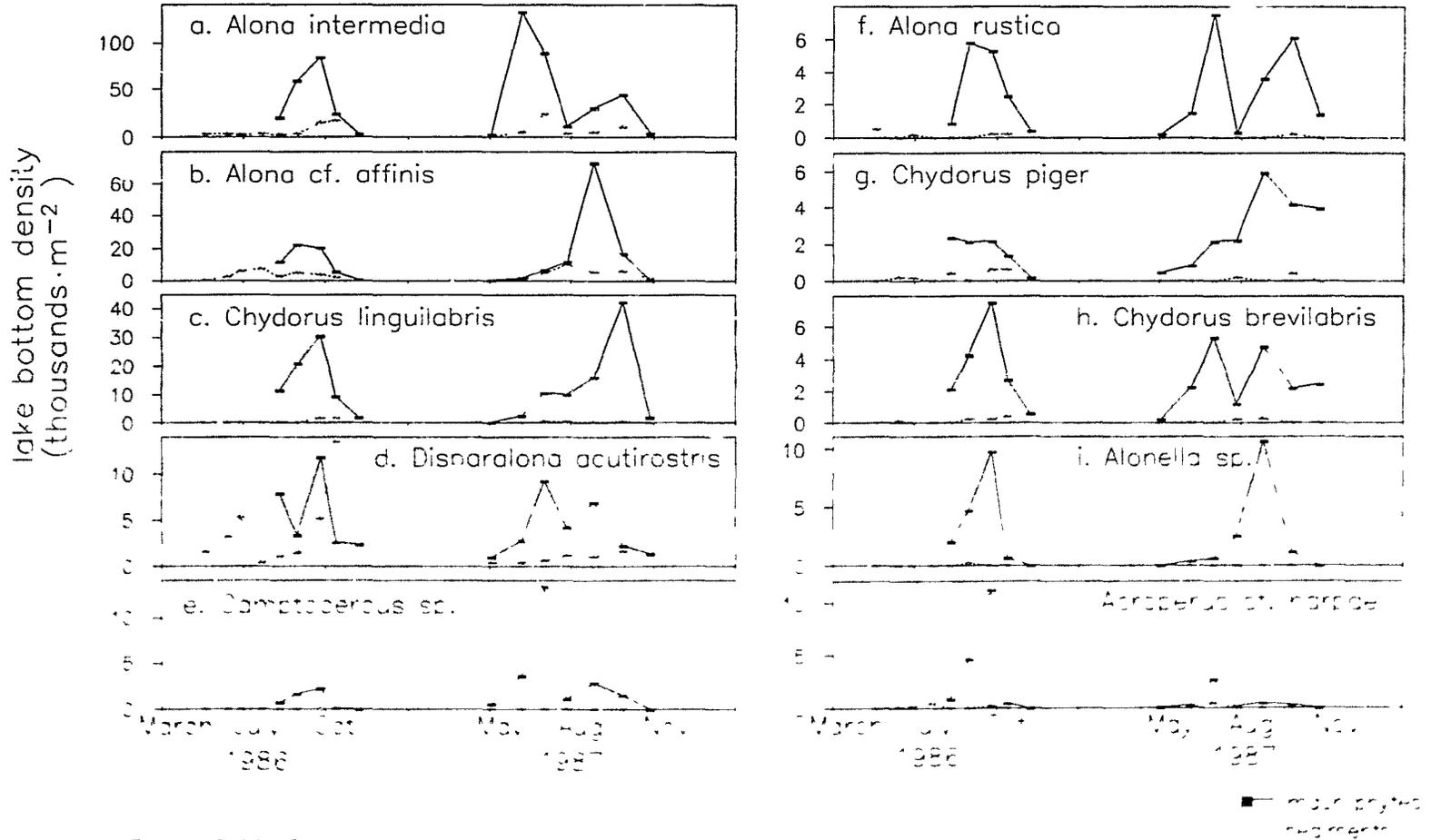


Figure 2.11. Seasonal changes of lake bottom densities for different species of chydorid Copepoda. Note different density scales.

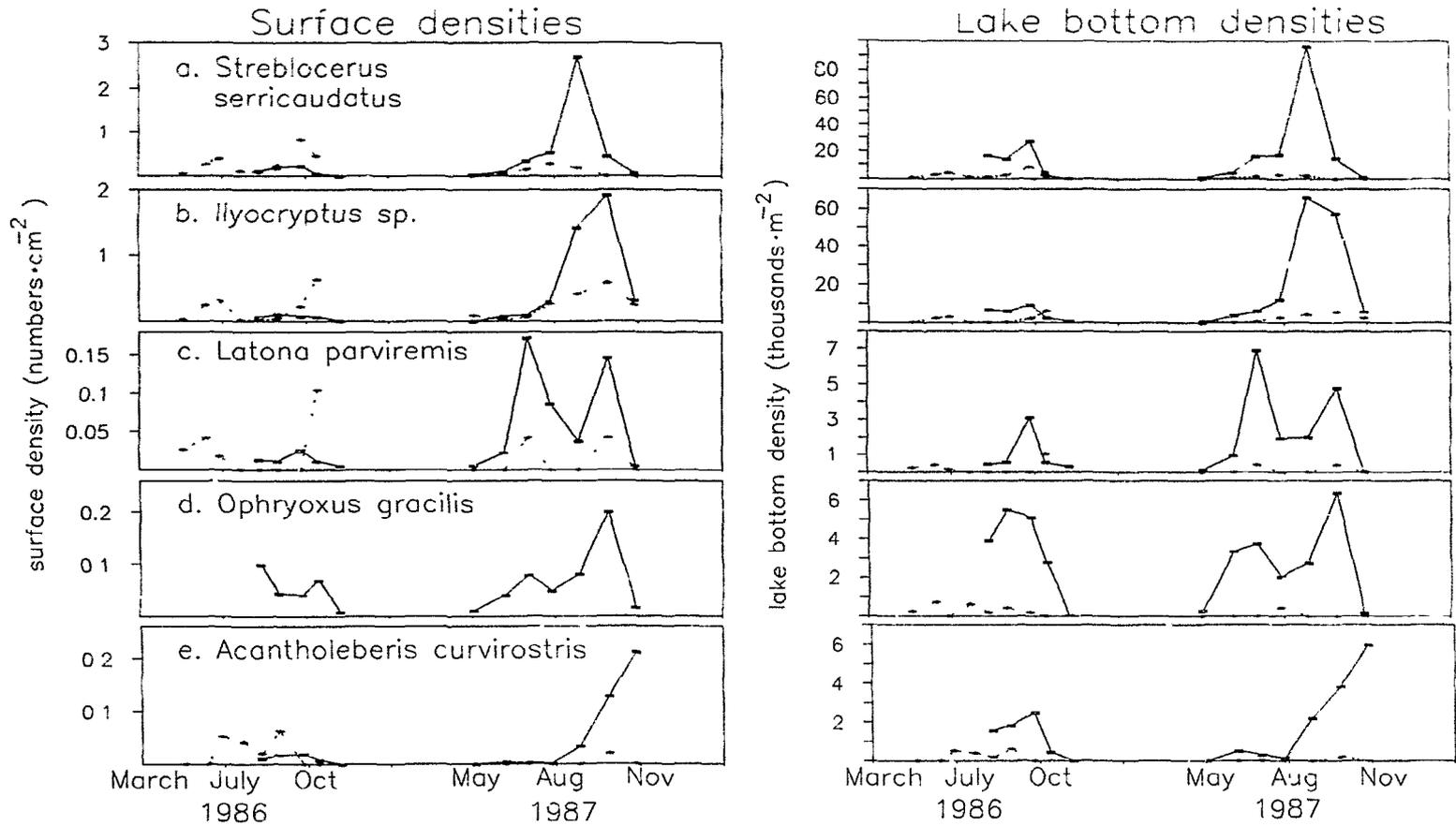


Figure 2.12. Seasonal changes of surface and lake bottom densities for different species of non-chydorid Cladocera. Note different density scales.

October, except benthic populations of Alona cf. affinis. Numbers of all Cladocera, except Chydorus piger, Chydorus brevilabris and Acantholeberis curvirostris, declined in November. Small populations of Alona cf. affinis, Alona rustica, Disparalona acutirostris, Ilyocryptus sp., and Simocephalus sp. persisted under the ice (Table 2.1).

The seasonal dynamics of littoral Cladocera in Jack Lake were similar to patterns observed in other studies (Smyly 1957; Straskraba 1963; Goulden 1971; Keen 1973, 1976; Daggett and Davies 1974a; Smirnov 1974; Whiteside 1974; Whiteside et al. 1978; Frenzel 1982; Lemly and Dimmick 1982; Williams 1982; Sharma and Pant 1984; Flossner 1985; Schoenberg 1988; Robertson 1990). In almost all lakes and streams that have been investigated, epiphytic and benthic Cladocera have had spring and fall peaks of abundance. The similarity of seasonal changes in many different systems suggests common underlying causes.

Seasonal changes in the mean size of common Cladocera in 1987 are depicted in Figure 2.13. The percentage of juveniles in each population is presented in Figure 2.14. With the exception of Ilyocryptus sp., cladoceran populations in May contained a high proportion of small juveniles that presumably hatched from ephippial eggs. The mean size of most species changed little between June and October. In November, production of ephippial eggs increased and fewer juveniles were encountered. As a result, the mean size of

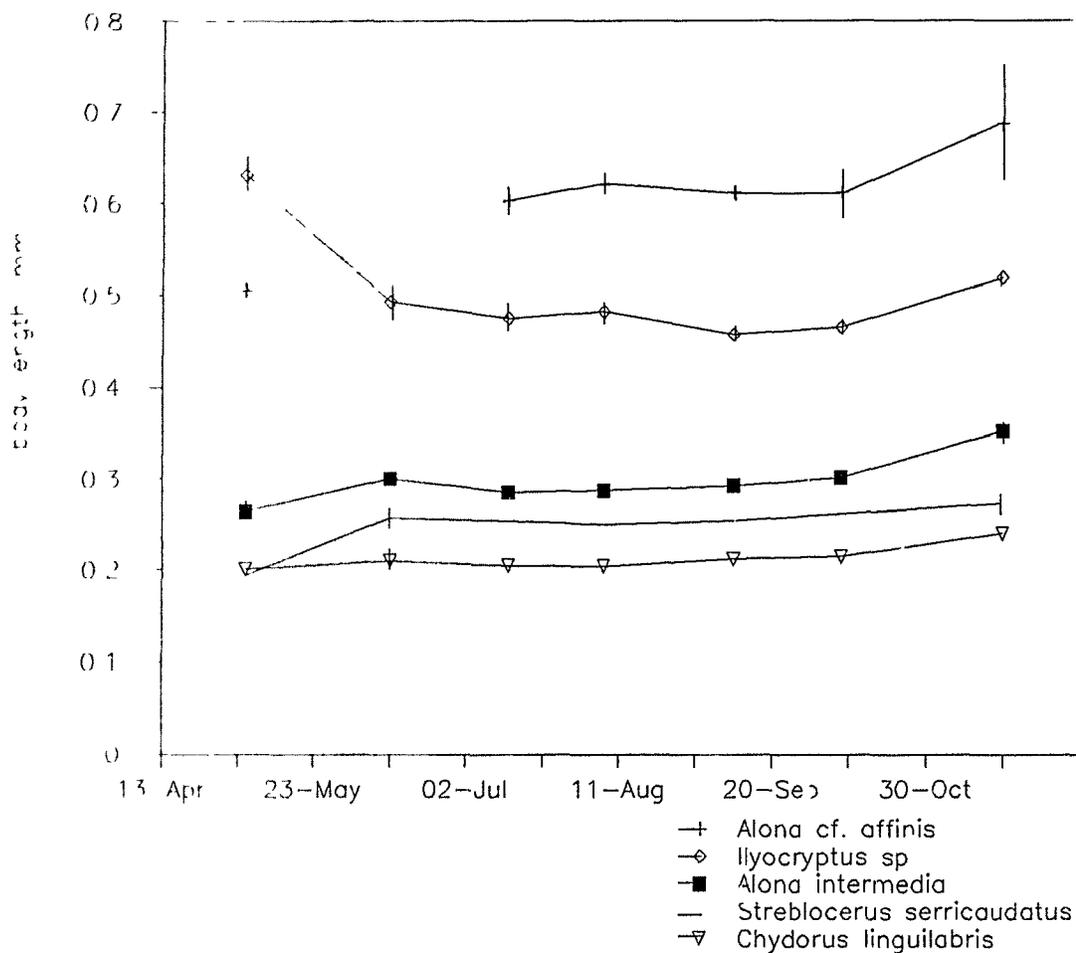


Figure 2-13. Seasonal changes of mean body length of common Cladocera, 1987. Vertical lines represent \pm one standard error. Standard errors less than .01 mm are not shown. Mean length of *Alona cf. affinis* in June is omitted because of insufficient data.

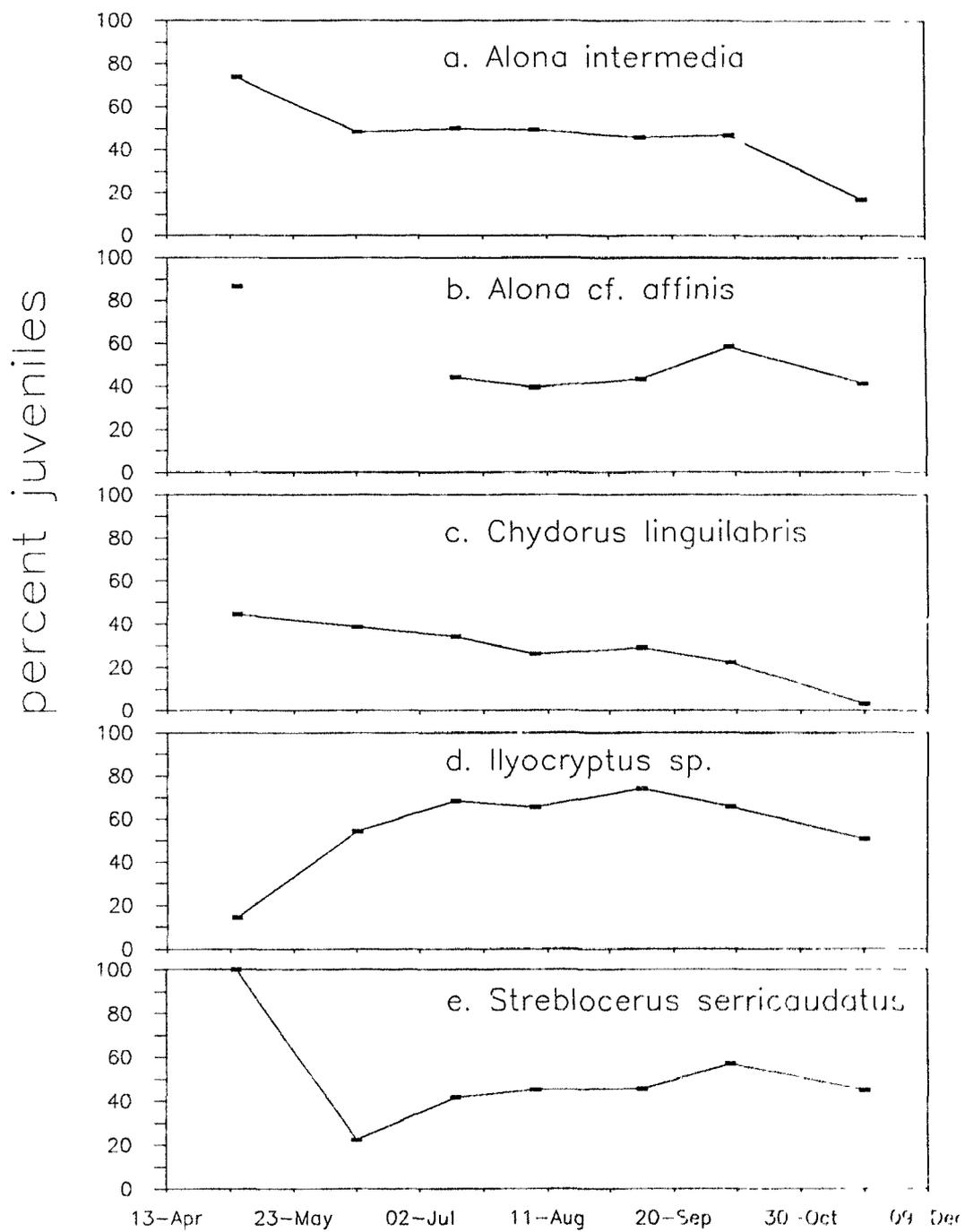


Figure 2.14. Seasonal changes in the proportion of juveniles in populations of common Cladocera, 1987.

common Cladocera increased slightly. Similar patterns have been observed by Keen (1973) and Daggett and Davis (1974a). Obvious seasonal changes in the morphology of cladocerans, such as the development of spines, etc., were not observed.

The low percentage of juveniles of Ilyocryptus sp. in May was unique among common Cladocera. This may indicate low reliance on the hatching of ephippial eggs by this species. Males and ephippial females of Ilyocryptus were never encountered in Jack Lake and it was the most abundant cladoceran encountered under the ice (Table 2.1). Overwintering populations of parthenogenetic Ilyocryptus have also been observed by Smyly (1957) and Daggett and Davies (1974a).

Seasonal changes in clutch sizes and birth rates of common Cladocera are depicted in Figure 2.15. Clutch sizes of all species were low in early spring and in late October-November. The clutch sizes of members of the family Chydoridae (Alona intermedia, Alona cf. affinis, Chydorus linguilabris) are limited to two eggs and mean clutch sizes did not vary dramatically between June and October. Average clutch sizes of the two macrothricid cladocerans (Ilyocryptus sp., Streblocerus serricaudatus) increased from June to July-August and decreased again in September-October. Birth rates for all species were low in May-June, highest in July-August, and low again in October-November.

Changes in birth rates failed to explain many of the

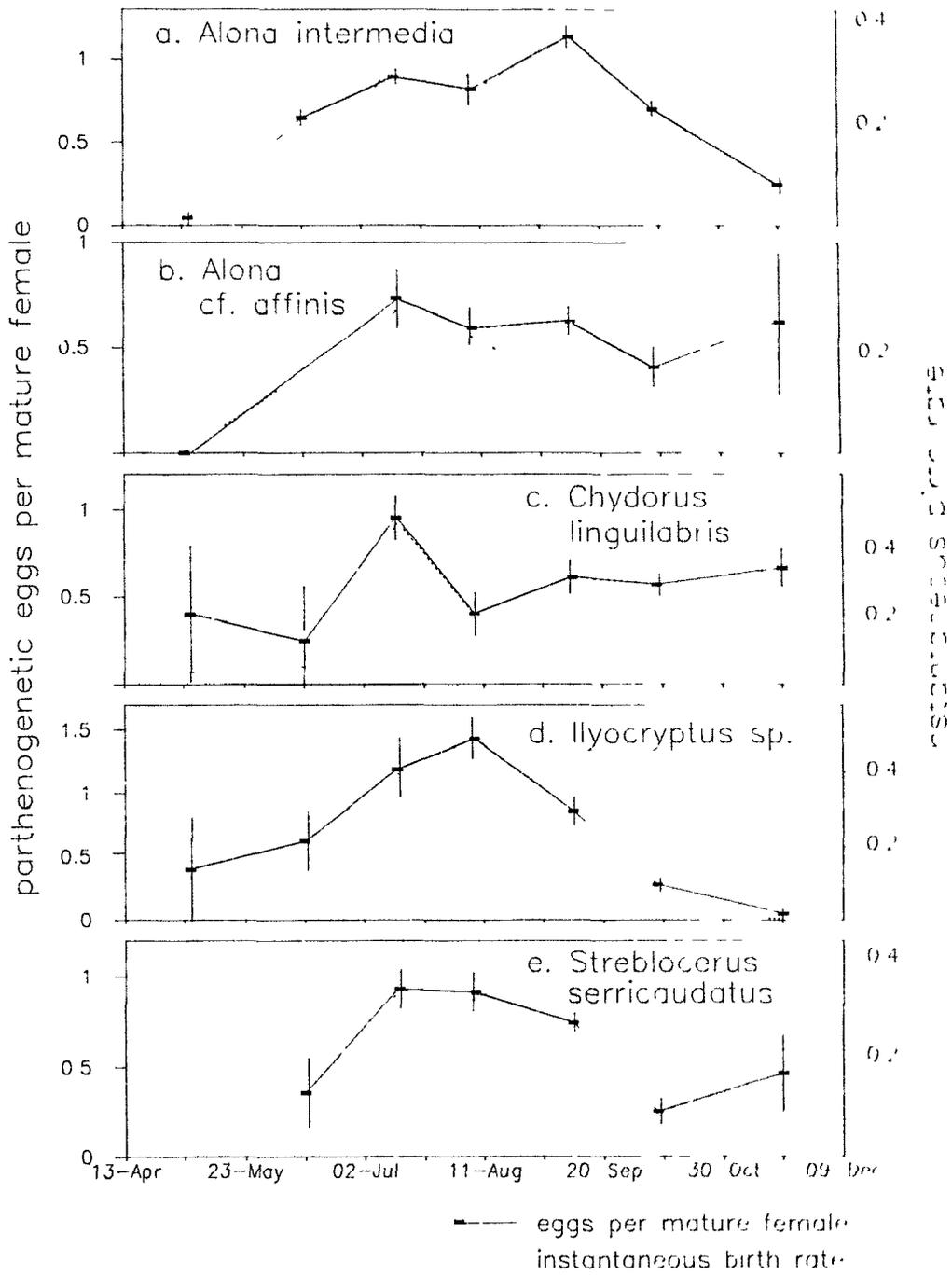


Figure 2.15. Seasonal changes of clutch sizes and birth rates for common Cladocera, 1987. Vertical lines for egg data represent \pm one standard error. Birth rates and clutch sizes for *Alona cf. affinis* (June) and *Streblocerus serricaudatus* (May) are omitted because of insufficient data.

fluctuations in cladoceran abundance described in Figures 2.10-2.12. Cladoceran populations were apparently limited from November to May by low water temperatures, low egg production, and resulting low birth rates. With warming of the lake in June, increased egg production and hatching of ephippial eggs apparently caused numbers of A. intermedia to increase rapidly. Numbers of other species did not increase at this time. Although birth rates and clutch sizes for all species were high in July-August, abundances were low. The decline in the abundance of A. intermedia in August was not the result of shifts in birth rates. The numbers of each cladoceran population increased in September despite declining birth rates. Because population sizes reflect a balance between gains (births and immigration) and losses (deaths and emigration), these results imply that seasonal changes in loss rates strongly affected littoral cladoceran population dynamics. Apparently, loss rates were highest in July-August (high birth rates and low abundance) and lower in September-October (lower birth rates and increasing abundance).

Clutch sizes of Cladocera usually decrease with declining food availability or with adverse chemical conditions (Slobodkin 1954; Green 1956, 1966; Richman 1958; Hall 1964; Davis and Ozburn 1969; Weglenska 1971; Biesinger and Christensen 1972). Hence, it is unlikely that high loss rates in August were caused by starvation or physiological

stress because clutch sizes did not decline at this time. There is also little evidence that the August decline of A. intermedia reflects senescence of a cohort hatched from ephippial eggs in May-June. Such a population decline should be accompanied by shifts in population age structure, with a high percentages of adults accumulating prior to the decline (cf. Slobodkin 1954). The size and age structure of the A. intermedia population was stable between June and October. Note that the interpretations presented above assume that large, transient shifts in birth rates and age structure were not missed between sampling dates.

High chydorid birth rates in combination with low midsummer population sizes have been reported by several researchers (Keen 1973; Williams and Whiteside 1978; Doolittle 1982; Robertson 1990). Previous studies have used shorter sampling intervals than those employed in Jack Lake and have minimized the probability of missing transient changes in birth rates. Despite a paucity of direct evidence, midsummer declines in littoral cladoceran abundance have usually been ascribed to the effects of invertebrate and vertebrate predation (Goulden 1971; Keen 1973; Daggett and Davis 1974a; Whiteside 1974; Phoenix 1976; Williams and Whiteside 1978; Doolittle 1982; Fairchild 1982, 1983; Williams 1982; Robertson 1990). Jack Lake is devoid of fish and other vertebrate predators. The hypothesis that the seasonal dynamics of epiphytic and benthic Cladocera in Jack

Lake were largely determined by invertebrate predation is examined in detail below.

4) Invertebrate predators

a) Gut content analyses and identification of important invertebrate predators of microcrustacea: Many of the invertebrates encountered in Jack Lake could potentially feed on littoral microcrustacea (Chapter 1). The most common predator groups were water mites, cyclopoid copepods, tanypod chironomids, and odonates. Potentially important secondary predators were Chaoborus americanus and Cernotina sp. The results of gut content analyses of Jack Lake invertebrates are summarized in Table 2.2.

i) Copepoda: The guts of adult and c5 M. albidus frequently contained remains of Cladocera (Table 2.2, Figure 2.16a). Fryer (1957a) also found that M. albidus was highly predaceous. Animal remains were not observed in the few guts of c1-c4 M. albidus examined from Jack Lake. Nauplii and early copepodid stages of most predaceous cyclopoids are largely herbivorous, with increasing carnivory with age (Smyly 1970; Dodson 1975; Gophen 1977; Jamieson 1980). The predation rates of early instar copepodids are always much less than those of c5 or adult stages (Jamieson 1980).

Guts of copepods other than M. albidus contained few or no animal remains (Table 2.2). Fryer (1957b) and Dodson (1975) reported that Eucyclops agilis was primarily herbivorous. Although the small size of Diacyclops nanus suggests that it

Table 2.2. Percent composition of animal prey in guts of common invertebrates in Jack Lake. Prey are abbreviated as follows: Cl (Cladocera), Cop (Copepoda), Dip (Diptera), Od (Odonata), Tri (Trichoptera), Olig (Oligochaeta), Mite (Acari), Prey (mean number of animal prey per gut), Num (number of guts examined).

Potential predator	Cl	Cop	Dip	Od	Tri	Olig	Mite	Prey	Num
Copepoda									
<u>Acanthocyclops</u>									
<u>vernalis</u>							0		6
<u>Diacyclops</u>									
<u>nanus</u>							0		3
<u>Eucyclops</u>									
<u>agilis</u>							0		10
<u>Macrocyclus</u>									
<u>albidus</u>	86	6				8		.86	57
<u>Epischura</u>									
<u>nordenskioldi</u>	100							.06	16
Diptera									
<u>Procladius</u> sp.	82	8	8			1	1	4.3	54
<u>Ablabesmyia</u> sp.	93	1	2			2	1	5.2	22
non-tanypod									
Chironomidae								0	4
<u>Chaoborus</u>									
<u>americanus</u>	50	48						3.6	2
Trichoptera									
<u>Cernotina</u> sp.	25	31	13		13		6	2.3	7
<u>Oxyethira</u> sp.								0	2
<u>Phryganea</u> sp.								0	3
Odonata									
<u>Enallagma</u>									
<u>carunculatum</u>	44	16	32	1		1	4	3.0	76
<u>Aeschna</u>									
<u>interrupta</u>	26		63	6	2		1	8.1	10
<u>Cordulia</u>									
<u>shurtleffi</u>	44	3	38	9	1	2	2	3.6	36
<u>Leucorrhinia</u>									
<u>glacialis</u>	47	12	30	5	1	1	1	3.7	40

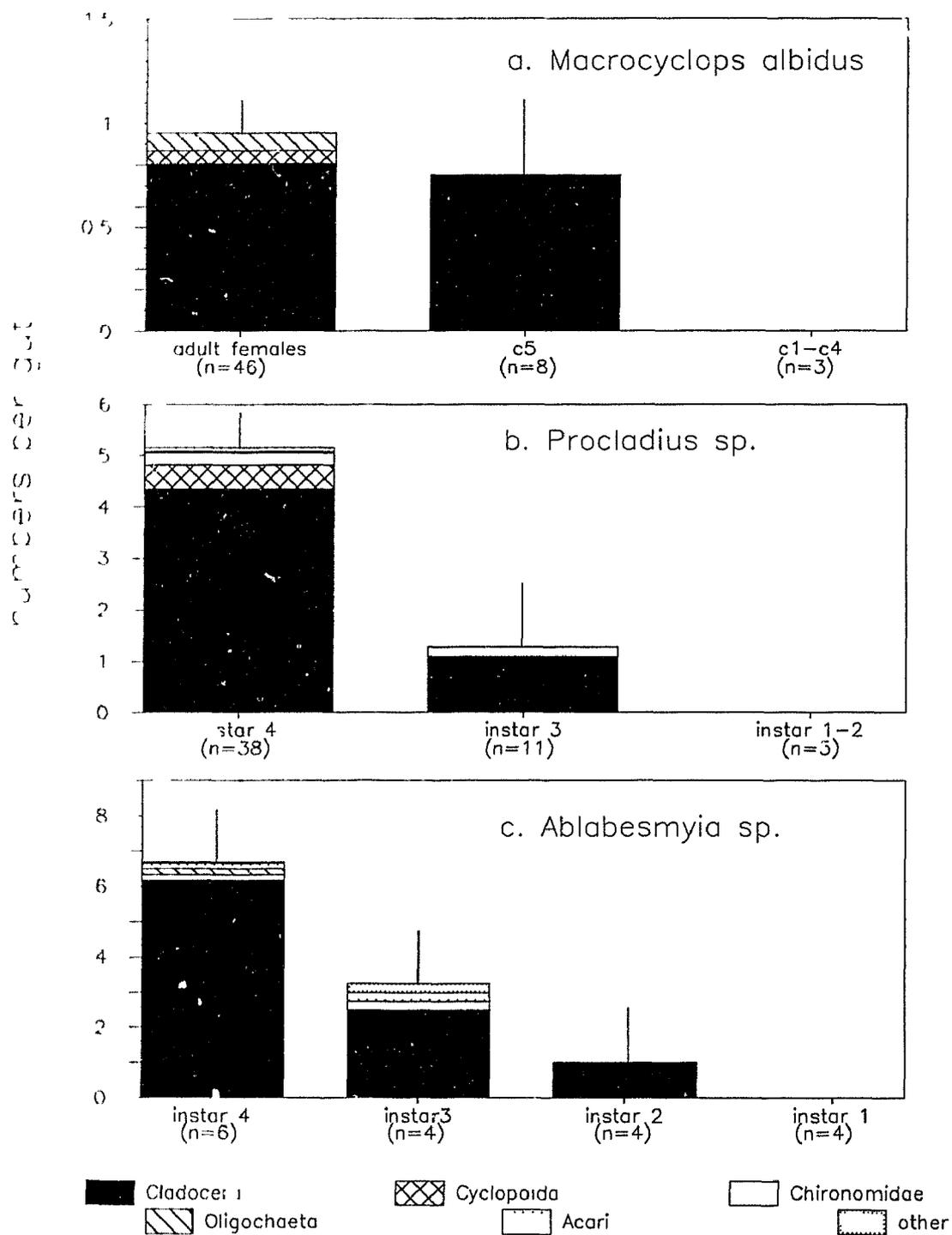


Figure 2.16 Mean numbers of animal remains encountered in guts of *Macrocyclus albidus* and tanypod chironomids. Vertical lines are \pm one standard error.

does not feed on microcrustacea, its feeding habits are unclear. Strayer (1985) reported finding rotifer remains in the gut of one D. nanus, suggesting that it preys on small invertebrates. Adult and c5 Acanthocyclops vernalis have been frequently identified as predators on rotifers and microcrustacea (Fryer 1957b; Anderson 1970; Monokov 1972; Brandl and Fernando 1974; Dodson 1975; Kerfoot 1977). The absence of animal remains in the guts of A. vernalis from Jack Lake is probably an artifact of the small number of animals examined. Although few animal remains were encountered in Epischura nordenskioldi guts, this planktonic calanoid probably has a diet similar to its close relative, Epischura lacustris. E. lacustris feeds on planktonic rotifers and microcrustacea (Confer and Blades 1975; Kerfoot 1977, 1978, 1987; Li and Li 1979; Chow-Fraser and Wong 1986).

ii) Chironomidae: Instars-3 and -4 of two tanypod chironomids, Ablabesmyia sp. and Procladius sp., fed heavily on Cladocera in Jack Lake (Table 2.2; Figure 2.16b,c). A high percentage of guts also contained detritus and algae (particularly desmids). Tanypod midges have been reported to feed on chironomids, oligochaetes, microcrustacea, algae, and detritus (Armitage 1968; Kajak et al. 1968; Roback 1969; Tarwid 1969; Thut 1969; Izvekova 1971; Monokov 1972; Loden 1974; Baker and McLachlan 1979; Dusoge 1980; Menzie 1980; Titmus and Badcock 1981; Vodopich and Cowell 1984; Hershey 1986). Few remains of microcrustacea were found in the guts

of instar-1 and -2 tanypods. The head capsules of these instars were less than 600 μm long and probably precluded feeding on microcrustaceans. Early instar Procladius and Ablabesmyia apparently rely on a diet of algae, detritus, and protozoa (Armitage 1968; Baker and McLachlan 1979).

