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## Resource Partitioning in Summer by Salmonids in South-Central Lake Ontario

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**Abstract.**—During the summers of 1981 and 1982, we studied resource partitioning by stocked lake trout *Salvelinus namaycush*, brown trout *Salmo trutta*, and chinook salmon *Oncorhynchus tshawytscha* by fishing vertical gill nets at six distances from shore in south-central Lake Ontario. The nets were set at depths of approximately 15–45 m (nearshore stations, <4 km offshore) and more than 55 m (offshore stations, 4–24 km offshore). Salmonids were concentrated near shore, where they partitioned available habitat and, thus, food resources. Horizontal habitat was partitioned with respect to distance from shore; vertical habitat was partitioned in relation to temperature and the thermocline. Salmonids foraged for the most available prey items within their habitat. Overlaps in both food use and horizontal habitat use were inversely related to overlap in use of vertical habitat. There was increased habitat separation between sexes for those species caught farther from shore. At the salmonid stocking and prey density levels existing during our study, lake trout, brown trout, and chinook salmon appeared to partition resources and minimize deleterious trophic interactions during thermal stratification.

Sympatric species often partition resources (Schoener 1974; Werner et al. 1977). The manner in which partitioning occurs is important in defining niche dimensions and species interactions (Pianka 1983). For example, differences in resource use are often magnified by interactions between sympatric species (Nilsson 1967). This process of “interactive segregation” is a behavioral phenomenon that is expressed in various ways (Nilsson 1963; Werner and Hall 1979), and may be accomplished through habitat partitioning (spatial or temporal), food partitioning, or both. By comparing resource use of species living sympatrically and allopatrically, one can determine the importance of factors influencing fish distribution.

Since 1970, Lake Ontario has been stocked primarily with five salmonid species. Large numbers of lake trout *Salvelinus namaycush* are stocked in a continuing effort to redevelop a self-sustaining population (Elrod 1983). Stocking of coho salmon

*Oncorhynchus kisutch*, chinook salmon *O. tshawytscha*, brown trout *Salmo trutta*, and rainbow trout *Oncorhynchus mykiss* (formerly *Salmo gairdneri*) supports a sizeable sport fishery. Similar stocking efforts occur in the other Great Lakes, yet little information exists on the interactions of these stocked species. Thus, there is potential for deleterious trophic interactions to affect the reestablishment of a self-sustaining lake trout population.

Elrod (1983) and Christie et al. (1987) noted that juvenile lake trout feed on slimy sculpin *Cottus cognatus*, switching to rainbow smelt *Osmerus mordax* and alewives *Alosa pseudoharengus* as they grow larger. Chinook salmon caught by anglers feed on alewives (Brandt 1986), suggesting that adult lake trout and chinook salmon may compete for food. Although numerous studies of resource partitioning have been conducted on prey fish in the Great Lakes (Evans and Loftus 1987), studies of their predators, the salmonids, have not focused on the partitioning of more than one resource. Given this lack of information, we used vertical gill nets set at six distances from shore to examine patterns of resource partitioning in summer by adult salmonids in south-central Lake Ontario. Data on prey distributions were collected simul-

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taneously with the catch of salmonids. The objectives were to define the dimensions of salmonid niches and to examine predator-prey interactions. From these data, we evaluated the importance of factors influencing salmonid distributions in Lake Ontario.

### Methods

From 1 July to 7 September 1981 and from 2 April to 10 September 1982 (61 sampling dates), we collected salmonids and their prey fish with vertical gill nets fished off the south shore of Lake Ontario near Hamlin Beach State Park, Monroe County, New York. Vertical gill nets were made of panels, 4.9 m wide  $\times$  15 m deep, of either 114- or 140-mm-stretch mesh (salmonid nets) or 25- and 50-mm-stretch mesh (prey fish nets). Panels of equal mesh size were fished either singly or joined end to end to form columns 15, 30, or 45 m deep. Columns of net were suspended from float bars.

Usually, a gang of three vertical nets was set, but on occasion this was doubled to six nets to increase effort. During 1981, a gang contained only salmonid nets; in 1982, it contained two salmonid nets and one prey fish net.

