

A FURTHER INVESTIGATION OF THE HOMING BEHAVIOUR OF
THE INTERTIDAL COTTID, OLIGOCOTTUS MACULOSUS GIRARD

BY

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ABSTRACT

The purposes of this study were to find the causes of the variability previously observed in the homing behaviour of Oligocottus maculosus Girard and to attempt to clarify the mechanisms by which the fish homes; in particular whether olfaction is the major sensory mechanism involved. The study was conducted at 12 sites on the southwest coast of Vancouver Island, British Columbia. Variability in homing behaviour and morphological characters between fish in different tidepool and inlet areas, as well as age, year-class and length differences in homing behaviour in one tidepool area were examined. Consideration of the sensory mechanisms involved in homing behaviour included: interactions between resident and introduced fish, the nature of movement between the transplant and home pools, detection of chemosensory clues, the use of the paired fins to detect touch and/or chemosensory clues and in greatest detail, the roles of vision and olfaction in homing behaviour.

Prior to investigating age and year-class differences, a method of age determination using otoliths was developed and compared with results from vertebrae and length-frequency analysis. At any one time there are three major age groups in the population with decreasing numbers of age 3 and 4 fish. Age-length relationships differed between areas.

Differences were found in homing behaviour between areas, which could be related to wave action (turbulence) and

the topographical irregularity (roughness) of the terrain. With decreasing turbulence and increasing regularity of the terrain, fidelity is shown to an increasing number of pools or a wider area and, in tidepool areas, increasing percentages of fish show homing behaviour. However, the fish which do home in turbulent rough areas show highest percentages returning to the home pool. In inlets, little homing behaviour is expressed. With decreasing turbulence and increasing regularity of the terrain, decreasing numbers of fish remain in the transplant area. These findings can be related to the reduced high tide activity of O. maculosus in turbulent areas shown by Green (1971b,c).

No consistent differences, which could be related to exposure or homing behaviour, were found in the meristic and morphometric characters of O. maculosus in different areas. Investigation of cirri on O. maculosus in different areas showed that there is a variable increase in the number of cirri, on all parts of the body, with length and age. There are differences in these relationships between areas but they do not seem to be related directly to exposure. Year-class differences in cirri numbers are not apparent. The function of the cirri could not be determined.

Age related differences in homing behaviour are apparent, although year-class differences are not. Examination of the age differences in homing behaviour by smaller size-classes than one year age groups showed that there is an improvement in the percentage successfully homing with length up

to about 5 cm. Homing is best expressed in fish between 5 and 7 cm (age 2) and after this size there is a decrease in the percentage successfully homing. The percentage of homing fish returning to the home pool appears to be about equal for all size classes. There is a decline in the percentage remaining in the transplant area with length except in the largest size classes of fish.

Juvenile fish (about 2.3 to 2.7 cm) which have moved into lower tidepools from the high tidepools in which they settle, show extensive movement between tidepools and appear to begin showing evidence of home range fidelity and homing behaviour at about 3 cm. It is suggested that during this period of extensive movement, the area is in some way "learned" and "memorized".

Investigation of the sensory mechanisms involved in homing behaviour did not produce any evidence to show that pool density or "space", behavioural interactions, touch or taste clues detected by the paired fins or taste receptors located elsewhere on the body are involved in homing. Some evidence was found to suggest that movement between the transplant and home pool is directed. Vision and olfaction appear to be involved in homing, a combination of blindness and anosmia being the most effective in reducing homing success to low levels. Both senses are essential to the successful homing of juvenile fish but vision and subsequently olfaction become unnecessary in older fish. It is suggested that adult fish are unable to home unless

one of these senses is available. Because of the difficulties of appreciating how either olfaction or vision can be used over any distance in the turbulent intertidal, it is suggested that olfactory and visual, and perhaps other clues from particular pools are used to home and that the fish moves from "pool" to "pool" to home. However, neither conspicuous visual landmarks nor olfactory clues emanating from the home pool were shown to be recognized by O. maculosus. The data from this and a related study (Khoo, 1971) suggest that the relative importance of sensory mechanisms may differ both in the development of homing behaviour and between areas.

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I. GENERAL INTRODUCTION

Various aspects of homing behaviour have been studied in about a dozen different intertidal fishes (Hubbs, 1921; Gerstacher and Denison, 1930; Beebe, 1931; Aronson, 1951, 1971; Williams, 1957; Peppar, 1965; Gibson, 1967; Stephens et al., 1970; Green, 1971a,b,c, 1973; Khoo, 1971, 1974). The majority of intertidal fish examined in this regard appear to show some evidence of limited home range and in some species, evidence of the ability to return to a small area when displaced, that is, homing. For only one intertidal fish, Bathygobius soporator (Cuvier and Valenciennes), does there appear to be relatively clear evidence of the primary sensory mechanism involved: vision (Aronson, 1951, 1971).

The intertidal fish which has received the most attention with respect to home range, homing behaviour and sensory mechanisms involved in homing, is the tidepool sculpin, Oligocottus maculosus Girard, which ranges from northern California to the Bering Sea, Kuril Islands and Okhotsk Sea (Hart, 1973). Gersbacher and Denison (1930) suggested, on the basis of finding tagged O. maculosus in the same pool over a period of at least 10 days, that the fish showed relatively restricted movement. Green (1971b) demonstrated that O. maculosus showed homing behaviour. Subsequently, Khoo (1971, 1974) undertook a comprehensive examination of various aspects of the homing behaviour of O. maculosus at Port Renfrew. He found, in contrast to the suggestions of Green, and Gersbacher

and Denison, that O. maculosus individuals rarely restricted their natural movement to one pool, and showed that their home range was usually a small group of pools with a maximum extent of about 30 m. He found that O. maculosus could home from up to 300m away and that the effect of increasing distance on homing ability was modified by wave action. Adverse weather, rough terrain and deep subtidal areas decreased homing success and there was a difference in homing performance between naive and experienced fish, although after one displacement there was no improvement in homing performance of repeatedly displaced fish. Sex and size (from 4.5 to 9.0 cm total length) appeared to have no effect on homing performance. From sensory impairment experiments he concluded that touch or taste clues detected by the paired fins were not involved in homing, but that vision and olfaction were, olfaction being more important than vision. He concluded that O. maculosus uses olfaction and/or some kind of exploratory search process to home.

This study was designed to continue the work of Khoo, investigating the homing behaviour of O. maculosus. The two purposes of this study were: to find the causes of the variability in homing success observed by Khoo and to examine further the sensory mechanisms involved in homing, to determine whether olfaction is the major mechanism involved and whether other mechanisms are also involved.

The variability in the percentage of fish successfully homing observed by Khoo led him to suggest that there were

homing and non-homing members of the population. To attempt to elucidate the factors that cause variability in homing performance, several approaches were taken. Homing behaviour in different areas was examined to determine whether any variability existed between areas and if it could be related to a particular factor. In addition, homing behaviour was investigated by age, year class and length to determine whether these factors affect homing performance. In the study of length differences in homing performance, particular emphasis was placed on juvenile fish. It was felt that following the development of homing behaviour in juvenile fish might be more productive than examination of homing performance in adults in which this behaviour is relatively well developed.

The investigation of the sensory mechanisms involved in homing behaviour was chiefly designed to clarify the role of olfaction in homing, since the mixing processes of the intertidal make it difficult to understand the existence and utilization of distinct odour streams, as suggested by Khoo. Additional mechanisms were examined to investigate whether they played any role in homing behaviour. The role of sensory mechanisms in the homing behaviour of juvenile fish was also investigated.

In this study, home range in tidepool areas is used in the way in which it was used by Khoo (1971) and Gerking (1959), as the area covered by the fish during normal travel (modified from Hayne, 1949). Thus, the home range is regarded as an area

of limited extent, covering the tidepools in which an O. maculosus individual is found. In non-tidepool areas, home range was regarded as a small area comparable to a group of tidepools. In this study, the term homing was also used in the way it was used by Khoo (1971), as the return to the home range when experimentally displaced.

This study is composed of five parts. Since the effects of age and year-class on homing were to be investigated, it was necessary to develop a valid method of age determination. Thus the first section is concerned with ageing studies. Investigations of behavioural differences in homing and morphological differences between populations in various areas comprise the following two sections. The fourth section is concerned with the investigations of age, year-class and length differences in homing behaviour. The final section considers the role of various sensory mechanisms in homing.

II. DESCRIPTIONS OF STUDY SITES AND CAPTURE METHODS

1. Major study site

First Beach

First Beach is situated on the east side of Trevor Channel in Barkley Sound (48°49'N, 125°10'W) (Figures 1 and 2, site L). This site was chosen as the major study area because it offered a large selection of tidepools at both the north and south ends of the beach and because it permitted access from both Trevor Channel and the head of Bamfield Inlet (Figure 3). The beach is moderately exposed since prevailing adverse weather (from the southeast and particularly the north) produce relatively large waves breaking outside the bay. Further description of this area is provided in Appendix 1.

The majority of experimental work conducted at First Beach was carried out in two groups of tidepools at either end of the southern rocky shelf. The distance between these two groups of pools is about 60 metres. There were six pools in each group, but for most experiments only about four of the six pools in each group were used to trap fish. The choice of pools depended largely on the season and abundance of O. maculosus. Both groups of pools ranged between about the 1 and 2.5 m tide level. Since the vertical distribution of O. maculosus in the

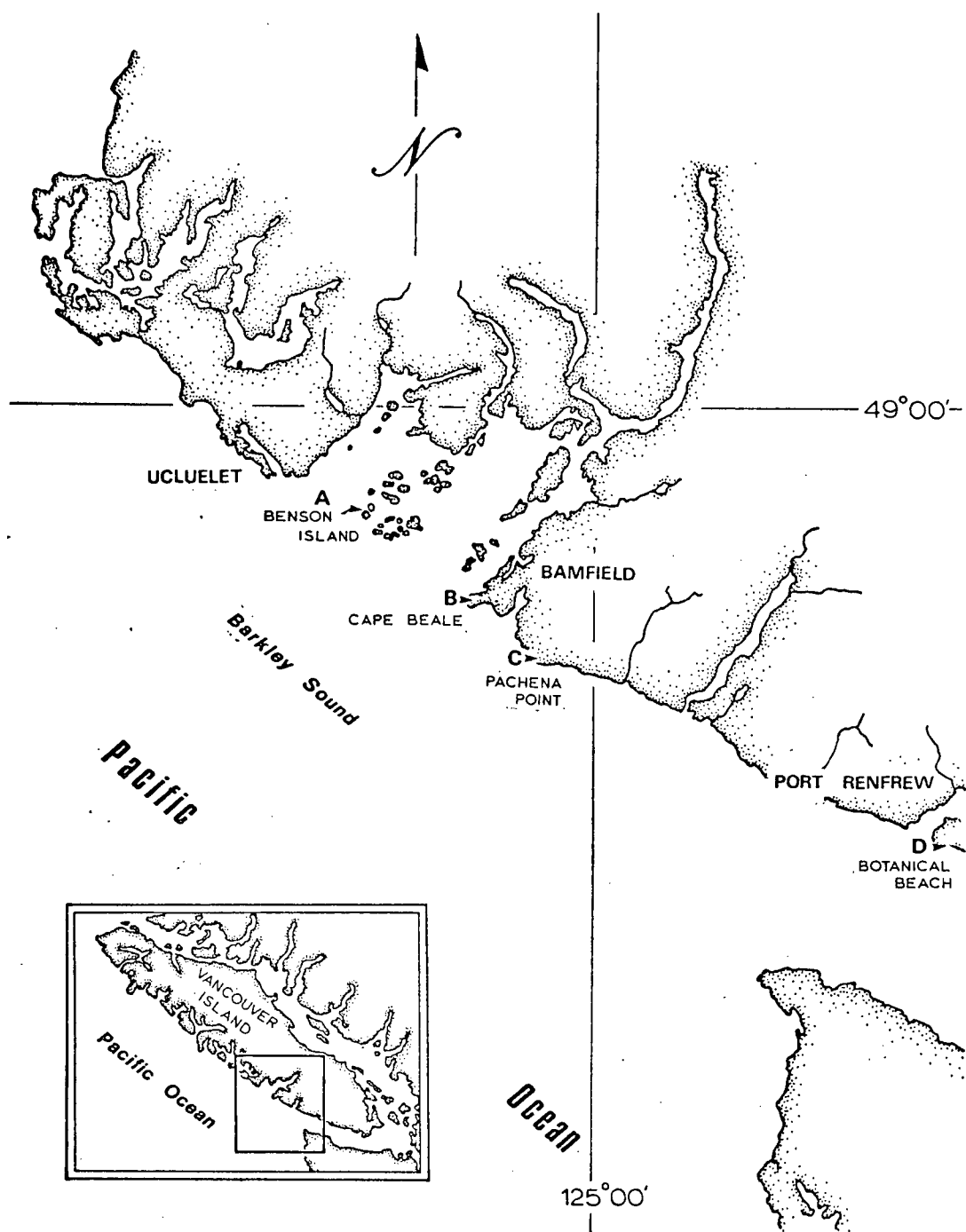


Figure 1 General location of study sites

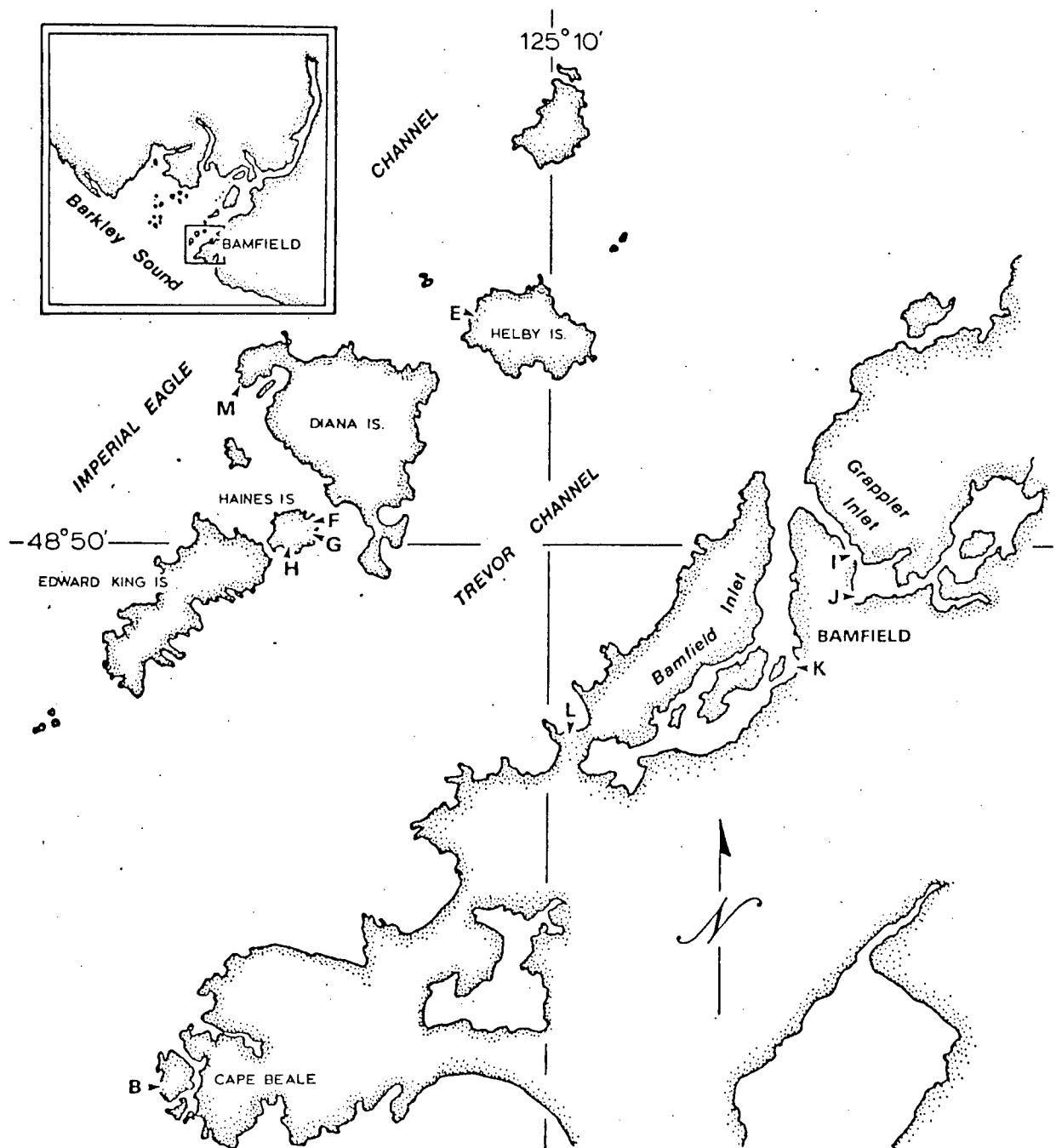


Figure 2 Locations of study sites



Figure 3 Aerial view of First Beach

intertidal is related to the size of the fish (Green, 1971a), there was some size selectivity in the fish used in experiments. At Port Renfrew, Green found that few fish less than 3.5 cm (total length) occurred below about the 2 m level and few fish less than 5.0 cm occurred below about the 1.5 m level. Although larger fish occurred in tidepools at all levels, fish larger than 5.5 cm did not normally inhabit tidepools less than 10 cm deep. At First Beach, few pools in the upper intertidal are deeper than 10 cm, so there are relatively few large O. maculosus at high levels. Since settlement of O. maculosus appears to occur largely in high shallow tidepools, there is a movement of fish down the intertidal as they increase in size. Thus, at First Beach, some O. maculosus between about 2.0 to 3.0 cm (total length) can be found in tidepools at about the 1.5 to 2 m tide level in about mid-June. The number of fish less than 4.0 cm increases in pools at and below this level as the summer progresses.

2. Other study sites

Exposed study sites

Benson Island ($48^{\circ}53'N, 125^{\circ}22'W$) is situated in the southwest of the Broken Group in Barkley Sound. The study site chosen on Benson Island is a narrow, steep rocky shelf facing northeast to east (Figure 1, site A). While the majority of oceanic swells and severe storms come from the southeast, the study site is relatively unprotected and thus was selected as an exposed site.

Cape Beale is situated at the mouth of Barkley Sound on the east side of Trevor Channel ($48^{\circ}47'N, 125^{\circ}13'W$) (Figure 1, site B). The study site chosen at Cape Beale was a narrow, rocky shelf directly in front of the lighthouse facing west across Barkley Sound. The site was chosen as an exposed site since even on a calm day large waves can be seen breaking on the offshore reefs surrounding Cape Beale, and on the shore itself.

Botanical Beach at Port Renfrew, hereafter referred to as Port Renfrew, is located on the west coast of Vancouver Island near San Juan Inlet ($48^{\circ}32'N, 124^{\circ}27'W$) (Figure 1, site D). The beach consists of extensive sandstone and shale shelves. Although it is situated in the Strait of Juan de Fuca, the beach faces in a westerly and north westerly direction onto

the Pacific Ocean. Thus it receives the full effect of Pacific swells. For this reason it was selected as an exposed site.

The beach designated as Pachena Point in this study is situated on the west coast of Vancouver Island about one kilometre north of the Pachena Point lighthouse ($48^{\circ}43'N, 125^{\circ}07'W$) (Figure 1, site C). The beach faces southwest directly onto the Pacific Ocean and thus was selected as an exposed site. The upper intertidal is composed of a steeply sloping gravel beach, below which lies a broad flat sandstone shelf, in which most of the experimental work was conducted. On either side of this shelf are lower rocky shelves with larger tidepools and scattered boulders.

Kirby Point is situated on the southwest corner of Diana Island in the Deer Group ($48^{\circ}51'N, 125^{\circ}12'W$) (Figure 1, site M). Two study sites were used at Kirby Point, both consisting of relatively narrow rocky shelves facing southwest, and thus receiving the impact of oceanic swells.

More detailed descriptions of these areas are provided in Appendix 1.

Moderately exposed study sites

Haines Island is situated towards the southern end of the Deer Group of islands in Barkley Sound. The southeast side of Haines Island consists of a large rocky shelf which is

exposed at low tide ($48^{\circ}49.9'N, 125^{\circ}11.7'W$). Since the strongest prevailing winds are generally from the southeast, an area on the shelf facing this direction was chosen as a moderately exposed study site (Figure 2, site H).

Helby Island is situated in the Deer Group of islands in Barkley Sound. The site selected for study is a rocky shelf on the southwestern side of the island, facing Ohiat Island and Imperial Eagle Channel ($48^{\circ}51'N, 125^{\circ}11'W$) (Figure 2, site E). Although the beach is somewhat protected by Ohiat Island, the numerous drift logs and absence of low brush just below the tree line suggest that the beach is moderately exposed.

More detailed descriptions of these sites are provided in Appendix 1.

Sheltered study sites

Grappler Inlet is situated on the eastern side of Trevor Channel in Barkley Sound. Two sites in the inlet were chosen as major study sites. One, on the south side of the inlet, is a small relatively sheltered bay ($48^{\circ}49.9'N, 125^{\circ}07.7'W$) and the second, an extremely sheltered mudflat, adjacent to the Government Wharf in Port Desire ($48^{\circ}49.8'N, 125^{\circ}07.6'W$) (Figure 2, sites I and J respectively).

A second site on Haines Island was selected as a sheltered study site ($48^{\circ}50.1'N, 125^{\circ}11.7'W$). On the eastern

side of the island is a large irregular area of rock exposed at low tide. Between the island itself and the rocky shelf is an extremely large tidepool, which partially drains at low tide into Dodger Channel (Figure 2, site G). The pool is relatively protected from swells from Trevor Channel by the rocky outcrops on its southern and eastern sides.

One site on the Haines Island side of Dodger Channel was selected for study ($48^{\circ}50.1'N, 125^{\circ}11.8'W$) (Figure 2, site F). The site was selected as a sheltered site since it remains calm during most storms. A bed of Zostera marina extends along the Haines Island shore of Dodger Channel and the site chosen was at the eastern end of the bed.

An area of the intertidal between Rance Island and the south east side of Bamfield Inlet ($48^{\circ}49'N, 125^{\circ}8'W$) was chosen as a sheltered study site (Figure 2, site K). At low tide there is a shallow channel of water surrounding Rance island and joining up with Bamfield Inlet. Two specific areas were chosen for study. One was a large tidepool adjacent to Rance Island, which is isolated from the main channel at low tide. The other was an area in the main channel adjacent to the mainland.


More detailed descriptions of these sites are provided in Appendix 1.

3. Enclosure

A large enclosure containing artificial tidepools and spanning the intertidal from about the 1 m level to about the 3.5 m level was constructed in the small bay in Grappler Inlet (48°49.9'N, 125°07.7'W) (Figure 2, site I).

The enclosure was designed to serve several purposes in the study of homing behaviour of O. maculosus. In homing experiments conducted in the field, a large percentage of O. maculosus individuals which do not home are lost for study. In a completely enclosed system of tidepools, those fish which do not home may be collected for examination of any differences between homing and non-homing O. maculosus. The other major reason for the construction of the enclosure was to investigate the pool fidelity and homing behaviour of juvenile O. maculosus. Following the development of homing behaviour of tagged juvenile fish in the field as they moved into lower tidepools would entail tagging large numbers of small fish. The relatively controlled environment of the enclosure offered the possibility of introducing large numbers of juvenile O. maculosus and monitoring their movements and homing behaviour much more readily.

The enclosure was constructed on a relatively steep rocky outcrop in the otherwise gently sloping bay. The

framework of the enclosure, 10 m long, 3.5 m wide and 5 m high at the seaward end was made of two  shaped constructions of 7.7 cm galvanized pipe embedded in concrete at either end. On top of these supports two logs were lashed to the outer edges of the horizontal pipes. Wooden poles embedded in concrete served as intermediate supports along the sides of the enclosure. Several diagonal and cross supports were added to the enclosure to increase stability (Figure 4).

