tory cortex continuing to receive some bulbar input after partial LOT section performed in neonates but not in adults. This may well account for the relative deterioration of mating behavior in this group of animals. Thus, in all four experimental groups, mating behavior appears to depend on the extent of the olfactory bulb's projection, either total cortical area innervated or input into caudal structures specifically (Fig. 1, A and B) (*6, 16*).

The postsurgical rearrangement of transected LOT axon populations suggests that individual axons grow much like trees (Fig. 1C). When all of the axons' distal branches are severed ["pruned" (*3*)] by complete LOT section at 3 days of age, their proximal branches compensate by sprouting new collaterals, some of which apparently reinnervate part of the denervated cortex behind the cut. After partial LOT section at this age, the cut fibers undergo similar compensatory sprouting. The distribution of the uncut fibers, however, also becomes rearranged; their mid-level branches proliferate to fill in the otherwise denervated wedge of cortex just caudal to the cut, and, apparently in compensation, the most distal axonal branches become foreshortened. This may reflect the retraction of these distal arborizations (*17*). It is more likely, however, that in response to the abnormal occupation of terminal sites vacated as a result of the cut, growth of the most distal branches of the uncut fibers is stunted so that they can no longer keep pace with the ballooning size of the underlying cortex. Thus, by undergoing compensatory sprouting and compensatory stunting, growing axons would tend to conserve their total amount of axonal arborization (*3, 4*). Furthermore, while in some circumstances the sprouting of new connections may lead to functional recovery, the compensatory stunting of normal connections elsewhere may have pathological consequences.

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11. Residual debris from the prior LOT cut disappears quickly. Thus, it does not obscure one's view of the fibers that survived the cut and were present during the period of behavioral testing, and were later visualized by the histological procedure. Silver staining was done by the first method of R. P. Fink and L. Heimer [*Brain Res.* **4**, 369 (1967)], with 4-day survival after bulbectomy. For the autoradiographic determinations, animals were killed 1 day after intrabulbar injection of ^{35}S-labeled methionine tracer [A. M. Graybiel, in *The Use of Axonal Transport for Studies of Neuronal Connectivity*, M. Cuénod and W. M. Cowan, Eds. (Elsevier, Amsterdam, 1975), pp. 175–216, and (*4*)].
12. Mann-Whitney U test, 1-tailed.
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14. This sparing might represent the recovery of olfactory function lost after the cut, rather than the preservation of a function never lost. Thus, normal pups 3 days of age show strong preferences for certain odors (*18*). When such pups are given complete unilateral LOT sections combined with contralateral bulbectomy, however, they show a severe odor-preference deficit when tested at 7 to 12 days of age (*18*). Neonatal LOT section apparently disrupts the sense of smell, which only subsequently recovers. This conclusion is tentative, however, because the pups' responsiveness to sex-related odors (*7, 8*) was not investigated.
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Niche Analysis of a Zooplankton Community

Abstract. *The division of the niche hyperspace has been demonstrated for the limnetic zooplankton community of Mirror Lake, New Hampshire. The niche structure of the zooplankton community is conceived as an intensive or intracommunity population continuum corresponding to the niche hyperspace. The community of zooplankton is a system of interacting populations whose adaptive centers do not overlap and have evolved toward dispersion in relation to the complex gradients of food size, depth, and time.*

The limnetic zooplankton community of oligotrophic Mirror Lake, New Hampshire, consists of at least 18 species of Cladocera, Copepoda, and Rotifera. If a vertical tow with an appropriate net were made, most of these species would be found to coexist in the lake on any given day during summer. Is this coexistence of 18 species of zooplankton a refutation of the competitive exclusion principle?

The competitive exclusion principle contends that no two species can coexist in the same niche; that is, complete competitors cannot coexist (*1*). Unfortunately, the term niche has been used in more than one sense. The functional niche has been defined as the position or role of a species within a given community (*2*), and the spatial or habitat niche may be thought of as the distributional relation of a species to a range of habitats (*3*). Furthermore, the fundamental niche of a species has been defined as a multidimensional hypervolume bounded by species tolerance limits in relation to environmental variables (both physical and biological) within a given biotope and community (*4*).

In a recent attempt to clarify the use of the terms niche and habitat, Whittaker *et al.* (*5*) restricted the term habitat to intercommunity variables, that is, environmental variables with an extensive spatial component. The term niche (*5*) was restricted to intracommunity variables, that is, intensive or local environmental variables. To complete the definition of niche, some measure of the population response to environmental variables is added, for it is the response of the range of genotypes in the population to the complex of environmental variables that is of concern. The niche variables may be viewed as axes of an *n*-dimensional coordinate system defining the niche hyperspace. That part of the hyperspace that each species in the community (*6*) utilizes, occupies, or is affected by is the niche hypervolume. Within this hypervolume the species' response to niche variables is expressed by population measurements, and the population response surface to the niche variables provides the best characterization of the niche. This concept of niche is used in the study reported here.