During 1981 and 1982, two gangs of vertical gill nets were generally set three times per week (i.e., six sets), the sets being rotated among three "near-shore" areas. The water depths at the nearshore areas were 15, 30, and 45 m, and the distances from shore were approximately 1, 2, and 3 km, respectively. In nearshore areas, the entire column of water was fished from surface to bottom. In 1982, vertical gill nets were also set at approximately 8, 16, and 24 km from shore ("offshore" areas), where water depths ranged from 56 to 174 m. At the offshore areas it was not feasible to fish the entire water column; however, the 45-m columns of net extended from the surface well into 4°C water of the hypolimnion, where catches were extremely low. During 1981, a 91.4-m-wide  $\times$  2.5-m-deep horizontal gill net (114-mm-stretch mesh) was fished at the bottom near the vertical gill nets to test whether this stratum of water was adequately sampled; in the spring of 1982, horizontal gill nets were also fished close to shore in water 2-8 m deep. Each gill net set started before dusk and lasted 12-28 h.

We recorded depth of capture for all fish and assigned a temperature to each depth from an average of the temperature profiles measured when we set and pulled the nets. After we recorded their

total lengths and weights, salmonids were sexed, and their stomach contents were recorded as percent volume (water displacement method) and frequency of occurrence for each species consumed. We determined percent resource overlap between species by Schoener's (1970) method.

Because we examined densities of fish between divisions along a given niche dimension, as opposed to numbers caught, catch per unit effort (CPUE) was computed as the number of fish caught per square meter of net fished at each 1-m depth or 1°C temperature increment divided by the number of hours fished. For example, when temperature was the variable examined, the catch at a given temperature was divided by the square meters of net fished at that temperature and then divided by the hours fished. This method of determining catch per unit effort was also used for distance from shore, depth below the surface, distance from the bottom, and distance from the thermocline. Large amounts of a vertical gill net may fish depths not representing a species' habitat, and effort would be artificially increased if all the net area were included in calculations of horizontal distributions. Therefore, when calculating catch per unit effort for distance from shore, we counted as effort only the netting that fished "available" habitat, which we defined as depths encompassing two standard deviations of each species' mean temperature of capture.

The 1981 and 1982 data on catch per unit effort were initially examined separately, but the results were almost identical so the data were combined. Analyses of seasonal trends in depth distribution were facilitated by dividing the netting data into six intervals that corresponded with phases of the thermocline formation: 1 April-30 June, 1-15 July, 16-31 July, 1-15 August, 16-31 August, and 1-10 September. We calculated distance from the bottom for those fish caught in nearshore areas, where the entire water column was fished, and summer temperature use for those fish caught after a thermocline (i.e., 1°C change per meter change in depth) had developed. Mean values for a given niche dimension were determined after the catch was adjusted for effort.

### Results

During 1981 and 1982, we caught 207 lake trout, 120 brown trout, 26 chinook salmon, 4 rainbow trout, and 4 coho salmon (total lengths ranged from 330 to 820 mm). Species composition remained the same between 1981 and 1982 (*G*-test

TABLE 1.—Habitat selection by three salmonid species and two prey species in Lake Ontario. Except for distance from shore in spring 1982, all data are from the period of summer thermal stratification in 1981 and 1982 for salmonids and in 1982 for prey. Values are mean  $\pm$  1 SD; sample sizes are in parentheses. Significant differences<sup>a</sup> between species or sexes were determined by *t*-tests; lower case letters indicate  $P < 0.05$  and capital letters indicate  $P < 0.01$ .