To eliminate escape of introduced fish the four sides of the enclosure were covered with an exterior layer of 2.5 cm mesh chicken wire and an interior layer of fibreglass window screening. The small mesh of the window screening served to prevent escape of juvenile fish. In the first summer of operation, the chicken wire and window screening were attached continuously down the sides and across the bottom of the enclosure. This proved unsatisfactory because walking on the mesh produced large numbers of holes. In the second summer, the mesh and chicken wire on the sides were fastened to 2.5 cm x 10 cm planks embedded in concrete at the base of the sides. The bottom was left uncovered.

Deep (30 cm) and shallow (15 cm) plastic dishpans (40 cm in diameter) served as tidepools. These were attached with polypropylene lines tied to eyebolts embedded in the substrate with hydraulic cement. This arrangement allowed alteration of the positions of particular tidepools. Gravel, pebbles and small rocks with attached Fucus sp. and Mytilus edulis were



Figure 4 Enclosure from outside (above) and inside (below)

placed in the tidepools.

A shallow concrete trough was constructed at the seaward end of the enclosure to enable the fish which did not return to a tidepool at low tide but followed the receding water level to remain in water at tide levels lower than that of the seaward end of the enclosure.

A large wooden plank was placed on top of the cross supports about one metre from the top of the enclosure to enable viewing from above at high tide.

Around the outside of the enclosure, a small boom of logs and tires was constructed to provide a partial barrier to boat wake, which had severe effects on the screening. A greater problem was the effect of waves and strong winds caused by winter storms. Several severe storms were sufficient to destroy the screening. Thus, experiments in the enclosure were only feasible during the summer months.

4. Capture methods

Two methods of capture were used. The vast majority of O. maculosus used in homing experiments were caught using wire minnow traps. A piece of mussel (usually Mytilus californianus) was attached to a hook centrally located in the trap. Traps were placed in pools for about four hours around low tide (depending on weather conditions and tide height). When reciprocal transplants were being conducted and an insufficient number of O. maculosus had been captured from one group of pools, small dipnets were sometimes used to catch the necessary remaining fish.

Minnow traps collect few fish less than about 3.5 to 4.0 cm (total length) because the size of the wire mesh allows smaller fish to enter and exit anywhere in the trap. Thus, since the majority of homing experiments were conducted in pools up to about the 2.5 m tide level, juveniles for specific studies (fish less than about 3.5 to 4.0 cm) were collected with small dipnets.

To catch fish for cirri counts and age determination studies a combination of minnow traps and dipnets were used. In pool population studies, pools were bailed by bucket until very little water remained. Fish were then captured using small dipnets and by hand.

III. AGE DETERMINATION IN O. MACULOSUS

To evaluate the effect of age and year-class on homing behaviour and other factors, it was necessary to develop a valid method for determining the age of O. maculosus individuals. Initially, rings on otoliths were interpreted and validation of this method of ageing was attempted by examining rings on vertebrae and by using the graphical method of separating age groups devised by Cassie (1954).

1. Methods

Age determination using otoliths

Following collection, O. maculosus individuals were preserved in 10% formalin. Within 48 hours of collection and after soaking in fresh water, the fish were measured (total length)¹ with a dial caliper to the nearest 0.005 cm, sexed and both left and right otoliths removed and stored in glycerin. Otoliths were examined while immersed in water under reflected light on a black surface, using 30 x magnification.

¹All length measurements of O. maculosus in this study were made of total length, except in the analysis of meristic and morphometric characters, where standard length was used. For conversions from total length to standard length and vice versa, see Appendix 2.

Initially, a large number of otoliths were examined to determine whether there was evidence of growth rings. After it was established that a consistent pattern of rings existed, at least two readings were made of one otolith from each pair. Either otolith was used, since there was no difference between left and right otoliths in the number or form of opaque and hyaline rings. The numbers of opaque and hyaline zones and the consequent age of the fish was noted. Disagreements between the first and second readings were resolved by further examination of both otoliths until a decision was reached. Otoliths were read without prior reference to length or sex.

Six collections totalling 365 O. maculosus were made at First Beach. The collections were taken on 9 February, 1976; 1 June, 1976; 21 July, 1976; 29 September, 1976; 5 December, 1976 and 12 February, 1977.

Functional regressions of length on age were constructed to examine the nature of the growth relationship shown by otoliths. Regressions were calculated separately for males and females. Since external sex determination is impossible for O. maculosus juveniles less than 3.50 cm (total length), age data for this group of fish (22 fish) were included in both the male and female regressions. The regressions were compared to determine whether they were statistically different, and, if not, the data were combined to form a single regression. In the combined regression the data from juvenile fish were included only once.

Age determination using vertebrae

To attempt to validate the results of age determination using otoliths, the vertebrae and otoliths were extracted from O. maculosus individuals in two of the collections made at First Beach. These collections were taken on 5 December, 1976 and 12 February, 1977 and involved 177 fish.

Vertebrae were extracted after measuring and sexing the fish and removing the otoliths. An oblique forward pointing cut was made between the first and second dorsal fins and forceps were used to hold the vertebrae while twisting until the vertebral column broke and it was possible to extract several vertebrae. The vertebrae were rinsed in water and placed in a solution of trypsin and water to digest the attached tissue. After several days, the vertebrae were removed from the trypsin solution, rinsed in water and allowed to dry for several days, prior to being stored in glass vials.

Examination of the vertebrae was made under 30 x magnification on a black surface using reflected light. A single vertebra was cut away from the group and the centrum examined for evidence of growth rings. After examining a large number of vertebrae to determine whether there was any consistency in the patterns of rings, all the vertebrae were read and the number of opaque and hyaline zones and the age of the fish were noted. Two readings were made of all vertebrae

and disagreements were resolved by further reference to the single vertebra extracted and if necessary, to other vertebrae extracted. Readings of vertebrae were made without prior reference to length and sex. Although otoliths were also extracted from these fish, readings of vertebrae were made without reference to otolith readings.

Functional regressions of length on age were calculated separately for males and females to examine the growth relationship. As in the case of otoliths, data from fish less than 3.50 cm (total length) were included in both male and female regressions, but only once in the combined regression, which was calculated if there was no significant difference between the separate regressions for each sex.

A comparison of the age of each fish determined by otoliths and vertebrae was made using the method of Yasuda (1940) to determine the degree of agreement between the two methods.

Analysis of length frequency data

During the course of the study a considerable number of collections of O. maculosus were made at First Beach for various purposes: pool population studies, homing behaviour experiments, investigation of morphological characteristics and ageing studies. Except in the case of fish collected for the last two purposes, all fish were measured with a ruler to the

nearest 0.1 cm (total length) and sexed. Fish used for morphological and ageing studies were measured with a dial caliper to the nearest 0.005 cm and sexed. For the purposes of this analysis, the lengths were rounded to the nearest 0.1 cm.

The length data from these collections were combined in the case of closely associated collections and were used to construct length-frequency histograms spanning a period from May, 1975 to February, 1977.

The length-frequency histogram from the October, 1975 collection was selected (because of the relatively large sample size) for analysis of age groups using the graphical method developed by Cassie (1954). A percent cumulative frequency curve was constructed on probability paper, the points of inflection determined and the various age groups extracted.

A length-age functional regression was then calculated using the original length data as classified by age from the graphical analysis. The regression obtained was compared with the length-age regressions obtained using otoliths and vertebrae. A significant difference between the three regressions might suggest that age determination using otoliths was an invalid technique.

As a further possible corroboration of age groups in the population, the length-frequency histograms over time were examined to determine whether the modes of size groups, corresponding to derived ages, could be followed over the months

represented throughout the population.

Finally, data from tagged fish measured and sexed when initially caught for behavioural experiments and subsequently measured at a later date when retrapped, were investigated to determine whether they provided any support for the growth rates suggested by the methods outlined above. These data were collected intermittently over the duration of the research.

Age-length relationships

First Beach

To enable the determination of age for any given length of O. maculosus, predictive regressions of age on length were calculated separately from data obtained from otolith readings. As in the case of the length-age regressions, data for O. maculosus less than 3.5 cm (total length) were used in both male and female regressions since sex determination was not possible. The regressions were compared to determine whether they were significantly different, and if not, they were combined into one age-length regression, including the data from juvenile fish only once.

Other areas

Collections of O. maculosus were made at eight other areas on the west coast of Vancouver Island to determine the age-length relationship in each location for use in cirri analysis. Collections were made at Port Renfrew, Pachena Point, Benson Island, Cape Beale, Helby Island, Haines Island (large tidepool), Grappler Inlet (bay) and Rance Island. In each case, fish were fixed in 10% formalin immediately following collection. Within 48 hours and after rinsing with water, the fish were measured with a dial caliper to the nearest 0.005 cm (total length) sexed and the left and right otoliths removed and stored in glycerin. The procedures followed in reading the otoliths were the same as outlined for otoliths extracted from O. maculosus individuals from First Beach.

For each area, predictive age-length regressions were calculated separately for males and females. In cases where juvenile O. maculosus less than 3.50 cm (total length) had been collected, the age-length data were used in both male and female regressions, and only once in the combined regression calculated if there was no significant difference between the separate male and female regressions. The regressions for all areas (including First Beach) were compared to determine whether there were any differences in the age-length relationship between locations.

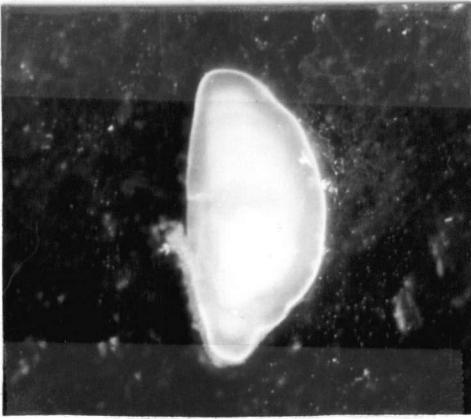
2. Results

Otoliths

From inspection of otoliths it is evident that the first summer growth zone appears as a broad opaque band of numerous finer almost hemispherical rings surrounding the central nucleus (Figure 5). This opaque zone does not usually form a complete circle. The first winter zone is (usually) a narrower hyaline band. Opaque growth zones in the second and subsequent summer are generally narrower than that of the first summer and form complete circles. These opaque growth zones are clearly separated by translucent hyaline zones (Figure 5). An indirect indication of the validity of otolith readings is the occurrence of a broad opaque band and a thin hyaline zone in juvenile fish caught in late summer. Stein (1973) investigating laboratory reared O. maculosus larvae in California found that the adoption of a benthic habitat occurred six to seven weeks after hatching and that after 51 days, one juvenile was 12.2 mm and metamorphosis was well advanced. Thus juveniles collected in August can be expected to have been spawned earlier that year (also see Atkinson, 1939).

The onset of growth in the second summer as shown by otoliths may start as early as February or as late as May,

Age 1



Age 2



1.0 mm

Age 3

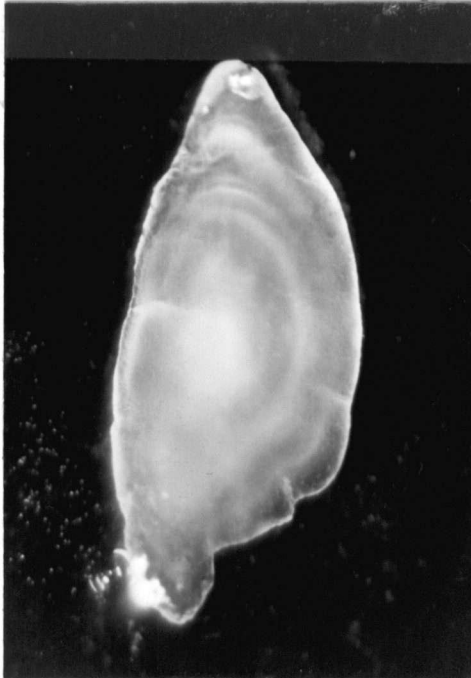


Figure 5 Otoliths of O. maculosus showing opaque and hyaline zones (all taken on 30 August)

depending on location and probably seasonal conditions. It appears that fish showing small opaque growth zones for the first summer's growth commence the second summer's growth prior to fish showing a wide growth zone for the first summer.

The cessation of yearly growth, as shown by otoliths, appears to occur sometime after July. Again fish with relatively small growth zones appear to continue growing longer than fish with wide growth zones.

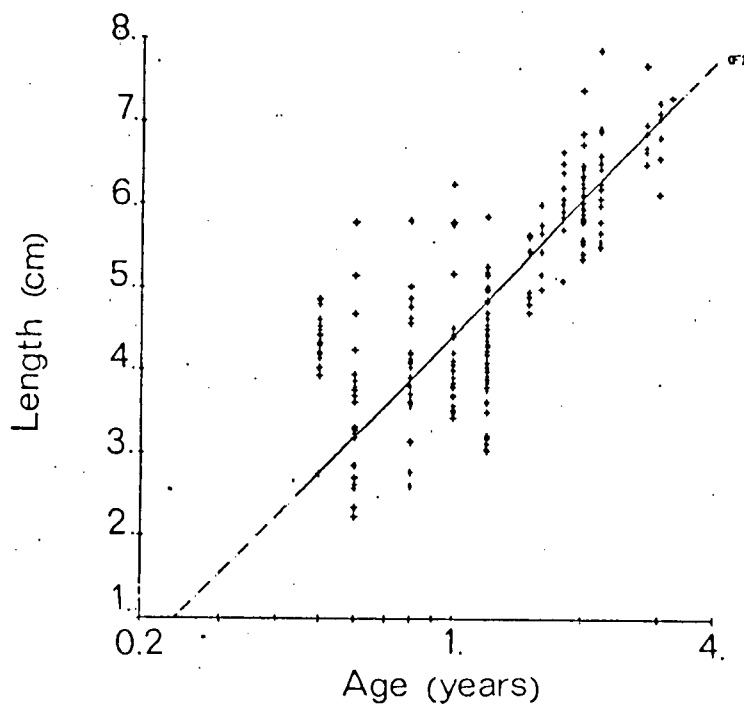
For the functional regressions of length-age for males and females separately (Figure 6), log to the base 10 transformations of the age values were made as suggested by the untransformed data. Inspection of the 95% confidence limits of v (slope) of the regressions (Table 1) results in rejection of the null hypothesis that males grow more rapidly than females. Thus the length-age data for males and females were combined to produce a single regression.

Vertebrae

The opaque and hyaline zones are more difficult to see in vertebrae than otoliths. Frequent moving of the vertebra is necessary to permit the light to shine through the centrum at an angle which allows resolution of the rings. However the patterns of rings are similar to those of otoliths except that on vertebrae there are fine ridges in the opaque zones (which Chadwick (1976) interpreted as annual marks) (Figure 7). The

First Beach O. maculosus female (otoliths)

$$Y = 4.420 + 5.492 \times \log X \quad N = 228$$



First Beach O. maculosus male (otoliths)

$$Y = 4.446 + 5.138 \times \log X \quad N = 160$$

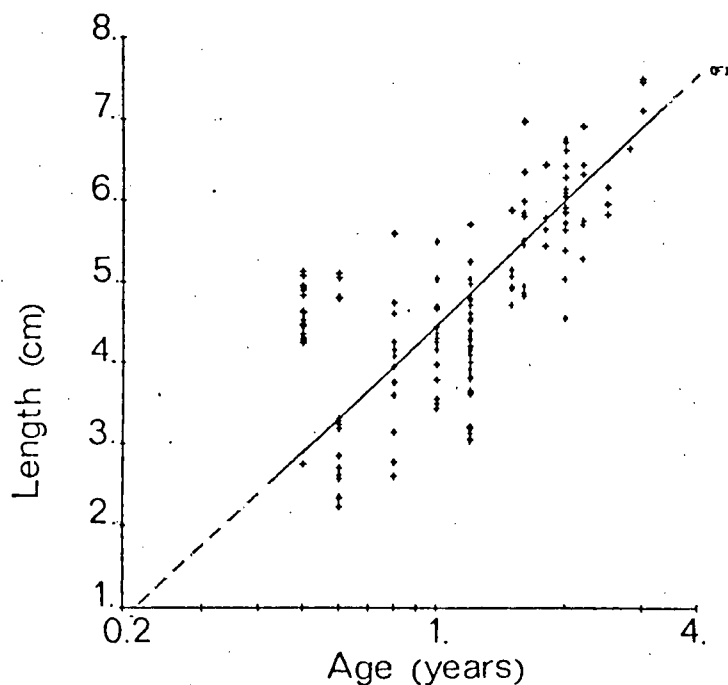


Figure 6 Length-age regressions of First Beach O. maculosus determined by otoliths (males and females separately)

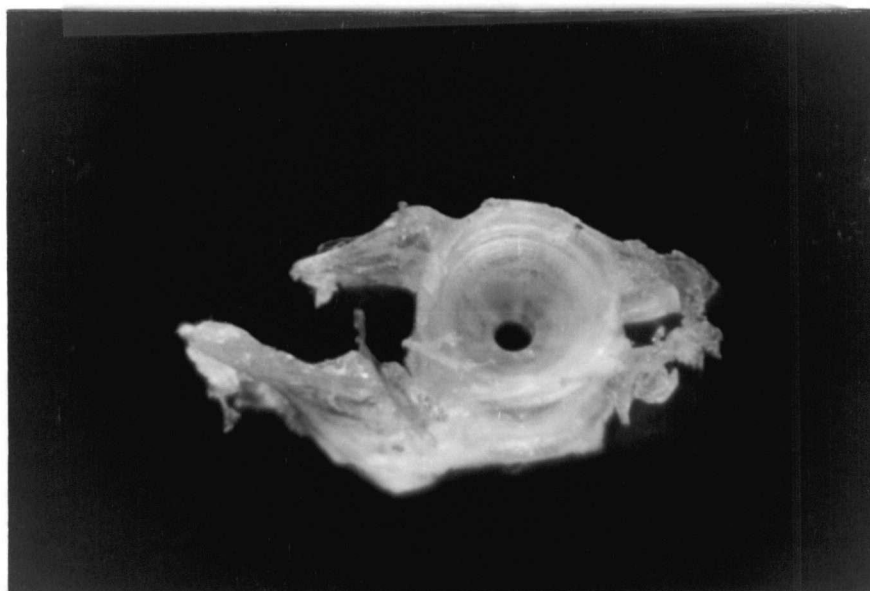
Table 1

First Beach Oligocottus maculosus (otoliths)

Length-age functional regression statistics

 $\log x$ vs y : $y = u + v \log x$

Statistic	Males	Females
u	4.446	4.420
v	5.138	5.499
Lower 95% confidence limit of v	4.511	5.021
Upper 95% confidence limit of v	5.765	5.977
N	159	228



—
0.5 mm

Figure 7 Vertebrae of age 3 O. maculosus showing opaque and hyaline zones (all taken on 5 December)

position of these ridges does not always correspond with the edges of the opaque growth zones which were used in this study.

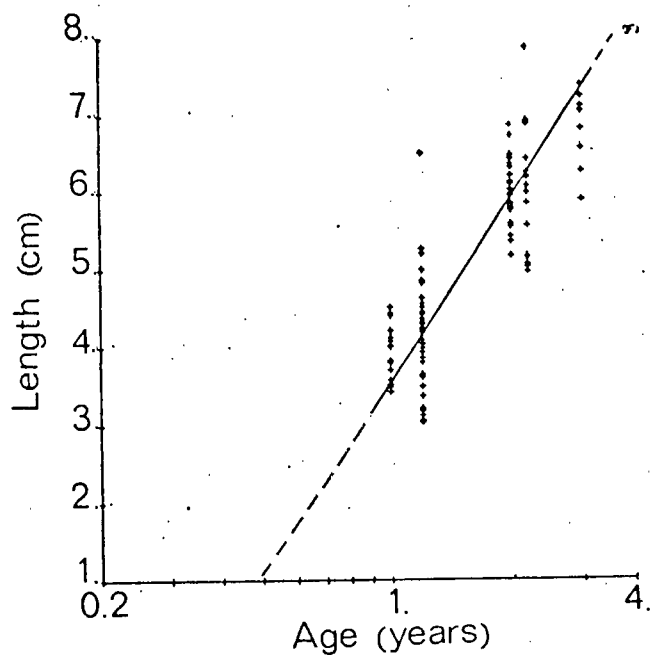
Figure 8 shows the calculated length-age regressions for males and females separately as determined by vertebrae. Again, inspection of the 95% confidence limits of v (slope) of the regressions (Table 2) results in rejection of the null hypothesis that males grow more rapidly than females. Thus the length-age data for males and females were combined in a single regression.

Graphical analysis of length-frequency data

Graphical analysis of a length-frequency distribution using the method of Cassie (1954) (Figure 9), provides the mean lengths for each age group which can be compared with the mean lengths for each age from otolith and vertebrae analysis (Table 3). Although the standard deviations for the mean lengths at each age derived from Cassie's method are rather large, there is fairly good agreement in mean lengths between the three methods.

