Ann. Zool. Fennici 19: 349–356. 1982

Competition in zooplankton communities

Paul D. N. Hebert

Hebert, P. D. N. 1982: Competition in zooplankton communities. — Ann. Zool. Fennici 19: 349–356.

Freshwater zooplankton communities are not speciose — it is rare to find as many as 10 species in even a large lake. This number is usually a small subset of the available species pool. It has been accepted for some 30 years that competitive interactions are important in limiting local species richness. Support for this view has been drawn from the fact that coexisting zooplankton species often differ in size, suggesting that size separation (and presumed reduced food overlap) is required for coexistence. In cases where species of similar size co-occur, niche analysis has shown spatial or temporal isolation. The view from nature has been reinforced by laboratory studies which have regularly shown competitive exclusion. Over the past decade evidence has accumulated to challenge this notion of strict niche separation. Co-occurring species often show significant concordance in life history traits, suggesting usage of common resources; and competition has now been documented in several cases. Studies on zooplankton species reproducing asexually have provided the most striking evidence of niche overlap. They have shown that local populations include a number of different clones. These clones are ecologically very similar, though not identical. Clonal diversity is maintained because of temporal shifts in the environment.

Paul D. N. Hebert, Biology Department, University of Windsor, Ontario N9B 3P4, Canada.

1. Introduction

Hutchinson's (1951) view that competition plays an important role in limiting the species richness of local zooplankton communities has been widely accepted. The present paper aims both to review the data which support this conclusion and to summarize more recent studies which indicate that substantial niche overlap is compatible with long-term coexistence. In any study of competitive interactions it is important to restrict considerations to a single guild. Thus this paper aims not to provide a broad overview of diversity patterns in zooplankton communities, but instead focuses on the nature of interactions among limnetic herbivorous crustaceans. It is apparent that the generality of patterns which emerge in this restricted study will need to be established by studying other zooplankton guilds such as the limnetic predators, or benthic herbivores.

The diversity of freshwater herbivores is much less impressive that that of their terrestrial counterparts. Even the ancient freshwater lakes such as Baikal contain few zooplankton species. In part the low species richness within habitats is a consequence of low species richness on a global basis. Thus there are only 7 major genera of planktonic cladocerans containing fewer than 200 species, and the calanoid copepods, while more diverse, probably include fewer than 500 species on a global basis. However, the number of species in any habitat is not only a small fraction of the global pool, but also of the local species assemblage. Thus Canadian freshwater habitats contain an average of 4 calanoid and cladoceran species (Table 1), although within a local region 4–5 times as many species are present. The diversity data for Canada are not unusual. Timms (1968) reported an average of 2.0 calanoids and 1.5 cladocerans in a survey of Australian habitats,

Table 1. Average number of limnetic zooplankters in a variety of Canadian habitats. The bracketed figures indicate the total number of species encountered in each survey.

Habitat type	Number of habitats surveyed	Average number of species per habitat Cladocerans	Calanoids
Rocky Mountain lakes & ponds (Anderson, 1974)	340	1.6(26)	1.1(21)
Ontario lakes (Patalas, 1971)	40	3.7(13)	2.0(7)
Tundra ponds (Hebert, pers. obs.)	135	0.9(4)	1.9(5)

while Pennak's (1957) global values average 2.7 copepod and 2.8 cladoceran species per habitat.

