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HABITAT SHIFTS AND BEHAVIOURAL INTERACTIONS
BETWEEN SYMPATRIC AND EXPERIMENTALLY ALLOPATRIC
CUTTHROAT TROUT AND DOLLY VARDEN CHAR

by

JOYCE H. ANDREW

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Department of Zoology

The University of British Columbia
1956 Main Mall
Vancouver, Canada
V6T 1Y3

Date 22 January 1986

ABSTRACT

The role of competition in structuring a lacustrine community of two salmonid species, cutthroat trout (Salmo clarki Richardson) and Dolly Varden char (Salvelinus malma Walbaum), was investigated in three coastal B.C. lakes. Habitat utilization of both species alone (allopatric) and in coexistence with each other (sympatric) was determined by gill netting at depth contours from lake surfaces to bottoms such that littoral, epipelagic, pelagic, and epibenthic habitats were sampled. From June to October, trout utilized mainly surface habitats (littoral and epipelagic) in sympatry and allopatry. Char utilized all habitats in allopatry, and exhibited generalist feeding behaviour by opportunistically utilizing different habitats as prey abundance varied between sampling periods. However, in sympatry, char shifted to deeper habitats not occupied by trout. In sympatry, trout and char were spatially segregated with depth. However, temporal segregation was not pronounced. The habitat shift by char supports an hypothesis of competition between sympatric trout and char for habitat resources, where competition acts more strongly on char. However, food abundance partly explained patterns in fish distribution.

The hypothesis that habitat segregation between sympatric trout and char is based on behavioural interactions was investigated in laboratory experiments. There were changes in the type and intensity of interaction between trout and char with irradiance level that were consistent with their

distribution and depth of habitat. At high irradiance levels such as occur in surface habitats, trout were more aggressive to char than at low irradiance levels. In sympatry with trout, char may seek refuge from aggression by trout in deeper habitats with lower irradiance levels. The feeding performance of char in interspecies pairs dominated by trout increased with decreasing intensity of behavioural interactions. However, the feeding performance of these char did not improve at low irradiance levels, presumably because char continued to display subordinate behaviours while confined in an aquarium with dominant trout. Whether the shift to deeper habitats by lake-dwelling sympatric char is a result of interference mechanisms is not clear. However, an hypothesis involving an interactive mechanism of segregation and interference competition along irradiance level gradients cannot be rejected by this study.

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1.0 INTRODUCTION

The continuing debate during the past twenty years over the role of interspecific competition in structuring animal communities has remained largely unresolved (Connell 1983, Roughgarden 1983, Simberloff 1983). A great deal of research has focused on testing the 'competitive exclusion principle', which states that two non-interbreeding populations occupying the same niche cannot coexist indefinitely (Harden 1960). Either one species will become extinct locally (Hutchinson 1957), or ecological differences between the species will be magnified and the two species will segregate into different niches. Interspecific competition determines the number of species that can coexist at stable population levels in an area, and limits the similarity of competing species in relation to the abundance and diversity of critical resources (Werner 1977). Therefore, interspecific competition is potentially strongest between closely related species because their preferred niches are often similar or overlapping. Niche shifts in food or habitat utilization between species coexisting (sympatric) in one location and separately (allopatric) in different locations are generally considered to produce the strongest evidence supporting the premise that competition influences the structure of particular communities (Zaret and Rand 1971, Schoener 1974a, 1975, Werner and Hall 1976, Connell 1983). The addition or removal of competitors alters niches or abundances by varying levels of competition (Connell 1975, Colwell and Fuentes 1975).

Competition has been implicated as an important selective

force in fish communities (Yoshiyama 1980, Schoener 1983). A number of studies have demonstrated the occurrence of competition between fishes as well as food and habitat partitioning, and temporal segregation (reviews in Schoener 1983, Connell 1983).

Fish species may exclude potential competitors from particular habitats by either depleting food resources (i.e. exploitative competition) or through aggressive interactions (i.e. interference competition). Nilsson (1967) identified two types of segregation - interactive and selective - in fish communities. Interactive segregation implies that ecological differences such as food or habitat selection are magnified through direct behavioural interaction, while selective segregation occurs between species which have evolved differences sufficiently great to be ecologically isolated in their use of one or more critical resources (see also Brian 1956). Many fish species possess a broad repertoire of behaviours (Hoar 1951), and several studies have shown that spatial segregation of species results from interspecific aggression and territorial behaviour of salmonids in streams (Kalleberg 1958, Hartman 1965, Hartman and Gill 1968, Everest and Chapman 1972, Cunjak and Green 1984) as well as other fishes on coral reefs (Low 1971, Myrberg and Thresher 1974). In a review of 164 studies on competition among animals, Schoener (1983) found that territorial competition prevailed among fishes.

Natural sympatric populations of two salmonid species,

Dolly Varden char (Salvelinus malma Walbaum) and cutthroat trout (Salmo clarki Richardson), coexist in Loon Lake, B.C. Individuals from these populations were experimentally segregated in 1974 - 1976 (Hume 1978), thereby creating allopatric populations of cutthroat trout (herein referred to as trout) and Dolly Varden char (herein referred to as char) in Eunice and Katherine lakes, respectively. These allopatric populations are self-sustaining, and several naturally produced generations are now present in these lakes.

Spatial segregation between trout and char in Loon Lake and other nearby lakes was clearly demonstrated by Andrusak and Northcote (1971), Armitage (1973) and Hume (1978). Trout and char segregate with depth, trout inhabiting surface and midwater zones and char occupying deeper water. Evolved differences between these populations have also been demonstrated. Solitary and paired trout and char from natural sympatric populations differ in their orientation in the water column in laboratory studies (Schutz and Northcote 1972) and each is more efficient than the other at feeding on prey items at its own preferred height in the water column (Schutz and Northcote 1972, Hume 1978). There is a major dietary overlap in limnetic zooplankton (Armitage 1973) although trout have higher capture efficiencies on zooplankton species (Hume 1978).

Henderson and Northcote (1985) found that irradiance level is an important factor which determines the success of prey acquisition by trout and char in Loon Lake. Trout are superior at prey detection and foraging efficiency in relatively high

irradiance (e.g. littoral and shallow limnetic habitats) and char are superior at visual detection and chemoreception of benthic and pelagic prey in relatively low irradiance (e.g. diurnal deep water habitats and nocturnal shallow water feeding). Despite evidence that trout were dominant over char in interspecific pairs used in feeding trials (Schutz and Northcote 1972) and in stream aquaria (Rosenau 1978), it has been concluded in previous studies that segregation of lake populations is largely selective rather than interactive. However, as indicated by Henderson (1982), segregation between sympatric trout and char need not always be interactive or selective. Interactive segregation may occur in the early stage of coexistence when trout dominates and outcompetes char for food, but then selective pressures may cause genetic changes in various morphological and behavioural characters, resulting in selective segregation.

There are two major objectives in this study. The first is to determine whether habitat segregation between trout and char in Loon Lake is due to competitive interaction, and the second objective is to determine whether the behavioural interactions between trout and char differed with irradiance level in a way that would support a hypothesis of segregation based on interspecific aggressive interactions. The hypotheses to be tested are as follows:

1. Trout and/or char have undergone a spatio-temporal habitat shift from sympatry to allopatry such that experimentally segregated trout and char occupy more similar habitats than when in sympatry.

This hypothesis will be examined by comparing spatial and temporal habitat uses by sympatric populations in Loon Lake with those of experimental allopatric populations of trout and char (Loon Lake stock) in Eunice and Katherine lakes, respectively. If differences are found, this would suggest that habitat segregation may be due to competition between the two sympatric populations. A habitat shift by only one species would indicate that the species which does not shift is the superior competitor.

Based on the results of the field study reported herein, the following hypothesis will be tested to investigate the possible relationship between irradiance level and the effectiveness of aggressive behaviour by trout in excluding char from habitats:

2. There are changes in the intensity and type of agonistic behaviour between trout and char with changes in irradiance level that are consistent with their distribution with depth in Loon Lake.

This hypothesis will be examined in a laboratory experiment using interspecific pairs of trout and char. If there is a reduction in aggressive behaviours with decreasing irradiance level, low irradiance habitats may provide refugia for char (the inferior competitor, according to the field results reported

herein) if it is able to acquire food resources in these habitats. Therefore, the following hypothesis will be tested:

3. The rate of planktivorous feeding of char (in the presence of trout) is reduced by aggressive behaviour of trout.

2.0 MATERIALS AND METHODS

2.1 Study Area

The present study was conducted in three small, oligotrophic lakes in the University of British Columbia Research Forest (49° 19'N, 122° 34'W), near Haney, B.C. (Figure 1). The lakes are situated in coastal mountain uplands at elevations between 340 m (Loon Lake) and 505 m (Katherine Lake). The surrounding topography is characterized by steep slopes covered by western hemlock forest with stands of alder, birch, and planted Douglas fir (Feller 1975). There are granitic outcrops of quartz iodite in the northern portion of the Research Forest and gradual slopes of forest-covered glacial till in the south (Roddick and Armstrong 1956). The climate is wet and mild (Efford 1967). Eunice and Katherine lakes freeze over in winter but Loon Lake is ice-covered only in occasional winters.

Each of the three lakes is almost entirely surrounded by forest to the water's edge. Loon Lake contains patches of water lily pads (Nuphar polysepalum) along approximately one-fourth of the shoreline, and beds of horsetail (Equisetum fluviatile) and pondweed (Potamogeton spp.) in the littoral zone near the south end of the lake. In Eunice Lake, there are floating mats of bog vegetation along the south shore of the main part of the lake. Similarly to Loon Lake, Eunice Lake contains patches of water lily pads, but also has sparse patches of skunk cabbage (Lysichiton americanum), ferns, and shrubs near the shoreline.

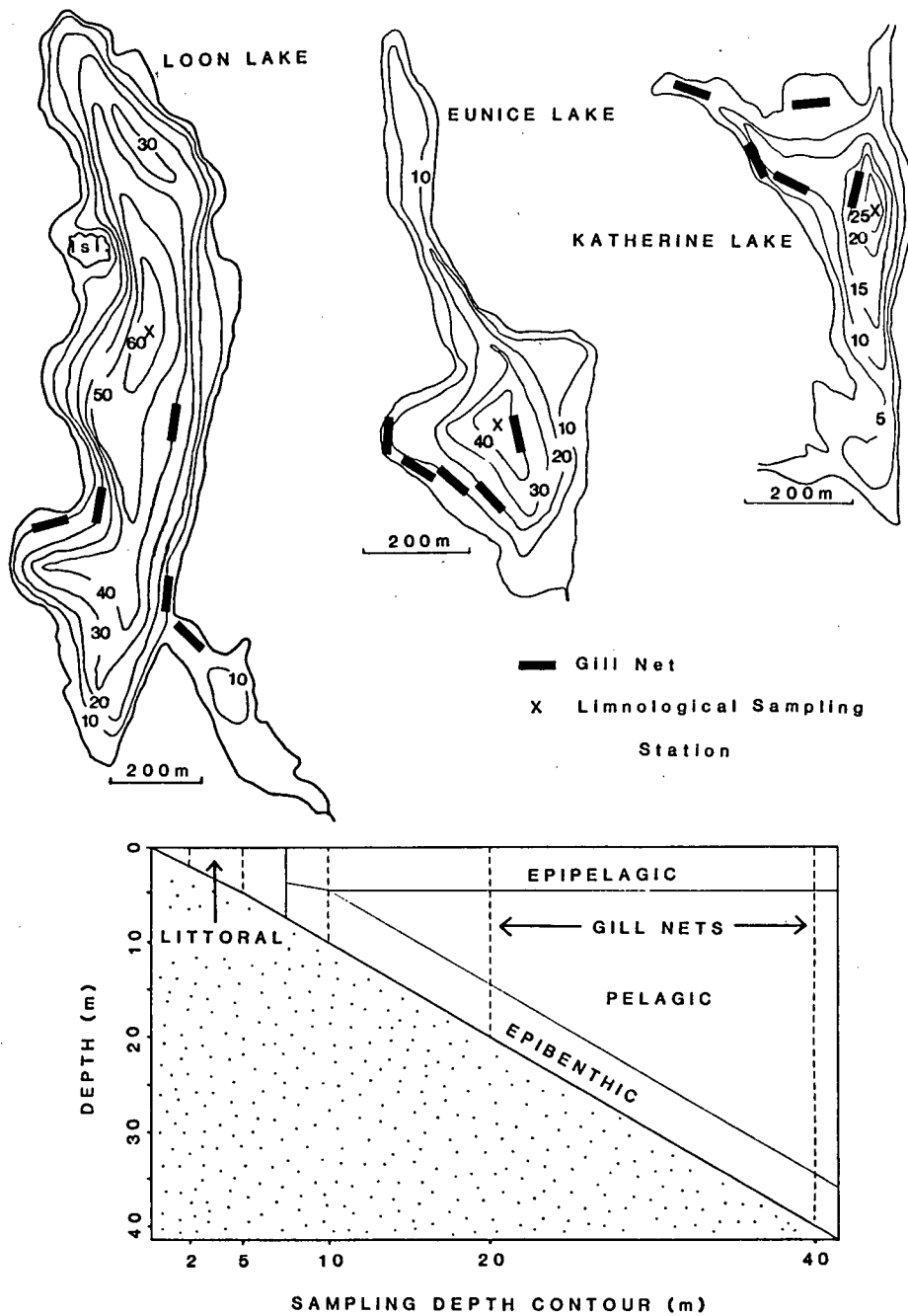


Figure 1. Map of gill net sampling stations and lake habitats used in the analysis of spatial distribution of trout and char in Loon, Eunice, and Katherine lakes, University of British Columbia Research Forest.

Katherine Lake has more abundant growth of aquatic macrophytes in the littoral zone than the other two lakes, especially near its north and south ends. The littoral zone contains patches of grasses and reeds (Graminae), water lily pads, and other submerged vegetation.

Loon Lake contains coexisting native populations of cutthroat trout and Dolly Varden char, but no other fish species. Abundance of adults of these species was estimated by the Schnabel method during the period 1974 - 1976 to be 7300 and 3100 fish, respectively (Hume 1978). Eunice and Katherine lakes were both fishless until 1974. Between October 1974 and June 1976, a total of 1571 cutthroat trout and 881 Dolly Varden char were transplanted from Loon to Eunice and Katherine lakes, respectively (Hume 1978). The numbers transferred were sufficient to assume genetic homogeneity between donor and transplanted stocks (Ryman and Stahl 1980). The transplanted populations reproduced successfully in each of the new lake systems so that by 1982 there could have been up to eight successive year classes recruited to them and at least two generations that completed their entire life cycle within the recipient lakes.

2.2 Spatial and Temporal Distribution

Spatial distributions of fish populations were assessed during three sampling periods in 1982: (1) 22 June to 5 July (hereafter referred to as the June sampling period), (2) 16 to 25 August, and (3) 30 September to 10 October (hereafter referred to as the October sampling period).

Gill Netting

Fish were captured in nylon monofilament gill nets. Each gill net gang was composed of seven 5 m long panels of increasing mesh sizes (20, 25, 31, 38, 44, 51, and 60 mm stretched diagonal mesh). Nets were either 2, 5, or 10 m deep and were marked at 1 m intervals to facilitate determination of capture depth of fish. Sampling stations at Loon and Eunice lakes were located along the 2, 5, 10, 20, and 40 m depth contours, and in Katherine Lake at the 2, 5, 10, and 20 m depth contours (Figure 1). Stations were marked with buoys and retained throughout the study. Gill nets were set during day (8.0 ± 4.5 h) and night (13.5 ± 4.0 h) periods. During each sampling period all stations were sampled from surface to bottom at least twice. At the 10, 20, and 40 m stations gill nets were set successively so that all depths at every station were sampled. For example, at the 40 m station, a 10 m deep gill net was set at 0-10 m, 10-20 m, 20-30 m, and 30-40 m on four sequential days to complete one "day sample". In addition to experimental sampling, an extra set was performed in Katherine

Lake to supplement low August catches. The net was set overnight on the bottom 2 m, the net extending from the shore to deep benthic habitats of the lake.

One potential problem with this sampling design is that catch per unit effort may decrease with repeated sampling at each station. Since each depth was sampled four times (two day and two night sets), day or night catches may be higher if the first sampling was respectively a day or a night set. Day and night catches per unit effort were significantly different for each population in June ($\chi^2=3.84$, $p<.05$, $df=1$), and in three out of four fish populations the greater catch was obtained during the time consistent with first net exposure. However, differences in day and night catches should not affect this part of my study whose purpose was to compare distributions of fish populations and not total catch between lakes. First net exposure may bring about a non-random depletion of the population in the vicinity of each station so that by fishing first at the shallower layers of the water column, the catches at depths of 10 m to 40 m may be reduced, which would bias distributions and make them appear shallower. However, every population was fished in the same manner and distributions therefore would be biased in the same way if such depletions occur.

There are some difficulties in determining fish density and distribution by inference from results of gill net sampling (Andreev 1955), although researchers frequently have used gill nets for this purpose (e.g. Horak and Tanner 1964). Gill nets

are passive sampling devices in that the capture of fish is due to their swimming into the net and becoming gilled and entangled. If fish are more active at certain times of the day or in certain habitats (presumably due mainly to foraging or spawning activity), a higher catch per unit effort will result in that sample. In addition, fish may be able to visually perceive and avoid capture by gill nets better during the day than night. Because the efficiency of gill nets varies with irradiance level and activity of fish, the accuracy of the interpretation of catch per unit effort as "fish density" varies between samples. However, conditions of irradiance with depth and the diel illumination cycle were similar among lakes and habitats, and sampling dates of fish populations. Furthermore, since foraging or reproductive activities are obviously related to the "importance" of habitats to fish, a higher catch per unit effort biased by these activities is indicative of a habitat which is "useful" to fish. In any case, biases in the measurement of catch per unit effort probably were similar for all populations, lakes, and habitats so that comparisons between them would be biased in much the same way.

Fish removed from gill nets were sampled at a field laboratory at Loon Lake. Depth of capture (within 1 m depth intervals) was recorded as fish were removed from gill nets. At the laboratory, species, date and location (lake and station) of capture, fork length (± 1.0 mm), weight (± 0.1 g), sex and state of sexual maturity were recorded. Females with eggs up to pinhead size and males with testes enlarged up to half the body

cavity length were recorded as immature (juvenile) fish. If gonad development was more advanced the state of sexual maturity was recorded as mature (adult), following Dahl (1917). Ages were determined later using otoliths (details in Jonsson et al. 1984).

Limnological Sampling

To test the hypothesis that niche utilization of allopatric and sympatric populations is the same, lake environments should be identical with respect to limnological features, as well as prey types and sizes. Such ideal conditions are rarely if ever met in whole lake experiments. However, to determine whether there were important differences between lakes and seasonal differences within lakes, limnological measurements and sampling of prey types were conducted during each of the three gill netting periods. Temperature, dissolved oxygen concentration, and light penetration profiles were determined at the deepest point of each lake (Figure 1). Temperature and oxygen concentration were measured using a YSI Model 57 meter with a 15 m cable and probe. Measurements of temperature and dissolved oxygen at depths greater than 15 m were obtained using the same apparatus, but water samples were brought to the surface in a 3 l Van Dorn bottle. Light penetration was measured by a standard Secchi disc and/or Licor Model LI-185A light meter.

Invertebrate prey types, densities and distributions were determined by Hindar et al. (in prep.) concurrently with my study and are summarized in Section 3.1.3. Zoobenthos were

sampled with a 9 x 9" Ekman dredge at the gill netting stations in all sampling periods. Five parallel samples were taken at each station. Zooplankton were sampled by diagonal hauls with Clarke-Bumpus gear (0.08 mm net) from the depths 0-5, 5-10, 10-20, and 20-40 m. Surface arthropods were sampled with a net (frame size 30 x 30 cm, 0.2 mm mesh) at distances of 50-150 m towed from the bow of a boat along the shore line and in mid-water (6 samples per lake per month).

Data Analyses

Numerical catch data from the three lakes were used to determine spatial and temporal habitat use of trout and char. The distribution of each species in sympatry and allopatry was compared to determine whether one or both species had undergone a habitat shift. A second test was performed to determine the relative similarity of habitat use by the two species by comparing habitat use by trout and char in sympatry with habitat use in allopatry. An hypothesis of competition predicts that the two species prefer more similar habitats than they occupy in sympatry.

Spatial and temporal distributions of populations were compared using the Kruskal-Wallis extension to two and three factor nonparametric analyses of variance on ranked values (Zar 1984, p.219-222, 249). In the model for analysis of variance (ANOVA), depth is nested in station, because variation in catch with depth is confounded by the sloping lake bottom. For example, the catch at depth equal to 2 m at the 2 m contour has

a benthic influence whereas this component is absent at the same depth at the other stations. To avoid this confoundment, results from gill netting stations and depths were assigned to four habitat zones. The littoral zone included the 2 m and 5 m stations, the epipelagic habitat included the upper 5 m of the 10 m, 20 m, and 40 m stations, and the pelagic habitat included the 5 to 15 m depth zone at the 20 m station and 5 to 35 m depth zone at the 40 m station. Katherine Lake had reduced sampling effort in the latter three habitat zones because it lacked a 40 m contour. A 5 m deep gill net set was considered to be one sampling unit. All samples were corrected to catch per unit effort (individuals captured/100 m² net area/12 h set).