The small sample numbers at the upper end of the length distribution and the absence of any fish for several length values make interpretation of the upper end of the percent cumulative frequency curve somewhat difficult. While the inflection point at 98.5% theoretically marks the upper length of the four year age group, the paucity of data (four fish unevenly distributed) for the remaining four lengths

First Beach O. maculosus female (vertebrae)
 $Y = 3.535 + 7.978 \times \log X$ $N = 114$



First Beach O. maculosus male (vertebrae)
 $Y = 3.394 + 8.269 \times \log X$ $N = 73$

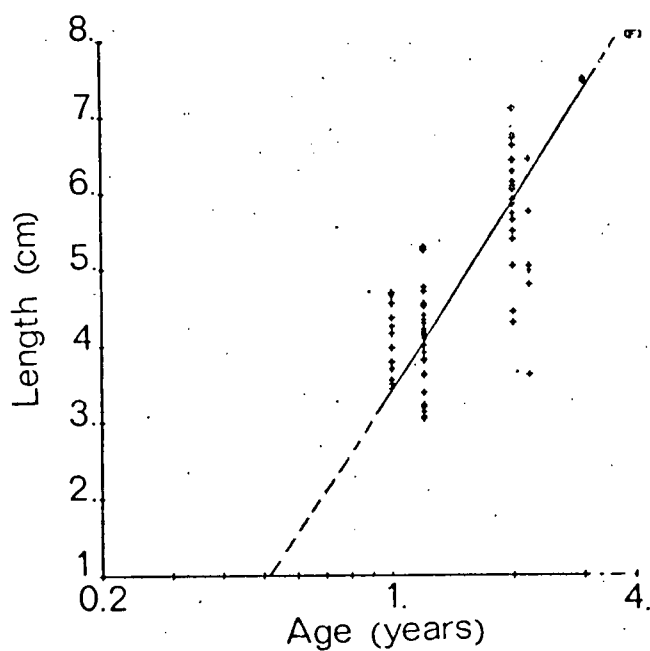


Figure 8 Length-age regressions of First Beach O. maculosus determined by vertebrae (males and females separately)

Table 2

First Beach Oligocottus maculosus (vertebrae)

Length-age functional regression statistics

 $\log x$ vs y : $y = u + v \log x$

Statistic	Males	Females
u	3.394	3.535
v	8.269	7.978
Lower 95% confidence limit of v	7.047	7.214
Upper 95% confidence limit of v	9.492	8.743
N	73	114

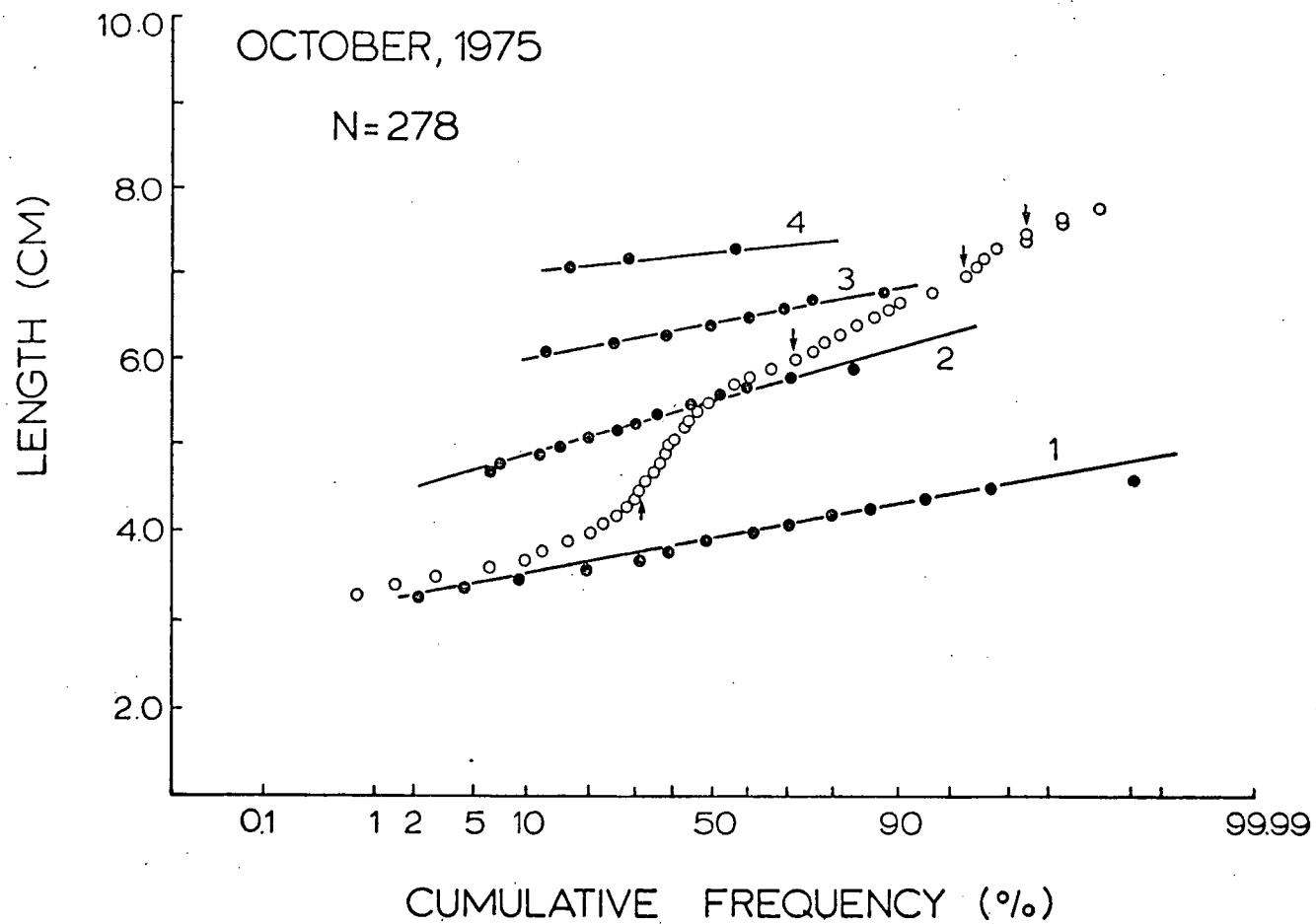


Figure 9 Length frequency analysis of age groups using Cassie's method

Table 3

Mean lengths (cm) for each age group
determined by three different methods

Length Statistics		Otoliths	Vertebrae	Cassie's method
Age 1	\bar{x}	4.21	4.02	3.9
	s.d.	.73	.38	.30
	N	127	26	89
Age 2	\bar{x}	5.01	4.99	5.5
	s.d.	.96	1.19	2.41
	N	194	119	111
Age 3	\bar{x}	6.49	6.14	6.4
	s.d.	.60	.84	3.49
	N	43	32	67
Age 4	\bar{x}	7.30		7.3
	s.d.			.21
	N	1		7
Age 4+	\bar{x}			7.8
	s.d.			.13
	N			4

theoretically classifies them as four plus age group fish although they probably belong to the four year age group.

In the calculation of the length-age regression using the information obtained from Cassie's method (Figure 10), fish of the four plus age group were not considered since a definite age could not be ascribed to them. For the purposes of comparison the regressions calculated for males and females (combined) from otolith and vertebrae analysis are also shown in Figure 10. Inspection of the relevant statistics for the three regressions (Table 4) suggests that there is good agreement between the growth relationships described by otoliths and Cassie's method, but that growth described by vertebrae may not fit into this pattern.

Several reasons may account for the difference between the regressions for otoliths and vertebrae. Although there is agreement between the age determined by vertebrae and otoliths for 86% of the fish from which both were extracted (Table 5), the Kolmogorov-Smirnov test (Siegel, 1956) shows a significant difference between the two methods in age determination ($p < .05$). Examination of each age group individually reveals no significant differences between the methods for age one or two fish ($p > .05$), but a significant difference for age three fish ($p < .05$). Thus, there is a tendency for data derived from otoliths from older fish to show more rapid growth than that derived from vertebrae. Vertebrae appear to be a successful method of validating age determination using otoliths, at least

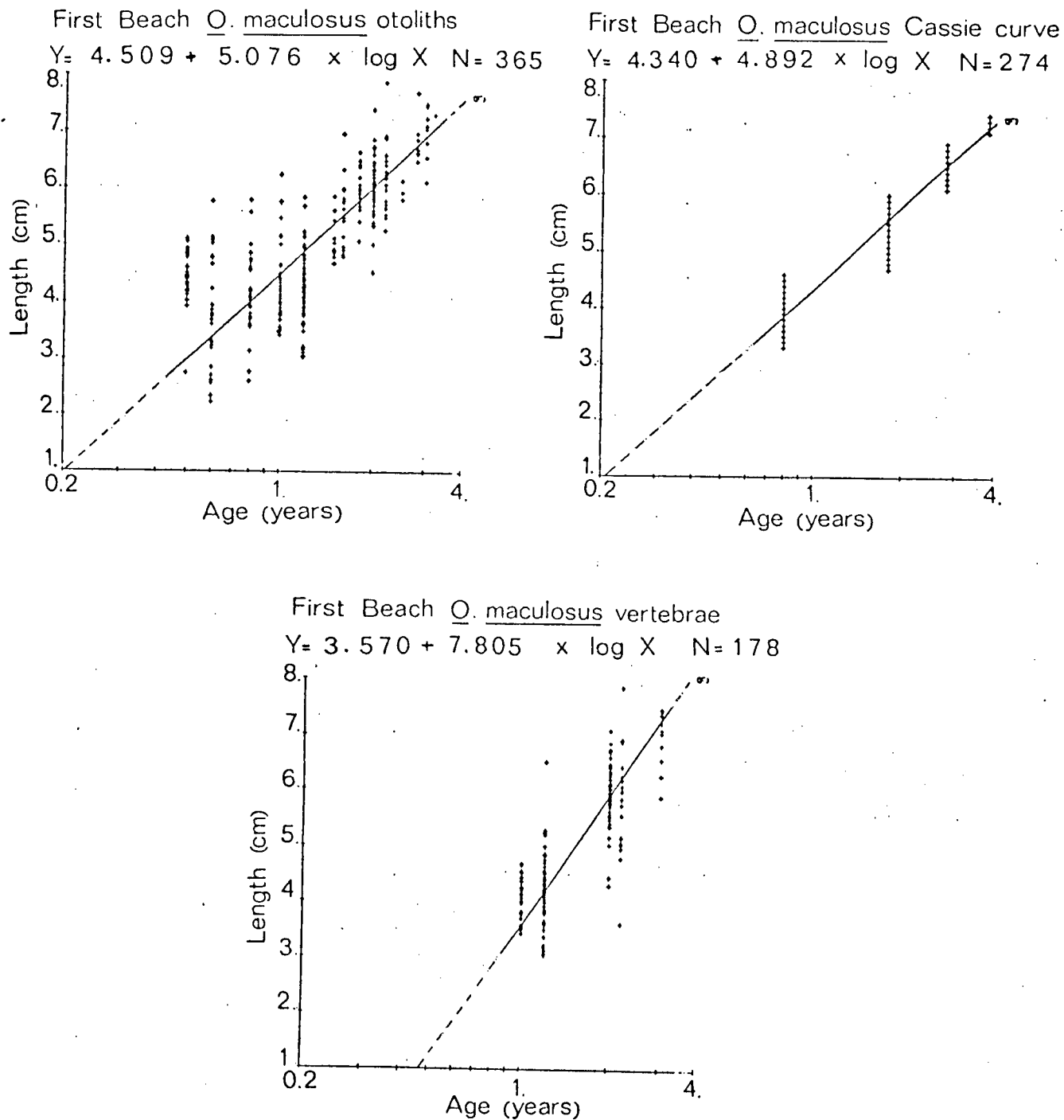


Figure 10 Length-age regressions of First Beach O. maculosus determined by otoliths, vertebrae and length frequency analysis (males and females combined)

Table 4

Oligocottus maculosus (First Beach)

Length-age regression statistics from
three different methods of age determination

$$\log x \text{ vs } y: y = u + v \log x$$

Statistic	Otoliths	Vertebrae	Cassie's method
u	4.509	3.570	4.340
v	5.076	7.805	4.892
Lower 95% confidence limit of v	4.702	7.162	4.708
Upper 95% confidence limit of v	5.451	8.447	5.076
N	365	178	274

Table 5

Comparison of age determined
by otoliths and vertebrae of the
same Oligocottus maculosus individuals

Vertebral age (years)	Otolith age (difference from vertebrae)		
	-1	0	+1
1	0	25	1
2	8	107	4
3	11	21	0
% of total	10.7	86.4	2.8

+: age determined by otoliths greater than by vertebrae

0: age determined by otoliths equal to that by vertebrae

-: age determined by otoliths less than by vertebrae

for age one and two fish. The other possible reason for the difference between the regressions is that the samples for vertebrae analysis contain few juveniles less than 3.50 cm (total length) and few fish in the one year age group, compared with the data for otolith and length-frequency analysis. Taking these factors into consideration, there appears to be good agreement in age determination between otoliths and Cassie's method of length-frequency analysis, and good agreement between these methods and vertebrae for at least age one and two fish.

Further validation of two major age groups and progressively smaller numbers of three and four year age group fish existing in the population is provided by analysis of length-frequency histograms over time (Figure 11). The variation in the size of any one length class is a reflection of the purpose for which, and the relative height of the pool in which, the fish were caught. Collections for behavioural experiments (in pools up to about the 2.5 m level) tended to produce more larger sized fish than pool population collections (in pools around the 2 to 3 m level). Following the modes over the months shown makes it evident that the young of the year appear in pools below about 3 m between May and July, that the majority of growth takes place starting sometime between February and May (probably April or early May) and continues until about July or August, after which there is very little growth (particularly in older fish) until the following spring. The data suggest that the young of the year appear in lower

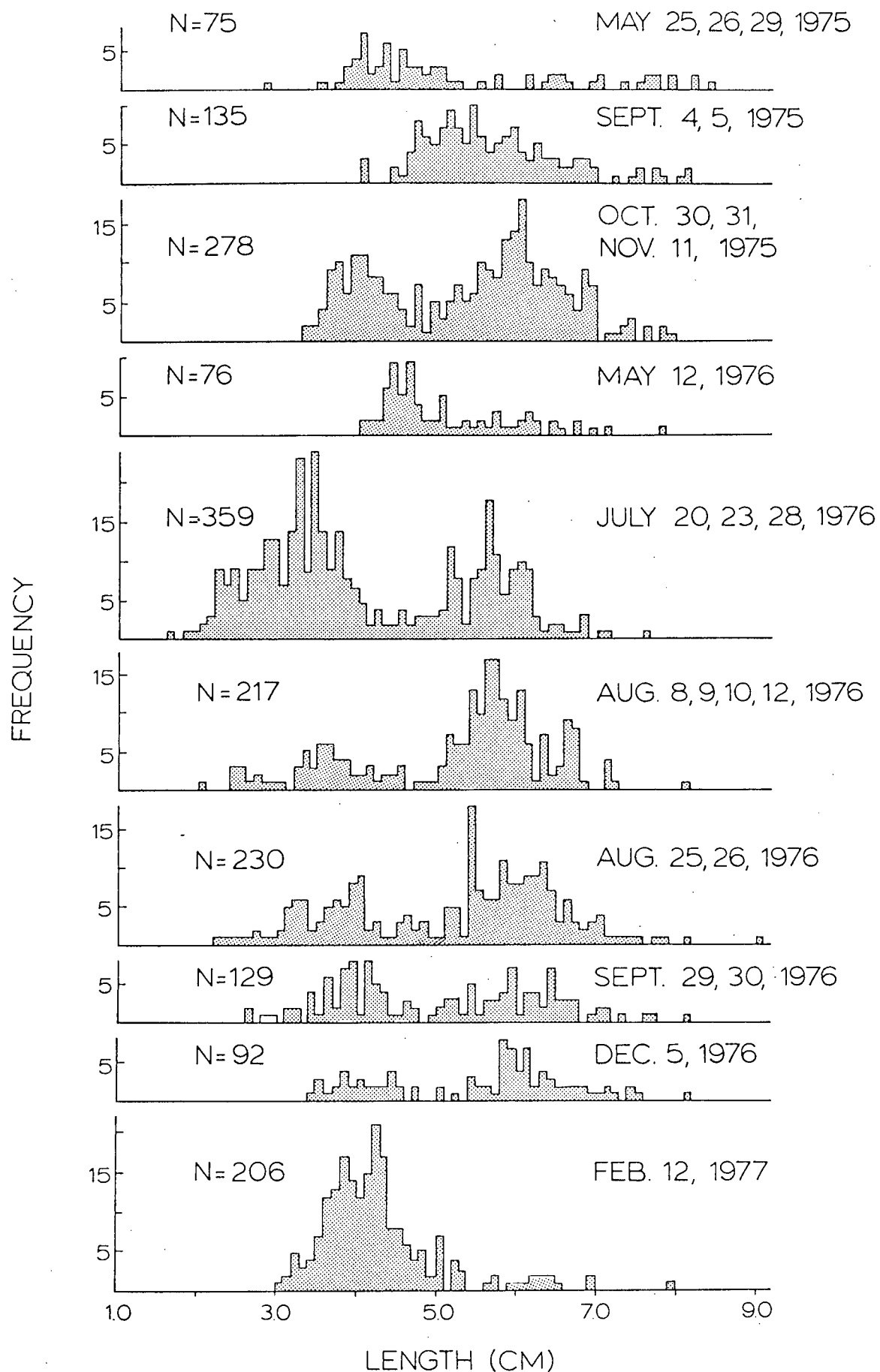


Figure 11 Length frequency histograms of *O. maculosus*

tidepools at a mean size of about 3.0 cm and grow to a mean size of about 4.0 cm by the end of one growing season. In their second year they appear to grow to about 6.0 cm mean size and in their third year to about 7.5 cm mean size.

While no fish have been tagged prior to the summer growth period and thus no direct estimate of growth over the entire period is available, the amount of growth shown by tagged fish is not inconsistent with other derived values, although it may be somewhat lower (Table 6). One fish which was tagged in mid-summer 1976 and recaptured in mid-summer 1977 showed growth consistent with that described by the length-frequency histograms. It is evident that very little, if any growth occurs after September until the following spring. The data are insufficient to conclude that tagging retards growth, as has been found for other fish (Ricker, 1971).

Age-length relationships

First Beach

For the regressions calculated for males and females (Figure 12 and Table 7) log to the base 10 transformations were made of both age and length data. Both regressions are significant ($p < .01$). On the basis of the results from analysis of covariance, which showed no significant differences between male and female regressions in variances, slopes or intercepts

Table 6

Growth of tagged Oligocottus maculosus individuals

Month first trapped	Month last trapped	Initial length (cm)	Final length (cm)	Growth (cm)
May	October	4.0	5.7	1.7
		5.2	6.1	0.9
		5.7	6.5	0.8
		5.7	7.8	2.1
	December	4.7	5.4	0.7
August	October	5.1	5.2	0.1
		5.5	5.7	0.2
		6.3	6.6	0.3
	November	6.6	6.6	0
	July	3.9	6.2	2.3
September	October	5.4	5.6	0.2
		6.1	6.2	0.1
		6.2	6.3	0.1
		6.6	6.8	0.2
		6.7	6.8	0.1
		6.8	6.8	0
October	November	4.6	4.8	0.2
		4.8	4.8	0
		6.9	6.9	0

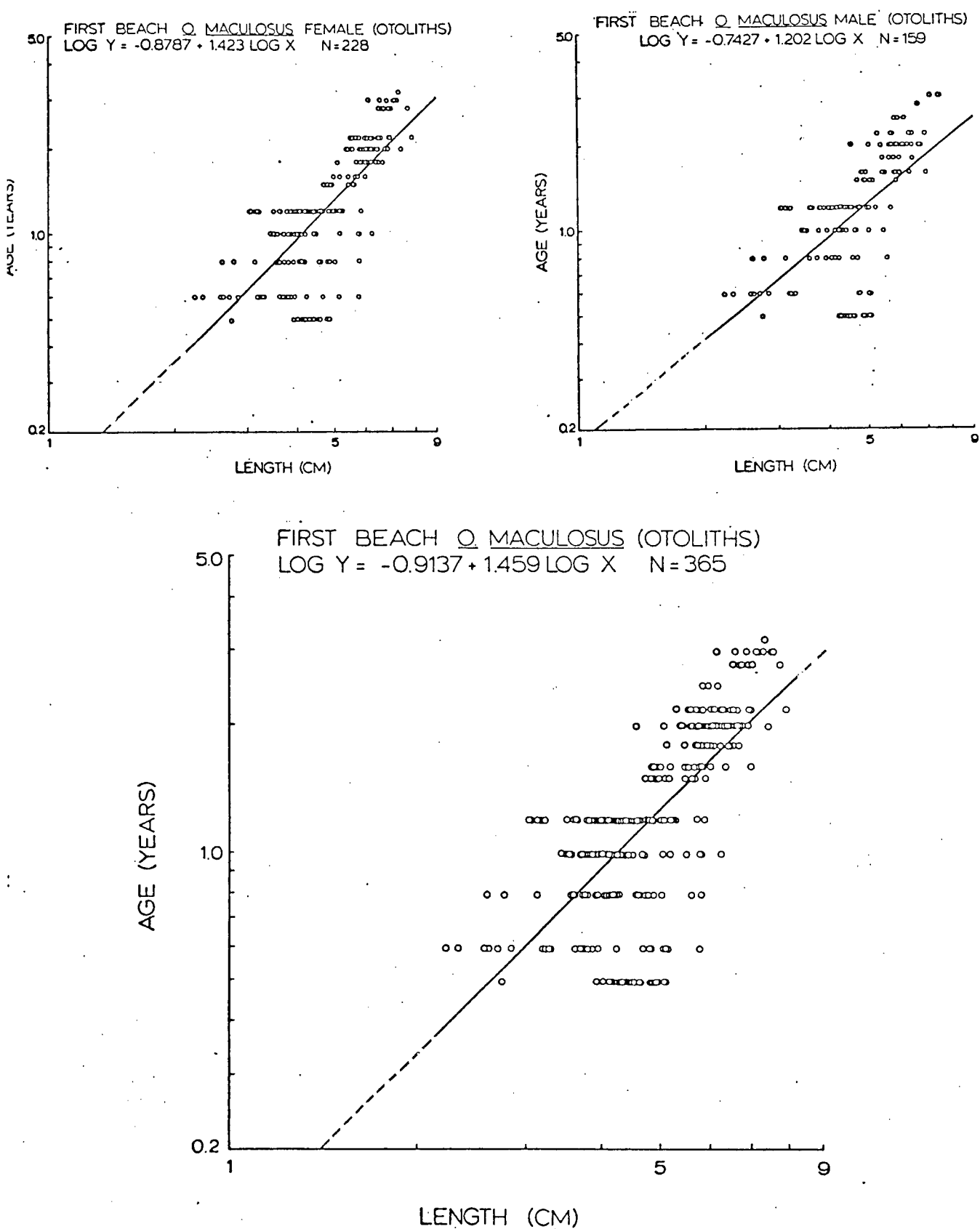


Figure 12 Age-length regressions of First Beach *O. maculosus* determined by otoliths (males and females separately and combined)

Table 7

First Beach Oligocottus maculosus (otoliths)

Age-length regression statistics

$$\log x \text{ vs } \log y: y = a + b(x - \bar{x})$$

Sex	a	b	\bar{x}	N	s.e. of b	F	p<
Females	.08	1.42	.67	228	.091	244.0	.01
Males	.05	1.20	.66	159	.12	86.73	.01
Combined	.08	1.46	.68	365	.085	249.7	.01

Analysis of covariance

Males vs females

Source	F	p
Common variance	1.33	.024
Different slopes (b)	2.07	.151
Different intercepts (a)	.464	.496

($p > .01$) (Table 7), the data were combined into a single age-length regression for First Beach (Figure 12 and Table 7). This regression was also significant ($p < .01$).

