AN EXPERIMENTAL STUDY OF FEEDING BEHAVIOR AND INTERACTION OF COASTAL CUTTHROAT TROUT (*Salmo clarki clarki*) AND DOLLY VARDEN (*Salvelinus malma*)

by

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ABSTRACT

Differences in food habits and spatial distribution of sympatric Dolly Varden (Salvelinus malma) and cutthroat trout (Salmo clarki clarki) in a small coastal lake were documented by Andrusak (MS 1968). Segregation was inferred to be of the interactive type hypothesized by Nilsson (1965, 1967).

The object of this study was to describe feeding behavior of individuals from these sympatric populations, and to evaluate the importance of food exploitation to the segregation process. Individual and paired fish were studied in the laboratory throughout the spring, summer and autumn.

The different food habits were found to be due to a number of basic behavioral and morphological differences between the species. Dolly Varden oriented to and rested on the bottom. Cutthroat rested in the water column and were frequently surface oriented. Searching behavior differed between the species. Dolly Varden swam faster and at relatively constant rates. They sampled "mouthfuls" of substrate as they searched. Trout alternately hovered and cruised, sampling specific items. At low light intensities they were much less successful than the char at finding benthic food items. The mouth of the Dolly Varden is small and "scoop-like" compared to that of the cutthroat, and seems particularly well adapted for benthic feeding. Dolly Varden searched persistently for benthic organisms in the absence and presence of surface insects. Cutthroat rapidly switched from bottom to surface

feeding if insects were presented there.

The observed differences between species were fully expressed in isolated individuals. There was no evidence of the differences being magnified through interspecific competition. These differences, believed to be inherent, were considered sufficient to keep the species segregated without the involvement of competition. Segregation was concluded not to be of the interactive type, even though the populations still retained considerable plasticity enabling them to switch diets or habitats when necessary or advantageous. The period of intense competition and food exploitation was considered to have occurred and ended during earlier stages of the coexistence.

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INTRODUCTION

Throughout northern temperate regions there are numerous examples of coexisting closely related fishes. Many of these are salmonids, and examples are described by Kalleberg (1958), Nilsson (1965), Newman (1956), Everhart and Waters (1965), and Hartman (1965). All salmonid species are similar in morphology and trophic adaptations, and are therefore potential competitors.

Nilsson (1967) points out that though it is often easy to demonstrate segregation of coexisting fishes it is difficult to determine if the segregation is interactive or due to completed ecological divergence. Nilsson (1955, 60, 61, 63, 65, 67) has looked in detail at coexisting populations of *Salvelinus alpinus* and *Salmo trutta* in Sweden, and has developed the hypothesis that their co-existence is due to interactive segregation. He suggests that most species of fish in northern temperate regions may provide examples of interactive segregation since the faunas are young and the ecosystems are still evolving relatively rapidly. The term, interactive segregation, was originally used by Brian (1956), and means that any ecological differences, such as food or habitat selection, between the species are enlarged considerably when the species are sympatric.

Nilsson (1967) suggested the following mechanisms are possibly involved in interactive segregation:

a. Exploitation - "one species is more efficient in a habitat than another, perhaps because it can find and use vacant resources more quickly than the other" (Brian 1956).

b. Territoriality

c. Food fighting

d. Predation

e. Other interferences.

A second type of segregation defined by Brian is selective segregation. This type he says "consists of the selection by instinctive behavior of totally different habitats (that is resources and modifying factors combined)". Nilsson (1965) mentions that the work of Fryer (1959) on Lake Nyasa cichlids indicates selective segregation. Selective segregation could theoretically be an end result with interactive segregation an intermediate step.

In British Columbia Andrusak (MS 1968) studied allopatric and sympatric populations of cutthroat trout (Salmo clarki clarki) and Dolly Varden (Salvelinus malma) in three small coastal lakes. He described distinct spatial and food segregations during the summer for the sympatric populations in Marion Lake which suggests interactive segregation is present between these species in much the same manner as described by Nilsson (1967) for Salvelinus alpinus and Salmo trutta.

Andrusak's field study clearly demonstrates a seasonal segregation of the two species in Marion Lake. The study did not include any detailed investigation of mechanisms involved in the segregation process.

The objectives of my study were twofold:

1. To describe in detail the feeding behavior of lake dwelling coastal cutthroat and Dolly Varden.
2. To look specifically at food exploitation as a mechanism for segregation; viz, to determine if there were differences in the feeding behavior of the two species, that could contribute significantly to their segregation.

Based on field observations and Andrusak's earlier study it was hypothesized that Dolly Varden were more successful predators than cutthroat on benthic organisms, and that cutthroat were more successful than Dolly Varden feeding on surface organisms. Experiments were then conducted to test these hypotheses.

Brian's (1956) definition of the exploitation mechanism states that one species is more efficient than another, but does not define what is meant by efficient. In this study the term, more efficient, means that one species caught significantly more food than the other in a given time. No attempt was made to relate energy obtained to energy expended.

MATERIAL AND METHODS

THE FISH

Experimental fish used in the study were mature coastal cutthroat (*Salmo clarki clarki*), and coastal Dolly Varden (*Salvelinus malma*).

Cutthroat were typical coastal specimens as described by Carl, Clemens, and Lindsey (1959) or Clemens and Wilby (1961). The jaw was long, extending well beyond the posterior margin of the eye, and the snout was relatively pointed.

Dolly Varden from Marion Lake differed considerably from the general description of the species given by the above authors. Clemens and Wilby (1961) say that the head and mouth are large with the maxillary reaching to a point behind the posterior margin of the eye. This description is very similar to that of the cutthroat's head. Marion Lake Dolly Varden had small heads and mouths compared to Marion Lake cutthroat (Fig. 1). The mouth was nearly subterminal and the snout blunt, whereas the cutthroat's mouth was distinctly terminal and the snout pointed.

Marion Lake fish were used exclusively for all experiments except those involving paired cutthroat and Dolly Varden. A few individuals in this series came from other coastal lakes. All cutthroat were angled and all Dolly Varden gill netted. Most of the data came from four cutthroat and four Dolly Varden from Marion Lake. These will be referred to as CT #1, #2, #3, #4, and DV #1, #2, #3, and #4. All were approximately equal in size (Table I).

Fish used in the study all appeared to be in good

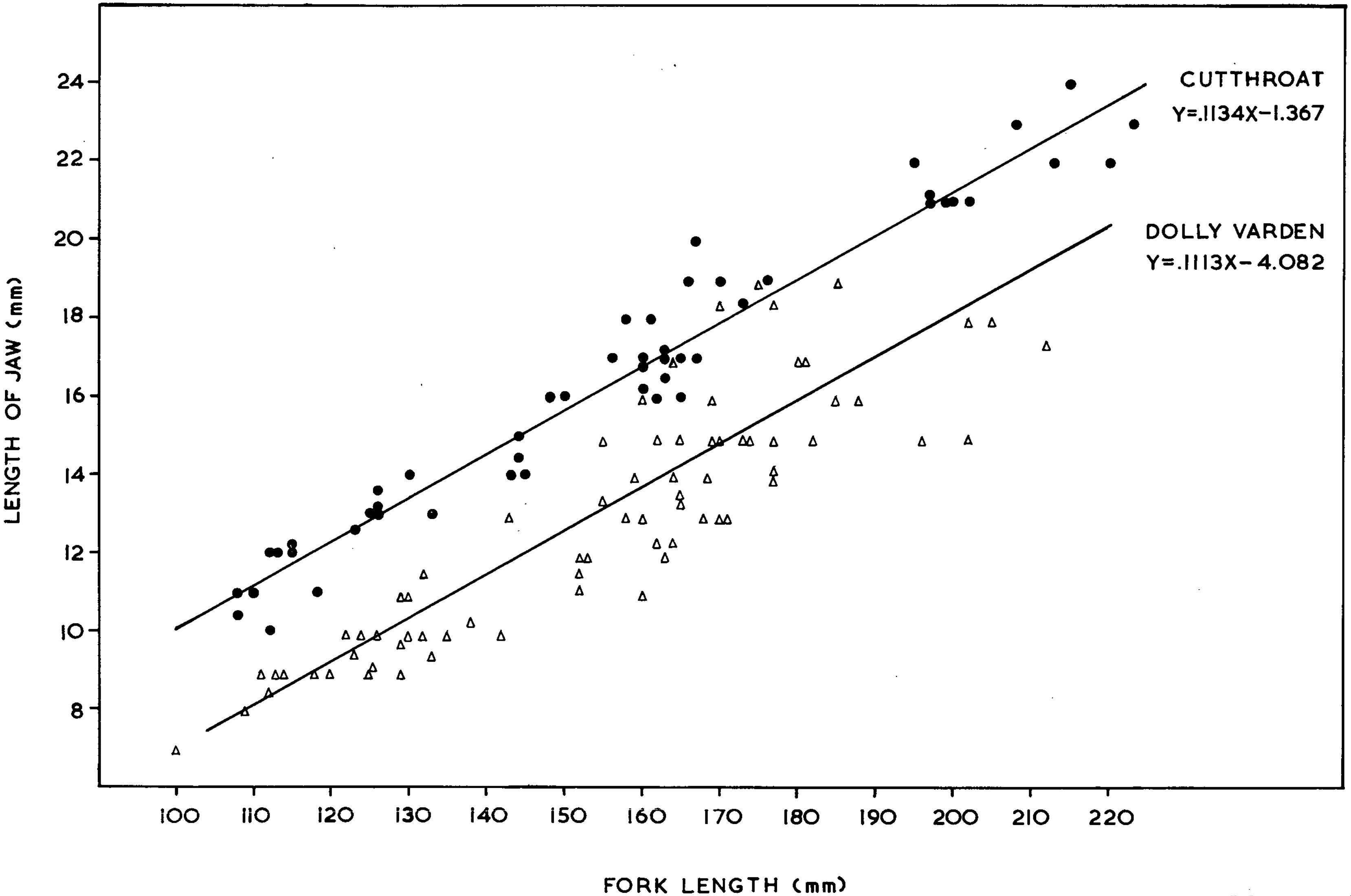


FIG. 1 Differences in mouth size between Marion Lake cutthroat and Dolly Varden.

TABLE I. Length and weight of experimental fish.

	Weight (g)	Length (mm)	Date of length-weight measurements
CT #1	97.5	212	December/68
CT #2	57.5	171	October/68 *
CT #3	54.2	174	December/68
CT #4	64.5	185	December/68
DV #1	79.3	192	December/68
DV #2	64.6	182	October/68 *
DV #3	69.8	182	December/68
DV #4	70.0	179	December/68

* Fish died in October

condition. If an individual did not seem healthy then it was not used. Cutthroat #2 and Dolly Varden #2 died suddenly from unknown causes in October 1968. Otherwise all fish seemed to grow and survive well during the experiments.

CT #1 gained 39 g and grew 32 mm between April 1, 1968 and December 15, 1968. DV #1 gained 33 g and grew 27 mm in the same period. During this time the fish were fed an excess of frozen brine shrimp each evening, but their stomachs were frequently evacuated the following morning.

OBSERVATIONS OF FISH IN MARION LAKE

Most observations were made from a row boat with the aid of a plexiglass viewing box. Two persons were in the boat, one observing, the other steering with oars and recording data. It was seldom necessary to row since prevailing breezes moved the boat sufficiently. The viewing box was moved slowly from side to side behind the transom to scan as wide a field as possible. A few fish sightings were made from the boat through polaroid sun glasses, and others by swimming along the surface with mask and snorkel.

Sightings were restricted almost exclusively to one 100-meter section of the lake, parallel to the shore and including depths to 4 meters. This region had a gently sloping mud bottom, many rooted aquatics, and submerged logs.

All observations were made between 0900 and 1500 hours since shadows from the surrounding mountains made spotting and identification difficult before and after this period.

HOLDING FACILITIES IN THE LABORATORY

Fish were held indoors in two concrete troughs 366 cm x 41 cm x 38 cm. Densities varied from 20 to 30 fish per trough and included both species.

A steady flow of water was maintained in the holding tanks with complete exchange taking about three hours. Water temperature was usually about 1 C higher than the incoming city water, and ranged from 6 C in January to 14 C in August.

Photoperiod in the holding area was natural, the overhead fluorescent fixtures being controlled by a photoelectric cell located outside.

EXPERIMENTAL FACILITIES IN THE LABORATORY

Observation Tanks

The four experimental tanks were housed in a 3.3 m x 4.5 m room where noise and interference were negligible. The tanks 122 cm x 61 cm x 61 cm were made of painted plywood with plexiglass fronts. Three of them were subdivided in the middle by removable fiberglass screen dividers. A Dolly Varden was held in one end and cutthroat in the other. Screened lids kept the fish from jumping out. The fourth tank was not divided and was used for the daily experiments. Vertical lines on the plexiglass front defined four equal quadrants.

Each tank was illuminated by a single "cool white" General Electric fluorescent lamp providing surface illumination of approximately 500 lux. Illumination at a depth of 48 cm (8 cm from the tank bottom) was approximately 240 lux. This was as close to the bottom as the phototube could be placed. All feeding experiments, unless stated otherwise, were at this light intensity. Photoperiod in the observation room consisted of 14 hours "days" and 10 hours "nights" for the duration of the study. Black plastic curtains were hung between and above the tanks to keep the room relatively dark. Observations were made from a chair 1 to 3 meters in front of the tank.

Water temperature and flow were similar to conditions described for the concrete holding tanks.

Recording Equipment

Behavior was recorded with the aid of a tape recorder, eight key multiple counter, and stop watch.

Illumination levels were varied by replacing the fluorescent lamp with two 60 watt "Shadow Ban" white incandescent bulbs in circuit with a Variac voltage regulator.

Light intensities were measured with a Photovolt Model 514 M photometer fitted with phototube C and a scotopic (human eye) correction filter. The phototube was calibrated in June 1968 using a N.B.S. foot candle lamp. It was housed in an underwater case with an opal diffusing glass producing a reasonably close fit to a cosine response curve. By controlling illumination levels with the Variac, spectral characteristics of the light were altered considerably, the reds predominating at the lowest intensities. Readings in foot-candle or lux units were therefore very approximate.

Stomach Pump

Stomachs were evacuated with a stomach sampler similar to that described by Seaburg (1957). The sampler used had a 1.5 mm inside diameter copper inlet tube and 6 mm I.D. outlet tube. Both tubes were 140 mm long. The pump was 100% efficient in recovering chironomid larvae eaten in the preceding hour. This was established from numerous trials in which larvae in the tank were counted before and after a feeding session, and the differences checked against the number evacuated from the stomach. Fish were anaesthetized in a .06% solution of 2-phenoxyethanol prior to pumping. No adverse effects from this procedure were evident. CT #1 had its stomach evacuated approximately 85 times between June 20 and November 30, 1968. Behavior and condition of this fish appeared "normal" for the duration.

GENERAL LABORATORY ROUTINE

Dolly Varden and cutthroat in use were held in three of the four aquaria in the observation room. All experiments involving single fish were conducted in the fourth tank, the experimental fish being lifted into the tank immediately prior to the experiment and removed immediately following it.