Occasionally, invertebrate remains have been encountered in the guts of non-tanypod chironomids, particularly Cryptochironomus and Endochironomus (Armitage 1968; Thut 1969; Izvekova 1971; Loden 1974; Soszka 1975b). A cursory examination failed to reveal animal remains in guts of non-tanypod chironomids from Jack Lake.

iii) Odonata: In Jack Lake, both zygopteran and anisopteran Odonates fed on a wide variety of invertebrates, with remains of microcrustacea and chironomids predominating in faecal pellets (Table 2.2, Figure 2.17). These results match findings from many other studies (Pritchard 1964; Lawton 1970a; Pearlstone 1973; Thompson 1978a; Baker and Clifford 1981; Folsom and Collins 1984; Johnson et al. 1984; Merrill and Johnson 1984; Blois 1985a,b; Johnson 1985; Johnson et al. 1985; Bryant 1986). As odonates increased in size, numbers of remains per gut increased and larger prey items, such as chironomids, trichopterans, and odonates, were added to the diet. There was no sign that smaller items (primarily microcrustacea) were dropped. Similar results have been reported by Pritchard (1964), Lawton (1970b), Pearlstone (1973), Thompson (1978a), Blois (1985a), and Baker

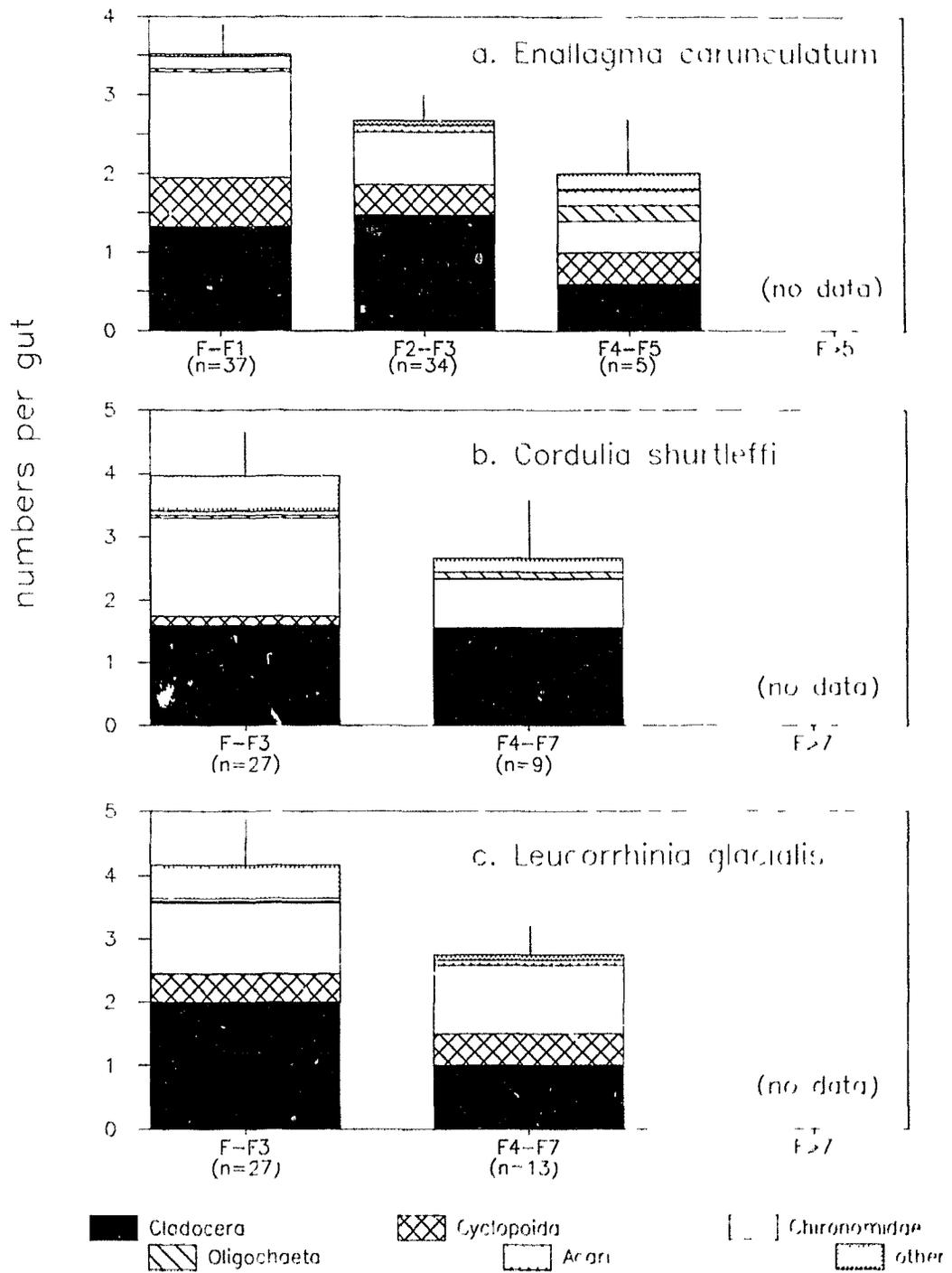


Figure 2.17. Mean numbers of animal remains encountered in guts of odonates. Vertical lines are \pm one standard error.

(1986). Faecal pellets from early-instar odonates could not be analyzed. Lawton (1970b) reported that instars 1-3 of a zygopteran odonate, Pyrrhosoma nymphula, fed on protozoa, rotifers, and, occasionally, small Cladocera.

iv) Trichoptera: In Jack Lake, guts of Cernotina sp. contained remains of microcrustacea, chironomids, trichopterans, and water mites (Table 2.2). Other members of the trichopteran family Polycentropidae have been identified as important predators of invertebrates in streams (Townsend and Hildrew 1979; 1980; Hildrew and Townsend 1982). No animal remains were encountered in guts of Phryganea sp., although Winterbourn (1971) indicates that other members of the family Phryganidae may occasionally consume microcrustacea.

v) Selectivity: In general, insufficient numbers of predator guts were examined to allow accurate assessment of selectivity. Some broad trends were obvious, however. The proportion of copepod and water mite remains in odonate guts was always much less than in samples collected from Jack Lake. Negative selection of copepods or mites by odonates has also been reported by Pritchard (1964), Merrill and Johnson (1984), Blois (1985a), and Johnson et al. (1984, 1985). Low numbers of chironomid, copepod, and mite remains in tanypod guts also suggest negative selection for these items in Jack Lake. This contrasts with previous studies that indicate that tanypods prefer small chironomids to

microcrustacea (Kajak et al. 1968; Baker and MacLachlan 1979; Dusoge 1980; Vodopich and Cowell 1984). Negative selection of copepods by tanypods has been noted by Roback (1969). There was no evidence of selection by any predators for different species of littoral Cladocera in Jack Lake. Similar results were reported by Goulden (1971). Remains of planktonic microcrustacea (calanoid copepods, Holopedium gibberum) were rarely encountered in the guts of cyclopoid copepods, tanypod chironomids, or odonates.

There is little evidence that invertebrate predators actively select prey. Instead, selection seems to be determined primarily by encounter rates and the effectiveness of prey defence strategies (Kerfoot 1977; Crowley 1979; Williamson 1983; Peckarsky 1984; Cooper et al. 1985). Relatively low numbers of copepod and mite remains in odonate and tanypod guts may have occurred for several reasons: 1) Predators and prey may have occupied different microhabitats in Jack Lake. Examination of spatial distributions of tanypods, odonates, copepods, and mites (Chapter 1) provided little support for this hypothesis. 2) If remains of copepods and mites are less easily identified or pass through the guts of predators more quickly than other invertebrate remains, apparent negative selection may result. Although the digestion times of different prey are unknown, the large disparity between densities of copepods and mites in the lake and in faecal pellets suggest that the apparent negative

selection was not an artifact. 3) Copepods and mites may be less susceptible to invertebrate predation than other invertebrates in Jack Lake. The "hop and sink" movement of cyclopoid copepods may decrease encounter rates with predators (Pearlstone 1973; Cooper et al. 1985) and their strong escape responses may further reduce capture probabilities (cf. Williamson 1983; Cooper et al. 1985; Browman et al. 1989). Water mites are unpalatable to many aquatic predators (Pritchard 1964; Pieczynski 1976; Kerfoot 1982).

b) The seasonal dynamics of invertebrate predators of littoral microcrustacea: In the discussion below, I describe the seasonal dynamics of common invertebrate predators in Jack Lake and discuss their potential impact on epiphytic littoral Cladoceran populations. In particular, I discuss evidence that invertebrate predation was highest in July-August and lower in September-October. Less emphasis is placed on the effects of predators on cyclopoid copepods because 1) gut content analyses suggested that invertebrate predators in Jack Lake fed most heavily on Cladocera, and 2) the impact of predators on cyclopoid populations was more difficult to evaluate. Birth rates of cyclopoids were not estimated and seasonal changes in abundance were strongly affected by life-cycle processes. For example, peaks of total cyclopoid abundance in June and September coincided with the maturation of two generations of nauplii to c1-2

copepodids.

i) Predatory copepods: The seasonal dynamics of M. albidus were described above (Figure 2.7). Peak numbers of the most predaceous stages of M. albidus (c5, c6) coincided with periods of maximum cladoceran abundance in June and September. As a result, predation by M. albidus probably does not account for the midsummer decrease or autumn increase of Cladocera.

In laboratory studies, maximum predation rates of adult planktonic cyclopoid copepods feeding on microcrustacean prey rarely exceed 3 prey.predator⁻¹.d⁻¹ (except with nauplii as prey) (McQueen 1969; Anderson 1970; Smyly 1970; Jamieson 1980; Brandl and Fernando 1974, 1975; Williamson 1983). Stemberger (1986) reports gut passage times of 7-10 hours at 16° C for adult Diacyclops thomasi. If M. albidus have similar gut passage times, this implies mean predation rates of approximately 1 to 3 prey.predator⁻¹.day⁻¹ at these temperatures in Jack Lake. Consumption at these rates by c5 and c6 M. albidus between June and October 1987 would result in average daily mortality of 4 to 30% of the population of epiphytic Cladocera. This is within the range of estimates of predation by cyclopoid copepods on planktonic microcrustacea (Confer 1971; Brandl and Fernando 1979).

ii) Tanypod chironomidae: Procladius sp. had a univoltine life history in Jack Lake and emerged in May (Figure 2.18). Instars-1 and -2 were abundant in June and these developed

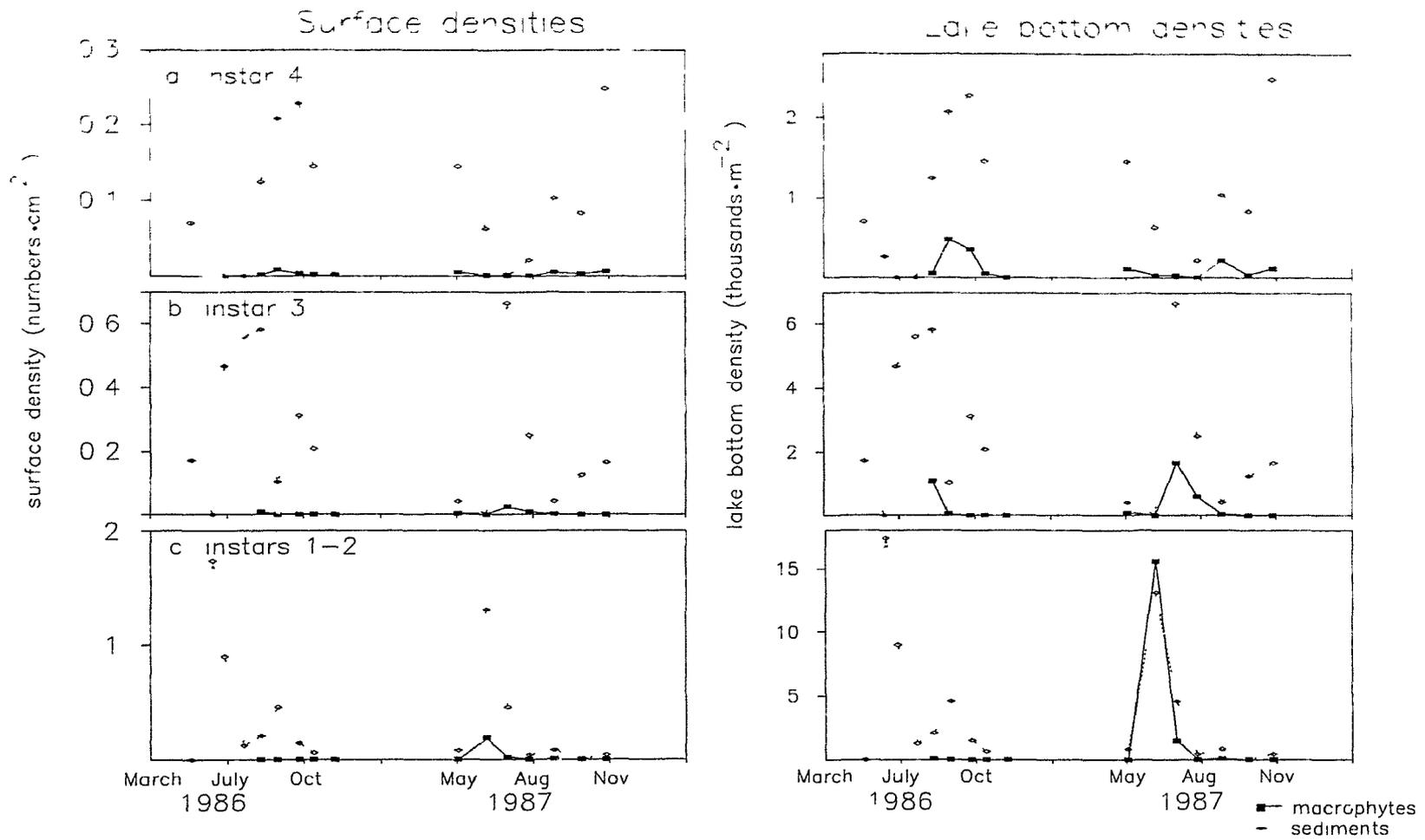


Figure 2.18 Seasonal changes of surface and bottom densities of different instars of *Procladius* sp. Note different density scales

to instar-3 by July-August and instar-4 by September-November. Most Procladius overwintered in the 4th instar (Table 2.1).

The life history of Ablabesmyia in Jack Lake is uncertain. A small peak of instar-1 larvae occurred in June and a second, larger peak from September to November (Figure 2.19). Many Ablabesmyia overwintered in the first instar (Table 2.1) and instar-2 larvae became common in May and July. Instar-3 Ablabesmyia were abundant in sediment samples collected in July and in macrophyte samples collected in October-November. Instar-4 larvae were encountered only between June and August. Because Ablabesmyia was identified only to genus, it is possible that more than one species occurred in Jack Lake and that each had a different life-history.

There are few estimates of feeding rates of tanypod midges. The gut analyses suggested that only instar-3 and -4 tanypods fed heavily on microcrustacea. Laboratory studies in small containers indicate that potential feeding rates of instar-4 Procladius may be as high as 9 chironomids per day (Dusoge 1980; Vodopich and Cowell 1984; Hershey 1986). I estimated tanypod predation rates on Cladocera by using the results of the gut content analyses and assuming that gut passage times fell between 4 and 18 hours. This implies that instar-3 tanypods ate between 2.5 and 6 Cladocera·predator⁻¹·d⁻¹ and that instar-4 tanypods consumed 7 to 21 Cladocera·predator⁻¹·d⁻¹. If predation rates are in this range, 5 to 17% of

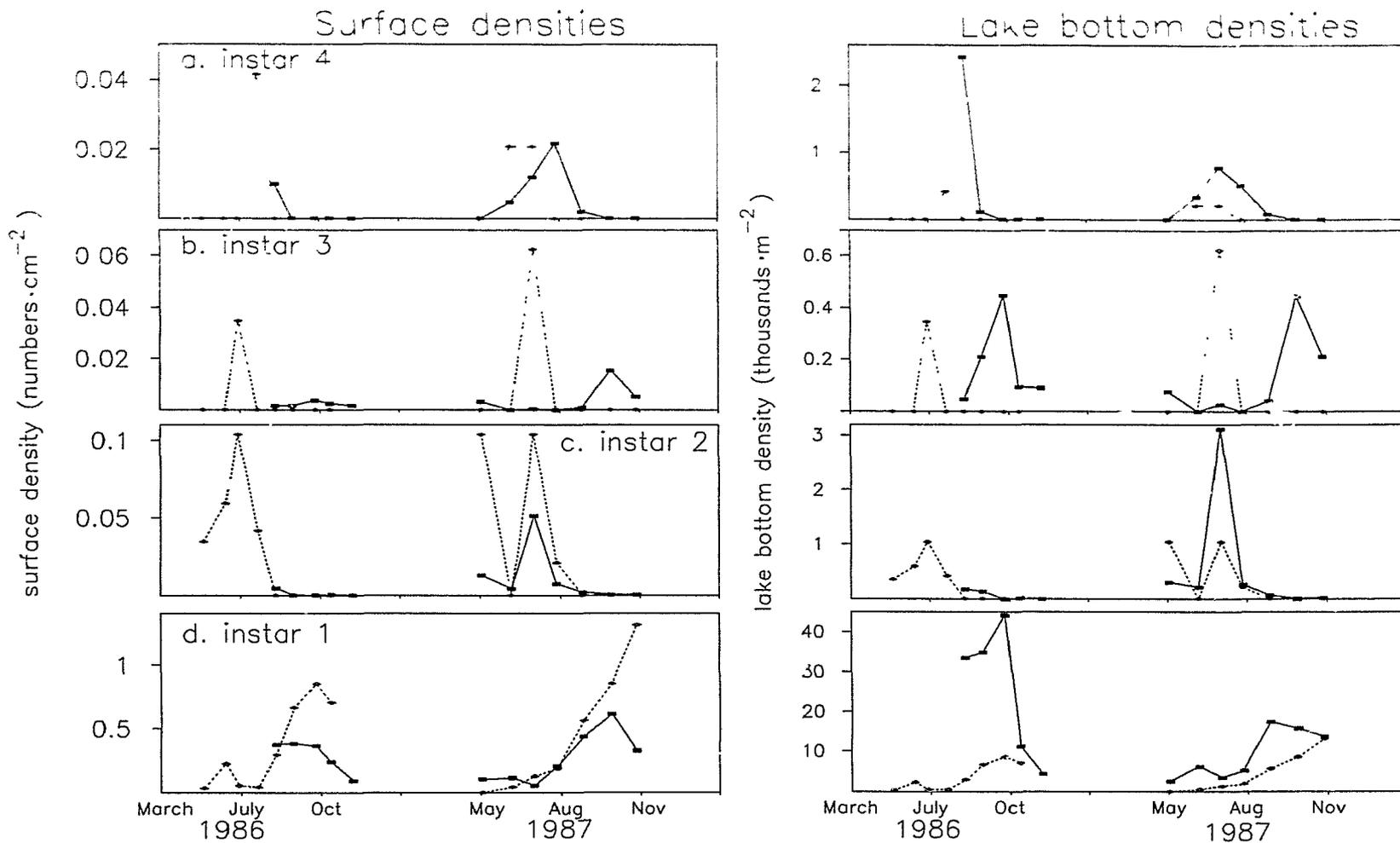


Figure 2.19. Seasonal changes of surface and bottom densities for different instars of *Ablabesmyia* sp.. Note different density scales.

epiphytic Cladocera would be consumed daily by tanytoids in July-August 1987. At other times, less than 5% of epiphytic Cladocera would be consumed daily.

Seasonal changes of predation by Procladius probably did not strongly affect littoral Cladocera in Jack Lake. The predatory instars-3 and -4 occurred primarily in sediments and were spatially segregated from the large numbers of Cladocera on macrophytes. Coexistence of high numbers of instar-4 Procladius and benthic Cladocera in September and October further suggest that this predator did not strongly affect cladoceran seasonal dynamics. In contrast, the seasonal dynamics of Ablabesmyia suggest potentially strong interactions with epiphytic and benthic microcrustacea. Instar-4 Ablabesmyia fed heavily on Cladocera and maximum surface and bottom densities coincided with midsummer declines of epiphytic and benthic Cladocera.

iii) Odonates: The odonate assemblage in Jack Lake was dominated by a zygopteran, Enallagma carunculatum, and two anisopterans, Cordulia shurtleffi and Leucorrhinia glacialis.

E. carunculatum, had a semi-voltine life history (Figure 2.20). Oviposition occurred in August and large numbers of newly hatched larvae appeared in September (Figures 2.21). Growth was minimal between October and May and resumed in June. The second winter was spent in instars F-F4 and emergence occurred the following July. The biomass of E. carunculatum was greatest in spring and fall, with a

Enallagma carunculatum

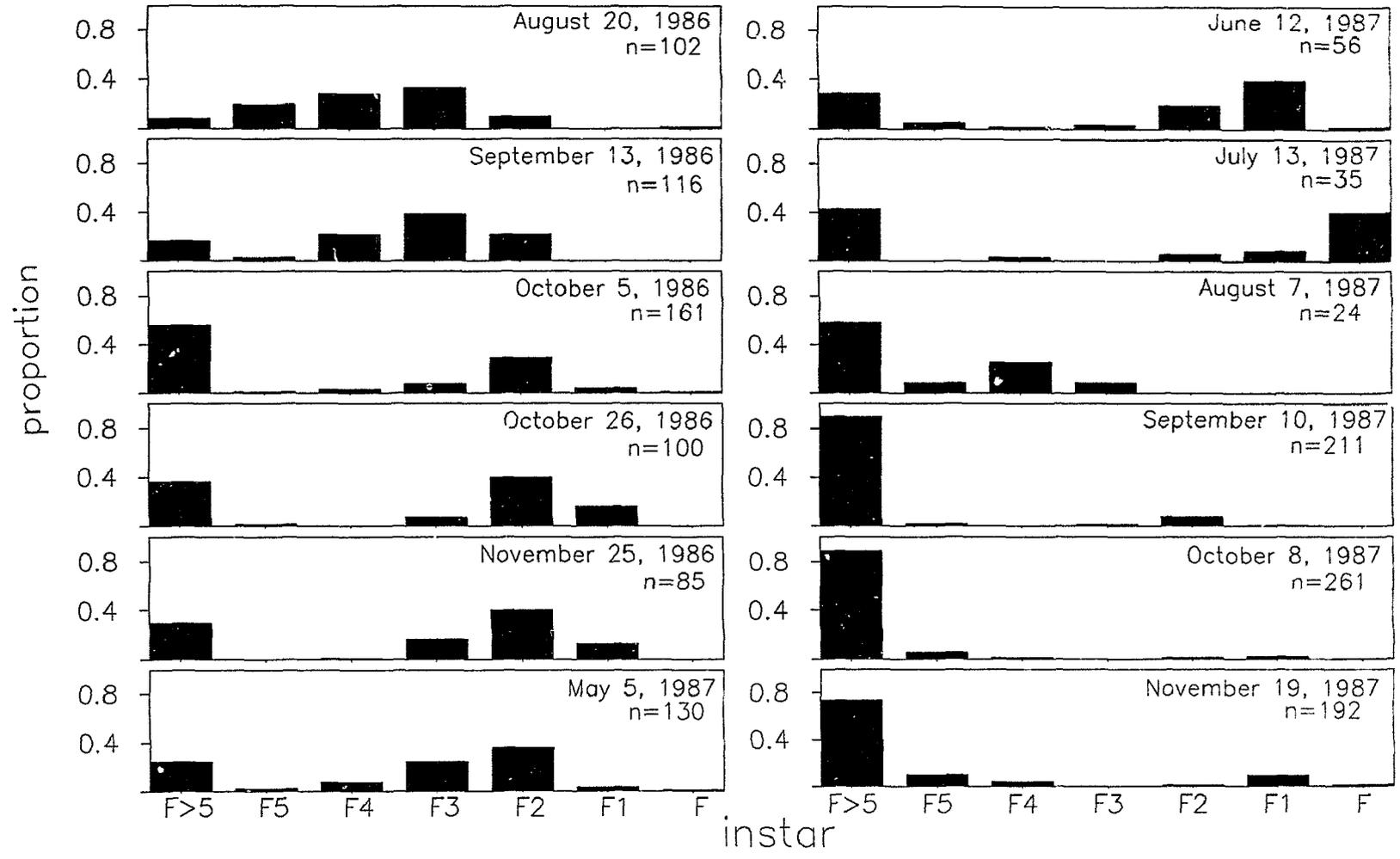


Figure 2.20. Relative frequency of different instars of *Enallagma carunculatum*.

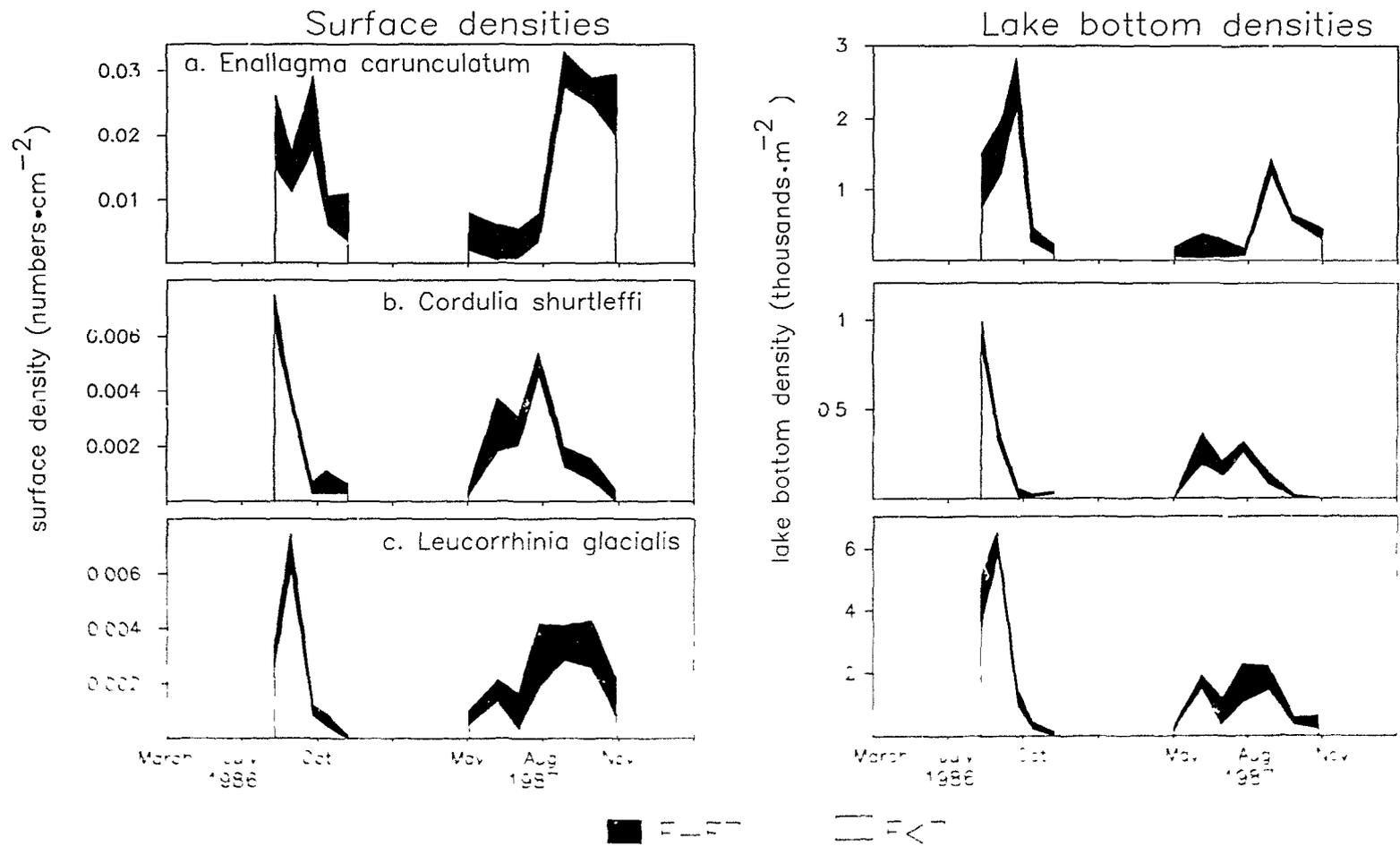


Figure 2.11 Seasonal changes of surface and bottom densities of common caddisflies. Note different density scales.

midsummer low in August (Figure 2.22). This pattern roughly follows changes in the abundance of Cladocera and there is little evidence that E. carunculatum strongly affected cladoceran seasonal dynamics.