To determine the spatial and temporal distribution of fish populations, catch per unit effort ANOVAs were determined with respect to habitat, time of day, and sampling month. Diel and seasonal movements of fish between habitats were inferred when the relative catch per unit effort in lake habitats changed with time of day or month, respectively. Whether habitat shifts occurred between sympatric and allopatric populations was determined by catch per unit effort ANOVAs of either trout or char with respect to lake (Loon Lake versus Eunice or Katherine Lake), sampling month, time of day, and habitat. Tukey's multiple comparison of means ($p=.05$) was used to determine homogeneous sets of means from ANOVAs (Zar 1984, p.199). Genlin software was used throughout the analyses.

2.3 Laboratory Experiments

Trout and char were collected in May 1984 from experimental allopatric populations (Hume and Northcote 1985) from Eunice and Katherine lakes, respectively. Collections were made with monofilament gill nets of stretched mesh sizes 20 to 60 mm. Despite a relatively high initial mortality in the laboratory, adequate numbers were maintained there for four months before experiments started. The two species were held separately at temperatures seasonally ranging from 6.0 to 12.5 °C in large oval fibreglass aquaria (137 x 78 x 70 cm deep) with flow-through providing water replacement every 2.3 hours. Fish were fed daily rations of chopped chicken liver; some char would not eat liver and were fed Neomysis mercedis, a mysid shrimp. Fish used in the experiments were segregated from the rest of the stock and held individually or in mixed-species pairs for 3-6 days in similar but smaller aquaria with water replacement rates of approximately one hour (112 x 50 x 36 cm deep). These fish were fed ad libitum daily rations of Neomysis mercedis.

Agonistic behaviour of six mixed-species pairs of trout and char was recorded at four irradiance levels. Each pair of fish was considered to be one replicate. Each pair was held for 2-5 days at the highest irradiance level until one fish became "dominant" and the other "subordinate". Based on the results of my field study, trout are superior competitors to char in Loon Lake, therefore only pairs in which the trout was dominant were used in the experiment. Although trout were dominant in eight out of the ten size-matched interspecies pairs used in the

laboratory, there was no significant difference at $p=.05$ in frequency of dominance by trout and char with this small sample size (binomial test, one-tailed, $p=.055$). Since decreased light level was the experimental treatment, the highest irradiance level was the control, and was used to establish baseline levels of aggression. The three levels were then presented in the next three consecutive days. Rather than using different fish pairs at each treatment level, behaviours were recorded for each fish pair at each treatment level. Although this procedure was used to avoid logistical problems, it violated the assumption of inferential statistics of independence of data at treatment levels. To partially circumvent this problem, treatments were presented to fish pairs in random order so that prior experience at other irradiance levels was randomized (Table 1). Fish were allowed at least one day of acclimation to each light level before data on behaviour were recorded. Two trials of 30 minutes duration were performed each day, one before and another after feeding. Trials were conducted between 10:00 and 17:00 PST. Each replicate pair was held in the experimental aquarium until data on behaviour at each light level had been recorded. Following each replicate, fish were anaesthetized in 2-phenoxyethanol and were measured and weighed to verify size-matching of pairs (Table 1).

Pairs were held together in the experimental aquarium prior to treatments until the fish were acclimated to the aquarium and aggression between the trout and char had stabilized (see Section 3.4.1).

Table 1. Fish sizes and order of irradiance level treatments.

Replicate	Pair ¹	Order of Treatments ²	Trout		Char	
			Length (cm)	Weight (gm)	Length (cm)	Weight (gm)
1	T1-C1	I-III-IV-II	24.1	125.0	23.0	112.5
2	T2-C2	I-II-III-IV	22.4	115.0	22.3	98.0
3	T3-C3	I-IV-III-II	25.5	157.5	25.8	156.0
4	T3-C4	I-II-IV-III	25.5	157.5	26.5	175.5
5	T4-C5	I-III-II-IV	24.0	122.5	23.2	108.0
6	T4-C6	I-III-IV-II	24.0	122.5	24.5	114.0

¹T=trout; C=char

²Irradiance level treatments:

I = 3.0×10^{18} photons/m²/s

II = 1.5×10^{16} photons/m²/s

III = 5.0×10^{15} photons/m²/s

IV = 3.0×10^{15} photons/m²/s

During the establishment of dominance and the period of data recording, fish in the experimental aquarium were fed daily rations of 25 live Neomysis mercedis. Neomysis were collected from the Main Arm of the Fraser River, east of the George Massey tunnel. Neomysis were not present in Eunice and Katherine lakes, therefore both species were equally inexperienced with this prey prior to the experiment. Neomysis is a relatively large planktonic or epibenthic invertebrate, and its swimming movements make it a highly visible prey to both trout and char. The mean length of Neomysis used was 11.23 ± 2.76 mm (mean \pm standard deviation) total length (anterior end of carapace to tip of telson), and was not significantly different between samples (F-test, $p > .05$, $F = 2.46$, $df = 4, 115$).

2.3.1 Irradiance Levels

Experiments were conducted in a glass-fronted brown wooden aquarium (118 x 56 x 30 cm deep) with a sand substrate and flow-through providing water replacement every 1.8 h. Water temperature varied seasonally from 9.0 to 13.0 °C. The tank was illuminated by two Vita-lite fluorescent tubes, mounted in a light-proof housing and suspended 50 cm above the water surface. The spectral distribution of Vita-lites approximates that of the sun (Henderson 1982, his Figure 2). The three lower irradiance levels were obtained by sliding a board with a lengthwise 0.64 cm slit under the housing, and placing layers of black cloth over the slit.

The highest irradiance level used (3.0×10^{18} photons/m²/s)

was greater than the saturation irradiance threshold (SIT) of char and near that of trout. The SIT is the minimum quantity of irradiance that maximizes reaction distance to prey (Henderson and Northcote 1985). According to Henderson and Northcote, both species use visual prey detection above the SIT and trout always use visual prey detection. The lowest irradiance level used (3.0×10^{15} photons/m²/s) was at the visual irradiance threshold (VIT) of trout but greater than that of char. The VIT is the maximum quantity of irradiance resulting in zero reaction to prey, below which prey targets are not detected visually (3.0×10^{15} and 7.0×10^{14} photons/m²/s for trout and char, respectively; Henderson and Northcote 1985).

2.3.2 Behavioural Interactions

Several categories of agonistic behaviour, which included both aggression and submission, were recorded (Table 2). Despite improved visibility to the observer using the special video camera, observations at the lower irradiance levels were limited. Therefore, only relatively obvious behavioural acts were recorded to ensure regularity and reliability in recording. More subtle behaviours such as threat postures (e.g. fin raising) were not recorded. Similar procedures were used on inter- and intraspecific pairs as well as solitary fish of both species.

Observations of fish were made from outside the light-proof room which housed the experimental aquarium. For purposes of observation, the aquarium was illuminated with infrared light of

Table 2. Agonistic, swimming, and feeding behaviours recorded in the experiment.

Behavioural Act	Description
A. Aggressive Behaviour	
Charge	Aggressor rapidly darts at body of submissive fish, but aggressor does not chase submissive fish if it attempts to escape.
Chase	Aggressor chases submissive fish down length of aquarium, usually at burst swimming speed.
Nip	Aggressor bites or nips tail or other body parts of submissive fish.
B. Submissive Behaviour	
Avoidance	Submissive fish avoids an aggressive interaction by fast swimming (usually < burst speed) down length of aquarium when the aggressor approaches.
C. Swimming Behaviour	
Swimming activity	Movement in horizontal position in aquarium to a different quartile = one unit of activity. Recorded only during lulls in aggression.
Bottom rest	Occurred in char only; resting on substrate on pectoral and caudal fins.
Diagonal hover	Submissive fish hovers in water column, usually near surface, in a non-horizontal position (approximately 30° angle) with its head up. Fish may be stationary or move forward slowly, but most movements are balancing movements, mainly of the pectoral fins.
D. Feeding Behaviour	
Feeding strike	Rapid forward movement at prey, not necessarily resulting in capture; occurred in feeding trials only.

two incandescent lamps shielded by 12.7 cm Kodak Wratten Series 88A filters. The lamps were placed at an angle on top of the aquarium near the front so as not to block light from the Vitalites. Henderson (1982) found that the mean reaction distances of trout and char were not significantly different in the presence or absence of infrared light when Vita-lite levels were 4.2×10^{17} and 3.0×10^{15} photons/m²/s for trout and char, respectively. However, other fish species can perceive far-red light up to 740 nm (Beauchamp et al. 1979), and there is no evidence that salmonids do not have similar high red sensitivity in sufficient light intensity (R.D. Beauchamp, pers. comm.).

Fish were observed on a video monitor through a Sanyo Silicon Diode video camera (VCS 3000) fitted with a Fujinon T.V. EE 1:1.4 25 mm photomultiplier lens and a Viticon tube which is sensitive to infrared light. Behaviours were recorded on an electronic hand-held event recorder (Observational Systems OS-3).

2.3.3 Data Analyses

The statistical test used to analyze the experimental results was one-way ANOVA for single-factor experiments with repeated measures (Winer 1971, Rodgers 1977). In all ANOVAs, the number of behavioural interactions was transformed using $\log_{10}(\text{behavioural interactions} + 1.0)$ to normalize the Poisson distribution of the data. Minitab software was used throughout the analyses.

3.0 RESULTS

3.1 Study Lake Environmental Conditions

3.1.1 Morphometric Comparisons

Loon Lake is larger and deeper than Eunice and Katherine lakes based on surface area, depth, and volume comparisons (Table 3). Loon Lake has over twice the surface area and volume of either of the other two lakes. The three lakes have similar shoreline development (D_c), which ranges from 1.5 (Eunice Lake) to 2.2 (Loon Lake). However, Katherine Lake has a larger percentage of its surface area formed by littoral zone than does Eunice or Loon Lake (Table 3). Almost one-fourth of the surface area of Katherine Lake is less than 2 m deep, while Loon and Eunice have much smaller littoral zones (7.1% and 10.4% of their surface areas, respectively).

3.1.2 Temperature, Oxygen, and Irradiance Levels

During each of the three sampling periods, all lakes were thermally stratified with well-developed thermoclines (Figure 2). The epilimnial depths were similar for all lakes (Table 3). Maximum epilimnial temperatures were similar in all lakes (approximately 20 °C) during summer but decreased (12-15 °C) and deepened (6.5-8.5 m) during autumn. In October, erosion of epilimnia had begun but fall turnover had not yet occurred.

During each of the three sampling periods, the dissolved

Table 3. Physical and chemical characteristics of Loon, Eunice, and Katherine lakes, University of British Columbia Research Forest.

	Loon	Eunice	Katherine
Elevation (m)	340	480	505
Surface area (ha)	48.6	18.2	20.7
Maximum depth (m)	62	42	29
Mean depth (m)	27.5	15.8	7.5
Volume ($\text{m}^3 \times 10^4$) ¹	1336	288	175
Shoreline development (D_L) ¹	2.2	1.5	1.9
Shallow littoral area (0-2 m) (percent of lake area)	7.1	10.4	24.5
Epilimnion depth in 1982 (m)			
June	5.5	3.5	4.5
August	6.5	6.0	6.0
October	8.5	6.5	7.5
Secchi disc transparency in 1982 (m)			
June	9.3	8.5	9.1
August	8.1	4.0	7.3
October	7.5	-	-
Irradiance extinction coefficient (η)	1.1	1.7	1.4
pH ²	6.4-6.7	6.4	6.6
Color (Pt units) ²	<5	15	10-15
Total dissolved solids (mg/L) ²	32	16	15

¹Hume 1978

²Northcote and Clarotto 1975

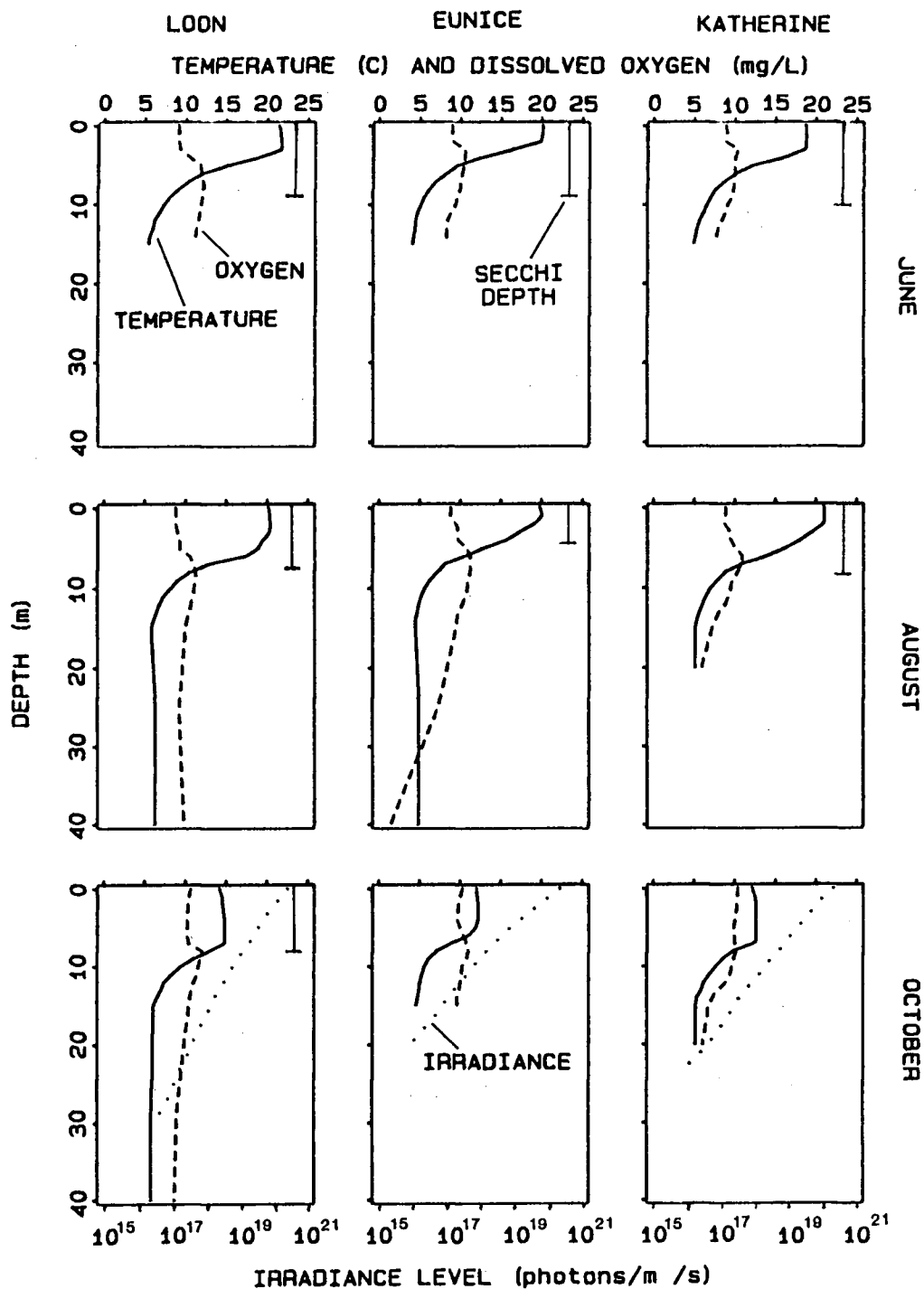


Figure 2. Temperature, dissolved oxygen concentration, and midday irradiance profiles of Loon, Eunice, and Katherine lakes. (Surface conditions in October: 7.53×10^{19} photons/m²/s; flat calm; no cloud)

oxygen profiles of the lakes usually exhibited positive heterograde curves. The only exceptions were Katherine and Eunice lakes in October, where dissolved oxygen concentration decreased with depth. The dissolved oxygen concentration maximum at the thermocline may be a result of decreased solubility of oxygen in the epilimnion due to high summer temperatures, oxygen consumption in the hypolimnion (typical of clinograde reduction with depth), and production of oxygen by phytoplankton at the thermocline (Wetzel 1983). The latter process was probably not important, as dissolved oxygen maxima seldom exceeded 110%. Eunice Lake was anoxic near the sediment in deep parts of the lake during August.

Secchi disc transparencies of the lakes were similar during June (Table 3). In all lakes, water transparency decreased between June and October, perhaps due to accumulated phytoplankton biomass over the growth season. Irradiance profiles in October indicate that light extinction with depth is more rapid in Eunice and Katherine lakes than in Loon Lake (Table 3). However, the pattern of light extinction in the three lakes is typical of coastal oligotrophic lakes.

The study lakes tend to be slightly acidic (pH 6.4-6.7), and Pt values range from <5-15 units (Table 3). Although Loon Lake has approximately twice the total dissolved solids content of Eunice or Katherine lakes, all three lakes are within the low range typical of coastal British Columbia lakes (Northcote and Larkin 1956).

3.1.3 Fish Prey Distributions

The study lakes share similar prey types (Table 4), densities, and distributions (Hindar et al. in prep.). The densities of surface arthropods (mainly winged insects) were not significantly different between the lakes in 1982, and were less than 2 individuals/m² during all sampling periods except Eunice in August and Katherine in October, when both exceeded 4 individuals/m². The proportion of large (≥ 4 mm) surface arthropods was highest in July and in Katherine in October. Limnetic zooplankton densities were highest (9000 - 23000 individuals/m³) at 0-5 m, and decreased with depth in all samples except Katherine in October, when the density was highest at 5-10 m (18846 individuals/m³ at 5-10 m versus 8734 individuals/m³ at 0-5 m). From spring to autumn, densities at depths greater than 10 m (10-20 and 20-40 m sampling intervals) were always higher in Loon (379-4264 individuals/m³) than the other lakes (287-1023 individuals/m³ and 489-1887 individuals/m³ in Eunice and Katherine lakes, respectively). There was a relatively low proportion of large size classes of zooplankton in all lakes in July and in Eunice Lake in August.

The densities of littoral zoobenthos (mainly Hyalella azteca, Pisidium sp., and chironomid larvae) were highest at the 2 m depth contour in October in all lakes (1500 - 2200 individuals/m²). There was a significant increase with depth in the proportion of large (≥ 8 mm) zoobenthos in all lakes except Katherine in July. Profundal zoobenthos was almost exclusively chironomid larvae, and showed density maxima at 40 m in Loon,

Table 4. Zooplankton species in Loon, Eunice, and Katherine lakes.¹

	Loon	Eunice	Katherine
A. Cladocera			
<u>Daphnia rosea</u>	*** ²	***	**
<u>Bosmina longirostris</u>	***	***	***
<u>Holopedium gibberum</u>	**	***	***
<u>Diaphanosoma brachyurum</u>	**	***	**
<u>Polyphemus pediculus</u>	**	**	**
<u>Leptodora kindtii</u>	**	**	-
<u>Ceriodaphnia pulchella</u>	***	*	-
B. Copepoda			
<u>Diaptomus kenai</u>	**	**	**
<u>Diaptomus leptopus</u>	**	**	**
<u>Diaptomus oregonensis</u>	***	-	-
<u>Diaptomus tyrrelli</u>	-	**	**
Cyclopoda	***	**	**

¹Data from Hindar et al. in prep., Hume and Northcote 1985, and Northcote and Clarotto 1975.

²*** very common; ** common; * uncommon; - rare

usually at 20 m in Eunice, and at 10 m in Katherine Lake.

3.2 Length, Weight, and Age of Trout and Char

Size differences between fish in sympatric and allopatric populations were not as pronounced in 1982 as they were in 1976 (Table 5). Trout and char transferred in 1974 - 1976 to Eunice and Katherine lakes, respectively, grew quickly following the experimental transfers to previously fishless lakes with abundant food resources (Hume and Northcote 1985). This conclusion was based on comparisons of length distributions, length-weight relationships, and increases in the growth rates of individual fish from sympatric and allopatric populations. In 1976, the mean lengths of allopatric trout and char (209.9 and 237.2 mm, respectively) were significantly greater than mean lengths of fish in their sympatric donor populations (180.0 and 172.0 mm, respectively; t-tests, two-tailed, $p < .001$; Hume 1978). Six years later, the mean length of allopatric char (197.2 mm) was still significantly greater than sympatric char (182.2 mm; t-test, two-tailed, $p < .001$) although the difference was not so great as in 1976, but the mean length of allopatric trout (165.9 mm) was significantly less than sympatric trout (178.4 mm; t-test, two-tailed, $p < .001$; Table 5, Figure 3). Differences in fish sizes between years may be attributed to the wider range of gill net mesh sizes used in 1982 (20-60 mm) than in 1976 sampling (25-51 mm stretched diagonal mesh).

Since trout and char are native in Loon Lake and have coexisted for centuries, these populations may be assumed to be

Table 5. Comparison of fork length of trout and char captured in Loon, Eunice, and Katherine lakes in 1976 and 1982.

=====						
		Fork Length (mm)			t-Test	t-Test
		-----			Between	Between
	N	Range	Mean	Standard	Lakes	Years
		min,max		Deviation	(df) ¹	(df) ²

A. 1976 (Hume 1978)						
Trout						
Loon	218	111,233	180.0	18.4	7.272*** ³ (430)	
Eunice	214	116,310	209.9	41.8		
Char						
Loon	25	112,217	172.0	24.8	6.957*** (148)	
Katherine	125	134,337	237.2	45.4		

B. 1982						
Trout						
Loon	1066	77,332	178.4	30.1	21.776*** (1981)	.000ns (1282)
Eunice	917	82,270	165.9	26.5		19.311*** (1129)
Char						
Loon	288	96,220	182.2	14.7	5.633*** (678)	3.105** (311)
Katherine	392	100,323	197.2	43.4		8.861*** (515)
=====						

¹H₀: Mean length in experimental lakes = mean length in Loon Lake

²H₀: Mean length in 1976 = mean length in 1982.