2. Factors restricting diversity

The fact that one finds only a portion of the local species pool in any habitat can be attributed either to chance or to the presence of predators, competitors, or unsuitable environmental conditions. The possibility that a species is absent from an otherwise suitable habitat simply because of its failure to colonize it cannot easily be ruled out. Genetic studies have suggested that the movement of dispersal propagules among habitats is more limited than had been expected. There is good evidence of a positive relationship between habitat size and species richness for a number of freshwater taxa (Dickson & Cairns 1972, Colinvaux & Steinitz 1980, Holland & Jain 1981), but information on the zooplankton remains largely anecdotal. Thus it is generally recognized that lake habitats contain more zooplankton species than do ponds. In North America, for example, an individual lake may contain as many as 6-7 *Daphnia* species, while ponds invariably have fewer than half as many. Patalas (1971) showed statistically that large lakes contain more zooplankton species than small lakes. Similarly, Good (1981) documented a positive correlation between pool volume and zooplankton species richness. This correlation can be explained on island biogeographic terms — habitat size is likely to be directly correlated with colonization rate and inversely with extinction rate. However, the correlation between species richness and habitat size may equally well be a consequence of increased microhabitat diversity. Colonization processes are obviously not the sole agents limiting species distributions. The role of unsuitable environmental conditions in limiting zooplankton distributions has been recognized for some 50 years (Hutchinson 1933). Over the past 15 years, the impact of predation on the species composition of zooplankton communities has also been well documented. It is now generally accepted that the absence of large bodied zooplankton species in lakes is a consequence of fish predation, while their prevalence in habitats lacking fish results from their relative immunity to invertebrate predators (Zaret 1980). There is no doubt then, that both physical factors and predator constellations have the effect of restricting the number of species from the local species assemblage which can colonize any habitat. It remains to be determined how important competition has been in further reducing the number of species present in a habitat.

3. The impact of competition — a classical view

In his 1951 paper Hutchinson argued that coexisting copepods were not a random assemblage of the local species pool, but that coexisting species tended to differ widely in size. He hypothesized that these size differences were related to the use of different foods and that instances of coexistence between species of similar size were not seen because of competitive exclusion. Additional supporting data have been obtained. Thus Bayly (1964) has shown that large and small calanoids coexist in Australian and New Zealand habitats, but that similar sized species do not. However, exceptions to the generalization have been detected. Rigler & Langford (1967) showed that many Ontario lakes contain several calanoid species of similar size. A more fundamental criticism can be levelled against these community assembly observations. In no case have the observed assemblages been compared with those expected on the basis of chance (Connor & Simberloff 1979, but see Diamond & Gilpin 1982, and Gilpin & Diamond 1982 for difficulties in carrying out such a test). In 1965 Brooks and Dodson provided additional support for the view that competition has played an important role in determining the species composition of zooplankton communities. Specifically they argued that the predominance of large zooplankton species in habitats lacking fish was a consequence of their competitive superiority over smaller species. However, a number of both theoretical (Hall et al. 1976) and experimental studies (Sprules 1972, Dodson 1974, Dodson et al. 1976) soon indicated weaknesses in this size-efficiency hypothesis and there is now considerable support for the alternative hypothesis (Dodson 1974) that the dominance of large zooplankters in pond habitats is primarily a consequence of their resistance to invertebrate predation.

Other independent support for the importance of competition in structuring zooplankton communities has been obtained from niche analysis studies (Miracle 1974, Lane 1975, Makarewicz & Likens 1975, Williams 1982). The conclusions of the several studies have been congruent — coexisting zooplankters are found in different parts of the water column at different times of the year. For instance, Makarewicz & Likens (1975) showed that the time and place of peak abundance for each of the three cladoceran species in Mirror Lake were not similar. Indeed, even when density isoclines were plotted, little overlap was evident. Many observations of a similar sort have been made. For example, many European lakes contain two *Daphnia* species, with *D. longispina* found in the surface waters, and *D.*

longiremis restricted to the hypolimnion. Similarly, Threlkeld (1979) suggested that *Daphnia pulicaria* and *Daphnia galeata mendotae* coexisted in a Michigan lake due to differences in habitat preference, migration, feeding efficiencies and life histories. However, such studies have one major failing — they do not show that the disjunct distributions are the result of competition (Lawlor 1980). Indeed they don't even rule out the possibility of competition; for the circulation of water means that a herbivore confined to the surface waters may well reduce food availability for a species restricted to deep water.

Further support for the importance of competition has come from laboratory studies, which have shown swift competitive exclusion. For instance, Frank (1957) showed that *D. pulicaria* excluded *D. magna* whether the cultures were fed yeast or alga. His choice of competitors was somewhat odd, for the two species do not ordinarily coexist and the stocks used in the experiments were from Michigan and California respectively. Similarly, most of the laboratory competition experiments carried out prior to 1970 dealt with species pairs which do not coexist in nature.

In conclusion three lines of work — community composition, niche analysis, and laboratory competition studies supported the notion that in natural habitats zooplankton species occupied discrete niches and that competition between coexisting species was rare. When competitors met, the outcome was swift competitive exclusion. The adequacy of the observations used to establish this generalization has been challenged because the remainder of this paper aims to establish that niche overlap in zooplankton communities is in fact substantial and that competition among species is commonplace.