Habitat character	Lake trout	Brown trout	Chinook salmon	Rainbow smelt	Alewife
Distance from shore (km)					
Spring 1982	2.6 $\pm$ 3.2(13)	0.1 $\pm$ 0.0(30)	1.0 $\pm$ 0.0(3)		
Summer	1.9 $\pm$ 0.7(191) Z	1.4 $\pm$ 0.7(87) Y	2.8 $\pm$ 1.4(23) x	2.6 $\pm$ 1.9(48)	2.5 $\pm$ 3.4(174)
Males	1.8 $\pm$ 0.7(126) W	1.3 $\pm$ 0.6(31)	2.1 $\pm$ 0.7(12) w		
Females	2.1 $\pm$ 0.5(65)	1.3 $\pm$ 0.6(55)	4.3 $\pm$ 3.1(10)		
Depth of capture (m)	25.4 $\pm$ 8.9(180) Z	14.6 $\pm$ 6.7(83) y	18.3 $\pm$ 7.3(23) X	26.1 $\pm$ 13.5(48) V	6.1 $\pm$ 4.4(174)
Distance above (+) or below (-) thermocline (m)	-7.2 $\pm$ 6.7(144) Z	+3.1 $\pm$ 7.1(81)	+6.3 $\pm$ 7.8(23) X	-15.5 $\pm$ 13.3(48) V	+7.3 $\pm$ 4.2(174)
Temperature selection (°C)	10.1 $\pm$ 2.8(180) Z	13.4 $\pm$ 3.7(83)	14.4 $\pm$ 2.9(23) X	11.1 $\pm$ 3.7(48) V	17.4 $\pm$ 4.3(174)
Distance from bottom (m)	16.2 $\pm$ 14.5(180)	13.5 $\pm$ 11.1(83) Y	26.0 $\pm$ 12.7(23) X	17.2 $\pm$ 13.1(48) V	28.7 $\pm$ 12.5(174)

<sup>a</sup> Significant differences: Z,z = lake trout versus brown trout; W,w = males versus females; Y,y = brown trout versus chinook salmon; V,v = rainbow smelt versus alewife; X,x = chinook salmon versus lake trout;

= 5.1,  $P > 0.10$ ; Sokal and Rohlf 1981). Analyses of resource use were largely limited to lake trout, brown trout, and chinook salmon because few rainbow trout and coho salmon were caught.

#### Horizontal Habitat

In spring 1982, before Lake Ontario thermally stratified, salmonids occupied nearshore areas (Table 1). Brown trout were the closest to shore of these species, in water less than 5 m deep; chinook salmon were at intermediate depths and lake trout at deeper nearshore areas. Two rainbow trout were captured during this time in 3 m of water. Only two salmonids (lake trout) were caught offshore before thermal stratification occurred.

During thermal stratification, 92% of the chinook salmon and all lake trout and brown trout were captured in the three nearshore areas (Figure 1), as were two rainbow trout and four coho salmon. Although nets were fished at the deeper offshore stations in 1982, mean distance from shore where fish were captured remained the same as it was in summer 1981. Extensive netting efforts in the offshore area captured few salmonids. Within the relatively shallow nearshore areas, the species partitioned habitat (Figure 1). Brown trout occupied the areas closest to shore (particularly area 1), and first lake trout and then chinook salmon were centered farther offshore. Female lake trout and chinook salmon were caught farther from shore than were males (Table 1).

#### Vertical Habitat

Lake trout, brown trout, and chinook salmon also exhibited significant differences in vertical habitat selection (Table 1). Although vertical distributions were wide (depths of capture ranged from 1 to 46 m), there were seasonal trends (Figure 2). Regression analyses of depth of capture versus seasonal time interval indicated that all three species moved progressively deeper in the water column from 1 April through 15 August ( $P < 0.01$ ). From 15 August through 10 September,

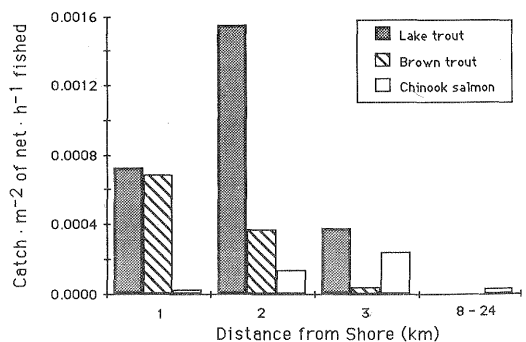


FIGURE 1.—Catch of salmonids per unit effort with vertical gill nets at three "nearshore" areas (1, 2, and 3 km from shore) and at the "offshore" area (8–24 km from shore) in south-central Lake Ontario during the 1981 and 1982 summer periods of thermal stratification. Area 1 = 1 km from shore, 15 m depth; area 2 = 2 km from shore, 30 m depth; area 3 = 3 km from shore, 45 m depth; area 4 = 8–24 km from shore, 56–174 m depth.