³*** p≤.001; ** p≤.01; * p≤.05; ns=not significant p>.05

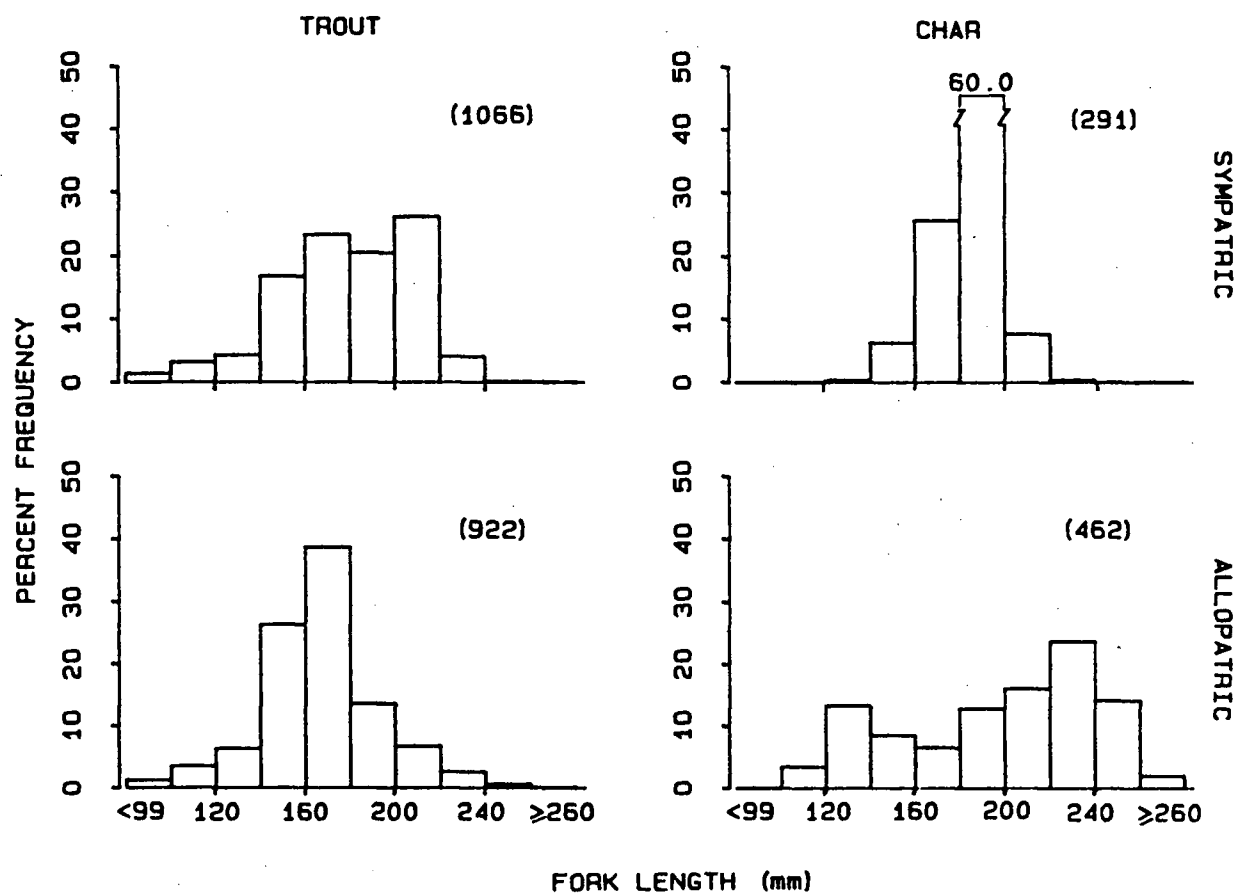


Figure 3. Length frequency distribution of trout and char captured from Loon, Eunice, and Katherine lakes. (Sample sizes are shown in parentheses.)

stable, and the Malthusian parameter (r) equal to zero (Jonsson *et al.* 1984). The mean length of trout in Loon Lake did not differ significantly between 1976 and 1982 (t-test, two-tailed, $p > .05$), but that of char was significantly longer in 1982 (t-test, two-tailed, $p < .01$). The result for char, however, is questionable due to the relatively low sample size in 1976 ($n=25$). The mean lengths of allopatric trout and char in 1982 were significantly shorter than those in 1976 (t-tests, two-tailed, $p < .001$).

Sympatric trout and char captured in 1982 had the same patterns of length versus weight as those captured in 1976. Functional regression of the logs of weight and length (Ricker 1973) of 1982 Loon trout resulted in a slope which overlapped the 95% confidence limits of the length-weight relationship for 1976 (slope = 2.73 ± 0.105 , cf Figure 4). Loon char captured in 1982 also had a length-weight relationship that overlapped the 95% confidence limits of those captured in 1976 (slope = 2.82 ± 0.305 , cf Figure 4). This provided further evidence that the native fish populations in Loon Lake were stable with respect to their length-weight relationship.

Trout and char captured in 1982 ranged in age between 0+ and 12+ years (Figure 5). Fish captured in 1975 - 1976 were determined to be a maximum of age 4+ years using probability paper analysis (Hume 1978), which was corroborated with scale analysis (Armitage 1973). The maximum age of fish between 1976 and 1982 probably did not differ by eight years, but rather the age difference is an artifact of the difference in technique of

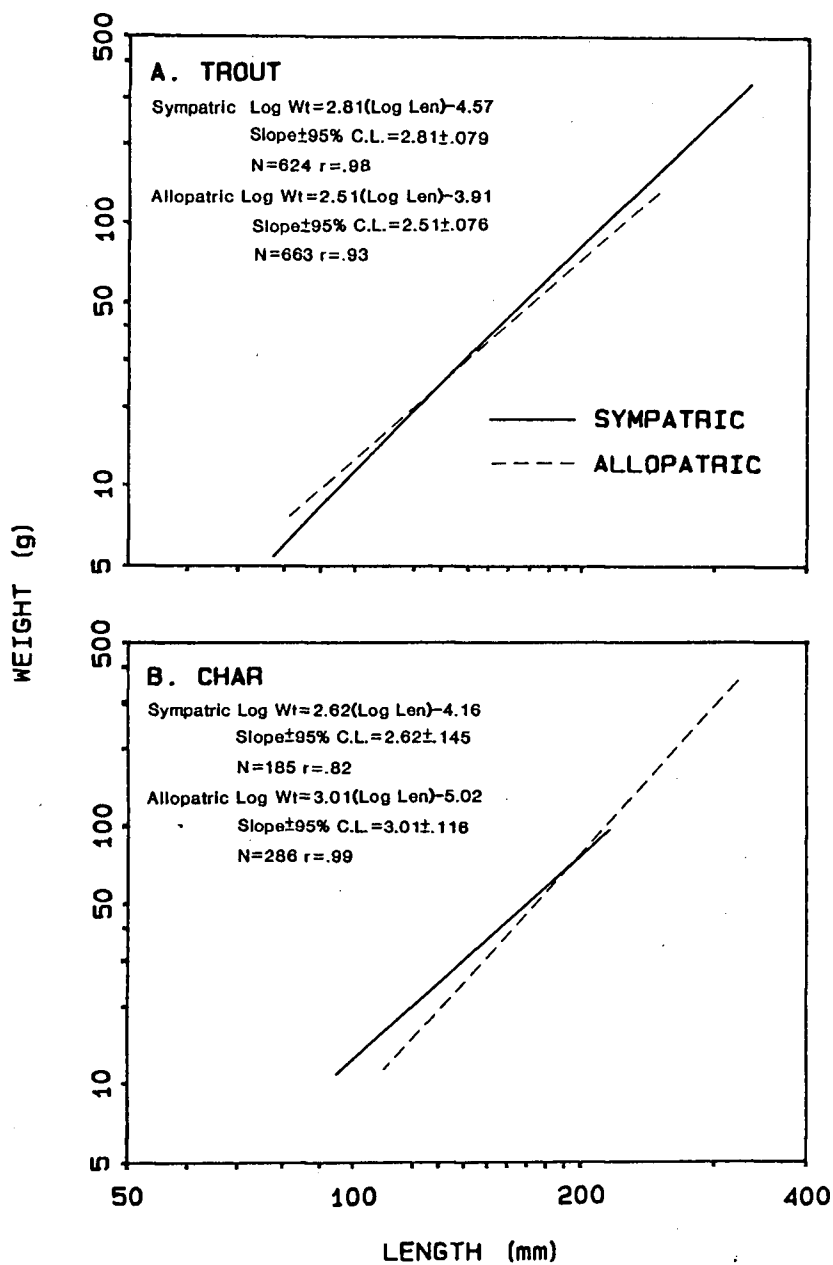


Figure 4. Length-weight relationship and functional regression lines of trout and char from Loon, Eunice, and Katherine lakes. (Data points are omitted for clarity.)

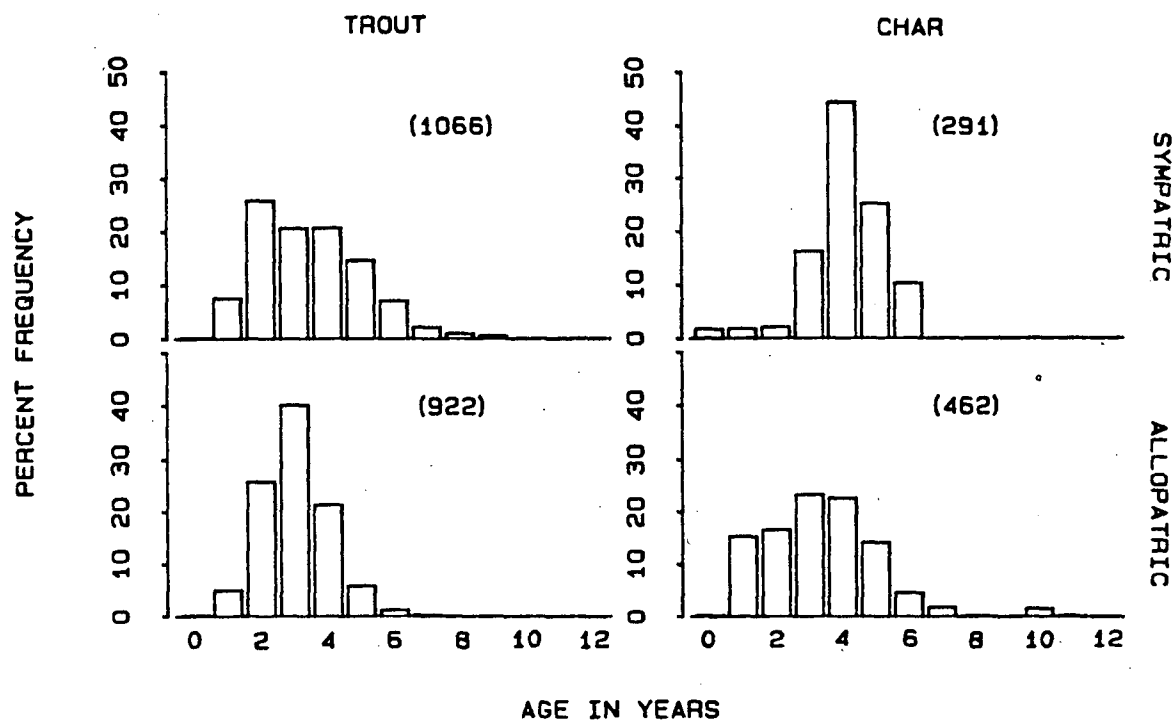


Figure 5. Age composition of trout and char from Loon, Eunice, and Katherine lakes. (Ages were determined using otoliths. Sample sizes are shown in parentheses.)

age determination. Allopatric trout and sympatric char had relatively strong age 3+ and 4+ year classes, respectively (Figure 5). This is also reflected in length distributions (Figure 3) and age-length relationships (Figure 6). Allopatric trout are shorter at a given age than sympatric trout, but allopatric char are longer (Figure 6). There was no significant difference in growth rate between allopatric and sympatric trout, but allopatric char had a faster growth rate than sympatric char (Jonsson et al. 1984, their Table 2).

In 1976, the larger length classes of allopatric trout and char of a given length tended to weigh more than the same species in Loon Lake (Hume 1978). In 1982, this was still true of char, but allopatric trout were not able to maintain the same growth rates in weight throughout the lengths sampled (Figure 4).

3.3 Effects of Coexistence on Spatial and Temporal Distribution

In Tables 6-7 and 9-10, the ANOVA terms that indicate differences in spatial use of habitat and diel differences in habitat use of individual populations are "habitat" and "time*habitat", respectively. Seasonal differences in habitat use and diel movement are indicated by the interaction terms "month*habitat" and "month*time*habitat", respectively. In Tables 8 and 11, the ANOVA terms that provide information on differences in spatial and diel use of habitats between fish populations are the interaction terms "lake*habitat", and "lake*time*habitat", respectively. In Tables 12-13, the ANOVA

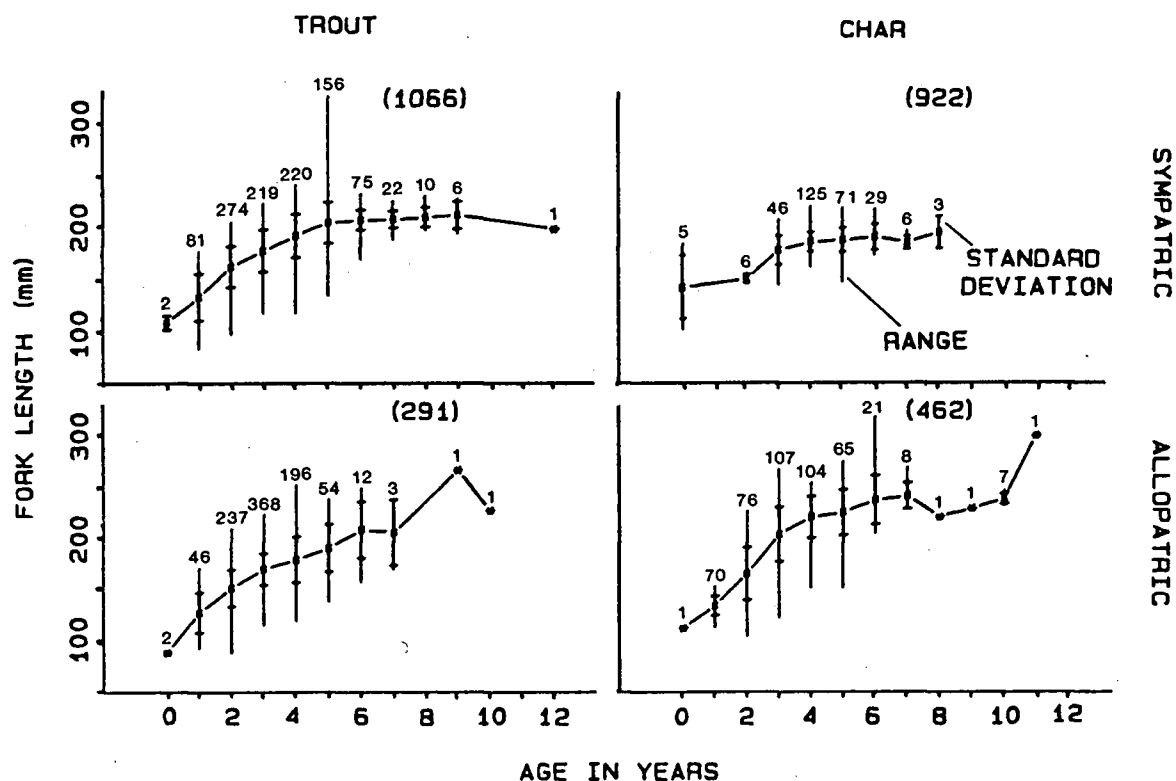


Figure 6. Age-length relationship of trout and char from Loon, Eunice, and Katherine lakes. (Sample sizes are shown on bars. Total sample sizes are shown in parentheses.)

terms that indicate differences in spatial and diel use of habitats between trout and char populations are the interaction terms "species*habitat" and "species*time*habitat", respectively.

3.3.1 Trout

Sympatric Trout in Loon Lake

Sympatric trout mainly occupied depths between 0-10 m from June to October (Figure 7), and were most dense (in the sense that CPUE was highest; see Section 2.2) in littoral habitat, and secondarily in epipelagic habitat, while epibenthic and especially pelagic habitats were little utilized, according to relative CPUEs between habitats (Kruskal-Wallis H-test (herein referred to as H-test), $p < .001$; Table 6). There were no significant diel or seasonal movements between habitats from June to October (H-test, $p > .05$; Table 6). (Movement between habitats is inferred when the relative CPUEs change between day and night (diel) or from month to month (seasonal movement); see Section 2.2). However, there was some evidence of a shoreward movement at night (Figure 7). Trout utilized pelagic habitat to a greater extent in October than during June and August although this trend was not statistically significant (H-test, $p > .05$; Table 6D).

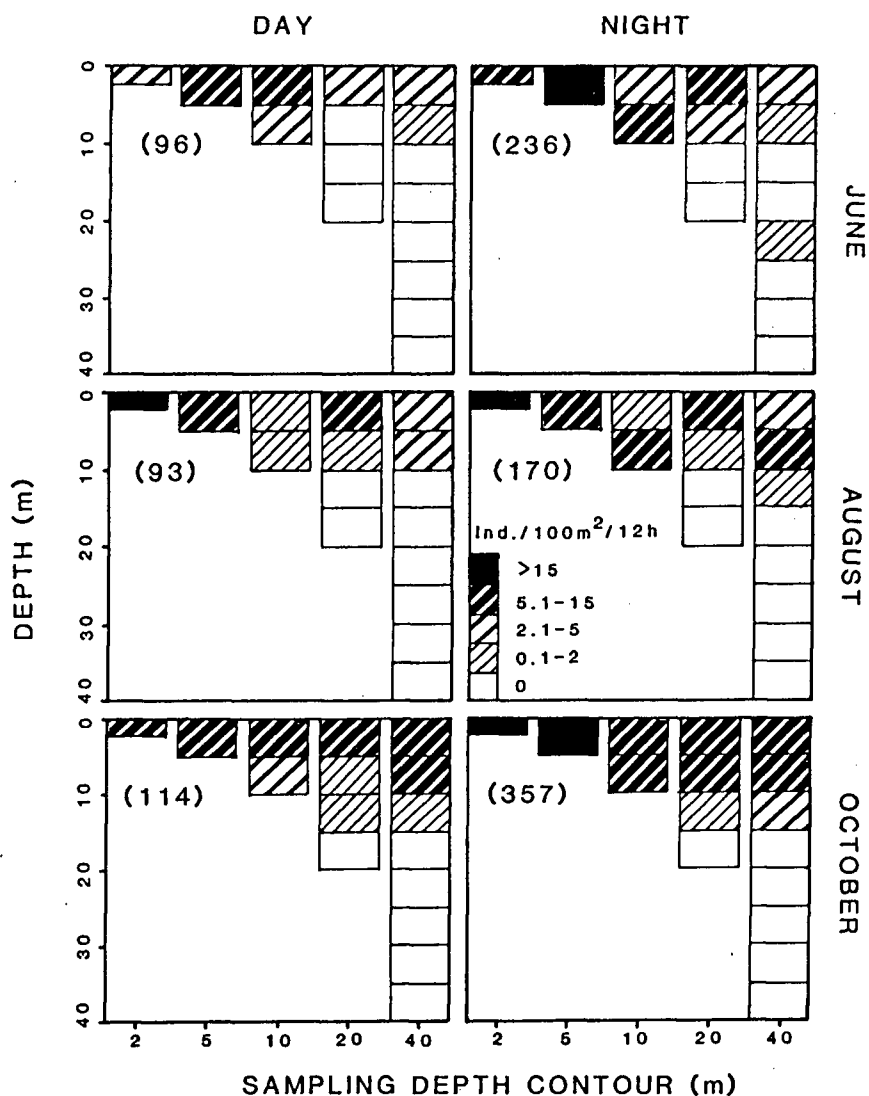


Figure 7. Spatial and temporal distribution of sympatric trout in Loon Lake. (Mean catch per unit effort in 5 m deep gill net sets in units of individuals/100 m² net area/12 h set. Numbers of individuals captured are shown in parentheses.)

Table 6. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Loon Lake sympatric trout by time of day (D=day, N=night), habitat (L=littoral, EP=epipelagic, P=pelagic, EB=epibenthic), and month (J=June, A=August, O=October).

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
=====			
A. June (N=332)			
time of day	2.97, 1	ns ²	ns
habitat	50.52, 3	***	<u>L</u> <u>EP</u> <u>EB</u> <u>P</u>
time*habitat	.93, 3	ns	ns
B. August (N=263)			
time of day	.05, 1	ns	ns
habitat	42.03, 3	***	<u>L</u> <u>EP</u> <u>EB</u> <u>P</u>
time*habitat	.30, 3	ns	ns
C. October (N=471)			
time of day	.91, 1	ns	ns
habitat	39.68, 3	***	<u>L</u> <u>EP</u> <u>P</u> <u>EB</u>
time*habitat	.54, 3	ns	ns
D. Pooled (N=1066)			
sampling month	4.15, 2	ns	ns
time of day	2.93, 1	ns	ns
habitat	117.33, 3	***	<u>L</u> <u>EP</u> <u>EB</u> <u>P</u>
month*time	1.22, 2	ns	ns
month*habitat	3.43, 6	ns	ns
time*habitat	.80, 3	ns	ns
month*time*habitat	.87, 6	ns	ns
=====			

¹Factor levels are listed in descending order of means; homogeneous subsets are underlined.