Other areas

The regression statistics calculated separately for males and females at each area (Table 8) were all significant ($p < .01$). For Rance Island, there were insufficient data to calculate separate male and female regressions, thus a single combined regression only was calculated for this area. Analysis of covariance statistics comparing male and female regressions for each area (Table 9) show values to two decimal places except where the probability was close to zero, in which case three decimal places are shown. It is evident that for all areas except Grappler Inlet and Pachena Point there are no significant differences between male and female regressions in variances, slopes and intercepts ($p > .01$). Thus combined regressions were calculated for each area (Figure 13 and Table 10). The combined regressions are all significant ($p < .01$). In the case of Pachena Point the regressions were combined since the agreement between slopes and intercepts was good. The difference between variances was probably due to the preponderance of age two females relative to males. In the case of Grappler Inlet, the regressions are evidently significantly different in variances and slopes ($p < .01$). The regression for males shows good agreement with regressions for both sexes for all places except

Table 8

All areas Oligocottus maculosus (otoliths)

Age-length regression statistics

Males and females separately

 $\log x$ vs $\log y$: $y = a + b(x - \bar{x})$

Area		a	b	\bar{x}	N	s.e. of b	F	p<
<hr/>								
Cape	F	.21	1.18	.63	41	.10	140.32	.01
Beale	M	.27	1.23	.66	23	.15	57.153	.01
Benson	F	-.092	1.31	.55	36	.12	125.00	.01
Island	M	-.14	1.20	.52	30	.13	88.802	.01
Port	F	.18	.796	.67	49	.10	68.239	.01
Renfrew	M	.18	.772	.66	18	.17	20.494	.01
Pachena	F	.24	1.47	.70	46	.062	556.91	.01
Point	M	.32	1.42	.76	26	.14	95.790	.01
Helby	F	.17	1.43	.65	50	.14	109.83	.01
Island	M	.21	1.56	.68	37	.19	64.981	.01
Haines	F	.23	1.33	.73	42	.11	146.43	.01
Island	M	.18	1.36	.71	30	.21	40.338	.01
Grappler	F	.11	.846	.67	23	.16	28.891	.01
Inlet	M	.22	1.37	.74	17	.054	629.33	.01

Table 9

All areas analysis of covariance statistics

Males vs females

Area	F (va)	p	F (b)	p	F (a)	p
<hr/>						
Cape Beale	1.47	.14	.092	.76	1.85	.18
Benson Island	1.17	.34	.41	.53	.119	.73
Port Renfrew	1.08	.40	.15	.90	.602	.44
Pachena Point	2.60	.003	.15	.70	.263	.61
Helby Island	1.57	.07	.32	.57	.059	.81
Haines Island	1.02	.49	.012	.91	2.22	.14
Grappler Inlet	5.42	.001	10.07	.003	3.69	.06

va: variance, b: slopes, a: intercepts

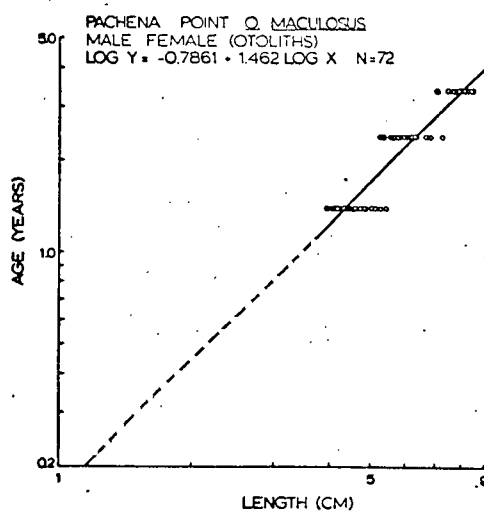
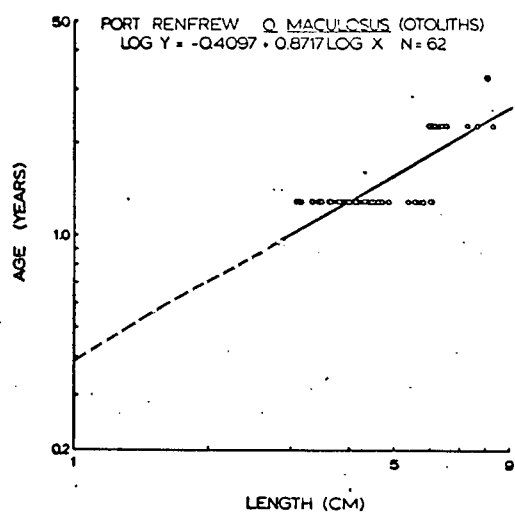
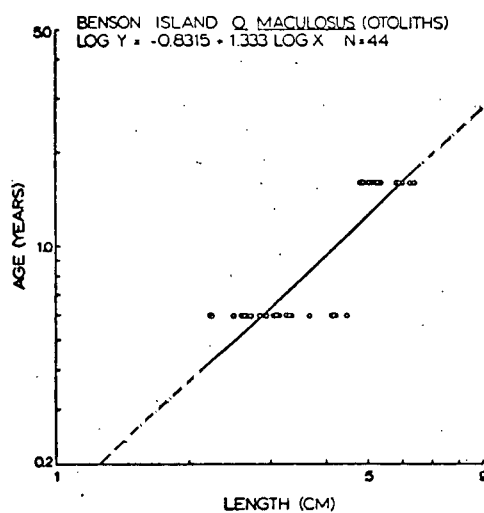
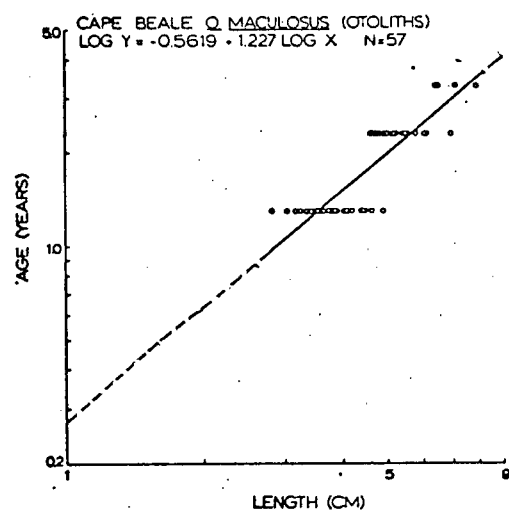


Figure 13 Age-length regressions of *O. maculosus* from eight areas determined by otoliths (males and females combined)

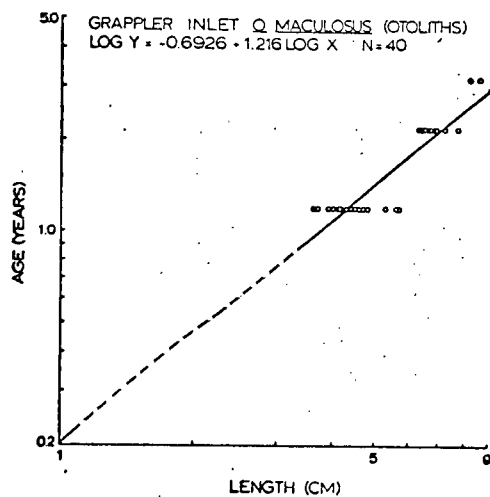
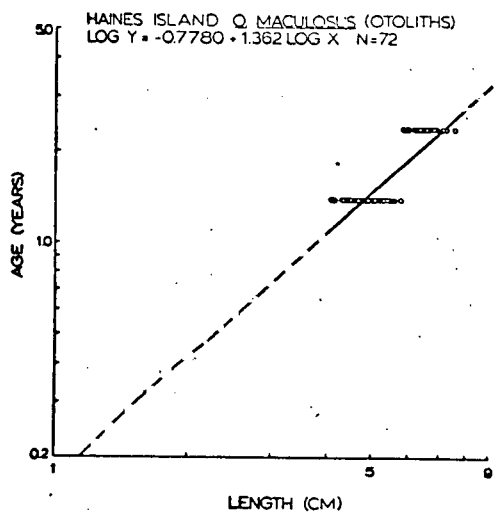
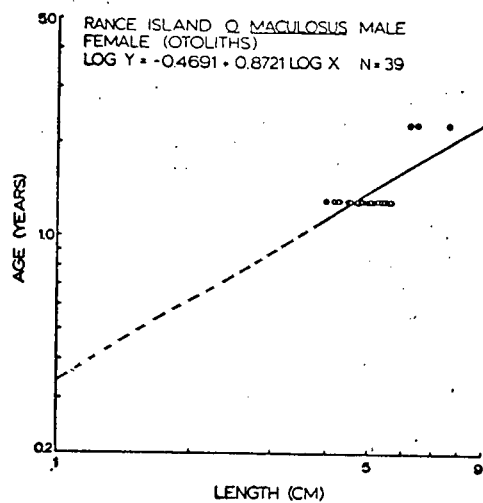
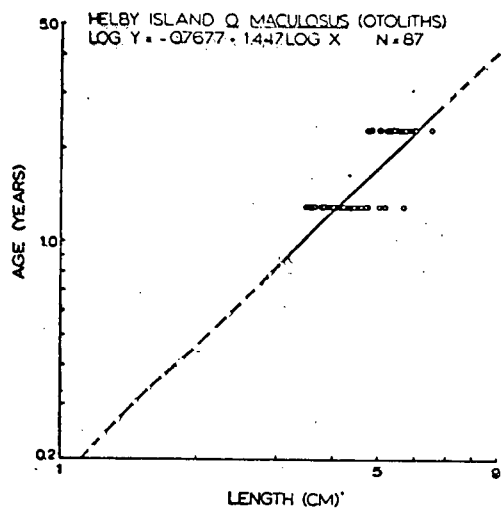


Figure 13 (continued)

Table 10

All areas Oligocottus maculosus (otoliths)

Age-length regression statistics

Males and females combined

 $\log x$ vs $\log y$: $y = a + b(x - \bar{x})$

Area	a	b	\bar{x}	N	s.e. of b	F	p<
<hr/>							
Cape Beale	.24	1.23	.66	57	.094	169.60	.01
Benson Island	-.057	1.33	.58	44	.11	146.12	.01
Port Renfrew	.18	.872	.68	62	.086	106.63	.01
Pachena Point	.27	1.46	.72	72	.061	570.60	.01
Helby Island	.19	1.45	.66	87	.11	173.19	.01
Haines Island	.21	1.36	.72	72	.10	201.77	.01
Grappler Inlet	.16	1.22	.70	40	.088	189.96	.01
Rance Island	.13	.872	.69	39	.14	40.570	.01

Port Renfrew, but the regression for females does not. The difference may be at least partially accounted for by one four year old male and no corresponding females, which, given the small sample size, may produce significant differences. In view of the good agreement between male and female regressions at all other places and the absence of any obvious reason for a significant difference between male and female age-length relationships in Grappler Inlet, the regressions were combined into a single regression for the area. Analysis of covariance statistics for all sites (Table 11) show significant differences between the regression lines; the slopes are significantly different ($p=.01$) and the adjusted group means differ significantly ($p<.01$). Inspection of the lines and their relevant statistics suggests that the regressions for Port Renfrew and Rance Island are different from the other sites.

3. Discussion

The study of age determination in O. maculosus at First Beach revealed three major age groups and a fourth smaller age group. This is in contrast to the work of Chadwick (1976) whose study of age determination using vertebrae of O. maculosus at Port Renfrew and Bruels Point, California led him to suggest that there were six age groups at both localities. The single collection of fish he made at Port Renfrew was taken in late July at which time the young of the year have appeared in

Table 11

Analysis of covariance

All sites males and females combined

Source	d.f.	Mean Square	p
<hr/>			
Difference between group means slope and common slope	1	.055	.05
Group means from their line	7	.50	0
Between individual lines	8	.034	.01
About individual lines	820	.014	
<hr/>			
Probability of common variance 0			
Slope of group means		1.35	
Common slope of lines		1.62	
<hr/>			

tidepools. Chadwick's length-frequency distribution curve (using a moving average of three and standard length) shows one prominent mode at about 2.5 cm and another less prominent one at about 1.5 cm. These correspond to his I and 0 age classes, respectively. If age class I was recruited to the population in the previous year, and taking growth after July into account, it should be possible to find a size class of fish of less than 2.5 cm (about 3.0 cm total length) between October and May. Reference to the length-frequency histograms of Figure 11 shows no such size class at that time and shows that Chadwick's 0 and I year-classes belong to the one year age group defined here.

This analysis of the length-frequency histograms for First Beach is supported by Green's (1967) length-frequency histograms for O. maculosus at Botanical Beach, and Atkinson's (1939) length-frequency histograms for O. maculosus at Puget Sound, Washington.

Other studies of age determination in marine cottids are few. Chadwick (1976) conducted age determination studies in Clinocottus globiceps (Girard), and as for O. maculosus concluded that there are six age classes. Weiss (1969) examined ageing in the more euryhaline Leptocottus armatus Girard, a cottid which has been reported to grow to 46 cm (Hart, 1973). He examined fish up to about 25 cm (total length) and on the basis of otolith readings suggested ten age groups. McElderry (1975) examined the age-length relationship of Clinocottus analis (Girard) in California. On the basis of otolith

examination he concluded there were seven age classes, although few fish were more than two years old. O'Connell (1953) conducted ageing studies, using otoliths, in the cabezon, Scorpaenichthys marmoratus (Ayres), a large subtidal cottid, and found thirteen year old females and nine plus males. Length-frequency data from rotenone collections in kelp beds in Barkley Sound suggest that Artedius harringtoni (Starks), a cottid which is recorded to grow to 10 cm (Hart, 1973), comparable to O. maculosus, shows two and possibly three age groups within the population, the approximate mean lengths of which correspond to those for O. maculosus age groups. Although there are fewer data on which to base conclusions, Artedius lateralis (Girard), another essentially subtidal cottid, appears to show at least two age groups (Bruce Leaman, personal communication).

IV. VARIABILITY IN HOMING BEHAVIOUR

1. Tagging and recapture methods

Tagging methods

Tags for adult O. maculosus consisted of three coloured beads and monofilament line. Nineteen colours of beads were used. A piece of monofilament (usually 4 or 6 lb test, but heavier when this was not available) about 20 cm long was threaded with a bead and attached with a double improved cinch knot, leaving one end about 3 cm long and the other about 15 cm long. Another bead was then threaded on the long end of the line. A large number of these were made prior to tagging fish, to expedite the actual tagging process.

The long end of the monofilament was threaded through a fine needle and the needle inserted through the dorsal musculature of the fish between the dorsal fins from the left to right sides of the fish. Another bead was threaded onto the line and the line threaded once more through the bead. This bead was then manoeuvred down to the right side of the fish so that the beads on both sides were adjacent to the body. The long end of monofilament was then looped and its free end wound through the loop five or six times.

A dissecting needle was inserted in the loop and

pushed down the line to the outer side of the bead. Both free ends of monofilament were then pulled, causing the last knot to tighten. The free ends of monofilament were then cut off. Once familiarity with the technique was gained, a fish could be tagged in well under one minute.

All fish were tagged with unique tags so that individual recognition was possible. Over 2800 fish were tagged using this technique. No anaesthetic was used. Tag loss, from fish greater than 2.5 cm, as indicated by recovery of fish with lesions on the dorsal musculature was very low (about 2%). Tagged fish were kept in the laboratory for varying periods from overnight to almost five months. The only mortality recorded from untreated, tagged fish occurred after blockages in the seawater system.

Several methods were attempted for the tagging of juveniles. Pieces of vaseline coated nylon thread about 5 cm long, and large (8 mm x 3 mm) and small (3 mm square) pieces of coloured surveyors' tape were attached through the dorsal musculature with nylon thread. However, within several days, the tags either came off or entangled the fish in assorted debris.

Finally juvenile fish were tagged with two coloured beads (one bead each side of the body) and monofilament line (2 lb test) in the same manner as adult fish. This method proved relatively satisfactory except for fish less than about 2.5 cm

(total length) for which no really satisfactory individual tag was developed.

Recapture methods

In homing behaviour experiments two methods were used to find tagged fish after release. At First Beach about once every two weeks, baited minnow traps were set in tidepools for about four hours around low tide. Traps were set only in pools used for capture and transplanting of fish. In addition, and whenever possible between trappings, pools were inspected thoroughly for tagged O. maculosus. The pools in which fish were captured and transplanted and pools between the home and release pools were examined, although the latter less thoroughly, except where otherwise stated.

In homing experiments conducted in other areas, a combination of trapping and observation was also used. In Grappler Inlet, traps were set, over two tidal cycles (approximately 24 hours), at least once every two weeks and frequently several times per week for the first month of an experiment. Simultaneously, observations from the surface were also made for tagged fish. In other places, the recapture schedule is outlined in the descriptions of experiments conducted there.

2. Homing in different locations

First Beach

Home range and area fidelity

Since the majority of investigations into homing behaviour of O. maculosus have been conducted at Port Renfrew, it was regarded as essential to investigate pool fidelity and size of home range of O. maculosus at First Beach, prior to commencing homing studies. In this study, the term home range is used as in Khoo (1971) as the area covered by the fish during normal travel.

Gersbacher and Denison (1930) and Green (1967) suggested that the majority of O. maculosus display rather strict fidelity to particular pools. Khoo's (1971) studies however, showed that the majority of fish move within a group of neighbouring pools. He suggested that the amount of movement between pools may depend on the size of the pools involved. Despite Green's observations that few fish are found more than three metres from their home pool, Khoo proposed that the maximum extent of the home range was not more than 30.5 metres.

Three experiments were conducted specifically to determine whether O. maculosus exhibited pool fidelity at First

Beach. These experiments were also designed to give an indication of the size of the home range. Analysis of data from other experiments on the pool movements after homing of untreated, tagged O. maculosus individuals was also undertaken to determine the degree of natural movement between tidepools.

Methods

In the first experiment a total of 33 O. maculosus were tagged and returned to the tidepool in which they were captured. Fish were collected from three adjacent tidepools. In the second experiment, a total of 76 O. maculosus were tagged and returned to the pool in which they were captured. Fish were collected from two groups of three and five pools each. In the third experiment, a total of 44 O. maculosus were captured from two groups of two and three pools each and returned to the pool in which they were captured. The pool in which a fish was captured was termed the home pool.

All observations of tagged fish in any pool over four months, 10 weeks and five weeks, respectively, were recorded and used for analysis. Percentages of tagged fish found in the home pool only, in the home and nearby pools and in distant pools were calculated.

To provide an indication of the pool fidelity of individual O. maculosus, location records of individuals from the second replacement experiment seen at least five times over

a period of at least 28 days were analyzed. These fish were regarded as having relatively extensive location records. The period over which the fish was seen, the number of pools in which the fish was seen and the number of times seen in each pool were calculated.

Results

The results of the three replacement experiments (Table 12) show that in each experiment, about 30 to 40% of the fish were subsequently found only in the home pool. About the same or slightly higher percentages of fish were found in the home and nearby pools. In each case, a majority of the fish replaced were found in the area of the home pool (either the home pool only or the home and nearby pools), that is, the home range. Several fish were found in distant pools from 30 to 60 m away from the home pool.

It thus appears that in addition to a small percentage of fish which stray widely, equal proportions of O. maculosus show fidelity to a particular pool, as to a small group of pools. This group comprises usually about two or three pools, but occasionally up to five, covering an area with a diameter of about 10 to 15 m maximum.

From the analysis of long term pool fidelity from the second replacement experiment (Table 13) it is evident that some O. maculosus show strict fidelity over a long period to one

Table 12

First Beach replacement experiments

Date released	28 May 75	2 June 75	Total	30 June 77	9 Aug 77
Number released	19	14	33	76	44
Number found in home pool only	9	2	11	27	17
Percent found in home pool only	47	14	33	36	39
Number found in home and nearby pools	7	2	9	40	18
Percent found in home and nearby pools	37	14	27	53	41
Number found in home pool and home and nearby pools	16	4	20	67	35
Percent found in home pool and home and nearby pools	84	29	61	88	80
Number found in distant pools	0	2	2	2	2
Percent found in distant pools	0	14	6	3	5

Table 13

Long term pool fidelity of individual Oligocottus maculosus

from 30 June replacement experiment

(long term: seen at least five times over at least 28 days)

One pool		Two pools		Three pools		Four pools		Five pools	
Days over which observed	Number of times observed per pool	Days over which observed	Number of times observed per pool	Days over which observed	Number of times observed per pool	Days over which observed	Number of times observed per pool	Days over which observed	Number of times observed per pool
61	12	75	17,1	75	19,1,1	58	7,4,4,1	70	10,8,7,1,1
61	25	74	15,3	75	21,2,1	60	15,7,2,2	75	12,4,3,2,1
75	20	75	18,7	75	17,4,2	60	13,5,4,1		
75	18	71	9,8	42	7,2,1	57	5,2,1,1		
74	25	75	26,1	60	7,5,2				
61	11	48	17,1	41	4,3,3				
38	17	58	17,1	37	2,2,1				
61	7	58	7,2						
52	12	74	6,1						
58	5	30	6*						
34	7	43	8,4						

* always found in a different pool from the pool of first capture

pool. This was also evident from the location data of some of the fish used in homing experiments: for example, one O. maculosus was seen 17 times after homing over 179 days, always in the same pool; another was seen 41 times over 83 days after homing always in the home pool; two fish which were released in 1976 were found eleven and twelve months later in their original capture pools. There is no doubt that some O. maculosus display very strict fidelity to a particular pool.

Examination of the number of times that individuals were observed in pools of the home range shows that in a majority of cases, there is one pool within the group of pools around which the fish moves, to which greater fidelity is shown. Again, this result is supported by analysis of pool location records from O. maculosus seen over long periods of time after homing: for example, two fish were seen in two pools a total of 16 times each over a period of 101 days, one fish 15 times in one pool and once in the other, the other fish 11 times in one pool and five in the other; a fish was seen a total of 29 times in four pools over 83 days, the number of times in each pool being 18, 6, 4 and 1. From 10 homing experiments involving untreated, tagged fish which successfully homed and were subsequently seen at least five times over a period of at least 28 days, 37 were found only in one pool and 56 were found in more than one pool. Of those 56, 42 (75%) were found in one pool more than twice as many times as any other pool. Thus it appears that the majority of O. maculosus show greater fidelity

to one particular pool than to other pools in the home range. This pool is termed the preferred pool.

Homing behaviour

Two experiments were conducted specifically to determine whether O. maculosus at First Beach demonstrate homing behaviour, that is, return to the home range when experimentally displaced. The experiments were also designed to compare the difference, if any, in homing behaviour between reciprocal and non-reciprocal transplants of fish. Analysis of data from other homing experiments involving untreated, tagged O. maculosus was also undertaken to provide a more comprehensive picture of homing behaviour at First Beach.

Methods

In the first experiment, a total of 42 tagged O. maculosus taken from a group of five pools were transplanted to a pool about 60 m away. All observations of tagged fish in any pool over a four month period were recorded and used for analysis.

The second and subsequent experiments investigated the effect of approximately maintaining the number of O. maculosus in the study tidepools while transplanting fish. In the second experiment O. maculosus were collected from two groups of pools

about 60 m apart. A total of 54 fish were tagged, 20 from one pool in one group and 34 from four pools in the other group. Releases were made into the pool in each group from which the most fish were taken, so that in one pool 20 fish were removed and 34 introduced, and in the other pool 22 fish were removed and 20 were introduced. Data collected over a four month period were used in the analysis.

The analysis of data from other experiments involved examining the homing performance of untreated, tagged O. maculosus used in seven experiments designed to examine the sensory basis of homing, and one transplant experiment (4 July, 1977). In all cases, fish were taken from two groups of pools about 60 m apart. Reciprocal transplants were made as far as possible, so that the number of fish transplanted to each pool was equal to the number of fish removed (and transplanted to pools in the other group). In the first two experiments conducted in 1977, about 25% of the fish released in each experiment were less than 4.0 cm (total length), which was not the case for the other experiments. Data collected over a four month period were used in the analysis except in the cases of the experiments starting on 23 August, 1976, 15 September, 1976, 4 July 1977, 16 July 1977 and 9 August 1977 for which data collected over 3.5, 2.5, 2+, 2 and 1+ months, respectively, were used.

Following the method of Khoo (1971), homing was regarded as successful if a tagged O. maculosus returned to its

home range (either the home pool or nearby pools). The first pool in the home range in which a tagged fish was found was regarded as the pool to which the fish homed, even if the fish subsequently was located in another pool. A record was kept of fish located in pools other than those of the home range. Calculations were made of the percentage of O. maculosus homing, the percentage of homers returning to the home pool and the percentages of released fish remaining in the transplant area for any period of time.

Results

Although there is considerable variability in the results from the ten homing experiments (Table 14) and some of the percentage returns are small, there is definite evidence to indicate that a majority of O. maculosus individuals are able to return to a relatively small area when displaced.

In nine out of the ten experiments the percentage of successfully homing fish which returned to the home pool was considerably greater than the percentage returning to the home range. Although many of these fish were subsequently found in other pools in the home range, the fact that they initially returned to the home pool demonstrates the ability of O. maculosus to return to a small area from a considerable distance.

It is interesting to note that in all experiments,

Table 14

Homing performance of untreated Oligocottus maculosus
at First Beach

Date released	26 May	11 Aug	4 Sept 1975	21 Sept	16 May	23 Aug 1976	15 Sept	4 July	16 July 1977	9 Aug
Number released	42	54	69	33	38	31	20	60	45	32
Number homed	15	30	52	24	20	15	14	31	19	20
Percent homed	36	56	75	73	53	48	70	52	42	63
Number found in transplant area	6	8	17	3	8	8	4	27	26	14
Percent found in transplant area	14	15	25	9	21	26	20	45	58	44
Days spent in transplant area										
a. homers	1,1, 1,1	13,22, 25,41	1,1,1, 1,1,4, 6,6,7, 17,18	4	2,27	2	1,1	1,1,2, 2,4,7	2,2,2, 2,5, 42	3,3, 8,18
b. non-homers	1, 102	1,21, 42,82	6,6,7, 13,22, 42	3,78	2,2, 73,73, 83, 110	1,2, 10,11, 46,80, 104	10,26	1,1,2,2, 2,4,10,10, 16,17,17, 18,21,21, 22,26,26, 44,54,57,58	1,1,1,2, 2,5,6,6, 6,13,14, 14,14,27, 27,32,55,55, 59,59	1,3,3,3, 8,8,11, 11,18,30
Percent of homers returning to home pool	73	87	73	60	70	60	64	65	42	60

considerable numbers (from 9% to 58%) of fish remained in the transplant pool area for variable periods of time (from 1 to 104 days) after being released. This implies that while the majority of O. maculosus individuals show homing behaviour, there is a reasonable number of fish which do not demonstrate this behaviour. Of those fish, a considerable percentage (up to 77% of non-homing fish) remain in the transplant area.