4. Competition revealed through regression analyses and field experiments

Exploitative competition often results from the use of a shared food resource. Direct analysis of dietary overlap among zooplankters is difficult — in part because zooplankton consume a wide variety of items including organic debris, bacteria and algae. However, a more serious problem arises because there is no easy way to determine the relative nutritive value of items present in the gut. A zooplankter may assimilate 93 % of the caloric value of a cryptomonad, but less than 5 % of the caloric value of a blue-green. Fortunately, there is an indirect way to assess food availability. Zooplankton grow larger and produce more eggs when food is abundant (Hutchinson 1967). Analysis of variation in body size and egg production can provide indications of food overlap.

There are two common herbivorous calanoids in tundra ponds near Churchill, Manitoba. *Diaptomus arcticus* is a large species with mature females averaging 2.23 mm in length. Adult females of *D. tyrrelli* are considerably smaller, averaging 1.68 mm. Adult size in these species is not constant. Variation in size among individuals within a specific pond is usually small, but size differences among adults from different ponds is often dramatic. Variation in mean length of *D. tyrrelli* females from 1.43 to 1.85 mm was encountered in a survey of 20 ponds. This length variation corresponded to a four-fold variation in weight. The same sort of size variation was seen among populations of *D. arcticus*. Figure 1 shows, moreover, that there is a strong positive correlation in size of the two species. Ponds with large adults of *D. tyrrelli* have large adults of *D. arcticus*. The parallel size trends may indicate the use of common resources, and thus significant dietary overlap between species which differ in size. This line of analysis has a weakness — it is not possible to rule out the possibility that the two species use different food items which covary in abundances.

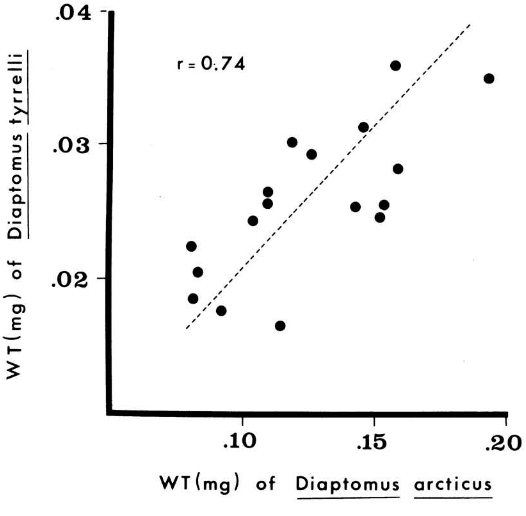

Fig. 1. Correlation between the body weights of two herbivorous calanoids cohabiting in arctic tundra ponds (Churchill, Manitoba).

This possibility can be tested if one has density data. Data of this sort are not available for the arctic copepods, but were collected during a study on Australian *Daphnia* species. In many Australian

Table 2. Multiple regression analysis of the factors affecting standard egg production in *Daphnia carinata* and *Daphnia cehpalata* when living in isolation, and when cohabiting. *$p<0.05$, **$p<0.01$.

Independent variables	*T*-ratio	
D. carinata (alone)		
Temperature	-1.99*	
Number of adults in sample	-3.29**	$R^2=0.28$
Number of adults 1 month prior	-1.89**	$F=4.49$**
D. cephalata (alone)		
Temperature	1.79*	
Number of adults in sample	-5.42**	$R^2=0.29$
Number of adults 1 month prior	-3.37*	$F=9.99$**
D. cephalata (cohabiting)		
Temperature	0.80	
Number of *cephalata* adults in sample	-1.43*	$R^2=0.26$
Number of *cephalata* adults 1 month prior	-1.77**	$F=3.86$*
Number of *carinata* adults in sample	-1.86*	
Number of *carinata* adults 1 month prior	-1.26*	