Mirror Lake represents a discrete ecosystem; biological, physical, and chemical components interact to produce a multitude of environmental variables, integrated to form a functioning whole. Within the boundaries of this ecosystem each species population of the zooplankton community is subjected to and interacts within a range of these environmental variables. Changing patterns of the possibly important variables temperature, light intensity, water chemistry, predation pressure, and trophic interactions in lakes correspond with depth and time. Depth and time may consequently be thought of as complex gradients, each comprising numerous factor gradients that may change together (but are not all strongly correlated). Particular components of the complex gradients (such as temperature and phytoplankton biomass) may ascend and descend with time over a yearly cycle.

Productivity, the rate of synthesis of organic matter per unit time, is a useful measure of species importance values. When plotted (*7*) on axes of depth and time, species importance values form a population surface, which is a measure of the species' response to the environmental variables it encounters (Fig. 1). In this study where both axes are expressions of intracommunity variables, the population surface describes major features of the species' niche.

Before any information can be extracted from these graphs, it is necessary to separate species by their mode of feeding—carnivorous versus herbivorous. Species considered to be predators are grouped in Fig. 1A: *Mesocyclops edax* (*8*), *Cyclops scutifer* (*9*), and *Asplanchna priodonta* (*10, 11*). Two of these species are univoltine species, present in the lake throughout the year but possessing a niche center restricted to a specific season. This is a reflection of the alternation of timing in life history between *M. edax* and *C. scutifer*, which is similar to the alternation in the life history of *Cyclops strenuus* and *Mesocyclops leuckarti* observed in Lago Maggiore, Italy (*12*). Since the copepodids and adults are carnivorous and the nauplii are filter feeders (*13*), the alternation of life history reduces competition between these species; for the adults of each species cooccur with the immatures of the others. Each of the species *M. edax* and *C. scutifer* possesses its own distinctive niche response, clearly separated in time and space from that of the other species and from *A. priodonta.*

A further division of feeding behavior can be based on the size of the food utilized by the herbivorous zooplankton. Considering *Daphnia cucullata*, *Bosmina coregoni*, *Eudiaptomus graciloides*, and rotifers, Gliwicz (*10*) has demonstrated the ability, presumably mechanical, of zooplankton to concentrate food in different size ranges.

However, many irregular, bizarre-shaped, relatively large algae, such as *Asterionella* and *Staurastrum*, which, according to the results of experiments with artificial particles (*10*), should not be ingested by zooplankton, appear to be broken and then ingested (*14*). This mechanism of feeding is probably of little significance in Mirror Lake since large, irregularly shaped algae make up only 2.7 percent of the total annual phytoplankton biomass.

The niche responses of the macroconsumers *Holopedium gibberum*, *Daphnia catawba*, and *Diaptomus minutus* are separated in time and space (Fig. 1, B and C). In relation to depth (at a given time), or in relation to time (at a given depth), the distributions of these species should form bell-shaped curves, except for one case. *Diaptomus minutus* has a bimodal distribution curve resulting from the growth of adults in May and of nauplii in the hypolimnion during July (Fig. 2). The different feeding behaviors of the life stages (adults as macroconsumers and nauplii as microconsumers) of this species result in two different niche response surfaces.

The niches of the microconsumers *Keratella taurocephala*, *Kellicottia bostoniensis*, *Keratella crassa*, and *Con-*

