A COMPARATIVE STUDY OF THE BEHAVIOUR OF TWO SYMPATRIC SPECIES OF FRESHWATER SCULPINS, *Cottus asper* Richardson AND *Cottus aleuticus* Gilbert, IN RELATION TO THEIR DIFFERENCES IN MICROHABITAT

by

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ABSTRACT

The behaviour of two sympatric species of sculpins, *Cottus asper* and *Cottus aleuticus*, which occupy different microhabitats, was studied by the comparative method. The aim of the study was to determine some of the important behavioural adaptations to the differences in their microhabitats.

C. asper occurs in areas of slow current and fine substrate and *C. aleuticus* in areas of fast current and coarse substrate.

The posture, orientation to the current, and locomotary and feeding behaviour of the species were examined in the laboratory under different conditions of current and substrate.

C. asper responds to a current by lying flat on the substrate. *C. aleuticus* also exhibits this posture on sand, but on a gravel substrate, raises the body by spreading the pectoral fins.

C. aleuticus adopts a parallel orientation to the current more frequently than a broadside orientation, but *C. asper* "prefers" the broadside position. However, both species assume the broadside position more frequently on sand than on gravel, and the parallel orientation more frequently on gravel than on sand.

C. asper is a much poorer swimmer than *C. aleuticus*, especially in a current. *C. aleuticus* is much more active than *C. asper* at all times of day and under all conditions of current tested.

C. asper is a lurking predator and takes food from the surface of the substrate. *C. aleuticus* is a more active feeder, and feeds by swimming to the water surface, by taking food from the substrate surface and by foraging in the crevices of the gravel.

From laboratory observations it appears that *C. aleuticus* relies on sight in food detection to a greater extent than does *C. asper*.

The findings of this study were compared with field observations and with previous studies of other cottid species. It was concluded from this that *C. aleuticus*' posture, orientation to the current, and locomotory and feeding behaviour are a reflection of a more active way of life and are related to the special problems of life in a strong current. *C. asper*, however, is typical, both in behaviour and morphology, of bottom-dwelling, sedentary fish, of reclusive habits.

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INTRODUCTION

This thesis is concerned with a comparative study of the behaviour of two closely related species of freshwater sculpins, family Cottidae. *Cottus asper* and *Cottus aleuticus* are known to differ in their microhabitats with respect to the nature of the substrate and the current velocity (Taylor, 1966). The present study was a comparison of the behaviour of these species under different conditions of current and substrate to determine which are the important behavioural adaptations to these differences in microhabitat.

One of the distinguishing features of the family Cottidae is the absence of a swimbladder. As would be expected from this, the group as a whole is benthic. Cottids occur over rubble (Bailey, 1952), gravel (Simon and Brown, 1943), and mud and sand (Taylor, 1966). They are found in pools (Taylor, 1966), in slow streams (Smyley, 1957), and in torrents (Carl *et al*., 1951), and riffles (Bailey, 1952). Each species is commonly collected in association with a specific substrate type and a certain current velocity.

It has been suggested (Bailey, 1952) that the principal factor governing habitat choice, at least in the spawning season, is the nature of the substrate, and that a given current speed is only apparently selected owing to its association with certain substrate types (Zarbock, 1951). Bailey (1952) found that although *C. bairdi* apparently chose its spawning sites on the basis of substrate type, most of the nests were found in areas where the surface velocity was quite high. However, water movements inside the nest itself were rather gentle.

Another common feature of the freshwater sculpins is that they usually occur in groups of two or more species, each one of which is more frequent in some parts of the river or stream than in others, according to the distribution of current speed and substrate type (Straskaba et al., 1966; Bailey, 1952; Smyley, 1957; Taylor, 1966). Coastal British Columbia is comparatively "impoverished," in that only two species, the prickly sculpin, Cottus asper Richardson, and the Aleutian sculpin, Cottus aleuticus Gilbert, are present. This area therefore presents a somewhat simplified situation, amenable to study.

Sculpins all over the northern hemisphere appear to have rather similar diets, chiefly consisting of bottom dwelling invertebrates (Smyley, 1957; Bond, 1964; Northcote, 1954). They eat organisms within certain size ranges that depend on the mouth size of the sculpin. The size of food taken therefore differs not only between species, but also during the lifetime of a single individual.

Cottus asper and Cottus aleuticus are sympatric in the Little Campbell River of southwest British Columbia. Collection studies (Taylor, 1966) indicate that they differ in their microhabitats, C. asper inhabiting areas of slow current and finely textured substrate, and C. aleuticus occurring in areas of swift current and coarse substrate. These microhabitats overlap to some extent, and where C. asper is scarce or absent,

C. aleuticus may occupy C. asper type habitats.

Laboratory studies (Taylor, 1966) indicate that these species exercise some degree of selectivity in their environment with regard to substrate type and current velocity. In the laboratory C. asper and C. aleuticus tend to choose current and substrate conditions that resemble those occurring in their natural habitat. However Taylor did not examine the animals' behaviour once the choice was made to determine if the species' behaviour differed in a way that could be correlated with the substrate and current type that they had chosen.

It seems likely that these differences in microhabitat would be reflected in the everyday behaviour of the sculpins. Consequently C. asper and C. aleuticus were observed in laboratory situations in which current speed and substrate type were varied. Their behaviour in these various circumstances was noted, and experiments were then conducted to examine further any differences which these observations had indicated.

The feeding behaviour of C. asper and C. aleuticus was also studied, as it appeared to be related to the differences in the behaviour of the two species in current conditions.

The present study was, in a sense, a departure from "classical" vertebrate ethology, in that the behaviour considered was not a form of social behaviour, but the means used by the individual to meet the problems of food getting and locomotion that the environment presents daily.

Throughout this study the comparative method was chosen as the most fruitful means of discovering the significance of behavioural differences as ecological adaptations (Lack, 1965).

MATERIALS AND METHODS

Description of Species

C. asper and C. aleuticus are rather similar in appearance (see Carl et al., 1959, for complete description). However, they do differ morphologically in several respects that have a bearing on their behaviour in different current and substrate conditions.

C. asper is the larger species, attaining a length of up to 150 mm. A few individuals may be up to twice this size. C. aleuticus, however, rarely exceeds 100 mm in length. C. asper has a very large, broad head and mouth relative to body size, but C. aleuticus has a mouth and head more in proportion to the rest of its body. C. asper's body is somewhat dorso-ventrally compressed, and the width of the body decreases markedly from head to tail. C. aleuticus is more cylindrical in shape and has a less pronounced tapering from the anterior to the posterior of the body.

Collecting and Holding Conditions

C. asper and C. aleuticus were collected from the Little Campbell River in a seine net (2.4 m x 1.6 m x 3 mm mesh) equipped with aluminum poles and heavy weights. Roller type leads were used as these effectively stirred up the substrate and disturbed the sculpins. At times the seine was held stationary while the substrate was disturbed by someone splashing downstream towards the net. However, best results were usually obtained by taking short, deep drives in deep pools, from the middle of the streambed towards the shore, or by making long sweeps upstream in shallower water. Large C. aleuticus were sometimes collected by jabbing the aluminum poles under the overhanging banks in riffle areas and suddenly lifting the net with a scooping motion.

The fish were held in four outdoor troughs (7'2" x 16" x 8") with running dechlorinated water and air hoses. Some fish were also held in a small unheated hut, in two plywood tanks (40" x 12" x 18½") and in one metal tank (8' x 10½" x 8¼") with running dechlorinated water and air hoses. The plywood tanks were each equipped with three plexiglass windows on one side, and were used to observe the general behaviour of the fish. These tanks had gravel substrates of varying depths. The gravel at the deep water end of the tank was 2 3/4" thick, and the depth of the substrate gradually increased until at the shallow water end the gravel was 10½" to 11 3/4" thick. Both species were held at various times in bare troughs, over gravel, or over sand.

The indoor tanks were provided with "hides" in the form of halved clay flowerpots. The outdoor tanks were partially covered to give the fish a refuge.