ponds one finds two or more species belonging to the *Daphnia carinata* complex. These species are similar in size and closely related genetically (Hebert 1977a). The two commonest species around Sydney are *D. carinata* and *D. cephalata* (Hebert 1977b). In the genus Daphnia 95 % of the energy in excess of maintenance requirements is diverted to egg production (Richman 1958). Brood size is determined by food availability in the preceding moult interval (2 days at 20°C to 7 days at 10°C) and thus responds rapidly to changing food levels. If one monitors egg production in a population, large temporal shifts are common. Typically, these shifts are related to population density — as density increases, brood sizes decline (Hebert 1977b). Egg production patterns and population densities of *Daphnia* were studied in 50 ponds near Sydney. In 15 of these ponds *D. carinata* lived alone, while in 15 other ponds only *D. cephalata* was present. In the remaining 20 ponds the two species coexisted. Multiple regression analysis showed that in ponds containing only *D. carinata* egg production was depressed by increased population density (Table 2). Populations with a high density history produced few eggs. The same trend was evident among populations of *D. cephalata*. At sites where the two species coexisted a striking result was obtained. Egg production in *D. cephalata* was depressed not only by the density of conspecific individuals, but also by the density of *D. cephalata*. This study provides clear evidence of competition between the species, most likely via a shared food resource base.

Within the past decade a number of other studies have provided evidence of significant overlap in food use among coexisting zooplankton species. Thus, Allan (1973) found that *Daphnia parvula* and *Holopedium gibberum* showed significant resource overlap, while Lynch (1978, 1979) produced strong evidence that *Daphnia pulex, Ceriodaphnia reticulata,* and *Bosmina longirostris* all compete for resources. DeMott & Kerfoot (1983) produced additional evidence of competition for food between *Daphnia* and *Bosmina,* while Smith & Cooper (1982) documented competition among *Daphnia, Moina,* and *Ceriodaphnia.* Other workers have found evidence of food overlap among more closely related taxa. Thus Jacobs (1977b, 1978) showed significant resource overlap among cooccuring *Daphnia* species, and Kerfoot (1975, 1977) found overlap among morphs (probably sibling species, Kerfoot & Peterson 1982) of *Bosmina.* These studies have indicated that competition between species normally results in reduced growth and egg production. It can also, when food levels are very low, be reflected in reduced survivorship. Juveniles tend to be particularly susceptible to starvation (Neill 1975) perhaps because of their limited lipid stores (Goulden & Horning 1980, Tessier & Goulden 1982).

5. Predator balancing of competitive systems

There seems little doubt that overlap in resource use and competition for food are common among coexisting zooplankters. The failure of this competition to result in exclusion has been attributed in nearly all cases to the interaction between competition and predation. Thus it has been shown that the competitively superior "short-featured" form of *Bosmina longirostris* is also more susceptible to predation (Kerfoot 1975, Kerfoot 1977, Kerfoot & Pastorak 1978). Spatial heterogeneity in predator densities permits the two forms of *Bosmina* to coexist — the short-featured form predominates in areas with low predator density and the long-featured form in regions with more predators. Similarly, in all of the other examples previously discussed the competitive dominant was judged more sensitive to predation (Allan 1973, Jacobs 1977a, b, 1978; Lynch 1978, 1979, DeMott & Kerfoot 1983). Differential susceptibility to predation is likely also important in explaining seasonal cycles in abundance of *D. carinata* and *D. cephalata*. *D. carinata* predominates in winter, while *D. cephalata* reaches greatest abundance in summer (Hebert 1977b). *D. carinata* lacks a helmet, while *D. cephalata* produces an enormous crest in response to a water soluble substance released by notonectids (Grant & Bayly 1981). The crested from of *D. cephalata* is protected from notonectid predation. The predominance of *D. cephalata* during the summer months is undoubtedly related at least in part to the coincident rise in notonectid densities. However, a difference in birth rates also exists between the species. *D. carinata* produces more eggs than *D. cephalata* when water temperatures are low, and the reverse is true at high temperatures (Hebert 1977b). In this case, the continued coexistence of these two species appears to depend upon both predation, and the effect of temperature on the natality of the two species.