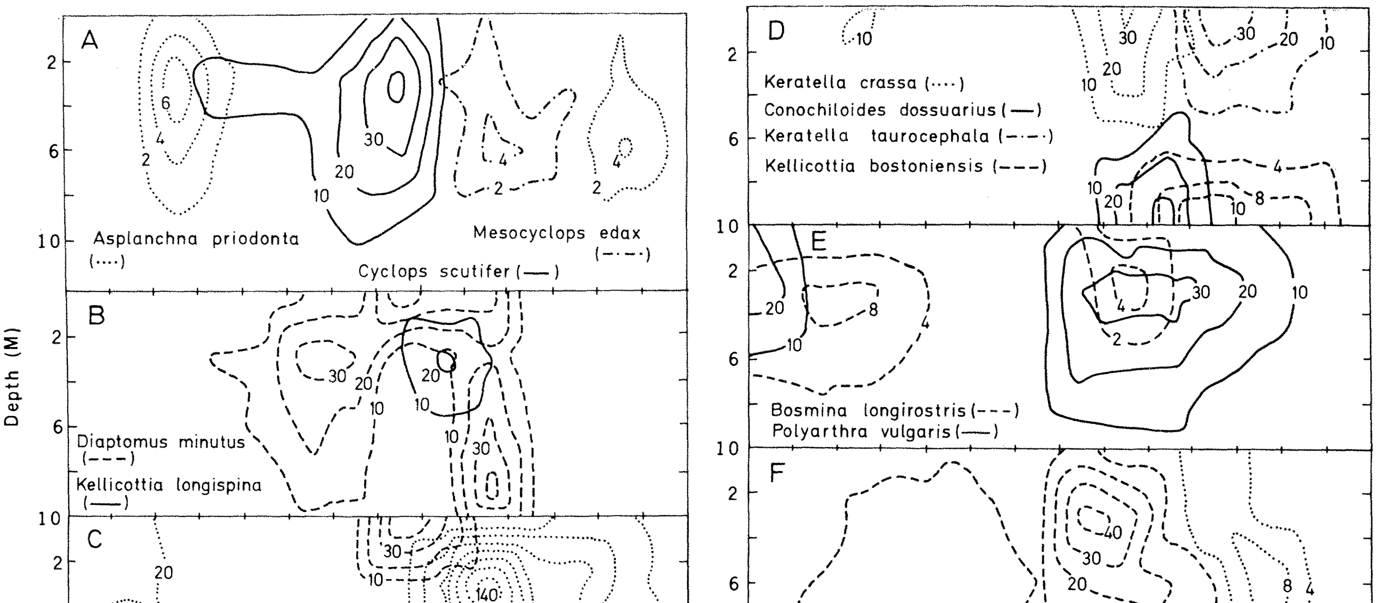

Fig. 1. Population response surfaces of: (A) *Cyclops scutifer, Mesocyclops edax*, and *Asplanchna priodonta*; (B) *Diaptomus minutus* and *Kellicottia longispina*; (C) *Daphnia catawba* and *Holopedium gibberum*; (D) *Keratella crassa, Conochiloides dossuarius, Keratella taurocephala*, and *Kellicottia bostoniensis*; (E) *Bosmina longirostris* and *Polyarthra vulgaris*; (F) *Keratella cochlearis* and *Conochilus unicornis*. Isolines are drawn from mean monthly production values (in micrograms of dry weight per liter per month) measured at 0, 3, 6, and 9 m.

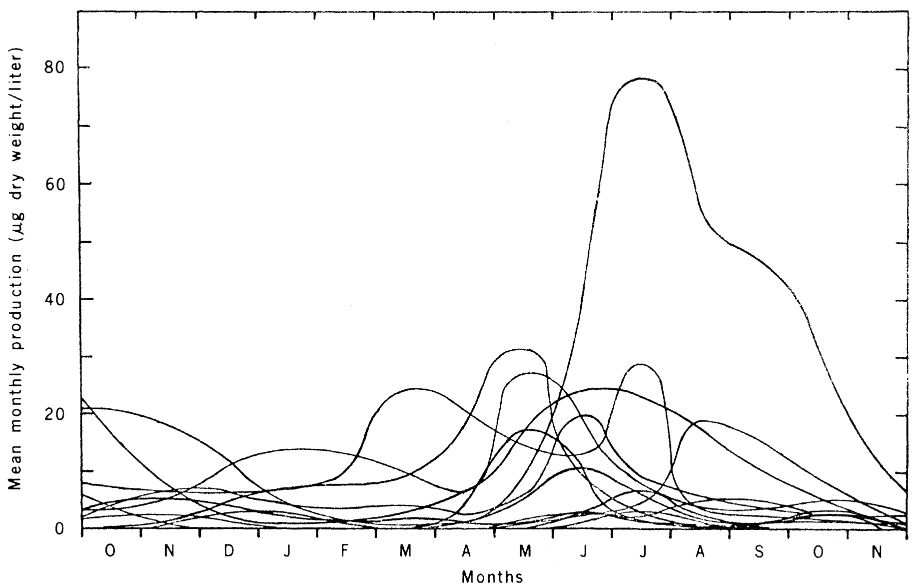

Fig. 2. Distribution of zooplankton populations in Mirror Lake along the complex gradient of season.

ochiloides dossuarius* are distinctly separated into the top 2 m of the lake and into the hypolimnion (Fig. 1D) (*15*). The response surface of the remaining rotifers would lie in the strata of water between 2 m and the hypolimnion, if no food selectivity were involved. This is the case with the remaining microconsumers. The adaptive center of *Conochilus unicornis* (Fig. 1F) is generally located in the metalimnion in September, whereas *Kellicottia longispina* (Fig. 1B), *Keratella cochlearis* (Fig. 1F), and *Polyarthra vulgaris* (Fig 1E) are at 3 to 6 m in the spring and early summer.