²*** p≤.001; ** p≤.01; * p≤.05; ns=not significant p>.05

Allopatric Trout in Eunice Lake

From June to October, allopatric trout mainly occupied depths from 0-5 m (Figure 8), and were most dense in epipelagic habitat and secondarily in littoral habitat, while pelagic and epibenthic habitats were little utilized (Table 7). In June, the mean CPUE of trout in epibenthic habitat was higher than in pelagic habitat (Table 7D), but this pattern was not maintained in August or October (Table 7B and C). There were no significant diel or seasonal movements between habitats from June to October (H-tests, $p > .05$; Table 7). In August and October, there seemed to be a shoreward movement to the littoral zone at night (Figure 8), but this trend was not statistically significant (H-tests, $p > .05$; Table 7B and C).

Sympatric versus Allopatric Trout

In August and in all sampling months pooled, sympatric and allopatric trout were distributed differently between habitats (H-tests, $p < .05$; Table 8B and D). Sympatric trout utilized (in order of decreasing CPUE) littoral, epipelagic, epibenthic, then pelagic habitats, whereas allopatric trout utilized epipelagic, littoral, pelagic, then epibenthic habitats. However, both populations were most abundant in littoral and epipelagic habitats, while fewer trout were found in epibenthic and pelagic habitats. In general, the vertical distribution of allopatric trout was more restricted to shallow habitats than that of sympatric trout. There was no difference in diel patterns of

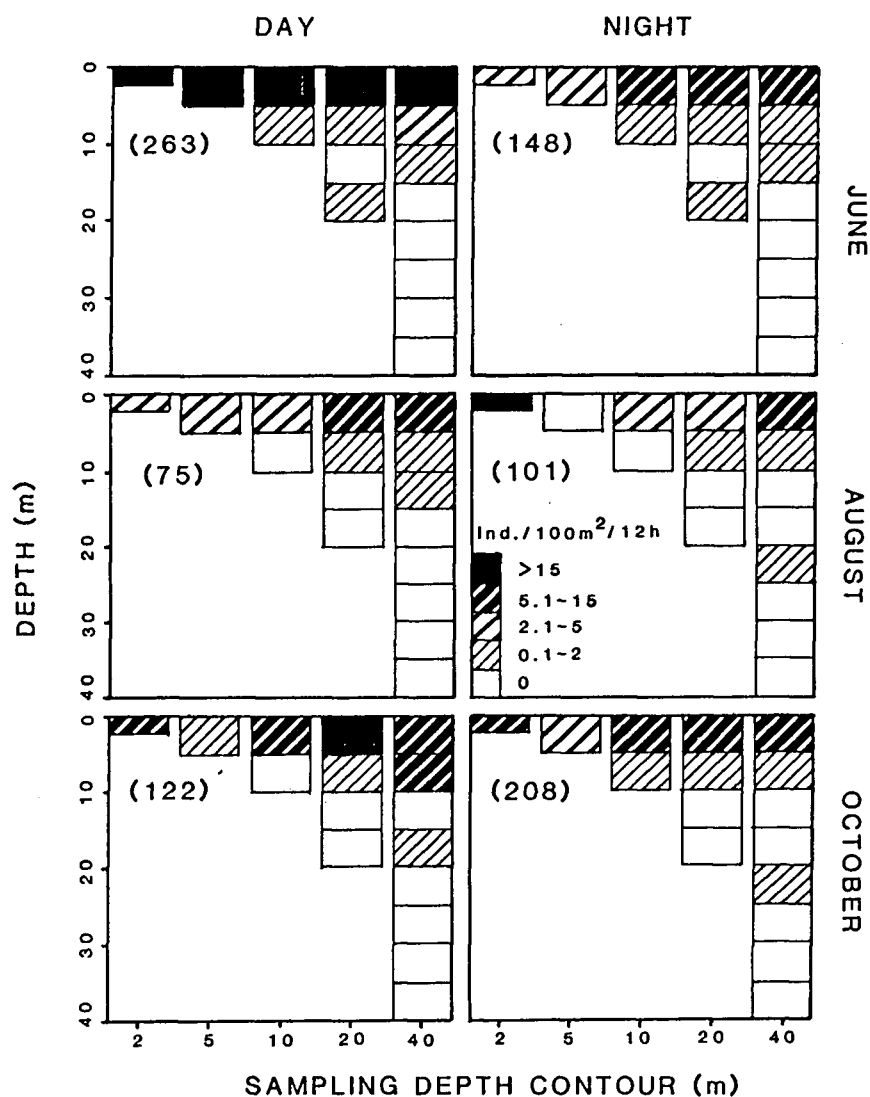


Figure 8. Spatial and temporal distribution of allopatric trout in Eunice Lake. (Mean catch per unit effort in 5 m deep gill net sets in units of individuals/100 m² net area/12 h set. Numbers of individuals captured are shown in parentheses.)

Table 7. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Eunice Lake allopatric trout by time of day (D=day, N=night), habitat (L= littoral, EP=epipelagic, P= pelagic, EB=epibenthic), and month (J=June, A=August, O=October)

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
=====			
A. June (N=411)			
time of day	1.32,1	ns ²	ns
habitat	48.66,3	***	<u>EP L</u> <u>EB P</u>
time*habitat	8.51,3	ns	ns
B. August (N=176)			
time of day	.07,1	ns	ns
habitat	40.09,3	***	<u>EP L</u> <u>P EB</u>
time*habitat	.46,3	ns	ns
C. October (N=330)			
time of day	.02,1	ns	ns
habitat	42.87,3	***	<u>EP L</u> <u>P EB</u>
time*habitat	1.32,3	ns	ns
D. Pooled (N=917)			
sampling month	5.05,2	ns	ns
time of day	.24,1	ns	ns
habitat	130.70,3	***	<u>EP L</u> <u>P EB</u>
month*time	1.50,2	ns	ns
month*habitat	3.74,6	ns	ns
time*habitat	1.12,3	ns	ns
month*time*habitat	1.74,6	ns	ns
=====			

¹Factor levels are listed in descending order of means; homogeneous subsets are underlined.

²*** p≤.001; ** p≤.01; * p≤.05; ns=not significant p>.05

Table 8. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Loon Lake sympatric trout versus Eunice Lake allopatric trout by lake (L= Loon, E=Eunice), time of day (D= day, N=night), habitat (L=littoral, EP= epipelagic, P=pelagic, EB=epibenthic), and month (J=June, A=August, O=October).

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
=====			
A. June (Loon N=332, Eunice N=411)			
lake	.27,1	ns ²	ns
time of day	.06,1	ns	ns
habitat	90.31,3	***	<u>EP L EB P</u>
lake*time	4.10,1	*	<u>E-D L-N E-N L-D</u>
lake*habitat	1.13,3	ns	ns
time*habitat	.41,3	ns	ns
lake*time*habitat	1.75,3	ns	ns
B. August (Loon N=263; Eunice N=176)			
lake	1.71,1	ns	ns
time of day	.13,1	ns	ns
habitat	72.35,3	***	<u>L EP EB P</u>
lake*time	.00,1	ns	ns
lake*habitat	9.60,3	*	<u>L-L E-EP L-EP E-L</u> <u>L-EB L-P E-P E-EB</u>
time*habitat	.62,3	ns	ns
lake*time*habitat	.17,3	ns	ns
C. October (Loon N=471; Eunice N=330)			
lake	1.87,1	ns	ns
time of day	.61,1	ns	ns
habitat	78.35,3	***	<u>L EP P EB</u>
lake*time	.26,1	ns	ns
lake*habitat	3.35,3	ns	ns
time*habitat	1.78,3	ns	ns
lake*time*habitat	.33,3	ns	ns

..Continued

Table 8. Continued

=====			
D. Pooled (Loon N=1066; Eunice N=917)			
lake	1.85,1	ns	ns
month	7.08,2	*	<u>O J A</u>
time of day	.68,1	ns	ns
habitat	236.02,3	***	<u>L EP P EB</u>
lake*month	2.68,2	ns	ns
lake*time	2.33,1	ns	ns
lake*habitat	10.45,3	*	<u>L-L E-EP L-EP E-L</u> <u>L-EB L-P E-P E-EB</u>
month*habitat	3.67,6	ns	ns
time*habitat	1.62,3	ns	ns
lake*month*habitat	3.55,6	ns	ns
lake*time*habitat	.33,3	ns	ns
=====			

¹Factor levels are listed in descending order of means;
homogeneous subsets are underlined.

²*** $p \leq .001$; ** $p \leq .01$; * $p \leq .05$; ns=not significant $p > .05$

habitat use (H-test, $p > .05$; Table 8), nor seasonal differences in habitat use (H-test, $p > .05$; Table 8D) between sympatric and allopatric trout.

3.3.2 Char

Sympatric Char in Loon Lake

Sympatric char were captured with the highest CPUE in epibenthic habitat, secondarily in pelagic habitat, thirdly in epipelagic habitat, and most sparse in littoral habitat (Figure 9; H-test, although not significant at the usual level of $p = .05$, was significant at $p = .068$; Table 9D). This pattern of distribution was found in August (H-test, $p < .01$; Table 9B) and October (H-test, although not significant at the usual level of $p = .05$, was significant at $p = .058$; Table 9C) with the exception that char were more dense in littoral than epipelagic habitat in October. Char were not distributed differently between habitats in June (H-test, $p > .05$; Table 9A), although at night, most char were found between depths 0-10 m at the 5-20 m contours. There were seasonal differences in the distribution of char between habitats (H-test, $p < .01$; Table 9D), which involved a movement from relatively shallow habitats in June to habitats greater than 5 m deep in August and October (Figure 9). There were no diel movements between habitats (H-test, $p > .05$; Table 9), although there was some evidence that char utilized shallower habitats at night in August and October (Figure 9). It should be noted that char spawn during autumn. Although many char in

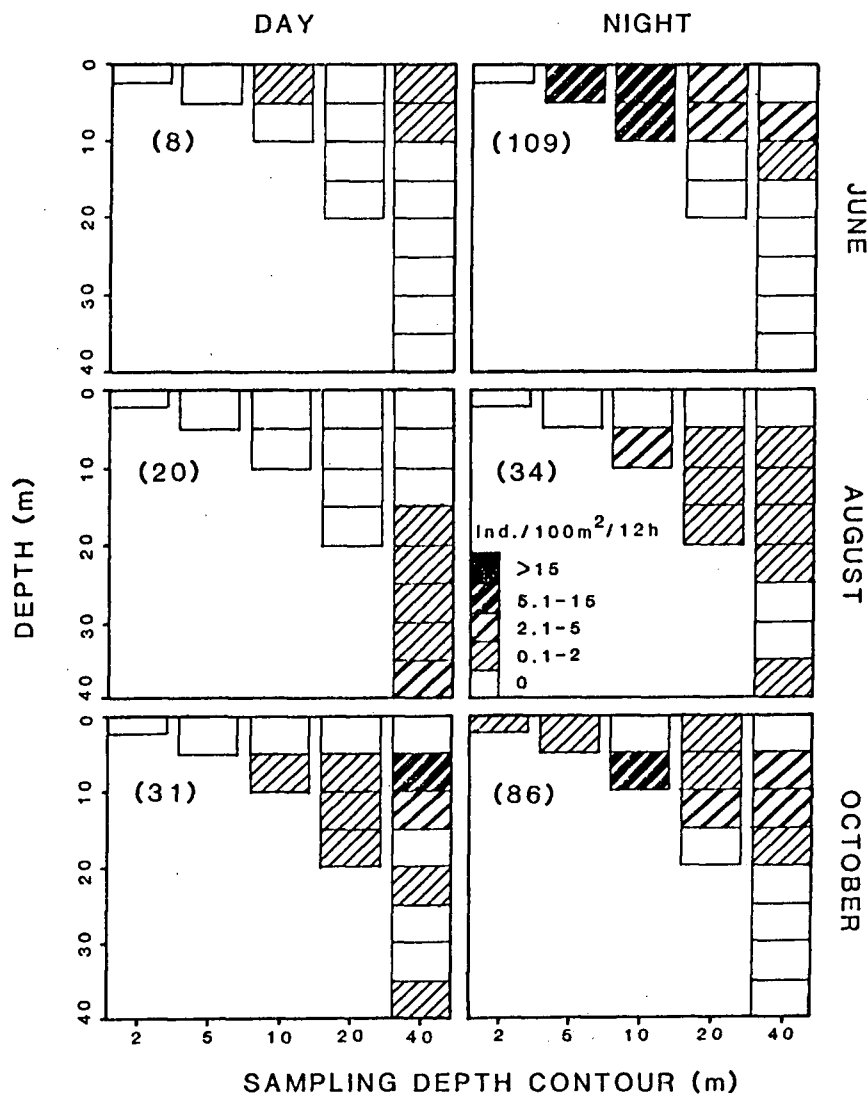


Figure 9. Spatial and temporal distribution of sympatric char in Loon Lake. (Mean catch per unit effort in 5 m deep gill net sets in units of individuals/100 m² net area/12 h set. Numbers of individuals captured are shown in parentheses.)

Table 9. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Lön Lake sympatric char by time of day (D=day, N=night), habitat (L= littoral, EP=epipelagic, P=pelagic, EB=epibenthic), and month (J=June, A=August, O=October).

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
=====			
A. June (N=117)			
time of day	8.79,1	** ²	<u>N D</u>
habitat	5.07,3	ns	ns
time*habitat	.69,3	ns	ns
B. August (N=54)			
time of day	.78,1	ns	ns
habitat	14.52,3	**	<u>EB P EP L</u>
time*habitat	1.09,3	ns	ns
C. October (N=117)			
time of day	2.05,1	ns	ns
habitat	7.49,3	ns ³	ns (<u>EB P L EP</u>)
time*habitat	3.47,3	ns	ns
D. Pooled (N=288)			
sampling month	3.59,2	ns	ns
time of day	9.34,1	**	<u>N D</u>
habitat	7.14,3	ns ⁴	ns (<u>EB P EP L</u>)
month*time	2.29,2	ns	ns
month*habitat	18.28,6	**	<u>J-EP O-EB A-EB O-P</u>
			<u>A-P O-L J-L J-EB J-P O-EP A-EP A-L</u>
time*habitat	1.10,3	ns	ns
month*time*habitat	5.35,6	ns	ns
=====			

¹Factor levels are listed in descending order of means; homogeneous subsets are underlined.

²*** p≤.001; ** p≤.01; * p≤.05; ns=not significant p>.05

³p=.058

⁴p=.068

spawning coloration were captured during October, no spawning aggregations were observed.

Allopatric Char in Katherine Lake

Allopatric char occupied depths from the surface to the bottom of Katherine Lake (Figure 10), but were distributed differently between habitats in each sampling month (H-test, $p < .01$; Table 10). In June and August, CPUEs were highest in epibenthic habitat, secondarily in littoral habitat, and thirdly in either pelagic or epipelagic habitat (H-tests, $p < .05$; Table 10A and B). The extra gill net set overnight in Katherine Lake in August captured 11.71 char/100 m²/12 h in littoral habitat, and 15.24 char/100 m²/12 h in epibenthic habitat. These supplemental catches corroborated the results from experimental sampling. In October, char were most dense in epipelagic habitat and littoral habitat, and least dense in pelagic and epibenthic habitat (H-test, $p < .05$; Table 10C). During October, char were observed to rise for surface prey over the whole lake. Due to the small sample sizes of allopatric char, especially during the day in June (N=16) and August (N=2), the distributions were "driven" by nocturnal catches. The large number of char captured at night in October (N=209) came mainly from the littoral zone and were chiefly large adult males and females in spawning coloration.

Although there were no significant diel movements between habitats (H-test, $p > .05$; Table 10), in June and October there was a marked increase in the density of char in littoral habitat

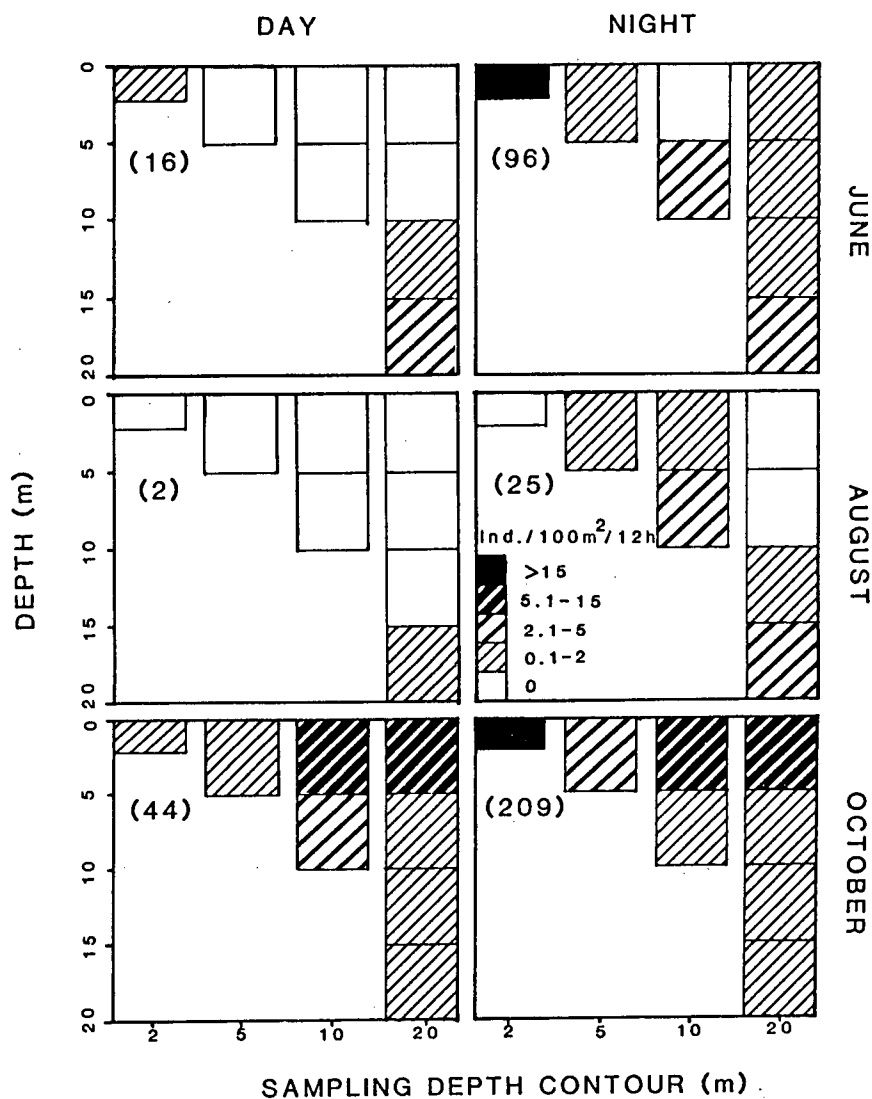


Figure 10. Spatial and temporal distribution of allopatric char in Katherine Lake. (Mean catch per unit effort in 5 m deep gill net sets in units of individuals/100 m² net area/12 h set. Numbers of individuals captured are shown in parentheses. Note change in depth scale from Figures 9-11.)

Table 10. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Katherine Lake allopatric char by time of day (D=day, N=night), habitat (L=littoral, EP=epipelagic, P=pelagic, EB=epibenthic), and month (J=June, A=August, O=October)

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
=====			
A. June (N=112)			
time of day	11.92,1	*** ²	<u>N D</u>
habitat	9.05,3	*	<u>EB L P EP</u>
time*habitat	3.35,3	ns	ns
B. August (N=27)			
time of day	15.91,1	**	<u>N D</u>
habitat	15.51,3	*	<u>EB L EP P</u>
time*habitat	5.97,3	ns	ns
C. October (N=253)			
time of day	5.92,1	ns	ns
habitat	5.58,3	*	<u>EP L P EB</u>
time*habitat	5.53,3	ns	ns
D. Pooled (N=392)			
sampling month	25.60,2	***	<u>O J A</u>
time of day	14.86,1	***	<u>N D</u>
habitat	3.48,3	ns	ns
month*time	1.59,2	ns	ns
month*habitat	18.44,6	**	<u>O-EP O-L J-EB J-L</u>
			<u>O-P A-EB O-EB J-P A-L A-EP J-EP A-P</u>
time*habitat	5.51,3	ns	ns
month*time*habitat	5.33,6	ns	ns
=====			

¹Factor levels are listed in descending order of means; homogeneous subsets are underlined.

²*** p≤.001; ** p≤.01; * p≤.05; ns=not significant p>.05

at night (Figure 10).

Sympatric versus Allopatric Char

In June and October, sympatric and allopatric char were distributed differently between habitats (H-tests, $p < .05$ and $p < .01$, respectively; Table 11A and C), but in August and in all months pooled, there was no significant difference in their distribution between habitats (H-tests, $p > .05$; Table 11B and D). The small number of char captured in August created a relatively large variance in catch per unit effort which may have obscured differences in distribution between habitats. Although both populations were most dense in epibenthic habitat in August, allopatric char were found in greater relative abundance in littoral habitat than sympatric char. Sympatric and allopatric char exhibited significantly different seasonal movements between habitats (H-test, $p < .001$; Table 11D). Seasonal differences in habitat use were due to opposite trends of vertical movement between the two populations. Sympatric char utilized shallow habitats in June and mainly epibenthic habitat in August and October, but allopatric char utilized epibenthic habitat in June and August and shallower habitats in October.

There was no statistical difference in diel use of habitats between sympatric and allopatric char (H-tests, $p > .05$; Table 11). However, in October, there was some evidence that sympatric char used shallower parts of the water column at night while allopatric char (mainly spawners) used littoral habitat to a greater extent at night than during the day.