Experimental fish in the observation room usually had their stomachs evacuated in the morning if experiments were scheduled for later in the day. This was done in an attempt to standardize hunger levels. No experiments were run until at least an hour after evacuation, although the fish would feed within 5 to 10 minutes of recovery from the anaesthetic. The stomach pump was also used at the end of each feeding experiment to get a direct count of the number of invertebrates captured.

Fish in the holding troughs were fed daily. Their food alternated between frozen brine shrimp, frozen fish, and horse heart.

FIELD OBSERVATIONS IN MARION LAKE

Results of gill netting and stomach analysis by Andrusak (MS 1968) indicated that during July and August Marion Lake Dolly Varden fed predominantly on the benthos and cutthroat at the surface (Fig. 2). Field studies were conducted to try to substantiate Andrusak's findings by direct observation.

SPATIAL DISTRIBUTION

All observations were restricted to depths of 4 meters or less (Table II). Within this zone 40% of the Dolly Varden observed were swimming within a few centimeters of the bottom and 60% were in mid-water. The absence of resting fish may have been partially due to the difficulty of seeing immobile fish lying on the bottom. No Dolly Varden were seen between the shore and the 2-meter contour.

All cutthroat seen were within 1 to 2 meters of the surface. Fifty five per cent of these were inside the 2-meter depth contour, but none was closely associated with the bottom. Cutthroat were frequently hovering in the shallows when first spotted, but within seconds moved away. They seemed more wary than the Dolly Varden who could often be watched for several minutes before being disturbed. The observed vertical distribution corresponded closely with Andrusak's gill net results (Fig. 3).

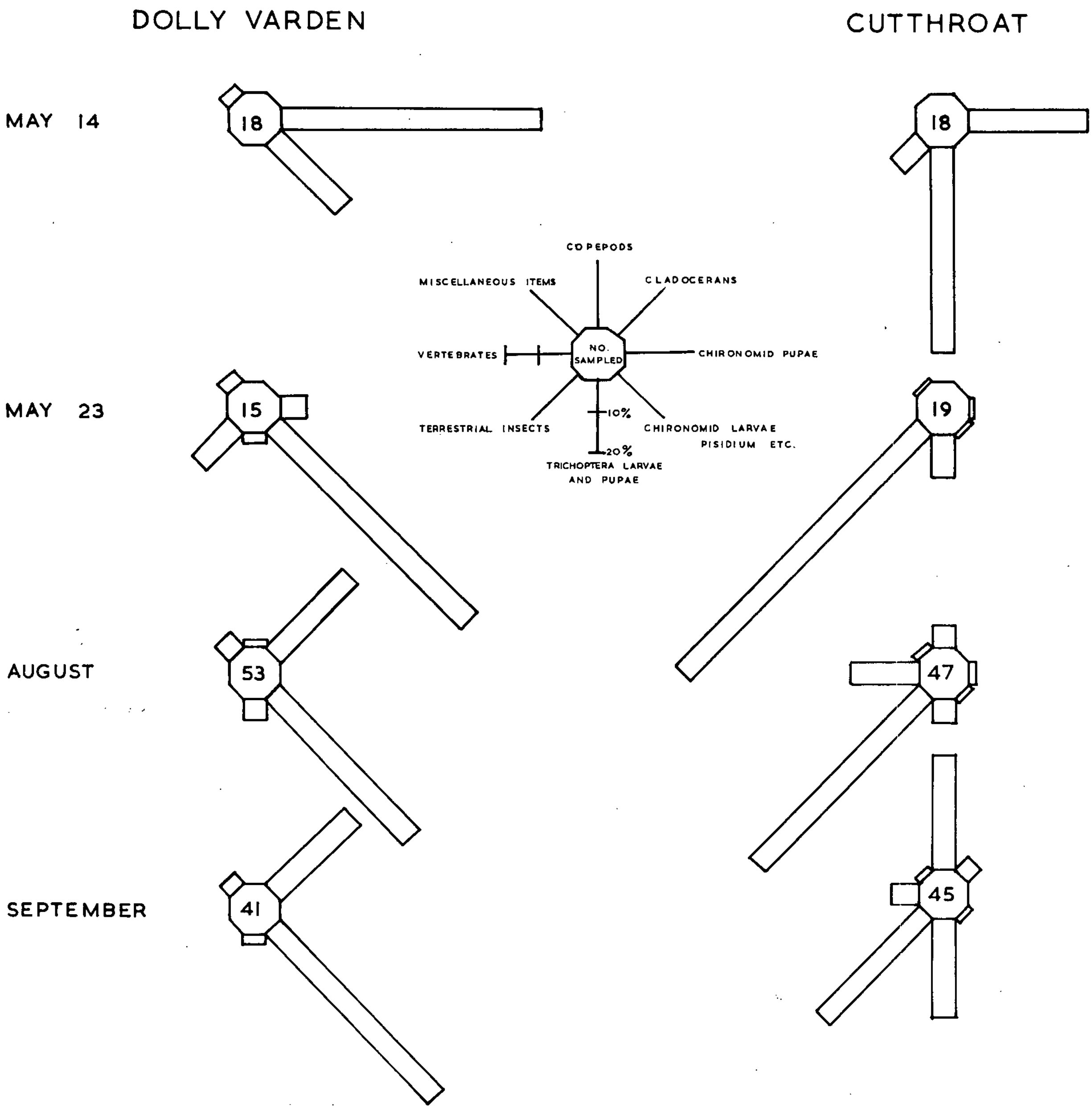


FIG. 2 Stomach analysis of Marion Lake Dolly Varden and cutthroat trout in average per cent volume, May, August, and September, 1967 (adapted from Fig. 17, Andrusak 1968 MSc Thesis).

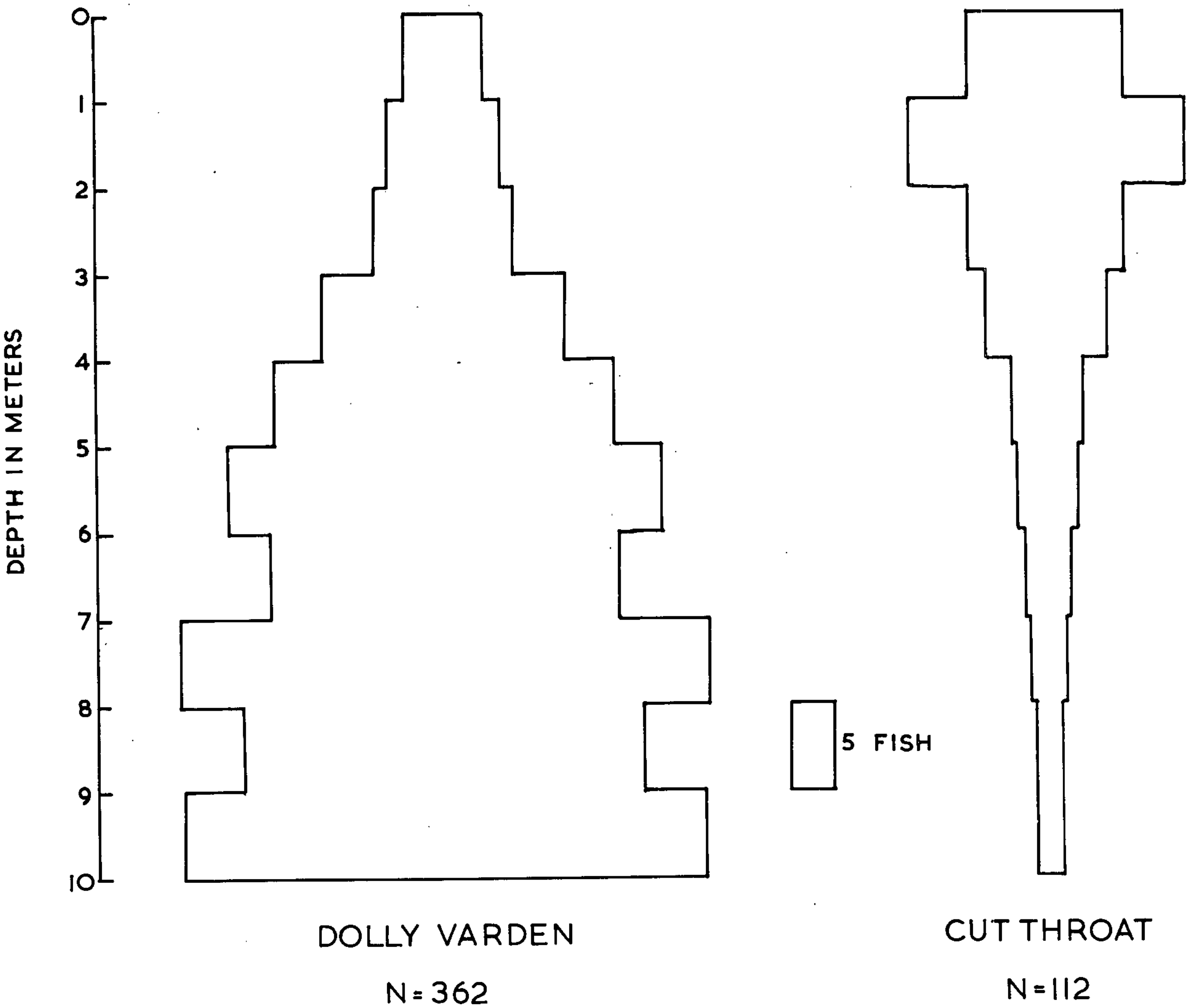


FIG. 3 Vertical distribution of Dolly Varden and cutthroat trout caught in 10 m floating nets in Marion Lake, May 15 - Sept. 15, 1967 (from Fig. 12, Andrusak 1968 MSc Thesis).

TABLE II. Depth at which fish were observed in Marion Lake, August and September 1968.

	0 meters to 2 meters		2 meters to 4 meters	
	Bottom	Midwater	Bottom	Midwater
Cutthroat	0	14	0	11
Dolly Varden	0	0	30	48

FEEDING BEHAVIOR

Dolly Varden were frequently observed feeding on the benthos and in the water column in Marion Lake (Table III). Feeding cutthroat were only positively identified two or three times and all were taking surface insects. It seems likely that the reason more feeding trout were not seen is that they were close to the surface and therefore frightened by the boat before being observed. Probably the majority of fish surfacing in the lake were cutthroat. During the summers of 1967 and 1968 approximately 75 were angled with worms, artificial flies, or spinners within a meter of the surface. Only three Dolly Varden were caught in this manner.

Dolly Varden feeding on the benthos swam slowly, parallel to the bottom, with frequent momentary stops as they dipped to pick up and then reject bottom materials. Those feeding on plankton constantly changed direction both laterally and vertically as they "mouthed" at objects in the water column.

TABLE III. Feeding locations of Dolly Varden and cutthroat observed in Marion Lake, September 5 and 6, 1968.

	Feeding on benthos	Feeding on midwater plankton	Angled with fly at surface
Cutthroat	0	0	20
Dolly Varden	13	12	0

Sixty five of the 78 Dolly Varden observed were small (100 - 150 mm). Andrusak (MS 1968) noted that Dolly Varden caught during the summer in three meters or less were often small. Forty six of the 65 Dolly Varden in this small size class were seen in mid water whereas 11 of 13 in the 150 - 200 mm size class were very close to the bottom (Table IV). This corresponds with Andrusak's findings that the smaller Dolly Varden fed heavily on plankton in late summer whereas the 100 - 200 mm group fed primarily on bottom fauna.

TABLE IV. Size differences of Dolly Varden seen near the bottom and in the water column of Marion Lake, August and September 1968.

	Bottom	Midwater
Small (< 150 mm)	19	46
Large (> 150 mm)	11	2

Dolly Varden appeared to be much more gregarious than cutthroat. Bottom-feeding individuals repeatedly were seen travelling in twos and threes and plankton feeders were seen in loose aggregates of up to six or more (Table V). Minimum distances between individuals were estimated to be about 10 cm. Two pairs of cutthroat were observed. The others were all singles. Andrusak's gill net data showed that Dolly Varden were highly clumped during the summer, and cutthroat distributions were either dispersed or random.

TABLE V. Numbers of fish seen together in Marion Lake, August and September 1968.

	Singles	Twos	Threes	Fours	Fives	Sixes	>Six
Cutthroat	23	2	0	0	0	0	0
Dolly Varden	16	6	6	1	0	2	1
Combined cutthroat and Dolly Varden		0	0	0	0	0	0

LABORATORY EXPERIMENTS

To test the hypotheses that Dolly Varden feed more successfully than cutthroat on benthic organisms, and that cutthroat are the more successful species at the surface, a series of laboratory experiments were conducted. These experiments were designed to determine spatial preferences, and to compare the rate of learning and feeding efficiency of individuals from each species when offered surface organisms only, bottom organisms only, or a combination of both.

SPATIAL DISTRIBUTION

Dolly Varden and cutthroat in the laboratory differed considerably in their resting habits. These differences were quantified by watching isolated individuals of each species periodically throughout the day, and recording the time spent at each location.

Between feedings Dolly Varden (1 per tank) spent an average of 50 to 75% of their time lying on the tank bottom. It was uncommon to see them resting anywhere else (Table VI). This behavior seems typical of the genus Salvelinus. Newman (1960) described it for Dolly Varden, Nilsson (pers. comm.) for arctic char (S. alpinus), and Newman (1956) for brooktrout (S. fontinalis). Resting Dolly Varden sometimes lay on their bellies, but frequently the body was held off the bottom by the caudal, pelvic, and pectoral fins.

When not resting Dolly Varden usually swam vigorously around the tank. This swimming was frequently up and down in the tank corners and back and forth against the plexiglass front. It was considered to be a type of escape activity and persisted intermittently in some fish for months.

Isolated cutthroat in aquaria generally hovered in one place in the water column for most of the time. It was difficult to tell if hovering fish fixed their positions in relation to distance off the bottom or from the surface. Some hovered just beneath the surface while others stayed within 2 or 3 cm of the bottom. In either case they were never more than 50 cm from the air-water interface, and most seemed to be visually oriented to the surface.

TABLE VI. "Resting" positions of 10 cutthroat and 10 Dolly Varden in observation tanks (single fish in tanks; data represent one hour of "resting" time per fish).

	Bottom	Distance above the bottom			
		2-10 cm	11-20 cm	21-30 cm	31-40 cm
Cutthroat	1	3	2	3	1
Dolly Varden	9	0	0	1	0

Trout and char in the holding troughs were held together in mixed groups. The troughs were not suitable for lengthy observation work, but usually one could get a brief look at the fish before frightening them. Most of the Dolly Varden lay on the bottom and a few were always cruising or hovering, but all of the cutthroat hovered off the bottom.

FEEDING BEHAVIOR

1. Learning and prey recognition

During the first two weeks in the laboratory when experimental techniques were being improved, and pilot experiments tried, it became apparent that the Dolly Varden and cutthroat in use (DV #1 and CT #1) improved in their ability to capture chironomid larvae for four or five consecutive days. On each of these days the fish spent one 30 to 40 minute period searching for the larvae. Thereafter, additional experience no longer resulted in increased captures per unit of time. The number of larvae caught in subsequent half-hour feeding sessions levelled off with slight daily variation in either direction.