The temperatures in these tanks fluctuated from 0°C in the month of February to 16°C in July. C. aleuticus is not as tolerant of high temperatures as C. asper, and is usually not collected in areas with a seasonal high temperature of greater than 15°C (Taylor, 1966). Consequently, most of the C.

aleuticus were kept in the indoor troughs as the summer temperature in the hut could be kept lower than outdoors. All fish were exposed to the natural seasonal and daily light variations.

The cottids were fed thawed, concentrated brineshrimp. The diet was varied with small fish, such as guppies, gouramis and small goldfish. Feeding times were unscheduled, and at irregular intervals they received no food for a day or two. This was done not only to prevent the fish from developing a conditioned activity cycle, but also because it was found that the cottids ate more if they were deprived of food one or two days in every week.

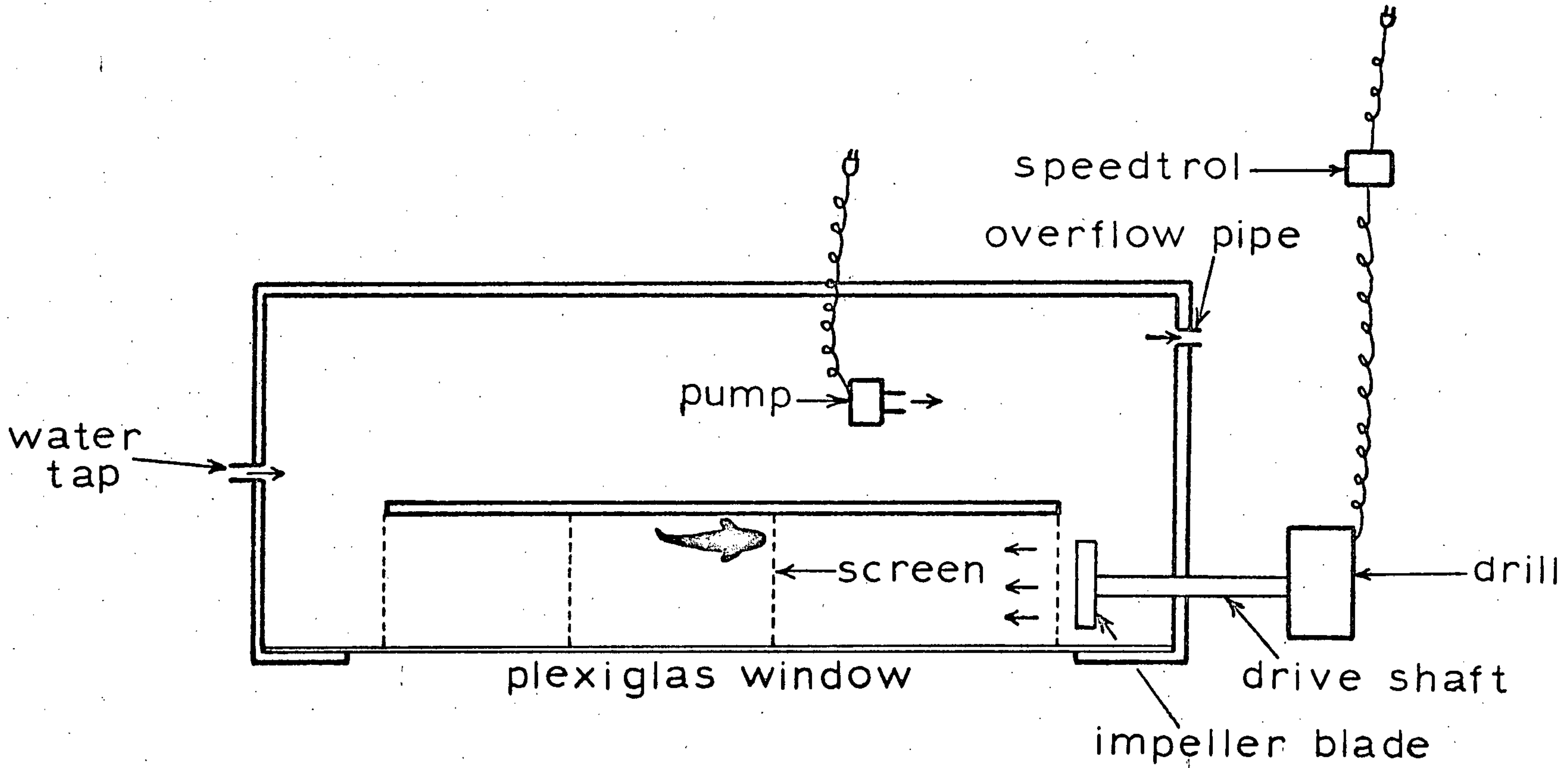
All tanks were treated regularly with one or two drops of a 1% solution of malachite green, as a fungicide.

Flow Tank

For several experiments it was necessary to produce currents of several different speeds. A flow tank was constructed (8' x 20½" x 14½") of ½" plywood and ¼" plexiglas. This tank (Fig. 1) consisted of two channels separated by a plywood partition (6'2" x ½" x 14½"). One channel (5'8" x 9½" x 14½") had a plexiglas wall through which the fish were observed, and the other (8' x 9½" x 14½") was for the recirculation of water. The ends of the viewing channel were screened and at times the fish were restrained in the middle portion of the channel in a wire fence (23" x 9¼" x 15½").

A small submersible pump (Little Giant model 1,115 volts) was placed in the recirculation channel to provide a constant

Figure 1. The flow tank and current producing apparatus used in locomotion, orientation, and posture experiments.


speedtrol
overflow pipe
pump
water tap
screen
drill
plexiglas window
drive shaft
impeller blade

slow current of less than 6 cm/sec. This was current 1, equivalent to Taylor's (1966) "noncurrent."

Other current conditions were produced by a 5" impeller blade mounted in the water behind the screen at one end of the viewing channel. This was connected by a rubber insulated driveshaft to a heavy duty industrial drill (Rockwell 758R; ½") suspended outside the tank. The drill speed was regulated by a speedtrol (Model SC1000; C.C. Industries Inc., Philadelphia, Pa.). With this apparatus surface velocities of 13, 20, and 25 cm/sec were obtained (currents 2, 3 and 4). Various quantities of a 1% solution of methylene blue were placed in this system to study the pattern of the current. The current appeared to be rather uniform from the water surface to the surface of the substrate, except in the area immediately in front of the impeller blade, where there was much turbulence.

Times of Observations

The fish used in this study were held either in outdoor troughs or in a small hut which was panelled in fibreglas sheets which admitted diffuse natural light. They were therefore observed under natural daylight conditions. It soon became apparent that both species were more active at some times of day than at others. Both C. asper and C. aleuticus were rather active until approximately 11 am, after which activity was maintained at a lower level until about 1 pm, and there was then very little activity until early evening, about dusk. The C. asper were less active at all times of day than the C.

aleuticus, and they remained motionless under their flowerpot "hides" throughout most of the afternoon.

It was suggested that perhaps this low level of daytime activity in C. asper was compensated for by a higher nighttime activity. Experiments were therefore conducted, using apparatus designed by Byrne (1968), to see if the activity cycles of the two species differed radically in shape. The locomotary sp activity of four fish of each species was recorded automatically. Recordings were made continuously of C. asper for ten days and of C. aleuticus for twenty-one days.

It was discovered that in both species there was a slightly higher level of activity during most of the night than during the day, and a brief burst of activity shortly after dusk. Both species were more active in the early morning than in the late afternoon.

It was therefore decided that experiments should be conducted in the early morning to ensure that the fish would be observed at a time when they were normally active and under light conditions suitable for observation.

RESULTS

Orientation With Respect to the Current

A. Observation

When C. asper and C. aleuticus were observed at rest under current conditions, it was noted that they aligned themselves in a rather specific manner with respect to the direction of flow of the current. On all but a very few occasions, they could be classified as either parallel to or broadside to the direction of flow. Further, it appeared that the two species differed in their preference for one of these positions.