Comparison of the percentages homed between the non-reciprocal transplant and the reciprocal transplants shows that increasing the density or reducing the "space" does not appear to be a factor influencing successful homing. It is possible, however, that the number of non-homing fish remaining in the transplant area is influenced by this factor.

A number of fish which successfully homed were located at least once in pools between the transplant pool and the home range. The majority of fish were found on the periphery of the home ranges. For example, one fish displaced to a high pool in the intertidal was found in a lower pool the day following release and was back in the home range for a period of 3 to 33 days after release. Another fish, originally captured in a high tidepool and transplanted was observed after release in a low pool in its home range after five days, the next highest pool after seven days and the higher home pool many times from 17 to 98 days after release. Not all fish displayed this apparent type of movement between pools. Some were observed in pools at or outside the edges of the home ranges in the mid-intertidal.

A few fish were observed in a series of mid-intertidal pools from the release pool to the home range. Several fish which were found out of the transplant and home areas after release were found in pools up to 30 m away from the transplant area and in the opposite direction from the home pool.

Inlets

Home range and area fidelity

Homing behaviour of O. maculosus has to date, only been examined in tidepool areas (Gersbacher and Denison, 1930; Green, 1967; Khoo, 1971). In several areas of Barkley Sound (Grappler Inlet, Rance Island and Dodger Channel) large, but particularly in Dodger Channel, seasonal populations of O. maculosus can be found.

If homing is defined as the return to a home range when experimentally displaced, it is necessary to establish whether inlet O. maculosus display fidelity to a particular area. One experiment was conducted to determine whether O. maculosus can be regularly found in a restricted area of an inlet, comparable to a group of tidepools.

Methods

A total of 58 fish from two sites on the south side of Grappler Inlet were tagged and replaced in the area in which they were captured. Of these fish, 43 O. maculosus were captured and released in the small bay about halfway along the inlet and 15 fish were captured and released at the mudflat in Port Desire. At each site a series of minnow traps was spread in a line parallel with the shore line and covering a linear distance of about 7 to 10 m. Traps were always set at low tide, however the level of the intertidal at which the traps were set depended on the height of the tide. At higher low tides, the traps were set at a higher water level but in the same transect perpendicular to the shore as the lowest trapping site. Trapping was conducted and observations were made only at the two sites. Data were collected over a four month period.

Results

The relatively low percentages of fish resighted suggest that in inlets O. maculosus individuals do not display the same degree of fidelity to a small area comparable to that shown by O. maculosus individuals found in tidepools (Table 15). One tagged fish was located three times at the capture site (50, 52 and 64 days after release), but the majority were seen again only once after release, and within the first month. One tagged

Table 15

Grappler Inlet replacement experiment

	Bay	Mudflat	Total
Date released	2 October 1975		
Number replaced	43	15	58
Number resighted there	12	6	18
Percent resighted there	28	40	31

O. maculosus was observed a number of times at the small bay, at varying tide levels from 0.5 to 3 m. This fish was always found about 0.6 m below the water level, apparently following the tide.

It is possible that the home range of inlet O. maculosus is larger than the areas trapped or observed. It is also possible that the efficiency of trapping and observations is considerably less in inlets than in tidepools where much better defined areas are under consideration. However the low percentages trapped or seen again over the duration of the experiment appear to suggest that some inlet O. maculosus show some fidelity to a particular area but that the majority range over a wider area. Even those fish which do display a degree of association with a small area appear to do so only for a limited period of time.

Homing behaviour along inlets

Although the degree of fidelity to a particular area shown by inlet O. maculosus appears to be small, two transplant experiments were conducted to determine whether O. maculosus displays homing behaviour in inlets, that is, returns to a small area (as in tidepool O. maculosus) when experimentally displaced.

Methods

In the first experiment a total of 78 O. maculosus were collected from the two sites in Grappler Inlet, 42 from the bay and 36 from the mudflat. The fish were reciprocally transplanted (although the numbers were not quite equal). Trapping was conducted and observations were made only at these two sites. Data were collected over a four month period.

In the second experiment a total of 88 O. maculosus were collected, 64 from the bay and 24 from the mudflat. These fish were released at a site approximately halfway between the capture sites. At the release point, O. maculosus does not appear to occur in any numbers, as three days by trapping prior to the experiment produced only four O. maculosus. Following release, trapping was conducted and observations were made at all three sites. Data were collected over a four month period.

Analysis of data involved calculating percentages successfully homing and percentages remaining in the transplant area.

Results

The low percentages successfully homing (Table 16) suggest that homing behaviour is not well developed in O. maculosus found in inlets. Even when the distance to home was considerably reduced the percentages homing were small.

In the first experiment the percentages remaining in the transplant area were small. In the second experiment no fish were found at the transplant site. Few untagged O. maculosus were trapped at this site. The data from the first experiment may imply that the slightly more exposed area (the bay) is a more desirable habitat than the mudflat. The absence of tagged fish at the transplant site in the second experiment suggests that while they move away from the transplant area, the majority did not return to the capture site, as shown by the percentage successfully homing.

Compared with homing behaviour of O. maculosus in tidepool areas, it appears that homing behaviour is not as well developed in inlet fish. An attempt was made to determine whether inlet fish showed improved homing performance in a tidepool situation. On 17 October, 1975, 71 tagged O. maculosus from Grappler Inlet were introduced to a group of tidepools at First Beach. In three of the tidepools an equal number of fish was removed as was replaced (31 fish). It was intended that the movements of the fish between tidepools be monitored for some

Table 16

Homing behaviour along Grappler Inlet

	Bay	Mudflat	Total	Bay	Mudflat	Total
Date released	2 October 1975			4 February 1976		
Number released	42	36	78	64	24	88
Number homed	5	3	8	2	3	5
Percent homed	12	8	10	3	13	6
Number staying in transplant area	1	5	6	0	0	0
Percent staying in transplant area	2	14	8			
Days staying in transplant area						
a. homers						
b. non-homers	4	1, 15				
		20, 22,				
		54				

period of time and if fidelity to a pool or group of pools became apparent, transplant experiments were to be conducted to examine homing behaviour.

Following the introduction, severe storms occurred resulting in a noticeable decrease in both natural tidepool populations of O. maculosus and tagged O. maculosus. In the first two weeks after release 23 fish were located. The majority were found in the group of pools into which they were introduced and adjacent pools. Of those fish seen after release, about equal percentages were introduced into cleared and uncleared pools. Most showed some tendency to move from the release pool to other pools. After the first two weeks only one tagged O. maculosus was located, 54 days after release in a pool about 60 m away from the release area. Thus it was not possible to conduct any transplant experiments to examine homing ability.

Homing behaviour across inlets

Carlson and Haight (1972) found that the yellowtail rockfish, Sebastes flavidus (Ayres) was unsuccessful in homing if the area between the displacement and home sites included deep water. Green (1975) found that the cunner Tautogolabrus adspersus (Walbaum) was unable to home over deep water. Khoo's (1971) work at Port Renfrew showed that rough terrain or deep subtidal areas appeared to have adverse effects on the homing ability of O. maculosus.

To determine whether deep water has adverse effects on the homing ability of inlet fish, two experiments were conducted on the homing ability of O. maculosus across Grappler Inlet, at the same time as the homing experiments along Grappler Inlet were conducted. Although the ability of inlet O. maculosus to home is not as well developed as in tidepool fish, there apparently is a small percentage which are able to home successfully.

Methods

A total of 72 O. maculosus (56 from the bay and 26 from the mudflat in Grappler Inlet) were transplanted to a site on the north side of Grappler Inlet directly opposite the small bay. The distance across the inlet is approximately 80 m and the depth in the middle of the inlet about 12 m at high tide. Trapping was conducted and observations were made at the release site for one month after release and at the capture sites for four months after release.

In the second experiment 44 O. maculosus were transplanted from the bay on the south side of Grappler Inlet to the release site directly opposite on the north side of the inlet. Trapping and observations at the release site were conducted for one month after release and at the capture site for four months after release.

Results

Table 17 makes it abundantly clear that inlet O. maculosus are unable to home over deep water. It is interesting to note that although there are considerable numbers of O. maculosus at the release site, none of the transplanted fish was found at this site after release. Since no fish were removed from the transplant site prior to releasing fish, density dependent exclusion cannot be eliminated.

3. Homing with respect to exposure

Khoo (1971) found that O. maculosus at Port Renfrew were rarely restricted to one particular pool. This study has shown that in the course of their normal movements at First Beach, equal proportions of fish show fidelity to a particular pool as to a group of pools, and that in the latter group there is usually one preferred pool. In inlets, O. maculosus appear to show little fidelity to a particular area, comparable to a group of tidepools.

With respect to homing behaviour, O. maculosus at both First Beach and Port Renfrew show moderate to high, but variable percentages homing and O. maculosus in Grappler Inlet show little evidence of homing. The work of Green (1967) at Port

Table 17

Homing behaviour across Grappler Inlet

	Bay	Mudflat	Total	Bay
Date released	16 October 1975			4 Feb 76
Number released	56	26	72	44
Number homed	0	0	0	0
Number staying at transplant site	0	0	0	0

Renfrew showed that the vast majority of transplanted O. maculosus left the transplant pool within a few tidal cycles. In a number of experiments Green found that only four fish out of over 100 transplanted fish remained in the transplant pool for any period of time: one was taken with poison the day following release, two remained three weeks and one about four weeks. The latter three subsequently homed. Khoo (1971) trapping on a two-weekly basis found that all fish left the transplant pool at the end of the first two weeks. At First Beach a sizeable percentage of fish remained in the transplant area for considerable periods of time, either prior to homing or to taking up residence in the area.

It thus appears that there may be differences in homing behaviour of O. maculosus in areas of different exposures (substrates). Results from First Beach and Grappler Inlet and the work of Green and Khoo at Port Renfrew suggest that in more exposed tidepool areas, O. maculosus displays less fidelity to particular pools and fewer fish remain in the transplant area. In sheltered inlet areas much less area fidelity is shown than in any tidepool area, few fish home and relatively few remain in the transplant area. Thus a series of experiments designed to compare homing behaviour simultaneously in exposed and sheltered areas was conducted.

Methods

Four experiments involving nine different locations of differing exposures were conducted to compare the homing behaviour of O. maculosus. Each site was initially classified as exposed, moderately exposed or sheltered according to location and observation. In each experiment releases, retrapping and observations of fish were made simultaneously in all locations as far as possible.

Homing behaviour was compared in O. maculosus from Port Renfrew (exposed), First Beach (moderately exposed), and Grappler Inlet (sheltered). A total of 286 fish were transplanted as follows: Grappler Inlet - two groups of 50 fish were reciprocally transplanted between the small bay and the mudflat on the south side of the inlet, a distance of about 120 m; First Beach - two groups of 49 fish were reciprocally transplanted between two groups of four pools each about 60 m apart; Port Renfrew - two groups of 44 fish were reciprocally transplanted between two groups of three and five pools each, about 60 m apart. Subsequent trapping was conducted and observations were made at two week intervals as far as possible, up to four months.

Homing behaviour was compared in O. maculosus from Benson Island (exposed) and Rance Island (sheltered). A total of 103 fish were transplanted as follows: Rance Island - two

groups of 17 and 34 fish each were interchanged between the two study sites in the inlet, about 50 m apart; Benson Island - two groups of 26 fish each were reciprocally transplanted between two groups of three pools each about 80 m apart. Subsequent retrapping and observations were attempted on a number of occasions for almost two months.

Homing behaviour of O. maculosus was compared on the south eastern side of Haines Island (moderately exposed) and the Haines Island shore of Dodger Channel (sheltered). A total of 88 fish were transplanted as follows: Dodger Channel - 34 fish were transplanted from the western to eastern end of the Zostera bed in the channel, about 70 m; Haines Island - two groups of 30 and 24 fish each were approximately reciprocally transplanted between two groups of three pools each, about 50 m apart. Subsequent retrapping and observing were conducted a number of times until the experiment was terminated after six weeks.

Homing behaviour and area fidelity were compared in O. maculosus from Kirby Point (exposed), First Beach (moderately exposed) and the large tidepool on Haines Island (sheltered). A total of 111 fish were transplanted as follows: Haines Island - a group of 52 fish were displaced about 60 m from the large tidepool to Dodger Channel, First Beach - 32 fish were approximately reciprocally transplanted between two groups of pools about 60 m apart; Kirby Point - one group of 18 fish and another of nine fish were approximately reciprocally transplanted between two groups of pools at two locations on the

point. In both cases the fish were displaced about 50 m. Percentages homing and remaining at the transplant areas were calculated for all nine sites.

In addition, a total of 123 fish were replaced in the area in which they were captured, as follows: Haines Island - 53 fish were replaced into the large tidepool in the area in which they were captured; First Beach - 44 fish were replaced into the tidepools in which they were first captured; Kirby Point - 26 fish were replaced into the pools in which they were captured. Subsequent retrapping was conducted and observations were made twice weekly at all sites until the experiment was terminated after five weeks. Percentages found in the home and home and nearby pools and in distant pools were calculated for each site.

Results

The results of the four transplant experiments (Table 18) show that in spite of the low percentages located after release in some areas, in each case the percentages successfully homing are greater in areas of moderate to greater exposure (tidepool areas) than in sheltered areas (inlets). However the percentages homing in different tidepool areas show a greater degree of variability than anticipated, and there appears to be no relationship between this variability and exposure as determined by location and observation. The percentages of O. maculosus remaining at the transplant sites are variable, but

Table 18

Homing behaviour in areas of different exposure

	P.R.	F.B.	G.I.	B.I.	R.I.	H.I. ¹	D.C.	K.P.	F.B.	H.I. ²
Date released	5 Nov 1975	2 Nov		4 June	2 June 1976	24 October 1976		8 Aug	9 Aug 1977	7 Aug
Number released	88	98	100	52	51	54	34	27	32	52
Number homed	18	35	3	2	0	27	1	7	19	2
Percent homed	20	36	3	4	0	50	3	26	59	4
Number staying in transplant area	0	2	4	33	0	3	0	11	13	0
Percent staying in transplant area	0	2	4	63	0	6	0	41	41	
Days staying in transplant area										
a. homers										
b. non-homers		15,26	23,39, 90,94	1x21, 28x9, 53x3		11,11 39		1,3,3,3, 3,3,10,22, 22,23,36	3,3,3,3, 1,3,3,3, 11,11,18 18,18	
Percent of homers returning to home pool	42	74		100		70		100	68	

P.R.: Fort Renfrew, F.B.: First Beach, G.I.: Grappler Inlet, B.I.: Benson Island,
R.I.: Rance Island, H.I.¹: Haines Island (south east side),
D.C.: Dodger Channel, K.P.: Kirby Point, H.I.²: Haines Island (large tidepool)

do not show increasing numbers of fish remaining at the transplant site in less exposed tidepool areas. Only in inlets and channels are the predicted findings confirmed.

In the first experiment the small percentage of fish located after release may be the result of a series of extremely severe storms which occurred just subsequent to transplanting. At both First Beach and Port Renfrew a reduction in the number of O. maculosus was evident following the storms. Khoo (1971) found an inverse relationship between homing performance and sea state conditions (as measured by percent observations of swells greater than or equal to six feet).

The second experiment (Benson Island and Rance Island) produced very unexpected results. At the time of trapping and release there were numerous O. maculosus in the inlet around Rance Island. Following release of the tagged fish, the population of O. maculosus in the area almost completely disappeared to be replaced by large numbers of Leptocottus armatus. Analysis of stomach contents of O. maculosus from this area showed a low diet diversity when compared with fish from First Beach and Port Renfrew (Ruth, 1976). The apparently unstable population of O. maculosus at Rance Island may be a reflection of this.

Although the third experiment (Haines Island and Dodger Channel) was conducted for only six weeks and at a time when there is a high frequency of storms, the percentage of

O. maculosus at Haines Island which had successfully homed by the end of this period was considerably greater than the percentage homing in Dodger Channel. No O. maculosus were seen or trapped at the western end of the eel grass bed and intensive trapping of this site prior to the experiment produced none. This and the low percentage homing suggest that while the release site was not feasible as an alternative habitat for the transplanted fish, homing behaviour is not strongly expressed in O. maculosus found in inlets.

The fourth experiment (Kirby Point, First Beach, Haines Island) was terminated after five weeks. Although this is a relatively short period of time, data from First Beach suggest that the majority of information is acquired in the first month following release. Since the weather was favourable almost simultaneous twice weekly visits to each site were possible for the duration of the experiment. In agreement with the other experiments, the data suggest that homing behaviour (that is, returning to the area of capture) is better developed or at least expressed, in tidepool than inlet areas, but fail to show that a gradient of ability in homing behaviour exists which corresponds to a visually determined exposure gradient.

From the results of the replacement experiment at Kirby Point, First Beach and the large tidepool on Haines Island (Table 19) it is evident that the percentage of fish found in the home pool only is much greater at Kirby Point than at First Beach, where the usual situation of equal percentages in the

Table 19

Area fidelity in sites of different exposures

Area released	K.P.	F.B.	H.I.
Date released	8 Aug 77	9 Aug 77	7 Aug 77
Number released	26	44	53
Number found in home pool only	23	17	1
Percent found in home pool only	88	39	2
Number found in home and nearby pools	2	18	
Percent found in home and nearby pools	8	41	
Number found in home pool and home and nearby pools	25	35	
Percent found in home pool and home and nearby pools	96	80	
Number found in distant pools	0	2	0
Percent found in distant pools	0	5	0

K.P.: Kirby Point, F.B.: First Beach, H.I.: Haines Island

home and nearby pools was found. As anticipated, little area fidelity was shown to the large tidepool on Haines Island.

The data suggest that my perception of exposure, based on location and observation, bears little relationship to the homing behaviour of O. maculosus. Since wave action (turbulence) has been demonstrated as important in the distribution and activity of O. maculosus (Green, 1971a,b,c), consideration of this and a related factor (the roughness of the terrain, in terms of the steepness and irregularity of the shore) with respect to the homing behaviour of O. maculosus, may be more relevant than an overall subjective impression of exposure. These factors are considered in the next section.

4. Measurement of wave action and topographical regularity

The problem of measuring the relative exposure in terms of wave action or turbulence in different localities has been attacked in a number of ways. Ballantine (1961) suggested eight biologically determined exposure categories, essentially based on the abundance of common species, ranging from extremely sheltered to extremely exposed. While biological scales are useful in a descriptive sense they are not easily generalized over wider areas.

Determinations of exposure or wave action based on wind measurements have been used by Moore (1935) and Southward

(1953), using the percentage of winds over 100 days blowing into the exposed aperture of a given locality and the percentage of winds equal to or greater than 10 knots which produced a wash at least one foot over the predicted tidal height, respectively. The former method does not take account of wind force or swells and the latter does not take into account the slope of the locality.

Green (1967) used a submersion-emersion sensor (Druehl and Green, 1970), bolted to the substrate at a known vertical height and attached to a recorder which recorded the times of emergence and submergence of tidepools. Comparing the actual times with predicted times of submergence enabled him to rate pools into four categories from exposed to sheltered. At least two such sensors are required to be positioned simultaneously. Jones and Demetropoulos (1968) developed a drogue attached to a spring dynamometer which records the maximum drag produced by waves in the locality. No measurement of frequency is provided. Harger (1970) measured wave impact over one tidal period by the movement down a nail of a steel plate held in position with a C clip. A method for measuring short term exposure was described by Muus (1968) in which Plaster of Paris balls are attached to steel rods embedded in the substrate and the weight loss of the balls compared to weight loss figures at known water velocities.

While these methods may be useful in some studies they do not provide a simple means of measuring exposure in a variety of widely spaced areas over a long period of time. In this

study a method was required which measured the exposure where the fish are located over a relatively extensive period. Thus the method used was based on the weight loss of cement blocks attached to the substrate (in pools and on rocks) but able to move in a hemisphere about the anchor and undergo abrasion by the action of waves moving the block over the substrate.

Initially, a pilot study was conducted lasting approximately two months. However, the weakness of the pins used resulted in a high loss of cement blocks in more exposed areas. Subsequently, a longer term study, lasting almost nine months was conducted. Only the results of the final study are reported.

The relative roughness of the terrain was evaluated by a subjective estimate based on observations of the study areas. The steepness of the rocky shelves and the degree of irregularity of these shelves were used in this estimate.

Methods

Styrofoam cups were cut down to make moulds 4.5 cm high. The cups were then greased with vaseline and eyebolts 6.35 cm long were inserted in the bottom of the cup so that part of the eye was inside the cup. Concrete was mixed using Portland CSA Type 20 cement in the following proportions - cement : sand : water - 5 : 1 : 3. This mixture was poured into the cups and allowed to set. The styrofoam cups were then

peeled off leaving a concrete block with an inserted eyebolt (Figure 14a). The blocks were weighed to the nearest gram.

The blocks were anchored in tidepools and to the substrate at nine sites on the west coast of Vancouver Island: Cape Beale, Port Renfrew, Benson Island, Pachena Point, First Beach, Helby Island, Grappler Inlet (bay), Rance Island and the large tidepool on Haines Island. Ten blocks were anchored at each site using a pin attached to an eyebolt embedded in hydraulic cement. To overcome the problem of the weakness of the shower curtain clips used in the pilot study, halibut snaps were used as the pin between the cement block and the anchored eyebolt (Figure 14b). In addition to the cement blocks anchored in the field, ten blocks each were anchored to bricks in the calm and "exposed" sides of a tank used in an experiment to determine whether greater numbers of cirri could be experimentally produced on fish in an "exposed" tank as opposed to a calm tank. This provided a measure of the effect of constant immersion on the blocks and the relative exposure of the side of the tank receiving waves.

All the cement blocks were put into position between 30 August and 12 September, 1976 and were removed between 21 May and 28 May, 1977. After removal the blocks were uniformly washed and scrubbed with steel wool, and then oven dried at 55°C for 48 hours. Keeping the blocks dry, they were again uniformly scrubbed with steel wool. This procedure succeeded in removing the attached animals, such as Spirorbis sp. The blocks were

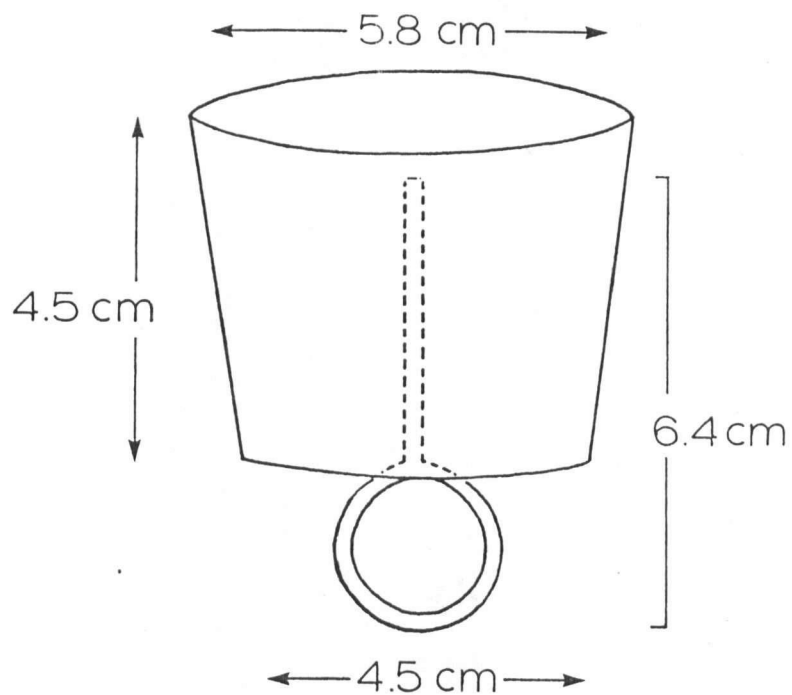


Figure 14a Cement block design



Figure 14b Cement block anchored in pool

weighed to the nearest gram.