An experiment was subsequently set up to compare the capturing abilities of "naive" and "experienced" fish of both species searching for chironomids. Naive fish were those that had been captured at Marion Lake 9 months earlier, and had at no time during these months been exposed to chironomid larvae. These fish were considered to be naive for only one feeding session on the larvae. Experienced fish were those that had previously reached a plateau in larvae captured.

Individual fish were given 30-minute feeding sessions on 50 red _Chironomus sp._ larvae in a sand and "leaf-litter" substrate. The substrate was a 5 mm deep mixture of five parts sand under one part leaf-litter. Leaf-litter consisted of the evergreen needle and twig residue left after sieving Marion Lake bottom samples.

Larvae were distributed in the tank 15 minutes before introducing the fish, at an average density of 1 per 132 cm^2. Approximately 10% buried themselves completely within minutes, but the majority remained exposed for the duration of the experiment.

Each fish was lifted in a dip net from its holding tank into the observation tank, and the feeding session was considered to have started when it made its first feeding intention movement. At the end of 30 minutes it was removed and anaesthetized. Captured larvae were recovered with the stomach pump.

Experienced cutthroat and Dolly Varden began to search within a minute or two of being placed in the tank. Naive fish were held in the observation room for only 24 hours prior to the experiment and many would not eat after being moved from one tank to another. To be sure that the naive experimental fish would eat, each was offered a small portion of brine shrimp at the start of the experiment. Those that refused the shrimp were not used.

During each feeding period the following elements of behavior were recorded:

1. "Bottom grabs" (B.G.) - included all attempts by the fish to pick up something from the bottom.
2. Quadrant changes - scored each time the fish moved from one to another of four equal sections in the tank.

The four naive cutthroat and five naive Dolly Varden captured an average of 13% and 12% respectively of the 50-chironomid ration. Experienced trout and char all scored between 25% and 30% (Fig. 4). Naive fish of both species made

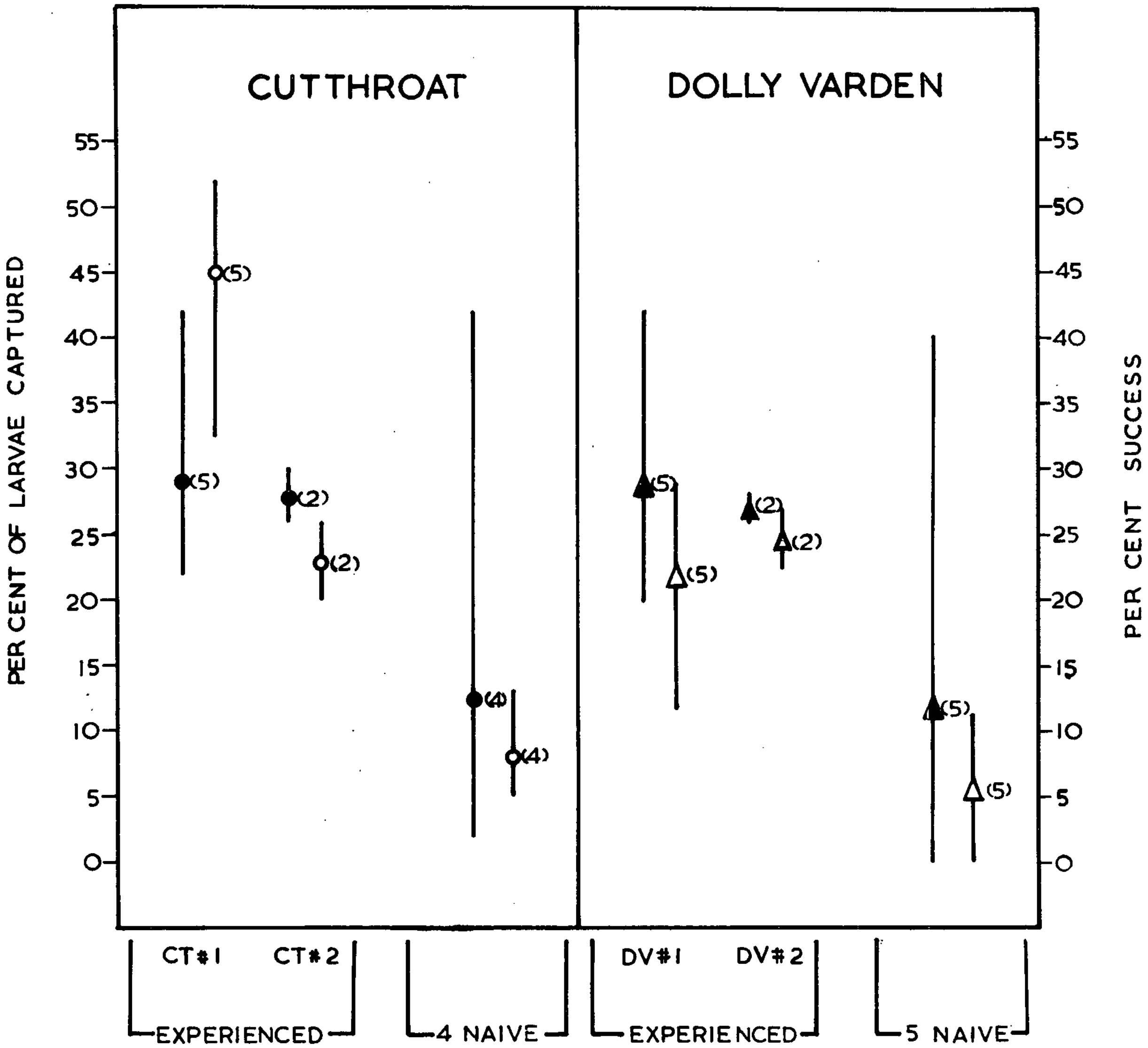


FIG. 4 Feeding success of individual experienced and naive cutthroat and Dolly Varden searching for 50 *Chironomus* larvae during a 30 minute feeding session. Mean per cent of larval ration captured = solid symbols. Mean per cent success (open symbols) = no. of captures no. of bottom grabs. Vertical lines indicate range; number of replicates in brackets.

proportionately more grabs at non-living objects than did the experienced fish. Per cent success was therefore lower for the naive than experienced predators. Naive fish did not seem to recognize larvae as readily as experienced ones. One cutthroat and one Dolly Varden captured as many larvae as the most successful experienced fish, but per cent success was only 14% and 11% compared to a mean of 25% or more for each of the experienced predators. These high capture scores were due to the fish sampling an exceptionally large amount of needles, sticks, and bottom debris. The results indicated that cutthroat and Dolly Varden have to learn to feed effectively on new types of prey. No differences were apparent between the trout and char.

A temporary shortage of red *Chironomus* larvae led to the next experiment. During a feeding session with one of the experienced Dolly Varden a 40-larvae ration was made up of ten *Chironomus* and 30 green *Psectrotanypus*. At the end of the period evacuation of the stomach revealed four *Chironomus* only. Before this observation it was assumed that once a fish commenced feeding on chironomid larvae, all exposed species would be vulnerable.

To test this assumption four cutthroat and Dolly Varden, experienced feeders on red *Chironomus*, were each given 10-minute feeding sessions on green *Psectrotanypus* on four consecutive days. Larvae were distributed on a sand substrate with no leaf-litter. These larvae did not burrow in the sand. The four predators had demonstrated previously that within

10 minutes each would pick up 20 or more red Chironomus larvae from an unburied ration of 25.

In the first test, three of the four fish captured no larvae in a ten minute feeding session; one took six larvae. During the next 3 days all fish increased their larval capture rate (Fig. 5), approximating the "plateaus" reached earlier for feeding on red Chironomus.

It appears from these experiments that Dolly Varden and cutthroat, if searching visually, must learn to recognize not only new types of prey, but also different colours or species of the same prey type. The red larvae were larger than the green ones, and appeared to move slightly more, but the latter were still very obvious to the observer as they lay on the sand. These data suggest a search image may be involved, but this aspect of learning was not investigated further.

2. Benthic oriented feeding - isolated predators

A. Substrate surface

(i) "Exposed" prey

Observations at Marion Lake and the gill net data of Andrusak indicated that Dolly Varden, particularly the 150 - 200 mm size class, fed more heavily on benthic organisms than did cutthroat. This suggested that Dolly Varden might be more successful predators than cutthroat on such organisms. To test this hypothesis an experiment was conducted with two experienced fish of each species and Chironomus larvae as prey. Rations and feeding periods were similar to those for the "learning"

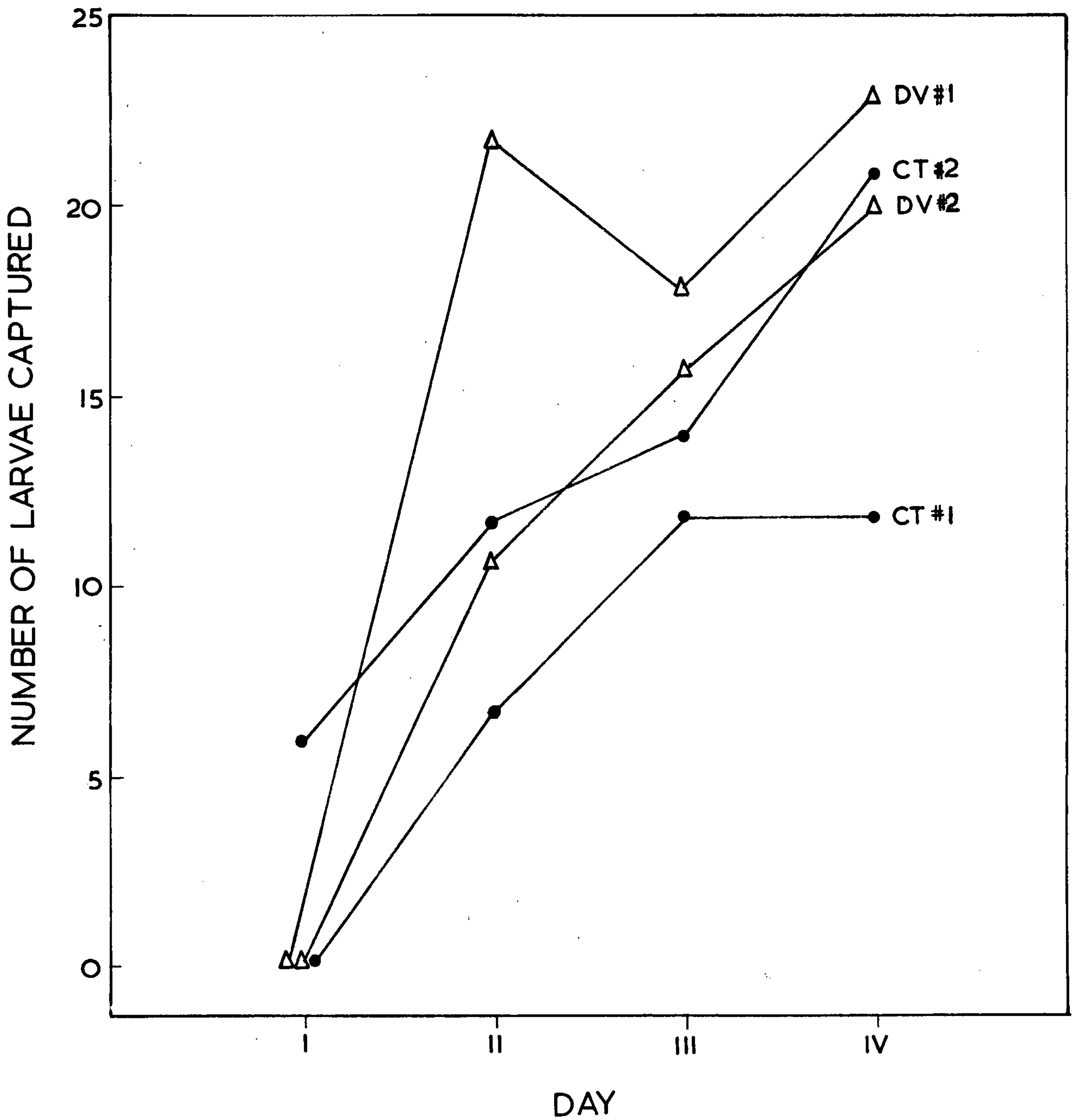


FIG. 5 Number of larvae caught (10 minute feeding session) on four consecutive days from a ration of 25 green chironomids by individual Dolly Varden and cutthroat trout.

experiments.

There was little difference between the four fish in number of larvae captured (Table VII) but differences in searching behavior between species were apparent. These will be described under the subheading "Searching components".

TABLE VII. Feeding success of individual cutthroat and Dolly Varden searching for 50 <u>Chironomus</u> larvae on a sand and leaf-litter substrate during a 30-minute feeding session.

	Number of Trials	Bottom grabs		Larvae captured	
		Mean	Range	Mean	Range
CT #1	5	32	22-44	15	11-21
CT #2	2	61	58-64	14	13-15
DV #1	5	67	41-85	15	10-21
DV #2	2	55	48-62	14	13-15

The lack of difference in success between species was not interpreted to mean that the trout were equally effective benthic predators as the char. The experiment was probably not a good test of this. Chironomid larvae used were large (13 - 15 mm) and red in colour. They were very obvious to a human observer as they lay on the substrate, and perhaps quite conspicuous to the fish. Both species appeared to search visually for these exposed prey.

(ii) "Camouflaged" prey

The combination of red *Chironomus* larvae on a light sandy substrate produced a striking colour contrast between prey and environment. Similar conditions would not likely be found in nature. In an attempt to produce a more natural colour combination, cryptically coloured (yellowish green) chironomids were used instead of *Chironomus* for the next series. They were also smaller than *Chironomus*, averaging 8 - 10 mm. These larvae were very difficult to see as they lay amongst the leaf litter and sand.

The same four predators were used, each having acquired previous experience with this larva during the "learning" experiments. Feeding time was reduced to 10 minutes and the ration cut to 25 larvae.

In most of the earlier feeding experiments it was noticed that the Dolly Varden gave up searching before the end of the session, and began a type of escape behavior. Cutthroat usually searched for the duration. Consequently a comparison of feeding success at the end of the period would not involve equal periods of searching. To eliminate this difficulty searching time was recorded with a stop watch for each of the species and both prey captured and bottom-grabs were calculated per searching minute. Fish were considered to be searching if they remained within 6 - 7 cm of the bottom, and appeared to be orienting to it visually.

On this basis each Dolly Varden averaged two to three times as many bottom grabs, and over three times as many captures as the most efficient cutthroat (Table VIII). A Mann-Whitney U Test (Siegel 1956) showed these differences to be statistically significant at the .01 level.

These results suggest that Dolly Varden may well have some advantages over cutthroat when feeding on the benthos. Behavioral differences were again obvious.

(iii) Searching components

The first obvious difference between the species concerned their pattern of swimming as they searched for chironomid larvae. Cutthroat alternated between hovering in the water column as they scanned the bottom for larvae, and cruising slowly not far above the substrate. Dolly Varden cruised almost constantly when searching (Fig. 6). Their only stops in the water column occurred occasionally when they were "chewing" and rejecting a mouthful of sand and litter. Usually this process of "sorting" and rejecting took place while the fish continued to swim. They searched within 5 cm of the bottom, frequently with pectoral fins brushing the substrate. Cutthroat scanned the bottom from 5 to 15 cm above it. Both species searched with bodies parallel to, or very slightly inclined to the substrate, tilting the head down only to investigate or pick up something.