6. Patterns of clonal diversity

The continued coexistence of species with significant overlap in resource use does not need to be predator balanced. In Australia, *D. carinata* often coexists with species so morphologically similar that they can only readily be distinguished electrophoretically. It is unlikely that such species differ in their susceptibility to predation. Further evidence of coexistence in the absence of significant morphological divergence has been derived from studies of clonal diversity in *Daphnia* populations reproducing by obligate parthenogenesis. In these species, which have abandoned sexual reproduction, each clone is a reproductively isolated unit; thus the maintenance of clonal diversity is analogous to the maintenance of species diversity. In a survey of 11 populations of *Daphnia pulex* in southwestern Ontario, 22 different clones were identified (Hebert & Crease 1980), and as many as seven were found in a single habitat. These results seem typical for *Daphnia* reproducing by obligate parthenogenesis. Table 3 shows that similar levels of clonal diversity were found in populations of *D. pulex* from both temperate and arctic regions, and in populations of *Daphnia middendorffiana*, another obligate parthenogen.

Table 3. Clonal diversity (mean ± *SE* and range) in populations of *Daphnia* reproducing by obligate parthenogenesis.

Species	Locale	Populations surveyed	Clones per habitat	
D. pulex	Windsor	11	3.6±.6	1-7
D. pulex	Kingston	10	3.0±.3	2-5
D. pulex	Churchill	10	3.1±.6	1-6
D. middendorffiana	Churchill	70	2.8±.2	1-10

Table 4. The results of pairwise competition experiments between clones of variable genetic similarity.

Competition between clones of groups	Mean genetic distance between competitors	Coexistence	Exclusion
3 × 3	0.110	9	6
1 × 2	0.175	29	15
1 × 3	0.205	1	35
2 × 3	0.215	1	22
$\chi^2_3 = 49.2$; $p<0.0001$			

Such regular coexistence of clones is surprising in light of Williams's (1975) comment that "if the competitive exclusion principle is ever to apply it should do so in the case of clones." One explanation for such coexistence is that the clones are ecological analogues. However, four lines of evidence indicate that there are ecological differences among clones. Firstly clone frequencies are not stable; major shifts in frequency occur during both annual cycles and between different years. These shifts must reflect fitness differences among clones, rather than drift because population sizes are large. Secondly, clonal distribution patterns seem not to be random. Analysis of genetic distance data using cluster analysis reveals that the Ontario clones of *D. pulex* fall into three rather distinct groups. Clones of two of these groups are regularly found in grassland and urban habitats, while clones in the remaining group are characteristic of forest pools. Aside from these two lines of indirect evidence of ecological differentiation, there are more direct indications of clonal differences in life history traits and competitive ability. An initial study of four clones; one belonging to group 1, two to group 2, and one to group 3 revealed significant clonal differences in rates of increase (Loaring & Hebert 1981). When competition experiments were carried out by making pairwise combinations of these clones, competitive exclusion normally occurred. The group 1 clone competitively excluded the remaining three clones at all three experimental temperatures, while the group 3 clone was excluded by each of the other clones. The two group 2 clones showed a switch in competitive superiority related to temperature and coexisted at 20°C. These experiments were run in 2 liter containers, but a similar outcome was observed in 500 liter tanks (Loaring 1982). The coexistence of the two most genetically similar clones in the first set of experiments, suggested the value of investigating the relationship between extent of genetic divergence and probability of coexistence in more detail. In a second experiment 37 different clonal combinations were made (Loaring 1982). The results indicated that there was a relation between genetic similarity and coexistence. Genetically closely related clones tended to coexist at the end of the experiment, while combinations of more distantly related clones resulted in exclusion (Table 4). The laboratory results accord with distributions seen in nature. Group 3 clones regularly coexist in nature as do clones of group 1 and 2. However, it is rare to find a group 3 clone in ponds containing clones belonging to the other groups.