The Kruksal-Wallis one-way analysis of variance by ranks, corrected for ties (Siegel, 1956), was used to compare the initial weights of the blocks at each site to determine whether there were any significant differences between the samples when they were installed.

Results

The Kruksal-Wallis one-way analysis of variance by ranks, corrected for ties, on the initial weights for all samples (Table 20) showed no significant differences between samples ($H=.958$, $p>.05$). Weight loss (mean grams and mean ranks) and the number of cement blocks remaining are also shown in Table 20. Examination of the mean ranks shows several clusters of ranks: Cape Beale and Benson Island; Port Renfrew, Pachena Point and First Beach; Rance Island, Helby Island, Grappler Inlet and the wave tank; Haines Island and the calm tank. Since only a relative exposure rating was required and since the individual sample sizes were small, especially for several groups, it appeared that considering the samples in the groups delineated above was the most useful approach.

Using the multiple comparisons test based on rank sums, and corrected for ties (Hollander and Wolfe, 1973; Dunn, 1964), the four groups of samples were compared with each other. Dunn suggests using a relatively high significance level (such

Table 20

Final study of relative exposure
Weight statistics of cement blocks

	Initial mean wt (grams)	Initial mean wt (ranks)	N	Mean wt loss (grams)	Mean wt loss (ranks)	N
<hr/>						
Cape Beale	175.9	56.1	10	32.0	80.3	2
Benson Island	174.6	47.2	10	53.8	75.1	4
Port Renfrew	176.2	56.7	10	21.3	59.6	7
Pachena Point	175.6	54.6	10	22.1	57.0	10
First Beach	176.1	56.4	10	29.0	63.4	7
Helby Island	176.0	57.0	10	17.0	38.8	6
Rance Island	175.9	56.4	10	19.2	49.9	9
Grappler Inlet	175.6	53.7	10	17.7	39.3	10
Haines Island	175.7	56.3	10	12.7	17.3	10
Wave Tank	176.0	57.0	10	17.1	38.3	10
Calm Tank	176.4	59.4	10	12.2	14.0	10

as 0.20) in such multiple comparison tests, since taking a more traditional level of 0.05 for example, "makes establishing substantial differences exceedingly difficult". Hence, comparisons were made using a value of 0.20.

This resulted in the following ranking of sites in order of decreasing exposure (with the mean number of cement blocks remaining in parentheses):

Cape Beale, Benson Island (3)

Port Renfrew, Pachena Point, First Beach (8)

Rance Island, Helby Island, Grappler Inlet, Wave Tank (8.75)

Haines Island, Calm Tank (10).

The four groups were all significantly different ($p < .20$) from each other except Cape Beale, Benson Island and Port Renfrew, Pachena Point, First Beach. However, since the lack of significance is primarily due to the small number of blocks remaining at these sites and since this in itself is an indication of relative exposure, Cape Beale and Benson Island are rated as more exposed than Port Renfrew, Pachena Point and First Beach.

The ranking of sites according to the relative roughness of the terrain resulted in a somewhat different order.

The sites at Cape Beale, Benson Island and Kirby Point are extremely irregular, with relatively narrow, sometimes steeply sloping shelves and small surge channels, compared with the wider, less perilous shelves at First Beach and the southeast side of Haines Island, and again with the broad, flat shelves at Port Renfrew and Pachena Point. In sheltered areas, Grappler Inlet and Rance Island appear to be more topographically irregular than the sand/mud flats of the large tidepool on Haines Island and Dodger Channel. Consideration of the results of the cement block evaluation of wave action together with the subjective estimates of roughness of the terrain suggests that evaluating the exposure of an area simply by observation and location may be somewhat misleading. An area which by location and observation might be classed among the most exposed (for example, Port Renfrew, Pachena Point) may, because of the regularity of the terrain, have a similar overall exposure to a site which by location appears more sheltered but which has a rougher terrain (for example, First Beach). In the following analysis of homing behaviour and exposure, the study sites and the homing behaviour observed there were classified initially into the groups suggested by the cement block ratings, and within these groups further divided by the topographical irregularity estimates to provide an indication of the effect of these two factors on homing behaviour.

5. Discussion

From Table 21 it is evident that with decreasing turbulence and increasing regularity of the terrain, the area to which fidelity is shown in tidepool areas, increases in size from one pool, to one preferred pool to a group of pools. In more sheltered topographically regular inlets, fidelity is shown to apparently larger areas. When displaced, fish in turbulent rough areas display less evidence of homing than fish in less turbulent, rough areas. However, those few fish which do home in turbulent rough areas return to the home range with greater precision than in other areas (that is, greater percentages return to the initial pool of capture, the home pool, than to other pools in the home range) in inlets few fish home. With decreasing turbulence and increasing regularity of the terrain, decreasing numbers of fish stay in the transplant area.

These results confirm and extend Khoo's (1971) findings that poor weather and rough terrain, in the form of steep trenches and abruptly sloping shelves adversely affect homing ability. The kind of homing behaviour exhibited apparently depends on the degree of wave action and roughness of the terrain.

Turbulence has been shown to play a major role in the vertical distribution, high tide distribution and activity of

Table 21

Homing behaviour according to topographical regularity and turbulence

	TIDEPOOLS			INLETS	
Turbulence	high		moderate	low	very low
Topography	highly irregular	irregular	relatively regular	regular	extremely regular
Area fidelity	particular pool	usually one preferred pool	group of pools	large area?	large area?
Homing behaviour					
Percent homing	relatively low	moderate to high	moderate to high	low	very low
Percent remaining in transplant area	moderate to high	low to moderate	very low	low	very low
Percent of homers homing to home pool	high	moderate to high	moderate to high		

O. maculosus (Green, 1971a,b,c). In exposed transects O. maculosus tends to be confined to higher tidepools, whereas in sheltered areas, it occurs throughout the intertidal. Seasonal changes in distribution are evident when storm induced disruption of pools occurs and the resident population is washed out of the pool or departs (Green, 1971a; personal observation). In winter months, when turbulence is greatest, a decline in fish numbers is evident. This has also been shown for another intertidal fish, Acanthocottus [= Enophrys] bubalis (Euphrasen) (Gibson, 1967).

At high tide, only O. maculosus in sheltered areas leave the pool (in some sheltered areas there is an almost complete onshore shift in the distribution of O. maculosus less than 5.5 cm); in exposed areas they seek cover until the pool is isolated again (Green, 1971b,c). In moderately exposed areas, the only time at which a significant proportion of fish leave the pool is in July, August and September, the calmest months of the year (Green, 1971b). Although these are also the hottest months of the year, and O. maculosus remain in or retreat to deeper water in pools at temperatures above 15° C, tidal flooding in June has been shown to reduce the temperature from 20°C to 11°C in the warmest parts of a pool within one hour (Green, 1971c). Green found the change during the fall from being active to inactive at high tide occurred first in the O. maculosus inhabiting the more exposed of two otherwise similar pools (1971a). Reduced activity during turbulent

periods has also been reported in Clinocottis analis (Williams, 1957).

There appears to be a relationship between the amount of wave action and the amount of high tide movement of O. maculosus, from virtually none in an exposed tidepool areas to an onshore shift in sheltered tidepool areas and possibly almost continual movement in inlets, as the fish follow the tide. Thus in rough turbulent areas, few fish leave the pool at high tide and hence display strict pool fidelity. When transplanted, fidelity is changed to the new pool and few fish home, although those which do home show greater precision in the area to which they return, presumably because they rarely move out of the home pool in their natural movements. In less turbulent, less rough areas, the degree of movement at high tide appears to depend on the regularity of the terrain. Where the terrain is more regular, presumably turbulence between pools is reduced and movement between pools less hazardous. When fish from these areas are displaced, the numbers remaining in the transplant area appear to depend on the roughness of the terrain; in more regular areas the fish leave the transplant pool. In sheltered inlets, where turbulence is never great and movement is possible at all times, a much greater amount of movement appears to take place, resulting in little area fidelity and homing success. The absence of distinct topographical irregularities also appears to reduce the occurrence of fidelity to a small area comparable to that of a

group of tidepools.

To my knowledge, there is only one published study comparing home range fidelity in the same intertidal species (Blennius pholis (Linnaeus) and Acanthocottus [= Enophrys] bubalis) in two semi-exposed (Ballantine, 1961) areas. Differences were noted in one species (Blennius pholis) which were suggested as possibly being due to the topographical dissimilarity of the two areas; the area where a higher frequency of return to the home pool after being absent was observed, is irregularly divided by vertical rock edges producing gullies, in contrast to the flatter, undivided rocky shore at the other site (Gibson, 1967).

Although there are few published data comparing home range in the same species in different areas, comparisons can be drawn between the fairly limited home ranges reported for tidepool fishes Amphigonopterus [= Micrometrus] aurora (Jordan and Gilbert) (Hubbs, 1921), Clinocottus analis, Girella nigricans (Ayres) (Williams, 1957), Acanthocottus [= Enophrys] bubalis, Blennius pholis (Gibson, 1967), Hypsoblennius gilberti (Jordan) (Stephens et al., 1970), Clinocottus globiceps (Green, 1973) and small coral reef fish Dascyllus aruanus (Linnaeus) (Sale, 1971), Holacanthus bermudensis Goode (Bardach, 1958), the somewhat larger but fairly restricted home ranges shown by near shore rocky and coral reef fish Sebastes flavidus (Carlson and Haight, 1972), Tautogolabrus adspersus (Green, 1975), Epinephelus striatus (Bloch), E. guttatus (Linnaeus) (Bardach,

1958) and the apparently comparatively poorly developed area fidelity shown by freshwater fish Galaxias bonghong Macleay (Berra, 1973), Cottus bairdi punctulatus (Gill) (Bailey, 1952), Cottus bairdi (Girard) (McCleave, 1964), Lepomis megalotis (Rafinesque) (Berra and Gunning, 1972) and in tidal creeks and salt marshes Menidia menidia (Linnaeus), Fundulus heteroclitus (Linnaeus) (Buttner and Brattstrom, 1960; Lotrich, 1975).

Comparison of the results of these studies appears to suggest that fish closely associated with the substrate where there are topographical irregularities, for example, pools, reefs, wrecked boats, boulder patches etc. show evidence of fairly restricted area fidelity. In addition, where turbulence can be considerable and the fish is liable to be swept out of the area, restricted area fidelity appears to be shown.

With regard to homing behaviour, there do not appear to be any published reports of differences in homing behaviour of the same intertidal species in different areas. Different species of intertidal fish have been shown to display varying success in homing performance, from high percentage returns in Clinocottus globiceps (Green, 1973) and Bathygobius soporator (Beebe, 1931), moderate to low returns in Hypsoblennius gilberti (Stephens et al., 1970), Blennius pholis, Acanthocottus [= Enophrys] bubalis, Ciliata mustela (Linnaeus) (Gibson, 1967), Girella nigricans (Williams, 1957), to almost complete inability to home in Clinocottus analis (Williams, 1957). Near shore marine fishes show similar variability from relatively high

percentage returns in Tautogolabrus adspersus (Green, 1975), moderate returns in Sebastes flavidus (Carlson and Haight, 1972), low to moderate returns in Epinephelus striatus and E. guttatus (Bardach, 1958) and inability to return from a considerable distance in Holacanthus bermudensis (Bardach, 1958).

In general, freshwater fish and fish in tidal creeks show much less success in homing than marine fishes in which this has been examined (Lotrich, 1975; McCleave, 1964; Berra, 1973; Gerking, 1959; Gunning, 1959).

While turbulence, topography (and distance displaced) evidently appear to have a general effect on homing success, other factors such as changes in area fidelity over the life of the fish and existence and size of home range may also be significant.

V. MORPHOLOGICAL DIFFERENCES BETWEEN FISH IN DIFFERENT LOCATIONS

1. Port Renfrew, First Beach, Grappler Inlet

The early suggestion that there were differences in homing behaviour of O. maculosus in areas of different exposures prompted further investigation of behavioural differences. At the same time as the first behavioural experiment investigating homing behaviour in different locations was conducted, examination of meristic and morphometric characters in these populations was undertaken to determine whether there were any differences between the populations. Such differences, if present, might conceivably be related to behavioural differences.

Methods

To examine meristic and morphometric characters, a total of 304 O. maculosus were collected as follows: 136 from the bay in Grappler Inlet (29 October, 1975), 53 from the mudflat in Grappler Inlet (1 November, 1975), 59 from First Beach (2 November 1975) and 56 from Port Renfrew (5 November, 1975). The fish were fixed in 10% formalin immediately after collection and later transferred to 37.5% isopropyl alcohol.

The fish were measured (standard length - for conversion to total length see Appendix 2) and sexed, and six characters were measured: head length, head depth, eye length, interorbital distance, distance between anterior nares and distance between posterior nares. All measurements were made with dial calipers to the nearest 0.005 cm. Head depth, length and eye length were expressed and examined as percentages of standard length. Interorbital distance and distance between anterior and posterior nares were expressed and examined as percentages of head length. Counts were made of dorsal fin spines and rays and anal fin rays.

Cirri were also examined with respect to number, their nature (single, bifid, triple etc.) and location (lateral line, around eye, head (orbit to occipit), maxillary, preoperculum, operculum and behind the opercular flap above the base of the pectoral fin).

Analysis of all characters except cirri was made according to the method of Hubbs and Hubbs (1953). The number of cirri and the number of lateral line cirri were calculated and plotted against length to determine if any relationship was apparent.

Results

From inspection of the graphical analysis of the eight characters examined (Figure 15), it is evident that there are no obvious or consistent differences in these characters between the four populations examined.

The analysis of total and lateral line cirri number against length suggested an exponential relationship, with the asymptotic number of cirri increasing in the order Grappler Inlet, First Beach and Port Renfrew. This raised the possibility that if cirri contained sensory receptors, there might be some relationship between exposure, homing performance and the number of such sensory receptors. If differences in homing behaviour could be related to differences in the number of sensory receptors, and if the nature of the sensory receptors could be determined (for example, chemoreceptors), an indication of both the mechanism and variability in its perceptiveness in relation to variability in homing behaviour might be provided. Hence a larger scale investigation of the number and distribution of cirri in areas of different exposure was undertaken. To determine experimentally whether cirri number is a function of exposure, each of two groups of small juvenile O. maculosus was exposed to either continuous waves or calm water in the laboratory. Exposure, using the same method as for the study sites, was examined for each of the two conditions.

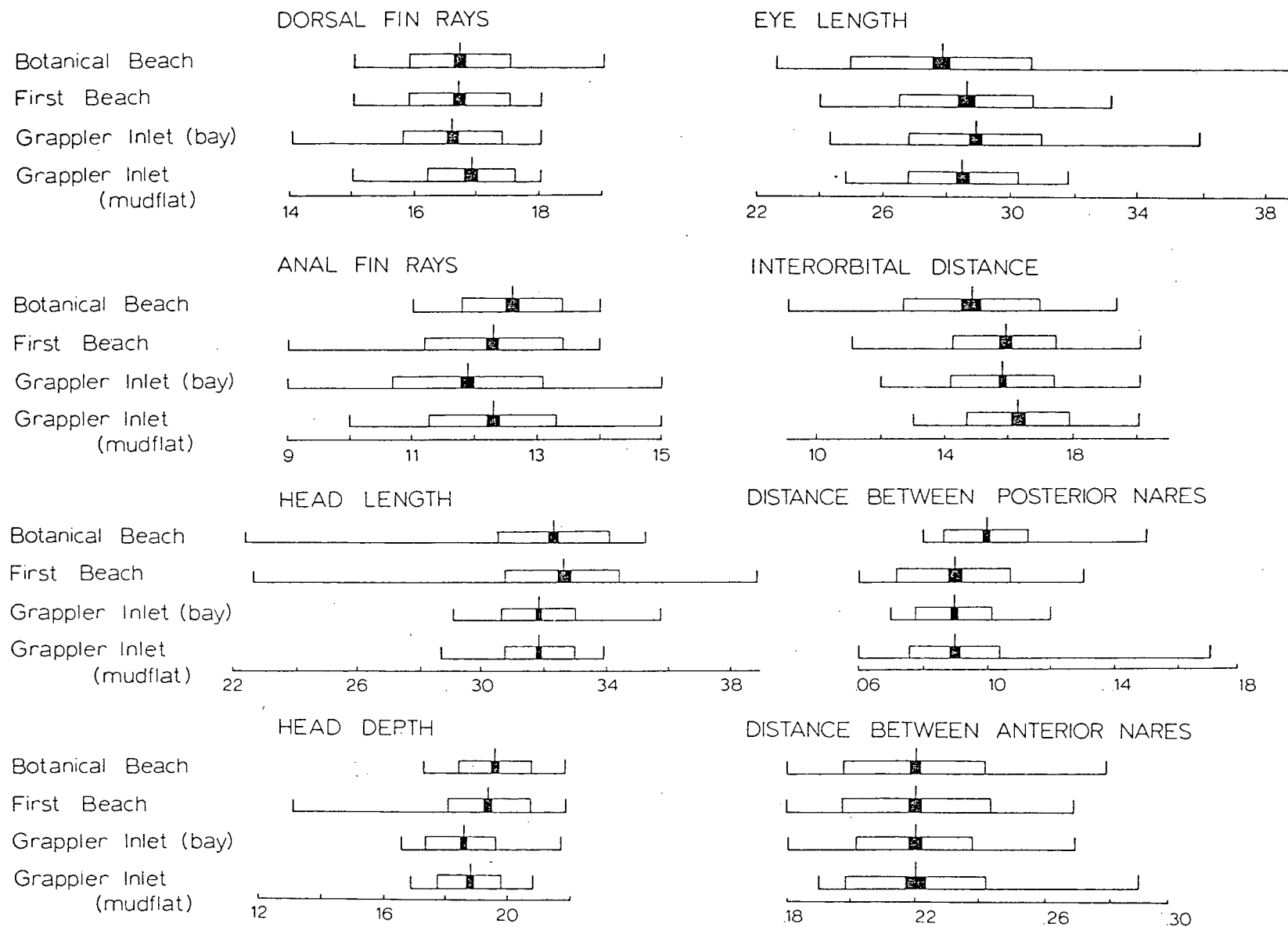


Figure 15 Graphical analysis of eight meristic characters at four areas

Finally, histological examination of the cirri was undertaken to determine whether any sensory receptors were apparent.

2. The relationship of cirri to exposure

Since the preliminary investigation of cirri on fish from three different areas suggested that fish in more exposed areas have more cirri (although little difference was subsequently found in relative exposure between Port Renfrew and First Beach) examination of this apparent phenomenon was undertaken. O. maculosus were collected from six additional sites on the west coast of Vancouver Island and five Alaskan collections were examined.

Methods

To add to the initial collections made at Port Renfrew, First Beach and both the bay and the mudflat in Grappler Inlet, further collections were taken at all sites except the mudflat for cirri analysis. Collections of O. maculosus for cirri analysis were also made at Cape Beale, Benson Island, Pachena Point, Helby Island, Rance Island and the large tidepool on Haines Island. The sites were chosen as covering a range of exposures, the relative positions of each site in an exposure scale subsequently being determined by the weight loss of the cement blocks installed at each site, except

the mudflat in Grappler Inlet.

Immediately after collection the fish were fixed in 10% formalin and later transferred to 37.5% isopropyl alcohol. The fish were measured (total length) to the nearest 0.005 cm, sexed and the cirri were counted and recorded according to their nature and location.

In addition, five Alaskan collections of O. maculosus from the U.B.C. Fish Museum were examined with respect to cirri to determine whether the apparent phenomenon is widespread. The collections examined were from Shelter Island (BC63-251: 58°26'N, 134°52'W), Fish Egg Island (BC63-151: 55°28'30"N, 133°11'15"W), Saginaw Bay, Kuiu Island (BC61-499: 56°55'N, 134°16'W), Tee Harbor, Cohen Island (BC63-87: 58°26'N, 134°46'50"W) and Little Port Walter, Baranof Island (BC63-1255: 56°23'N, 134°38'30"W). These areas were located on charts to obtain an estimate of their exposures relative to each other and in a general manner to the sites on Vancouver Island. However, since no objective measurement of the exposure of the Alaskan sites has been made, the exposure rankings must be regarded cautiously.

The fish from these collections were measured (total length) to the nearest 0.005 cm, sexed and the number of cirri recorded according to nature and location.

Total cirri number was examined with respect to length for each area and then evaluated according to exposure.

Functional regressions of total cirri number vs length were constructed for males and females separately and combined. In the case of juveniles (less than 3.5 cm total length) where sex could not be determined, the data on cirri were included in both the male and female regressions but only once in the combined regression.

Using the age-length regressions calculated for nine of the areas on the west coast of Vancouver Island, except the mudflat in Grappler Inlet, the ages of the fish from each area were calculated and total cirri number was examined with respect to age in each of these areas. Again, functional regressions were calculated for males and females separately and combined. Juveniles were included in both the separate male and female regressions but only once in the combined regression.

Using the age of fish from each of the areas where this could be calculated, the year-class of each fish was recorded. For each area, fish of each year-class were extracted and functional regressions of total cirri vs age were calculated. Since the sample sizes were small in some cases, only combined regressions were calculated.

Results

The distribution and nature of cirri are highly variable between fish. Young fish possess few cirri; the smallest O. maculosus examined (1.4 cm total length) had no cirri and on fish less than 2.0 cm few cirri are apparent. There is an increase in the number of cirri and the number of branched cirri with increasing length, as observed by Bolin (1944). Cirri increase in number on all parts of the body although multifid cirri do not appear to occur at all cirri locations, even in larger fish. Cirri appear first around the eye and on the top of the head prior to being found along the lateral lines and maxillaries, preoperculars, operculars etc. Cirri do not appear to be bilaterally symmetrical in distribution. Uneven distribution appears to be more common than not.

Along the lateral line cirri begin to appear in small fish immediately in front of the anterior pores. In larger fish the cirri precede the anterior half to two-thirds of the lateral line pores and are bifid and trifid in larger fish. Around the mid and upper margin of the eye, small specimens may have one or two cirri while large specimens may have up to nine cirri, many of them multifid.

On the top of the head the distribution is highly variable, although the pattern found on the fish examined in

this study does not appear to be the same as that described by Bolin (1944, p. 66):

"The general pattern in large adults is usually formed by a line of three multifid cirri extending along each fronto-parietal ridge, and a parallel series of two or three similar cirri slightly laterad to these, while two transverse series of up to three cirri each extend across the top of the head in the occipital region. One to three cirri often occur in the midline anteriorly. In juveniles the cirri on top of the head are all simple and may be limited to as few as four on each side."

The general pattern found on large adults in this study consisted of two parallel transverse pairs of frequently multifid cirri behind each eye. Posterior to these, two parallel rows of up to five (when this row occurred) and six (sometimes multifid) cirri respectively were found. Occasionally one or two cirri were found slightly behind and to the side of the last occipital row of cirri. One or two cirri were sometimes found in the midline anteriorly. In the smallest fish examined one or two symmetrical parallel pairs of unbranched cirri were found in the occipital region.