Dolly Varden usually swam more rapidly than the trout as they searched for larvae. To quantify this, the searching speeds of six different fish were recorded by timing their

TABLE VIII. Feeding success (means and ranges of 5 replicates) of individual cutthroat and Dolly Varden searching for 25 green *Psectrotanypus* larvae on a sand and leaf-litter substrate during a 10-minute feeding session.

	Bottom grabs		Larvae captured		Minutes spent searching		Bottom grabs per minute of searching	Captures per minute of searching
	Mean	Range	Mean	Range	Mean	Range		
CT #1	2.4	0- 5	0		1	0.5-2.0	2.4	0
CT #2	18.8	7-28	2.2	0-5	8.6	6.0-9.0	2.2	.26
DV #1	19.2	15-24	2.2	0-5	2.7	1.5-3.5	7.1	.81
DV #2	34.2	12-60	5.8	1-9	6.2	4.0-8.0	5.5	.94

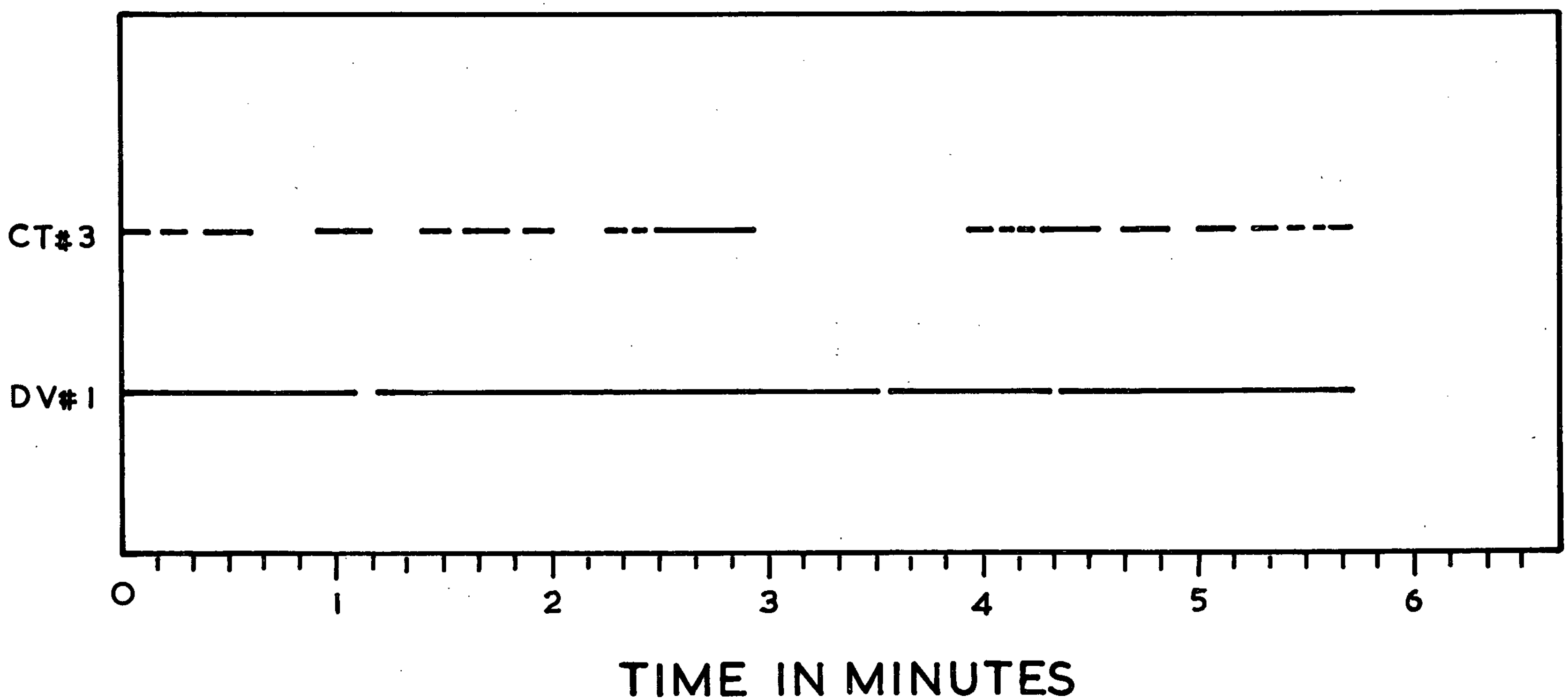


FIG. 6 Typical searching pattern of cutthroat and Dolly Varden looking for chironomid larvae in a sand and leaf-litter substrate. Solid lines indicate cruising; breaks indicate hovering. Data obtained with Rustrak event recorder.

movement over standard 26 cm courses (20 replicates each) within the observation tank. Fish were searching for approximately 25 Chironomus on the usual sand and leaf-litter substrate.

In addition to corroborating the previously observed intermittent swimming behavior of the trout versus the constant swimming of the char, the experiments showed that the average searching speed of Dolly Varden was about twice that of cutthroat (Table IX). Differences between species were highly significant ($F = 62.58$, 1, 118 df). This greater swimming rate was reflected by Dolly Varden moving more frequently from quadrant to quadrant. There was also some indication that their searching pattern within each quadrant was more complex than that of the trout. This was not quantified, but might well be worth future investigation.

TABLE IX. Average swimming speeds of individual cutthroat and Dolly Varden searching for Chironomus larvae on a sand and leaf-litter substrate.

Fish	Speed (cm/sec)
CT #1	2.7
CT #2	3.1
CT #3	3.0
DV #1	7.1
DV #2	5.4
DV #4	5.3

The results suggest that Dolly Varden would likely come into contact with benthic prey more frequently than would cutthroat.

Searching cutthroat and Dolly Varden seemed to have basic behavioral differences associated with picking up benthic prey. In all experiments with chironomids as prey both predator species seemed to respond to visual cues before picking up items from the bottom. As cutthroat scanned the bottom their eyes could frequently be seen shifting attention from one area to another, and at times their head was also moved from side to side. The cutthroat's "targets" were always specific items such as a single larva, evergreen needle, or stone. Very little of the surrounding substrate was picked up at the same time. Dolly Varden seemed less discriminatory as to what they sampled. They picked up and then rejected "mouthfuls" of litter and sand, dexterously retaining the larva while expelling the sand out the front and sides of the mouth. The Dolly Varden also seemed to scan the bottom as they cruised over it, but did not appear to visually select individual items to the same extent as did the trout. Cutthroat frequently spotted a target, swam over to it, and then moved on without picking it up. Dolly Varden on the other hand often would pick up and reject several consecutive mouthfuls of substrate with little delay between grabs. They tended to make more bottom grabs per unit of time than the cutthroat. There was no distinct division here between species, but the individuals making fewest grabs were cutthroat and the highest rates were by Dolly Varden (Table X).

Probably the difference in type of bottom grab is more significant than the difference in rate of grabs. Cutthroat picked up individual items from the substrate surface while Dolly Varden engulfed mouthfuls of the substrate.

On several occasions it appeared as if trout struck at but missed larvae. To test "strike success" of the two species 10 to 15 Chironomus larvae were scattered over a sand substrate a minute or two before introducing the predator. Many of the prey began burrowing in the sand immediately and were partially buried when the fish started to feed. Hollows and hillocks in the sand provided some degree of cover for unburied larvae. Each fish was tested on three or four different occasions. Strikes at larvae were scored as either captures or misses. No record was kept of strikes at objects other than larvae.

Cutthroat searched 5 to 15 cm above the sand and tended to dive down at larvae when sighted. They appeared to suck in individual larvae without picking up much of the surrounding sand. Consequently they frequently missed partially buried larvae or those in small depressions in the sand (Table XI).

Dolly Varden searched within 5 cm of the bottom scooping up considerable amounts of sand with each larva. Misses were rare. Three or four times a larvae was expelled with the sand, but in each case it was grabbed again immediately.

TABLE X. Number of bottom grabs by individual cutthroat and Dolly Varden during a 10-minute feeding session on *Chironomus* larvae.

1. Fifty larvae on a sand and leaf-litter substrate[1]

	Number of trials	Number of bottom grabs	
		Mean	Range
CT #1	5	15	6-21
CT #2	2	30	29-32
DV #1	5	29	16-42
DV #2	2	22	19-24
DV #6	2	49	43-56

2. Twenty five larvae on sand only (no leaf-litter).[2]

	Number of trials	Mean	Range
CT #3	3	48	41-54
CT #4	3	56	48-67
DV #3	3	56	49-66
DV #4	3	64	45-83

1 Differences between species were significant at the .05 level (Mann-Whitney U Test, $n_1=7$, $n_2=9$, $U=7$).

2 Differences were not significant at .05 level.

TABLE XI. Strike success of individual cutthroat and Dolly Varden feeding on red *Chironomus* larvae on a sandy substrate.

	Captures	Misses	Strike success (%)
CT #1	25	12	68
CT #2	45	9	83
CT #3	24	13	65
DV #1	28	0	100
DV #2	24	0	100
DV #3	25	2	93
DV #4	31	0	100

The preceding observations suggest that Dolly Varden are more effective than cutthroat in picking up and dislodging small invertebrates partially buried or in close association with the lake bottom. The method of bottom feeding employed by Dolly Varden might also give them the potential to exploit buried organisms unavailable to cutthroat.

B. Food within substrate

To test whether Dolly Varden and cutthroat would search within the substrate it seemed necessary to offer prey in a dense enough concentration that the predator's reward would be sufficient to keep it searching. Tubificid worms were chosen for this experiment. All experimental fish were fed *Tubifex* the day before the experiments started. Both species consumed the worms immediately.

On Day 1 of a 5 day series *Tubifex* were densely distributed in the observation tank. When most worms had buried themselves thoroughly in the 5 mm deep sand substrate a fish was introduced for a 10-minute feeding period. At the end of the period it was removed and ingested *Tubifex* recovered with the stomach pump. Recovered worms were commonly broken so any piece 10 mm or longer was scored as one worm. Substrate and *Tubifex* were not disturbed during the series except for the addition of more worms on Day 3. Predation had little effect on original densities. The four fish were tested in random succession each day.

Cutthroat caught only the worms that were fully exposed on top of the sand. They picked up little or no sand with each worm. Bottom grabs by trout were predominately at fecal material and a few evergreen needles present in the sand.

Dolly Varden began to successfully exploit buried *Tubifex* within a few minutes of their first exposure to them (Table XII). Feeding behavior consisted of slowly swimming several centimeters above and parallel to the bottom, then tilting at an angle of 45° to 60°, and driving and scooping into the substrate. Sand grains were frequently expelled from under the operculars, and often came to rest on the broad pectoral fins immediately after a scoop was made. Most sand was expelled from the front and sides of the mouth as worms were "sorted" from the sand. The sorting of prey from substrate involved a chewing movement and was very effective. Worms were retained in the mouth while virtually all of the sand was expelled. For example, DV #1 captured 53 Tubifex the first day but had only 20 sand grains amongst them.

It was difficult to determine how much the char relied on visual cues before making a grab. At times they seemed very "choosy" and appeared to look at and reject several areas before sampling Other times, particularly after catching some worms, bottom grabs seemed undirected.

TABLE XII. Feeding success of individual cutthroat and Dolly Varden searching for Tubifex in a sand substrate during a 10-minute feeding session.

	Number of trials	Number of bottom grabs		Number of worms ingested	
		Mean	Range	Mean	Range
CT #3	5	25	6-43	4	0- 9
CT #4	5	26	7-48	4	0-15
DV #1	5	51	38-60	74	53-115
DV #4	5	33	20-50	36	10-65

Both species found and ate unburied Tubifex with equal rapidity when tested at the end of the 5 day experiment (Table XIII).

These experiments suggest that Dolly Varden are able to exploit benthic organisms both on and within the substrate whereas cutthroat are largely limited to prey exposed on the substrate surface. The size class of Dolly Varden used (150 - 200 mm) did not expose the tank bottom when feeding, although sand was only 5 mm deep. Perhaps in a deeper and less dense substrate such as the mud of Marion Lake, organisms would be vulnerable at depths of a centimeter or more.

TABLE XIII. Time taken by individual cutthroat and Dolly Varden to pick up and consume 25 Tubifex on the bottom when no substrate present.

	Time (min.)
CT #3	5.0
CT #4	4.5
DV #1	4.0
DV #4	5.5

3. Surface oriented feeding - isolated predators

To test for differences in feeding abilities of cutthroat trout and Dolly Varden at the surface experiments were performed using Drosophila adults as prey. They were designed to test whether cutthroat were quicker than Dolly Varden to find and capture individual insects on the surface.

Three cutthroat and two Dolly Varden were used in the experiments. Each was tested once a day for four consecutive days. During the previous 60 days these fish had been feeding on bottom foods only (chironomid larvae and Tubifex).

At the start of each experiment approximately 25 freeze-killed Drosophila were clumped in one area of the observation tank. Then the experimental fish was introduced. The concentration of flies at the surface attracted the predator's attention and caused it to become "surface oriented". Once this original ration of flies was consumed single Drosophila were blown gently into the tank through an air hose, and the length of time from arrival on the surface until capture was recorded. Immediately after each capture another fly was introduced. This was repeated 15 times. Use of the long air hose permitted the observer to hide on the opposite side of the room while introducing flies into the tank.

During these feeding sessions it was not uncommon for the Dolly Varden to leave the surface area and go to the bottom. The number of trips to the bottom was recorded as was the length of time of each. A sand substrate covered the bottom of the tank but there was no benthic food present.

All fish quickly found and consumed the initial concentration of flies. Once cutthroat became surface oriented they cruised or hovered within 20 cm of the surface for most of the feeding period. Most flies appeared to be sighted from no more than 15 cm away. The trout tended to be more wary than Dolly Varden of going to the surface, and often would dart up for a fly, and then rapidly return to a hovering position 10 to 15 cm deep. When not so wary they leisurely swam within 2 or 3 cm of the surface quietly picking up flies one after another. The high average capture times for CT #1 and CT #4 on days two and three (Fig. 7) were due to the fish being unusually wary of the surface. As a result they hovered longer than usual before going for each fly.

Searching Dolly Varden cruised steadily within a few centimeters of the surface. They seemed to spot flies as quickly and from similar distances as cutthroat, and consequently were just as quick to catch flies when swimming near the surface. The major difference between Dolly Varden and cutthroat was the propensity of the Dolly Varden to return to the substrate even when flies were present. Cutthroat made no attempts to search the bottom when flies were present or had recently been at the surface. Each day the char concentrated less on the bottom, and more on the surface, thus decreasing their average capture times (Figs. 7 and 8).

4. Surface and benthic feeding - isolated predators

The presence of prey at only one level is unlikely to occur during the summer in most British Columbia lakes. Some organisms are probably always available at both the bottom and the surface. Following the experiments in which Dolly Varden and cutthroat were offered chironomid larvae only, their responses were examined when both chironomid larvae and surface insects were present.

Fifty *Chironomus* larvae were distributed on the sand and leaf-litter substrate as before, and in addition 25 live vestigial-winged *Drosophila* were scattered on the surface just before introducing the fish.