The orientation responses with respect to the current were so consistent that it was thought that they must be of considerable importance to the animals. Experiments were therefore conducted to determine the differences in the frequencies of the positions adopted by the two species. If one can demonstrate differences in the response of two sympatric species to changes in certain environmental parameters one may then speculate on the significance of these differences as ecological adaptations.

B. Method

To find the "preferred" direction of orientation with respect to the current, that is, the one most frequently assumed, ten fish of one species were placed in a bottomless wire cage in the middle portion of the flow tank, where a current of uniform velocity could be maintained. They were then exposed to a current of constant speed for fifteen minutes. At the end of this time the number of fish facing "into," "away" from and "broadside" to the current source was recorded. Three subsequent recordings were made at intervals of five minutes.

Each group of ten fish was tested at four current speeds; less than 6 cm/sec ("noncurrent"), and 13, 20, and 25 cm/sec. Forty fish of each species were tested on a gravel substrate, and thirty of each species on sand.

C. Results

In analysing these data, it was thought best to consider the parallel alignment as two categories, "into" and "away," as there would be a considerable difference in the pattern of current flow around animals in these positions.

The data obtained on sand and gravel substrates were tested by two analyses of variance (Tables I and II). In both cases the only one of the conditions that showed a significant difference at $p<0.01$ was the direction faced (D). The interactions species x direction (S x D) and direction x current (D x C) were also significant at $p<0.01$. In neither case was the second order interaction species x direction x current significant.

The means were compared by the Student-Newman-Keul test. As can be seen from Tables III and IV, *C. aleuticus* assumed the parallel alignment more frequently than the broadside, while *C. asper* did the reverse. At no time did *C. aleuticus* show a significant preference for the "broadside" over the "into" position.

TABLE I

The frequency with which C. asper and C. aleuticus faced "into," "away" from and "broadside" to the current on a sand substrate, at four current speeds.

SOURCE	SS	df	MS	F
Species (S)	0.0	1	---	---
Direction (D)	1157.25	2	578.625	186.89*
Current (C)	0.0	3	---	---
S x D	382.58	2	191.29	61.786*
S x C	0.0	3	---	---
D x C	53.91	6	8.985	2.902*
S x D x C	36.89	6	6.148	1.986
Error	817.37	264	3.096	
Total	2448.0	287	---	

*significant at $p<0.01$.

TABLE II

The frequency with which *C. asper* and *C. aleuticus* faced "into," "away" from and "broadside" to the current on a gravel substrate, at four current speeds.

SOURCE	SS	df	MS	F
Species (S)	0.0	1	---	---
Direction (D)	265.85	2	132.925	65.513*
Current (C)	0.0	3	---	---
S x D	237.95	2	118.975	58.637*
S x C	0.0	3	---	---
D x C	57.80	6	9.633	4.748*
S x D x C	15.33	6	2.556	1.259
Error	730.4	360	2.029	
Total	1307.33	383	---	

*significant at $p<0.01$.

TABLE III

The frequency with which *C. asper* and *C. aleuticus* faced in three directions at four current speeds on a sand substrate. Data are arranged to compare "into," "away" and "broadside" orientations at each of four current speeds. Tabulated values are means obtained from 30 fish of each species, observed 10 at a time.

C. asper

Current	Into	Away	Broadside
1	2.75	1.0	6.25
2	1.17	0.83	8.0
3	1.25	1.0	7.75
4	1.0	0.75	8.25

C. aleuticus

Current	Into	Away	Broadside
1	3.67	2.58	3.75
2	4.0	1.58	4.42
3	3.83	1.08	5.08
4	4.5	0.83	4.67

Means joined by dotted lines are significantly different at $p < 0.05$ by the Student-Newman-Keul test.

TABLE IV

The frequency with which *C. asper* and *C. aleuticus* faced in three directions at four current speeds on a gravel substrate. Data are arranged to compare "into," "away" and "broadside" orientations at each of four current speeds. Tabulated values are means obtained from 40 fish of each species, observed 10 at a time.

C. asper

Current	Into	Away	Broadside
1	2.25	2.75	5.0
2	2.69	1.81	5.5
3	2.38	1.56	6.06
4	1.31	2.88	5.81

C. aleuticus

Current	Into	Away	Broadside
1	3.75	3.13	3.13
2	4.0	3.25	2.75
3	3.56	2.63	3.81
4	3.13	2.94	3.94

Means joined by dotted lines are significantly different at $p < 0.05$ by the Student-Newman-Keul test.

C. asper behaved in much the same manner on sand as on gravel, except that the preference for the "broadside" position was more pronounced on sand.

C. aleuticus, however, showed considerable differences in this behaviour on gravel and on sand. On a gravel substrate no one position was preferred at either current 1 or current 4. At current 2 there was a significantly greater number of animals that assumed the "into" position. At current 3 "broadside" was more frequent than "away," but not more than "into." On a sand substrate *C. aleuticus* showed no preference at current 1, but at the other three current speeds "broadside" and and "into" were both more frequent than "away," although no significant difference could be found between "into" and "broadside."

The "away" category does not appear to follow an easily describable pattern. It was much more frequent in *C. aleuticus* than in *C. asper*, reflecting *C. aleuticus'* overall greater preference for the parallel alignment. At no time, however, was it more frequent than the "into" position in *C. aleuticus*. *C. asper* adopted the "away" position more frequently than the "into" at high current speeds on gravel.

As can be seen from Tables V and VI, current speeds had very little effect on the frequency with which *C. aleuticus* assumed any position. No significant differences were detectable by the Student-Newman-Keul test.

C. asper, however, did respond to changing current speed with a change in position. On a gravel substrate the frequency

TABLE V

The frequency with which *C. asper* and *C. aleuticus* faced in three directions at four current speeds on a sand substrate. Data are arranged to show the effect of four current speeds on a single orientation. Tabulated values are means obtained from 30 fish of each species, observed 10 at a time.

C. asper

Current	1	2	3	4
Direction				
Into	2.75	1.17	1.25	1.0
Away	1.0	0.83	1.0	0.75
Broadside	6.25	8.0	7.75	8.25

C. aleuticus

Current	1	2	3	4
Direction				
Into	3.67	4.0	3.83	4.5
Away	2.58	1.58	1.08	0.83
Broadside	3.75	4.42	5.08	4.67

Means joined by dotted lines are significantly different at $p < 0.05$ by the Student-Newman-Keul test.

TABLE VI

The frequency with which C. asper and C. aleuticus faced in three directions at four current speeds on a gravel substrate. Data are arranged to show the effect of four current speeds on a single orientation. Tabulated values are means obtained from 40 fish of each species, observed 10 at a time.

C. asper

Current	1	2	3	4
Direction				
Into	2.25	2.69	2.38	1.31
Away	2.75	1.81	1.56	2.88
Broadside	5.0	5.5	6.06	5.81

C. aleuticus

Current	1	2	3	4
Direction				
Into	3.75	4.0	3.56	3.13
Away	3.13	3.25	2.63	2.94
Broadside	3.13	2.75	3.81	3.94

Means joined by dotted lines are significantly different at $p < 0.05$ by the Student-Newman-Keul test.

of the "into" category decreased at the highest current speed used (4), and this was significantly different from the frequency at current 2. The frequency of the "away" category at first declined and then increased with current speed, significantly different means being obtained between currents 1 and 3, and currents 3 and 4. The "broadside" category remained at about the same frequency at all current speeds.

On a sand substrate the behaviour of C. asper was somewhat different. There was a decreasing frequency of the "into" category, the differences between currents 2 and 3 being significant. The "away" category remained about the same; rather it was the "broadside" frequency which changed. This category was of a significantly lower frequency at current 1, than at any of the other three current speeds.

Stance

A. Observation

Early in the course of this study it was noticed that C. asper and C. aleuticus had several characteristic postures with regard to the position of head and body and the degree of extension of the fins. There appeared to be a difference in the frequencies with which these "stances" were assumed by the two species. Further, it appeared to be possible to correlate a given condition of substrate and current with a stance for each species.