Up to four cirri were occasionally found at the posterior end of the maxillaries; one to three was more common. Maxillary cirri were absent in small specimens. Along the

preopercular margin, up to six cirri were found although two or three was more common. Small fish showed only one or two, if any were present. In larger fish, several cirri were located just above the base of the preopercular spine. At the upper end of the opercular flap larger fish showed up to ten cirri, while in smaller individuals one to four was usual and in the smallest specimens none was apparent. These cirri are not mentioned by Bolin (1944), although Hart (1973) mentions them, while omitting to mention cirri on the maxillary, eye, above the preopercular spine and posterior to the opercular flap above the base of the pectoral fin. In this last location, two or three cirri commonly occurred although up to five were found in larger fish. Smaller fish showed one, if any.

Functional regressions of total cirri number vs length (Figure 16 and Table 22) for Vancouver Island sites are arranged in order of decreasing exposure as shown by the cement block exposure rating. The mudflat in Grappler Inlet is arbitrarily classified as about the same exposure as the large tidepool on Haines Island. The graphs for the Alaskan sites are classified in order of decreasing exposure as determined from charts.

It is evident that there is considerable variability in the relationship of total cirri number with length, but that in all cases, the number of cirri increases with length. For areas where there are reasonably large sample sizes for both sexes and where the length distributions are similar, there is good agreement between the regressions for males and females,

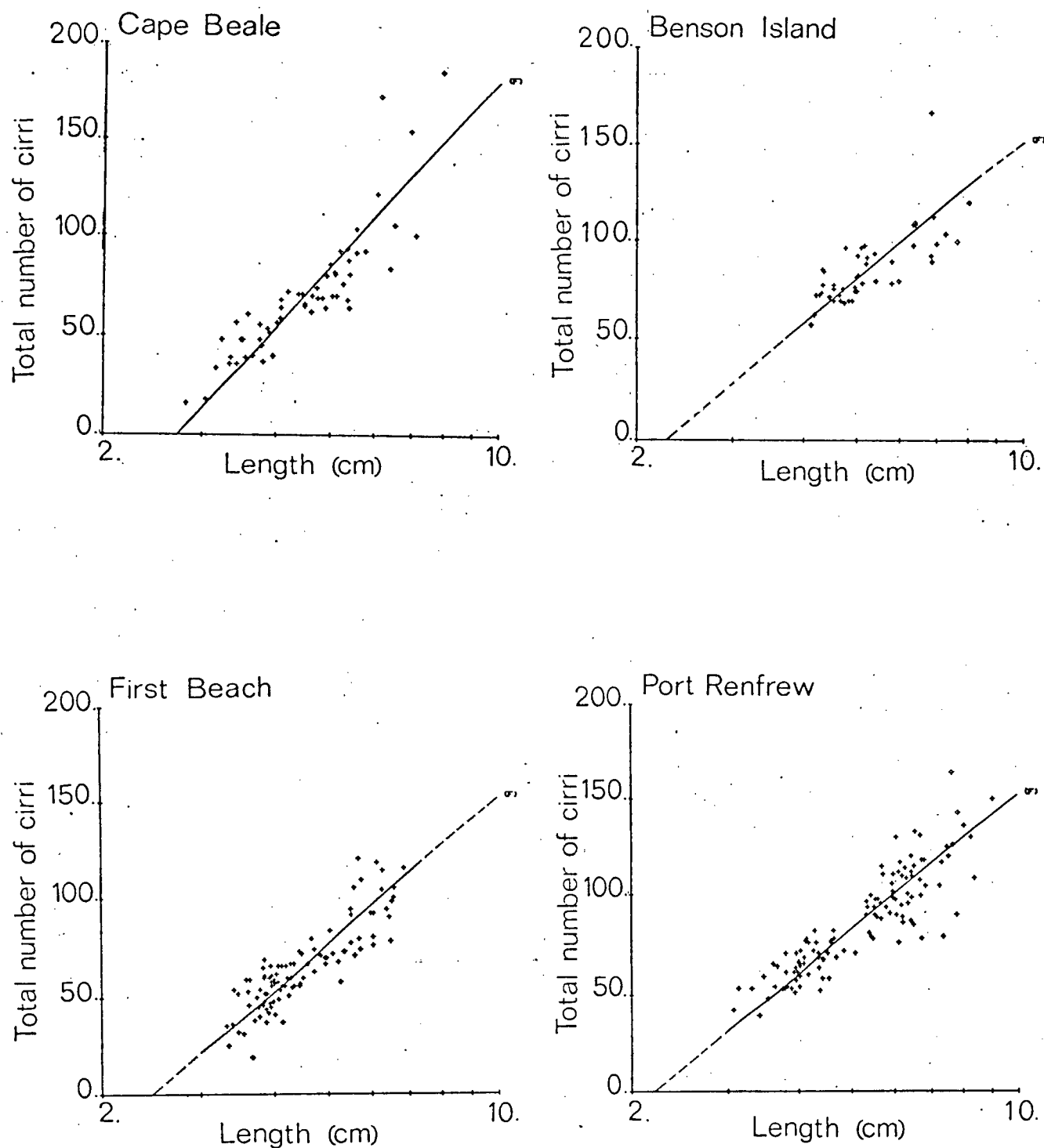


Figure 16 Total cirri-length regressions for *O. maculosus* from fifteen areas (males and females combined)

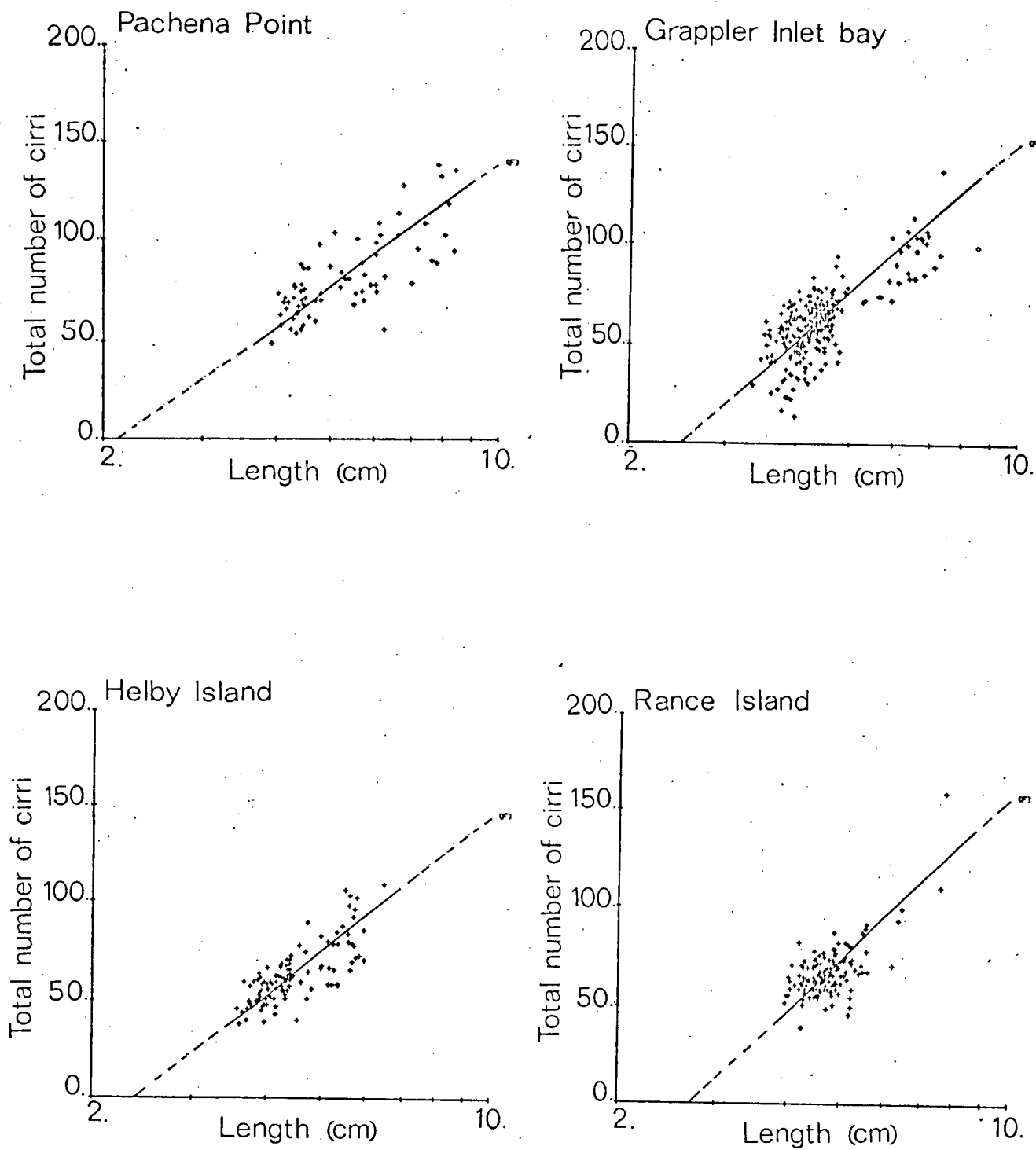


Figure 16 (continued)

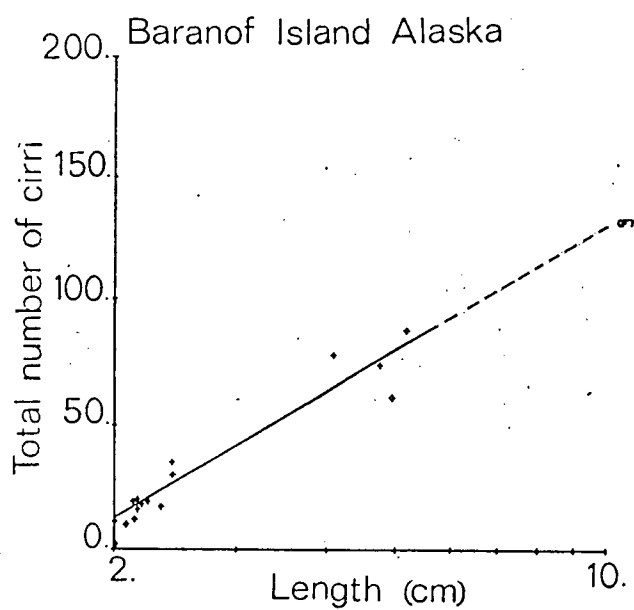
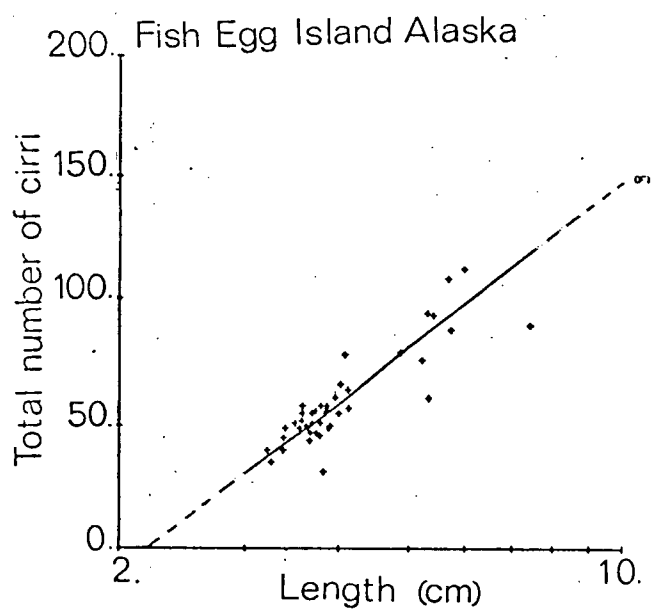
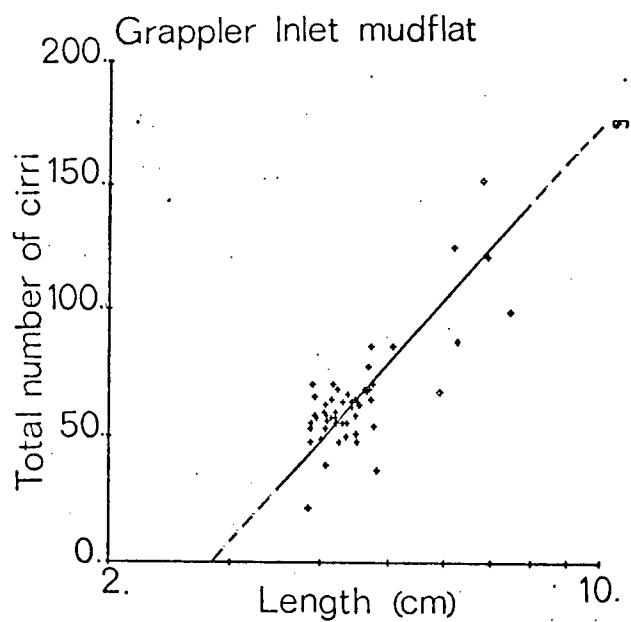
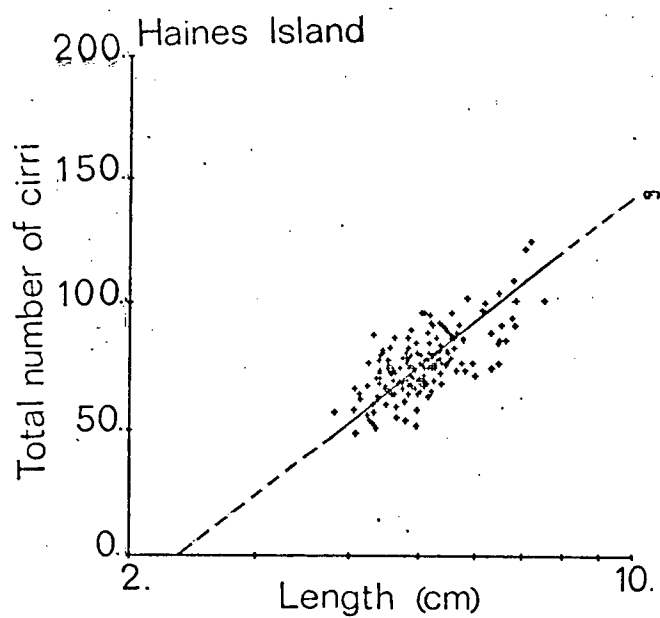


figure 16 (continued)

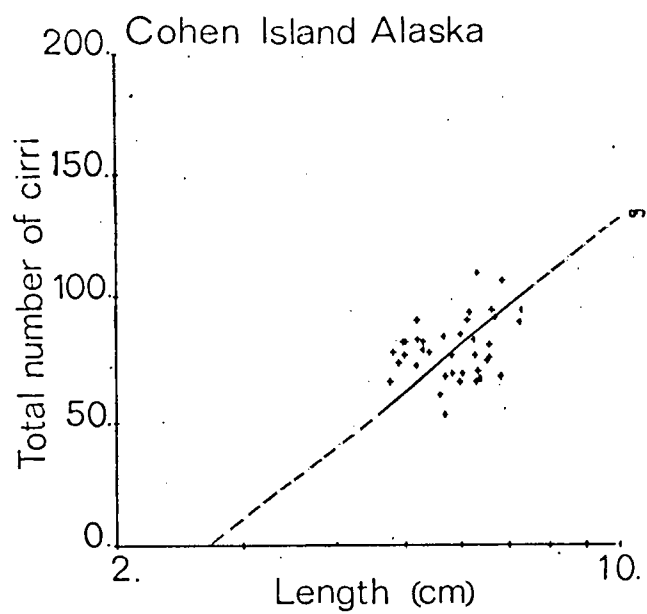
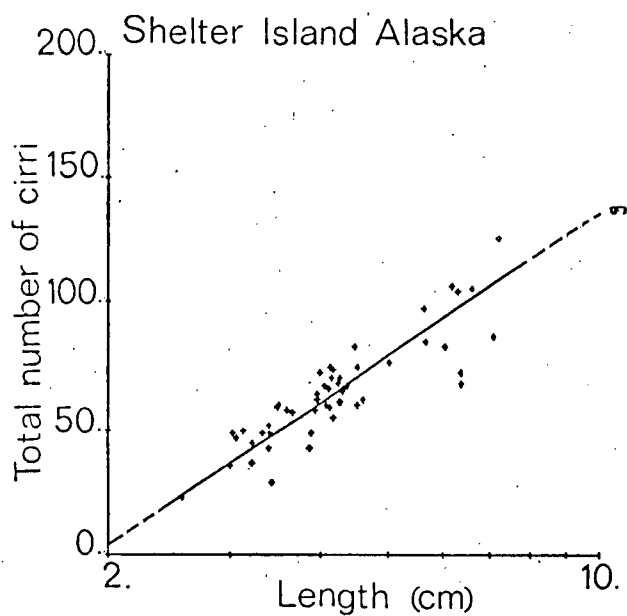
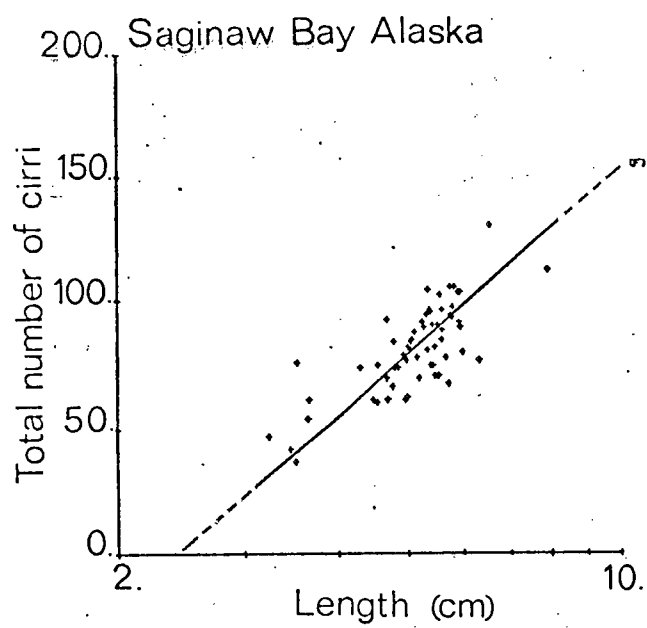


Figure 16 (continued)

Table 22

Oligocottus maculosus (15 areas) total number of cirri - length
functional regression statistics (males, females and sexes combined)

$$\log x \text{ vs } y: y = u + v \log x$$

		N	u	v	Upper 95% c.l. of v	Lower 95% c.l. of v
Cape Beale	Males	25	-102.7	261.8	306.9	216.6
	Females	42	-145.6	335.3	386.9	283.7
	Combined	58	-138.1	318.1	360.1	276.0
Benson Island	Males	16	-29.97	157.7	218.6	96.75
	Females	34	-107.9	271.97	332.8	210.6
	Combined	50	-83.17	234.2	279.1	189.2
Port Renfrew	Males	40	-63.13	210.7	241.7	179.7
	Females	83	-79.23	230.2	254.1	206.3
	Combined	118	-78.69	229.7	249.9	209.6
Pachena Point	Males	26	-112.4	262.0	325.0	198.9
	Females	46	-46.80	178.1	216.4	139.9
	Combined	72	-67.05	205.0	273.3	172.6
First Beach	Males	37	-105.7	262.7	300.7	224.7
	Females	71	-88.07	234.2	264.4	204.0
	Combined	102	-96.94	248.2	273.0	223.5
Helby Island	Males	46	-80.20	219.8	267.6	172.1
	Females	72	-94.74	244.0	275.9	212.1
	Combined	118	-86.97	231.0	257.0	205.0
Rance Island	Males	75	-90.76	236.6	285.2	188.0
	Females	79	-142.5	305.5	356.2	254.3
	Combined	154	-118.3	274.2	308.1	240.4
Grappler Inlet (bay)	Males	98	-89.45	233.9	261.5	206.4
	Females	179	-117.2	281.0	311.5	250.6
	Combined	275	-100.6	253.2	273.3	233.2

Table 22 (continued)

		N	u	v	Upper 95% c.l. of v	Lower 95% c.l. of v
Haines Island	Males	107	-102.4	253.9	294.3	213.6
	Females	79	-74.60	212.9	243.8	181.9
	Combined	186	-83.80	226.8	250.6	203.0
Grappler Inlet (mud)	Males	26	-78.04	213.6	275.2	152.0
	Females	28	-174.9	369.0	447.7	290.3
	Combined	54	-143.5	317.9	372.6	263.3
Fish Egg Island	Males	20	-74.83	218.2	267.1	169.2
	Females	30	-80.10	233.1	276.3	189.9
	Combined	45	-76.33	224.1	258.1	190.1
Baranof Island	Males	21	-35.31	159.0	182.0	136.0
	Females	21	-41.57	181.3	205.7	156.8
	Combined	23	-38.04	168.1	188.4	147.7
Saginaw Bay	Males	39	-70.46	210.0	255.5	164.4
	Females	24	-103.6	266.3	333.1	199.5
	Combined	62	-94.89	248.0	290.0	206.1
Shelter Island	Males	22	-46.56	174.7	211.9	137.4
	Females	45	-56.23	196.1	224.3	167.9
	Combined	54	-52.45	187.7	213.5	161.9
Cohen Island	Males	13	-166.4	315.4	515.0	115.8
	Females	26	-64.72	185.2	261.9	108.6
	Combined	39	-98.31	229.4	302.5	156.2

for example, Port Renfrew, First Beach and Helby Island. In cases in which the sample sizes are small, where length distributions are different, particularly in the larger size classes, and where one or two large fish in a sample show a large number of cirri and there are no fish of comparable size in the sample for the other sex, the regressions are widely divergent, for example, Benson Island, Cape Beale and Pachena Point.

No consistent differences are apparent between sexes and there is no evidence of a greater number of cirri on fish from more exposed areas. This is borne out by the combined regressions of total cirri vs length for each area. There is variability between areas but it does not follow a pattern consistent with relative exposure.

From the regressions of total cirri number vs age (Figure 17 and Table 23), it is evident again that there is considerable variability, for the same reasons that the length data show variability. Comparison of the regressions does not show any consistent differences between sexes or areas and the regressions for the sexes combined fail to show any consistent differences between areas related to exposure.