7. Entry requirements and taxon distributions

Our understanding of the assembly of zooplankton communities can perhaps be advanced by recognizing that species or clones colonizing a habitat must meet certain entry requirements — both physical and biological. Such entry requirements ensure that the species (or clones) exploiting a niche are ecologically convergent. A good example of this effect can be seen in tundra ponds near Churchill, Manitoba. Two species of *Daphnia* are present, *D. pulex* and *D. middendorffiana.* These species are fairly distinct morphologically — *D. middendorffiana* has a larger body size and longer tail spine than *D. pulex.* It produces smaller broods of parthenogenetic eggs, but its eggs and neonates are larger than those of *D. pulex* (Good 1981). *D. middendorffiana* is restricted to ponds with the predatory copepod *Heterocope septentrionalis,* while *D. pulex* inhabits ponds lacking the predator. This distribution pattern reflects the lower susceptibility of *D. middendorffiana* to predation and the greater competitive ability of *D. pulex* (Hebert & Loaring 1980, Good 1981). The checkerboard distribution of these species is reminiscent of that seen in the case of long and short featured forms of *B. longirostris,* except that at Churchill heterogeneity in predator densities occurs between rather than within habitats. Investigation at the species level overlooks the more complex problem of clonal distribution patterns, for there are more than a dozen clones of each species in the Churchill region (Hebert & McWalter 1982a). Each pond contains only a subset of these clones, and the proportion of a specific clone varies considerably among habitats. The factors governing clonal distributions are, with one exception, not clear. Three clones of *D. pulex* and six clones of *D. middendorffiana* produce a melanized cuticle, while the remaining clones are unpigmented (Hebert & McWalter 1982b). The melanized clones are restricted to ponds with little dissolved organic material, while clones lacking pigmentation are found in ponds containing large amounts of dissolved humics, which effectively absorb ultraviolet and blue light. Thus at Churchill one can identify a hierarchy of environmental factors which determine firstly species and then clonal distributions. One observes not the coexistence of ecologically different *Daphnia* species, or even morphologically differentiated clones, but rather the coexistence of clones which appear most ecologically similar.

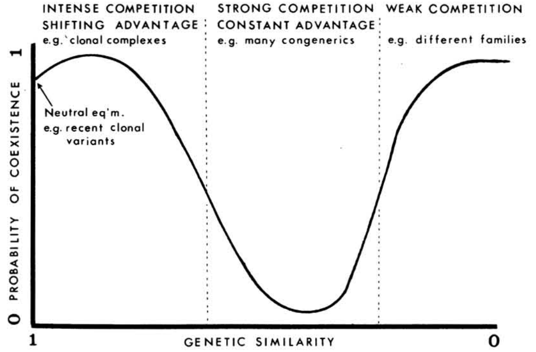

Fig. 2. A theoretical model for the probability of coexistence of taxa with different degrees of genetic similarity.

The studies at Churchill indicate that *D. pulex* competitively excludes *D. middendorffiana* from habitats lacking *Heterocope.* Yet these same ponds contain an array of ecologically similar clones of *D. pulex.* It is evident that ecological differentiation alone does not foster coexistence. Indeed the Churchill zooplankton communities suggest that the relationship between genetic similarity and probability of coexistence is bimodal. Such bi-modality can be justified on a theoretical basis (Fig. 2). In the absence of niche overlap coexistence is stable. Similarly in the case where two taxa are ecologically identical, they will coexist (neutrally), and if population sizes are large, any random walks in species abundance will be small. As this latter case illustrates, strong competition need not bring about rapid displacement. Indeed when taxa are very similar, competitive replacement will be slow because fitness differences will be small. In a stable environment, one taxon will, of course, eventually be excluded. However, in a variable environment, competitive advantage may shift from one taxon to the other. Seen from this light, clonal coexistence is not paradoxical. The requirement for long-term coexistence is that two taxa have similar mean fitness and such similarity is more likely in the case of closely rather than distantly related taxa. Competition between distantly related taxa will be less intense, because of reduced niche overlap, but one species is more likely to maintain a sustained fitness advantage resulting in exclusion. In conclusion, long-term coexistence between taxa with either great similarity or difference is likely. On the other hand, coexistence is less likely for moderately differentiated taxa. It is clear that most past research on zooplankton has ignored the coexistence of closely related taxa. The reasons for this are twofold. Most valid species probably fall into the right half of Fig. 2. Moreover, many of the morphologically similar species remain undetected. These undetected sibling species are precisely those which are most likely to provide examples which mirror those seen at the clonal level. Clearly, if this new view of zooplankton communities is verified, then competition can no longer be regarded as an infrequent, transient phenomenon.

References

Allan, J. D. 1973: Competition and the relative abundance of two cladocerans. — Ecology 54: 484—498.

Anderson, R. S. 1974: Crustacean plankton communities of 340 lakes and ponds in and near the National Parks of the Canadian Rocky Mountains. —J. Fish. Res. Board Canada 31: 855-869.