The most common posture assumed by C. asper when at rest on a sand substrate was to lie with the belly pressed flat against the sand, the head horizontal, the dorsal fins somewhat extended and the pectoral, pelvic and caudal fins folded.

C. aleuticus also assumed this posture on sand, but on a gravel substrate they more frequently extended the pectoral fins, thus lifting the body out of the hollows between the stones. Under many conditions of current and substrate C. aleuticus assumed the "head down" or "head up" positions (Fig. 2), in which the body was inclined at an angle to the substrate. The "head up" position was about as frequent as the horizontal, but the "head down" was usually only observed when the animal was foraging for food among the rocks, or if it was in an area of extreme turbulence.

The dorsal fins of C. aleuticus were most often extended, although under some conditions the folded posture was of equal frequency.

When C. asper were placed on a gravel substrate they retained their characteristic posture, so that they lay between the stones.

It seemed likely that the stances assumed by the two species would make a considerable difference to their exposure to the current. Experiments were therefore conducted to determine differences in the frequencies of the various postures between the species. By comparing the stances of the animals in a variety of conditions of current and substrate, one could speculate on the function of these postures.

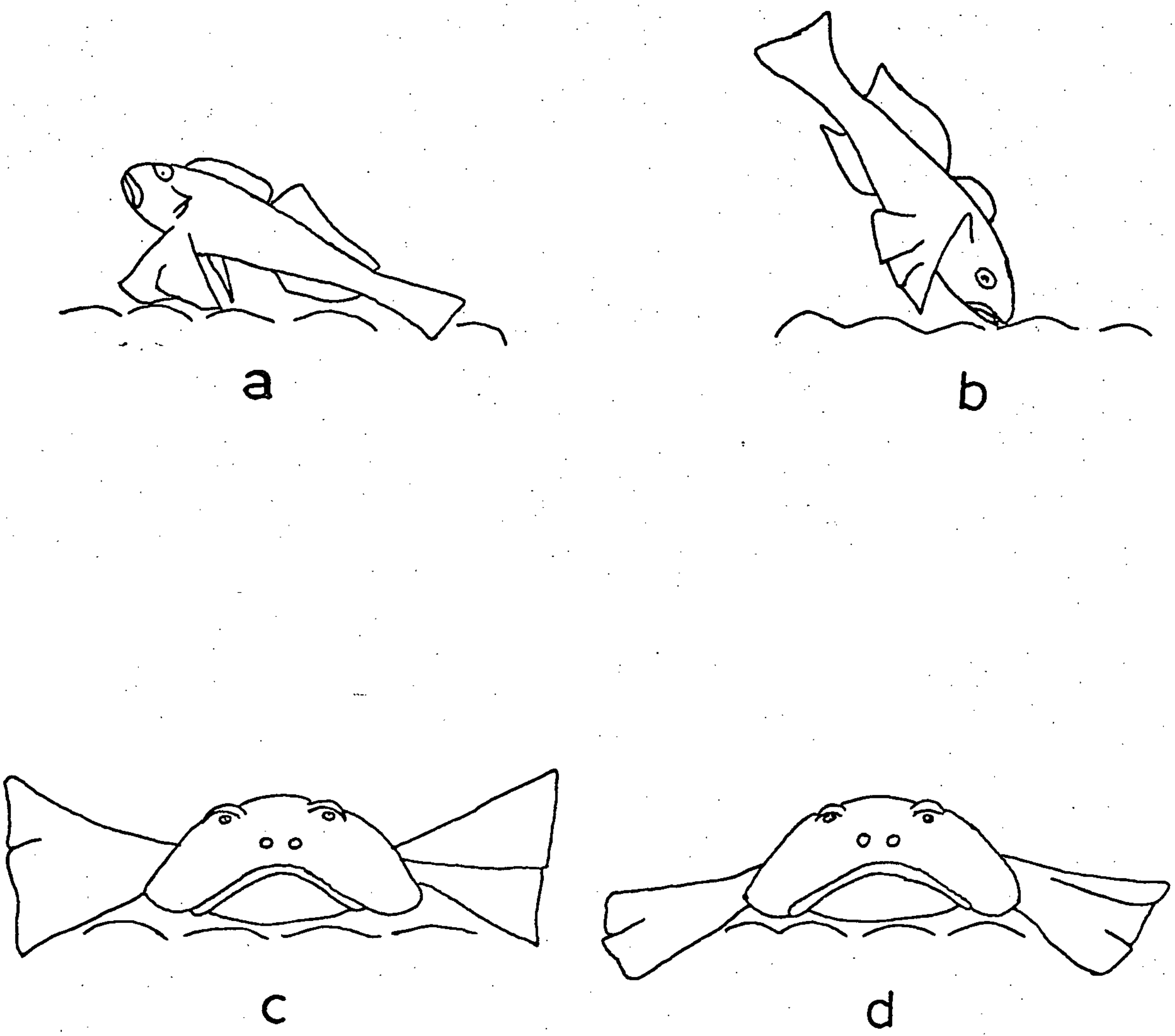
Figure 2. Four postures of C. asper and C. aleuticus

a) head up

b) head down

c) pectoral fins expanded

d) pectoral fins folded


a
b
c
d

B. Method

To determine the stance most commonly assumed in any given condition of substrate and current, five fish of one species were placed together in the flow tank and exposed to one of two current conditions, "noncurrent" (less than 6 cm/sec) and "current" (greater than 10 cm/sec). The fish were actually observed at three different current speeds, but since there was no detectable difference among these categories they were considered as one. Consequently there are three times as many recordings for "current" as "noncurrent." The position of the head and body, and the degree of expansion of the dorsal and pectoral fins were noted. The pectoral fins were not considered to be "expanded" if they were merely fanned out flat against the substrate, but only if they were held at an angle to the substrate (Fig. 2).

A total of 473 recordings were made, fifteen fish of each species being observed on sand, and fifteen on gravel. Recordings were made for approximately five minutes at a time.

C. Results

The counts obtained were grouped according to alternatives, e.g., "pectoral folded" (p.fol.) and "pectoral extended" (p.ex.). A series of X^2 tests were then performed on the groups (Tables VII and VIII).

C. asper assumed the folded position of the pectoral fins under all conditions tested, the most marked preference being shown with gravel and current (Table VII). The horizontal

TABLE VII

Postures assumed by *C. asper* on sand and gravel substrates under two conditions of current.[1]

	Sand		Gravel	
	Current	Noncurrent	Current	Noncurrent
Pectoral Fins				
Extended	14	3	5	0
Folded	33	13	57	15
X^2	7.68	6.25	43.6	15.0
Preferred	p.fol.	p.fol.	p.fol.	p.fol.
Dorsal Fin				
Extended	37	10	55	15
Folded	10	6	7	0
X^2	15.5	1.0*	37.16	15.0
Preferred	d.ex.	---	d.ex.	d.ex.
Head				
Horizontal	41	14	53	14
Head Up	5	2	9	1
Head Down	1	0	0	0
X^2	82.99	21.5	77.85	24.4
Preferred	hor.	hor.	hor.	hor.

[1]<6 cm/sec and >10 cm/sec.

*not significant at $p<0.05$.

TABLE VIII

Postures assumed by C. aleuticus on sand and gravel substrates under two conditions of current.[1]

	Sand		Gravel	
	Current	Noncurrent	Current	Noncurrent
Pectoral Fins				
Extended	26	3	95	80
Folded	45	17	62	5
X^2	5.08	9.8	6.93	66.18
Preferred	p.fol.	p.fol.	p.ex.	p.ex.
Dorsal Fins				
Extended	59	17	70	59
Folded	12	3	87	26
X^2	31.11	9.8	1.84*	12.81
Preferred	d.ex.	d.ex.	---	d.ex.
Head				
Horizontal	58	13	77	39
Head Up	12	7	75	42
Head Down	1	0	5	4
X^2	61.79	12.70	64.3	31.51
Preferred	hor.	hor.	hor./h.u.	h.u./hor.

[1] <6 cm/sec and >10 cm/sec.

*not significant at $p < 0.05$.