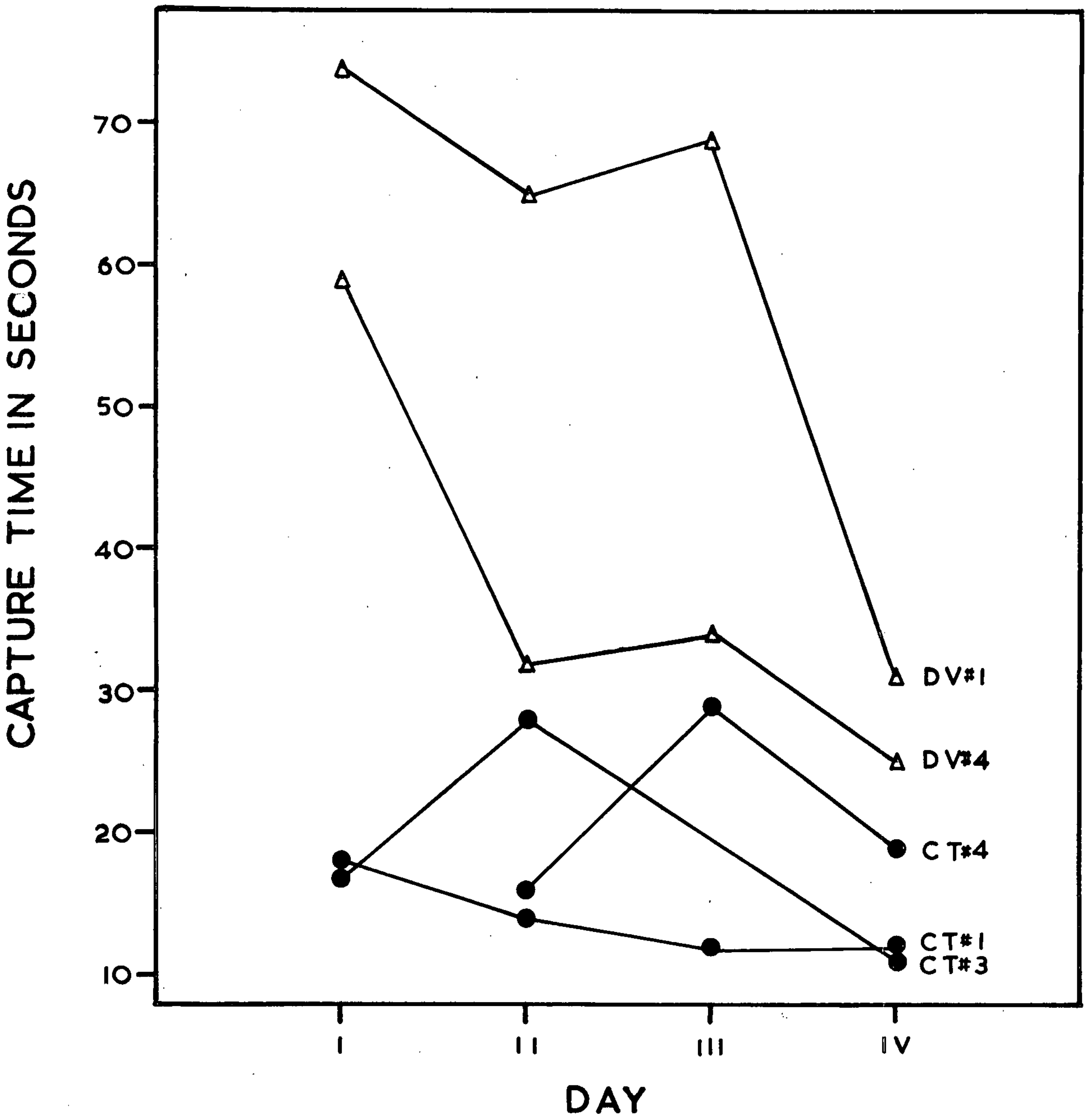


FIG. 7 Average time in seconds taken by Dolly Varden and cutthroat to capture single Drosophila adults during the first four days that flies were presented.

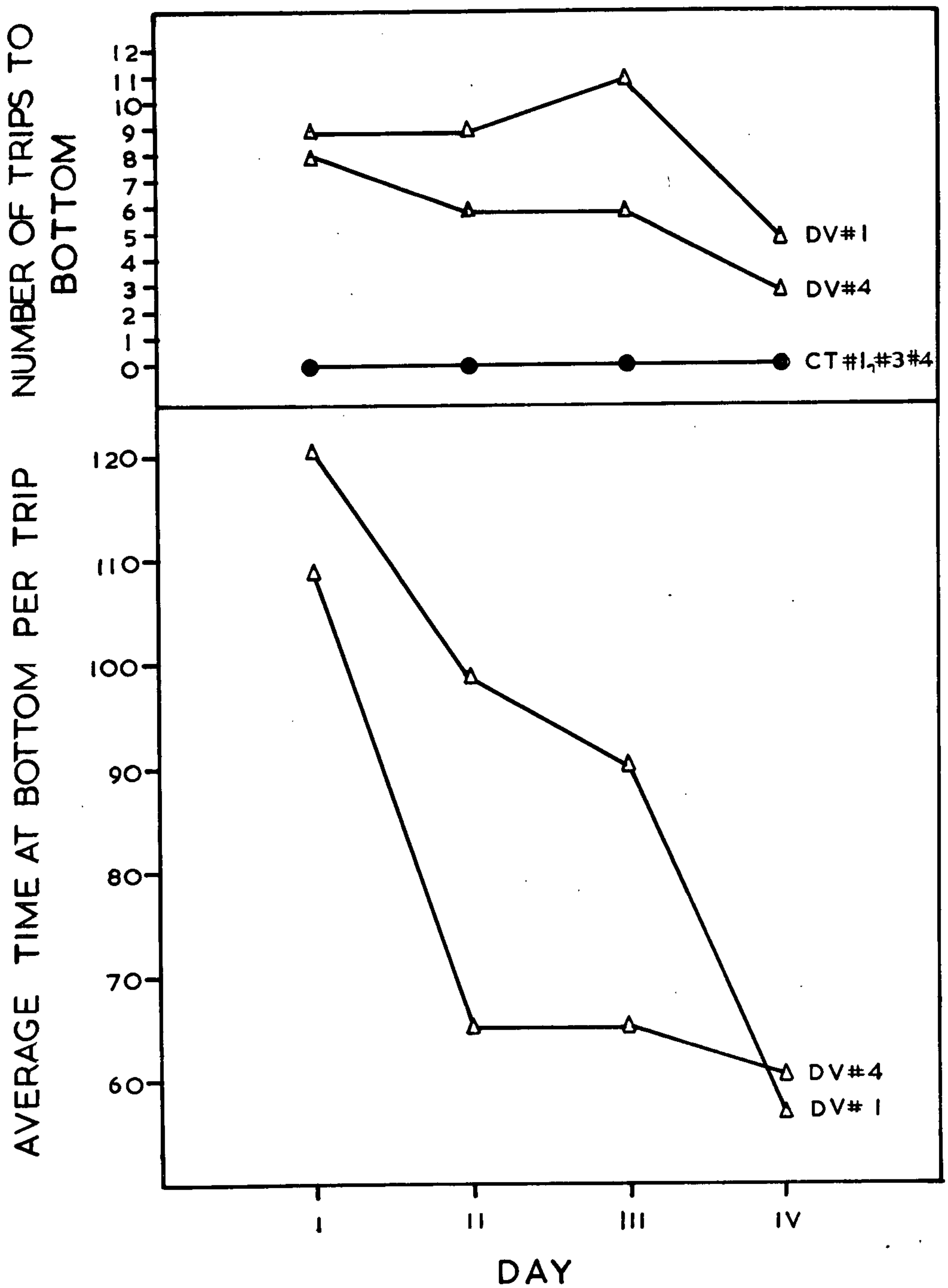


FIG. 8 Number of trips to the tank bottom and average time in seconds of each by cutthroat and Dolly Varden during their first four feeding sessions on Drosophila adults.

Bottom grabs were recorded as were the number of times a fish left the lower half of the tank, and moved into the upper half (a "surface trip"). "Surface grabs" were also scored each time the fish nipped at something floating on the water surface.

When fruit flies were present, cutthroat left the bottom once they discovered the flies, and exploited the surface almost completely before returning to search the bottom. Utilization of the surface food supply was probably complete within 5 to 15 minutes (Fig. 9). Cutthroat always captured 100% of the flies. Once they found the flies they cruised back and forth within 15 cm of the surface searching for more. The duration of each of the first few trips from the bottom to the upper half of the tank was long. After only one or two trips each cutthroat had averaged 20 to 25 surface grabs.

Dolly Varden did not stay at the surface for long at any one time. They oscillated between the surface and bottom making two to four surface trips every 5 minutes, and getting one to three flies per trip. After each brief trip to the surface they resumed searching for larvae. This pattern persisted for the full 30-minute feeding session, and usually resulted in incomplete exploitation of the fruit flies.

With flies present the cutthroat made fewer bottom grabs than when flies were absent, but the decrease was not statistically significant (p=.05). They did catch significantly

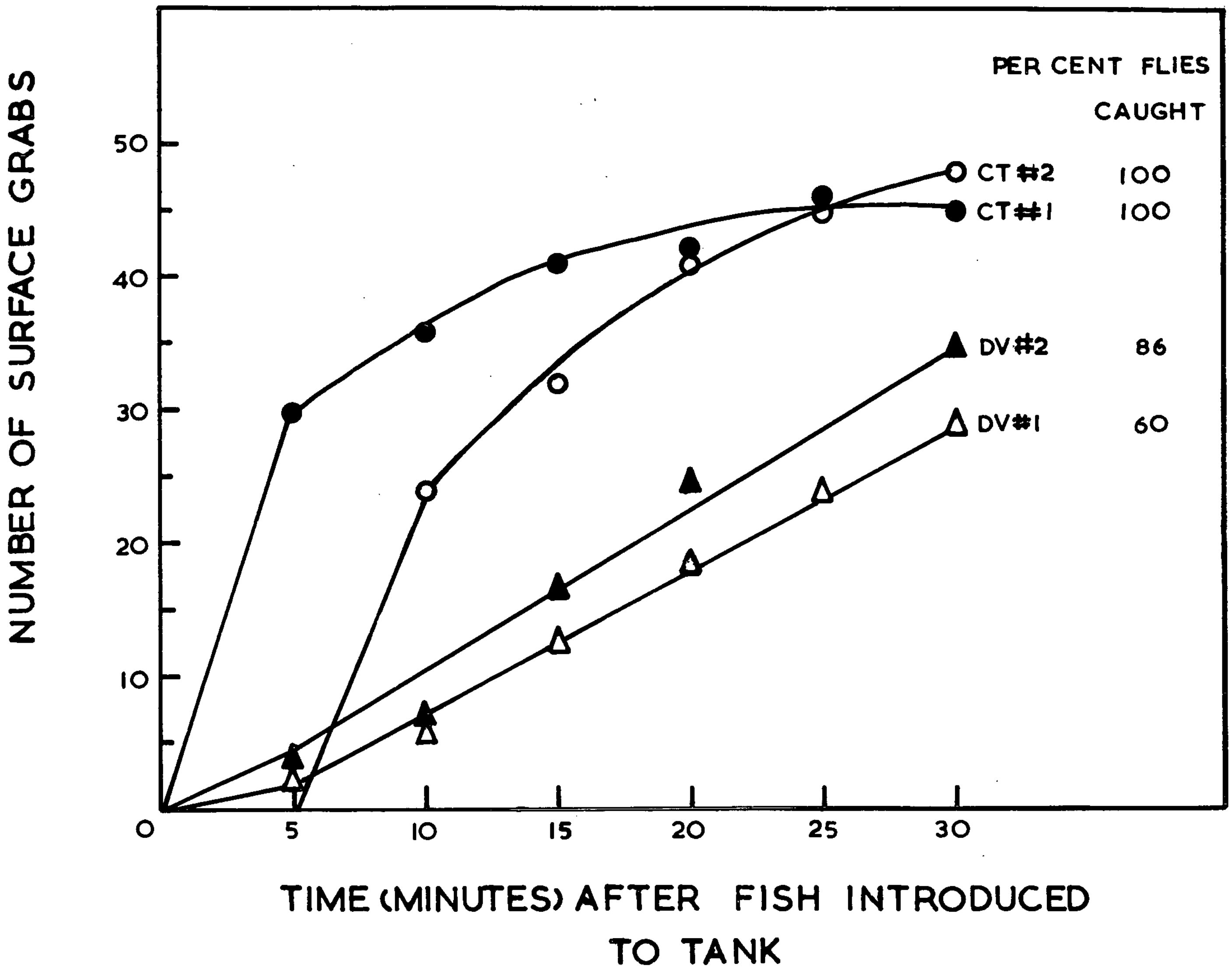


FIG. 9 Cumulative "surface grabs" by individual cutthroat and Dolly Varden feeding on a ration of 50 Chironomus larvae and 25 Drosophila adults. Each data point is the mean of four replicates.

fewer larvae (Mann-Whitney U Test, p=.05). Dolly Varden showed no significant change in bottom grabs or captures (Table XIV). The differences between species may have been more obvious if the feeding periods were shorter, involving only the time when both prey were present. In the 30-minute sessions cutthroat had a choice of flies or larvae for approximately 15 minutes, but thereafter only larvae were left. There were usually some flies present for the entire period when Dolly Varden were feeding.

The cutthroat's pattern of swimming changed from the typical hover-cruise routine to one involving a more steady patrolling of the tank and scanning of the surface. No change was evident in the Dolly Varden's swimming behavior.

The observed behavior of these four fish suggests that cutthroat are quick to leave the bottom and slow to return to it if food is available on the surface. Dolly Varden seem to be much less readily drawn to the surface, and persist on the bottom as long as food is present.

5. Interactive feeding - species pairs

In Marion Lake the division of food between Dolly Varden and cutthroat seems largely due to the location of the food, i.e. lake surface vs. lake bottom. There is some possibility that the above results were biased by differences in food preferences between species. Perhaps trout preferred fruit flies to larvae, and char preferred the larvae. Attempts to reveal such preferences were inconclusive. To investigate

TABLE XIV. Comparative feeding success during a 30-minute session of individual cutthroat and Dolly Varden searching for 50 *Chironomus* larvae in the presence and absence of a surface ration of 25 *Drosophila*.

	FLIES ABSENT			FLIES PRESENT		
	Number of trials	Number of bottom grabs	Number of larvae captured	Number of trials	Number of bottom grabs	Number of larvae captured
CT #1	5	32	15	6	22	10
		(22-44)	(11-21)		(14-30)	(3-15)
CT #2	2	61	14	6	50	11
		(58-64)	(13-15)		(38-68)	(6-15)
DV #1	5	67	15	5	51	15
		(41-85)	(10-21)		(46-55)	(14-19)
DV #2	2	55	14	6	73	17
		(48-62)	(13-15)		(28-100)	(10-24)

Data show averages; ranges in brackets.

the effect of location without the added complication of food preferences, experiments were made using a single food type, and paired Dolly Varden and cutthroat. Theoretically each species would exhibit its optimum feeding area under these conditions.

The experiments were of the "food scramble" type, and involved a scramble for food introduced item by item at the surface, the bottom, and simultaneously at both levels.