Table 11. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Loon Lake sympatric char versus Katherine Lake allopatric char by lake (L=Loon, K=Katherine), time of day (D=day, N=night), habitat (L=littoral, EP= epipelagic, P= pelagic, EB=epibenthic), and month (J=June, A=August, O=October)

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
A. June (Loon N=117; Katherine N=112)			
lake	7.11, 1	** ²	<u>K L</u>
time of day	20.12, 1	***	<u>N D</u>
habitat	1.66, 3	ns	ns
lake*time	.58, 1	ns	ns
lake*habitat	11.17, 3	*	<u>K-L K-EB K-P L-EP</u> <u>L-L L-EB L-P K-EP</u>
time*habitat	2.53, 3	ns	ns
lake*time*habitat	1.20, 3	ns	ns
B. August (Loon N=54; Katherine N=27)			
lake	.02, 1	ns	ns
time of day	4.86, 1	*	<u>N D</u>
habitat	22.05, 3	***	<u>EB P L EP</u>
lake*time	1.87, 1	ns	ns
lake*habitat	3.66, 3	ns	ns
time*habitat	3.60, 3	ns	ns
lake*time*habitat	.66, 3	ns	ns
C. October (Loon N=117; Katherine N=253)			
lake	19.09, 1	***	<u>K L</u>
time of day	3.29, 1	ns	ns
habitat	.42, 3	ns	ns
lake*time	.00, 1	ns	ns
lake*habitat	12.20, 3	**	<u>K-EP K-L K-P K-EB</u> <u>L-EB L-P L-L L-EP</u>
time*habitat	6.75, 3	ns	ns
lake*time*habitat	.60, 3	ns	ns

..Continued

Table 11. Continued

=====			
D. Pooled (Loon N=288; Katherine N=392)			
lake	18.31,1	***	<u>K L</u>
month	19.21,2	***	<u>O J A</u>
time of day	22.79,1	***	<u>N D</u>
habitat	6.12,3	ns	ns
lake*month	10.70,2	**	<u>K-O K-J L-O L-J</u> , <u>L-A K-A</u>
lake*time	1.29,1	ns	ns
lake*habitat	2.93,3	ns	ns
month*habitat	10.26,6	ns	ns
time*habitat	5.06,3	ns	ns
lake*month*habitat	23.86,6	***	<u>K-O-EP K-O-L K-J-EB</u>
K-J-L K-O-P K-O-EB K-A-EB K-J-P K-J-EP L-A-EB L-O-EB L-O-P L-A-P			
L-O-L L-J-L L-J-EB L-J-P K-A-L K-A-EP K-J-EP K-A-P L-O-EP L-A-EP			
L-A-L			
lake*time*habitat	1.99,3	ns	ns
=====			

¹Factor levels are listed in descending order of means;
homogeneous subsets are underlined.

²*** p≤.001; ** p≤.01; * p≤.05; ns=not significant p>.05

3.3.3 Trout versus Char

There were significant differences in habitat use between sympatric trout and char during each sampling month and all sampling months pooled (H-tests, $p < .001$; Table 12). In June, segregation between sympatric trout and char was based on differences in utilization of littoral and limnetic zones, where trout were most dense in littoral habitat and char were most dense in epipelagic habitat. However, during August and October, differences in habitat utilization were based on segregation with depth, where trout utilized mainly littoral and epipelagic habitats and char utilized mainly epibenthic and pelagic habitats. There were significant differences in habitat use between allopatric trout and char during June, August, and all sampling months pooled (H-tests, $p < .001$; Table 13A, B, and D). Although differences in habitat utilization between allopatric trout and char were mainly based on depth of habitat, littoral habitat was among the two more heavily used habitats for both trout and char. During October, differences in habitat use were not so significant as during other months (H-test, $p > .05$ (cf $p < .001$); Table 13C). In October, both allopatric populations were most dense in epipelagic, littoral, pelagic, then epibenthic habitats. However, trout were much less dense in pelagic and epibenthic habitats relative to the two heavily used (epipelagic and littoral) habitats (Table 13C).

There was no significant difference in diel movements between habitats between sympatric trout and char or between allopatric trout and char in any month or pooled months (H-

Table 12. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Loon Lake sympatric trout and char by species (T=trout, C=char), time of day (D=day, N=night), habitat (L=littoral, EP=epipelagic, P=pelagic, EB=epibenthic), and month (J=June, A=August, O=October).

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
=====			
A. June (Trout N=332; Char N=117)			
species	12.27, 1	*** ²	<u>T C</u>
time of day	8.21, 1	**	<u>N D</u>
habitat	34.38, 3	***	<u>EP L EB P</u>
species*time	.31, 1	ns	ns
species*habitat	16.89, 3	***	<u>T-L T-EP C-EP T-EB,</u> <u>C-L C-EB T-P C-P</u>
time*habitat	.54, 3	ns	ns
species*time*habitat	.72, 3	ns	ns
B. August (Trout N=263; Char N=54)			
species	12.06, 1	***	<u>T C</u>
time of day	.39, 1	ns	ns
habitat	11.23, 3	*	<u>L EP EB P</u>
species*time	.11, 1	ns	ns
species*habitat	45.62, 3	***	<u>T-L T-EP C-EB T-EB,</u> <u>C-P T-P C-EP C-L</u>
time*habitat	.70, 3	ns	ns
species*time*habitat	.13, 3	ns	ns
C. October (Trout N=471; Katherine N=117)			
species	17.93, 1	***	<u>T C</u>
time of day	1.83, 1	ns	ns
habitat	11.98, 3	**	<u>L EP P EB</u>
species*time	.00, 1	ns	ns
species*habitat	34.40, 3	***	<u>T-L T-EP C-EB T-P,</u> <u>C-P T-EB C-L C-EP</u>
time*habitat	1.02, 3	ns	ns
species*time*habitat	1.10, 3	ns	ns

..Continued

Table 12. Continued

=====			
D. Pooled (Trout N=1066; Katherine N=288)			
species	40.41,1	***	<u>T</u> <u>C</u>
month	6.66,2	*	<u>O</u> <u>J</u> <u>A</u>
time of day	7.88,1	**	<u>D</u> <u>N</u>
habitat	47.88,3	***	<u>L</u> <u>EP</u> <u>EB</u> <u>P</u>
species*month	.31,2	ns	ns
species*time	.32,1	ns	ns
species*habitat	89.14,3	***	<u>T-L</u> <u>T-EP</u> <u>C-EB</u> <u>T-EB</u> , <u>C-P</u> <u>T-P</u> <u>C-EP</u> <u>C-L</u>
month*habitat	8.96,6	ns	ns
time*habitat	.87,3	ns	ns
species*month*habitat	5.39,6	ns	ns
species*time*habitat	.50,3	ns	ns
=====			

¹Factor levels are listed in descending order of means;
homogeneous subsets are underlined.

²*** $p \leq .001$; ** $p \leq .01$; * $p \leq .05$; ns=not significant $p > .05$

Table 13. Kruskal-Wallis analyses of variance of gill net catch per unit effort for Eunice Lake allopatric trout versus Katherine Lake allopatric char by species (T=trout, C=char), time of day (D=day, N=night), habitat (L=littoral, EP=epipelagic, P=pelagic, EB=epibenthic), and month (J=June, A=August, O=October).

ANOVA Factor	H-statistic, Deg. Freedom	Probability of H	Tukey Multiple Comparison of Means (p=.05) ¹
=====			
A. June (Trout N=411; Char N=112)			
species	5.78, 1	* 2	<u>T C</u>
time of day	1.29, 1	ns	ns
habitat	32.62, 3	***	<u>L EP EB P</u>
species*time	8.79, 1	**	<u>T-D C-N T-N C-D</u>
species*habitat	31.07, 3	***	<u>T-EP T-L C-L C-EB</u> <u>C-P T-EB T-P C-EP</u>
time*habitat	1.69, 3	ns	ns
species*time*habitat	1.83, 3	ns	ns
B. August (Trout N=176; Char N=27)			
species	12.83, 1	***	<u>T C</u>
time of day	2.13, 1	ns	ns
habitat	24.30, 3	***	<u>EP L EB P</u>
species*time	1.05, 1	ns	ns
species*habitat	26.22, 3	***	<u>T-EP T-L C-EB T-P</u> <u>C-L C-EP C-P T-EB</u>
time*habitat	1.04, 3	ns	ns
species*time*habitat	1.23, 3	ns	ns
C. October (Trout N=330; Char N=253)			
species	.13, 1	ns	ns
time of day	.98, 1	ns	ns
habitat	49.40, 3	***	<u>EP L EB P</u>
species*time	.40, 1	ns	ns
species*habitat	5.39, 3	ns	ns
time*habitat	5.68, 3	ns	ns
species*time*habitat	1.24, 3	ns	ns

..Continued

Table 13. Continued

=====			
D. Pooled (Trout N=917; Char N=392)			
species	9.08,1	**	<u>T C</u>
month	19.16,2	***	<u>O J A</u>
time of day	3.89,1	*	<u>N D</u>
habitat	95.77,3	***	<u>EP L EB P</u>
species*month	8.12,2	*	<u>C-O T-J T-O T-A</u>
			<u>C-J C-A</u>
species*time	6.48,1	*	<u>T-D C-N T-N C-D</u>
species*habitat	53.61,3	***	<u>T-EP T-L C-EB C-L</u>
			<u>C-EP C-P T-P T-EB</u>
month*habitat	11.07,6	ns	ns
time*habitat	4.75,3	ns	ns
species*month*habitat	7.50,6	ns	ns
species*time*habitat	1.62,3	ns	ns
=====			

¹Factor levels are listed in descending order of means;
homogeneous subsets are underlined.

²*** $p \leq .001$; ** $p \leq .01$; * $p \leq .05$; ns=not significant $p > .05$

tests, $p > .05$; Tables 12 and 13). However, during June there was some evidence of a difference in the pattern of diel movement of allopatric trout and char between habitats (Figures 8 and 10). During June, although allopatric trout were most dense in epipelagic and littoral habitats during day and night, they were more dense in epibenthic habitat during the night than the day, and although allopatric char were most dense in epibenthic habitat overall, they were more dense in littoral habitat during the night than the day. These diel habitat shifts indicate that both allopatric trout and char make nocturnal use of habitats which are typical of the other species.

3.4 Effects of Irradiance Level on Behavioural and Feeding Interactions

3.4.1 General Behaviour

Establishment of Dominance

The establishment of dominance in fish pairs prior to experimental treatments followed a regular pattern of behaviour. To illustrate this pattern, agonistic interactions of one pair of fish are shown in Figure 11. Initially, the fish explored the aquarium and although swimming activity of both fish was relatively high, there were few behavioural interactions. This initial response was followed by a phase of relatively high interaction and reduced swimming activity, when dominance by trout was established. Once established, their dominance was

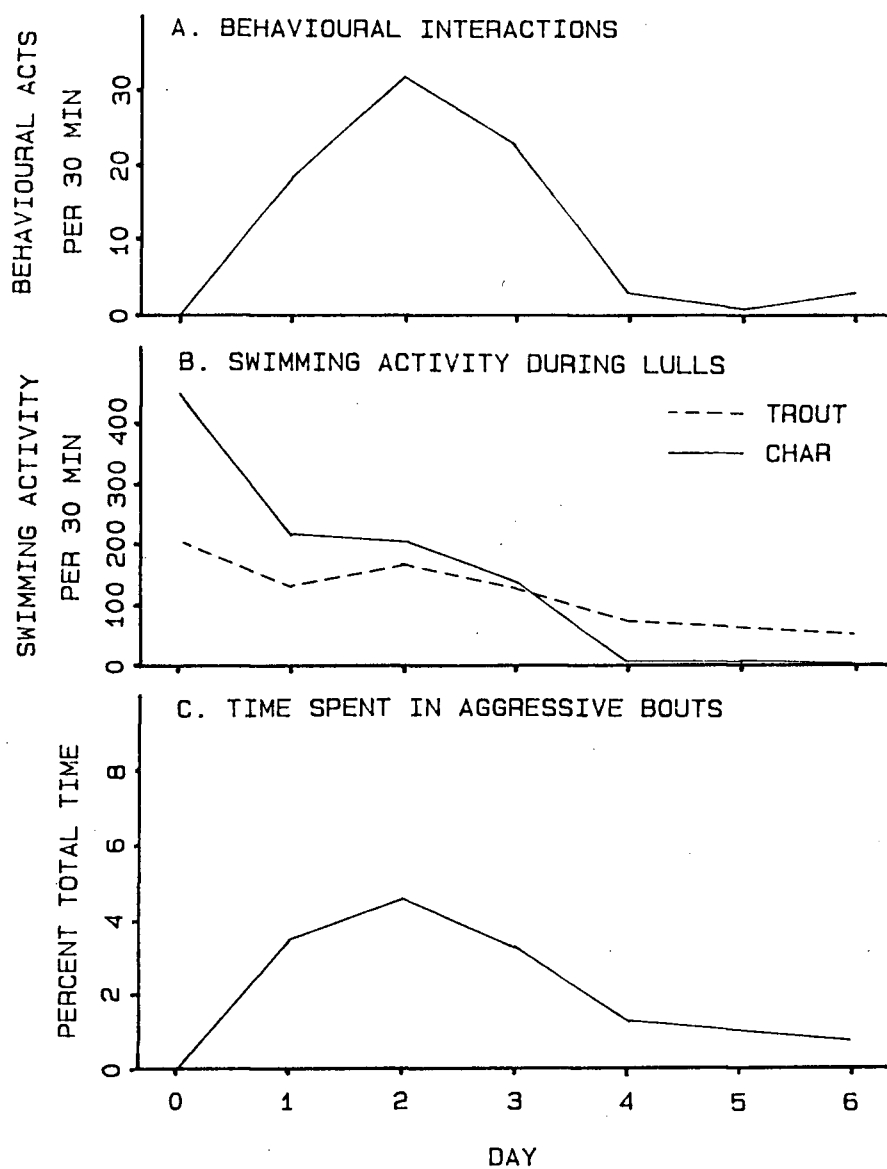


Figure 11. Behaviours associated with the establishment of dominance of trout over char.

maintained for the duration of the experiment in regular bouts of aggression, but the number of aggressive interactions and time spent in bouts markedly decreased (Figure 11). During this phase, the swimming activity of the char was very low and its use of the aquarium was restricted to one end (Figure 12). If the char strayed from this position, the trout immediately "responded" with aggressive behaviour. Once dominance was established, all aggressive behaviours were performed by the trout and all submissive behaviours by the char. Although data on establishment of dominance were not recorded for all pairs of fish, this sequence of behaviours was easy to recognize, and in each replicate, irradiance level treatments were not commenced until agonistic behaviours had stabilized.

Swimming Behaviour

The swimming activity of trout was significantly greater than that of char (F-test, $p < .001$, $F = 37.55$, $df = 1, 23$) in interspecific pairs (e.g. days 4-6, Figure 11B). Char in every replicate spent the majority of their time at either end of the aquarium, whereas trout either swam back and forth in the tank or hovered at the opposite end to the char (e.g. Figure 12).

Char had a different position in the water column than trout. Char often "rested" on the substrate, whereas trout always swam or hovered in the water column. Char in interspecific pairs rested on the substrate more often at low irradiance levels and always at the end of the aquarium. Solitary char behaved in the same way, but rested more

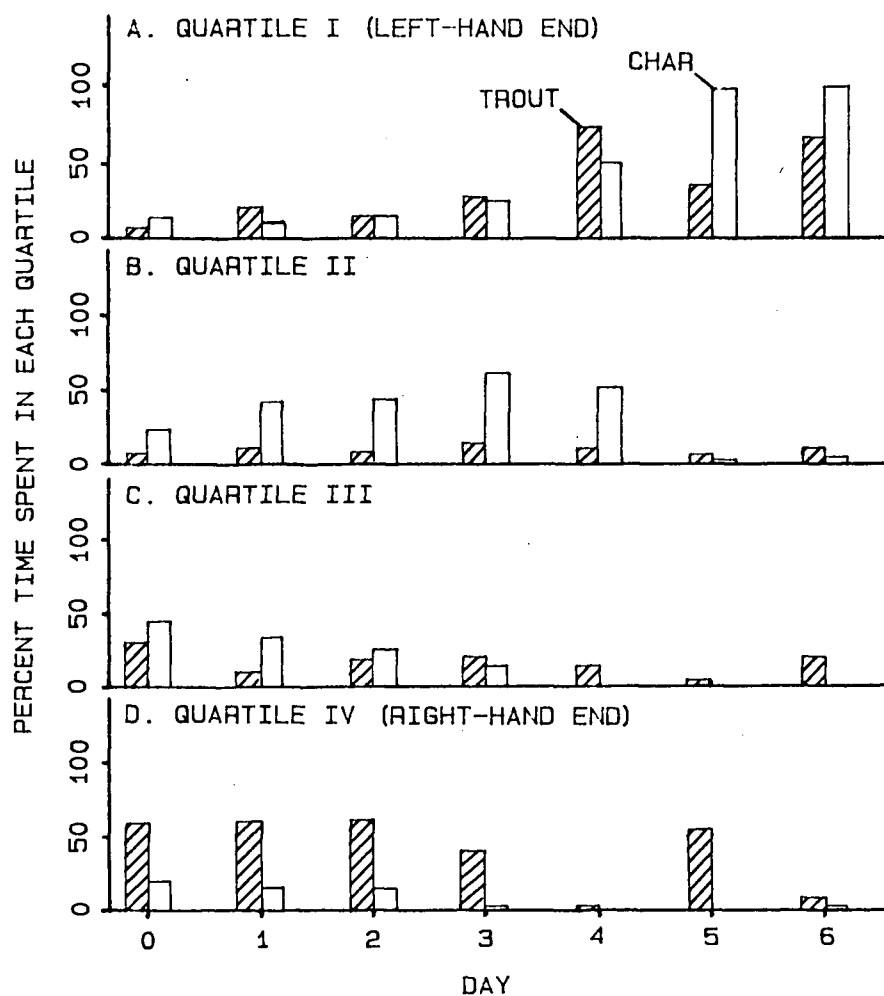


Figure 12. Horizontal position in aquarium during the establishment of dominance of trout over char.

frequently near the centre of the aquarium. Although char seemed to "prefer" resting on the substrate, char in interspecific pairs may have assumed this resting posture in an attempt to escape from aggression from trout. Char often swam to the bottom and became very still during an aggressive bout, leaving this position only to avoid the trout if it approached again to continue the bout. However, in some pairs, trout initiated aggressive bouts when char assumed a resting posture.

Another swimming behaviour performed by char but not trout in interspecific pairs was hovering in a non-horizontal position. This behaviour was performed by subordinate fish, and never by solitary individuals or dominant trout or char. Although the relevance of this behaviour is not known, it may be used by subordinate fish as a submissive display to reduce their apparent size from a vertical viewpoint.

Feeding Behaviour

During feeding trials, there were several behavioural changes in trout and char. Following the introduction of Neomysis, behavioural interactions were reduced initially for approximately 10 min while the fish exploited the prey, then interactions between trout and char became very frequent, but decreased within 30 minutes. However, there was no significant difference in the intensity of behavioural interactions between feeding and non-feeding trials (F-test, $p > .05$, $F = 3.25$, $df = 1, 23$). The increase in swimming activity of both trout (F-test, $p < .001$, $F = 20.67$, $df = 1, 23$) and char (F-test, $p < .01$, $F = 9.31$, $df = 1, 23$) was

highly significant, mainly due to increased searching activity (Table 14). However, the swimming activity of trout was significantly greater than that of char whether prey were present (F-test, $p < .001$, $F = 14.73$, $df = 1, 23$) or absent (F-test, $p < .001$, $F = 37.55$, $df = 1, 23$).

The vertical position of char in the water column (i.e. "resting" on bottom, swimming in the water column, or diagonal hover) was not changed from non-feeding trials.

3.4.2 Behavioural Interactions

The frequency of behavioural interactions between trout and char was reduced with decreasing irradiance level (F-test in two-way ANOVA (irradiance level (repeated measures) and order), $p < .05$, $F = 4.52$, $df = 3, 10$; Figure 13). There were virtually no interactions at the lowest irradiance level. The order in which irradiance levels were presented to each pair did not significantly affect the frequency of behavioural interactions (F-test in two-way ANOVA (irradiance level (repeated measures) and order), $p > .05$, $F = 0.23$, $df = 2, 10$).

At all irradiance levels, behavioural interactions were predominantly submissive acts of avoidance by the char. At the three lowest irradiance levels, there was an even greater predominance of submissive acts by the char, and aggression by the trout was virtually nil (Figure 13), although the dominance relationship was maintained at all irradiance levels.

At the lower irradiance levels, visual perception of char by trout may be limited due to reduced swimming activity of the

Table 14. Swimming activity of trout and char in feeding trials (F) and trials without prey present (NF). (Data from all irradiance levels pooled; N=24.)