(hor.) position of the body was similarly greatly preferred, the preference being more marked in current situations. The extended posture of the dorsal fins (d.ex.) was more frequent than the dorsal folded position (d.fol.) at all times and this preference was significant except under sand and noncurrent conditions.

C. aleuticus showed a much greater variability of stance with changing conditions. Like *C. asper*, *C. aleuticus* showed a distinct preference for the pectoral folded posture on a sand substrate. However, when placed on gravel *C. aleuticus* much preferred the pectoral extended posture. This was especially marked under noncurrent conditions.

C. aleuticus assumed the dorsal extended posture with a greater frequency than the dorsal folded in three out of four cases. The exception was a small nonsignificant preference for the dorsal folded position with gravel and current.

C. aleuticus favoured the horizontal position on sand, but on gravel the "head up" (h.u.) position occurred with equal frequency.

Thus the two species behaved in a very similar manner on a sand substrate, but differed markedly in their response to a gravel substrate.

Movement in Response to Current

A. Observation

It was observed that *C. asper* had great difficulty in moving around in the tank in a current of any magnitude, and that even in noncurrent conditions they did not move about as much as *C. aleuticus*.

C. aleuticus is a much better swimmer than *C. asper*. When attempting to move up or downstream in the presence of a current, *C. aleuticus* kept close to the substrate, particularly if it was gravel, and moved in a series of short, rapid leaps (Fig. 3a). Using this method, they had a remarkable ability to maintain their position in areas of extreme turbulence and to move upstream against a current capable of displacing the gravel.

C. asper attempted to move up or downstream by swimming up at an angle to the substrate (Fig. 3b). They were rarely able to make any advances upstream in any but the slowest currents, and their progress downstream was considerably hastened by the current. At times they appeared to be caught up by the current and swept helplessly along until they reached the end of the tank farthest from the current source. They were then able to right themselves by twisting their bodies until they were parallel to the substrate and to sink to the bottom of the tank.

Experiments were carried out to detect a quantitative difference in the amount of movement up or downstream by the two species under various current conditions.

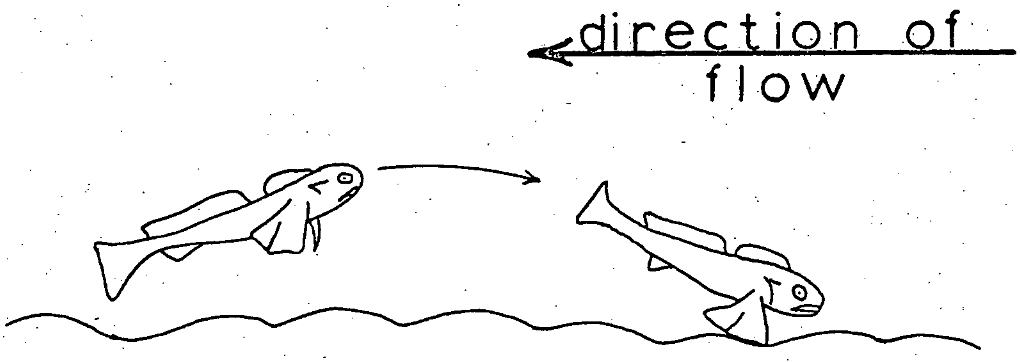
B. Method

To test the amount of movement of the species, a bottomless wire cage was placed in the middle portion of the flow tank, where a current of constant speed could be maintained. The side wall of the tank, above the plexiglas window, was marked off in

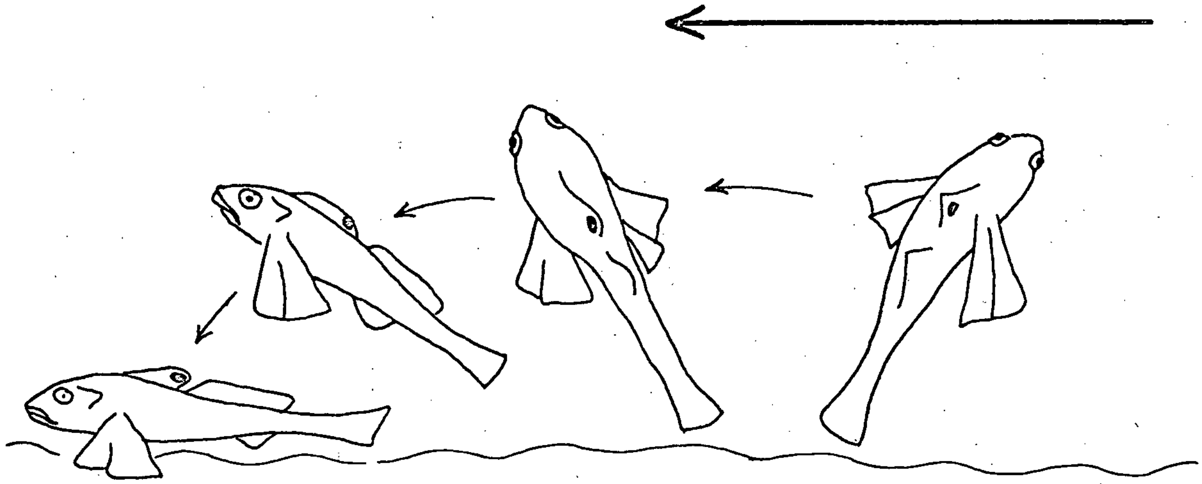
Figure 3. The methods used to swim in a current

a) C. aleuticus

b) C. asper



a



b

inches along the length of the wire fence, so that the fish's position could be determined at a glance through the window (Fig. 1). The posterior margin of the first dorsal fin was taken as a position marker, to eliminate the effect of changes in the direction faced without any movement up or down stream.

A single fish was introduced at the midpoint of the cage, and its position was recorded every three minutes for fifteen minutes while it was exposed to a current of constant speed. At the end of this time the fish was removed and an individual of the other species and approximately the same size was similarly tested. These fish were then discarded and another pair was tested at the same current speed.

A total of forty fish were tested, ten under "noncurrent" conditions (less than 6 cm/sec) and thirty at three different current speeds (13, 20 and 25 cm/sec).

This experiment was conducted on a gravel substrate.

C. Results

The data from this experiment were tested by an analysis of variance (Table IX). The species difference (S) was significant at $p<0.05$ ($F = 37.23$). Currents (C) and the species x currents interaction (S x C) were not significant.

The species means were compared by Tukey's w (Table X). *C. aleuticus* showed a greater amount of movement than *C. asper* under all current conditions.

The only significant change in amount of movement with increased current speed was a decrease in movement by *C. aleuticus*

TABLE IX

Total number of inches moved by *C. asper* and *C. aleuticus* in fifteen minutes at four current speeds.

SOURCE	SS	df	MS	F
Species	70.33	1	70.33	37.23*
Current	1.77	3	0.59	0.31
S x C	4.2	3	1.4	0.74
Error	60.48	32	1.89	
Total	136.78	39		

*significant at $p<0.05$.

TABLE X

Mean number of inches moved by *C. asper* and *C. aleuticus* in fifteen minutes at four current speeds. Comparison of species means.

Tukey's w = 2.3609.

CURRENT	1	2	3	4
Means for:				
C. asper	0.1	0.2	0.1	0.8
C. aleuticus	6.8	5.5	7.8	4.8
			----	----
Difference between the species' means	5.7*	5.3*	7.7*	4.0*

*significantly different at $p<0.05$.

----significantly different at $p<0.05$, when comparing within a single species at different current speeds.

between currents 3 and 4 (Table X). There is a definite but nonsignificant increase in movement by C. aleuticus between currents 2 and 3.

Feeding Behaviour

A. Observation

The superior swimming ability and greater "alertness" of C. aleuticus is reflected in the species' feeding behaviour.

The most common method in both species is to make short, horizontal darts across the bottom of the tank to seize food that is lying on the surface of the substrate or floating just above it. Such "darts and grabs" have been reported in another cottid species by Smyley (1957). This behaviour is sometimes directed towards inedible objects, which are then spat out. C. asper relied almost exclusively on this technique of food getting. The largest individuals, which spent most of the daytime in their hides, made brief sorties for food not far from the refuge, and quickly returned to it. This method was used for small food items such as brineshrimp, and also for small fish.