Bayly, J. A. E. 1964: A revision of the Australasian species of the freswhater genus Boeckella and Hemoboeckella (Copepoda: Calanoida). — Aust. J. Mar. Freshwat. Res. 15: 180-238.

Brooks, J. L. & Dodson, S. J. 1965: Predation, body size, and composition of plankton. — Science 150: 28-35.

Colinvaux, P. & Steinitz, M. 1980: Species richness and area in Galapagos and Andean lakes: equilibrium phytoplankton communities and a paradox of the zooplankton. — In: Kerfoot, W. C. (ed.), Evolution and ecology of zooplankton communities. University Press of New England, Hanover, N. H.

Connor, E. F. & Simberloff, D. 1979: The assembly of species communities: Chance or competition? — Ecology 60: 1132-1140.

DeMott, W. R. & Kerfoot, W. C. 1983: Competition among cladocerans: nature of the interaction between Bosmina and Daphnia. — Ecol. Monogr. (in press).

Diamond, J. M. & Gilpin, M. E. 1982: Examination of the "null" model of Connor and Simberloff for species co-occurences on islands. — Oecologia 52: 64-74.

Dickson, K. L. & Cairns, Jr., J. 1972: The relationship of freshwater macroinvertebrate communities collected by floating artificial substrates to the MacArthur-Wilson equilibrium. — Am. Midl. Nat. 88: 68-75.

Dodson, S. J. 1974: Zooplankton competition and predation: an experimental test of the size-efficiency hypothesis. — Ecology 55: 605-613.

Dodson, S. I., Edwards, C., Wiman, F. & Normandin, J. C. 1976: Zooplankton: Specific distribution and food abundance. — Limnol. Oceanogr. 21: 309-312.

Frank, P. W. 1957: Coactions in laboratory populations of two species of Daphnia. — Ecology 38: 510-519.

Gilpin, M. E. & Diamond, J. M. 1982: Factors contributing to non-randomness in species co-occurrences on islands. — Oecologia 52: 75-84.

Good, A. G. 1981: The ecology and biogeography of tundra zooplankton communities in the Churchill, Manitoba area. — MSc. thesis, University of Windsor.

Goulden, C. E. & Hornig, L. L. 1980: Population oscillations and energy reserves in planktonic Cladocera and their consequences to competition. — Proc. Natl. Acad. Sci. 77: 1716-1720.

Grant, J. W. G. & Bayly, I. A. E. 1981: Predator induction of crests in morphs of the Daphnia carinata King complex. — Limnol. Oceanogr. 26: 201-218.

Hall, D. J., Threlkeld, S. T., Burns, C. W. & Crowley, P. H. 1976: The size-efficiency hypothesis and the size structure of zooplankton communities. — Ann. Rev. Ecol. Syst. 7: 177-208.

Hebert, P. D. N. 1977a: A revision of the taxonomy of the genus Daphnia (Crustacea, Daphniidae) in southeastern Australia. — Aust. J. Zool. 25: 371-398.

—»— 1977b: Niche overlap among species in the Daphnia carinata complex. — J. Anim. Ecol. 46: 399-409.

Hebert, P. D. N. & Crease, T. J. 1980: Clonal coexistence in Daphnia pulex (Leydig): another planktonic paradox. — Science 207: 1363-1365.

Hebert, P. D. N. & Loaring, J. M. 1980: Selective predation and the species composition of arctic ponds. — Can. J. Zool. 58: 422-426.

Hebert, P. D. N. & McWalter, D. B. 1982a: Genetic variation in arctic Daphnia reproducing by obligate parthenogenesis. — Evolution (in press).

—»— 1982b: Cuticular pigmentation in arctic Daphnia: adaptive diversification of asexual lineages? — Am. Nat. (in press).

Holland, R. F. & Jain, S. K. 1981: Insular biogeography of vernal pools in the central valley of California. — Am. Nat. 117: 24-37.

Hutchinson, G. E. 1933: Experimental studies in ecology. I. Magnesium tolerance of Daphniidae and its ecological significance. — Int. Rev. Ges. Hydrobiol. Hydrogr. 28: 90-108.

—»— 1951: Copepodology for the ornithologist. — Ecology 32: 571-577.