C. shurtleffi and L. glacialis had long flight periods and asynchronous development in Jack Lake. C. shurtleffi emerged in June-July and had at least a semi-voltine life history (Figure 2.23). Numbers and biomass of C. shurtleffi were greatest in June and declined from October to May (Figures 2.21, 2.22). Numbers and biomass of L. glacialis were maximal between June and September (Figures 2.21, 2.22, 2.24).

Numbers of all species of odonates decreased between November and May and increased again in June. These density changes could not be caused by changes in total population size, because there was no emergence or oviposition at these times. Similar observations have been made by Macan (1964), Lawton (1970a), and Benke and Benke (1975) and probably indicate movement of animals from the study area. Many odonates move to deeper water in winter (Johannsson 1978; Bryant 1986; Wissinger 1988).

Laboratory studies suggest that odonates can be voracious predators. Maximum zygopteran predation rates of over 200 Cladocera per day have been reported by Johnson et al. (1975), Crowley (1979), and Jeffries (1988). It is unclear whether such predation rates are ever achieved in nature.

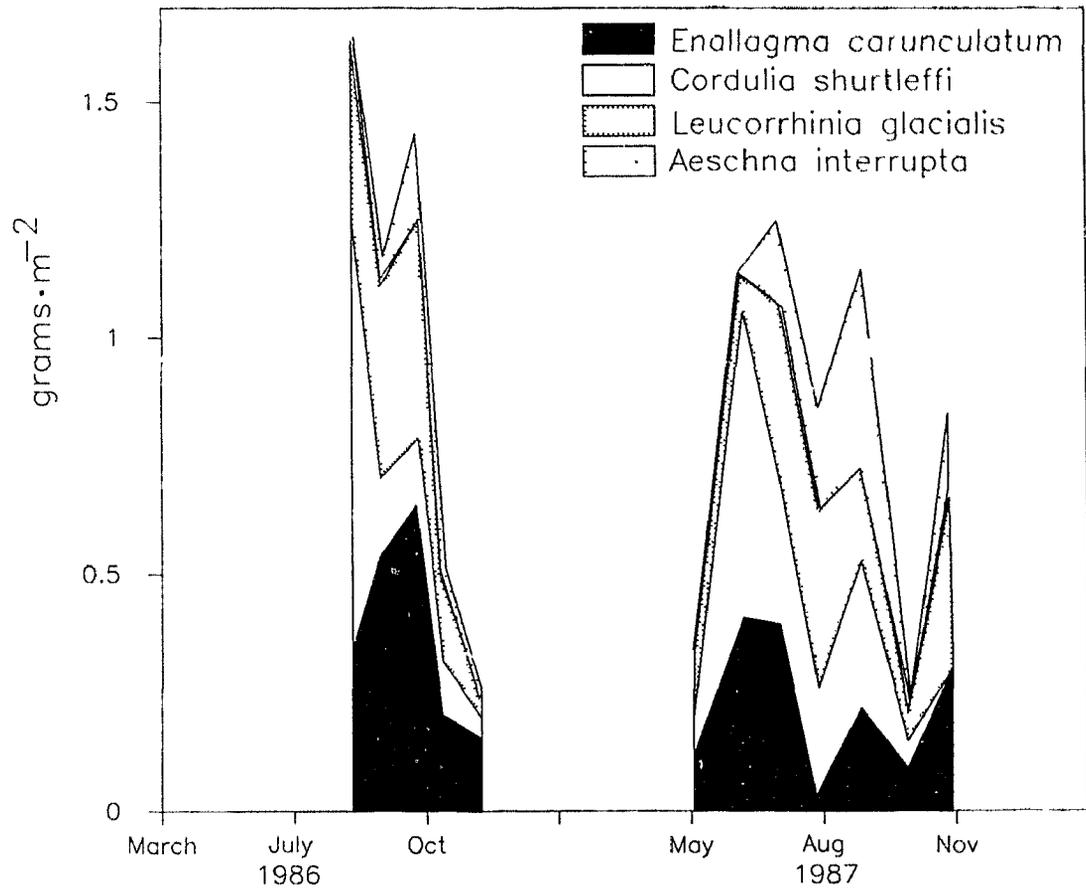


Figure 2.22. Seasonal changes in odonate biomass.

Cordulia shurtleffi

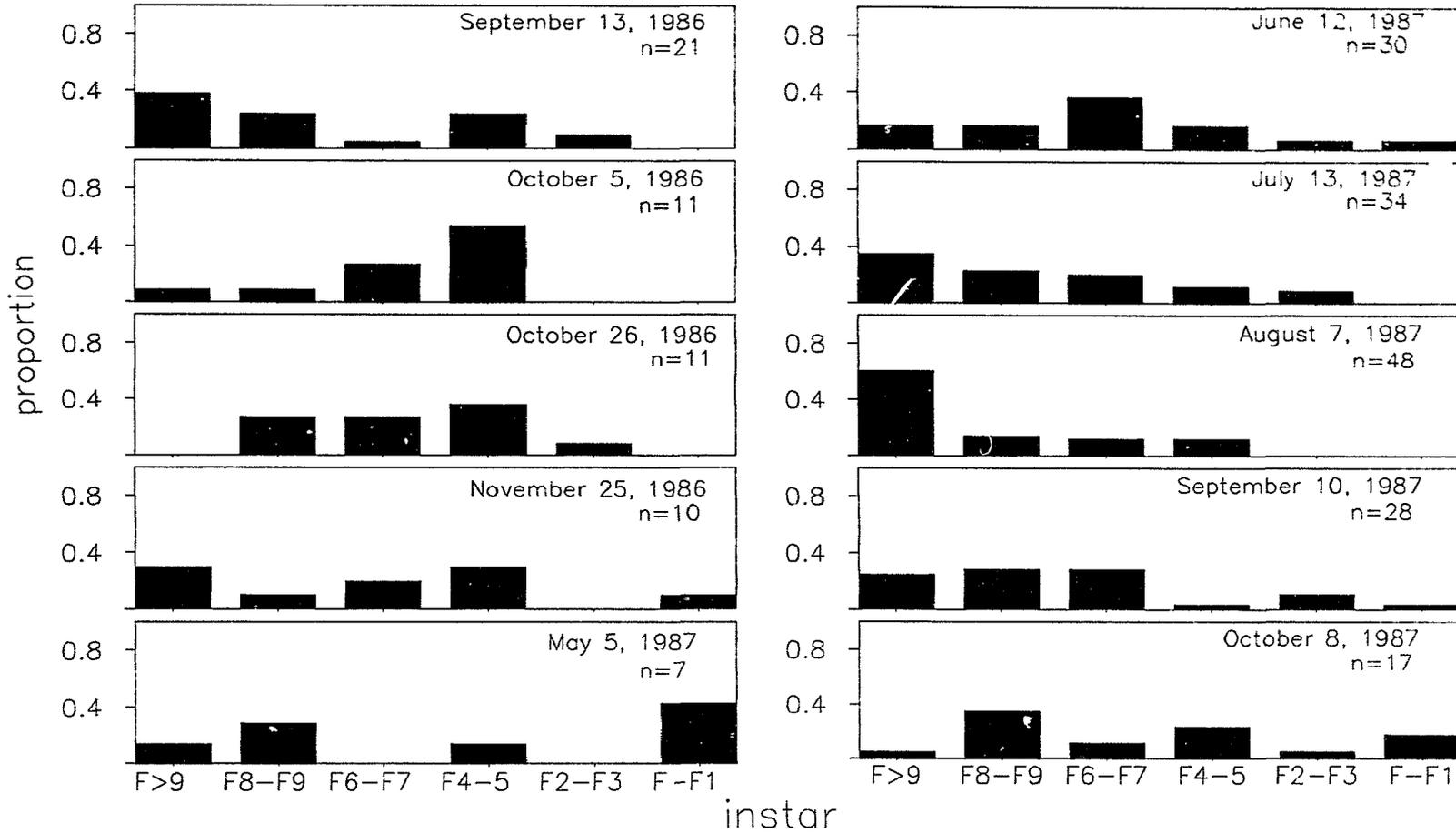


Figure 2.23 Relative frequency of different instars of *Cordulia shurtleffi*

Leucorrhinia glacialis

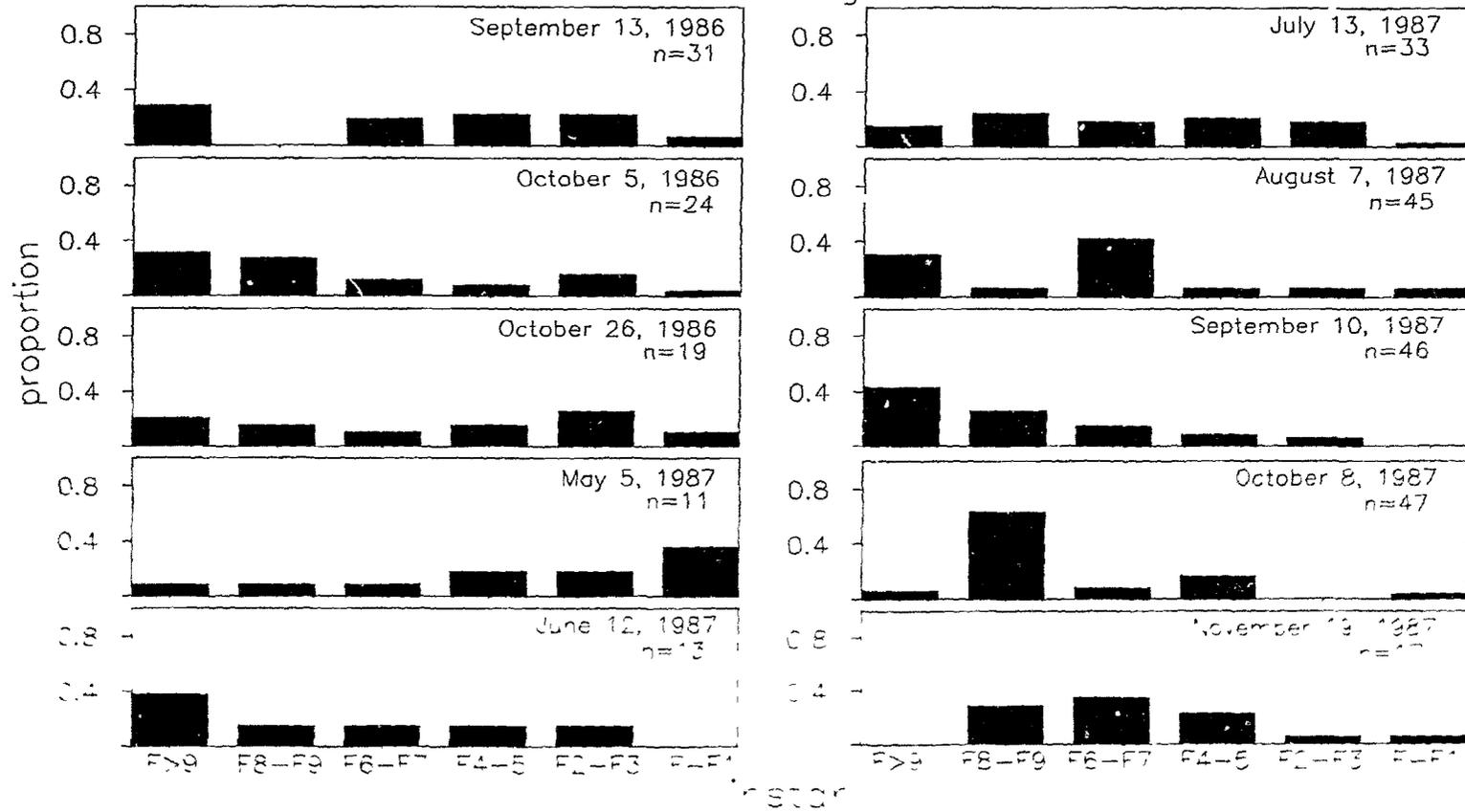


Figure 2.24 Relative frequency of different instars of *Leucorrhinia glacialis*

Mean gut passage times for odonates in Jack Lake varied between 5 and 10 hours at 22° C (Table 2.3), suggesting mean predation rates of less than 10 Cladocera per day. Lawton (1971a) found similar gut passage times for a zygopteran odonate, Pyrrhosoma nymphula, and estimated that natural feeding rates were 20-50% of maximum feeding rates determined in the laboratory. Because of the wide distribution of instars and the large potential range of predation rates within instars, the estimation of population predation rates for odonates is difficult. If odonates fed at a rate of 10 Cladocera·predator⁻¹·d⁻¹, they would consume between 3 and 9% of the epiphytic cladoceran population daily between June and August. Much higher rates are possible.

iv) Acari: Water mites were among the most common invertebrates in Jack Lake. Unfortunately, the species composition and feeding habits of water mites were not examined in detail. Nymphs and adults of two species encountered in Jack lake, Limnesia and Limnochares, are reported to eat Cladocera, chironomids, and other insect larvae (Paterson 1970; Pieczynski 1976; Smith 1987; Proctor and Pritchard 1990). Many other species are also highly predaceous (Smith 1987).

Over 95% of the mites in Jack Lake were small nymphs. In 1987, lake bottom densities of mites increased greatly from May to June, remained high until September and then decreased in October-November (Figure 2.25a). Numbers of mites did not

Table 2.3. Mean gut passage times (in hours) for three odonates from Jack Lake. Ranges are in parentheses.

<u>Species</u>	<u>22° C</u>	<u>14° C</u>
<u>Enallagma carunculatum</u>	5.0 (2.8 - 10.5)	21.1 (6.3 - 47.4)
<u>Cordulia shurtleffi</u>	6.7 (4.0 - 10.5)	31.6 (13.0 - 47.4)
<u>Leucorrhinia glacialis</u>	8.9 (5.0 - 10.5)	25.7 (13.0 - 39.6)

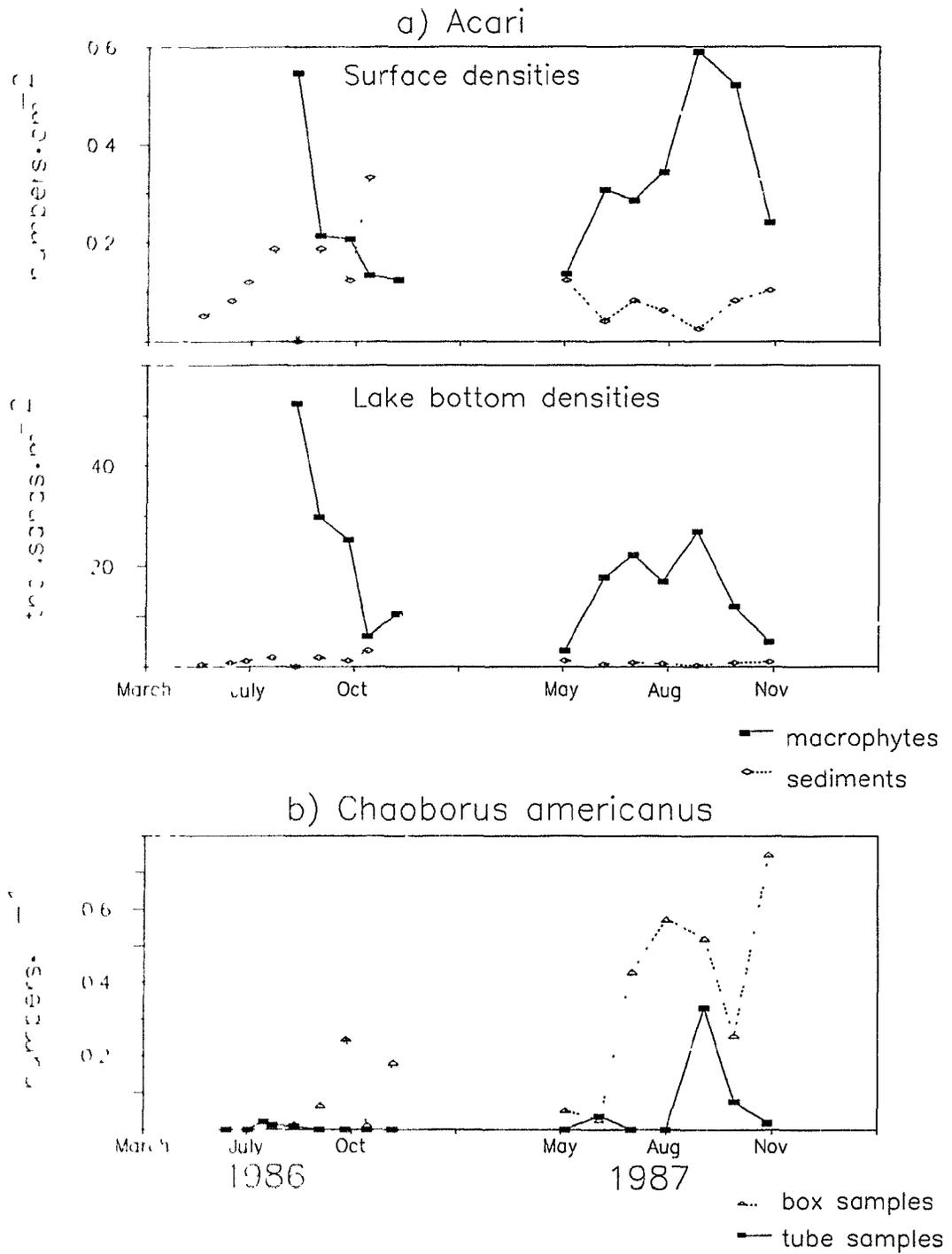


Fig. 2.25. Seasonal dynamics of a) water mites and b) *Chaoborus americanus*. Note different scales and units.

increase during the midsummer decline of Cladocera in 1987, and autumn increases of Cladocera preceded declines of mite abundance. Hence, mite predation does not appear to have strongly influenced microcrustacean seasonal dynamics.

Studies on planktonic mites have reported feeding rates on Cladocera of $3-168 \cdot d^{-1}$ for adults (Gliwicz and Biesiadka 1975; Lynch 1979; Riessen 1982; Matveev et al. 1989) and $2-3$ Cladocera $\cdot d^{-1}$ for nymphs (Riessen 1982). There are few studies of the feeding rates of littoral mites. Paterson (1970) found that adult Limnesia fed on chironomids in the laboratory at a rate of 26 chironomids per day. Consumption of Cladocera at these rates would rapidly eliminate littoral Cladocera from Jack Lake. In contrast, Anderson (1970) reported that "large red mites" consumed calanoid copepods at very low rates (less than $1 \cdot predator^{-1} \cdot day^{-1}$). As a result, the potential impact of mites on Cladocera in Jack lake is uncertain.

v) Chaoborus: Chaoborus is recognized as an important predator of planktonic microcrustacea (Allan 1973; Swuste et al. 1973; Federenko 1975; Lewis 1977; Pastorok 1980; Smyly 1980; Winner and Greber 1980; Elser et al. 1987; Jin and Sprules 1988; Mackay et al. 1990). Chaoborus americanus was regularly encountered in box and core samples from Jack Lake in close proximity to macrophytes and sediments. Although C. americanus is generally regarded as a planktonic predator, feeding on epiphytic and benthic organisms cannot be ruled

out.

There is little evidence that C. americanus strongly influenced the dynamics of epiphytic or benthic Cladocera. The abundance of C. americanus in box samples was much lower than that of most other predators. C. americanus was much more abundant in 1987 than 1986 (Figure 2.25b). In 1987, numbers of C. americanus were highest in box samples from June to September, decreased in October, and increased again in November. Epiphytic and benthic Cladocera displayed similar dynamics in both 1986 and 1987, despite large variations in numbers of C. americanus.

Although C. americanus probably did not affect the abundance of epiphytic and benthic microcrustacea, it may have affected planktonic species. Bosmina longirostris was abundant in 1986, but rarely encountered in 1987. B. longirostris and C. americanus apparently rarely co-exist (Von Ende and Dempsey 1981; Elser et al. 1987; Black and Hairston 1988). Increased abundance of H. gibberum in 1987 may result from decreased competition from B. longirostris. H. gibberum is surrounded by a gelatinous matrix that apparently reduces predation by Chaoborus (Allan 1973; Neill 1981; Stenson 1987). More data are required to test these hypotheses.

vi) Predatory trichoptera (Cernotina sp.): The size structure of Cernotina populations was determined only in 1987. Newly hatched individuals were common in samples

collected in July and August (Figure 2.26). These grew to instar-5 by October and emergence occurred the following June-July. Predation rates on Cladocera and relative predation by different instars is unknown. Under the assumption that instars-4 and -5 prey most on Cladocera, predation rates were highest in September-October and it is unlikely that predation by Ceratotina accounts for midsummer decreases of Cladoceran abundance.

5) Invertebrate predation and the seasonal dynamics of littoral microcrustacea: General discussion

The correlative nature of the observational data limits conclusions concerning the impact of predators on microcrustacean seasonal dynamics. Evidence that invertebrate predation strongly affected littoral cladoceran community dynamics was mixed. Seasonal changes in cladoceran birth rates were very different from changes in abundance, suggesting that variations in loss rates were important determinants of population size. Gut analyses indicated that many invertebrates fed on Cladocera and crude estimates of predation rates suggested that invertebrate predators may cause substantial mortality of epiphytic Cladoceran populations.

In contrast, seasonal changes in the abundance of most predators were not negatively correlated with littoral cladoceran abundance. Numbers of several common predators (c5 and adult M. albidus, instar-4 Procladius sp., Enallagma

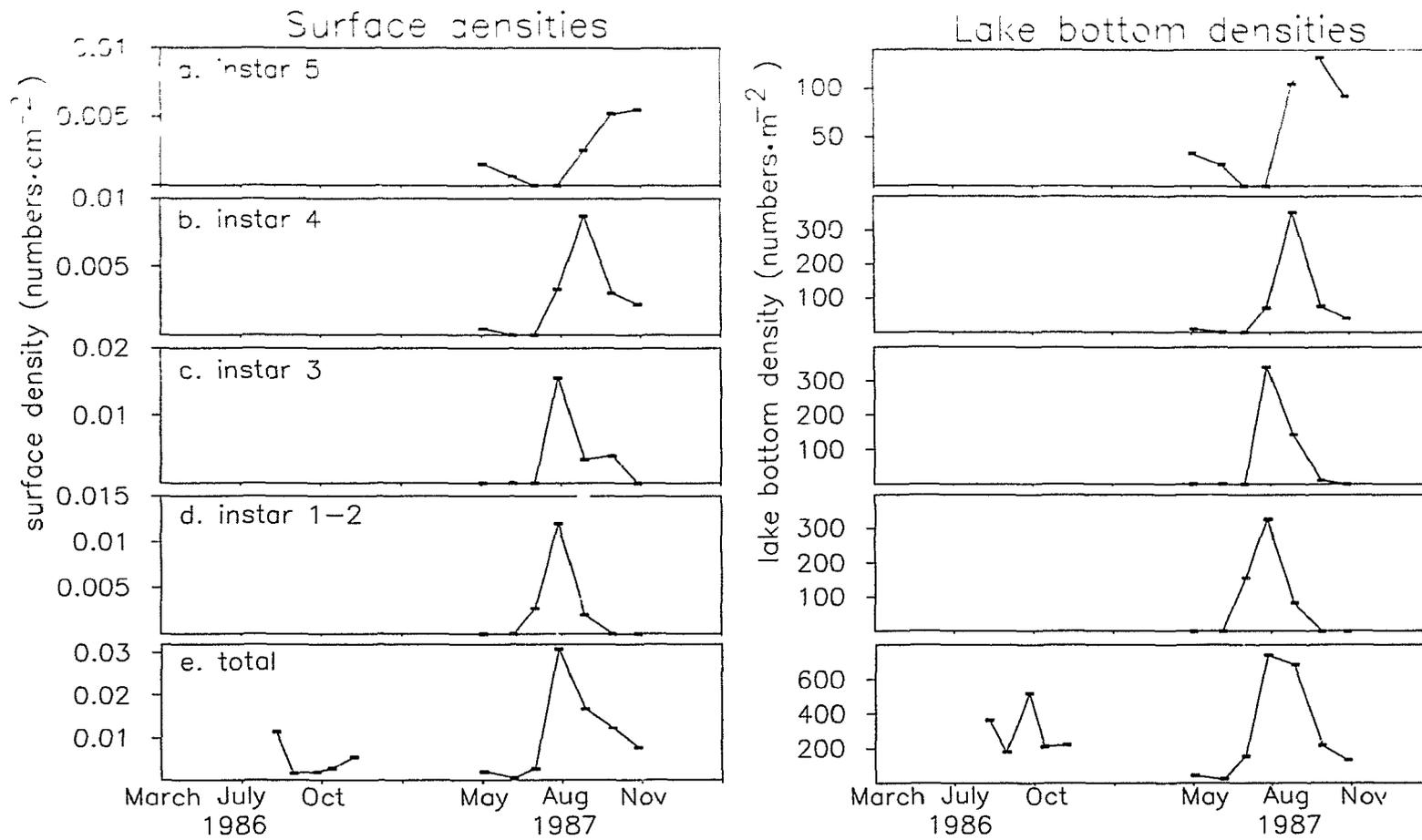


Figure 2.26. Seasonal changes of surface and bottom densities of different instars of *Cernotina* sp.. Note different density scales.

carunculatum, instar-4 and -5 Ceratotina sp.) were low in August, when birth rate estimates suggested that cladoceran loss rates were highest. Numbers of these predators also increased along with Cladocera in September-October. Seasonal changes in numbers of other predators (water mites, anisopteran odonates, Chaoborus americanus) seemed insufficient to explain changes in the abundance of epiphytic and benthic Cladocera.

The seasonal dynamics of Ablabesmyia sp. suggested the potential for strong interactions with littoral Cladocera. Goulden (1971) also concluded that tanypod chironomids were the most important invertebrate predators of benthic Cladocera and argued that they strongly influenced microcrustacean community dynamics. The influence of Ablabesmyia on microcrustacea in Jack Lake is examined further in Chapter 3.

The possibility that the seasonal dynamics of littoral microcrustacea reflected lagged responses to predator dynamics cannot be ruled out. For example, the decline in littoral cladoceran numbers in August may reflect a delayed response to high predation by Ablabesmyia, odonates, and M. albidus in July. Similarly, increases in Cladocera in September may be a response to decreased predation in August.

Total consumption rates by a predator population are a function of 1) predator numbers and 2) numbers of prey consumed per predator. Only seasonal changes in predator

abundance were estimated in this study. Consumption rates of individual predators are potentially affected by many factors including water temperature, alternate prey, macrophyte densities and species composition, interference among predators, prey size and morphology, prey behaviour, etc. The influence of these factors on seasonal changes in predation rates are considered briefly below:

a) Water temperature: The consumption rates of most invertebrate predators are positively correlated with water temperature (Lawton 1971a; Brandl and Fernando 1975; Federenko 1975; Gophen 1976; Thompson 1978b). The development rates of microcrustacean eggs increase with water temperature, so that increasing consumption rates by predators may be offset by increases of microcrustacean birth rates. In Figure 2.27, I compare literature data on the effects of temperature on chydorid cladoceran egg development rates and individual consumption rates by cyclopoid copepods and zygopteran odonate larvae. Data are expressed as proportions of rates at 10° C. These results suggest that increases of water temperature cause cladoceran egg development rates to increase at a proportionally faster rate than invertebrate predation rates. As a result, invertebrate predators should have a stronger impact on chydorid populations at low temperatures than at high temperatures (assuming that invertebrate predator numbers and cladoceran clutch sizes remain constant). This contention is also

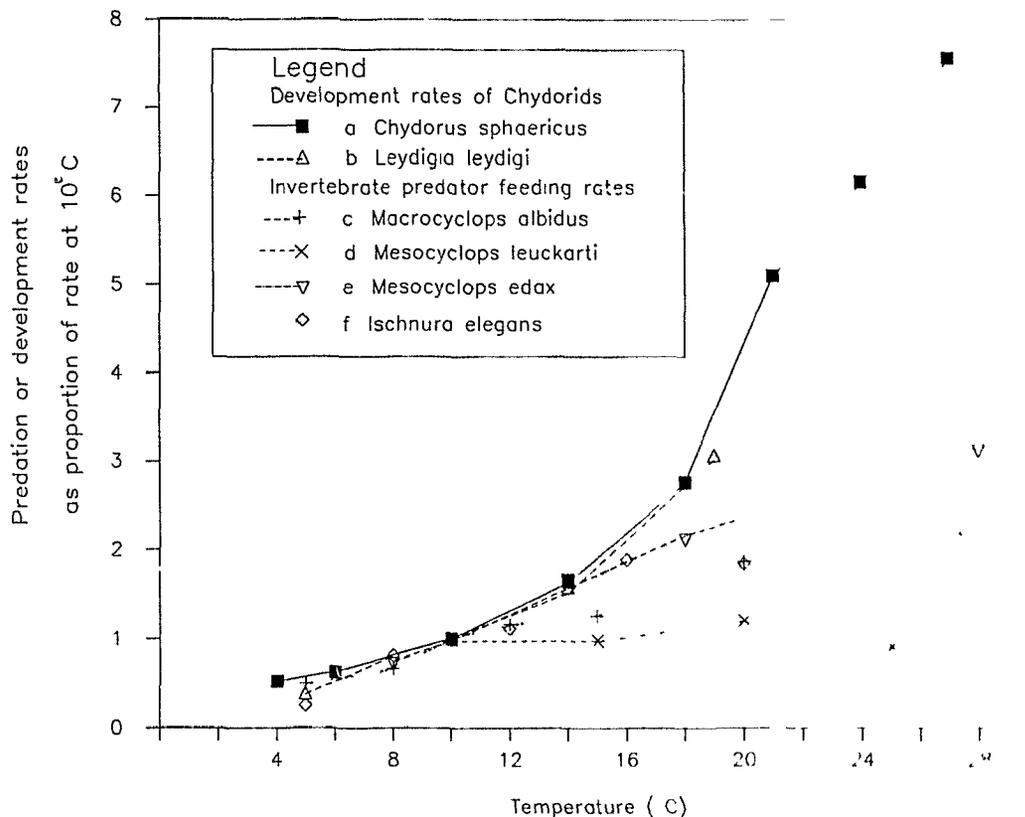


Figure 2.27. The relative effect of temperature on egg development rates of chydorid Cladocera and predation rates of cyclopoid copepods and zygopteran odonate larvae. a) Egg development rates for a chydorid cladoceran, *Chydorus sphaericus* (data from Keen 1973). b) Egg development rates for a chydorid cladoceran, *Leydigia leydigii* (data from Robertson 1988). c) Predation rates of a cyclopoid copepod, adult female *Macrocyclus albidus*, feeding on *Paramecium caudatum* (data from Laybourn Parry et al. 1988). d) Predation rates of a cyclopoid copepod, adult female *Mesocyclops leuckarti*, feeding on *Ceriodaphnia dubia* (data from Jamieson 1980). e) Predation rates of a cyclopoid copepod, adult female *Mesocyclops edax*, feeding on *Ceriodaphnia* sp. (data from Brandl and Fernando 1975). f) Maximum predation rates of a zygopteran odonate, instar-11 *Ischnura elegans*, feeding on *Daphnia* sp. (data from Thompson 1978b). Feeding rates at 10°C were estimated by linear interpolation.

supported by the results of Neill (1981). In a series of in situ enclosure experiments, Chaoborus reduced Daphnia populations only during years and seasons of low temperature. At other times, Daphnia was able to escape predator control through increased reproduction. Overall, these data suggest that September-October increases in littoral Cladocera in Jack Lake were not a function of temperature-induced decreases of consumption rates by individual predators.

b) Alternate prey: Many laboratory studies suggest that the predation rates of many invertebrates vary with the availability of alternate prey (Akre and Johnson 1979; Crowley 1979; Jamieson 1980; Kajak 1980; Williamson 1983; Jeffries 1988; Jin and Sprules 1988). Gut content analyses suggest that the most important non-crustacean prey of most predators in Jack Lake were chironomids and oligochaetes.