	Trout		Char	
	NF	F	NF	F
Swimming activity per 30 minutes (mean \pm standard deviation)	43.9 \pm 21.2	107.6 \pm 83.5	9.8 \pm 17.2	31.9 \pm 48.6

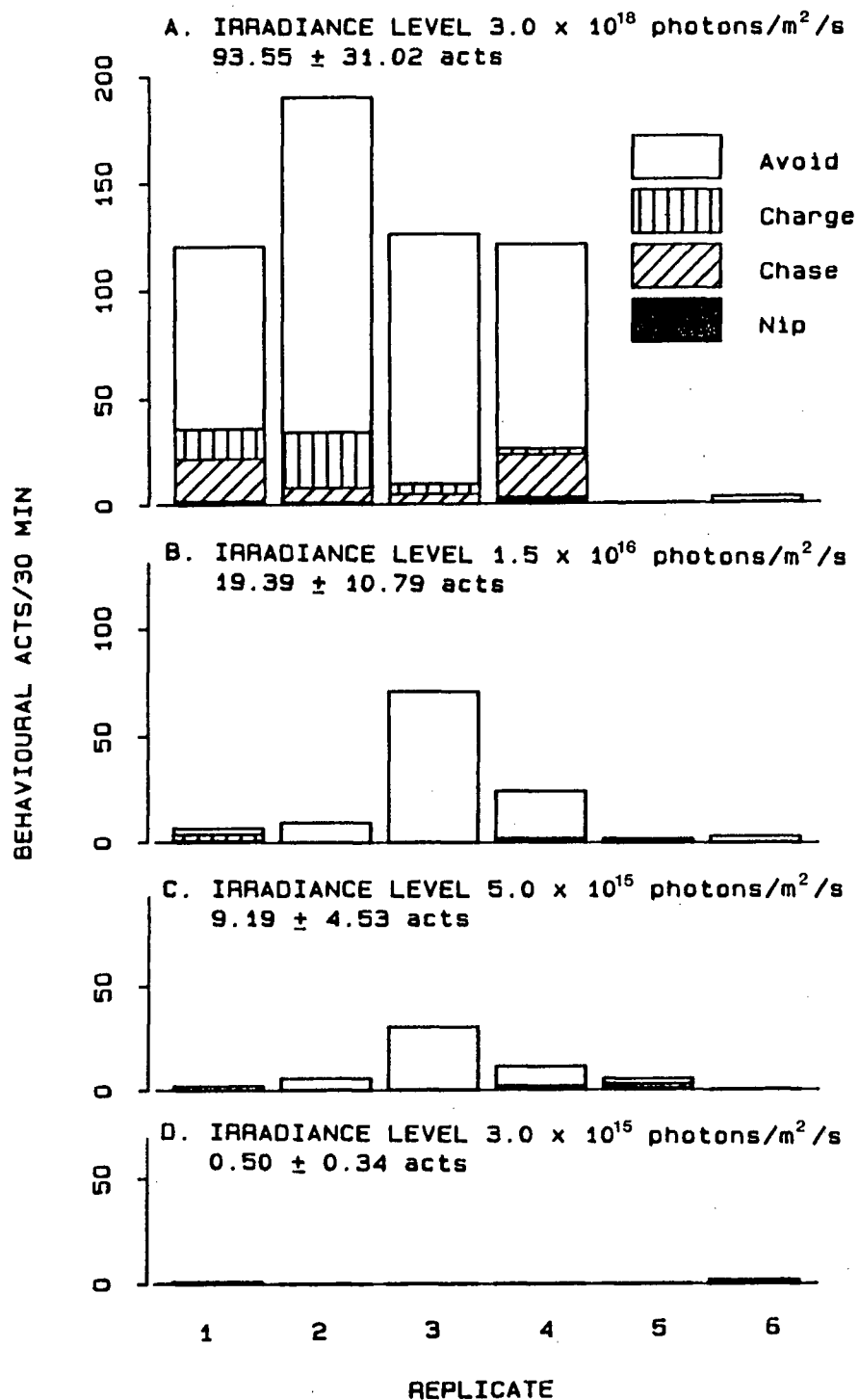


Figure 13. Type and intensity of behavioural interactions between dominant trout and subordinate char at four irradiance levels. (Mean behavioural acts per 30 min \pm standard error are shown.)

trout. With decreasing irradiance, trout must actively seek out char in order to perform aggressive acts. There was no significant difference in swimming activity of trout in interspecific pairs with char with decreasing irradiance level (F-test, $p > .05$, $F = 1.32$, $df = 3, 15$; Figure 14). However, solitary trout and intraspecific trout pairs exhibit reduced swimming activity with decreased irradiance level. The same is true of solitary and intraspecific pairs of char, but char in interspecific pairs with trout showed a highly significant reduction in swimming activity with decreasing irradiance level (F-test, $p < .01$, $F = 5.44$, $df = 3, 15$; Figure 14). Therefore, the swimming activity of trout appears to be influenced by the presence of char. Swimming activity of trout ($p < .05$, $r = .43$, $n = 23$) but not char ($p > .05$, $r = .37$, $n = 24$) was correlated with intensity of behavioural interactions, although the r value for trout was not much greater than that of char. It appears that under low irradiance, char continue to exhibit submissive behaviours (i.e. "avoidance"; Table 2) used at higher irradiance levels to avoid aggression by trout, and that subordinate char are less active than dominant or solitary fish. However, in several trials at the lower irradiance levels, char did not avoid trout, and some char appeared to be torpid in low irradiance (3.0×10^{15} photons/m²/s) because they did not respond to nudging by trout.

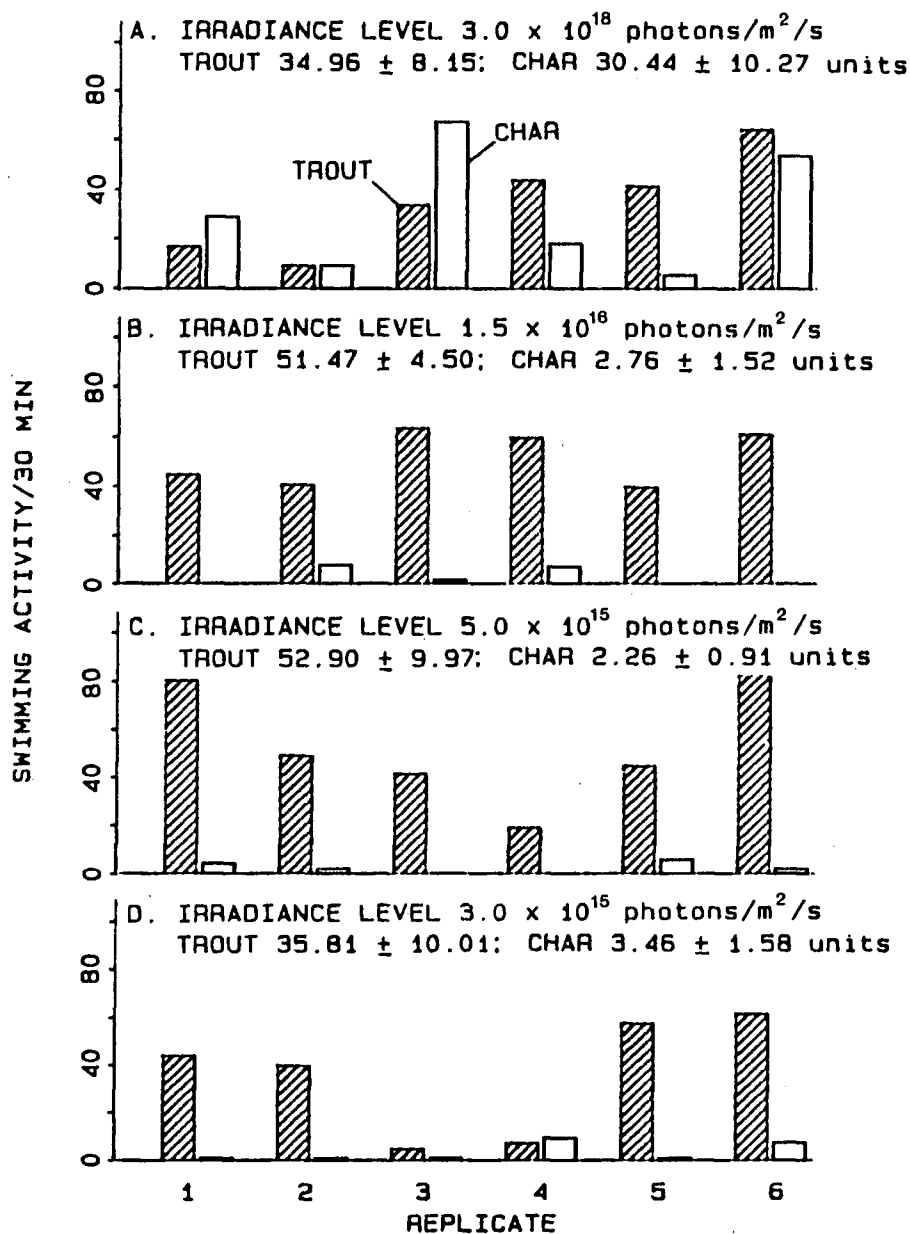


Figure 14. Swimming activity of dominant trout and subordinate char at four irradiance levels. (One swimming activity unit is entry to a new horizontal quartile of aquarium. Mean activity per 30 min \pm standard error are shown.)

3.4.3 Feeding Performance

The feeding performance of char in interspecific pairs dominated by trout increased with decreasing intensity of behavioural interactions (t-test, two-tailed, $p > .05$, $t = 5.41$, $df = 4$; Figure 15). Data used in this test were restricted to feeding trials at irradiance levels that maximized the reaction distance for both species (3.0×10^{18} photons/m²/s).

The difference in feeding performance of trout and char in interspecific pairs dominated by trout was highly significant (F-test, $p < .001$, $F = 24.29$, $df = 1, 23$; Figure 16). Trout made more feeding strikes than char in all replicates at all irradiance levels except for one trial (Replicate 2; Figure 16C). Neither trout (F-test, $p > .05$, $F = 2.39$, $df = 3, 15$) nor char (F-test, $p > .05$, $F = 1.92$, $df = 3, 15$) fed less frequently under lower irradiance level. The feeding performance of trout declined more rapidly with irradiance level than did that of char although this result was not statistically significant (Figure 16).

During feeding trials, char maintained similar behaviour to non-feeding trials, including subordinate behaviours, swimming activity, and orientation in the water column (Figures 17-19). As in trials without prey present, there was a highly variable intensity of interaction at the three highest irradiance levels, but there was a relatively low intensity of interaction and virtually no aggression at the lowest level in feeding trials (Figure 17, cf Figure 13). However, trout were dominant even at the lowest irradiance level, and the feeding performance of char was affected at all irradiance levels. There was a highly

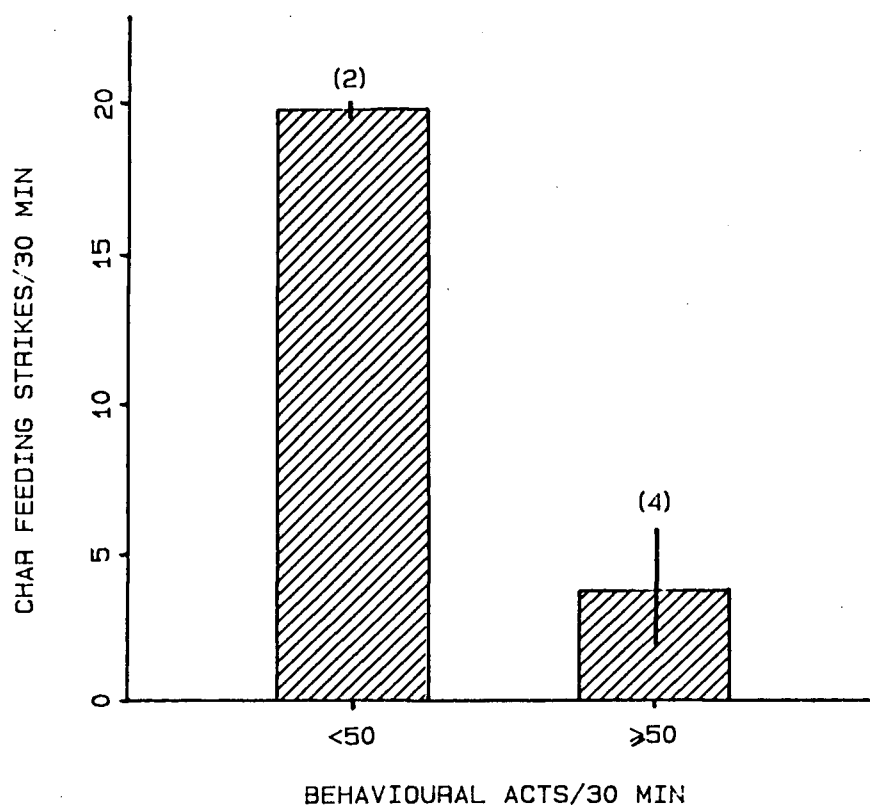


Figure 15. Effect of behavioural interactions between dominant trout and subordinate char on the feeding performance of char. (Irradiance level = 3.0×10^{18} photons/m²/s. Bars indicate \pm standard error. Sample sizes are shown in parentheses.)

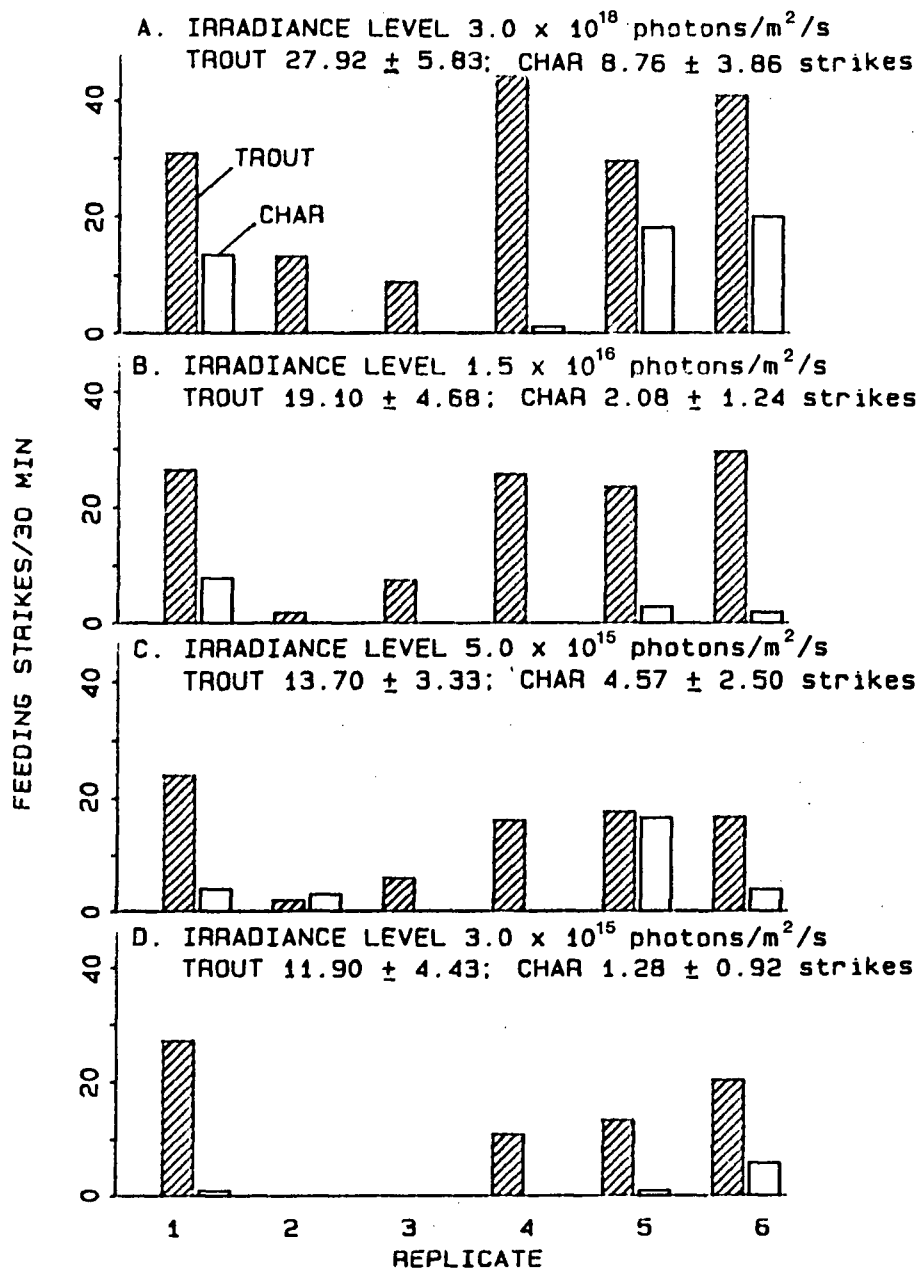


Figure 16. Feeding performance of dominant trout and subordinate char at four irradiance levels. (Mean feeding strikes per 30 min \pm standard error are shown.)

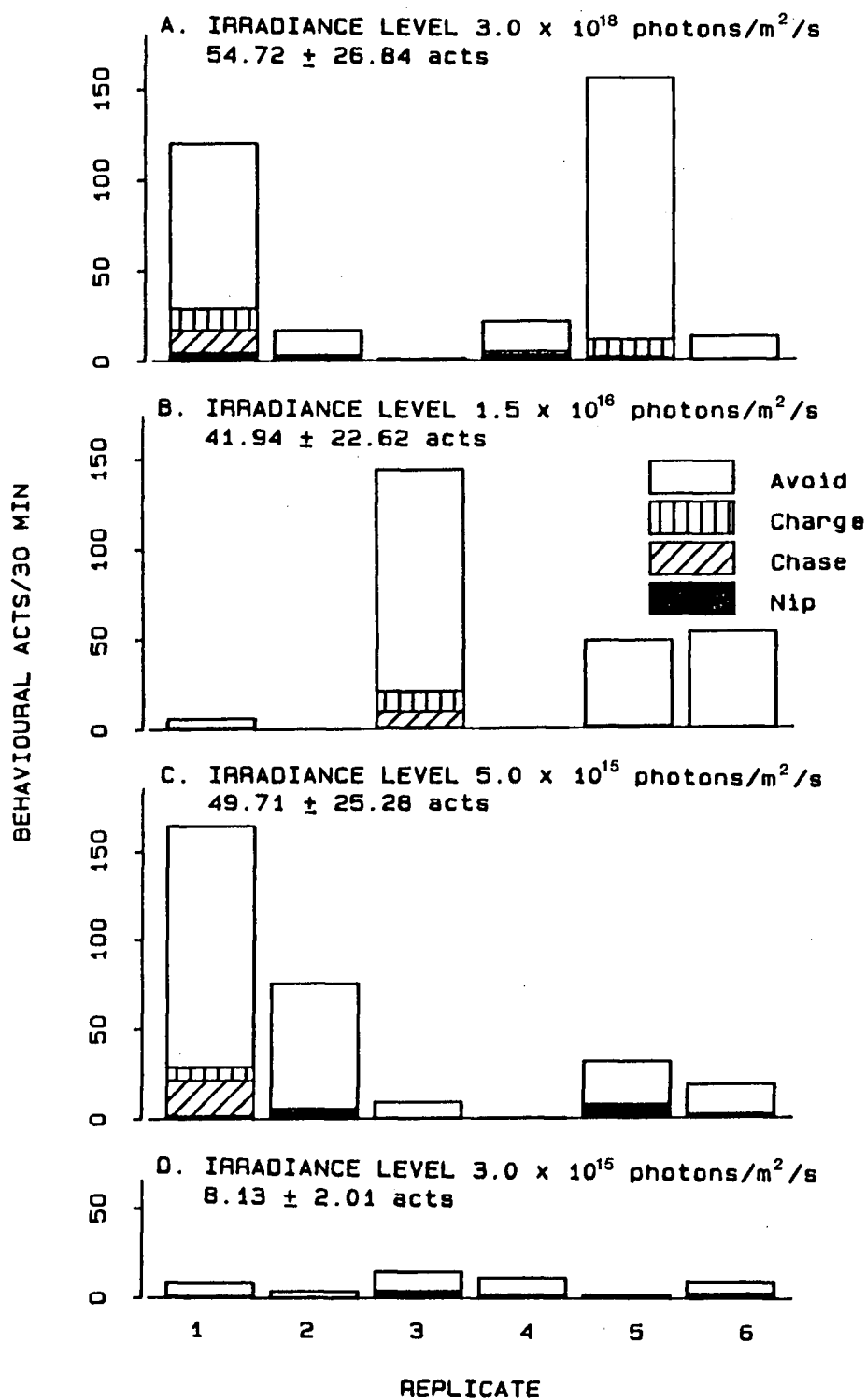


Figure 17. Type and intensity of behavioural interactions between dominant trout and subordinate char during feeding at four irradiance levels. (Mean behavioural acts per 30 min \pm standard error are shown.)

significant decrease in behavioural interactions in feeding trials with decreasing irradiance level (F-test, $p < .001$, $F = 15.13$, $df = 3, 40$). The swimming activity of char in feeding trials was significantly greater than non-feeding trials (F-test, $p < .01$, $F = 9.31$, $df = 1, 40$) but decreased with irradiance level similarly to non-feeding trials (F-test, $p < .001$, $F = 9.84$, $df = 1, 15$; Figure 18, cf Figure 14). The orientation of char in the water column was remarkably similar between feeding and non-feeding trials (Figure 19). However, vertical orientation varied between individual char. For example, the char in replicate 4 hovered in a diagonal position much more frequently than any other char. At the three lowest irradiance levels, the five other char never used the diagonal hover behaviour (with the exception of replicate 2 at 1.5×10^{16} photons/m²/s), but used bottom resting behaviour more frequently than at the highest irradiance level.