lake trout and brown trout moved higher in the water column ( $P < 0.01$ ). Although some chinook salmon also moved up in the water column during this time period, the overall trend was not significant ( $P > 0.05$ ). Low  $r^2$  values (0.18–0.62) indicated that seasonal time intervals were not always good predictors of depth distribution.

Thermal stratification was evident by early July. On a daily basis, temperatures within and about the thermocline were relatively stable. The mean width ( $\pm$ SD) of the thermocline was  $4.5 \pm 1.6$  m. As the thermocline moved progressively deeper through late August, depths selected by salmonids also increased (Figure 2).

Lake trout (94%) were found in or below the thermocline (Figure 3), whereas most brown trout (70%) were caught either in or within 5 m of the thermocline, and most chinook salmon (82%) were in or above the thermocline. Although brown trout and chinook salmon distributions did not differ significantly in relation to the thermocline, they were significantly different from those of lake trout. The only significant differences between sexes in distribution around the thermocline were for male (mean,  $+0.5 \pm 5.2$  m) and female (mean,  $+11.3 \pm 5.1$  m) chinook salmon ( $t = 5.28$ ,  $P < 0.001$ ; + indicates distance above the thermocline). The four coho salmon were captured 1–2 m below the thermocline and the one rainbow trout was captured 2 m above the thermocline.

As expected, trends in mean temperature of capture (Figure 4) closely paralleled the trends in distribution around the thermocline. Chinook salmon were captured at the same temperatures as brown trout, whereas lake trout occupied cooler water (Table 1). Most lake trout (71%) were at 8–12°C, whereas brown trout (23%) exhibited a peak at 13–14°C. Chinook salmon did not exhibit a sharp peak in temperature selection; however, as would be predicted from the thermocline data, male (mean,  $13.4 \pm 2.6^\circ\text{C}$ ) and female (mean,  $15.9 \pm 2.7^\circ\text{C}$ ) chinook used significantly different temperature zones ( $t = 2.36$ ,  $P < 0.05$ ). The four coho salmon were caught at 8–9°C and the single rainbow trout at 18°C.

Salmonid species differed in how closely they were associated with the bottom. Thirty-four percent of lake trout, 31% of brown trout, and only 8% of chinook salmon were caught within 5 m of the bottom. However, all three species ranged up to 40 m from the bottom. On one occasion, when the bottom of our 15-m vertical gill nets fished where the thermocline coincided with the bottom of the lake, 15 brown trout were caught. Twelve