Eighteen pairs of fish were tested but some individuals were used more than once. Eleven cutthroat and 13 Dolly Varden made up these pairs. The same pairs were not tested under all three different conditions. Fish of approximately equal lengths were paired.

The food used was frozen trout flesh cut into small pieces about 3 mm^3. During each 3 to 6-day series fish were fed no food other than that obtained in the experiments. Usually each pair of fish was tested in the morning and evening, but on some days only one session was completed. Tests were repeated five times for each pair.

There was no substrate in the observation tank, but a large boulder at each end provided cover for the fish.

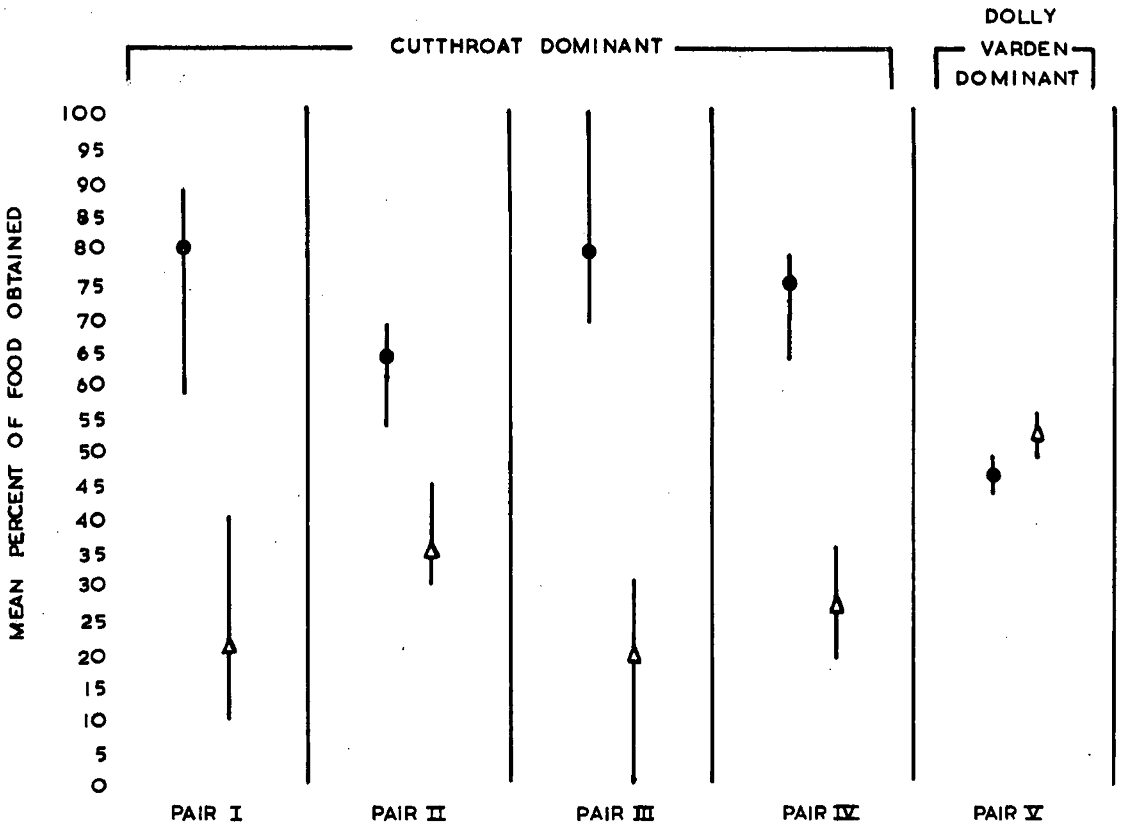
Most of the experimental fish were not conditioned to handling or the presence of humans. This problem was overcome by placing the paired cutthroat and Dolly Varden in the observation tank 24 hours prior to the first test, and leaving them in the tank for the duration of the experiment. The plexiglass windows in the tank were covered with half-aluminized plastic film which acts as a one-way mirror. Food was introduced through permanently mounted plastic inlet pipes that protruded from both ends of the tank.

A. Benthic feeding

Twenty pieces of food were flushed one at a time with water down the two inlet pipes. The food drifted out onto the tank bottom with no obvious turbulence or bubbles to mark its arrival, and usually the fish found each piece before the next one arrived.

Considerable aggression was observed in some pairs with the result that one fish usually became dominant. The number of aggressive nips was scored for three 10-minute periods before, during, and immediately after feeding. These scores were used to classify each fish as the dominant or subordinate of its pair.

In three of the seven pairs scrambling for bottom food a cutthroat dominated; no fish was obviously dominant in the other pairs. Dominant cutthroat always got 85% or more of the ration (Fig. 10). This was due to the intensely aggressive drives of the cutthroat quickly chasing the Dolly Varden under a rock or into an upper corner of the tank. Where dominance did not occur the Dolly Varden fared much better, getting the larger share of the ration in three of the four pairs. Mean transformed (angular transformation) scores of the Dolly Varden in this group were significantly greater than of the cutthroat



	PAIR I	PAIR II	PAIR III	PAIR IV	PAIR V
CUTTHROAT LENGTH (mm)	159	134	180	140	128
DOLLY VARDEN LENGTH (mm)	162	136	189	165	165
CUTTHROAT WEIGHT (g.)	37	24	58	30	20
DOLLY VARDEN WEIGHT (g.)	43	22	65	49	46

FIG. 10 Comparative success of paired Dolly Varden and cutthroat "scrambling" for 20 food items introduced one at a time at the bottom. Each data point is the average of 5 replications. Vertical lines indicate range; size and weight data given below.

CUTTHROAT = ●

DOLLY VARDEN = △

(t = 3.72, 3df), but variances between individuals exceeded those within (F = 3.74, 16 and 3d.f.).

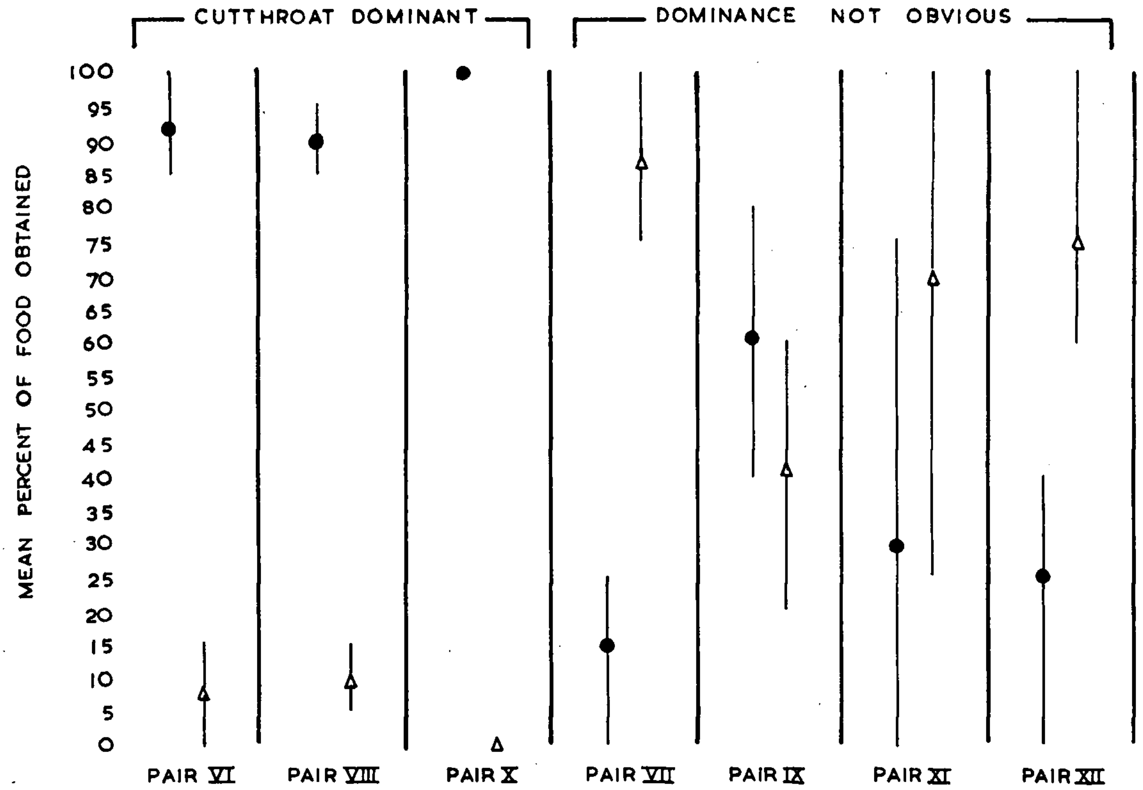
The species differed in their manner of searching the bottom. Dolly Varden moved around quickly exploring behind the boulders and in the corners, as well as the central region of the tank bottom. The cutthroat tended to alternate between hovering and slow cruising as described previously. They stayed in the central area of the aquarium, searching the corners rarely.

B. Surface feeding

The procedure here was the same as for the previous experiment with the exception that food items were introduced at the surface, each making a small disturbance as it entered the water.

In four of the five pairs cutthroat dominated, and in these pairs the cutthroat never obtained less than 55% of the ration (Fig. 11). Their mean share was significantly higher than the chars' (t = 8,3d.f.). The Dolly Varden was dominant in the fifth pair, but this was not unexpected since this was the only grossly mismatched pair used in the experiments. The char in this case weighed twice as much as the trout (Fig. 11). Even so the cutthroat's share of the ration was always in the 45% to 50% range.

Cutthroat appeared to "out-scramble" Dolly Varden as both responded to an introduced item. Frequently there was a race for the bit of food, but such races usually were won by



	PAIR VI	PAIR VIII	PAIR X	PAIR VII	PAIR IX	PAIR XI	PAIR XII
CUTTHROAT LENGTH (mm)	159	178	159	128	156	135	158
DOLLY VARDEN LENGTH (mm)	165	172	172	134	168	157	167
CUTTHROAT WEIGHT (g.)	37	51	37	19.5	29	23	40
DOLLY VARDEN WEIGHT (g.)	49	50	42	25.5	43	41	44

FIG. 11 Comparative success of paired Dolly Varden and cutthroat "scrambling" for 20 food items introduced one at a time at the surface. Each data point is the average of 5 replications. Vertical lines indicate range; size and weight data given below.

CUTTHROAT = ●

DOLLY VARDEN = △

the trout. It was not possible to determine whether the outcome was due to trout having superior means of detecting and responding to the food, or due to a hesitance of the Dolly Varden in the presence of a more dominant fish. There was more evidence of the latter than the former. Dolly Varden often left the mid-water area to briefly search the bottom. The trout rarely did this and consequently were in a better position spatially to respond to the next item.

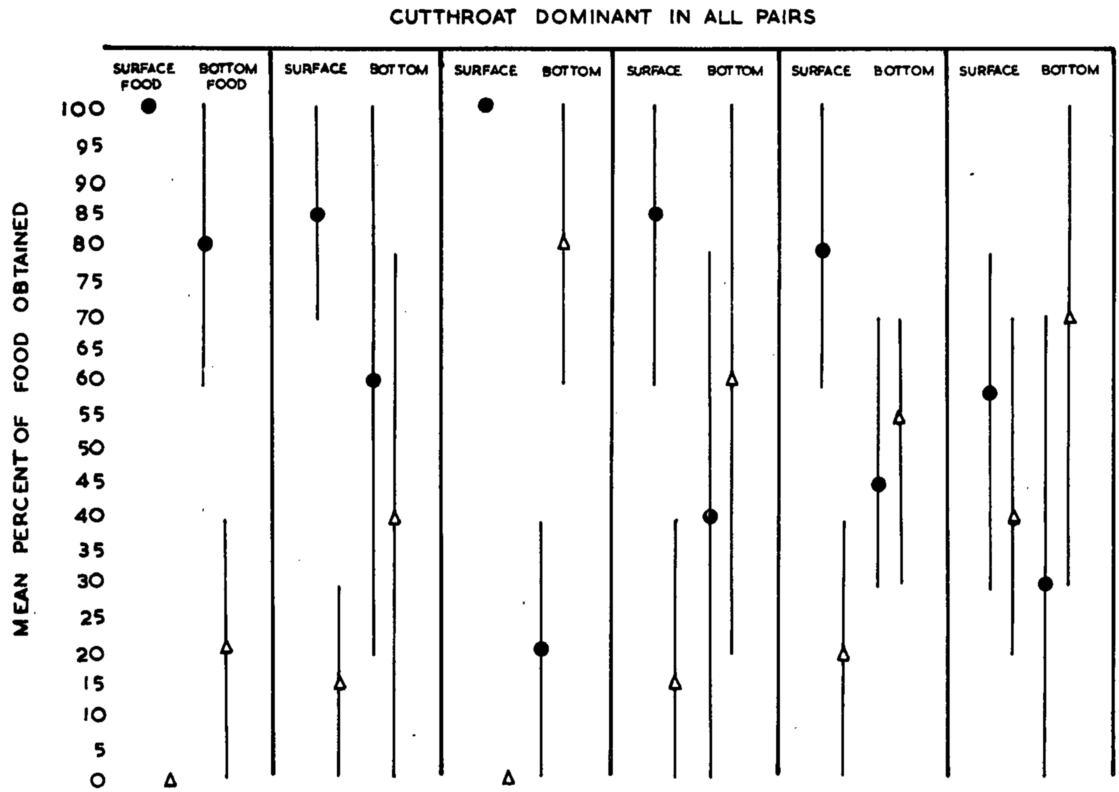
C. Benthic and/or surface feeding

(i) Observation tank.

Introduction of food at the surface or at the bottom only forced the fish to come to the same area of the tank for food. To permit a spatial segregation while feeding a third experiment was run, similar to the previous two, except that food was introduced simultaneously at the bottom and surface. The 20-item ration was introduced two pieces at a time, one at the surface and one at the bottom of the tank.

Six pairs of fish were tested and in each case the cutthroat was dominant. As in the situation when surface food only was presented, the cutthroat in each pair obtained an average of at least 60% of the surface ration (Fig. 12). Three of the six also got over 50% of the bottom rations as well. The difference in mean scores at the bottom between Dolly Varden and cutthroat was not significant ($t = .09$, 5d.f.).

There was not a distinct spatial segregation of paired fish in this series. Dolly Varden, as usual, spent the



	PAIR XIII	PAIR XIV	PAIR XV	PAIR XVI	PAIR XVII	PAIR XVIII
CUTTHROAT LENGTH(mm)	159	180	122	128	118	125
DOLLY VARDEN LENGTH (mm)	172	165	125	138	129	126
CUTTHROAT WEIGHT (g.)	37	58	18	20	16	22
DOLLY VARDEN WEIGHT (g.)	50	49	19	28	19	21

FIG. 12 Comparative success of paired Dolly Varden and cutthroat "scrambling" for 20 food items introduced simultaneously at surface and bottom (10 separate introductions of an item at the top and one at the bottom simultaneously). Each data point is the average of 5 replications. Vertical lines indicate range; size and weight data given below.