Seasonal changes in the abundance of chironomids, oligochaetes, and other non-predaceous invertebrates are depicted in Figure 2.28. Chironomids were the most abundant invertebrates in the Jack Lake littoral zone. In 1987, bottom densities of epiphytic chironomids increased from May to August and declined thereafter. A similar trend was evident in 1986. Numbers of oligochaetes, gastropods (Ferrissia sp.), and tardigrades were low in May, increased over the summer, and declined in November. The population size of a small trichopteran, Oxyethira sp., was greatest in September-October.

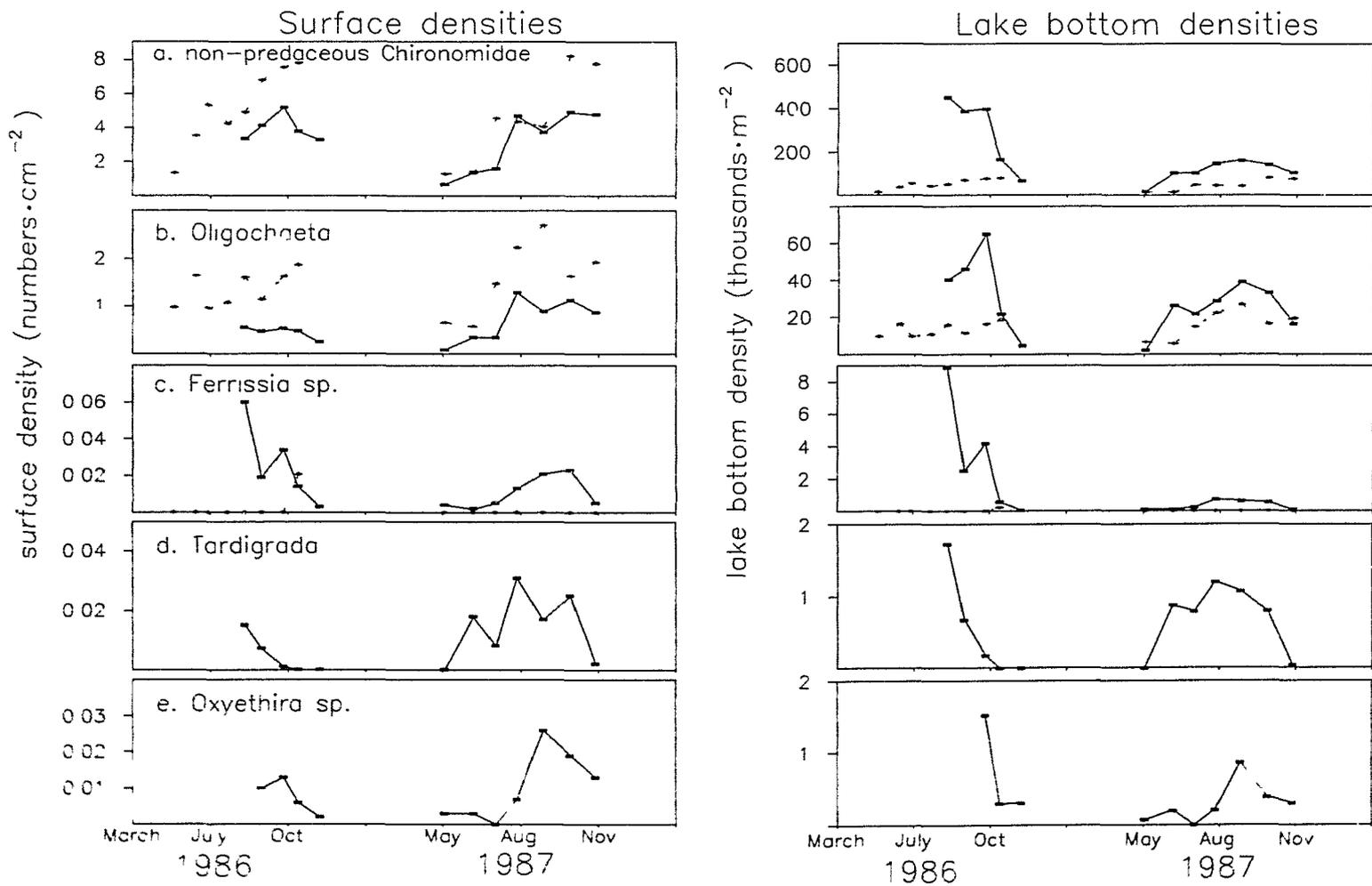


Figure 2.28 Seasonal changes of surface and bottom densities of non-predaceous macroinvertebrates. Note different density scales.

There is little evidence that changes in numbers of non-crustacean prey affected predation on Cladocera. Midsummer lows of cladoceran abundance did not coincide with low chironomid or oligochaete numbers. Possibly, increases in chironomid abundance in September-October caused decreased predation on microcrustacea. The effect of shifts in the availability of alternate prey is difficult to address, because many invertebrates feed selectively on different species and sizes of chironomids (Dillon 1985; Hershey 1986, 1987). The species composition and size structure of the chironomid community in Jack Lake was not examined in this study.

c) Macrophytes: Predation rates of many littoral predators are strongly affected by variations in the density and composition of macrophytes (Nelson 1979; Heck and Thoman 1981; Crowder and Cooper 1982; Stoner 1982; Coull and Wells 1983; Anderson 1984; Folsom and Collins 1984; Gilinsky 1984; Thompson 1987; Diehl 1988; Gotceitas and Colgan 1989; Dionne and Folt 1991). In both 1986 and 1987, increases of total cladoceran abundance in September-October coincided with increases in the biomass of Scirpus subterminalis and Potamogeton confervoides. Macrophytes also became covered by dense clouds of filamentous algae at these times and these may have provided a refuge for microcrustacea from some invertebrate predators. Anisopteran odonates and Procladius were rarely encountered on S. subterminalis or Potamogeton

confervoides (Chapter 1). More research is required before firm conclusions can be drawn.

d) Interference among predators: Many invertebrate predators display strong intraspecific interference competition and in extreme cases may actively consume members of their own species (Fischer 1961; Lane 1978; Baker 1980; Peckarsky and Penton 1985; Crowley et al. 1987; Matveev et al. 1989; Van Buskirk 1989; Wissinger 1989; Anholt 1990). Many small predators of microcrustacea in Jack Lake were also prey for larger predators and many invertebrates alter their behaviour with their own risk of predation (Sih 1982; Heads 1985; Crowley et al. 1987; Dixon and Baker 1987, 1988; Pierce 1988; Jeffries 1990; McPeck 1990). Although these behavioral shifts may have affected predation rates on Cladocera, it is unlikely that microcrustacean seasonal dynamics were strongly affected. Interference among predators should act to buffer the effects of variations of predator densities on total prey consumption.

e) Prey size and morphology: Variations in prey size and morphology affect the feeding rates of many invertebrate predators (Confer 1971; Thompson 1975; Thompson 1978b; Li and Li 1979; Jamieson 1980; Krueger and Dodson 1981; Pastorok 1981; Riessen 1982; Dillon 1985; Williamson 1986; Hershey 1987; Kerfoot 1987). The mean size of different species of Cladocera did not change between June and October in Jack Lake and obvious changes in morphology were not observed.

Both large species (Alona cf. affinis, Ilyocryptus sp.) and small species (Chydorus linguilabris, Streblocerus serricaudatus) of Cladocera increased in abundance in September-October.

f) Predator and prey behaviour: Seasonal changes in the behaviour of predators or microcrustacea may have affected predation rates. Many factors such as food availability, water clarity, the presence of competitors, etc. may alter the activity and behaviour of microcrustacea seasonally in Jack Lake. These behavioral effects could not be addressed in this study.

6) Summary

Large seasonal changes in the abundance of different species of epiphytic and benthic microcrustacea were encountered in Jack Lake. Examinations of cladoceran clutch sizes and birth rates in 1987 suggested that low numbers of Cladocera in May and November were the result of low birth rates caused by low temperatures. Seasonal changes of abundance at other times were apparently the result of seasonal shifts in loss rates. These patterns are similar to those observed in several other studies and have usually been interpreted as evidence of the effects of predation.

Based on relative abundance and gut content analyses, the most important predators of microcrustacea in Jack Lake were cyclopoid copepods (particularly M. albidus), tanypod chironomids (Ablabesmyia sp., Procladius sp.), odonate larvae

(Enallagma carunculatum, Cordulia shurtleffi, Leucorrhinia glacialis), and water mites. Only the dynamics of Ablabesmyia were suggestive of possible predator-prey interactions with epiphytic and benthic Cladocera. Unfortunately, conclusions concerning the potential impact of invertebrate predators in Jack Lake were limited by the lengthy sampling interval, an inability to assess the importance of lags in the response of prey populations, and the absence of direct estimates of invertebrate predation rates. As a result, the impact of several invertebrate predators is examined further in Chapter 3 using experimental approaches. A full discussion of factors affecting littoral microcrustacean seasonal dynamics in Jack Lake is deferred to Chapter 4.

Chapter 3

Experimental manipulations of invertebrate predator densities

A. Introduction

In this chapter, the effects of invertebrate predators on littoral microcrustacea are examined using in situ enclosures. Densities of odonates, adult water mites, and 3d and 4th instar Tanypodinae were manipulated in a series of six experiments using two enclosure designs. The following questions were examined in some or all experiments:

1) Do invertebrate predators affect the abundance of common littoral macro- and meiofaunal invertebrates? 2) Do invertebrate predators affect microcrustacean species composition? 3) Do invertebrate predators affect the size structure of littoral microcrustacean populations? 4) Do invertebrate predators affect the clutch sizes of common Cladocera? Clutch sizes have often been used as a correlate of competition intensity among Cladocera.

B. Methods

The timing and duration of the 6 experiments in Jack Lake are listed in Table 3.1.

1) Large enclosures (Experiments 1-3): The large enclosures were based on the design of Crowley et al. (1983) and were used for manipulations of odonate densities. Enclosures were cylinders of 100- μ m Nitex mesh supported by chicken wire and were placed in water 1 m deep. Bottoms were

Table 3.1. Summary of predator manipulation experiments in Jack Lake.

<u>Experiment</u>	<u>Predators manipulated</u>	<u>Duration</u>
1) <u>Large enclosures:</u>		
Experiment 1	large Odonates	Sept 2 - Oct 5, 1987
Experiment 2		June 15 - July 25, 1988
Experiment 3		Aug 17 - Sept 21, 1988
2) <u>Small enclosures:</u>		
Experiment 4	small Odonates Tanypodinae Acari	June 29 - July 10, 1988
Experiment 5		July 20 - Aug 3, 1988
Experiment 6		Aug 10 - Aug 24, 1988

670-cm² plastic flower pot plates that were isolated from lake sediments by the nylon mesh. Enclosure tops were open and extended approximately 20 cm above the lake surface. The nylon mesh allowed exchange of water and phytoplankton, but prevented passage of predators and most prey. Temperatures and oxygen concentrations in enclosures did not vary from those in the lake during the experiments.

At the start of each experiment, clumps of Pallavicinia lyellii, a rootless liverwort and the most abundant macrophyte in Jack Lake, were moved onto plastic plates on the lake bottom. After allowing three weeks for invertebrate colonization, the plates and macrophytes were enclosed in a 100- μ m mesh bag and brought to the surface by a SCUBA diver. On shore, the macrophytes were sorted and all odonates encountered were removed. Sorted material was mixed together and divided into equal allotments, one for each enclosure.

Each experiment had five randomly allocated replicates of two treatments: high and low odonates. Odonates were added to high odonate treatments at natural densities and the average proportions of different odonate species and instars were retained. Low odonate treatments contained only those animals missed during sorting. The initiation of different experiments was timed to include periods when crustacean numbers were both high and low in Jack Lake (Table 3.1). The duration of experiments was 5 to 6 weeks. P. lyellii in

enclosures remained green throughout the experiments.

At the termination of each experiment, enclosures were removed and invertebrates were washed from the nylon mesh and macrophytes. Material from enclosures was preserved in sugar-formalin, stained with rose-bengal, and sieved with a 600- μ m and a 125- μ m screen. All insects on the 600- μ m sieve (except non-predatory Chironomidae) were counted and then the 600- μ m fraction was recombined with material on the 125- μ m sieve. This volume was repeatedly subsampled with a wide-mouth pipette until approximately 400 microcrustaceans were counted. For abundant organisms, the standard error of subsamples was less than 10% of the mean and was ignored in subsequent analyses. Determinations of cladoceran clutch sizes, microcrustacean body lengths, invertebrate sizes and stages, and odonate biomasses are described in Chapter 2. In experiment 1, body lengths and clutch sizes were measured only for the most common crustacean species (Alona intermedia, Ilyocryptus sp., Chydorus linguilabris, Macrocyclus albidus). In experiments 2 and 3, body lengths of all microcrustacea were measured.

The success of odonate manipulations was assessed using t-test comparisons of the biomass of odonates in high and low-odonate treatments (Sokal and Rohlf 1981). A square-root transformation was most successful at reducing heteroscedasticity of odonate biomasses. The effect of odonates on numbers of common invertebrates was determined

by combining the results of the three experiments in a series of two-way ANOVAs (date X treatment (odonate density)) (Sokal and Rohlf 1981). Invertebrate abundances were fourth-root transformed before analysis. Size frequency distributions of common microcrustacea in low- and high-odonate treatments in different experiments were compared using Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1981). Size-frequency distributions for total Cladocera and Cyclopoida in experiments 2 and 3 were obtained by using size data for individual species, weighted by their abundance. These size distributions were compared with χ^2 tests (Sokal and Rohlf 1981). Degrees of freedom for Kolmogorov-Smirnov and χ^2 tests are presented in Figures 3.3 and 3.4 and in Appendix 4.

2) Small enclosures (Experiments 4-6): Water mites, tanypod midges, and early instar odonates were too small and abundant to be effectively manipulated in the large enclosures. To examine the impact of these predators, I conducted three experiments using small, 600-ml enclosures constructed of sections of 15.14-cm internal diameter plexiglass tubing. Tube ends were sealed with 63- μ m Nitex mesh.

Weighted plastic pot-scrubbers were left on the bottom of Jack Lake for three weeks to be colonized by a natural community of invertebrates (cf. Whiteside 1974). Scrubbers were then collected by a snorkeler and placed in a 100- μ m

Nitex mesh bag. On shore, all invertebrates and detritus on scrubbers were washed into a bucket and divided into equal allotments, one for each enclosure. Predators were removed from all allotments under a microscope using natural illumination. Predators were then returned to enclosures according to the experimental design. A pot-scrubber was added to each enclosure to provide cover. Enclosures were left on the bottom of Jack Lake in water approximately 1 m deep for 11-14 days (Table 3.1). At the termination of each experiment, the contents of each enclosure were washed through a 125- μ m sieve, preserved with a 5% formalin and sugar solution, and stained with rose-bengal. Microcrustacea and larger invertebrates in enclosures were counted without subsampling.

In each experiment, predators were manipulated according to a 2^3 factorial design (Box et al. 1978). The results of the different experiments were then combined and analyzed as a single $3 \times 2 \times 2 \times 2$ factorial design. The factors were the three experiments and all combinations of high and low levels of 1) third and fourth instar Tanypodinae (Procladius sp. and Ablabesmyia sp.), 2) adult water mites (Limnesia sp.), and 3) early instar odonates (Enallagma carunculatum, Leucorrhinia glacialis, and Cordulia shurtleffi with headwidths less than 1.75 mm). Enclosures with "high" levels of predators contained approximately natural densities that occurred on pot-scrubbers before sorting. At least two

predators were added to each enclosure and, consequently, initial predator-prey ratios were always slightly higher than in box samples collected from Jack Lake. Enclosures with "low" levels of predators contained only predators missed during sorting. There were two replicates of each combination of treatments for a total of 16 replicates in each experiment (48 replicates overall). Several enclosures containing only a pot-scrubber were left on the lake bottom and were used to assess immigration of invertebrates into enclosures.

Factorial designs are useful for exploring the effects of a broad range of treatments using a minimum number of replicates (Box et al. 1978; Sokal and Rohlf 1981). Although I was primarily concerned with the main effects of tanypods, odonates, and water mites on littoral microcrustacea, the factorial design allowed for the assessment of interactions among predators and dates. Furthermore, the main effects of predators were evaluated in a wide variety of conditions, adding robustness to the results (Qin and Threlkeld 1990). The main drawback of multifactorial experimental designs is that multiple comparisons are used to assess statistical significance (Wilkinson 1988). As a result, my analyses were restricted only to consideration of the impacts of predators on total numbers of Cladocera and Cyclopoida. All densities were log transformed before analysis to reduce heteroscedasticity. Statistical analyses were completed

using the SYSTAT 4.0 computer package (Wilkinson 1988) on an IBM personal computer clone.

C. Results

1) Large enclosures: At the termination of each experiment, mean odonate biomasses in low-odonate enclosures were between 10 and 25% of mean biomasses in high-odonate enclosures (Table 3.2). Biomass reductions in low-odonate enclosures were largely a result of decreased numbers of large anisopterans (headwidths greater than 2.5 mm). Zygopterans and small anisopterans were frequently missed during sorting and their numbers were not significantly reduced.

The abundance of common invertebrate groups varied considerably among experiments, but in no case was there a significant effect of odonate treatment (Figure 3.1, Table 3.3). The abundance of different species of microcrustacea was also not significantly different in low and high-odonate enclosures (Figure 3.2; see Appendix 5 for ANOVA tables). Numbers of total Cladocera and Cyclopoida were not significantly negatively correlated ($\alpha < 0.05$) with the biomass of any species of odonate or with total odonate biomass in any experiment. As a result, there is no evidence that large anisopteran odonates strongly affected the abundance of meio- or macrofaunal invertebrates in Jack Lake.

Size-frequency distributions for the most common species of Cladocera and Cyclopoida in each experiment did not vary significantly between low and high odonate treatments (Figures 3.3, 3.4; Kolmogorov-Smirnov tests, $\alpha = 0.05$;

Table 3.2. Mean biomasses of odonates ($\text{mg}\cdot\text{encl}^{-1}$) retrieved from enclosures and comparison of treatment means (t -tests; $\text{df}=8$). Standard errors of the mean are in parentheses. Biomasses were square-root transformed before applying t -tests.

	<i>Enallagma carunculatum</i>	<i>Cordulia shurtleffi</i>	<i>Leucorrhinia glacialis</i>	<i>Aeschna interrupta</i>	Total
<u>Experiment 1</u>					
Low odonates	3.99 (0.99)	5.43 (1.04)	6.23 (2.25)	0.0	15.66 (2.65)
High odonates	5.26 (1.02)	19.36 (2.65)	18.5 (5.37)	120.19 (12.26)	163.30 (13.23)
t -test	$p<.4$	$p<.05$	$p<.001$	$p<.001$	$p<.001$
<u>Experiment 2</u>					
Low odonates	2.41 (0.59)	17.38 (2.34)	7.25 (2.48)	0.0	27.04 (3.87)
High odonates	4.48 (1.58)	35.63 (10.75)	25.58 (6.24)	30.79 (2.99)	96.48 (5.14)
t -test	$p<.4$	$p<.5$	$p<.02$	$p<.001$	$p<.001$
<u>Experiment 3</u>					
Low odonates	1.07 (0.54)	11.87 (3.02)	5.05 (3.12)	0.0	17.99 (6.22)
High odonates	1.62 (0.52)	47.83 (5.39)	30.46 (6.78)	1.93 (1.93)	81.84 (6.7)
t -test	$p<.5$	$p<.001$	$p<.01$	$p<.001$	$p<.001$

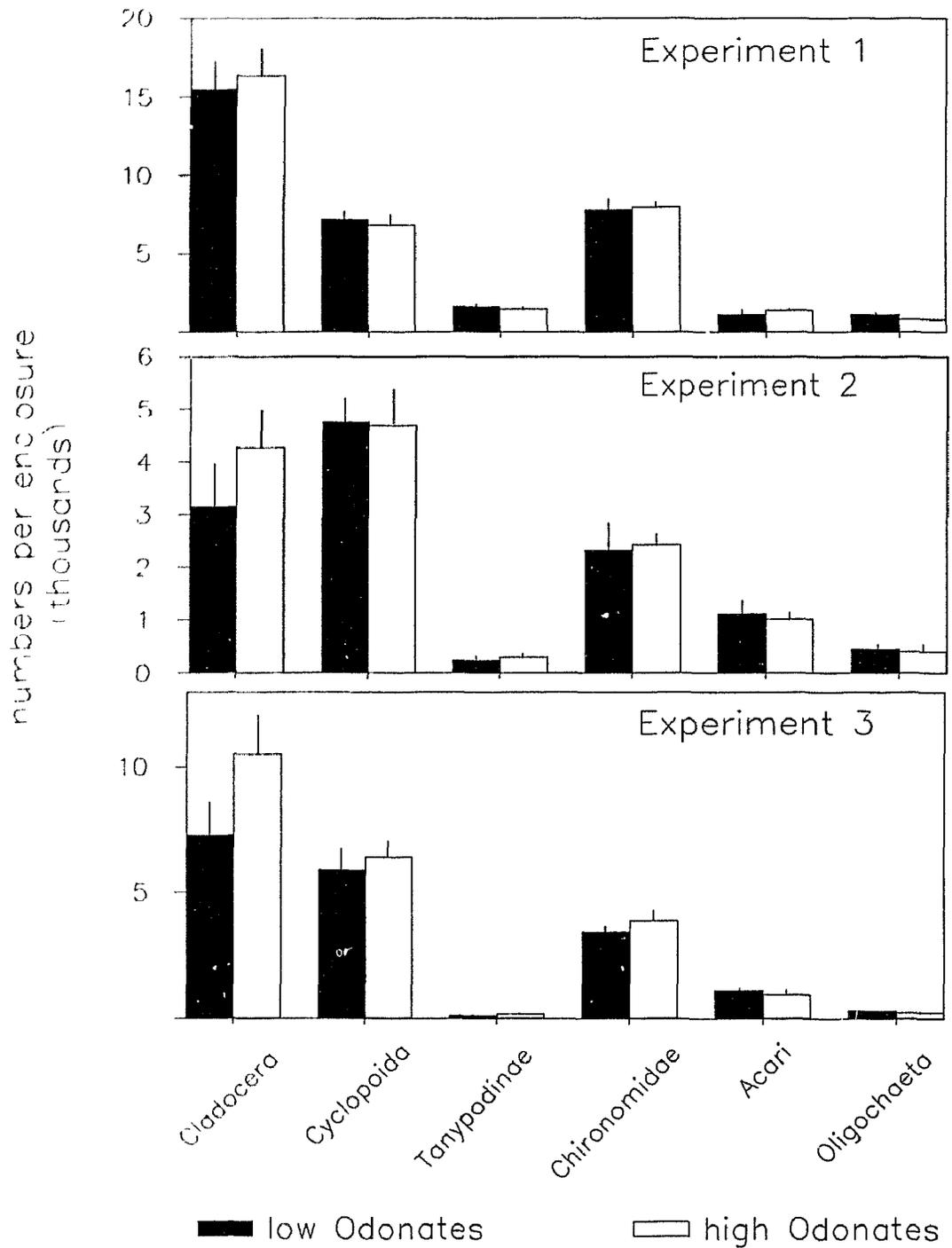


Figure 3.1. Final abundance of common invertebrate groups in large enclosures. Vertical lines are + one standard error.

Table 3.3. Two-way ANOVAs comparing abundance of common invertebrate groups in enclosures by experiment and treatment (high vs. low odonate abundance). All abundances were fourth-root transformed before analysis.

Source of variation	df	MS	F	P
<u>total Cladocera:</u>				
Experiment	2	31.751	37.752	<0.001
Odonates	1	2.700	3.210	0.086
Experiment X Odonates	2	0.346	0.411	0.667
Error	24	0.841		
<u>total Cyclopoida:</u>				
Experiment	2	2.02228	5.4444	0.011
Odonates	1	0.00007	0.0002	0.989
Experiment X Odonates	2	0.09491	0.2555	0.777
Error	24	0.37144		
<u>Tanypodinae:</u>				
Experiment	2	23.632	125.290	<0.001
Odonates	1	0.035	0.187	0.670
Experiment X Odonates	2	0.072	0.384	0.686
Error	24	0.189		
<u>non-predaceous Chironomidae:</u>				
Experiment	2	16.176	63.459	<0.001
Odonates	1	0.216	0.848	0.366
Experiment X Odonates	2	0.014	0.057	0.945
Error	24	0.255		
<u>Acari:</u>				
Experiment	2	0.109	0.075	0.928
Odonates	1	0.717	0.489	0.491
Experiment X Odonates	2	1.717	1.171	0.327
Error	24	1.466		
<u>Oligochaetes:</u>				
Experiment	2	5.386	18.156	<0.001
Odonates	1	0.624	2.105	0.160
Experiment X Odonates	2	0.065	0.220	0.805
Error	24	0.297		

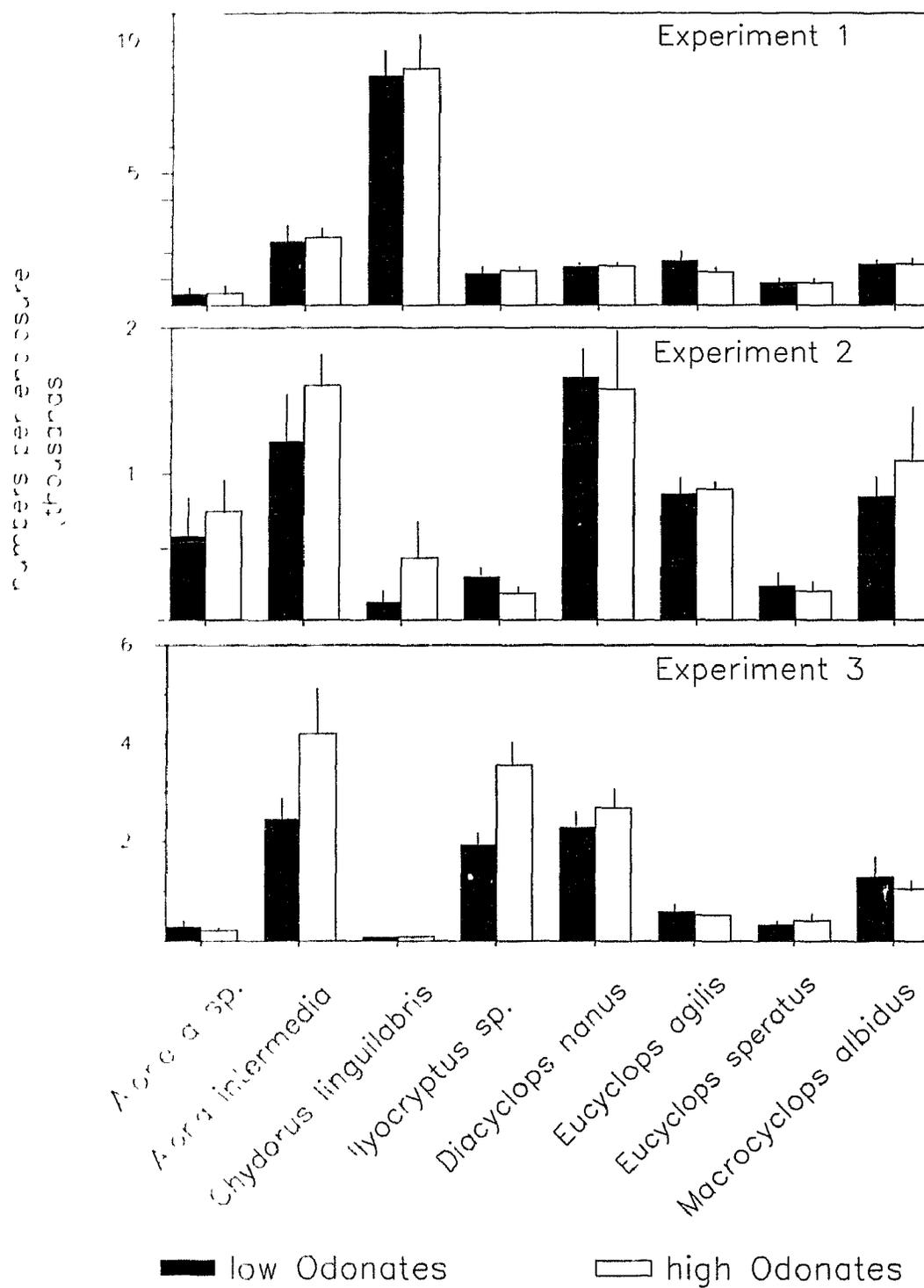


Figure 3.2. Final abundance of common microcrustacea in large enclosures. Vertical lines are + one standard error.