A method that was very rarely observed in C. asper but quite often in C. aleuticus was swimming to the water surface to get food that was drifting down. At times the fish's body would be almost perpendicular to the water surface, while the pectoral fins were used in a fanning motion, and the body undulated. This activity usually lasted less than thirty seconds and it was most commonly used when eating brineshrimp.

C. aleuticus would quite frequently move over the gravel, putting the head down in the crevices in the substrate to pick up food that had settled there. This foraging behaviour was used mainly in obtaining brineshrimp, although occasionally a guppy that was small enough to settle between the stones was eaten in this way.

C. aleuticus ate readily whenever food was available, even during the times of day in which their general level of activity was somewhat reduced. C. asper less often ate food as soon as it was presented, and during their relatively inactive period they would usually eat only if the food was deposited at the entrance of the hide.

C. aleuticus seemed to rely on sight to a certain extent in obtaining its food. The dropper by which the brineshrimp were introduced to the tank had only to appear above the water surface to set off a burst of activity in the fish; in particular, swimming to the water surface beneath the dropper.

C. asper were observed to roll their eyes up and to follow the food with their eyes as it drifted to the bottom of the tank.

The role of the chemical senses in obtaining food was more difficult to determine. Individuals of both species were observed to turn around and swim towards food that had been introduced out of line of their sight some distance away in a tank. But whether this was a response to chemical stimuli, or to the activity of other fish in the tank, or a chance sight of the experimenter, could not be determined.

B. Method

Preliminary tests were conducted in an attempt to ascertain the role that the chemical senses played in detecting the presence of food. The tests were conducted in a Y shaped maze (29" x 5¼" x 6½") (Fig. 4). The stem of the Y was partitioned off with a piece of black plexiglas (4" x 6" x 1/10") which could be raised or lowered on a string by the experimenter. The maze was completely enclosed by black polyethylene curtains with narrow slits through which the fish could be observed.

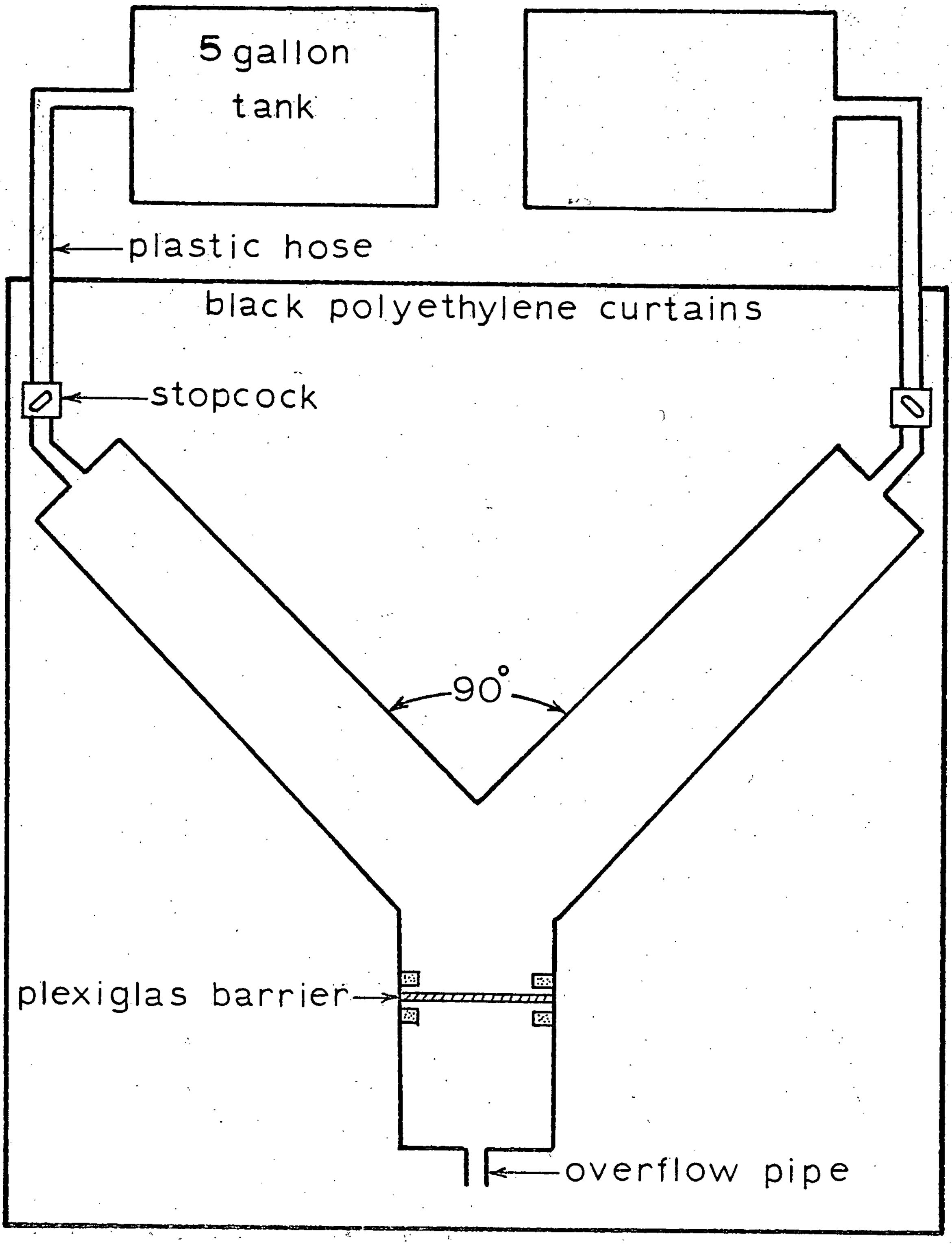
A continuous flow of dechlorinated water was provided by small (1/16") plastic hoses draining from two 5 gallon tanks on a shelf behind the enclosure. These hoses fed into the two arms of the Y and a siphon drained off the excess water at the stem of the Y. Water flow through the tubes was controlled by stopcocks.

A single fish that had been food deprived for about a week was placed in the stem of the Y behind the plexiglas barrier in the evening and left undisturbed overnight. The following morning approximately 5 ml of thawed brineshrimp was introduced into one arm of the Y. The barrier was then raised and the fish's movements recorded for 30 minutes.

Five fish of each species were tested in this way.

The direction and rate of diffusion of fluids in this maze were studied by observing the pattern of diffusion of various amounts of a 1% solution of methylene blue. It was found that the first traces of the dye were detectable by the human eye

Figure 4. The Y trough used for food detection experiments.


5 gallon
tank
plastic hose
black polyethylene curtains
stopcock
90°
plexiglas barrier
overflow pipe

at the stem of the Y a maximum of five minutes after the dye had been introduced to the arms of the Y. The maximum time for the diffusion of the heaviest concentration of the dye in this manner was fifteen minutes.

C. Results

The results of this experiment can only serve as an indication of the direction that future experiments should take, as the number of fish tested was limited by the time available for this study.

Four out of five C. aleuticus made "incorrect" first choices (Table XI). Only three C. asper made a choice, but all three chose correctly. This may be explained in part by certain differences in the behaviour of these species. When C. asper are disturbed they most often react by lying very still for some time after the stimulus is removed. C. aleuticus usually swim quickly away from the source of the disturbance (Appendix C). As a result, when the barrier was raised, the C. asper stayed in the stem of the Y for as long as 27 minutes before making their first choice (Table XI). Four out of five of the C. aleuticus, however, when disturbed by the barrier left the stem of the Y in the first thirty seconds after the barrier was raised. The three fish that swam into the incorrect arm moved to the correct after 6 to 6.5 minutes had elapsed.

TABLE XI

Ability to detect food by chemical senses. Correctness of first choice.