CUTTHROAT = ●

DOLLY VARDEN = △

majority of their time in the lower half of the tank. Much of this time involved avoiding the cutthroat. Cutthroat also spent more time cruising in the lower than in the upper half of the tank. This position was probably the most advantageous for spotting and responding to the surface food, which immediately sank. It also put them in position to scan the bottom. In general, the cutthroat did not actively search the bottom. The tank was bare and they could feed opportunistically as food appeared. They seemed to be more oriented to the surface than the bottom, and responded very quickly to food coming in overhead. Dolly Varden showed a weaker response to the surface food, but a more vigorous searching behavior on the bottom. Probably a deeper tank and floating surface food would have produced more spatial segregation.

(ii) Outdoor pond

In an attempt to eliminate the problems of aggression associated with the small tanks it was originally intended to repeat the preceding experiments in an outdoor concrete tank 2.4 x 4.5 x 0.6 m.

After losing "conditioned" fish to intermittent but persistent fungus attacks the pond was abandoned.

Some results were obtained. Two Dolly Varden and two cutthroat coexisted healthily for 24 days before being removed. During this period a peck order was established with the cutthroat ranking one and two in the order. Aggressive acts were never as intense in the pond as in the small observation tanks. If a subordinate was threatened it just moved out of the way. Nipping was rare. Subordinates had the opportunity of avoiding dominants and did so. Some nipping and chasing occurred when fish were competing for artificial food introduced one item at a time. When the fish were foraging for the chironomid larvae and small terrestrial insects present in the pond there was very little interaction. A Dolly Varden was observed defending a section of the tank wall one day as it grazed on chironomid larvae, but this was the only obvious example of food defense. Neither species exhibited strong territorial behavior in the pond. Cutthroat were more inclined to have "favorite" areas, but usually would tolerate a Dolly Varden resting within a meter or two.

A large population of small chironomid larvae flourished in the tank, most of them living on the four sides. Dolly Varden were frequently observed "grazing" on the tank walls, but cutthroat were never seen feeding in this manner. The char also spent more time actively searching the sandy substrate which had been seeded with Pisidium, a few chironomid larvae, and other invertebrates. When the fish were removed from the pond their stomachs were evacuated. The contents are listed in Table XV.

6. Light intensity and feeding

To test feeding ability of both species at low light intensities, individual fish were given 10-minute feeding sessions at four levels ranging from 500 lux to 0.003 lux at the surface. No fish were tested more than once per day. Prey consisted of 25 *Chironomus* larvae evenly distributed 10 minutes prior to introducing the fish. There was no substrate in the tank.

TABLE XV. Stomach contents of Dolly Varden and cutthroat held together for previous 24 days in outdoor pond.

	Pisidium	*Limnaea*	Chironomid larvae	Chironomid pupae	Winged insects
Dominant CT	0	1	2	9	3
Subordinate CT	0	0	2	32	63
Dominant DV	2	1	123	3	5
Subordinate DV	0	1	133	70	9

Pilot experiments with two Dolly Varden indicated that they could feed successfully at all of the above intensities if given a 10-minute dark adaptation period prior to feeding at the 0.02 lux and 0.003 lux levels. All six experimental fish were subsequently tested on this basis. After considering results of Brett and Ali (1958) for dark adaptation in young sockeye, I repeated the tests at the lowest light level, but with a 40-minute dark adaptation period.

At the maximum illumination tested cutthroat and Dolly Varden caught about equal numbers of larvae in the tank (Fig. 13). With the first reduction in light (surface = 0.13 lux) and no adaptation period the trout caught signif-

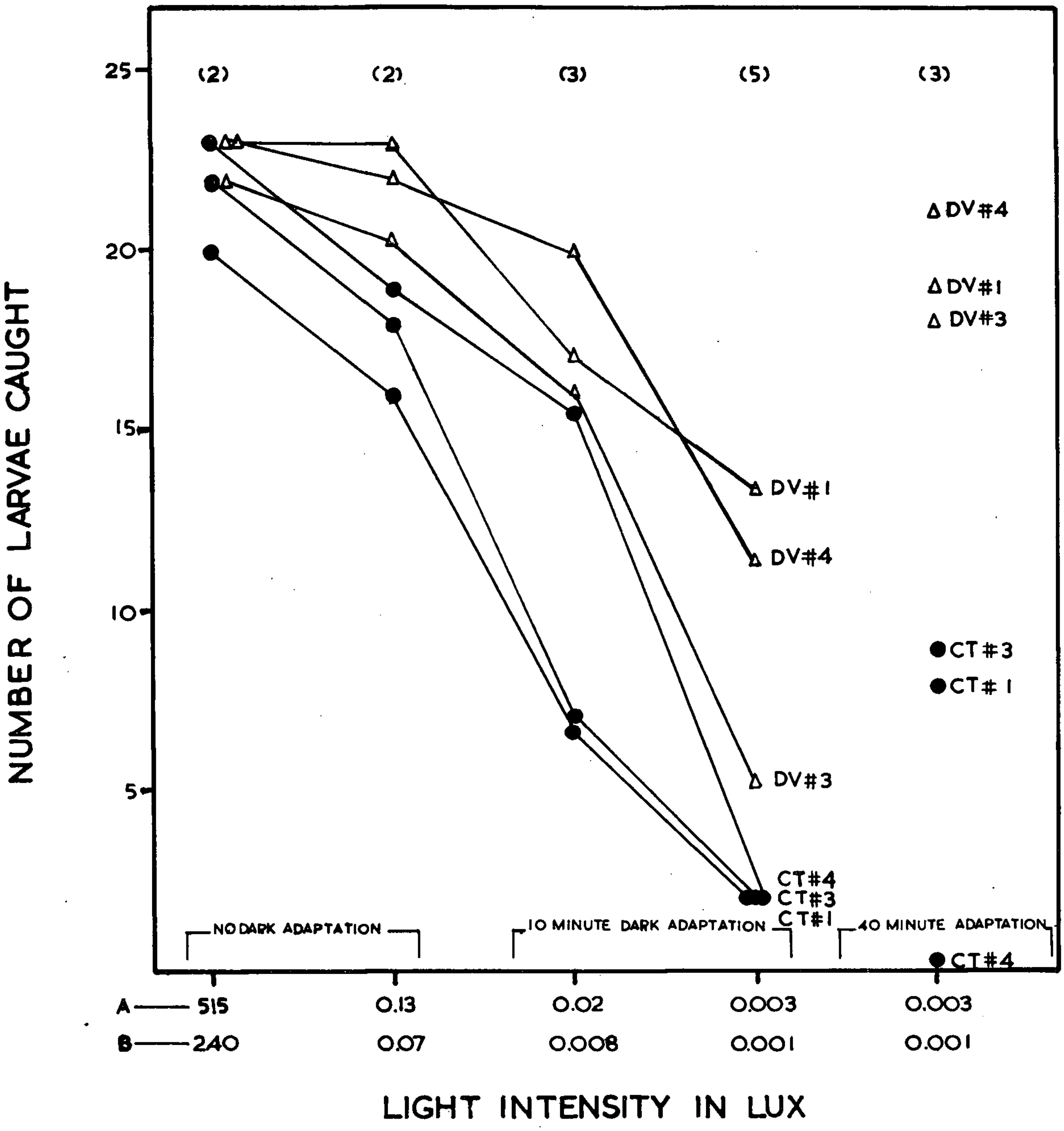


FIG. 13 Mean number of larvae caught from a ration of 25 Chironomus by individual Dolly Varden and cutthroat during a 10 minute feeding session. Number of replicate experiments per fish shown in brackets; A = water surface light intensity, B = 48 cm below surface or 8 cm above bottom.

icantly fewer than the char. (Mann-Whitney U Test $n_1 = 6$, $n_2 = 7$, $U = 8$, $p = .037$). The differences became greater with the next reduction in light. At the lowest illumination (surface = 0.003 lux) the average captures for the three trout had dropped to 9% of maximum success, and char to 44% of maximum.

When the dark adaptation period was lengthened to 40 minutes the success of both species increased sharply at the lowest illumination level. With this long adaptation period cutthroat reached 27% and Dolly Varden 83% of the success level established at the highest light intensity.

Fish were also tested occasionally in what was thought to be complete darkness. The results of these tests were not quantified since the experimental conditions varied. In most cases neither species caught any larvae, but infrequently a Dolly Varden did obtain one or two. Later it was realized that the room was not completely dark. Enough light filtered in around the covered windows to produce a reading of approximately 0.0003 lux at the tank surface.

The searching behavior of both species changed at low light levels. At the lowest level the fish of both species searched with their snouts almost touching the bottom, and their bodies tilted at angles of 45° or steeper. Cutthroat no longer hovered and scanned for food, but moved slowly and steadily across the bottom when searching. They showed a greater tendency than the Dolly Varden to give up searching under these conditions, and would then swim around in mid water. Both species appeared to move much slower than at the higher illuminations.

DISCUSSION

Distinct differences in the food habits and spatial distribution of sympatric Dolly Varden and cutthroat were documented by Andrusak (MS 1968) for Marion Lake, where they have apparently co-existed for many years. The major objective of the present study was to evaluate the contribution of food exploitation to the segregation of these species in Marion Lake. In Brian's (1956) words food exploitation may occur if one species "can find and use a vacant resource more easily and quickly than the other". Hardin (1960) says "ecological differentiation is the necessary condition for co-existence" and Brian (1956) means the same thing when he says "large scale co-existence is small scale segregation".

Laboratory experiments revealed a number of differences in the feeding behavior of cutthroat and Dolly Varden that might provide a means for ecological differentiation. Feeding habits seemed closely related to spatial positioning. Dolly Varden rested on the bottom when not feeding and cutthroat hovered in the water column (Table VI). When food was available at both surface and bottom the cutthroat exploited the surface first, but the Dolly Varden searched predominately on the benthos. During feeding experiments Dolly Varden often stopped swimming to rest on the bottom for a minute or two, and frequently located their next food item from this position.

Thomas (1962), discussing the different foods eaten by juvenile Atlantic salmon and brown trout, speculates that the trout get more winged insects due to spending their time in midwater. The salmon more often lie on the bottom and their food is predominately benthic. One might ask whether fish eat more benthic food because they rest on the bottom, or lie on the bottom because they are feeding there. For Dolly Varden the former seems to be the case. The resting habits of fish from a second lake, Dixon Lake, were the same as those for Marion Lake fish, but in Dixon Lake, where benthic organisms were relatively scarce, Andrusak (MS 1968) found that char fed predominately on midwater and surface foods. Therefore their resting positions obviously were not a result of their feeding habits.

In general, Dolly Varden seem to be a deep water fish compared to cutthroat, regardless of whether they are interacting with other species. Dixon Lake char are allopatric, but stay in deep water during the day and migrate vertically at dusk (Andrusak, MS 1968). Perhaps the char have a greater preference than trout for dark areas. This was not tested in the present study, but Gibson and Keenleyside (1966) noted that young Atlantic salmon spent more time than brook trout in lighted areas. They speculated that this may be significant in the segregation of these sympatric species.

Horizontal distribution and spacing of the fish are probably also interrelated with feeding behavior. The characteristic hovering by cutthroat suggests that they may take up feeding positions in the littoral zone. Cutthroat placed in the outdoor pond were observed to hover in specific spots, but there was little evidence of territoriality. In the lake, visual observations and gill net data showed cutthroat to be both randomly and widely spaced. This would seem to be advantageous for a surface feeder if surface food items are more dispersed than those on the bottom. In Marion Lake, direct observations and sampling with a sweep net indicated that floating insects were widely spaced.

Dolly Varden were often contagiously distributed in Marion Lake (Table V). There may be a definite functional significance to loose aggregates such as these when on the bottom. Keenleyside (1955) suggested that animals sometimes guide one another to food concentrations, and listed sticklebacks as an example. Benthic feeding Dolly Varden may do the same. Perhaps the combined feeding activities of a number of fish may stir up bottom organisms with the result that each fish gets more food than if it searched alone.

Significant differences in distribution and spacing of the two species have been described. Their methods of searching also differed considerably. Dolly Varden searched more vigorously than cutthroat, and travelled greater distances per unit of time (Table IX). They tended to be more exploratory, investigating the corners of the tanks, as well as around and behind large rocks. This type of searching would seem well suited for fish feeding on concealed or partially concealed benthic organisms. Beukema (1963) says that swimming activity is one of the most important factors determining area searched and prey encountered per unit time. The indication that Dolly Varden have a more complex searching pattern as well as a faster one is interesting. Beukema (1968) discusses how a high turning rate increases the predator's efficiency if prey are aggregated. Northcote (MS 1952) and others have shown that chironomid larvae are often distributed contagiously. Frequent turning by searching Dolly Varden would tend to keep the fish within such distributions. Cutthroat trout often hovered in one place, scanning the bottom or surface until finding a potential prey. Their habit of hovering in one place or alternately hovering and cruising is characteristic of many visual predators that wait for food to come to them. This pattern of searching would seem to be most advantageous to a piscivorous predator, but few of the trout in Marion Lake reached the size class ($>$ 200 mm) that fed on other fish. Drifting terrestrial insects and caddis fly larvae moving along the bottom are probably the most common prey.

Due to differences in searching behavior on the bottom, cutthroat have fewer benthic organisms available to them than Dolly Varden. Ricker (1954) and Tinbergen et al. (1967) suggest that there is a "maximum safe density" for prey. At this and lower densities predators will not find it rewarding to search for them, but predation will occur at higher densities.

In Marion Lake this density is probably higher for trout than for char. It was clearly demonstrated in the laboratory that cutthroat got only those organisms that were exposed on top of the substrate. The Dolly Varden's ability to feed on buried Tubifex (Table XII) indicates that it can prey on both exposed and buried organisms. In Marion Lake chironomid larvae and Pisidium were among the most important foods in the Dolly Varden diet, but made an insignificant contribution to the trout's diet. This held true even when surface insects were scarce in early May and trout were feeding on the bottom (Fig. 2). Chironomid larvae were readily eaten by trout in the laboratory. The absence of them in netted trout may be largely due to their unavailability to cutthroat in the lake. Pisidium are probably equally unavailable. They also seem to be relatively unpalatable to the trout. In the laboratory they were always rejected when intact and still ignored in most cases when the shells were crushed. Dolly Varden rejected them too in most instances but occasionally an individual would eat several in succession. In the lake they are an important food item. Andrusak (MS 1968) found them in one of every three Dolly Varden analyzed with up to 25 or more in some stomachs. This could be due to a relative scarcity of other benthic foods in the lake. He did not find a single Pisidium in trout stomachs.

Cutthroat trout in the laboratory were more "surface oriented" than Dolly Varden, and responded quickly to surface insects after weeks of feeding on benthic foods only.

Andrusak's data indicate that this also occurs in Marion Lake. On the day after the lake became ice-free, terrestrial insects made up 10% of the cutthroat stomach contents. Dolly Varden stomachs contained none. A week later this had risen to 86% for the cutthroat and about 12% for Dolly Varden (Fig. 2). This seems to be a clear example of one species finding and exploiting a food resource before the other. On the other hand it may just reflect a relative lack of searching at the surface by Dolly Varden even when food is reasonably plentiful. In the laboratory it was demonstrated that Dolly Varden would feed on winged insects, but were slower than trout to switch from benthic to surface feeding, and did so only when bottom food was absent or relatively scarce (Fig. 8). They did not orient to the surface as quickly or as persistently as cutthroat, but when they were near the surface seemed to locate individual flies as rapidly and from as far away as cutthroat. The cutthroat's habit of hovering in the water column, and the rapidity with which it becomes surface oriented after catching a surface prey are obviously advantageous for exploiting the surface. Andrusak (MS 1968) found that char in Marion Lake ate large numbers of winged insects during June, and he speculated that this may have been due to a temporary superabundance of surface food. The difference in time required and stimuli necessary to switch from bottom to surface food apparently is very significant in the segregation process.