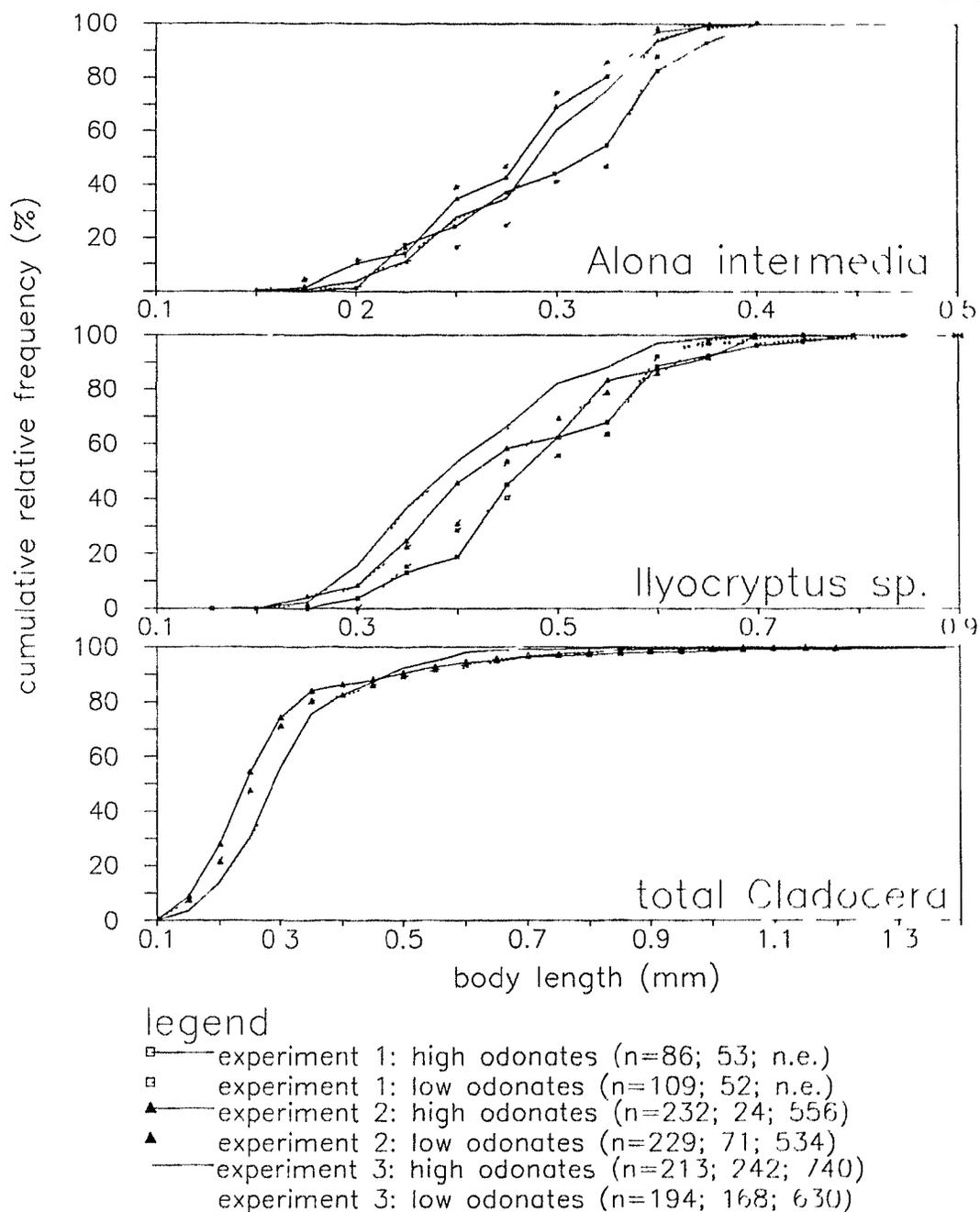
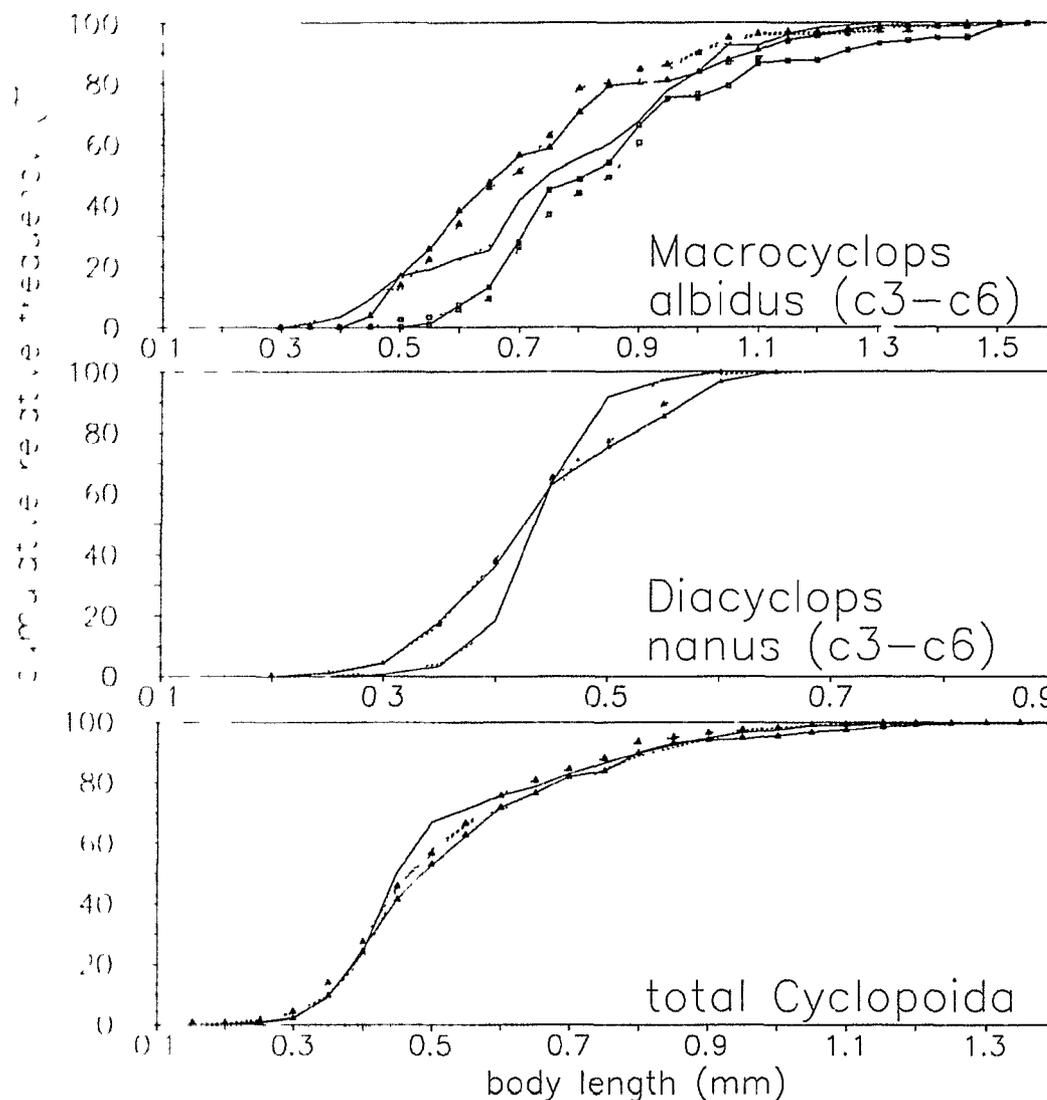


Figure 3.3. Cumulative relative size frequencies of body lengths of *Alona intermedia*, *Ilyocryptus sp.*, and total Cladocera in large enclosures. Sample sizes are presented in parentheses in the legend according to the following order: *A. intermedia*, *Ilyocryptus sp.*, total Cladocera. Sizes of total Cladocera were not estimated in experiment 1 (abbreviated as n.e. in the legend).



legend

- experiment 1: high odonates (n=90; n.e.; n.e.)
- experiment 1: low odonates (n=87; n.e.; n.e.)
- ▲ experiment 2: high odonates (n=110; 129; 430)
- ▲ experiment 2: low odonates (n=101; 209; 585)
- ▲ experiment 3: high odonates (n=86; 175; 493)
- ▲ experiment 3: low odonates (n=105; 186; 495)

Figure 3.4 Cumulative relative size frequencies of body lengths of *Macrocyclus albidus* (c3-c6), *Diacyclus nanus* (c3-c6), and total Cyclopoida in large enclosures. Sample sizes are presented in parentheses in the legend according to the following order: *M. albidus*, *D. nanus*, total Cyclopoida. Sites of *D. nanus* and total Cyclopoida were not estimated in experiment 1.

additional plots are presented in Appendix 4). The size distribution of total Cladocera and Cyclopoida also did not vary between treatments (χ^2 tests, $\alpha=0.05$). There was no tendency for microcrustacea in low odonate enclosures to be consistently larger or smaller than in high odonate enclosures.

Clutch sizes of common Cladocera were slightly larger in high-odonate enclosures, but these differences were never statistically significant (Table 3.4). In addition, there were no statistically significant correlations among the mean clutch sizes of common species of Cladocera, the density of each species, total Cladocera, or total microcrustacea. Hence, there is little evidence that the birth rates of Cladocera in enclosures were strongly affected by predation, intraspecific competition, or competition among microcrustacea.

The abundance and sizes of secondary predators also did not vary significantly between treatments in any experiment (see Figures 3.2 and 3.4 for M. albidus; Figure 3.1 for Acari; Figure 3.5 for other predators). There were no significant correlations among numbers of total Cladocera or Cyclopoida and the abundance of secondary predators in any experiment.

2) Small enclosures: Final numbers of predators were always significantly greater in "high-predator" enclosures than in "low-predator" enclosures and very few odonates or

Table 3.4. Mean numbers of parthenogenetic eggs per mature female of the most common Cladocera in high and low-odonate enclosures (+/- one standard error). P refers to significance level (t-tests). Each estimate is based on egg counts from at least 50 mature individuals.

<u>Species</u>	<u>low odonates</u>	<u>high odonates</u>	<u>P</u>
<u>Experiment 1:</u>			
<u>Alona intermedia</u>	0.73 (0.10)	0.89 (0.12)	0.32
<u>Chydorus</u> <u>linguilabris</u>	0.79 (0.11)	1.05 (0.13)	0.13
<u>Experiment 2:</u>			
<u>Alona intermedia</u>	0.75 (0.07)	0.78 (0.08)	0.78
<u>Alonella sp.</u>	0.39 (0.10)	0.46 (0.09)	0.62
<u>Experiment 3:</u>			
<u>Alona intermedia</u>	0.75 (0.08)	0.88 (0.08)	0.25
<u>Ilyocryptus sp.</u>	0.66 (0.13)	0.73 (0.13)	0.69

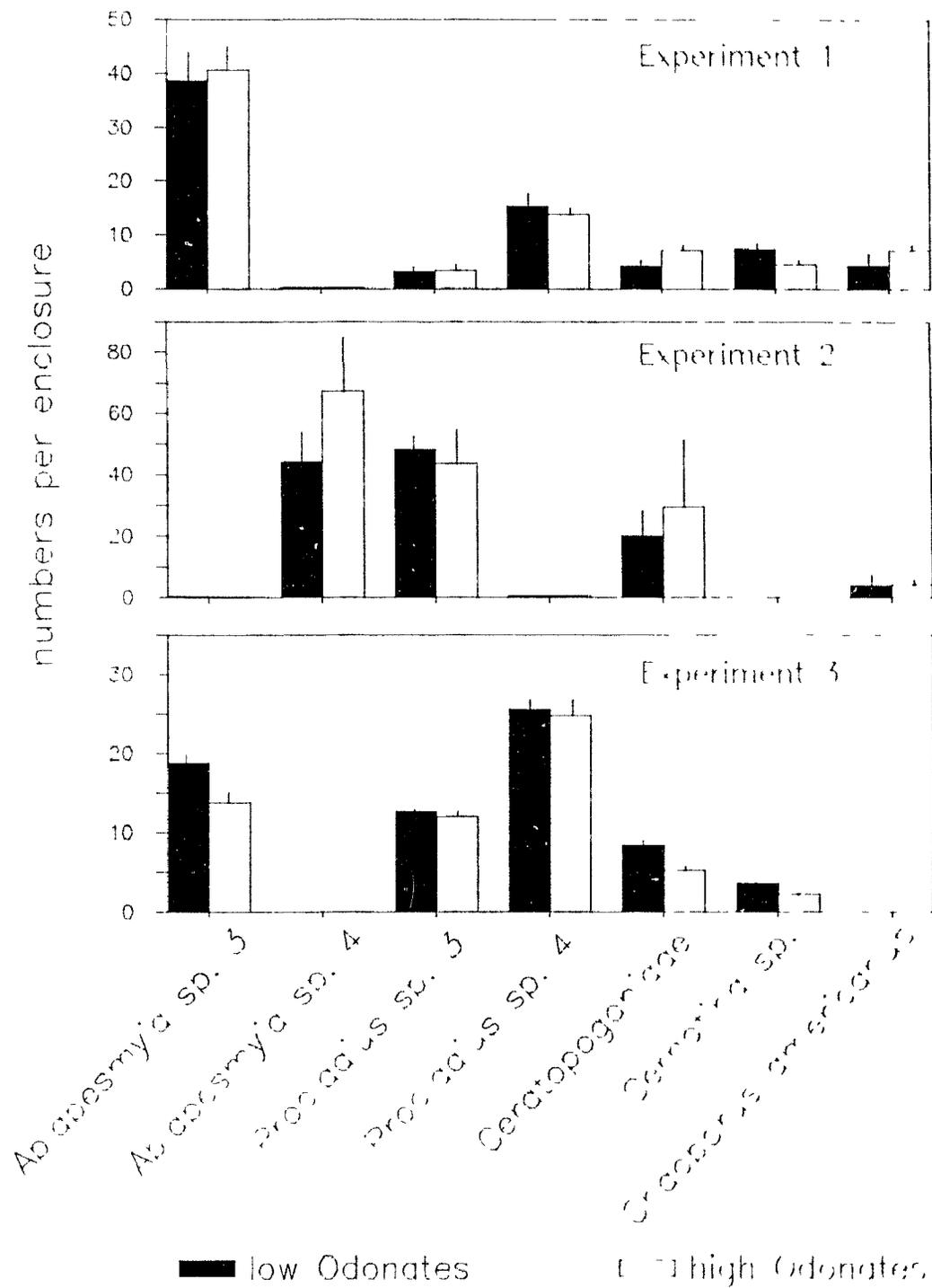


Figure 3.5. Final abundance of secondary predators in large enclosures. Vertical lines are + one standard error.

adult mites were missed during sorting (Table 3.5). Tanypod manipulations were less successful and large tanypods were frequently encountered in "low tanypod" enclosures. Presumably, these animals were missed during sorting or molted to larger instars during the experiment. In experiment 5, there was considerable mortality of tanypods. Instar-4 Ablabesmyia dominated at the experiment's initiation and presumably died while trying to emerge from the sealed enclosures.

Small numbers of early instar chironomids, cyclopoid copepods, and Cladocera and relatively high numbers of naid oligochaetes were able to enter enclosures through the 63- μ m screen (Table 3.6). Numbers of microcrustacean immigrants were apparently too low to affect final density estimates strongly.

The effect of predator manipulations on total Cladocera and cyclopoid densities is summarized in Figure 3.6 and Table 3.7. As in the large enclosure experiments, mean numbers of Cladocera and Copepoda varied considerably among the three experiments. None of the predator treatments had a statistically significant effect on total cladoceran numbers. Odonates significantly decreased numbers of cyclopoids, but water mites and Tanypodinae had no detectable effect. For both Cladocera and cyclopoids, all interactive effects were non-significant. There were statistically significant negative correlations ($p < .05$) between final numbers of

Table 3.5. Mean numbers of predators retrieved from small enclosures and comparison of treatment means. Standard errors of the mean are in parentheses. ANOVA probability values for the treatment are presented at the bottom of the table.

	Odonates	Acari	Tanypodinae
<u>Experiment 4</u>			
Low predators	0.0	0.25 (0.16)	1.88 (0.52)
High predators	2.25 (0.25)	1.50 (0.19)	3.25 (0.31)
<u>Experiment 5</u>			
Low predators	0.13 (0.13)	0.0	0.0
High predators	2.25 (0.41)	2.63 (0.26)	0.38 (0.18)
<u>Experiment 6</u>			
Low predators	0.38 (0.26)	0.13 (0.13)	1.63 (0.50)
High predators	2.75 (0.16)	3.75 (0.37)	3.50 (0.68)
<u>ANOVA (main effect)</u>			
	p<.001	p<0.001	p<0.019

Table 3.6 Mean numbers of invertebrates immigrating into empty enclosures (n=6, 2 enclosures from each experiment). Standard errors are in parentheses.

<u>Taxon</u>	<u>Mean numbers per enclosure</u>	
Cladocera	2.33	(1.23)
Cyclopoida	0.5	(0.5)
Chironomidae	2.17	(0.89)
Oligochaeta	38.0	(22.09)
Tardigrada	0.67	(0.33)

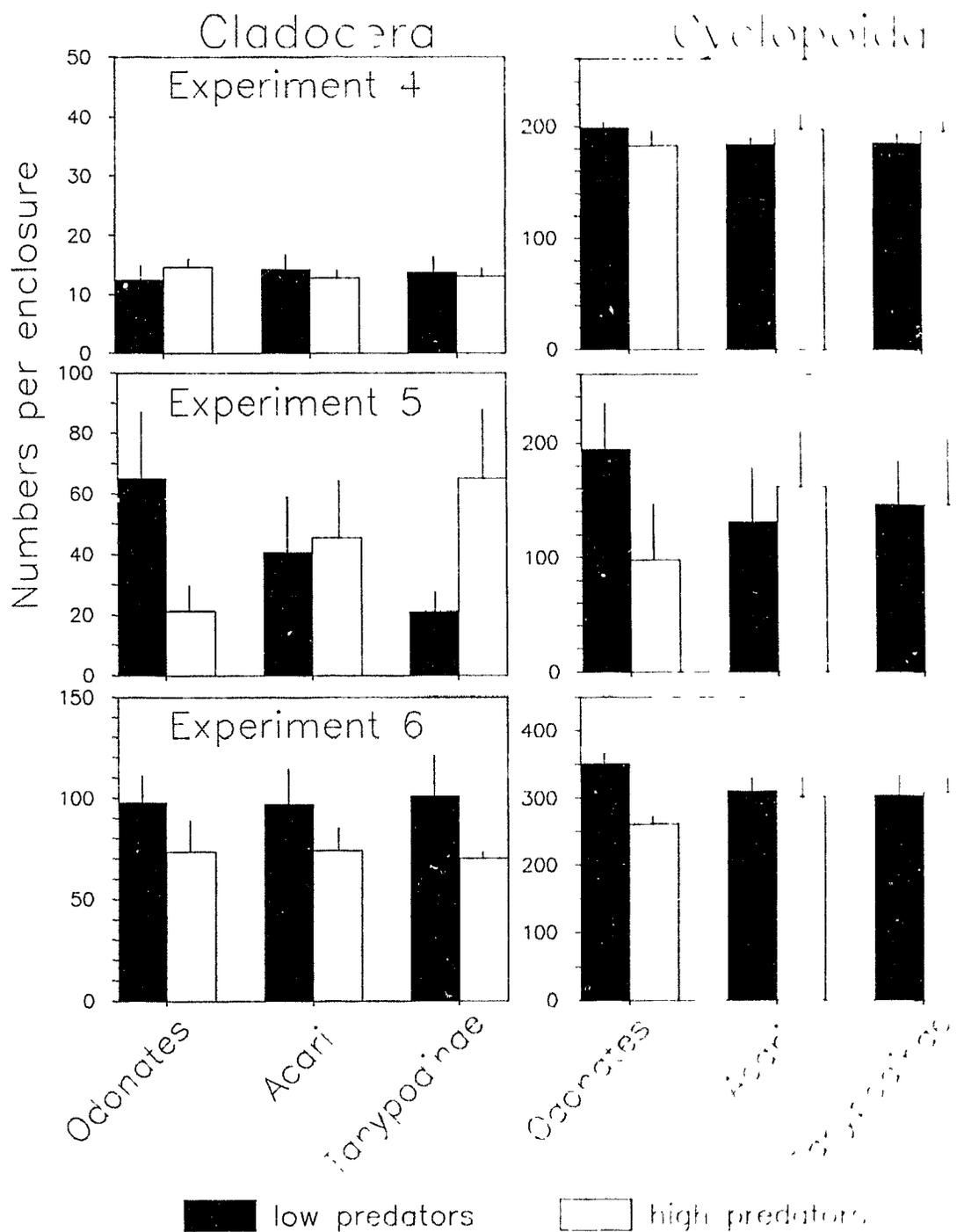


Figure 3.6. Summary of main effects of different predators on Cladocera and Cyclopoida in small enclosures. Vertical lines are + one standard error. Note different density scales.

Table 3.7. ANOVAs of total Cladocera and cyclopoid densities by treatment for small enclosure experiments. All densities were \log_{10} -transformed before analysis.

Source of variation	df	MS	F	P
<u>Cladocera</u>				
Experiment	2	0.552	7.152	0.004
Odonates	1	0.132	1.712	0.203
Acari	1	0.004	0.046	0.832
Tanypodinae	1	0.013	0.167	0.687
Date X Odonates	2	0.165	2.136	0.140
Date X Acari	2	0.125	1.617	0.219
Date X Tanypodinae	2	0.011	0.137	0.872
Odonates X Acari	1	0.0001	0.0001	0.993
Odonates X Tanypodinae	1	0.001	0.012	0.914
Acari X Tanypodinae	1	0.005	0.065	0.802
Date X Odonates X Acari	2	0.005	0.060	0.942
Date X Odonates X Tanypodinae	2	0.108	1.401	0.266
Date X Acari X Tanypodinae	2	0.008	0.102	0.903
Odonates X Acari X Tanypodinae	1	0.021	0.270	0.608
Date X Odonates X Acari X Tanypodinae	2	0.008	0.103	0.902
Error	24	0.077		
<u>Cyclopoida</u>				
Experiment	2	0.035	0.633	0.540
Odonates	1	0.299	5.397	0.029
Acari	1	0.043	0.784	0.385
Tanypodinae	1	0.030	0.545	0.468
Date X Odonates	2	0.153	2.757	0.084
Date X Acari	2	0.020	0.369	0.695
Date X Tanypodinae	2	0.024	0.439	0.650
Odonates X Acari	1	0.001	0.020	0.889
Odonates X Tanypodinae	1	0.046	0.824	0.373
Acari X Tanypodinae	1	0.023	0.422	0.522
Date X Odonates X Acari	2	0.0001	0.003	0.997
Date X Odonates X Tanypodinae	2	0.079	1.419	0.261
Date X Acari X Tanypodinae	2	0.009	0.158	0.854
Odonates X Acari X Tanypodinae	1	0.002	0.042	0.839
Date X Odonates X Acari X Tanypodinae	2	0.0001	0.006	0.995
Error	24	0.055		

cyclopoids and odonates in experiments 5 and 6 and between Cladocera and odonates in experiment 5. All other correlations among Cladocera, cyclopoids, and predators were not statistically significant. Qualitative examinations suggested that predators did not strongly affect the species composition of microcrustacea in enclosures. In each experiment, there were no statistically significant correlations between the mean clutch size of common Cladocera and the density of total Cladocera or microcrustacea.

D. Discussion

1) Predator effects:

a) Odonates: Over 3 to 4 week periods between June and October, numbers of total Cladocera, total Cyclopoida, and different microcrustacean taxa varied by as much as 400% in the littoral zone of Jack Lake (Chapter 2). Similar variations of numbers of microcrustacea were not observed in the large enclosures over analogous time periods. These results suggest that large odonates did not strongly influence seasonal fluctuations of microcrustacean numbers or species composition. Presumably, increased replication of treatments would lead to statistically significant results, but any observed effects would probably be small.

In the small enclosure experiments, there was a statistically significant decrease of cyclopoid copepod numbers in high odonate treatments. There was also a trend toward decreased numbers of Cladocera in high odonate enclosures in experiment 5. Despite these trends, evidence for a strong effect of small odonates was not overwhelming. Although the duration of the small enclosure experiments was only two weeks, their design was biased toward the detection of predator effects. Predator-prey ratios were greater and numbers of alternate prey were lower in enclosures than in box and core samples from Jack Lake. The small size of enclosures limited access of prey to natural refugia such as sediments and clouds of filamentous algae. The probability

of observing local-scale instabilities and strong predator effects increases in small enclosures (cf. Huffaker 1958; Maly 1978; DeAngelis and Waterhouse 1987; LaFontaine and Leggett 1987).

Manipulations of odonates in other studies have rarely resulted in large changes in invertebrate numbers or species composition (Hall et al. 1970; Benke 1978; Benke et al. 1982; Thorp and Cothran 1982; Morin 1984; Johnson et al. 1987). Odonate densities in Jack Lake are among the highest reported in the literature (Chapter 2) and their potential impact should be high. These results suggest that odonates rarely affect seasonal fluctuations of prey numbers.

b) Tanypods: Consistent trends toward decreased numbers of microcrustacea in enclosures with high tanypod abundance were not observed. Although variations of tanypod numbers in high and low-predator enclosures were less than for other predators, there was little evidence to suggest that tanypods strongly affected littoral microcrustacea. There have been few other experimental manipulations of tanypods to compare with Jack Lake. Kajak et al. (1968) and Dusoge (1980) found that addition of Procladius larvae to enclosures containing natural benthic communities led to significant decreases in numbers of microcrustacea, oligochaetes, and small chironomids. The relevance of these additions to natural variations of tanypod density remains unclear. Further study of the effects of tanypod chironomids on littoral

microcrustacean communities is warranted.

c) Water mites: Adult Limnesia sp. did not decrease numbers of microcrustacea in the small enclosure experiments in Jack Lake. This leads me to conclude tentatively that adult mites did not strongly affect microcrustacea seasonally in Jack Lake. Several other species of mites inhabit the littoral regions of Jack Lake, however, and their influence on microcrustacea was not assessed experimentally. Water mites are among the most abundant invertebrate predators in the littoral zone of many freshwater lakes (Pieczynski 1976). There is a need for more research on their role in littoral food web dynamics.

2) Was the absence of predator effects an artifact of enclosure design?:

Conditions within the enclosures necessarily varied from natural conditions encountered in Jack Lake. Several factors may have obscured the effects of predators on microcrustacea in the enclosure experiments:

a) Prey exchange rates: High rates of prey exchange between enclosure interiors and exteriors may swamp predator effects and lead to non-significant results (Cooper et al. 1990). In the small enclosure experiments, very few microcrustacea entered enclosures containing only a pot-scrubber. Although the absence of detrital and algal food may have influenced these results, exchange rates were apparently low. The nylon mesh in the large enclosure experiments was slightly larger

than that used in the small enclosures (100 μm vs 63 μm) and exchange rates were not assessed. It seems unlikely, however, that high rates of prey exchange can explain the absence of strong predator effects in these experiments.

b) Density dependent variations in birth rates: Reductions of prey densities may lead to density-dependent increases of prey birth rates that minimize the impact of predators in enclosures. There was little evidence that cladoceran birth rates were affected by predator or microcrustacean densities in either the large or small enclosure experiments.

c) Feeding by secondary predators: Increased feeding by predators remaining in low-predator enclosures may also have offset the impact of removed predators. Increased food availability usually leads to increased individual or population growth rates for invertebrate predators (Smyly 1980; Baker 1982; Anholt 1990). Although predator biomasses were not determined directly, there was little evidence of either developmental or numerical responses of predators in low-predator treatments. The abundance and average size of tanypods, Ceratotina sp., Chaoborus americanus, M. albidus, and water mites did not differ among treatments in the large or small enclosure experiments. In the large enclosure experiments, density-dependent variations in the size of odonates in high and low-odonate enclosures could not be assessed because of confounding treatment effects. Hence, increased feeding by small odonates in low-odonate enclosures

may have reduced the observed impact of manipulations of larger odonates.

d) Miscellaneous enclosure effects: The design of the enclosures may have prevented natural feeding by predators or provided artificial refuges for prey. For example, the pot-scrubbers may have limited access of some predators to microcrustacea. Qualitative examinations suggested that pot-scrubbers did not impede predators, but more detailed examinations would be useful. With the exception of tanypod chironomids in experiment 5, predators seemed healthy and active at the end of each experiment.

Many laboratory studies suggest that odonates, tanypods, and water mites can be voracious predators of microcrustacea (see Chapter 2 for references). Consequently, it is surprising that stronger predator effects were not observed in the enclosure experiments. In part, the failure to detect significant decreases of prey numbers may indicate that natural predation rates are far below maximum rates measured in the laboratory. Natural predation rates may vary from laboratory rates for several reasons: 1) Densities of prey are often unrealistically high in laboratory studies; 2) Microcrustacea that naturally coexist with littoral predators may be less susceptible than planktonic prey that are frequently used in laboratory studies (for example Daphnia). Several studies suggest that odonates feed on epiphytic or benthic Cladocera at much lower rates than on Daphnia

(Sadyrin 1977; Akre and Johnson 1979; Crowley 1979; Cooper et al. 1985; Jeffries 1988); 3) Increased spatial heterogeneity in the field may decrease invertebrate predation rates (Folsom and Collins 1984); 4) Predators in laboratory studies are frequently starved, artificially inflating predation rates (Lawton 1971b; Crowley 1979); 5) Interference competition and increased risk of predation may reduce feeding rates of predators in nature (Heads 1985; Pierce 1988; Jeffries 1990).

3) Summary: The results of the large and small enclosure experiments suggest that invertebrate predators did not strongly affect littoral microcrustacean communities over periods of 10 days to 6 weeks in Jack Lake. There was little evidence that predator effects were obscured by high prey exchange rates, increased prey production, increased predation by secondary predators, or by miscellaneous enclosure effects. More detailed study of these factors should be undertaken in future studies.

Chapter 4

Summary and General Discussion

In Jack Lake, large seasonal changes in the abundance and species composition of the epiphytic and benthic microcrustacean community were observed. Common species of cyclopoid copepods passed through two generations during the ice-free period, with peaks of adult numbers in June-July and October-November. Abundance maxima for total Cladocera occurred in June-July and September-October.

Populations of common littoral Cladocera in 1987 were apparently limited in May and November by low water temperatures and low birth rates. At other times, variations in birth rates failed to account for fluctuations in population sizes. Losses of common Cladocera were apparently highest in August and declined in September-October. Although transient shifts in birth rates may have been missed because of the long sampling interval in Jack Lake, my results are in accord with other studies in which more frequent sampling intervals were employed (Keen 1973; Williams and Whiteside 1978; Doolittle 1982; Robertson 1990). The similarity of seasonal changes in population sizes and birth rates in many lakes suggests that common factors widely influence littoral cladoceran dynamics. Birth and development rates of littoral cyclopoids were not determined in Jack Lake and, consequently, conclusions concerning the impact of predation on these organisms are more difficult to

reach.