	Time of First Choice (Minutes)	Correctness of First Choice	Time of First Correct Choice (Minutes)
C. asper			
1	11.5	correct	11.5
2	----	-------	----
3	----	-------	----
4	27.0	correct	27.0
5	19.5	correct	19.5
C. aleuticus			
1	0.5	incorrect	6.0
2	0.5	incorrect	6.5
3	0.5	correct	0.5
4	0.5	incorrect	6.5
5	20.0	incorrect	23.0

DISCUSSION

Discussion of Results

Since *C. aleuticus* on a sand substrate adopted a flat-lying posture (pectoral fins folded, dorsal fins extended, body horizontal) that was common in *C. asper* it is probable that this position is a response to *C. asper's* usual substrate. That this is indeed a reaction to a sand substrate is indicated by the fact that both species exhibited this posture on sand in current and "noncurrent" conditions. Smyley (1957) reported that *C. gobio*, which inhabits areas of slow to moderate current, and which exhibits many behavioural traits similar to those of *C. asper*, has a marked "preference" for keeping the body in contact with some surface.

The preference on the part of *C. aleuticus* for the extension of the pectoral fins on a gravel substrate was more marked in conditions of "noncurrent" than current. It may be that this position exposes the animal to a certain amount of current, but that the stance has a function that is sufficiently "important" to ensure that this posture will be retained in swift water, although at a reduced frequency. The significance of this raised posture might be that it permits the animal to catch food drifting in the water or to move with greater ease from stone to stone as it forages among the rocks. It would also allow the fish to maintain a more viligant watch on its surroundings.

In areas of extreme turbulence and current of greater than 25 cm/sec *C. aleuticus* put the head down into the current.

However this posture was uncommon in a regular, even current except when it was used for hunting for food. It might enable the animal to maintain position in areas of great turbulence.

The functional significance of the alignment with respect to the current is a matter for speculation, but it does appear to be related to the postures that the species assume. Animals which live in a strong current have special problems which they can meet in a variety of ways. Animals with streamlined body shapes that offer a minimum of resistance to the water can swim against the current. Those with flattened body shapes and clinging habits minimize the effect of the current by pressing against the substrate. And still others escape altogether and take shelter under rocks or in mats of aquatic vegetation (Needham *et al.*, 1935). It could be that facing parallel to the current and spreading the pectoral fins enables *C. aleuticus* to resist the current more effectively. However, *C. asper* presumably obtains an even greater degree of security by lying down between the stones of a gravel substrate. The advantages to *C. aleuticus* remaining on the surface of the stones must outweigh the increased exposure to the current.

The "into" position appears to have a special significance for *C. aleuticus*. Since *C. aleuticus* feeds partly on organisms floating in the water, the "into" position would enable them to detect food floating downstream and to intercept it more efficiently. If the fish faces away from the oncoming current it has to swim downstream after the food. If it faces into the current it can dart up to intercept it. Such quick darts and leaps are more characteristic of these species than prolonged swimming.

The fact that both species assumed the broadside position more frequently on sand than on gravel suggests that this position is an adaptation to a sand environment. It would seem unlikely that it has a function as a means of avoiding the current since it places more of the fish's body directly in the path of the current than any other position. However, C. asper employed this position more frequently in current than non-current, on sand. Since C. asper is a poor swimmer, especially in a current, the significance of this position might be that it enables the animal to move most of the time at an angle to the direction of flow, so that it is less easily displaced by the current.

In the light of their feeding behaviour observed in the laboratory it is likely that C. aleuticus depends on vision to a greater extent than C. asper does. C. asper probably depend mostly on their chemical senses to detect food and only use their vision to locate food more precisely as they dart forward to seize it. The ease and frequency with which C. aleuticus take floating food indicate that they depend on vision to some degree.

That at least some species of cottids rely on vision to some extent is indicated by Smyley (1957) and Phillips and Claire (1966), who studied C. gobio and C. perplexus respectively, and who found that these species preferred moving food.

C. asper's reluctance to feed during the day is probably related to its inhibition against leaving the hide during this period. Smyley (1957) noted that C. gobio ate very close to the hide and seldom emerged to hunt food, except at night.

The difference in swimming ability between these species is probably also related to their feeding behaviour, as C. asper appears to be a lurking predator, at least in the daytime, whereas C. aleuticus is an active forager and hunter.

General Discussion

Taylor (1966) attempted to determine the extent to which C. asper and C. aleuticus select the current and substrate types with which they are associated in the Little Campbell River. He presented individuals of three size groups (less than 40 mm, 40 to 85 mm and 85 to 90 mm) with a choice of fine (sand) or coarse (gravel) substrate. He also presented current (45 cm/sec) and "noncurrent" (less than 7 cm/sec) choices, and current and substrate choices simultaneously. His results are summarized on Table XII. Comparing this with the current and substrate conditions at the collection sites (Table XIII), one can see that C. aleuticus behaved as one would expect from field observations. All size groups selected current and gravel over noncurrent and sand. No significant difference was detected in the gravel/sand choice of the largest size group but this accords with their occurrence in the pool habitat. Similarly, the lack of preference with regard to current in the C. aleuticus fry corresponds with their collection in areas of slow current.

The results of the C. asper tests are less convincing in

TABLE XII

Summary of results of substrate/current velocity choice experiments (G. Taylor, 1966).

	Condition Selected When Presented With:		
Size Group	gravel/sand	noncurrent/ current	sand/gravel and noncurrent/ current
<40 mm (Fry)			
C. asper	gravel	no preference	no preference
C. aleuticus	gravel	no preference	current/gravel
40 to 85 mm			
C. asper	no preference	noncurrent	no preference
C. aleuticus	gravel	current	current/gravel
85 to 90 mm			
C. asper	no preference	no preference	no preference
C. aleuticus	no preference	current	current/gravel

TABLE XIII

Ecological data on the areas of the Little Campbell River from which *C. asper* and *C. aleuticus* were collected.

			Middle River	
	Estuary	Lower River	Pools	Riffles
Most Common Substrate	silt, mud, oyster shell	sand, silt, mud	sand, fine gravel	coarse and fine gravel
Current* cm/sec	0-30	0-45	<7.5	0-90
Species Collected	*C. asper*	*C. asper*	*C. asper* >100 mm	*C. aleuticus*
	C. aleuticus Fry (<40 mm)		*C. aleuticus* >80 mm	

*measured by Taylor (1966).

that a surprising lack of a preference for noncurrent is shown by two size groups. This may have been due to Taylor's experimental method, which involved checking the fish's position at intervals, rather than continuous observation. He reported that many C. asper never left the starting point where the current was rather low.

Taylor did find, however, that the greatest divergence in choice between C. asper and C. aleuticus occurred in the size group that was most sharply segregated in nature. Taylor's laboratory findings, when compared with his field observations, indicate that the laboratory conditions corresponded to the natural habitat. This enables one to assume that behaviour observed in these conditions is a real feature of the animal's response to its environment.

The findings of this study agree on the whole with Taylor's. C. asper tends to avoid current on a gravel substrate by lying down among the stones, and to minimize the effect of current on sand by keeping the body pressed flat against the substrate. C. aleuticus, however, adopts a posture and an orientation that actually exposes it to the effects of the current, on a gravel substrate.

That the species are differentially adapted to their microhabitats in some way is apparent from Taylor's results. The findings of this study indicate what some of the behavioural adaptations are.

The morphology of C. asper and C. aleuticus also reflects the differences in their habitats. Among related species of fish that differ in their swimming habits it is a general rule that the more active form has a slenderer caudal peduncle and a more streamlined shape than its sedentary relatives (Lagler *et al.*, 1962). Dorso-ventral depression is associated with bottom dwelling stream fish and it presumably aids them in keeping in position in a strong current (Lagler *et al.*, 1962). *C. asper* is thus typical of the trend in sedentary bottom dwellers and *C. aleuticus* is representative of more active fish.

C. asper and *C. aleuticus* lack swim bladders, as do many fish which inhabit swift streams (Lagler *et al.*, 1962). Although the absence of a swim bladder is no drawback to a sedentary bottom dweller, it might at first appear to be a disadvantage to a more active species. Swim bladders which function as hydrostatic organs enable fish to expend a minimum amount of energy in maintaining position (Lagler *et al.*, 1962). However, in a strong current to be of equal density with the water requires greater, not less, energy to maintain position (Lagler *et al.*, 1962).