—»— 1967: A treatise on limnology. Volume 2. Introduction to lake biology and the limnoplankton. — John Wiley & Sons. New York.

Jacobs, J. 1977a: Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. I. A model. — Oecologia (Berl.) 29: 233-247.

—»— 1977b: Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. II. Field data analysis of Daphnia. — Oecologia (Berl.) 30: 303-329.

—»— 1978: Coexistence of similar zooplankton species by differential adaptation to reproduction and escape in an environment with fluctuating food and enemy densities. III. Laboratory experiments. — Oecologia (Berl.) 35: 35-54.

Kerfoot, W. C. 1975: The divergence of adjacent populations. — Ecology 56: 1298-1314.

—»— 1977: Competition in cladoceran communities: the cost of evolving defenses against copepod predation. — Ecology 58: 303-313.

Kerfoot, W. C. & Pastorak, R. A. 1978: Survival versus competition: evolutionary compromises and diversity in the zooplankton. — Verh. Int. Ver. Limnol. 20: 362-374.

Kerfoot, W. C. & Peterson, C. 1980: Predatory copepods and Bosmina: Replacement cycles and further influences of predation upon prey reproduction. — Ecology 61: 417-431.

Lane, P. A. 1975: The dynamics of aquatic systems: a comparative study of the structure of four zooplankton communities. — Ecol. Monogr. 45: 307-336.

Lawlor, L. R. 1980: Structure and stability in natural and randomly constructed competitive communities. —

Am. Nat. 116: 394-408.

Loaring, J. M. 1982: The ecological genetics of Daphnia species. — MSc. thesis. University of Windsor, Windsor, Ontario.

Loaring, J. M. & Hebert, P. D. N. 1981: Ecological differences among clones of Daphnia pulex Leydig. — Oecologia (Berl.) 51: 162-168.

Lynch, M. 1978: Complex interactions between natural coexploiters — Daphnia and Ceriodaphnia. — Ecology 59: 552-564.

—»— 1979: Predation, competition and zooplankton community structure: an experimental study. — Limnol. Oceanogr. 24: 253-272.

Makarewicz, J. C. & Likens, G. E. 1975: Niche analysis of a zooplankton community. — Science 190: 1000-1003.

Miracle, M. R. 1974: Niche structure in freshwater zooplankton: a principle components approach. — Ecology 54: 1306-1316.

Neill, W. E. 1975: Experimental studies of microcrustacean competition, community composition, and efficiency of resource utilization. — Ecology 56: 809-826.

Patalas, K. 1971: Crustacean plankton communities in forty-five lakes in the Experimental Lakes Area, Northwestern Ontario. — J. Fish. Res. Board Canada 28: 231-244.

Pennak, R. W. 1957: Species composition of limnetic zooplankton communities. — Limnol. Oceanogr. 2: 222-232.

Richman, S. 1958: The transformation of energy by Daphnia pulex. — Ecol. Monogr. 28: 273-291.

Rigler, F. H. & Langford, R. R. 1967: Congeneric occurences of species of Diaptomus in southern Ontario Lakes. — Can. J. Zool. 45: 81-90.

Smith, D. W. & Cooper, S. D. 1982: Competition among cladocera. — Ecology 63: 1004-1015.

Sprules, W. G. 1972: Effects of size-selective predation and food consumption on high altitude zooplankton communities. — Ecology 53: 375-386.

Tessier, A. J. & Goulden, C. E. 1982: Estimating food limitation in cladoceran populations. — Limnol. Oceanogr. 27: 707-717.

Threlkeld, S. T. 1979: The midsummer dynamics of two Daphnia species in Wintergreen Lake, Michigan. — Ecology 60: 165-179.

Timms, B. V. 1968: Comparative species composition of limnetic planktonic crustacean communities in southeast Queensland, Australia. — Hydrobiologia 31: 474-480.

Williams, G. C. 1975: Sex and evolution. — Princeton University Press. Princeton. 200 pp.

Williams, J. B. 1982: Temporal and spatial patterns of abundance of the Chydoridae (Cladocera) in Lake Itasca, Minnesota. — Ecology 63: 345-353.

Zaret, T. M. 1980: Predation and freshwater communities. — Yale University Press. New Haven. 187 pp.

Received 15.IX.1982
Printed 30.XII.1982