In most previous studies, seasonal shifts in loss rates have been interpreted as evidence of variations in vertebrate and invertebrate predation intensity. Although several studies suggest that fish predation may affect littoral Cladocera (Straškraba 1965; Phoenix 1976; Doolittle 1982; Fairchild 1982; Bohanan and Johnson 1983), there have been few direct tests of the effects of invertebrate predation. Based on gut content analyses, relative abundance, and crude estimates of predation rates, the most important predators of microcrustacea in Jack Lake were cyclopoid copepods (particularly Macrocyclops albidus), tanypod chironomids (Ablabesmyia sp., Procladius sp.), odonates (Enallagma carunculatum, Cordulia shurtleffi, Leucorrhinia glacialis), and water mites. With the exception of Ablabesmyia sp., numbers of microcrustacea were not negatively correlated seasonally with predator abundance. Although direct estimates of invertebrate predation rates were not undertaken, seasonal shifts in feeding by individual predators were probably insufficient to account for apparent microcrustacean losses. In future studies, the role of seasonal changes in prey and predator behaviour, lags in prey population responses to predation pressure, the availability of alternate prey, and the availability of refuges for prey should receive increased attention.

The results of the enclosure experiments suggested that

invertebrate predators did not strongly influence littoral microcrustacea. The only statistically significant effect of manipulations of odonates, tanypod chironomids, and water mites was a slight decrease of cyclopoid copepods with odonates in small enclosures.

Many invertebrate predators are size-selective feeders (see references in Chapter 2) and, hence, shifts in predation pressure would be expected to influence the size structure of prey populations and communities (cf. Dodson 1974; Neill 1981; Elser et al. 1987; Black and Hairston 1988; Vanni 1988). Many planktonic microcrustacea also undergo morphological changes in the presence of invertebrate predators (Krueger and Dodson 1981; Kerfoot 1987). In Jack Lake, the size structure of populations of common littoral Cladocera was constant between June and October 1987, despite large variations in numbers of invertebrate predators. The sizes of microcrustacea in enclosures was also not affected by manipulations of invertebrate predator densities. Large changes in cladoceran morphology were not observed in either the observational or experimental studies. The mean size of adult cyclopoids decreased between July and September 1987. These decreases do not appear to have been linked to shifts in predation pressure. Several studies indicate that copepod sizes are negatively correlated with water temperature (McLaren 1963; Abdullahi and Laybourn-Parry 1985).

Taken together, the observational and experimental data do

not support the hypothesis that invertebrate predation strongly affected the abundance, species composition, or size structure of epiphytic and benthic microcrustacean communities in Jack Lake. There are several shortcomings of this study that limit the strength of my conclusions:

1) The sampling interval for seasonal observations was relatively long. As a result, transient shifts in invertebrate predator abundance and cladoceran birth rates may have been missed.

2) There were many difficulties encountered with the quantitative estimation of microcrustacean and predator population sizes (see Chapter 1). Qualitative seasonal patterns of abundance were similar regardless of the units of measure used, however.

3) There were no direct estimates of the feeding rates of invertebrate predators.

4) The role of secondary predators, such as Cernotina sp., Chaoborus americanus, Hydra sp., Utricularia spp., etc. may have been underestimated.

5) Seasonal changes in predation losses may have been caused by shifts in the behaviour of predators and microcrustacean prey. For example, Cladocera may have been more active in July-August than in September-October because of decreased food availability, temperature, chemical conditions, etc. Shifts in prey behaviour of this type could potentially affect predation losses without influencing

birth rates. These effects could not be detected in this study.

6) Repeated attempts to manipulate densities of M. albidus in enclosures were unsuccessful. Manipulations of tanypod chironomids were also less effective than manipulations of water mites and odonates. The effect of Ablabesmyia sp. on microcrustacean seasonal dynamics warrants more study. The midsummer depression of littoral cladoceran numbers closely coincided with increased abundance of instar 4 Ablabesmyia in Jack Lake. Goulden (1971) also found that midsummer declines of benthic chydorids coincided with increased numbers of late-instar tanypod chironomids. Addition of tanypod chironomids to sediment cores by Kajak et al. (1968) and Dusoge (1980) resulted in depressions of cladoceran and copepod abundances. The relevance of these enrichment studies to natural variations of predator numbers remains uncertain.

As a result of these limitations, the conclusions of this study must be considered tentative. It is also stressed that the conclusions apply only to seasonal variations in microcrustacean community structure. Invertebrate predators may be important determinants of littoral microcrustacean numbers among different lakes or among years in the same lake. Invertebrate predators had life spans that greatly exceeded the generation times of littoral Cladocera in Jack Lake. As a result, predators were incapable of numerical

responses to variations in prey density and could affect prey seasonally only through functional, developmental, survival, or aggregative responses (Johnson 1973; Benke 1978; Baker 1982; Peckarsky 1984). High prey densities may enhance emergence and oviposition of predators and increase predator densities in successive years. In this way, inter-annual predator-prey oscillations may result. Some species of microcrustacea may have been excluded from Jack Lake by the presence of certain invertebrate predators.

Aside from invertebrate predation, many other factors potentially affected the seasonal dynamics of epiphytic and benthic microcrustacea in Jack Lake. Some potentially important factors include competition and food availability, physical-chemical conditions, parasitism and disease, egg mortality, and immigration and emigration. These are discussed below.

Declines in food availability or increases in physiological stress from adverse physical-chemical conditions have been associated with declines in cladoceran egg production in many studies (e.g. Slobodkin 1954; Green 1956, 1966; Richman 1958; Hall 1964; Davis and Ozburn 1969; Weglenska 1971). Decreases in food availability also frequently lead to shifts in age structure of cladoceran populations through decreased juvenile survivorship (Slobodkin 1954). Seasonal changes in numbers of Cladocera were not associated with changes in clutch sizes or age structure in Jack Lake. The abundance

of many species of microcrustacea increased and decreased together, suggesting that interspecific competition did not strongly limit population sizes. Similar results have been observed in other studies (Goulden 1971; Keen 1973; Daggett and Davis 1974a; Whiteside 1974; Whiteside et al. 1978; Williams 1982; Sharma and Pant 1984; Robertson 1990). As discussed above, behavioral responses to changes in food availability may have interacted with predation to limit population sizes.

Aside from predation, potential sources of mortality of Cladocera in Jack Lake include egg mortality, parasitism, and disease, and interference competition. Threlkeld (1979) found that egg mortality in populations of Daphnia increased in the midsummer months. Populations of pelagic crustacea may also be reduced by parasitism or disease (Hoenicke 1984; Yan and Larsson 1988). Large numbers of moribund eggs or diseased or parasitized cladocerans were not observed at any time in Jack Lake. Evidence for strong interference competition is currently lacking for littoral Cladocera.

Immigration and emigration of animals to the littoral zone may also have affected population fluctuations in Jack Lake. Many studies suggest that littoral invertebrates migrate seasonally to different depths (Pieczynski 1964; Thut 1969; Johannsson 1978; Neubert and Frank 1980; Corkum 1984; Bryant 1986; Harper and Cloutier 1986; Wissinger 1988). There was indirect evidence that several invertebrate groups moved

among habitats in Jack Lake. Numbers of odonates declined from November to May and increased again in June, despite an absence of oviposition or emergence events at these times. Similar patterns have been observed in other studies and have been interpreted as evidence of migration of odonates to deeper waters in fall and winter (Macan 1964; Lawton 1970a; Bryant 1986; Wissinger 1988). Similarly, in both 1986 and 1987, numbers of epiphytic chironomids declined in October-November, while benthic chironomids increased in abundance. These patterns may reflect movement of chironomids from macrophytes to sediments (cf. Menzie 1980; Gilinsky 1984; Kornijow 1989).

The role of migration in littoral microcrustacean seasonal dynamics has received little attention. Littoral microcrustacea occurred abundantly at all depths in Jack Lake and movements among depth strata may have affected seasonal fluctuations of numbers in the shallow littoral zone. Tinson and Laybourn-Parry (1986) argue that benthic copepods migrate from deep waters to the shallow littoral zone with decreases in oxygen concentrations in the hypolimnion. More research is required to explore these possibilities.

Littoral microcrustacean community dynamics may also have been affected by immigration from buried ephippia (diapausing eggs). De Stasio (1989; 1990) found that the hatching of ephippial eggs of many microcrustacea is not restricted to the spring. He suggests that high percentages of some

microcrustacean populations may be derived from ephippial eggs and hatching of ephippia may influence seasonal population dynamics. Presumably, hatching of large numbers of ephippial eggs would lead to increased proportions of juveniles in affected populations. In Jack Lake, increased percentages of juveniles were observed only in May. Hence, there is little evidence of large hatches of ephippial eggs at other times.

Food web relations among invertebrates in the littoral zone of Jack Lake were highly complex. A clear hierarchy of predators and prey was not observed and ontogenetic diet shifts made many complex trophic paths possible. Small predators were frequently consumed by larger predators and predator-prey interactions could be reversed seasonally with changes in relative size. Many cyclopoid copepods and odonates may also be cannibalistic (Fischer 1961; McQueen 1969; Gophen 1976; Lane 1978; Crowley et al. 1987; Van Buskirk 1989). The early instars of many invertebrate predators were herbivorous or detritivorous and may have competed with organisms destined to become prey in later instars. The outcome of competitive interactions during early life stages may ultimately affect the success of later predatory stages (cf. Neill and Peacock 1980).

There was wide overlap in the diets and spatial and temporal distributions of many of the invertebrate predators in Jack Lake. Hence, potential for competition among

predators was high. In general, smaller items were not dropped from the diet of larger predators and diet width increased with predator size. As a result, competition among predators is likely to be asymmetrical, with small predators experiencing greater diet overlap with large predators than vice versa. Although the potential for competition was high, there was little evidence that predators depleted prey populations in Jack Lake. Consequently, it is unclear whether food was a limiting resource for invertebrate predators during the study years.

In summary, the results of this study suggest that invertebrate predation did not strongly influence littoral microcrustacean dynamics in Jack Lake. Littoral food web interactions are highly complex and the determination of important pathways of effect will be a difficult challenge.

Appendix 1. Transformation of data for multivariate analyses.

Data transformations of benthic invertebrate counts are usually required to stabilize variance and normalize distributions for parametrical statistical analysis (Downing 1979; Green 1979; France 1987). Many ecologists apply logarithmic or square-root transformations a priori. Downing (1979), however, argued that the log transform tends to overtransform benthic invertebrate data, whereas the square-root transform results in undertransformation. Downing proposed that a fourth-root transform ($X^{0.25}$) was a better compromise.

In this section, I examine the ability of the square root, log, and fourth root transformations to decouple the relationship between the variance and mean for Jack Lake invertebrate data. I sought a single, general transformation to simplify analyses.

Methods

Using techniques outlined in Chapter 1, I obtained estimates of the variance and mean of invertebrate counts in box and core samples from different sampling dates. Because these data are derived from a temporal series, they cannot be regarded as measures of aggregation, unless factors determining aggregation remained constant throughout the study.

I explored the relationship between variance and the mean

using Taylor's Power Law (Taylor 1961; Green 1979) where variance, σ^2 , is expressed as a function of mean abundance, μ :

$$\sigma^2 = a\mu^b$$

Substituting the sample statistics s^2 and X for σ^2 and μ , respectively, a and b can be estimated by linear regression:

$$\log_{10}s^2 = \log_{10}a + b \log_{10}X$$

The appropriate transformation can then be estimated from $Z = X^{1-(1/2)b}$, unless $b=2$, when $Z=\log_{10}X$ (where X is the untransformed variable and Z , the transformed variable). If $b=1$, a square-root transformation is appropriate, if $b=2$, a log transformation should be used, and if $b=1.5$, a fourth-root transform is best. The variance-mean relationship was also assessed after applying log, square root, and fourth root transformations to data for common taxa in Jack Lake (cf. Downing 1981b; France 1987). The best general transformation was determined to be the one with the lowest average rank of absolute r^2 for variance-mean relationship after transformation (cf. Downing 1981b; France 1987).

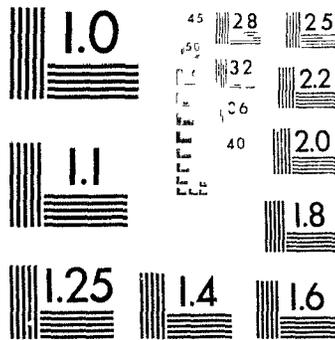
The deviation of resulting distributions from a normal distribution were examined with the Kolmogorov-Smirnov test (Sokal and Rohlf 1981) and by qualitative examination of normal probability plots (Sokal and Rohlf 1981; Wilkinson 1988).

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PM-1 3½"x4" PHOTOGRAPHIC MICROCOPY TARGET
NBS 1010a ANSI/ISO #2 EQUIVALENT



Results and Discussion

Variance was significantly ($p < .05$) related to mean numbers per box sample for all invertebrates investigated (Table A.1). Taylor's Power Law was of limited use for determining transformations because of wide variations of a (Taylor 1981). The fourth-root transformation was best, on average, at decoupling the mean-variance relationship. This was particularly true for epiphytic invertebrates. In sediment samples, the fourth-root transformation was generally either the worst or best transform. Hence, a single ideal transformation was not possible for all benthic invertebrates.

All distributions examined were highly skewed to the right, as is common for invertebrate populations. Log and fourth-root transformations were usually more successful than the square root transformation at reducing skewness. All distributions were significantly different from normal, regardless of the transformation used (Kolmogorov-Smirnov test $p < .05$). This result is not unusual, and most parametric statistical tests and multivariate analyses are robust to the assumption of normality (Cooley and Lohnes 1971; Green 1979; Legendre and Legendre 1983).

Conclusion

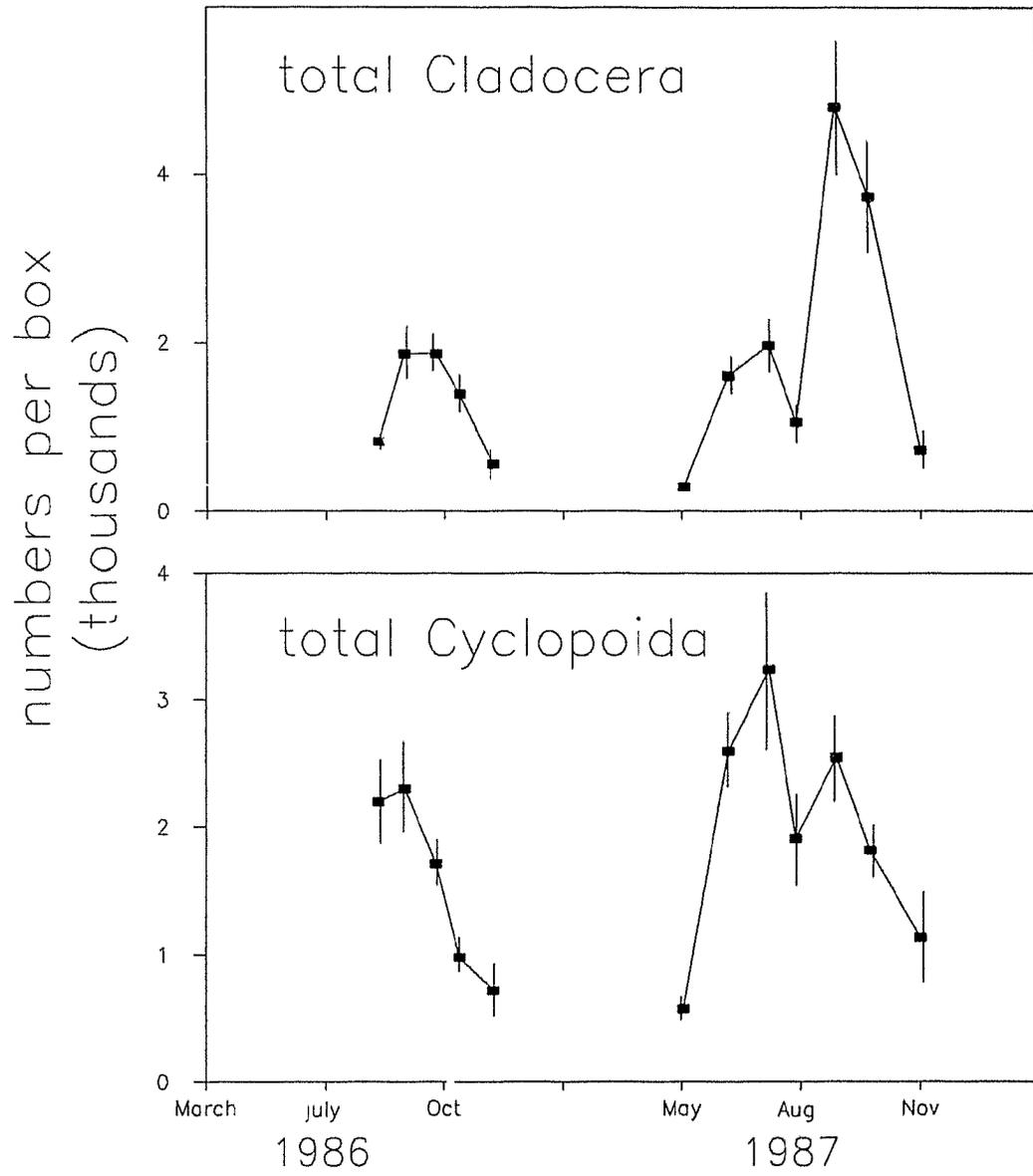
Although no single transformation was ideal for all the benthic data, the fourth-root transformation was deemed to

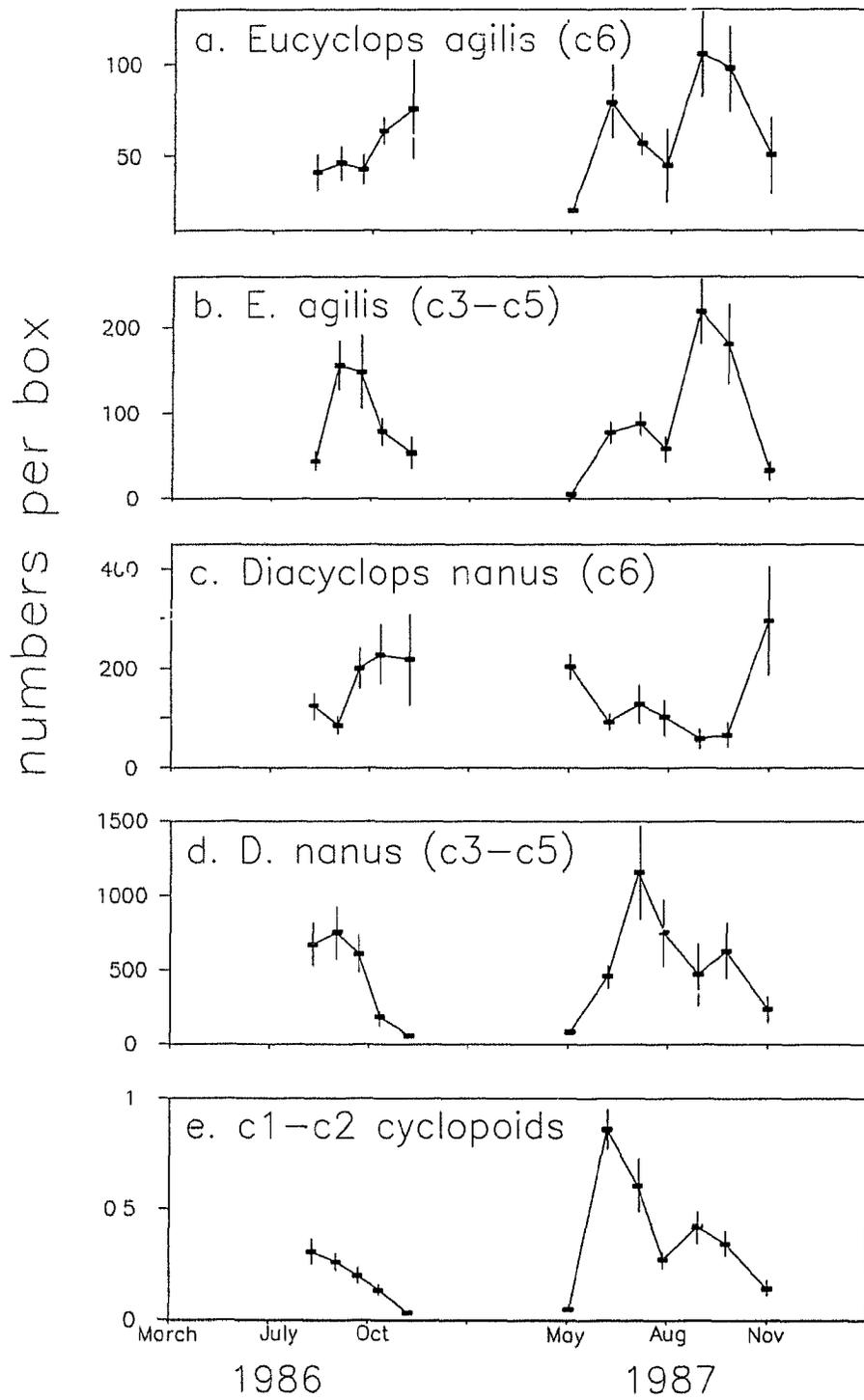
Table A.1. Variance-mean relationships for Jack Lake invertebrates. For both transformed and untransformed data, r^2 indicates the coefficient of determination between $\log_{10} S^2$ and $\log_{10} X$; a is the y-intercept and b is the slope for untransformed data. The rank of each coefficient for transformed data is given in brackets and the best overall transformation is that with the lowest overall rank.

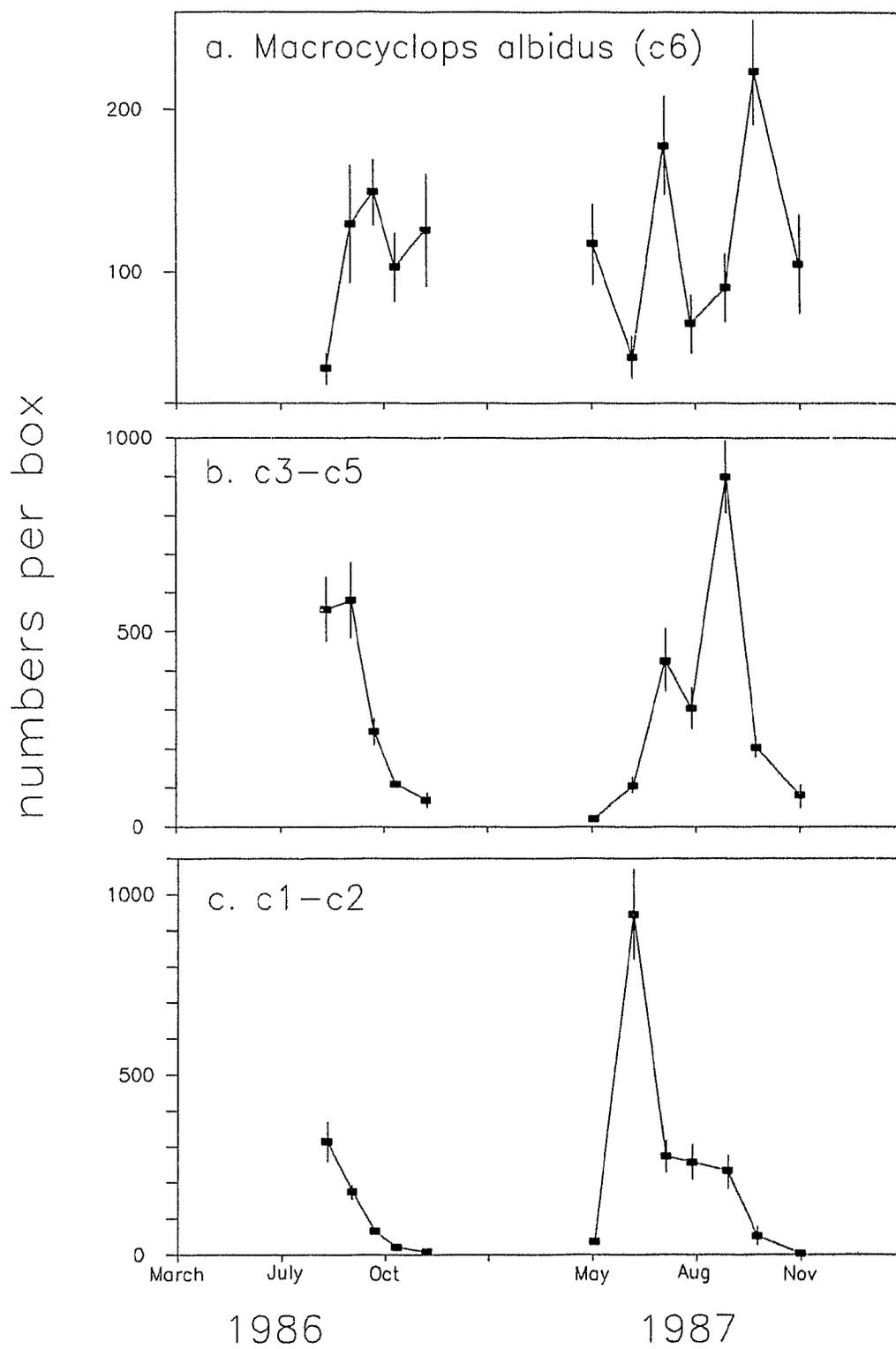
Taxa	Untransformed				Transformed (r^2)		
	n	r^2	a	b	$X^{0.5}$	$X^{0.25}$	$\log(X+1)$
Sediments							
<i>Alona intermedia</i>	15	.95	1.64	1.23	.15 (2)	.33 (3)	.01 (1)
<i>Alona cf. affinis</i>	15	.90	2.16	1.51	.29 (2)	.00 (1)	.60 (3)
<i>Disparalona acutirostris</i>	15	.93	1.43	1.62	.52 (3)	.22 (1)	.44 (2)
<i>Streblocerus serricaudatus</i>	12	.85	1.63	1.54	.4 (2.5)	.00 (1)	.4(2.5)
<i>Ilyocryptus</i> sp.	15	.96	2.06	1.50	.87 (2)	.67 (1)	.90 (3)
<i>D. nanus</i> (c6)	16	.58	1.29	1.18	.01 (2)	.21 (3)	.00 (1)
<i>D. nanus</i> (c3-5)	16	.89	1.55	1.57	.22 (2)	.38 (3)	.01 (1)
<i>Macrocyclus albidus</i> (c6)	16	.85	1.13	1.46	.15 (1)	.16 (2)	.24 (3)
<i>M. albidus</i> (c3-5)	14	.91	1.91	1.21	.13 (2)	.45 (3)	.01 (1)
<i>M. albidus</i> (c1-2)	15	.90	2.14	1.41	.38 (3)	.05 (1)	.09 (2)
Chironomidae	16	.50	1.61	1.37	.03 (1)	.17 (2)	.23 (3)
sum of ranks					22.5	21	22.5
Numbers per box sample							
<i>Alona intermedia</i>	12	.92	2.81	1.68	.60 (2)	.04 (1)	.69 (3)
<i>Alona cf. affinis</i>	12	.97	3.11	1.73	.88 (3)	.04 (1)	.35 (2)
<i>Chydorus linguilabris</i>	12	.95	.68	2.12	.73 (3)	.01 (1)	.09 (2)
<i>Streblocerus serricaudatus</i>	11	.94	2.13	1.77	.60 (3)	.08 (1)	.46 (2)
<i>Ilyocryptus</i> sp.	12	.98	2.66	1.78	.86 (3)	.04 (1)	.35 (2)
<i>Diacyclops nanus</i> (c3-5)	12	.94	1.31	1.91	.69 (3)	.09 (2)	.04 (1)
<i>Macrocyclus albidus</i> (c6)	12	.91	2.13	1.75	.46 (1)	.50 (2)	.52 (3)
<i>M. albidus</i> (c3-5)	12	.94	2.38	1.64	.60 (3)	.12 (1)	.55 (2)
<i>M. albidus</i> (c1-2)	12	.97	3.40	1.60	.80 (3)	.10 (1)	.29 (2)
Chironomidae	12	.72	4.02	1.61	.25 (3)	.00 (1)	.24 (2)
sum of ranks					27	12	21

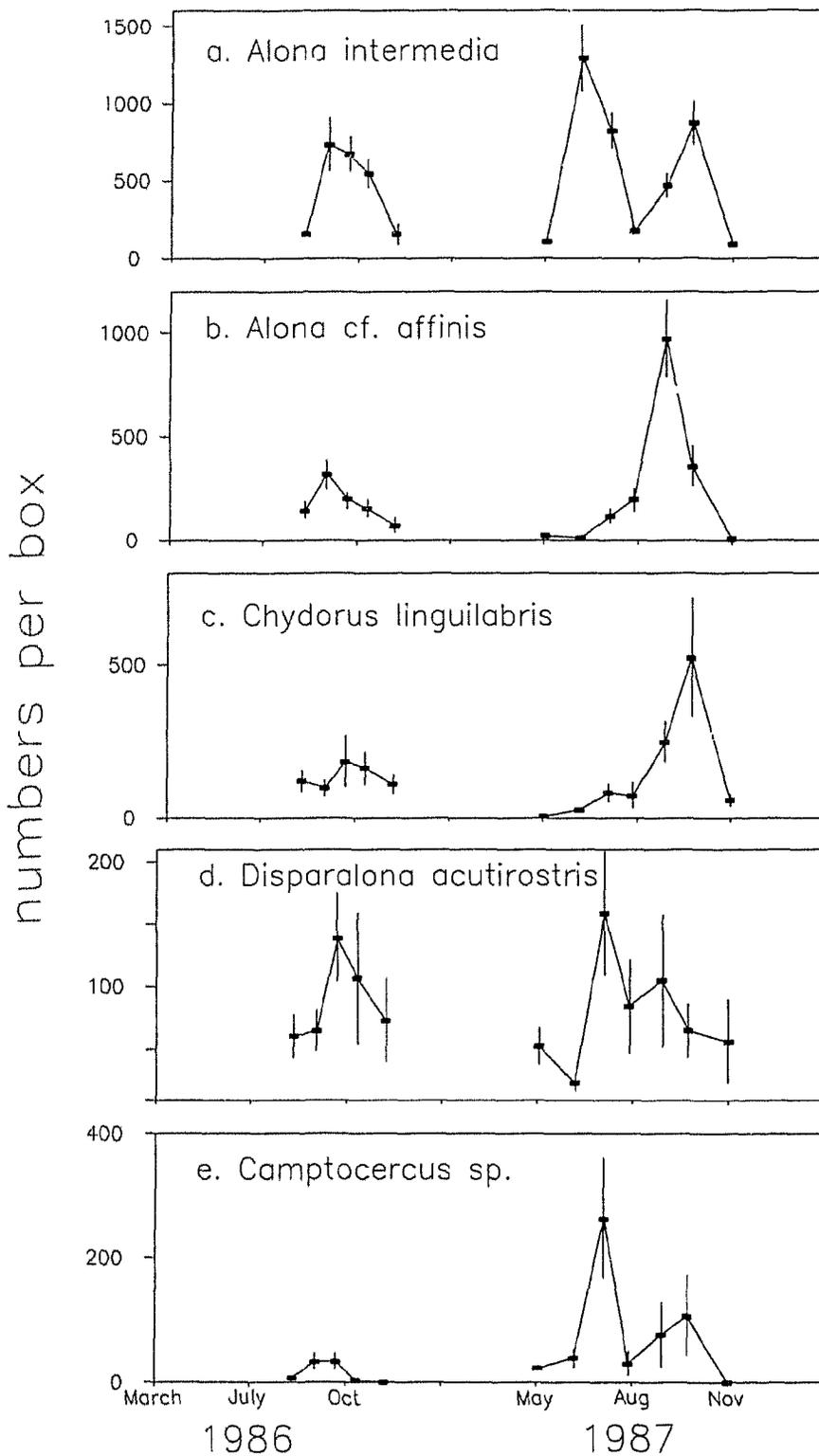
be the best on average.