The niche centers of *P. vulgaris* and *K. cochlearis* do overlap. However, their niches may be separated by virtue of differences in feeding behavior. Edmondson (*16*) has demonstrated that the abundance of the alga *Chrysochromulina* is reflected in the reproductive rate of *Keratella* but not of *Polyarthra*. *Polyarthra*'s reproductive rate increased with the abundance of the larger alga *Cryptomonas*. Sachse (*17*) also concluded that *Polyarthra* sp. feed mainly on *Cryptomonas*. Edmondson's study strongly suggests that *P. vulgaris* and *Keratella cochlearis* are feeding on organisms of different sizes. Even though the niche hypervolumes do overlap in Mirror Lake, they are apparently separated by a division of food (size) resources.

Edmondson (*16*) did not find any difference in feeding behavior between *Kellicottia longispina* and *Keratella cochlearis*. Any separation of niche would have to arise by some other mechanism. In Mirror Lake these two species are separated by time, space, and different types of vertical migration (Fig. 1, B and F).

One would not expect a difference between rotifers of the same genera in the size of food selected. However, Pejler (*18*) has suggested that differences in the size of rotifers are reflected in the size of the animal's food; that is, the larger the rotifer, the larger its food source. Bērzinš (*19*) used this hypothesis to define the niches of many of the species of *Polyarthra* found in Lake Skärshultsjön, Sweden. Although there are significant differences in the lengths of the three species of *Keratella* and two species of *Kellicottia* in Mirror Lake, it is not necessary to invoke size selectivity to explain their niches. Each species is separated from the other simply by time and space.

Bosmina longirostris (Fig. 1E) ingests particles in the same size range as the other Cladocera but feeds most intensively on particles in the size range 1 to 3 μ, which is also the optimum food range of rotifers. Thus, *Bosmina* does not fit into the arbitrary distinction between macro- and microconsumers but is adapted to a niche intermediate with (and overlapping broadly with) these groups. The degree of overlap of niches and the weak population (production) response of *B. longirostris* are probably reflections of intense competition between *B. longirostris* and the other herbivores in the lake. In the winter when *Daphina* and *Holopedium* are not present in the plankton, *B. longirostris* has a higher standing crop than in the summer. Moreover, a higher standing crop of *B. longirostris* is particularly evident in winters when the food supply is high.

Species populations of zooplankton are thus scattered in the niche hyperspace (*20*). However, the responses of the species to particular environmental variables may overlap broadly. Part of this overlap could be due to niche differences not presented in this treatment, such as vertical migration and kind of food (for example, animal versus plant versus dead material). Even so, overlap is not a contradiction of the exclusion principle; some overlap is to be expected, as in the formulation of May and MacArthur (*21*). Niche differentiation is revealed not in sharp boundaries between competing species but in relative differences in the locations of species centers in the niche hyperspace.

The overlapping curves together form a community continuum in time (Fig. 2) and depth. Certain species seem to have the modes of their distributions grouped together along the temporal complex gradient. This grouping of populations is apparent and not real. If another dimension, depth, were considered, a series of population surfaces overlapping with one another, but with no two distributions alike, would be evident. The finding parallels Ramensky's (*22*) and Gleason's (*23*) concepts of species individuality and community continuity. The niche structure of the zooplankton community should be conceived as an intensive or intracommunity population continuum corresponding to the niche hyperspace. In its continuity and the dispersion of species centers this intracommunity population structure is analogous to the extensive or intercommunity population continuum formed by communities in relation to habitat gradients (*24*).

The division of niche hyperspace now apparent in zooplankton of Mirror Lake is a result of predation, competitive displacements, and possible extinctions of species in the past. Competition among species certainly still exists. However, competition is reduced by the fact that the species select food of various sizes and by the partial separation in space and time of each species' niche response. In general, the limnetic zooplankton community of Mirror Lake can be conceived as a system of interacting populations whose adaptive centers have evolved toward dispersion in relation to the complex gradients of food size, depth, and time.