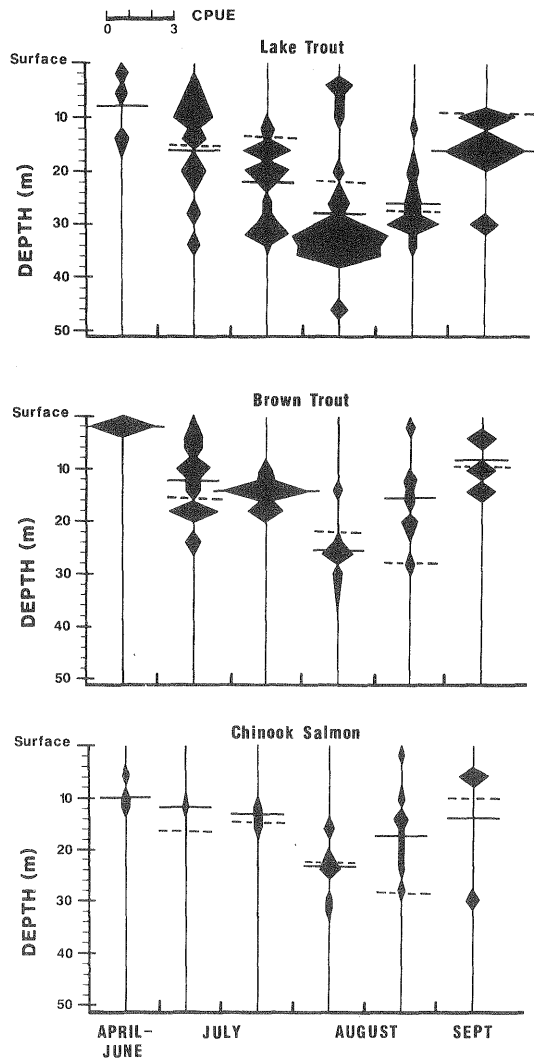


FIGURE 2.—Seasonal catch per unit effort (CPUE) with vertical gill nets in relation to depth for lake trout, brown trout, and chinook salmon during 1981 and 1982 combined, south-central Lake Ontario. The width of the frequency polygons represents catch per unit effort at each 2-m depth interval. Catch per unit effort (scaled upward by  $10^3$  for this figure) = numbers  $\cdot$  m $^{-2}$  of net fished  $\cdot$  h $^{-1}$ . The solid horizontal lines indicate mean capture depth, and the dashed lines mark the mean thermocline depth.

of these fish were caught, with only 10 m $^2$  of netting effort, less than 2 m off the bottom, suggesting that brown trout may concentrate where the thermocline and the bottom coincide. Although they occupied different horizontal and thermal habitats, lake trout and brown trout were captured at similar distances from the bottom, whereas chi-

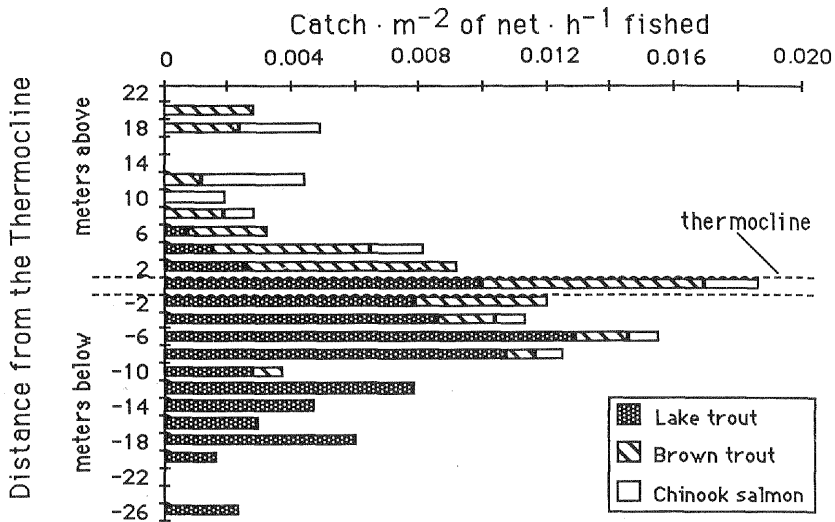


FIGURE 3.—Catch of lake trout, brown trout, and chinook salmon per unit effort with vertical gill nets relative to the distance from the thermocline during the 1981 and 1982 summer periods of thermal stratification, south-central Lake Ontario. The area between the dashed lines represents the thermocline. Depths above and below the thermocline are represented by positive and negative values, respectively.

nook salmon were found at a greater distance from the bottom (Table 1).

#### Diet and Prey Availability

All identifiable stomach contents consisted of rainbow smelt and alewives, except for a sculpin (Cottidae) in one lake trout stomach. Although lake trout ( $N = 207$ ) fed predominantly on rainbow smelt (45% by volume, 36% frequency of occurrence), they also consumed moderate numbers of alewives (19% by volume, 16% frequency of occurrence). Chinook salmon stomachs ( $N = 26$ )

contained exclusively rainbow smelt (47% by volume, 33% frequency of occurrence). Brown trout ( $N = 120$ ) fed selectively on alewives (52% by volume, 36% frequency of occurrence) and little on rainbow smelt (9% volume, 8% frequency of occurrence). Unidentifiable fish remains made up the remaining percentages of stomach contents.