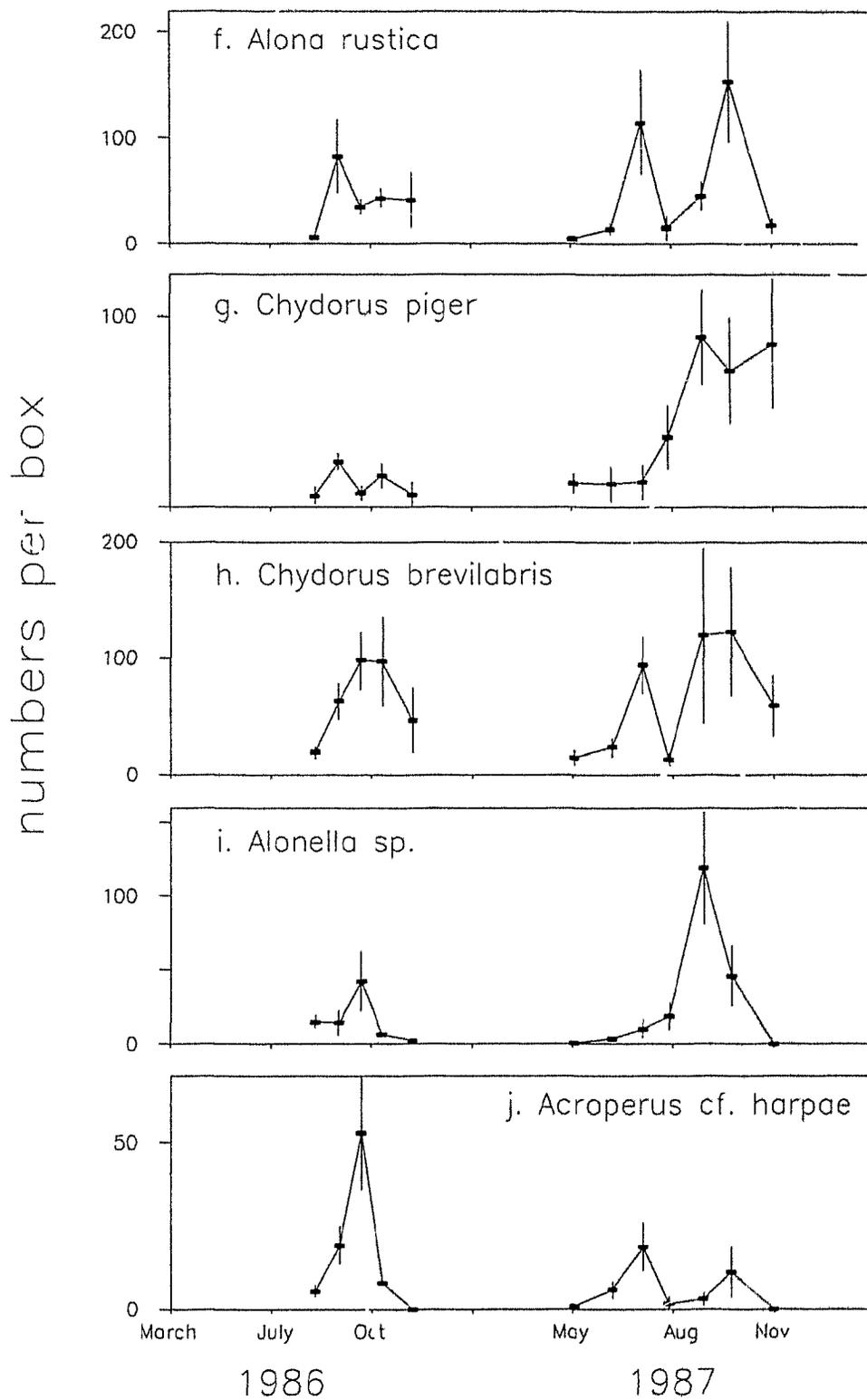
Appendix 2. Plots of mean numbers of invertebrates in box samples. Vertical lines are + one standard error. Plots for different taxa are in the same order as figures for surface and lake bottom densities in Chapter 2.

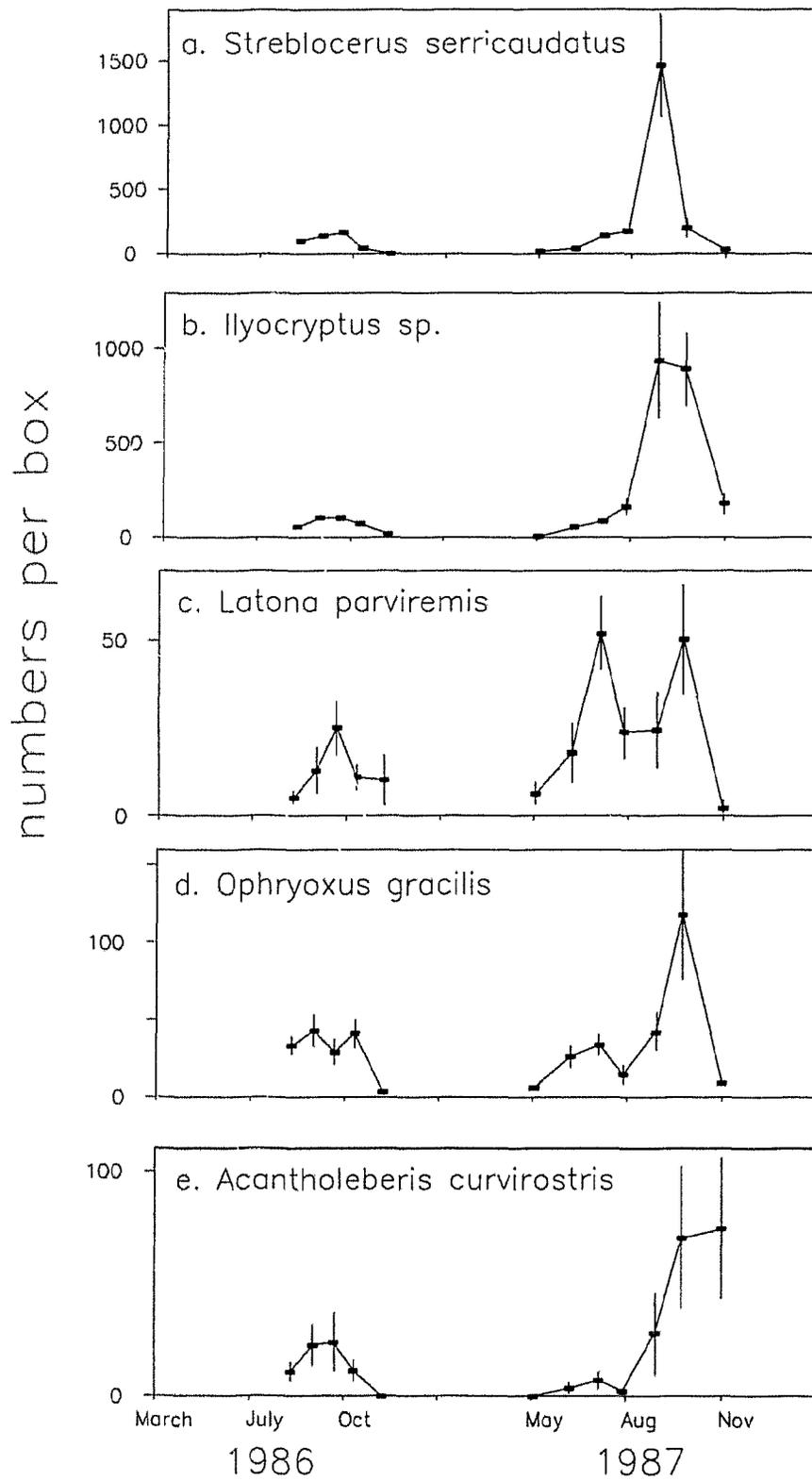




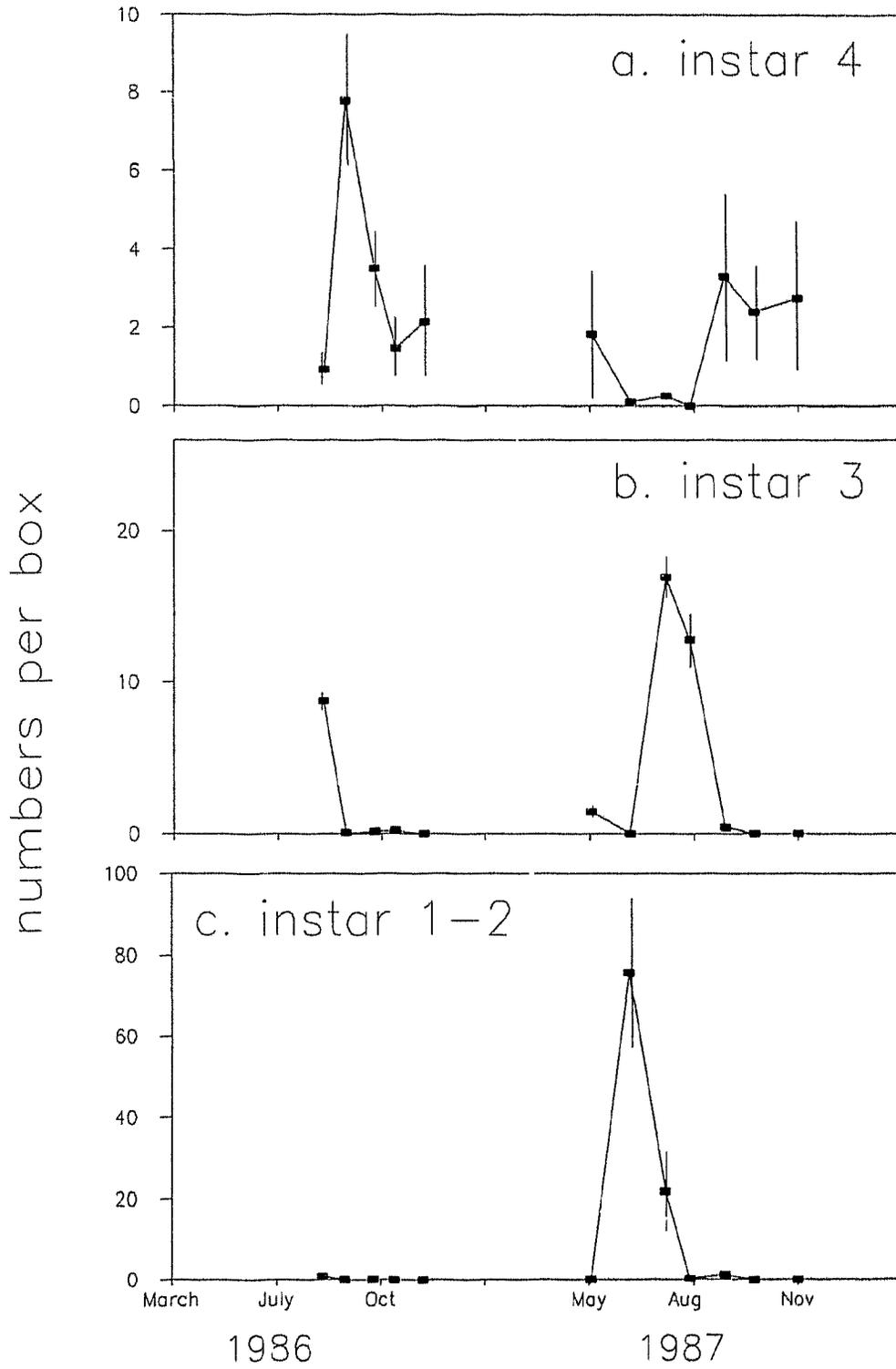




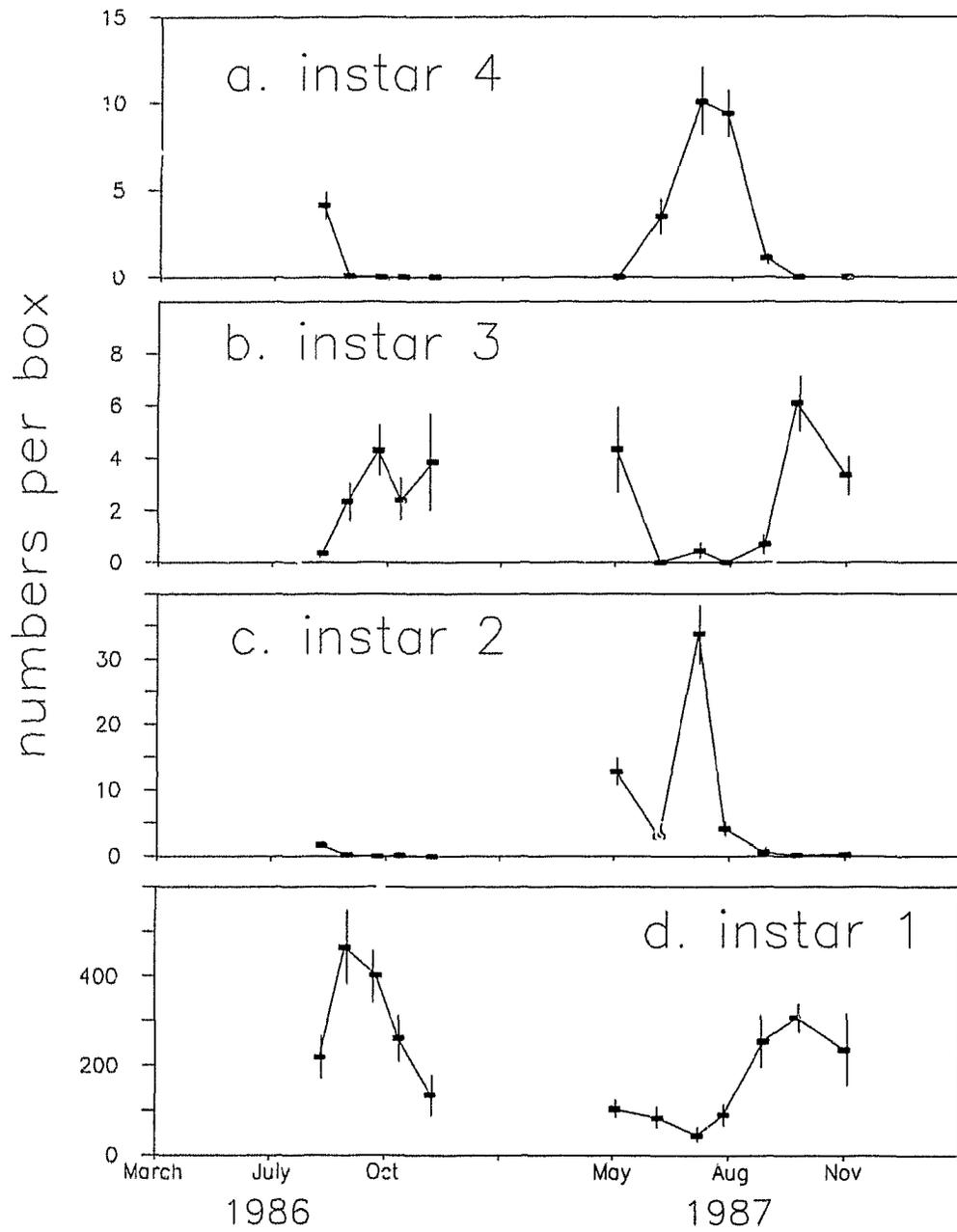


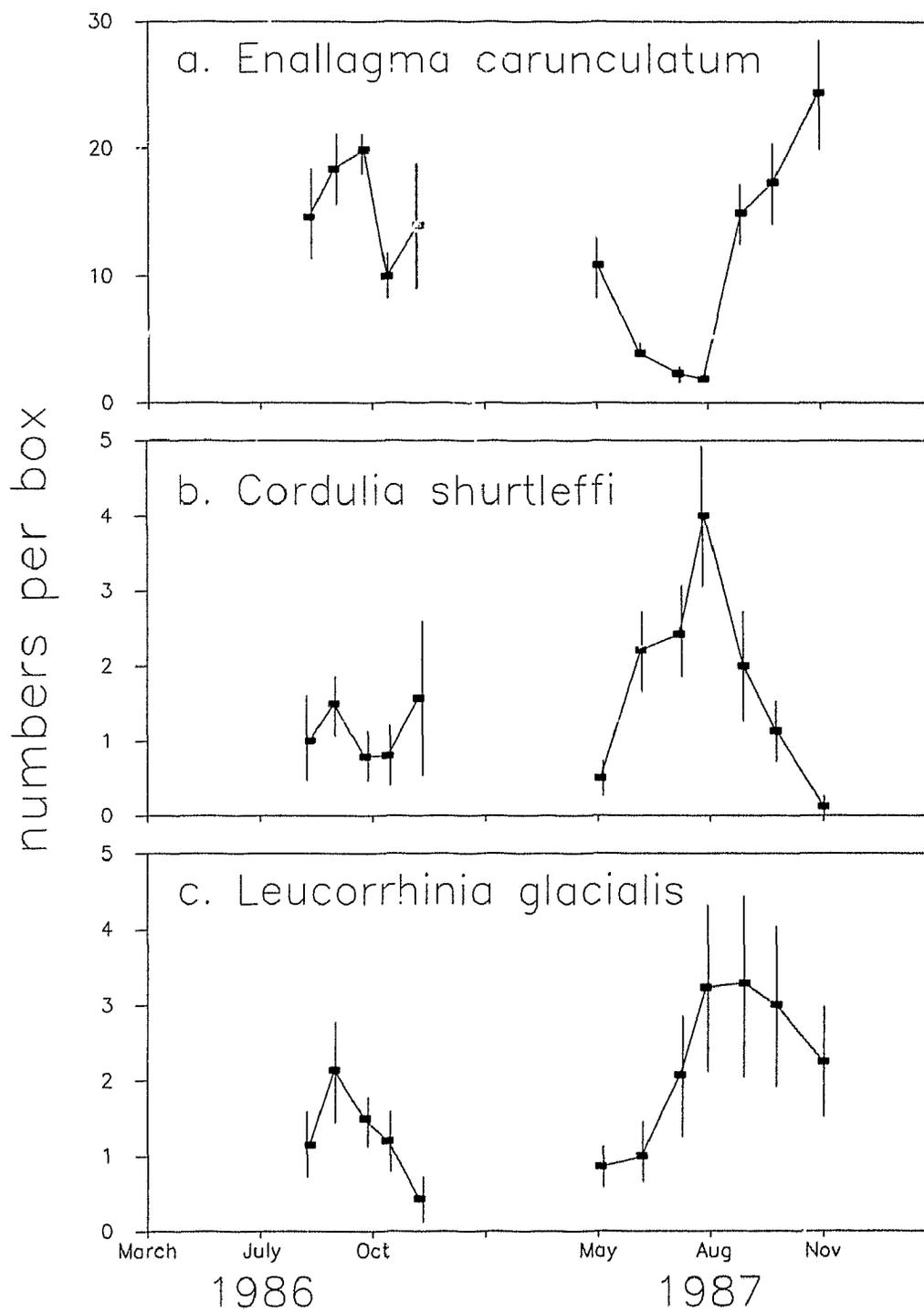


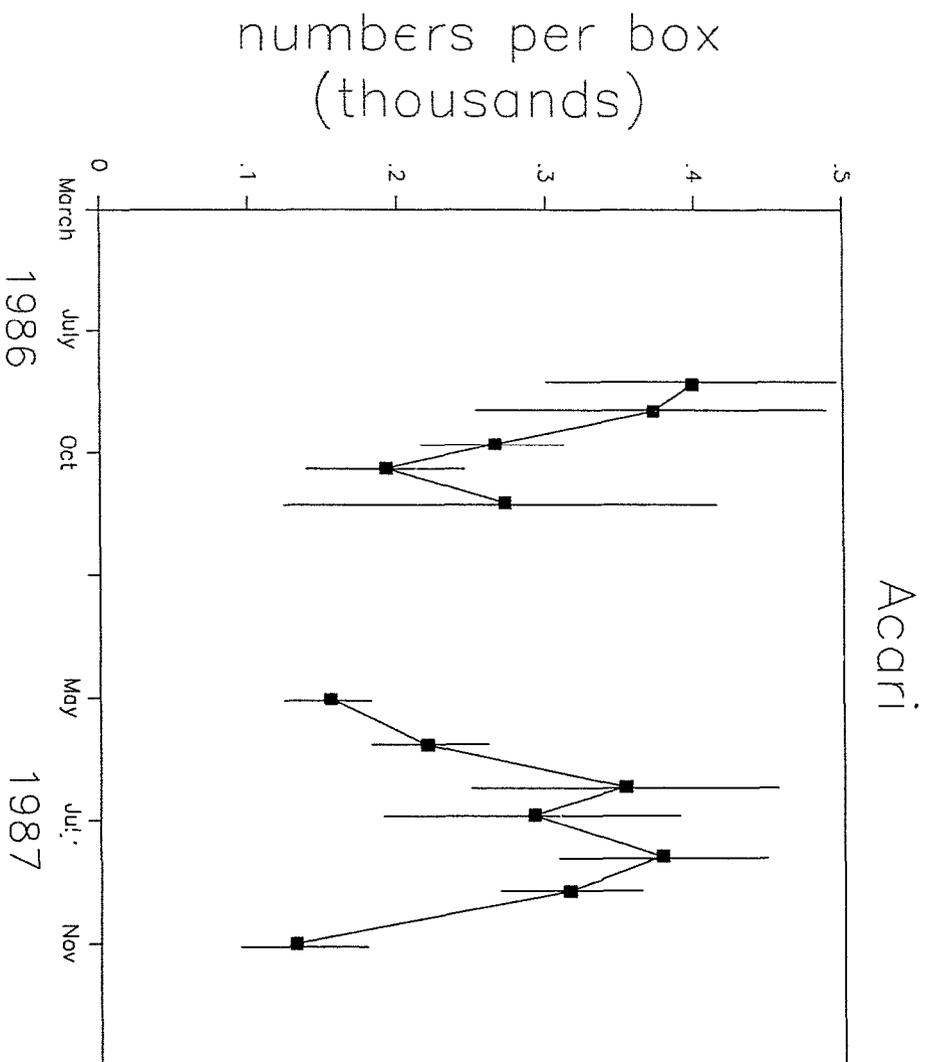
Procladius sp.



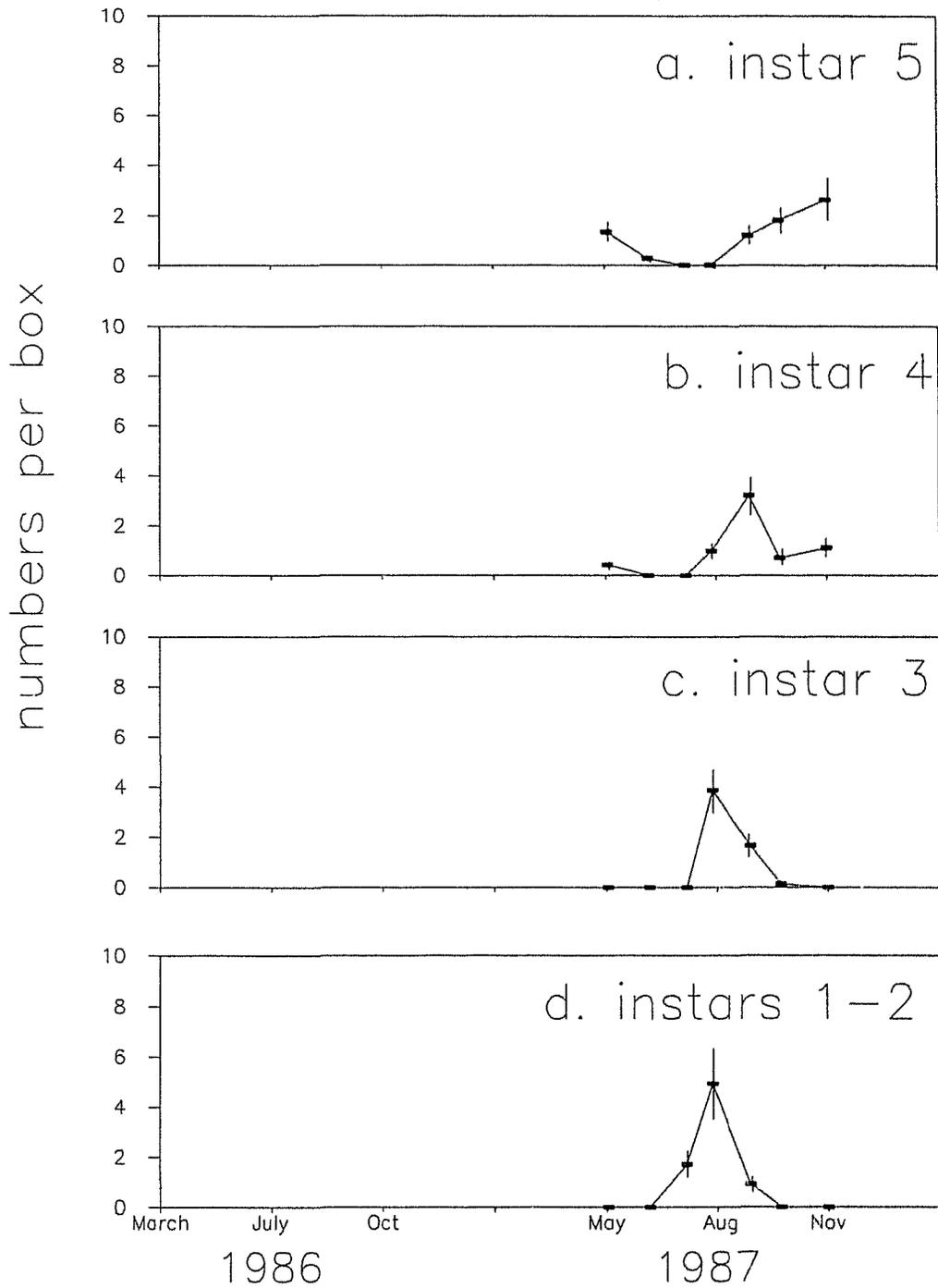
Ablabesmyia sp.