The mouth size of cottids is of the first importance, as it determines the size of the food that they eat (Northcote, 1954). Of the two species considered here, the larger *C. asper* also has the larger mouth relative to body size. In the laboratory they feed almost exclusively on organisms resting in the substrate or floating just above it. Northcote (1954) reported that *C. asper* of greater than 30 mm mainly eat aquatic insect larvae such as Plecoptera, Ephemoptera, Trichoptera, and Diptera (chironomids), which live among weeds and stones or burrow in sand or mud (Macan and Worthington, 1951). Sculpin fry eat the larger planktonic forms, such as Cladocera and Copepoda (Northcote, 1954), which, like all planktonic species, are rather small animals (Macan and Worthington, 1951). Active, small mouthed sculpins, such as *C. aleuticus*, could continue to exploit the plankten as an additional food source when adults. This would require a superior swimming ability and a greater dependence on vision than the bottom feeding habit. If the fish inhabits areas of strong current it must adopt modes of behaviour that enable it to obtain this kind of food in fast water. Thus *C. aleuticus* orients parallel to the direction of flow and lifts itself above the rocks on spread pectoral fins, permitting it to survey it's surroundings and to launch itself quickly upwards to catch floating food.

C. asper is a poor swimmer. Such a loss of swimming afficiency as a result of dorso-ventral depression is, however, offset by certain advantages. These include a gain in mimetic resemblance to the substrate (Appendix D), and in the efficiency of such secretive habits as the use of stones or other objects as shelter (Lagler *et al.*, 1962). *C. asper* is extremely secretive, spending most of the brightest hours of the day under logs or stones or in mats of vegetation.

SUMMARY

This study is an examination of the behaviour of two related sympatric species which occupy different microhabitats to determine which are some of the important behavioural adaptations to these differences in environment.

C. asper is collected in areas of slow current and finely textured substrate. *C. aleuticus* is most frequently found in areas of moderate to fast current and coarse substrate.

When exposed to a current in the laboratory *C. asper* presses the body against the substrate and lies at right angles to the current, thus avoiding the current, or at least minimizing its effects.

In a current *C. aleuticus* faces parallel to the direction of flow and on a gravel substrate raises the body by the expansion of the pectoral fins. One of the functions of this posture may be that it enables the animal to sight on and catch floating food. The spread pectoral fins might also enable the animal to resist the current.

In both species stance and orientation to the current seem to be in part a response to the nature of the substrate. Both *C. asper* and *C. aleuticus* adopt a typically *C. asper* posture and orientation on sand with a greater frequency than on gravel, and *C. aleuticus* type behaviour is more frequent in both species on gravel than on sand. However, *C. asper* still assumes the broadside position on gravel with an equal or greater frequency than the parallel, and *C. aleuticus* still shows a preference, although a reduced one, for the parallel alignment on sand.

Both species appear to employ vision and the chemical senses in obtaining food, but to different extents. C. aleuticus appears to employ vision more than C. asper does. However, C. asper would require some aid from vision to sight on the food before darting forward to seize it.

C. aleuticus relies on vision to locate its food when it feeds on floating organisms. However, the foraging behaviour shown by this species suggests that they also use the chemical senses in hunting, although perhaps their ability to detect food in this manner operates over a much shorter distance than in C. asper.

C. asper is a very poor swimmer compared to C. aleuticus and moves around much less in both current and noncurrent conditions. This corresponds with C. asper's reluctance to leave its hide during the daytime.

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APPENDIX

In the course of this study, many hours were spent simply observing the fish in a variety of situations, in an attempt to form a general impression of their behaviour. Many incidents were observed which were not further examined by experiments, but which have considerable bearing on this study. This Appendix, therefore, is an outline of some of the more pertinent of these observations, which make up the background for much of this research.

A. Adaptability to Laboratory Conditions

C. aleuticus appeared toadapt more quickly to the laboratory conditions than C. asper. C. aleuticus began to eat much sooner after they were brought into the laboratory. In inducing fish from the field to eat, it was noted that the smaller individuals of both species were the first to take the food. By placing individuals from a group of fish that were eating well in a group that were not eating, it was possible to induce the second group to eat.

Individuals of both species were kept alive and in apparent good health for over a year, indicating that they were well adapted to laboratory conditions.

B. Influence on Numbers on Behaviour

In keeping these fish and in observing their behaviour, the numbers of individuals kept in a single tank seemed to be of some importance. Both species exhibited very little aggressive behaviour among themselves, except when extremely crowded. Although cottids are territorial in the breeding season (Morris, 1954; Smyley, 1957) and the larger specimens (greater than 80 mm) were usually collected only a few at a time, there did not appear to be any necessity to separate the fish in individual aquaria. In fact, it was found that whenever the fish were isolated in this manner they stopped eating and soon died. This is not to say that the deaths were attributable to starvation, as in most cases the dead fish were of normal weight.

When ten to thirty fish were kept together, many individuals would associate under a single flowerpot. This was particularly marked in C. asper, which spent so much of their time in these refuges.

One male C. aleuticus in breeding condition established a territory in one flowerpot in a tank with about fifteen other fish, but very little response to his displays was noted in the other individuals.

Some aggressive behaviour was seen in connection with feeding when the animals were very crowded. This was particularly noticeable in C. aleuticus, which in these conditions customarily fed with its pectoral, caudal, and dorsal fins, and sometimes its operculum spread. This is very similar to the aggressive behaviour noted by Morris (1955) in C. gobio. Normally these "displays" did not result in any overt aggressive activity, although a few incidents were noted. The most common activity of this nature was pectoral fin biting, although there was also some chasing and nipping. Displays of this nature were also noted in C. asper, but less frequently, and overt aggressive behaviour was very rare.

Cases of aggregation behaviour have been reported in the field for both C. aleuticus (Greenbank, 1957) and C. asper (Northcote and Hartman, 1959).

C. Response to Unfamiliar Stimuli

On many different occasions these fish were observed when they were presented with unfamiliar objects or stimuli. Sometimes this was done deliberately, at others it occurred as a result of an experiment that was primarily designed for some other purpose.

When the stimulus was an unfamiliar variant of one which was common in the natural environment, such as frozen brine-shrimp, the fish did not behave in an "excited" manner. They might ignore the unfamiliar object for minutes or even days; then approach slowly, and finally exhibited no avoidance behaviour when another such object was introduced.

Stimuli which the human observer might expect to be frightening were reacted to in a variety of ways. An object, such as a styrofoam shape, dragged over the surface in rather deep water, elicited very little response other than upward eyerolling. However, if a handnet was dragged along the bottom of the tank both species became very "excited," swimming quickly away from the disturbed are of the substrate.

Lights of even very low intensity shone on a darkened tank, and tapping on the side of the tank, elicited somewhat different behaviour in the two species. The animal would either "freeze" in position and remain immobile, or it would swim quickly away, often to the nearest hide. The former reaction was most common in C. asper, the latter in C. aleuticus.

D. Cryptic Colouration

Both C. asper and C. aleuticus have a remarkable ability to alter the shade and pattern of their colouration to suit their background. This makes them very difficult to see, when they are observed from above.

On a uniform, pale coloured background, such as grayish sand, C. asper became uniformly pale gray, and their fins are nearly transparent. On a more varied background, such as gray and black gravel and/or brown sand with weeds, they are marbled, with five or six pronounced dark vertical saddles under the dorsal fins. The belly is light coloured.

In C. aleuticus, colouration is fairly characteristic of the individual animal. Most individuals are speckled gray and white, with three black saddle marks and black bars on dorsal, pectoral and caudal fins. A few fish, however, are speckled brown and white, producing a sandy colour, with very dark brown or black saddles. In all individuals on a highly variable substrate, such as gravel, the saddles are prominent, but they fade when the fish is placed on a uniform background.