The chief prey species of the salmonids, i.e., alewife and rainbow smelt, also showed habitat separation (Table 1). Alewives were almost entirely epilimnetic (92%), and 58% were captured 7–12 m above the thermocline. Rainbow smelt

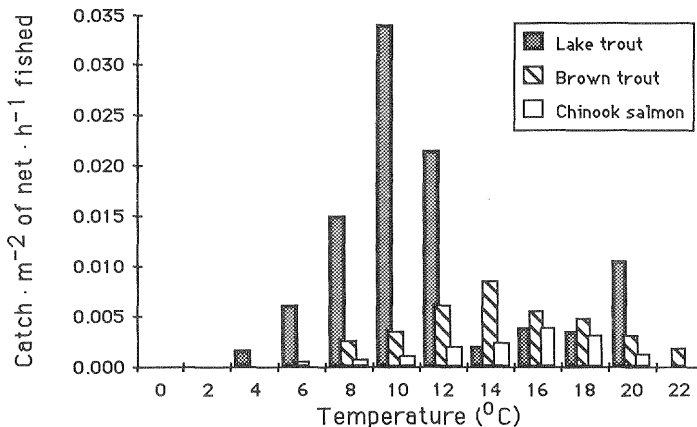


FIGURE 4.—Catch of lake trout, brown trout, and chinook salmon per unit effort with vertical gill nets relative to temperature during the 1981 and 1982 summer periods of thermal stratification, south-central Lake Ontario.

had a bimodal vertical distribution with a peak at the thermocline and one 20–30 m below the thermocline. Catch per unit effort was significantly greater for alewife ( $G$ -test = 22.9,  $P < 0.001$ ) and rainbow smelt ( $G$ -test = 4.2,  $P < 0.05$ ) in near-shore than offshore areas.

#### *Resource Overlap*

By comparing the degree to which the niches of the salmonids overlapped, we determined that percent overlap in horizontal distribution and food use was inversely related to percent overlap in vertical distribution. Chinook salmon and brown trout used similar vertical habitats (78% overlap) but were segregated based upon food types (15% overlap) and horizontal habitats (33% overlap). In contrast, lake trout and chinook salmon had a relatively high degree of overlap with respect to horizontal habitat (54%) and food types (70%) but lower overlap in vertical habitats (39%). Brown trout moderately overlapped lake trout on all three axes (45% food, 52% horizontal habitat, 50% vertical habitat).

#### **Discussion**

In south-central Lake Ontario, brown trout behavior during our study was consistent with that determined in prior research (Thorpe 1974; Svardson 1976), in which brown trout were most abundant in the shallow littoral zones of lakes. Similarly, earlier work showed that lake trout often occupy relatively deeper areas (Martin 1952; Galligan 1962; Dryer 1966; Lichorat 1982), and chinook salmon lead a pelagic existence farther from shore (Harden Jones 1970). Because these behavior patterns are commonly exhibited by these species in a wide variety of aquatic systems, it is likely that the mechanisms that elicit them are innate.

In our study, temperature preference appeared to be one of the more important innate mechanisms for habitat partitioning. Evidence that temperature is an ecological resource that can be partitioned by fish has been provided by Magnuson et al. (1979). Despite interlake differences in depth distribution and food use, lake trout are commonly most abundant in 8–12°C water (Martin 1952; Galligan 1962; Lichorat 1982; this study). In studies where lake trout were occasionally found in warmer water, the fish were believed to be making temporary excursions in pursuit of prey (Martin 1952; Galligan 1962). Brown trout, similarly, often select 13–14°C water (Coutant 1977; Reynolds and Casterlin 1979; this study). Although chi-

nook salmon are comparatively more eurythermal (Favorite and Hanavan 1963; Coutant 1977; Lichorat 1982; this study), they are often found either in or just above a thermal gradient. In the absence of a thermocline, chinook salmon increase their depth selection (Hasler 1971).