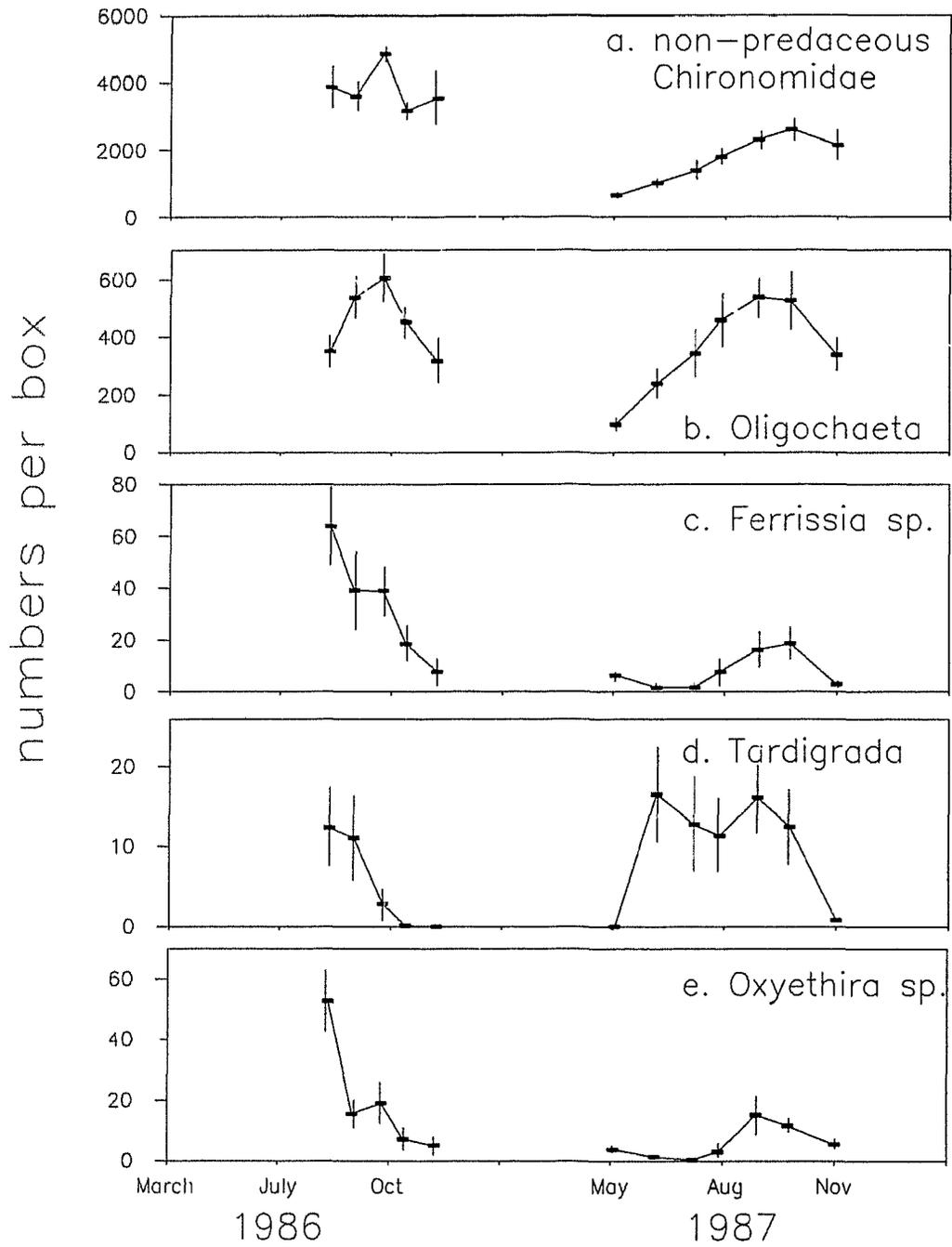




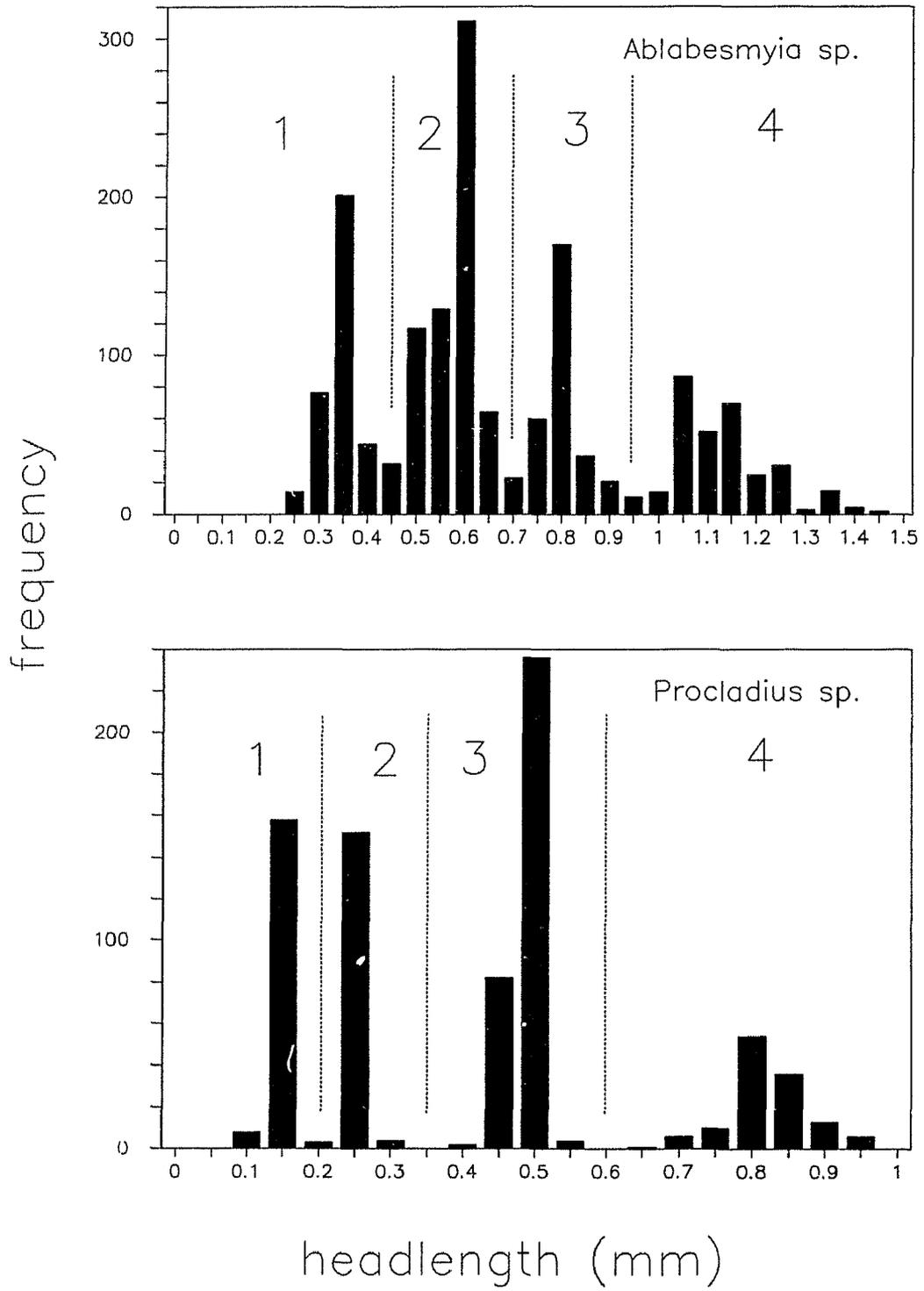


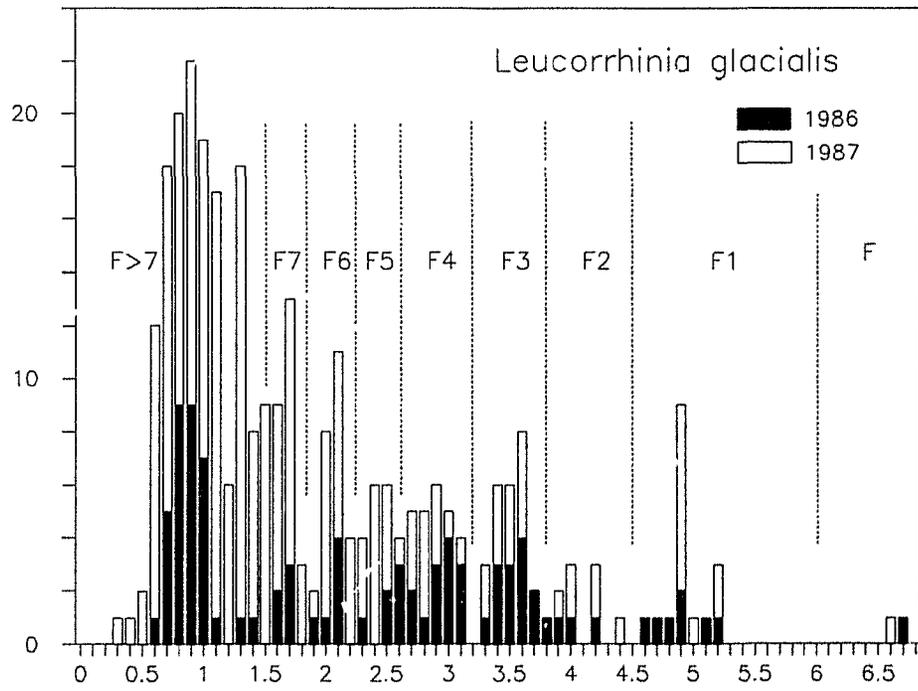
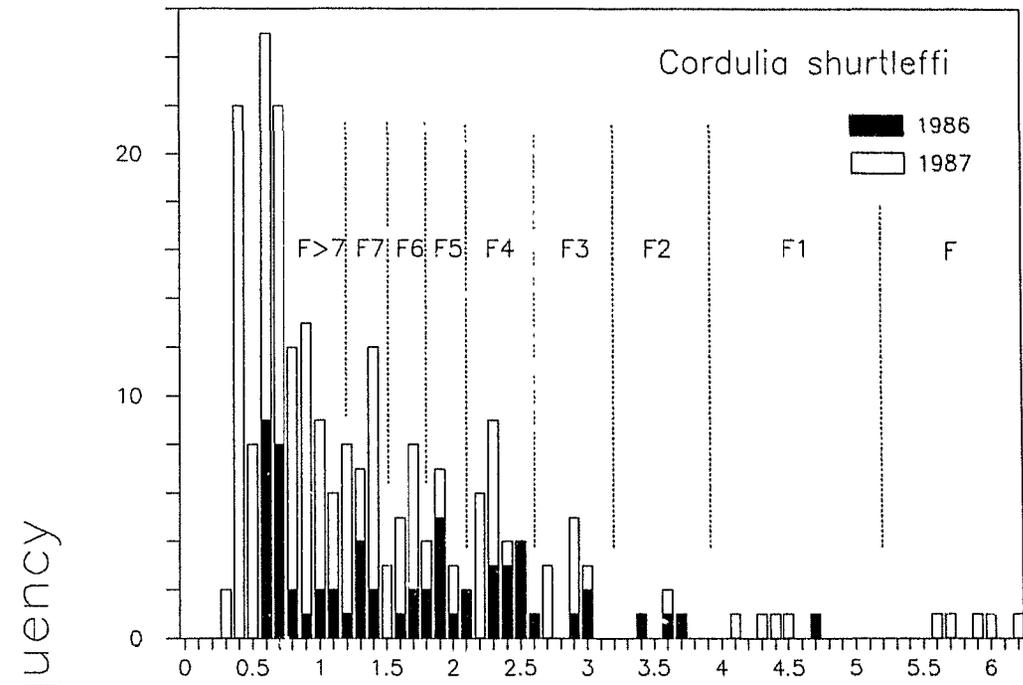
Cernotina sp.



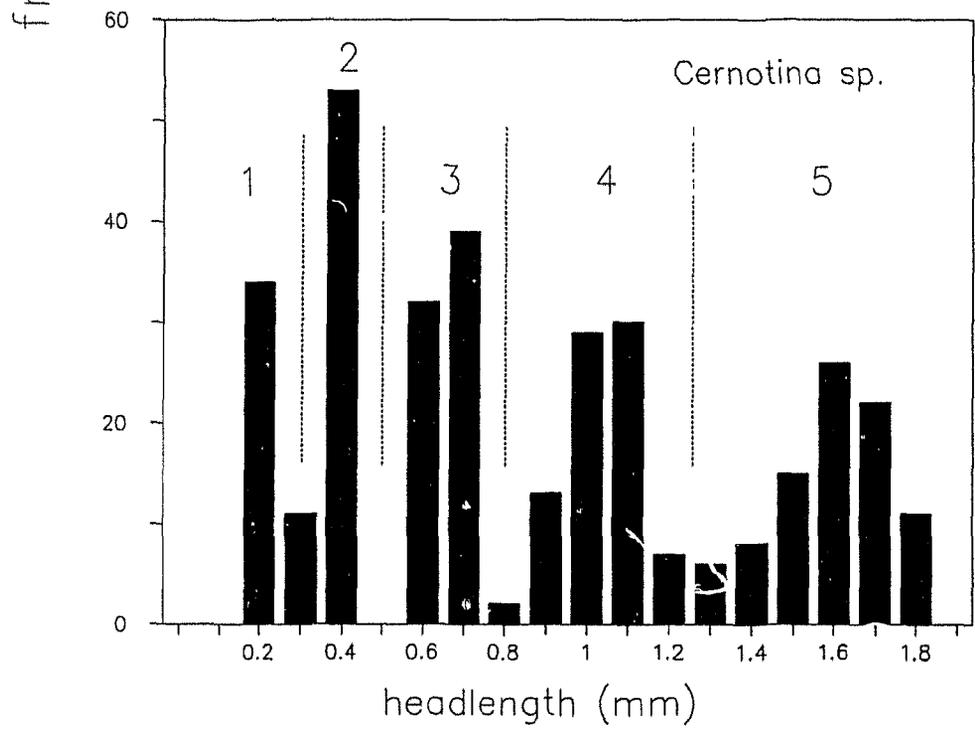
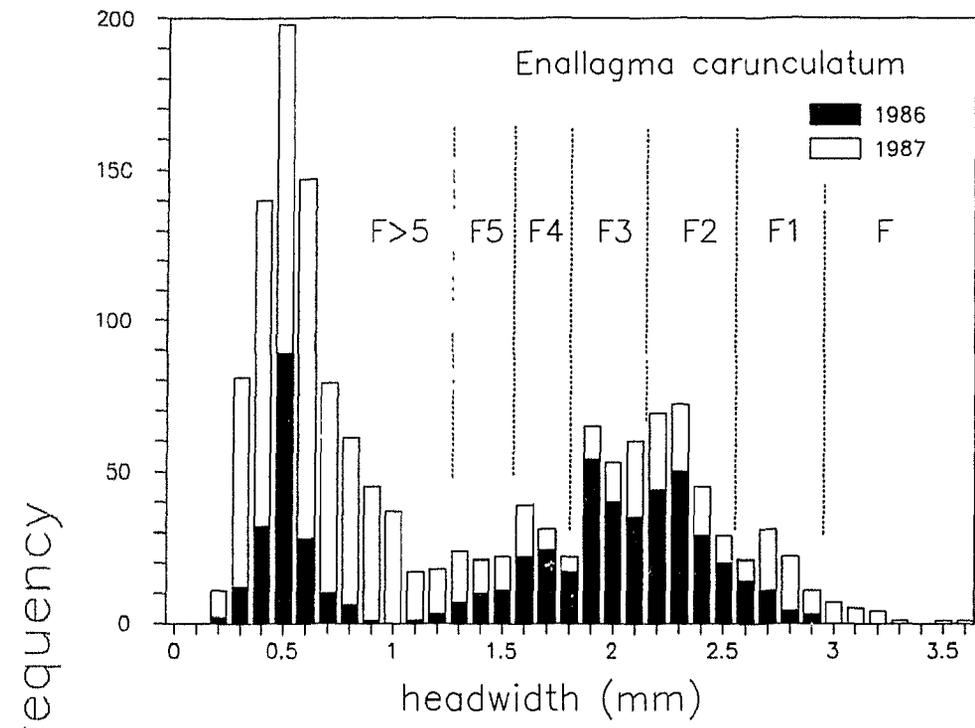


Appendix 3. Summary size-frequency histograms and instar designations for common invertebrate predators in Jack Lake.

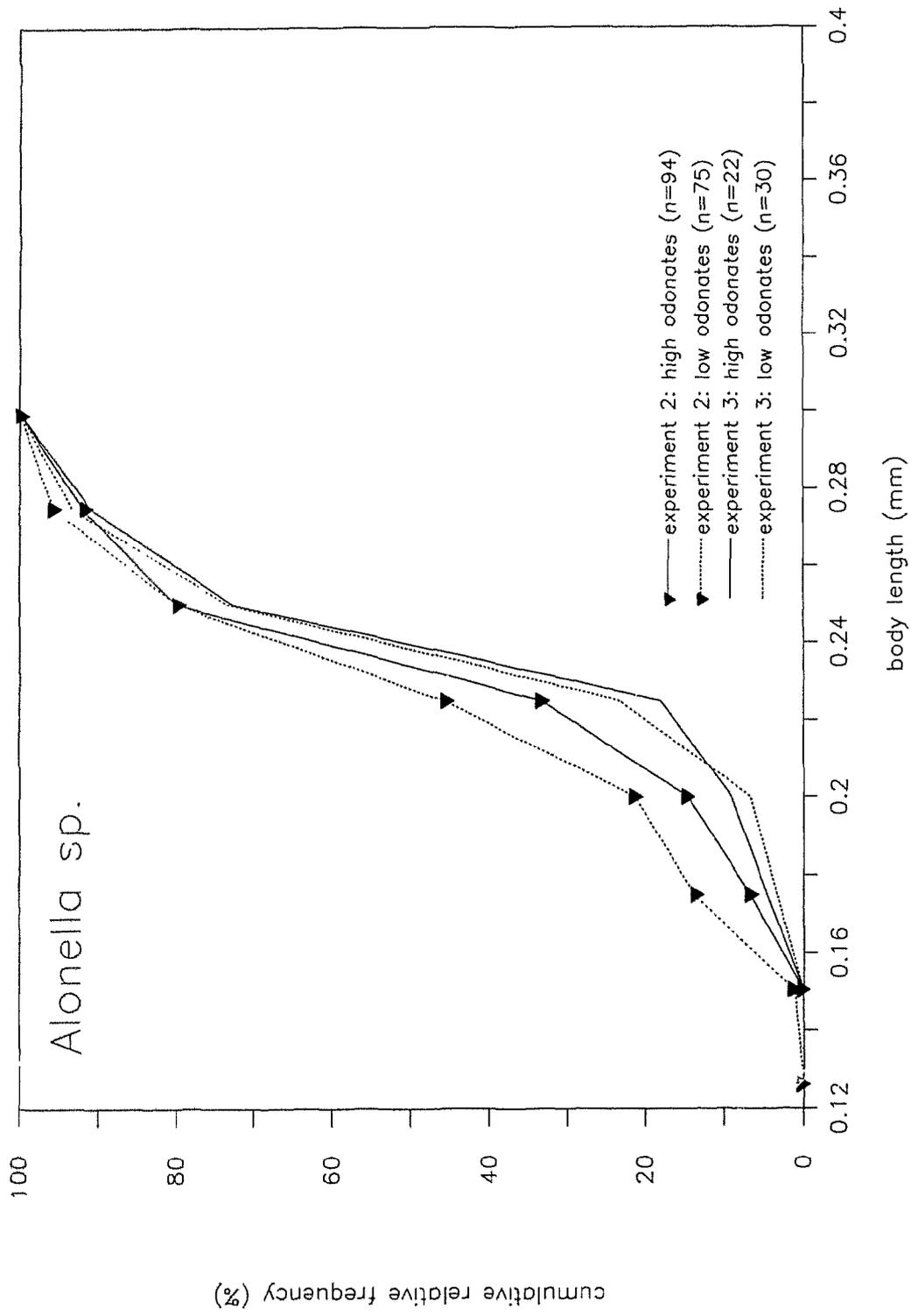


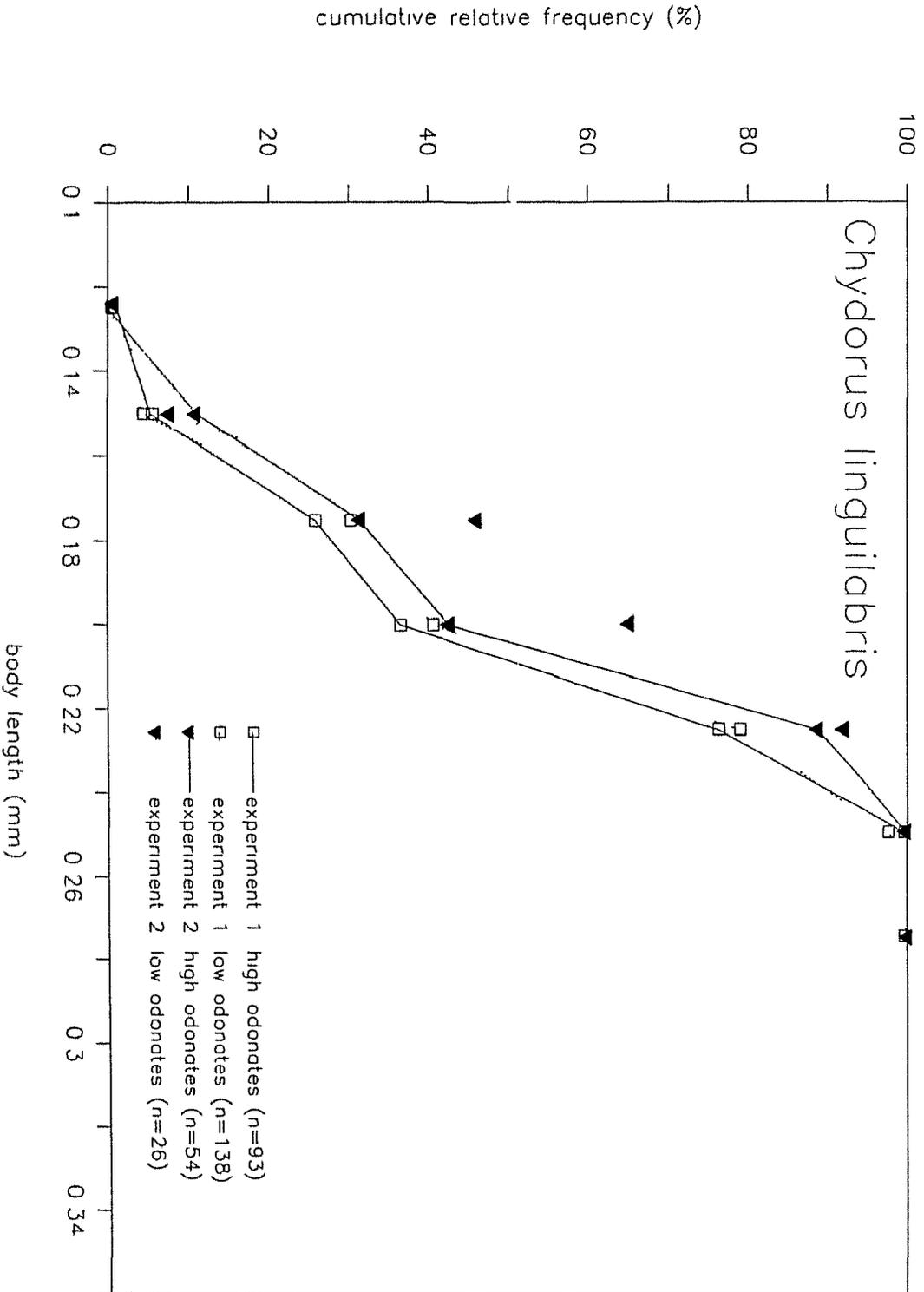


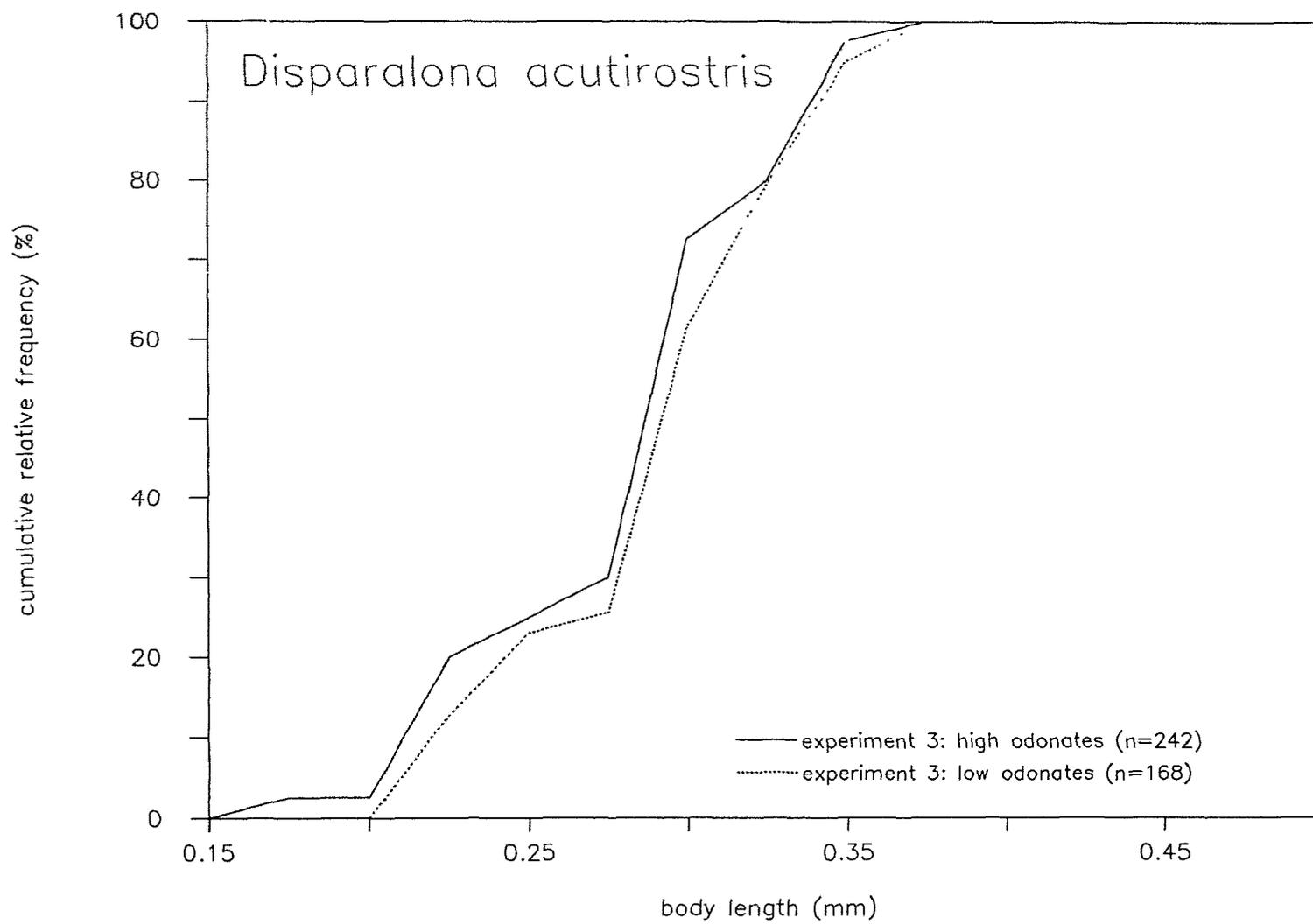
headwidth (mm)

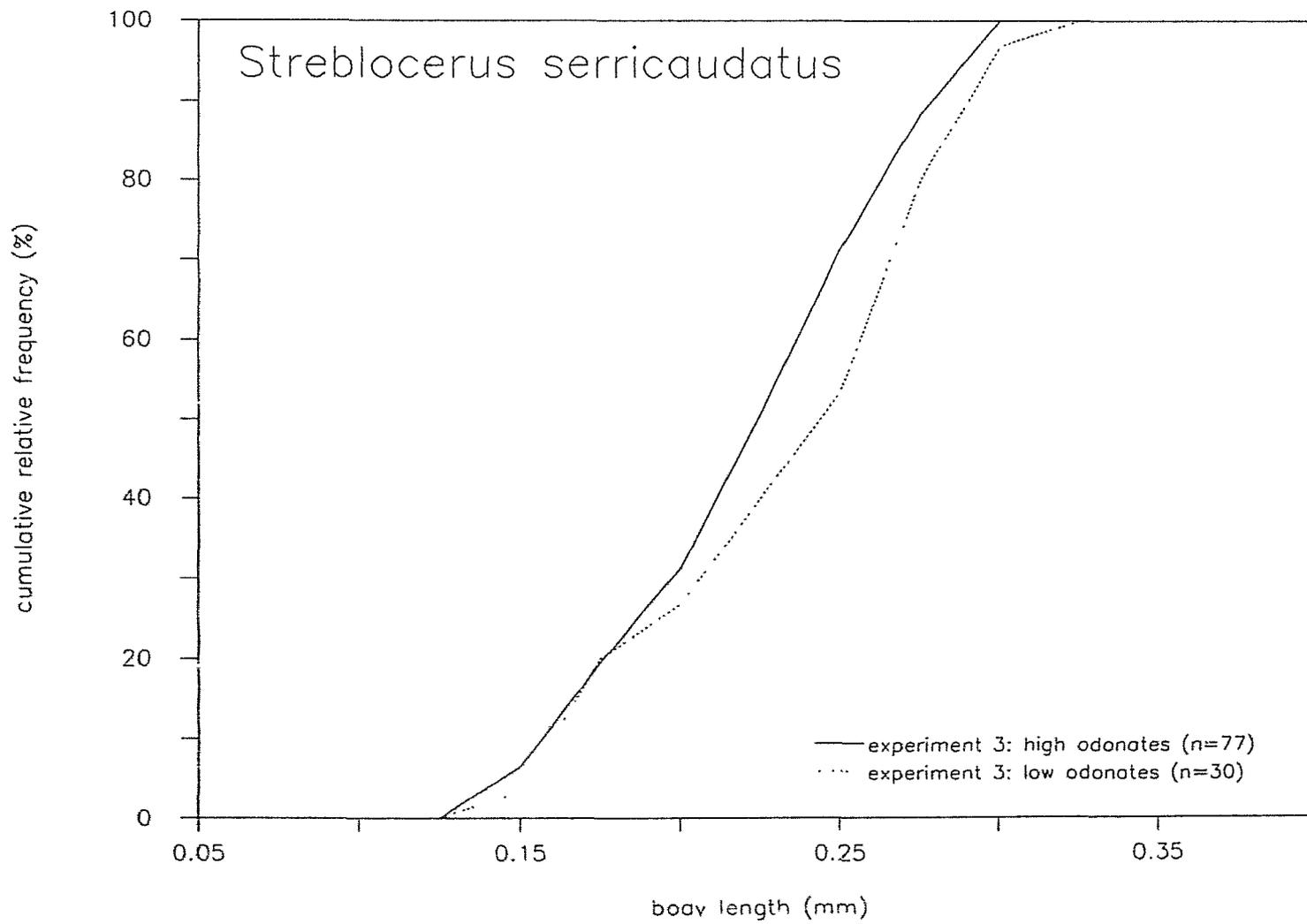


Appendix 4. Cumulative relative size frequencies of body lengths of Disparalona acutirostris, Alonella sp., Chydorus linguilabris, and Streblocerus serricaudatus in large enclosures (Chapter 3). Sufficient numbers of D. acutirostris were measured only in experiment 3, Alonella sp. in experiments 2 and 3, C. linguilabris in experiments 1 and 2, and S. serricaudatus in experiment 3. Sample sizes are presented in each figure.









Appendix 5. Two-way ANOVAs comparing abundances of common microcrustacea in large enclosure experiments (experiment X treatment (high vs. low odonate abundance). All abundances were fourth-root transformed before analysis.

Source of variation	df	MS	F	P
<u>Alonella sp.:</u>				
Experiment	2	3.754	1.486	0.246
Odonates	1	0.172	0.068	0.796
Experiment X Odonates	2	0.212	0.084	0.920
Error	24	2.527		
<u>Alona intermedia:</u>				
Experiment	2	4.501	5.121	0.014
Odonates	1	2.122	2.414	0.133
Experiment X Odonates	2	0.171	0.194	0.824
Error	24	0.879		
<u>Chydorus linguilabris:</u>				
Experiment	2	167.042	113.167	<0.001
Odonates	1	0.186	0.126	0.725
Experiment X Odonates	2	2.549	1.727	0.199
Error	24	1.476		
<u>Ilyocryptus sp.:</u>				
Experiment	2	27.547	136.379	<0.001
Odonates	1	0.558	2.764	0.109
Experiment X Odonates	2	1.532	7.584	0.003
Error	24	0.202		
<u>Diacyclops nanus (c3-c5):</u>				
Experiment	2	2.052	7.831	0.002
Odonates	1	0.015	0.056	0.816
Experiment X Odonates	2	0.137	0.522	0.600
Error	24	0.262		
<u>Eucyclops agilis (c3-c5):</u>				
Experiment	2	4.757	14.705	<0.001
Odonates	1	0.107	0.331	0.570
Experiment X Odonates	2	0.110	0.339	0.716
Error	24	0.323		

Appendix 5. Continued.

<u>Eucyclops speratus</u> (c3-c5):				
Experiment	2	7.087	12.289	<0.001
Odonates	1	0.002	0.004	0.952
Experiment X Odonates	2	0.071	0.123	0.885
Error	24	0.577		
<u>Macrocyclus albidus</u> (c3-c5):				
Experiment	2	1.894	2.544	0.100
Odonates	1	0.007	0.009	0.926
Experiment X Odonates	2	0.017	0.022	0.978
Error	24	0.745		

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