The results of experiments involving paired Dolly Varden and cutthroat were complicated by interspecific aggression, but did suggest trends in the feeding behavior of these fish when they coexist.

When food was presented at the surface only the cutthroat consistently "outscrambled" the Dolly Varden. Aggression was a factor here, but spatial position and orientation were also important. Even a small subordinate cutthroat obtained almost 50% of the food ration (Fig. 11).

When food was introduced at the bottom cutthroat got most of it if they were highly dominant. If dominance was in doubt or the feeding area was large enough, Dolly Varden apparently got significantly more than the trout, probably because of a more vigorous pattern of searching the bottom.

When food was presented at both levels the char seemed less distracted than the trout by the surface ration. In the six pairs tested the Dolly Varden in each pair got a greater share of the bottom food than of the surface ration. This may be largely due to the fact that the cutthroat monopolized the surface, leaving food available to the char at the bottom only. However, the experiments with individual Dolly Varden indicated persistence on the benthos when food was available at both levels, and no competitors were present.

Stomach analysis of the fish in the outdoor pond supported both laboratory and Marion Lake field data. Although only an isolated and non-repeated observation it gave additional evidence that when surface food is available the trout do not actively exploit chironomid larvae. The char on the other hand feed on them extensively.

The role of aggression during competition for food has been discussed at length by Magnuson (1962), MacPhee (1961), and others. Whenever Dolly Varden and cutthroat were paired in aquaria in the present study aggressive interactions resulted and in many cases were intense. Cutthroat dominated in 85% of the 25 pairs observed. The extreme intensity and frequency of aggression was thought to be mainly due to the small size of the tanks. The amount of aggression as Nilsson (1965), MacPhee (1961), and Magnuson (1962) all reported, was correlated with the amount of food present.

Food linked territoriality in streams has been reported by Kalleberg (1958) and Chapman (1966). A stream offers a variety of habitats such as riffles and pools, with room for many territories in each. In a lake where fish must forage for food rather than wait for drift to pass, it is difficult to imagine what advantages would result from frequent aggressive encounters. Perhaps lake dwellers are more likely to meet other fish as they search for food, and if so, are unlikely to establish recognizable peck orders, or afford the time and energy to fight with every "stranger". Chapman (1966) suggests that feeding territories in streams provide for optimal growth of individuals "with minimal wastage of energy in unnecessary aggression". Aggression must also be minimized somehow in lakes. Cutthroat might do this by mutual avoidance if they are not territorial. Dolly Varden are more gregarious and aggression is probably minimal other than at spawning time.

The aggressive behavior of Marion Lake cutthroat and Dolly Varden differed completely from that of the fish studied by Newman (1960). He described Dolly Varden as being extremely aggressive, and cutthroat as less aggressive than other salmonid species. It is difficult to explain the conflicting observations of Newman and myself. Perhaps aggressive tendencies vary considerably between populations, or the differences could result from variations in our experimental facilities. Newman speculated that the low aggression levels of dominant cutthroat "may have been related to poorer adjustment to aquarium conditions". This seems likely since newly caught cutthroat in the present study took longer to adjust to the aquaria. They were sometimes dominated by Dolly Varden during this period, but their positions reversed later.

It is not known at present what interaction may occur between juvenile trout and char in Marion Lake. The exact time and location of spawning has not been determined for either species. It is conceivable that sometime early in their life history, perhaps in a stream environment, Marion Lake Dolly Varden might gain a "direct appreciation of the unpleasant nature of the other species" (Brian 1956). If so, this could reinforce the spatial segregation attributed to feeding differences.

Marion Lake Dolly Varden and cutthroat differed considerably in the size of their heads and mouths (Fig. 1). The most striking feature was the small, slightly subterminal mouth of the Dolly Varden - a species usually described as predatory and possessing a large mouth. Freshwater fish communities in the northern hemisphere have been described by Hartley (1948) as being made up of a number of generalized feeders, all feeding on the same foods in various proportions. Other authors have stressed the differences rather than similarities in food habits, and have related these to mouth and body form. Keast and Webb (1966) studied 14 cohabiting fishes in an Ontario lake and concluded that each had specific adaptations for feeding on different prey, but still retained the ability to feed on a wide range of organisms. Northcote (1954) pointed out differences in mouth structure of two cottids and related these to feeding habits. The mouths of Marion Lake Dolly Varden looked much like the illustration of *Umbra's* mouth given by Keast and Webb (1966), and described by them as a scoop. Dolly Varden preying on *Tubifex* were observed to "scoop up" mouthfuls of sand and worms. Perhaps their mouths are particularly well adapted for this type of feeding. The cutthroat's mouth with its large gape is typical of an active predator, well suited for striking at and grasping individual prey. Vertebrates made only a small contribution to the stomach contents of cutthroat netted during July and August by Andrusak (Fig. 2), but were completely absent in the Dolly Varden. In the laboratory salmon fry were occasionally offered to individual fish. Cutthroat captured and consumed very efficiently. Dolly Varden attacked, but after each capture had difficulty in handling them, and usually the fry were rejected after being killed or crippled. This may have reflected the previous experiences of individual fish in Marion Lake, but also appeared to involve basic differences in feeding adaptations and behavior.

The differences in success between Dolly Varden and cutthroat feeding at low light intensities (Fig. 13) may be very significant. In the laboratory, Dolly Varden fed more successfully than trout on the benthos when illumination was adequate. If they are also capable of feeding in light regimes too low for the cutthroat their potential advantages on the bottom are increased considerably.

Chapman (1966) briefly discusses the importance of visual stimulation to feeding salmonids, and states that bottom organisms must move to be attacked. This generalization may hold true for cutthroat trout, but is less likely to apply to Dolly Varden. In the laboratory it was not the case for either species, but this might have been the result of the fish learning to recognize and to expect non-living foods. Dolly Varden caught more larvae than cutthroat at the low intensities either because they could see better, or because they were less dependent on vision. Obviously both species relied primarily on vision. This was indicated by the sharp increases in larvae captured following the longer period of dark adaptation. It was also suggested by the infrequent captures when the tank was intended to be in complete darkness, but actually had a surface illumination of about 0.0003 lux. At this intensity the extinction level was probably not far off. Brett and Groot

(1963) found that young salmon no longer caught *Daphnia* when surface illumination reached approximately 0.0001 lux. These prey were moving midwater forms. Girsa (1959) mentioned that gammarids were more accessible to fish at low light intensities if suspended by threads in midwater than if on the bottom or walls of the aquarium.

The Dolly Varden's superior ability to find larvae on the dark tank bottom is believed to be due to its less discriminatory sampling behavior. Many objects varying in shape and form are probably tasted first, and then rejected or accepted. The cutthroat under bright light selected specific individual targets. In the semi-darkness visual acuity is sacrificed for rod vision (Hoar 1966). The trout probably can no longer discern detail or slight movements of prey, and consequently pass them by. The possibility also exists that the char's night vision was superior to the trouts'. This was not tested.

Interactive segregation was described by Brian (1956) as the competitive method of segregation. Nilsson (1967) suggests competition and/or predation are involved. In both cases it is implied that interactive segregation results from competition between populations and is behavioral in nature.

The question of whether or to what degree food competition occurs between fish populations has been considered by many. In all cases the conclusions have been speculative owing to the near impossibility of measuring supply and demand of resources in the environment. Larkin (1956) discusses the subject in depth, and seriously questions whether competition for food between populations occurs to any measurable extent. Straskraba et al. (1966) concluded that competition was minimal between coexisting populations of sculpins, minnows, and brown trout. These species exploited different feeding areas in a common environment. Fish of different sizes may reduce competition by having dissimilar diets according to Keast (1965), and Keast and Webb (1966) emphasize that the coexisting species they studied each have morphological adaptations for preying on different prey. Intense competition between them is therefore unlikely.

If the segregation of Dolly Varden and cutthroat in Marion Lake is of the interactive type then by definition it involves interspecific competition. Andrusak (MS 1968) could not demonstrate, but did infer that such competition was a significant factor in the food segregation of these species. Newman (1956) felt that two salmonid species "are potentially their own greatest competitors, since they have not necessarily evolved mechanisms for interspecific toleration" but are biologically so similar.

The results of this study suggest that Marion Lake salmonids have evolved mechanisms for "tolerating" each other. Distinct differences in feeding adaptations and spatial preferences are involved, and these are as obvious in isolated individuals as in interacting pairs. It seems unnecessary to infer that food competition is largely responsible for the segregation of the populations. Even when the species were forced to feed together on the benthos due to ice cover in early May (Fig. 2) the diets varied considerably. One would have expected to see some chironomid larvae present in cutthroat stomachs at this time if competition for benthic foods was important to segregation. It seems reasonable that the observed food and spatial segregations are the logical results of two species exploiting the habitats they are best suited for - regardless of the presence of the other. Competition does not push them apart, but superabundance of food may bring them together.

The difference in mouth size between Marion Lake Dolly Varden and cutthroat may be a morphological feeding adaptation, and consideration should be given to the evolution of it and other feeding adaptations. Thomas (1962) says that if interspecific competition is the cause of these feeding adaptations the competition must have been between distantly related species during speciation, or through competition of sympatric sibling species after they become genetically unique. He sees a lack of evidence for interspecific competition, and concludes that physico-chemical and intraspecific factors are more important evolutionary forces.

The evidence for food competition occurring now between Dolly Varden and cutthroat populations in Marion Lake is weak, but the feeding adaptations seem to have evolved as specific benefits towards coexistence of these species. Is it not likely that when these salmonids first shared the lake competition between them would be intense? They no doubt were basically similar and their own greatest competitors, but natural selection can change gene frequencies quite rapidly. The evolving populations would tend to have increasing morphological and behavioral differences favourable to coexistence. This accentuation of differences in sympatric situations has been described as character displacement by Brown and Wilson (1956) and involves genetic changes in one or more characters. The characters may be behavioral, physiological, ecological, or morphological. Brown and Wilson say that following the initial contact of two similar species, the divergence of characters will tend to cause the sympatric species to be more different from one another than allopatric ones. Kohn and Orians (1962) agreed entirely with the above authors, and went on to stress the importance of the effects of natural selection on ecological characters. These characters, although often less obvious than the morphological ones, tend to be the most important in determining the degree of coexistence.

It is not surprising that evidence for food competition between fish populations is usually weak or lacking. The period of intense competition probably has ended before most investigations begin. The field study by Johannes and Larkin (1961) of sympatric redside shiners (<u>Richardsonius balteatus</u>) and rainbow trout (<u>Salmo gairdneri</u>) indicated that competition for <u>Gammarus</u> was negligible. Data of other workers for the previous 10 to 15 years revealed that at one time, shortly after the introduction of shiners, amphipods were the most important item of competition. Sympatric populations looked at may often be those that have, through natural selection, evolved ways to coexist with minimal interference. I believe this to be the case in Marion Lake. Is the observed segregation of Dolly Varden and cutthroat trout interactive or selective segregation? Nilsson chose the former term to avoid the ambiguities associated with the word competition, but perhaps the use of this term creates as many problems as it solves. It is difficult to decide at what point interactive segregation would become selective segregation if one continuous evolutionary process is involved. Certainly it is an oversimplification to think in terms of two distinct methods of segregation as suggested by Brian (1956). The methods both involve natural selection, the difference being the degree of selection attained. Perhaps the initial tendency to segregate is basically behavioral in nature and therefore of the interactive type, but even then the individuals from each population showing the greatest amount of segregation may be those best equipped genetically.

The comparison of fish living allopatrically and sympatrically does not alone appear to be a satisfactory approach to the study of interactive segregation. Unless the previous history of the sympatric populations is well documented it is not valid to assume that each population is similar in characters to some other allopatric population. Character displacement, as pointed out by Brown and Wilson (1956) may make them quite dissimilar.

Future tests of the interactive segregation hypothesis would be most meaningful if they included comparative studies of the behavior and physiology of the same species from allopatric and sympatric situations.

The introduction of species as suggested by Nilsson (1967) would be fruitful, but care should be taken in choosing the fish to be introduced. The best combination would be two species whose previous histories were entirely allopatric.

The objectives of this study were to describe the feeding behavior of the two species, and to evaluate the potential of food exploitation as a mechanism of interactive segregation. The hypothesis that Dolly Varden could feed more successfully on the benthos, and cutthroat at the lake surface was supported by the results of laboratory experiments. The observed differences in feeding behavior were certainly sufficient to permit exploitation by Dolly Varden at the lake bottom or cutthroat at the surface. However, there was little evidence that food exploitation occurs to any measurable extent. Exploitation involves one species finding and using a resource before the other. It seems unlikely that one species could "scramble away the resource in question before the other has tried to use it" as Nilsson (1967) suggests. I would expect more overlap in the diets of trout and char if exploitation were occurring. Each species would have some of the resource, but the more efficient one would have the bulk of it. It does not appear as if Marion Lake Dolly Varden try to utilize surface organisms when benthic foods are available, nor do the cutthroat try to use the same groups of benthic organisms as Dolly Varden if surface insects are present.

This study suggested that the segregation of fish in Marion Lake is not basically of the interactive type postulated by Nilsson. It does not deny the possibility of such segregation, but questions whether the methods or mechanisms are truly different from those of selective segregation.

SUMMARY

1. Individual Dolly Varden and cutthroat from the sympatric Marion Lake populations showed distinct differences in feeding behavior and spatial distribution in the laboratory.

2. Dolly Varden in aquaria were benthic oriented and rested on the bottom. Cutthroat were often surface oriented and rested in the water column.

3. Dolly Varden had small "scoop-like" mouths possibly well adapted for benthic feeding. Cutthroat mouths were large in comparison and probably better suited for seizing individual moving prey.

4. The steady swimming and frequent sampling by searching Dolly Varden is an efficient method of exploiting the benthos. The alternate hovering and cruising of searching cutthroat is more effective for detecting surface and actively moving prey.

5. Dolly Varden were capable of exploiting buried food organisms unavailable to cutthroat.

6. Dolly Varden fed more successfully than cutthroat on the benthos at low light intensities. This was believed due to them depending less on vision and more on taste than the trout.

7. The differences in behavior between Marion Lake Dolly Varden and cutthroat were obvious in isolated individuals. There was no evidence that these differences were magnified when the species were combined.

8. Behavioral and ecological differences were not unequivocally rigid. Each species was plastic enough to change habitat and diet when necessary or advantageous.

9. The potential for food exploitation existed due to species differences in feeding adaptations, but there was no evidence that exploitation occurred to any extent.

10. The segregation of Dolly Varden and cutthroat in Marion Lake was concluded to be the result of basic genetic differences in morphological, ecological, behavioral, and physiological characters, rather than an interactive segregation as inferred by Andrusak (MS 1968).

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