Given preferred thermal conditions, lake trout (Fry 1953; Dryer 1966) and brown trout (Thorpe 1974) tend to associate more closely with structures than do chinook salmon (Favorite and Hanavan 1963), helping to define resource partitioning further. The degree of association with structures is likely linked to different body forms and feeding behaviors of these species (Kalleberg 1958; Scott and Crossman 1974). In those areas of Lake Ontario that we sampled, the predominant habitat structure available was a gradually sloping bottom. Therefore, if brown trout and lake trout were to maintain an association with structure, while still occupying the temperatures discussed previously, they should be, as we found, relatively closer to shore than chinook salmon. Note that large proportions of the lake trout and brown trout populations were far from contact with the bottom, which may indicate the limited amount of structure available in an open environment like Lake Ontario.

Because fish often use habitats in which they are able to optimize yield of prey per effort expended foraging (Werner and Mittlebach 1981; Haraldstad and Jonsson 1983), it is likely that prey distributions influenced the concentrated use of near-shore areas by the salmonids in south-central Lake Ontario. All other factors being equal, a forager's yield per effort (MacArthur 1972) should be enhanced in areas of greater prey abundance. Our data indicate that, during thermal stratification, the major prey items (i.e., alewives and rainbow smelt) are most abundant in nearshore areas (Olson 1984).

In Lake Ontario, lake trout and brown trout distributions coincided closely with the distributions of their prey. In other lakes, these salmonid species tend to have diverse diets, yet they commonly use habitats similar to those they used in Lake Ontario (Scott and Crossman 1974). Therefore, we suggest that the lake trout and brown trout in Lake Ontario were consuming those prey most abundant in their habitats, rather than selecting habitats based upon prey preferences.

Surprisingly, chinook salmon ate rainbow smelt despite the epilimnetic preference of alewives that should have made these prey more available to the predator. A closer analysis indicated that ale-

wives declined in abundance with increasing distance from shore and decreasing water temperatures (Olson 1984). Although rainbow smelt were less abundant, their CPUEs peaked in cooler water and in areas farther from shore than those of alewives. In addition, the bimodal vertical distribution for rainbow smelt suggests that they may migrate up in the water column at dusk (Ferguson 1965), at which time they would become vulnerable to predation by chinook salmon. More recently, chinook salmon caught by anglers were feeding largely on alewives (Brandt 1986). This apparent switch in diet may reflect a recent decline in rainbow smelt numbers (Christie et al. 1987) or different sampling techniques.

In studies showing that interspecific resource overlap indices were inversely related, the correlation was often attributed to interspecific competition (Shoener 1974; Crowder et al. 1981). Although we found an inverse correlation between resource overlap indices for salmonids in south-central Lake Ontario, we deduced that, in this case, it was not a good indicator of competition because the resource partitioning could be almost entirely accounted for by intrinsic preferences and the recent independent evolutionary histories of these species. At the salmonid stocking and prey density levels that existed during our study, lake trout, brown trout, and chinook salmon appeared to partition resources and minimize trophic interactions during thermal stratification by means of previously evolved morphological and physiological traits.

Given our observations that salmonids concentrate in nearshore areas in south-central Lake Ontario, future consideration should be given to habitat limitations. At stocking levels of over  $8 \times 10^6$  salmonids/year in 1984 and 1985 (Brandt 1986), we conservatively estimate that 2,300 salmonids were stocked annually per square kilometer of surface area in our nearshore areas. This estimate includes large areas of water that have temperatures during the summer above salmonids' thermal needs. Thus, space could become a limiting factor for survival in Lake Ontario. In addition, because brown trout tend to be antagonistic and territorial (Kalleburg 1958; Nilsson 1963, 1967), they may in effect further reduce the amount of habitat available to conspecifics and other species, perhaps diminishing the prospect of redeveloping a self-sustaining lake trout population. Fishery managers should attempt to match stocking quotas to community structure as well as to angling demands, recognizing that brown trout concen-

trate as close to shore as temperature permits and that all three salmonid species are using nearshore areas.

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