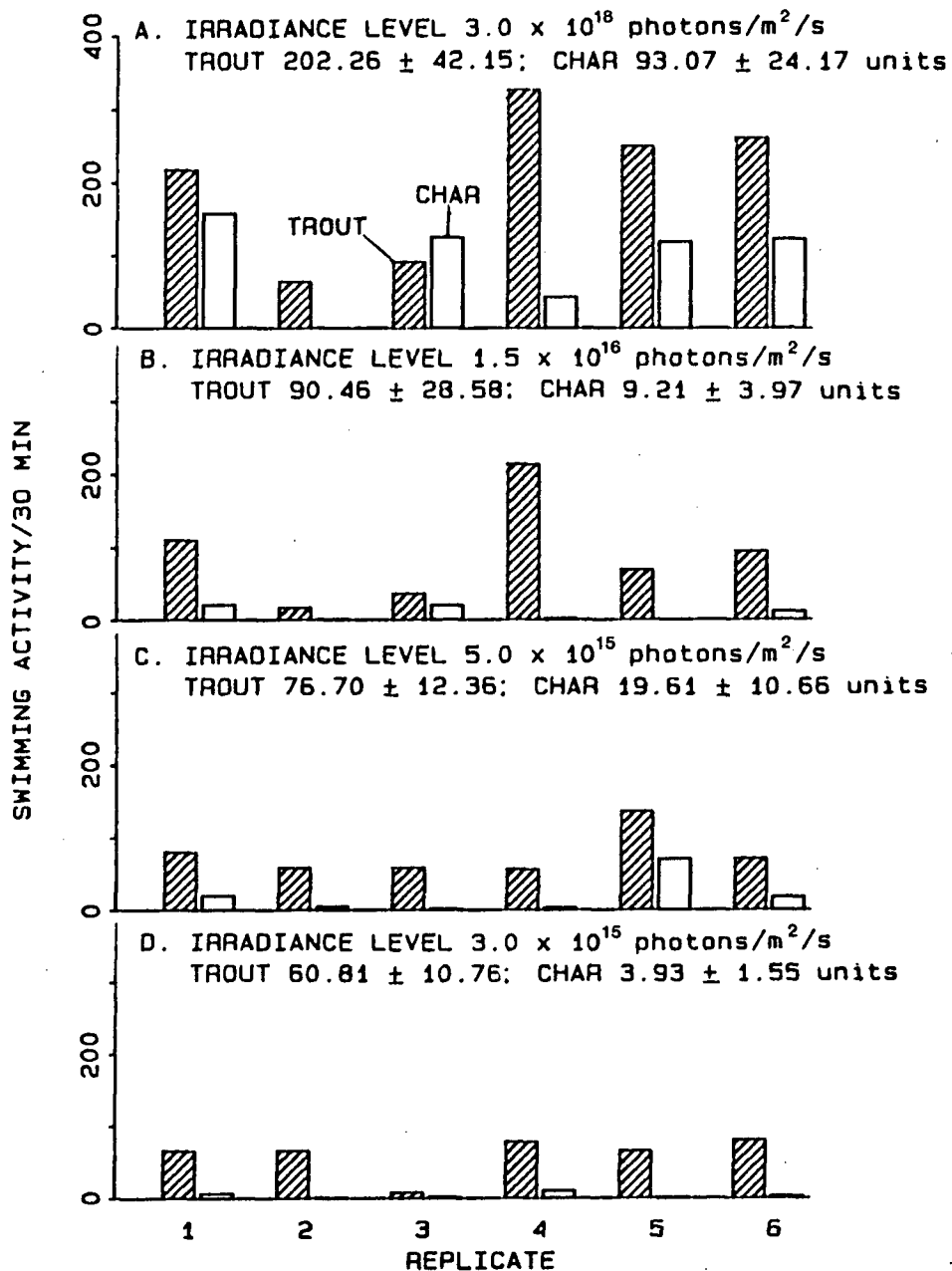


Figure 18. Swimming activity of dominant trout and subordinate char during feeding at four irradiance levels. (One swimming activity unit is entry to a new horizontal quartile of aquarium. Mean activity per 30 min \pm standard error are shown.)

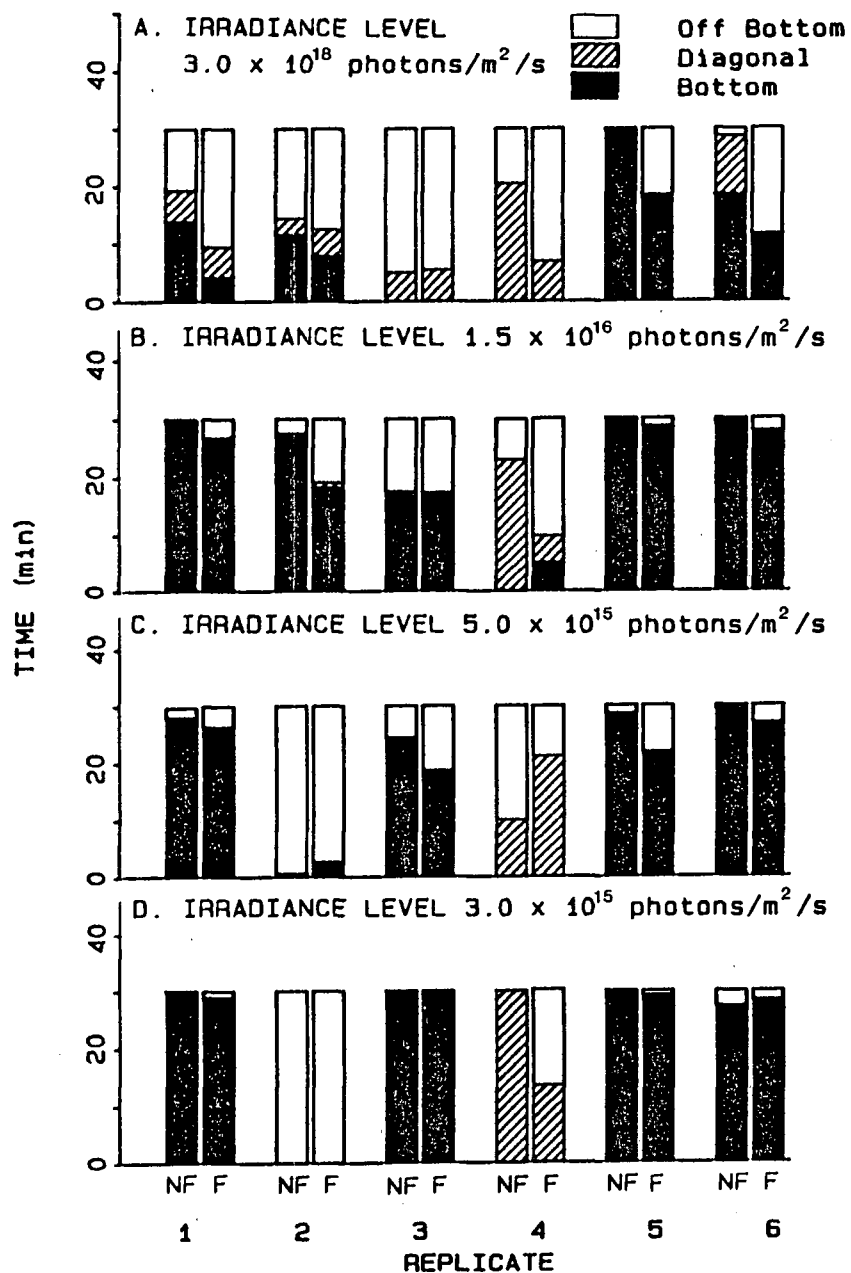


Figure 19. Vertical position in the water column of subordinate char at four irradiance levels. (NF=no prey present; F= Neomysis mercedis present. See text for explanation of terms.)

4.0 DISCUSSION

4.1 Spatial and Temporal Distribution

Habitat partitioning is common in fish communities (Nilsson 1967, Keast 1970, 1978, Zaret and Rand 1971, Moyle 1973, Werner et al. 1977, Gorman and Karr 1978). A "habitat" is a place with a particular kind of environment inhabited by organisms (e.g. littoral zone), where "environment" is a collective term for the conditions in which an organism lives (e.g. temperature, irradiance level, other organisms). The preferred habitat of a species is commonly thought to be based mainly on the abundance and type of food resources present. The habitats used in my study were defined by their proximity to either the lake surface or bottom, or a combination of the two boundaries: epipelagic, proximity to the surface; epibenthic, proximity to the bottom; littoral, proximity to both; and pelagic, proximity to neither boundary. Each habitat had similar environmental conditions of temperature, oxygen, and irradiance level in the study lakes. In addition, prey types were distributed in similar relative abundance among habitats in the lakes (with some exceptions, as discussed below).

If resource use patterns are affected by interspecific competitive interactions, then addition or removal of competitors should cause species to "shift" their niche in response, either away from or towards the resources used by the competitor, respectively (Eadie 1982). A niche is a particular role or set of relationships of an organism in an ecosystem,

which may be filled by different species in different geographical areas. A niche is composed of many "dimensions", the most important of which are trophic relationships, habitat or spatial dimension, and temporal dimension or time of activity (Pianka 1975). Species may undergo shifts in particular dimensions of their niche. A habitat shift is the divergence of sympatric species from each other so that each then occupies a different part of the site, thereby allowing coexistence under the pressure of competition (Schoener 1974a, Connell 1980). Although species may compete for space per se (e.g. Fausch and White 1981), competition between fish for space is usually closely associated with competition for food resources contained within particular habitats (Magnuson 1962, Gustafson et al. 1969, Dill et al. 1981). Segregation by habitat is one of the most important means by which ecologically similar species partition food resources (Schoener 1974a). Niche or habitat shifts are often cited as evidence of competition in fish communities (Nilsson 1960, 1963, Schoener 1974b, 1974c, 1975, Werner and Hall 1976, 1977, 1979, Werner 1977, Nilsson and Northcote 1981, Magnan and Fitzgerald 1982, Larson and Moore 1985). An hypothesis of competition between trout and char in Loon Lake would be supported by a habitat shift in one or both species between sympatry and allopatry.

There were significant differences between habitat use of the sympatric and experimental allopatric trout populations in August and all sampling months pooled. Allopatric trout were captured in greatest relative abundance in epipelagic habitat,

sympatric trout were captured in greatest relative abundance in littoral habitat, and epibenthic and pelagic habitat were less utilized by both populations. Differences in prey distributions between Loon and Eunice lakes could in part explain this apparent habitat shift. Zoobenthos, zooplankton, and surface prey were distributed in a similar way within each lake in June and August, except that surface arthropods were much more abundant in Eunice (4.06 individuals/m²) than in Loon (0.23 individuals/m²) during August (Hindar et al. in prep.). Allopatric Eunice trout may have utilized epipelagic habitat in August to consume surface arthropods. The distribution of trout in Eunice mainly in the upper 5 m of the water column rather than the upper 10 m as in Loon is consistent with the hypothesis that trout in epipelagic habitat in Eunice were consuming the abundant surface arthropods in August. However, Hindar et al. (in prep.) found that sympatric and allopatric trout consumed the same prey types, and in similar relative proportions during each month. In any case, despite the apparent preference of allopatric trout for epipelagic habitat, sympatric trout probably preferred littoral over epipelagic habitat, or at least were not outcompeted or excluded by char from epipelagic habitat, because char were not abundant in epipelagic habitat in Loon Lake. There was no significant difference between diel or seasonal use of habitats by sympatric and allopatric trout. I conclude that these data provide no clear evidence of a habitat shift in trout between sympatry and allopatry in habitat use, diel differences in use of habitats,

or seasonal differences in use of habitats.

There were significant differences in habitat use between sympatric and allopatric char in June and October, but no difference in August or in all months pooled. In June, allopatric char were most dense in epibenthic and littoral habitats but sympatric char utilized all habitats equally, including epipelagic and littoral habitat that was utilized by trout. This shift in habitat use in June does not support an hypothesis of competition between trout and char in Loon Lake because sympatric char shifted to habitats which were more similar to typical trout habitat than the epibenthic and littoral habitats most heavily utilized by allopatric char. However, in June, the main food item of allopatric char was Zygoptera larvae, which were abundant in the littoral zone (Hindar et al. in prep.). The high abundance of this prey in Katherine Lake during June probably had a strong influence on the attraction of allopatric char to littoral, and possibly epibenthic, habitats. In October, the results of habitat shifts contradict those of June, as epipelagic and littoral habitats that were used most heavily by allopatric char were least utilized by the sympatric population. These results support an hypothesis of competition between trout and char in Loon Lake, because sympatric char shifted to habitats that were less similar to trout habitat than habitats used most heavily by allopatric char. During October, allopatric char were probably attracted to the epipelagic zone to prey upon surface arthropods, as this prey type was over twice as dense during

this sampling period (4.5 individuals/m²) than in any other lake or month (Hindar et al. in prep.). During October 1982, char were observed to rise to the lake surface to consume floating prey items, and surface arthropods were a more important dietary item to char than in any other lake or month. During October, allopatric char were probably not attracted to epipelagic habitat (0-5 m) to consume zooplankton prey, as this prey type was more dense at 5-10 m in pelagic habitat. Since the density of surface arthropods in Loon Lake during October was not comparable to that in Katherine Lake, habitat shifts should be interpreted with caution, because prey abundance may partly explain the shift.

The distribution of allopatric char from the surface to the bottom of the lake and of sympatric char from approximately 5 m deep to the lake bottom also support the hypothesis that trout and char compete in Loon Lake. There was a significant difference in seasonal use of habitats between sympatric and allopatric char. The seasonal movement of sympatric char from mainly surface habitats in June to primarily epibenthic and pelagic habitats in August and October (H-test, $p < .001$; Table 12D) resulted in a greater segregation between sympatric trout and char from June to August and October. These data indicate that sympatric char undergo a habitat shift in October to habitats that are not utilized by trout. Sympatric char may also undergo a habitat shift in August, but the evidence for this shift is not conclusive.

There were no statistical differences between the two

populations in diel use of habitats, although in August and October there was some evidence that sympatric char used shallower habitats at night, while allopatric char used littoral habitat more at night than during the day. Prior to sampling in the lakes, I predicted that sympatric, but not allopatric, char would move at night to shallow habitats occupied by trout as irradiance levels decreased. In shallow habitats at night, char could exploit abundant zooplankton or even surface arthropod prey, since char are more efficient than trout in the detection of prey at low irradiance levels (Henderson and Northcote 1985). Even though sympatric char do not clearly show this pattern of diel movement, the diel vertical movement of allopatric char is puzzling. Why are allopatric char not distributed in shallow habitats during the day? One possible reason is that risk of avian predation is greater at the surface than in deeper habitats. Risk of predation is known to affect the choice of foraging habitat by fish (Mittlebach 1981, 1984, Werner et al. 1983). Belted kingfisher (Megaceryle alcyon), great blue heron (Ardea herodias), and common loon (Gavia immer) have been observed in the U.B.C. Research Forest (J. Werring, pers. comm.) and, although these bird species are not common, may act as predators at the lake surface during the day but not at night at all three study lakes. Another reason may be that char prefer the deepest water and lowest irradiance level that still allows maximum reaction distance to prey. Without hindering visual perception of food items, utilizing low irradiance level habitats may provide concealment from predators. The reaction

distance of char is maximized at a relatively low irradiance level ($\geq 3.0 \times 10^{16}$ photons/m²/s; Henderson and Northcote 1985) and during the day this irradiance level is relatively deep (>40 m on a clear July day; Henderson and Northcote 1985, their Figure 4). However, at night, when irradiance levels at all depths decrease, char must migrate to shallower water to maintain maximum reaction distance (Henderson and Northcote 1985, their Figure 5). These data do not provide evidence that char in sympatry with trout undergo a temporal niche shift, as both sympatric and allopatric char used shallower limnetic or littoral habitats at night.

An hypothesis of competition between trout and char in Loon Lake predicts, in addition to habitat shifts of one or both species, that habitat utilization of the two species is more similar when both species are in allopatry than when they coexist in Loon Lake. Habitat utilization of sympatric trout versus char, and of allopatric trout versus char were significantly different during June and August (H-tests, $p < .001$; Tables 12 and 13). However, in October, there was no significant difference in habitat utilization between allopatric populations (H-test, $p > .05$; Table 13D), while that of the sympatric populations remained significantly different (H-test, $p < .001$; Table 12C). The result in October is consistent with the pattern of habitat overlap shown in Figure 20. There were no differences in diel use of habitats between sympatric populations or between allopatric populations from June to October. However, at night in June, there was some evidence

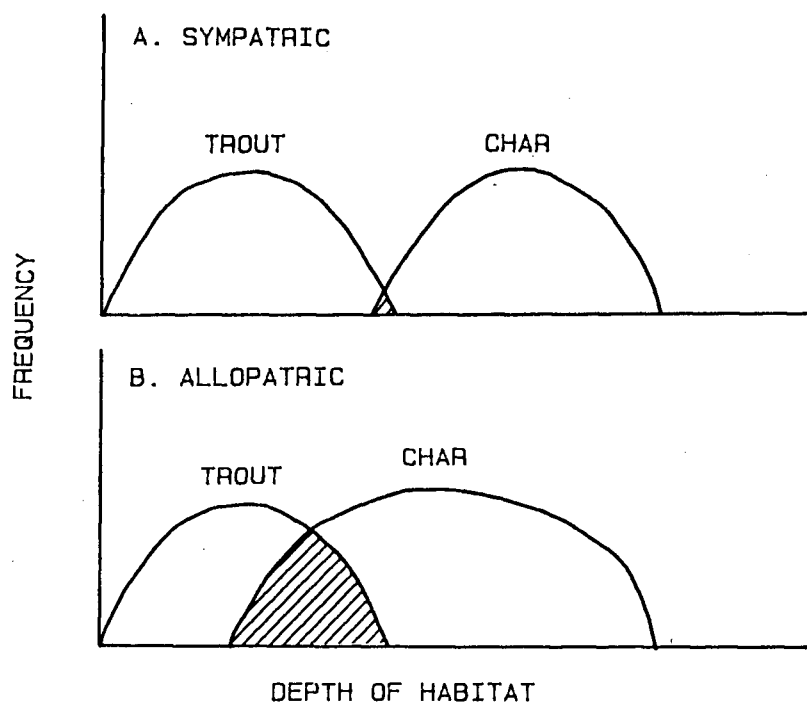


Figure 20. Schematic diagram of habitat overlap of sympatric Loon Lake trout and char and experimentally allopatric Eunice Lake trout and Katherine Lake char.

that allopatric trout moved to typical char habitat (epibenthic) and allopatric char moved to typical trout habitat (littoral). Fish distributions in October support an hypothesis of competition between trout and char in Loon Lake based on a comparison of habitat separation between the two sympatric populations with that of the two allopatric populations, but there is insufficient evidence in June and August to support the hypothesis. The lack of evidence in June and August is due to the fact that the habitat utilization of trout and char was significantly different at all times, thereby preventing "quantification" of niche separation.

Although trout did not undergo a habitat shift or expand their vertical distribution in allopatry, the habitat shift of char and expansion of their habitat utilization to the surface layers of the lake in allopatry is consistent with the hypothesis that interspecific competition occurs between trout and char in Loon Lake. In addition, the habitat shift by char but not trout is consistent with the hypothesis that competition acts more strongly on char. Although niche shifts are generally accepted as evidence of competition within communities, there are specific criteria that must be met for competition to occur. Competition occurs when two or more organismic units use the same resources that are in short supply, and this reduces the fitness and/or equilibrium population size of each (Pianka 1983, p.184). Trout and char populations in Loon Lake consume at least some of the same prey species (Schutz and Northcote 1972, Hume and Northcote 1985, Hindar et al. in prep.). In allopatry,

similar genetic stocks of these species consume virtually all of the same prey categories as each other, although not in the same relative proportions (Hindar et al. in prep.). The rapid growth of Loon Lake trout and char stocks transferred to previously fishless lakes with abundant food resources (Hume and Northcote 1985) indicates that these species are food-limited in Loon Lake. The limited growth of trout and char in Loon Lake most likely results in reduced reproductive potential (i.e. fecundity) and potential population size, and therefore reduces their fitness. Although Pianka's criteria have not been addressed directly in this study, they could provide a focus for further studies on these fish populations.

Part of the difficulty in drawing a strong conclusion from this field experiment is the lack of a rigid control for the experimental transfer of fish between whole lake environments. Although the study lakes had similar limnological features and fish prey distributions, even subtle differences in lake environments may influence how fish utilize habitats. Differences in lake morphometry, especially littoral development, and invertebrate distributions are probably among the most important of these factors in this experiment. In addition, intraspecific competition pressure influences how populations respond to interspecific competition, and this has not been addressed in this experiment. The relative importance of these factors on habitat utilization by trout and char is difficult to quantify.

The conclusion that trout is a superior competitor to char

is corroborated by evidence from diets and physiological performance based on growth rates and size. Char, but not trout, showed a niche shift in diet relative to the sympatric donor stock (Hindar et al. in prep.). Sympatric and allopatric trout had a marked food resource overlap from June to October, and fed mainly on littoral zoobenthos, surface insects, and cladocerans. Sympatric and allopatric char overlapped in food resources in October only, although food resource availability may partly explain this result. Sympatric char consumed mainly littoral zoobenthos, chironomids, and zooplankton, whereas allopatric char consumed mainly littoral zoobenthos in June and August, and surface arthropods and zooplankton in October (Hindar et al. in prep.). Allopatric char improved relative to the sympatric population with respect to the life history variables growth rate (higher, $p < .001$) and size (fork length longer, $p < .001$), while growth rate of allopatric trout was the same as that of the sympatric stock ($p > .05$) and mean fork length was shorter ($p < .001$; Jonsson et al. 1984, their Table 2). However, differences in growth rates and size between sympatric and allopatric stocks as indicators of competitive pressure in Loon Lake must be interpreted with caution, as allopatric populations are not necessarily at carrying capacity, while the populations in Loon Lake are stable (Section 3.2).