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Vespula squamosa: A Yellow Jacket Wasp Evolving Toward Parasitism

Abstract. *Evidence from behavior and from nest architecture implicates* Vespula squamosa *as a temporary, apparently facultative social parasite of* V. maculifrons. *Analysis of 66* V. squamosa *nests collected in northern Georgia revealed that 54 were initially built by* V. maculifrons. *Three very young* V. maculifrons *nests, each with a* V. squamosa *queen and workers of both species, confirmed the parasitic propensity.*

Social parasitism, in which the young of one species are actively raised by another, has arisen repeatedly among such divergent animal groups as birds and insects. It is widespread in the eusocial Hymenoptera, particularly among the ants, among whom it occurs repeatedly in quite unrelated stocks; among eusocial wasps, however, only four genera are known to contain social parasites (*1, 2*). Among the three dozen species of socially parasitic wasps, most have a relationship involving obligatory and permanent coexistence between intruder and host; the parasite queen usurps the host queen's position but produces no worker caste and depends on host workers to rear her reproductive forms (*3*). However, this common and rather extreme form of parasitic dependence (inquilinism) tells us little of the evolutionary pathways by which it was achieved. We now report on a notable exception, a temporary and apparently facultative social parasite—the yellow jacket wasp *Vespula squamosa* (Drury)—that seems to be crossing the evolutionary threshold from a free-living existence to parasitism.

Over most of its range, *V. maculifrons* is sympatric with *V. squamosa*. Although *V. squamosa* is common and widely distributed throughout eastern North America from New York to southern Mexico (*4*), few biological data exist for this species, except for reports of unusual nests and various miscellaneous observations (*5*). The only previous indication of its possible parasitic propensity is the single report that a queen was found in West Virginia in a *V. vidua* (Saussure) nest (*6*). In 1974, however, in collecting 66 *V. squamosa* and 63 *V. maculifrons* (Buysson) colonies from northern Georgia for analysis of nest architecture and population structure, we found evidence that *V. squamosa* queens regularly usurp established colonies of *V. maculifrons*.

A number of characteristics easily distinguish nests of the two species, especially nonoverlapping differences in the size of worker cells, and envelope paper—*V. maculifrons* nests are always tan and of a fragile, flaky texture, but *V. squamosa* makes a much tougher gray paper. In 54 (82 percent) of the outwardly typical *V. squamosa* nests, we found distinguishable central cores of smaller tan cells in the initial worker combs. Remains of a tan, fragile envelope covered the top of the oldest comb (Fig. 1). Supports between combs in the oldest part of the nest had the grainy, brittle, sawdust texture of *V. maculifrons* nests, in contrast to the hard, glossy gray *V. squamosa* supports in the rest of the nest. Typically, the number of *V. maculifrons* cells was low compared with the number of *V. squamosa* cells, which indicated that usurpation occurred quite early in the nesting season. Excluding two unusual nests (*7*), an average of 278 *V. maculifrons* cells (range, 58 to 479) occupied the central core of initial combs of usurped nests, only 1 to 19 percent of the total worker cells ($\bar{X} = 6$ percent).

Direct behavioral confirmation of usurpation was obtained in June 1975, when two *V. maculifrons* nests were discovered into which individuals of both species carried provisions and pulp loads. Upon dissection, one nest the size of a baseball was found to contain 16 *V. maculifrons* workers, 58 *V. squamosa* workers, and a single *V. squamosa* queen, with no trace of the host queen. Cells of the three combs were all small and tan; the predominantly tan nest envelope contained gray bands intermixed in the most recently constructed portions. The smaller second nest that was usurped contained 245 tan cells and harbored seven *V. maculifrons* workers, 35 *V. squamosa* workers, and a single *V. squamosa* queen, again with no trace of the host queen. A third usurped *V. maculifrons* nest, transplanted into an observation nest box, contained an estimated 330 tan cells and harbored only 13 host workers, one newly eclosed parasite worker, and the parasite queen; but again there was no host queen.

The above evidence indicates a socially parasitic existence for *V. squamosa*, in which a fertile overwintered queen searches out and invades an established young colony of *V. maculifrons* and somehow eliminates the host queen. Laying her own eggs within the nest, the *V. squamosa* queen relies on *V. maculifrons* workers to raise her first brood of workers. After a week or so, since no further *V. maculifrons* eggs are being laid, host workers begin to dwindle in number, and eventually a "pure" *V. squamosa* colony results, with parasite workers and finally with reproductives. This relationship is termed temporary social parasitism; the only other vespid wasp at a similar evolutionary level is a hornet, *Vespa dybowskii* Andre, a facultative temporary social parasite of two other Oriental species of *Vespa* (*8*).

While over four-fifths of our *V. squamosa* nests constituted unequivocal cases of usurpation, 12 nests showed no trace of a *V. maculifrons* heritage. These may repre-