The habitat segregation of trout and char in Loon Lake is mainly with depth of habitat. Seasonal and daily differences are not common. The morphological and ecological specializations, or selective differences, of these closely

related species are in accordance with their pattern of habitat use. Char feed more successfully on benthic prey, and trout on surface prey in laboratory experiments involving solitary individuals and interspecies pairs exposed to food in benthic, surface, and both locations (Schutz and Northcote 1972, see also Hume 1978). Differences in feeding performance on prey types may be related to differences in mouth morphology of trout and char (Hespenheide 1973). The mouth of char is subterminal and "directed" downwards at benthic prey whereas the mouth of trout is terminal, which may allow trout to feed more effectively on zooplankton or surface prey. Deep-dwelling char have a SIT and VIT that are one and two orders of magnitude lower, respectively, than those of the more surface-dwelling trout (Henderson and Northcote 1985). These differences in visual ability of trout and char are related to differences in the eye morphology and the ratio of rods to cones in the retina (Henderson 1982), and enable each species to detect prey in its habitat. In addition to visual perception of prey, char are capable of chemoreception of prey below their VIT, and the greater maximum reaction distance and foraging velocity of trout enable trout to visually search a volume of water seven times greater than char for a zooplankter such as Diaptomus kenai on a summer day (Henderson and Northcote 1985). The specializations of trout make it superior to char in the exploitation of food resources in shallow, well-illuminated habitats, and vice versa for char in deeper, less well-illuminated habitats. However, these specializations do not explain the absence of char from

shallow habitats in sympatry with trout in Loon Lake.

In addition to selection of habitat based on food resources, trout and char may also use other environmental factors such as temperature and irradiance level to provide a cue for habitat partitioning with depth. Apart from differences in prey type and abundance with depth, the limnetic zones of lakes are homogeneous in many respects. Temperature is an important determinant of physiological and biochemical rates (Fry 1971). The behavioural thermoregulation of fish is well-documented (Ferguson 1958, Brett 1971, Neill and Magnuson 1974, Coutant 1977), and the success of a fish in achieving its fundamental thermal niche can contribute to its fitness in terms of growth (Brett 1970, Magnuson et al. 1979). Recent studies have documented thermal habitat partitioning by fish in lake bottom habitat (Brandt et al. 1980), seasonal habitat shifts along temperature gradients (Matthews et al. 1985), thermal habitat shifts resulting from competitive interaction (Beitinger and Magnuson 1975, Crowder and Magnuson 1982), and complementarity in the use of food and thermal habitats in a lake (Crowder et al. 1981). Magnuson et al. (1979) stressed that temperature is an ecological resource and is one axis of an animal's multidimensional niche. The fundamental temperature niche of trout and char is probably similar to that of juvenile rainbow trout, which McCauley and Pond (1971) found to be 17-20 °C. It is intuitive that the fundamental irradiance niche of both trout and char is one which maximizes the reaction distance to prey targets. Therefore, habitat preference of both trout

and char based on temperature and irradiance level preferences is in warm epilimnial waters of littoral or epipelagic habitat. Since the reaction distance of char is maximized at a lower irradiance level than trout (Henderson and Northcote 1985), the fundamental habitat of char extends deeper in the water column than that of trout. In allopatry and sympatry, trout occupy their fundamental niche based on temperature and irradiance preferences. Although sympatric char occupy habitats deeper in the water column than trout, in allopatry they are found in shallower habitats that are more similar to their preferred thermal and irradiance niche. Therefore, an hypothesis of habitat selection based on temperature and irradiance level preferences is supported by the distribution of allopatric trout and, to a lesser extent char. The habitat shift of char in sympatry to colder habitats with lower irradiance levels is in accordance with the hypothesis that competition between trout and char in Loon Lake acts more strongly on char.

When competition concerns direct utilization of limiting resources and deprives other individuals of the benefits to be gained from those resources, the mechanism of competition is said to be exploitative. If competitive ability is based on interference phenomena and individuals harm each other by aggressive encounters, producing toxins, and so on, which prevent a competitor from gaining access to resources, the mechanism of competition is said to be interference (Crombie 1947, Elton and Miller 1954, Brian 1956, Miller 1967, Schoener 1983, Pianka 1983). Local extinction occurs only where species

niches overlap, thereby allowing populations to coexist in contiguous allopatry (Miller 1964). Based on his work with gopher species, Miller (1964) stated that, as a general principle, whenever competitive exclusion occurs and the fundamental niche of one species is included within the fundamental niche of another species, the first species with the specialized niche must be the superior competitor in order to survive. Miller's results are paralleled by the results of the present study, where the preferred habitat (i.e. fundamental niche) of trout is included within that of char, and trout is the superior competitor.

Connell (1961), Werner and Hall (1977), and Nilsson (1960, 1963) also obtained similar results. Connell found that the barnacle Cthamalus stellatus survived at all water levels in the intertidal zone, but persisted in competition with the superior competitor Balanus balanoides only by occupying a part of the environment where B. balanoides did not survive. Werner and Hall found that bluegill sunfish (Lepomis macrochirus) were more flexible in habitat use than green sunfish (L. cyanellus), which were limited to littoral habitats. In sympatry with aggressive green sunfish, bluegills shifted to smaller, less preferred food items in the open water column, while green sunfish remained in the littoral zone and exploited larger food items. The open water column provided a competitive refuge for the bluegill, which handled small foods more efficiently than did green sunfish. Nilsson found that brown trout (Salmo trutta) and arctic char (Salvelinus alpinus) in Sweden preferred similar

prey, but in sympatry, char shifted to offshore prey, primarily zooplankton, whereas trout continued to feed on preferred prey types in the littoral zone. The trout were more effective than char in exploiting preferred prey items and were much more territorial and aggressive in interspecific encounters. In each case cited above, the competitor that was a specialist in habitat or food selection (e.g. trout in the present study) was a superior competitor to the generalist competitor (e.g. char), and interference competition was the mechanism of exclusion of the generalist from its usual habitat.

Habitat selection behaviour of species evolves because organisms in some habitats leave more descendants than organisms in other habitats; such behaviour can be very exact and specialized in predictable environments (Krebs 1978). However, generalists often occur where they have few competitors (Morse 1980), perhaps due to their competitive exclusion by superior specialist competitors.

Allopatric populations of trout and char used in the present study both demonstrated plasticity in prey selection in the 18 mo following segregation in 1974 - 1976 (Hume and Northcote 1985). Both populations switched to abundant Chaoborus larvae in pelagic habitats. However, this switch in prey type represented a greater change in habitat selection by char than trout. Individual char were previously highly benthofagous in sympatry with trout, whereas trout occupied shallow habitats in Loon Lake. Therefore, char can be concluded to be more generalist, opportunistic predators than trout. In

the present study, allopatric char were more general in habitat utilization than trout. However, fluctuations in abundances of different prey types may partly explain the apparent diet expansion of allopatric char because Katherine Lake may have had more erratic fluctuations in food types and abundances than Loon or Eunice lakes (Hindar et al. in prep.). The habitat shift of char to less preferred habitats in the presence of trout may be based on interference by trout. Schutz and Northcote (1972) found that trout were aggressively dominant to char in most interspecies pairs in laboratory aquaria, and Rosenau (1978) found that trout were more aggressive than char in stream aquaria.

In summary, the present study showed evidence consistent with the hypothesis that trout and char were in competition in Loon Lake. Based on distribution between habitats in allopatry, char are generalists in habitat selection and trout are relative specialists. In sympatry, trout remain in shallow habitats similarly to allopatric trout, and may competitively exclude char from this zone. Diel and seasonal temporal differences are not important to habitat utilization of trout. The mechanism of competition of trout and char in Loon Lake is at least partially exploitative, based on selective differences between the two species. However, a mechanism of exploitative competition does not explain why char are not present in typical trout habitat. Other studies suggest that interference competition is usually the mechanism of competition when a generalist competitor is excluded from the preferred habitat of a specialist competitor.

In addition, the superior aggressiveness of trout is consistent with an hypothesis of segregation with depth based on interference competition. It is suggested that trout and char are segregated with depth in Loon Lake based on interference competition by trout, and that this mechanism is moderated by irradiance level, an environmental cue which provides structure in the pelagic environment.

4.2 Behavioural Interactions and Irradiance Level

If interactive segregation occurs between populations, the following criteria must be met:

1. The populations must be segregated spatially and/or temporally, at least during critical periods of resource acquisition.
2. The populations must be competitors, or potential competitors, for an essential resource such as food or space.
3. The populations must have a communication system of recognizable signals, which may take the form of aggressive or agonistic behaviours that signal dominance or territoriality to individuals or groups of the other population.
4. To avoid local extinction, both populations must be able to maintain growth and reproduction.

In accordance with Criterion 1, trout and char in Loon Lake are segregated spatially with depth (Armitage 1973, Hume 1978,

my field study). Furthermore, in accordance with Criterion 2, I presented evidence in my field study that trout and char are in competition. In sympatry, there is a habitat shift by char, but trout occupy their preferred habitat. Trout in sympatry with char in Loon Lake have similar spatial and temporal distributions as trout in allopatry in Eunice Lake; they are most dense in littoral and epipelagic habitats. However, char in Loon Lake have a restricted spatial and temporal distribution in relation to char in allopatry in Katherine Lake. In allopatry, char occupy the entire water column, but in sympatry with trout, char are found in deep limnetic water. It was concluded from the field study that trout and char in Loon Lake are in competition and that trout is the superior competitor. However, at this point it has not been shown whether competition is of the exploitative or interference type. My laboratory experiments address Criteria 3 and 4, and investigate behavioural interaction (interference competition) as a possible mechanism of interactive segregation between trout and char.

In conjunction with Criteria 3, one requisite of the establishment of a dominance relationship is a communication system of recognizable signals between dominant and subordinate individuals. The repertoire of behaviours encompassing aggressive behaviours performed by dominant individuals and submissive behaviours performed by subordinate individuals are termed "agonistic behaviour". The aggressor is identified by overt defense of its territory as attacking, chasing, or threatening, or displays which may be overt or ritualized (Morse

1980). Interspecific patterns of aggressive behaviour in animal groups studied to date resemble intraspecific patterns (Morse 1980, p.267), and in closely genetically related species such as trout and char, communication signals may be more similar than behavioural signals of species which are not closely related.

Aggressive behaviour and dominance-mediated interspecific relationships have been reported for many animal taxa, including mammals, birds, fish, lizards, salamanders, starfish, insects, crustaceans, spiders, and limpets (reviewed in Morse 1980, p.267). These relationships occur over a wide range of social situations, including both strict territorial situations and ones in which no stationary area is defended (Morse 1980). If the dominance relationship involves territoriality, aggressive behaviour is associated with a clear reference point in space (concept developed by Schjelderup-Ebbe 1922, cited in Morse 1980). The function of aggressive behaviour, then, is to gain access to resources (e.g. food, space, or mates) while restricting the availability of resources to another individual or group.

In accordance with Criterion 3, there is evidence that trout and char possess a common system of communication. Aggressive behaviours of trout such as nip, charge, and chase, and the submissive behaviour of char such as avoiding or fleeing from its aggressor combined to produce a dominance relationship in interspecies pairs in the present study. The dominance relationship in the laboratory aquarium may be associated with territoriality, as evidenced by the restriction of char to one

end, and the more general use of the aquarium by dominant trout (Figure 12). Fish may use the aquarium walls or substrate to visually locate territories. However, there would seem to be an absence of such spatial markers to locate territories in lake pelagic environments. Unless fish are closely associated with the lake surface or bottom, there are few visual cues for a fish as to its location. Therefore, how is segregation between Loon Lake populations of trout and char maintained?

One environmental cue which may provide a vertical "spatial" marker for trout and char in Loon Lake is irradiance level. Irradiance level is an important factor in selective differences between the two species in the procurement of food resources (Henderson 1982). Since trout are less able to perceive prey in low irradiance, the preferred habitats of trout have relatively high irradiance levels. If trout are dominant to char in Loon Lake, char will experience strong aggression in high irradiance habitats occupied by trout and char may flee to low irradiance habitats to seek refuge.

The laboratory experiments reported herein provide evidence for reduced intensity of behavioural interactions between trout and char as irradiance decreases to the visual threshold of trout. Assuming that aggression is based on visual cues, one explanation for reduced aggression by trout with decreasing irradiance level is that the ability of trout to visually perceive char declines over the range of experimental irradiance tested. The visual ability with respect to reaction distance to prey of trout and char certainly declines over this range

(Henderson 1982).

In addition to the reduced capability of trout to see char with decreasing irradiance level, the swimming activity of trout is another factor which would affect the frequency of visual contact of char by trout. Although the swimming activity of trout in interspecific pairs with char did not decrease significantly with irradiance level (F-test, $p > .05$), solitary trout were less active in low irradiance. Therefore, the presence of subordinate char may stimulate the swimming activity of trout to reinforce the dominance relationship. The confinement of trout and char in relatively small laboratory aquaria at almost fifty times the natural fish density in Loon Lake "forced" more intense interactions between the fish than they would likely experience in their natural environment. Since trout in Loon Lake are not confined in close proximity with char as they are in experimental aquaria, their swimming activity would probably be more similar to that observed in solitary trout. Therefore, in low irradiance habitats in Loon Lake, trout would have very little visual contact with char due to reduced visual ability and swimming activity.

Although aggression by trout decreased to a very low intensity at their visual irradiance threshold, the dominance relationship with char persisted. Although most behavioural interactions at all irradiance levels were submissive acts by char (i.e. "avoidance"), the proportion of submissive acts increased with decreasing irradiance level. In Loon Lake, a dominance relationship between individual interacting pairs of

trout and char would possibly not be established nor would it persist as observed in the experiments, because the char would be able to flee from its aggressor. In low irradiance habitats, char would have a relatively low encounter rate with trout, and the low intensity of aggression might then not be strong enough to establish a dominance relationship.

In Loon Lake, trout and char segregate spatially on an irradiance gradient, where trout use relatively high irradiance level habitats and char use deeper habitats with lower irradiance levels. Competitively inferior char experience differences in intensity of aggression by trout along this gradient, and the distribution of the two species is consistent with these differences. If char can learn to associate relatively high irradiance level with a greater intensity of aggression from trout, the hypothesis that habitat segregation is maintained by aggressive interspecific interactions by competitively superior trout cannot be rejected. The ability of char to associate irradiance level with aggression by trout was not tested in this study.

Further investigations, particularly direct field observations, are required to test the application of this laboratory study to interactions of trout and char at irradiance levels in their natural lake environment. A more rigorous laboratory test of the hypothesis that segregation between trout and char is maintained by a mechanism of interactive segregation based on irradiance levels would be to conduct similar experiments to mine but in larger aquaria. Use of 10 x 10 m

aquaria would scale the experimental fish density to approximately the natural density in Loon Lake. In aquaria of this size, behavioural interactions between interspecies pairs would probably be much less intense than I observed, but would probably reflect more accurately the natural rate of interaction. However, the results of my laboratory experiments may be indicative of interactions that take place in the natural environment in a more subtle form.

The fourth criterion for interactive segregation is that populations must be able to obtain adequate food resources to maintain growth and reproduction, thereby avoiding local extinction. It is not known whether the trout and char populations in Loon Lake are at stable levels but the fact that char have persisted in Loon Lake for many decades if not centuries indicates that they have been able to obtain adequate food resources for growth and longterm reproduction (see also Jonsson et al. 1984). However, in coexisting populations of trout and char, the exclusion of char from its preferred habitat or distribution probably means that char are restricted to less than optimal foraging patches, since habitat selection is ultimately based in its contribution to fitness of the individual (Alcock 1975, Werner et al. 1981). A reduction in energy intake per foraging effort by char due to less dense prey, smaller prey, and increased search and/or handling time in such patches obviously results in decreased fitness. A strong reduction in fitness would result in the eventual extinction of the population. One mechanism the char may use to obtain

adequate food resources is to occupy low irradiance habitats to forage unhindered by aggressive trout. The feeding performance of char may improve when aggression by trout is reduced. The feeding experiments in this study were performed to test whether the feeding performance of trout and char was consistent with an hypothesized mechanism of interactive segregation on irradiance level gradients in Loon Lake.

My experiments provide evidence that in an irradiance level that maximized reaction distance of char and very nearly maximized that of trout (3.0×10^{18} photons/m²/s), the feeding rate of char on Neomysis mercedis was adversely affected by aggressive behaviour of trout. Char which had more behavioural interactions with trout made fewer feeding strikes (Figure 15). However, in Loon Lake habitats below the visual irradiance threshold of trout (3.0×10^{15} photons/m²/s), trout would not detect prey items visually (Henderson and Northcote 1985) and would presumably not see char, thereby removing the stimulus for aggressive behaviour of trout. Moreover, below this threshold, trout would not restrict the feeding performance of char through aggressive behaviour, and char could forage as if trout were not present, detecting prey items visually to their visual irradiance threshold (7.0×10^{14} photons/m²/s), and below this level detecting prey using chemoreception (Henderson 1982).

The feeding rate of char was inferior to that of aggressively dominant trout at all irradiance levels above the visual irradiance threshold of trout. As described in the foraging model of Henderson and Northcote (1985), the greater

reaction distance and swimming activity of trout (Figures 14 and 18) allowed trout to search a larger volume of water than char thereby increasing prey encounter rate. In my experiment, char were subordinate at all irradiance levels and were restricted to one end of the aquarium. They behaved like "sit and wait" predators, and were only able to search for prey in a hemispherical volume of water, with reaction distance as the radius. The feeding performance of char in interspecific pairs dominated by trout (8.76 ± 9.47 (mean \pm standard deviation) strikes per 30 minutes, $n=6$) was significantly less than that of solitary char (48.14 ± 6.86 strikes per 30 minutes, $n=2$), but was not significantly different from that of char dominating interspecific or intraspecific pairs (27.4 ± 20.1 , $n=4$ and 7.72 ± 7.81 , $n=2$ strikes per 30 minutes, respectively). The feeding performance of both trout and char was reduced with decreasing irradiance level. However, feeding strikes by trout declined more rapidly than those of char (Figure 16). It should be noted that feeding strikes included both successful and unsuccessful attacks on Neomysis prey, and that the proportion of unsuccessful strikes probably increased with decreasing irradiance level, especially for trout. Prior to performing the experiment, it was expected that the feeding performance of char would improve with decreasing irradiance level while aggression by trout was less frequent. However, at all irradiance levels above the visual irradiance threshold of trout, the feeding performance of trout was superior to that of char (Figure 16). This is probably because the dominance relationship between the

fish persisted to the visual irradiance threshold of trout. For reasons already given, in Loon Lake, the dominance relationship would probably break down in low irradiance habitats, and therefore the feeding performance of char might then improve.

In any case, char are certainly more capable than trout of procurement of food resources in low irradiance habitats (Henderson and Northcote 1985). Henderson showed that, although the maximum reaction distance for visual prey detection by char at their saturation irradiance level of 3.0×10^{16} photons/m²/s, char use visual prey detection down to their visual irradiance threshold of 7.0×10^{14} photons/m²/s, below which they use chemoreception of prey. Trout are only able to use visual prey detection down to an irradiance level of 3.0×10^{15} photons/m²/s, which corresponds to a depth of below 40 metres in Loon Lake on a sunny summer day. For approximately 5.5 h per night, not even surface waters are illuminated sufficiently for prey detection by trout (Henderson and Northcote 1985, their Figure 5). Therefore char are able to capture prey in these darker spatio-temporal habitats in the absence of trout.

4.3 Concluding Statement

Segregation of trout and char in Loon Lake is certainly selective due to behavioural (Schutz and Northcote 1972) and physiological (Henderson 1982) differences that affect prey acquisition. However, competition plays a role in habitat utilization of sympatric trout and char. Trout occupy surface habitats whether allopatric or in sympatry with char. On the

other hand, char undergo a habitat shift between sympatry and allopatry. In allopatry, char occupy different habitats seasonally, in accordance with food abundance, but in sympatry, char shift to deeper, less well-illuminated habitats. Temporal segregation between trout and char was not pronounced. It is concluded that trout are competitively superior to char, based on the lack of habitat shift by trout and the accompanying habitat shift by char, although this result is interpreted with caution since differences in prey distributions partly explain habitat utilization. Difficulties in drawing strong conclusions from the field results arise due to the lack of rigid controls in such whole lake experiments. In particular, the influence of differences in littoral development and prey distributions on habitat utilization by fish are difficult to quantify.

Other studies have shown that trout are very aggressive towards char in lake (Schutz and Northcote 1972) and stream (Rosenau 1978) laboratory aquarium studies. It is concluded from my laboratory experiments that behavioural interactions between dominant trout and subordinate char decrease with irradiance level. If this holds true in lake environments, char may seek refuge from aggression by trout by shifting to low irradiance habitats. Char do switch to such habitats in sympatry with trout, but whether their habitat shift in Loon Lake is a result of interference mechanisms is not clear. This relationship might be confirmed in an appropriate study based on field observations. Although the feeding performance of char improves with decreasing intensity of aggression by trout, my

laboratory experiment did not show that decreasing irradiance level per se produced the same effect. This is probably because in my experiment, the dominance relationship between trout and char persisted in conditions of low irradiance due to the continued confinement of fish pairs in aquaria.

This study corroborates the scenario proposed by Henderson (1982) that when trout and char invade a fishless lake, trout through their aggressive highly competitive behaviour, are able to occupy their "optimal" habitat based on food preferences and restrict char to other portions. However, the habitat occupied by char in sympatry with trout may be "optimal" for char, since food, competition, and predators are important variables determining the habitat for each species. Segregation of populations need not be exclusively selective or interactive, and although the segregation of trout and char in Loon Lake is certainly selective, an hypothesis involving an interactive mechanism of segregation and interference competition along irradiance level gradients cannot be rejected.

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9. Hindar, K., J.H. Andrew, B. Jonsson and T.G. Northcote. (in preparation) Feeding strategies of sympatric and experimentally allopatric cutthroat trout and Dolly Varden char.

RESEARCH PRESENTATIONS

1. Pacific Ecology Conference, Bamfield, B.C., 21-24 February 1985.
2. SCWIST Society for Canadian Women in Science and Technology Symposium, Cowichan Bay, B.C., 26-28 April 1985.
3. Institute of Animal Resource Ecology, UBC Research seminar, 9 September 1985