The regressions of total cirri number vs age by year-class are simply a good illustration of the hopelessness of constructing regressions on few points (Figure 18 and Table 24). The variability is such that comparisons are rendered

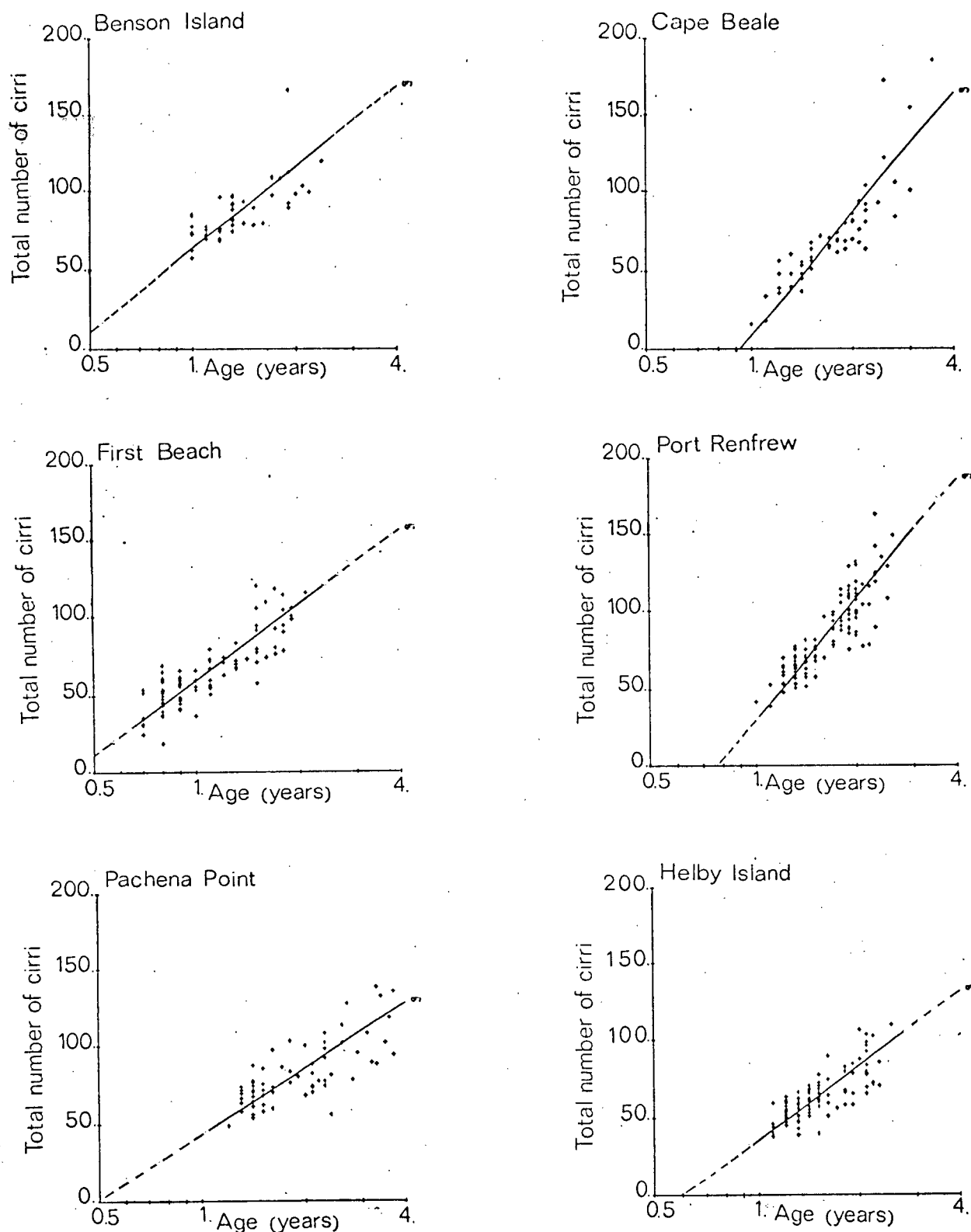


Figure 17 Total cirri-age regressions for O. maculosus from nine areas (males and females combined)

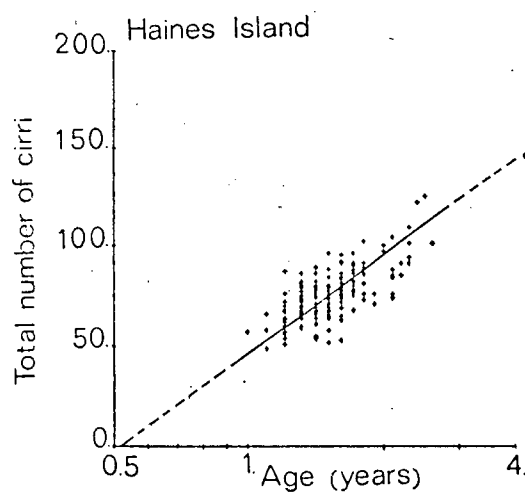
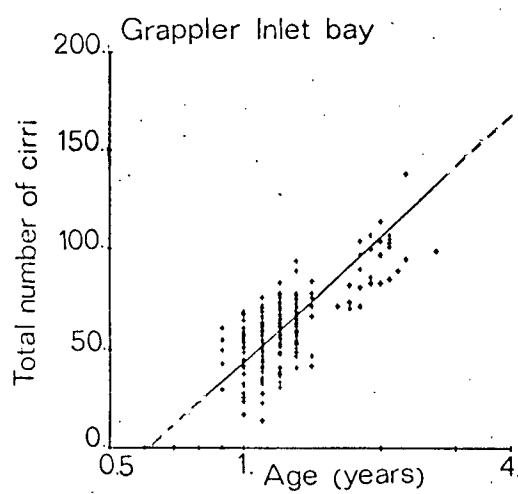
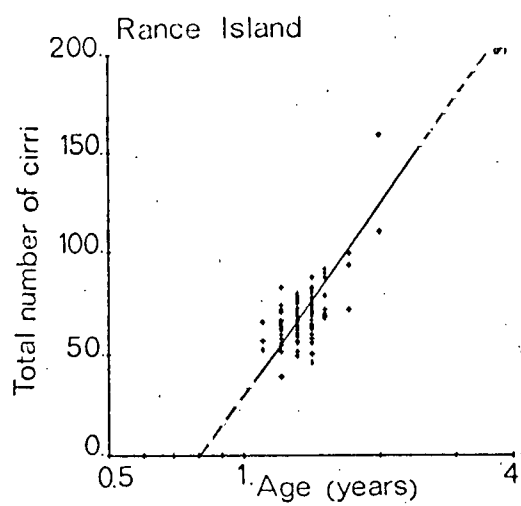


Figure 17 (continued)

Table 23

Oligocottus maculosus (9 areas) total number of cirri - age
functional regression statistics (males, females and sexes combined)

$$\log x \text{ vs } y: y = u + v \log x$$

		N	u	v	Upper 95% c.l. of v	Lower 95% c.l. of v
Cape Beale	Males	25	17.44	214.2	251.3	177.2
	Females	42	9.183	270.4	312.1	228.7
	Combined	58	8.847	256.9	290.9	223.0
Benson Island	Males	16	69.02	117.1	162.8	71.40
	Females	34	62.15	201.5	247.8	155.2
	Combined	50	63.44	174.2	208.1	140.3
Port Renfrew	Males	40	36.66	238.6	273.6	203.5
	Females	83	30.08	259.0	286.3	231.7
	Combined	118	30.45	258.6	281.5	235.6
Pachena Point	Males	26	29.74	176.2	219.1	133.2
	Females	46	48.90	121.8	143.8	95.35
	Combined	72	43.33	139.8	162.1	117.5
First Beach	Males	37	59.67	170.8	197.0	144.6
	Females	71	59.75	150.4	170.4	130.4
	Combined	102	59.60	159.9	176.5	143.4
Helby Island	Males	46	36.08	152.1	185.4	118.8
	Females	72	35.15	166.6	188.6	144.6
	Combined	118	35.82	158.0	175.9	140.1
Rance Island	Males	75	38.95	247.5	299.3	195.7
	Females	79	22.04	352.0	409.7	294.4
	Combined	154	29.73	311.0	349.6	273.0
Grappler Inlet (bay)	Males	98	43.97	190.9	213.8	167.9
	Females	179	42.89	229.3	254.5	204.1
	Combined	275	43.70	206.8	223.4	190.2
Haines Island	Males	107	43.80	182.9	212.3	153.5
	Females	79	48.00	151.8	174.7	128.9
	Combined	186	46.61	162.0	179.7	144.9

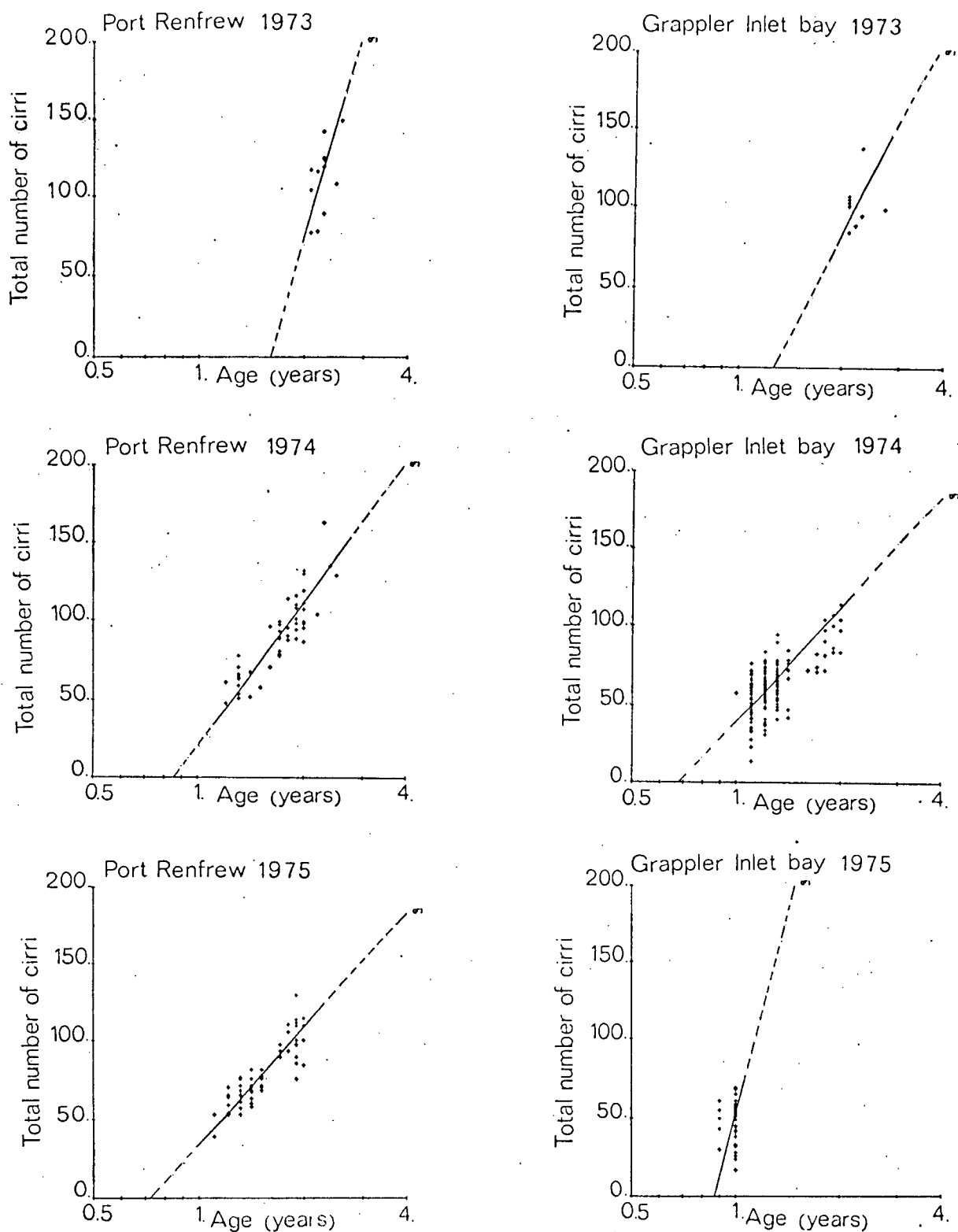


Figure 18 Total cirri-age by year-class regressions for *O. maculosus* from two selected areas (males and females combined)

Table 24

Oligocottus maculosus (9 areas) total number of cirri - age by year-class

functional regression statistics (sexes combined)

$$\log x \text{ vs } y: y = u + v \log x$$

		N	u	v	Upper 95% c.l. of v	Lower 95% c.l. of v
Cape Beale	1974	16	-101.3	533.7	788.2	279.2
	1975	41	23.60	183.2	207.7	158.7
Benson Island	1974	3	-18.21	359.5	2710	-1991
	1975	37	55.91	224.0	278.6	169.4
Port Renfrew	1973	13	-150.4	744.4	1173	315.3
	1974	48	20.80	301.1	344.4	257.8
	1975	56	34.51	245.6	277.0	214.1
Pachena Point	1973	8	-363.4	882.3	1742	22.27
	1974	19	-59.25	395.8	576.5	215.2
	1975	44	34.79	215.3	271.3	159.2
First Beach	1974	29	44.28	231.8	298.7	164.8
	1975	60	60.23	154.7	181.0	128.4
	1976	12	64.43	204.9	338.0	71.78
Helby Island	1974	16	-129.7	637.6	990.9	284.3
	1975	102	35.26	166.9	190.7	143.2
Rance Island	1975	154	29.73	311.3	349.6	273.0
Grappler Inlet (bay)	1973	9	-41.57	417.0	787.6	46.32
	1974	223	39.99	238.1	261.7	214.5
	1975	43	53.45	875.4	1151	599.4
Haines Island	1974	15	-79.95	500.0	708.8	291.3
	1975	170	43.67	183.9	207.5	160.4

impossible.

The analysis of total cirri number by length, age and age by year-class with respect to exposure confirms the increase in number of cirri with length and age. It also indicates that there is a great deal of variability between populations with respect to total cirri number, but that this variability is not a direct function of exposure, as measured by the cement block evaluation of wave action.

3. Experimental manipulation of cirri number

In an attempt to determine experimentally whether the number of cirri is a function of exposure (essentially determined by wave action), equal numbers of juvenile O. maculosus were placed into two separated sides of a large tank, half of which was subjected to almost continuous waves and the other half of which remained calm, except for a constant water inflow.

Methods

A large plywood tank, 183 cm x 122 cm x 31 cm was divided in half lengthways and to a height of 34 cm with a piece of 1.9 cm plywood, to provide "calm" and "exposed" sides of the tank. At one end of the tank on the exposed side a wave tank

was erected (Figure 19).

The wave tank, based on one at the Scripps Institute of Oceanography, was constructed of plexiglass and was supported by and pivoted on two threaded rods passing through the top end of 5 cm x 10 cm wooden uprights screwed to the inside corners of the exposed tank. By drilling a quincunx of holes through each of two 10 cm x 10 cm x 5 cm blocks of plexiglass attached to each side of the wave tank, it was possible to alter the pivoting point of the tank and thus manipulate the amplitude and frequency of the waves. The wave tank was filled with water from an overhead pipe until the maximum equilibrium level was exceeded, at which time the sloping edge of the tank would begin to fall and the water would be emptied out as a wave. The empty tank would then right itself and refill. The tank was positioned for the experiment so that a frequency of one wave every 20 seconds with a volume of approximately 13 cm³ was established. A constant flow of water was maintained into both sides of the tank as far as the seawater system permitted.

The end of the tank at which the wave tank was positioned was raised 10 cm to facilitate the flow of waves to the outlet end of the tank, the last 0.6 m of which was covered with nitex screening to permit fish from being washed out by waves. An identical piece of nitex was fitted to the calm side of the tank, to maintain uniform conditions. On each side of the tank, "shelter" was provided in the form of connected styrofoam egg cartons and a sheet of fruit box packing stapled

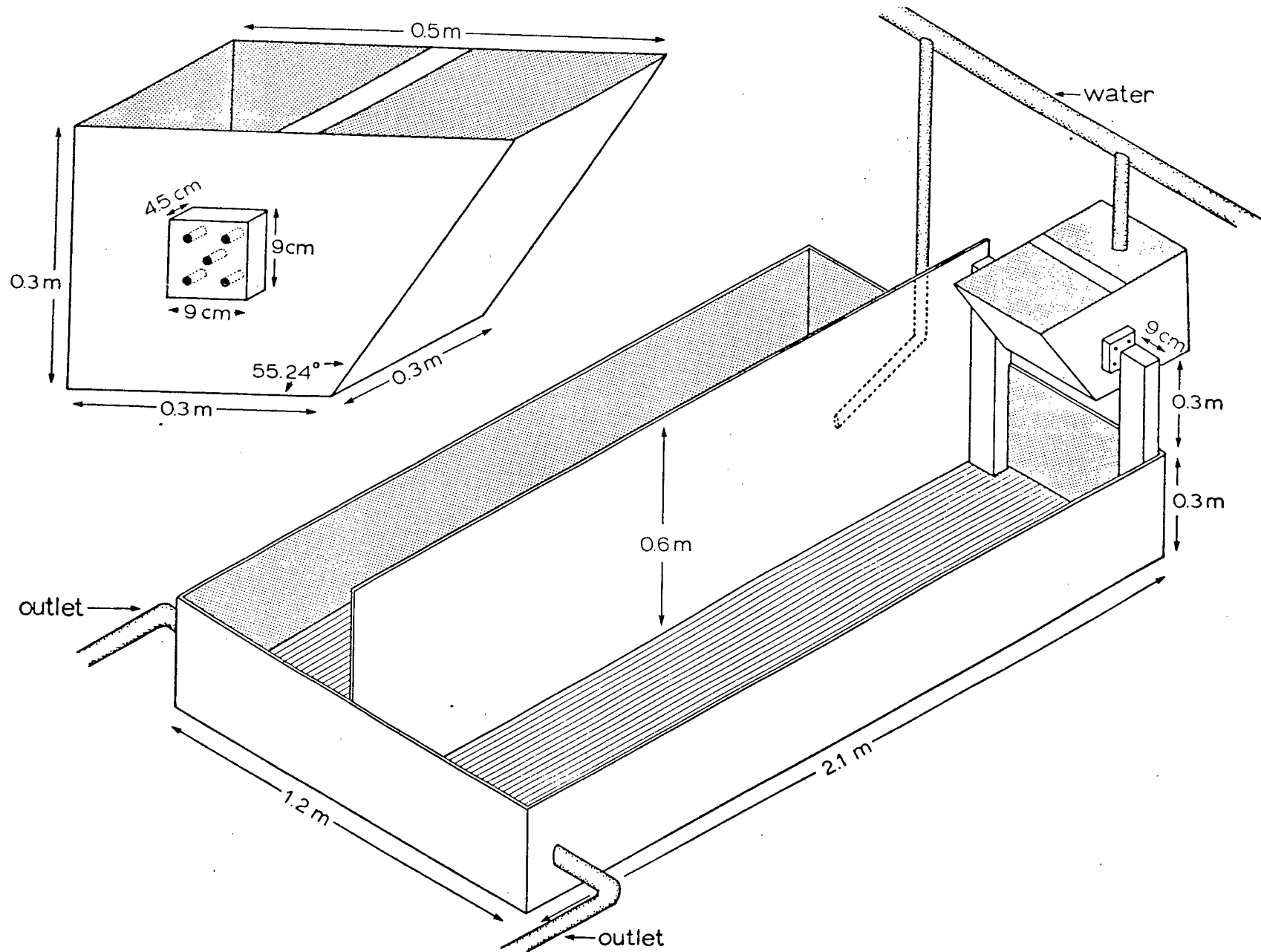


Figure 19 Design of experimental tank showing calm and exposed sides and wave making tank

to the bottom. In addition, ten cement blocks attached to eyebolts anchored in hydraulic cement to 5 bricks were spaced throughout each side of the tank, to determine the relative exposure of each side.

Juvenile O. maculosus were collected from First Beach and divided into three groups. One group was placed in the exposed side of the tank, one in the calm side and the third group was fixed and preserved for cirri counts. Four introductions of fish were made between 6 July and 19 August 1976 giving a total of 102 fish in each of the three groups. The juveniles preserved at the time of introduction were measured (total length) to the nearest 0.005 cm and cirri were examined to provide data on initial cirri nature and distribution for the juvenile fish in the calm and exposed tanks.

The fish remained in the tanks until 16 December 1976, a period of approximately four months, during which time they were fed pieces of mussel (mostly Mytilus californianus but occasionally M. edulis), chopped frozen euphausiids and fresh amphipods. Fresh food was always used in preference to frozen food. To enable the fish in the exposed side of the tank to feed without danger of being washed out of the tank, the water into the wave tank was turned off for several hours each time the fish were fed.

When the fish were removed from each side of the tank

at the conclusion of the experiment, they were fixed and preserved. Subsequently, they were measured (total length) to the nearest 0.005 cm and cirri number and location examined to see if there were any differences between the two groups.

Functional regressions of total cirri vs length were calculated for the fish preserved at the time of introduction and the fish removed from each side of the tank at the conclusion of the experiment. Log to the base 10 transformations of length were made as suggested by the untransformed data.

Although the fish were removed after approximately four months the tank was maintained for a longer period. The cement blocks were removed in May 1977 and the considerable flora and fauna which had developed were removed over a period of several weeks in late August and early September 1977 and identified. The tank was inside from its construction (July) until January, 1977, after which time it was moved outside, thus receiving considerably more light.

Results

Subsequent to this experiment manipulating cirri number, the exposure of the exposed side of the experimental tank relative to other areas in Barkley Sound was shown by the loss of weight of the cement blocks to be about equivalent to that of Grappler Inlet, Rance Island and Helby Island,

significantly more exposed than the calm side of the tank, but significantly less exposed than the majority of tidepool areas.

Inspection of the lists of algae and invertebrates in each side of the tank appears to provide some biological indication of the degree of wave action, since presumably the chance of settlement in either side of the tank was equal (Appendix 3). The kinds of species found also shows the effect of raising deep water (20 m) into a shallow tank exposed to a great deal of light. Many of the species found are not common in the mid to upper intertidal and are characteristically found in the lower intertidal and subtidal.

Comparison of the distributions of cirri with respect to length from the sample preserved at the time of introduction of juvenile O. maculosus into the experimental tank and on fish from First Beach used in cirri analysis shows a considerable difference (Figure 20 and Table 25). This is probably a result of the different length distributions on which the regressions were constructed, since there is very little overlap in length distribution between the two samples.

From the regressions of total cirri vs length of fish from the calm and exposed sides of the experimental tank (Figure 21 and Table 25), it is evident that in both sides of the tank there was high mortality (77% and 84% in the calm and exposed sides respectively). The fact that so few fish survived precludes any definite conclusions.

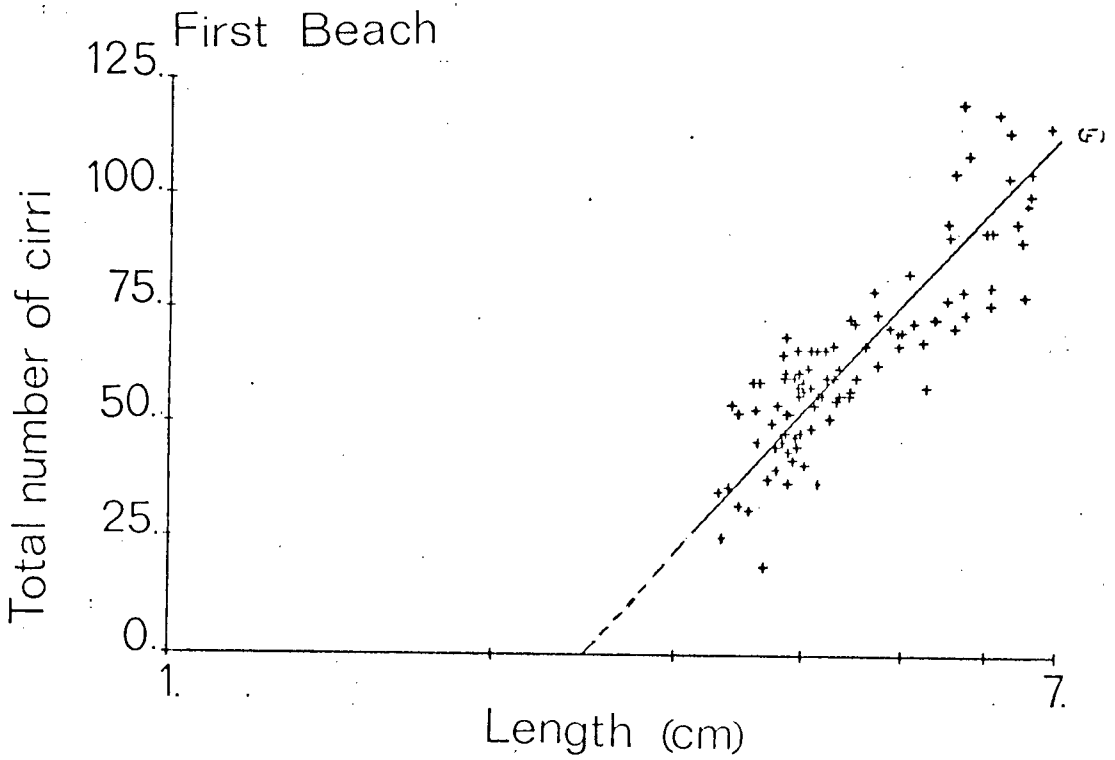
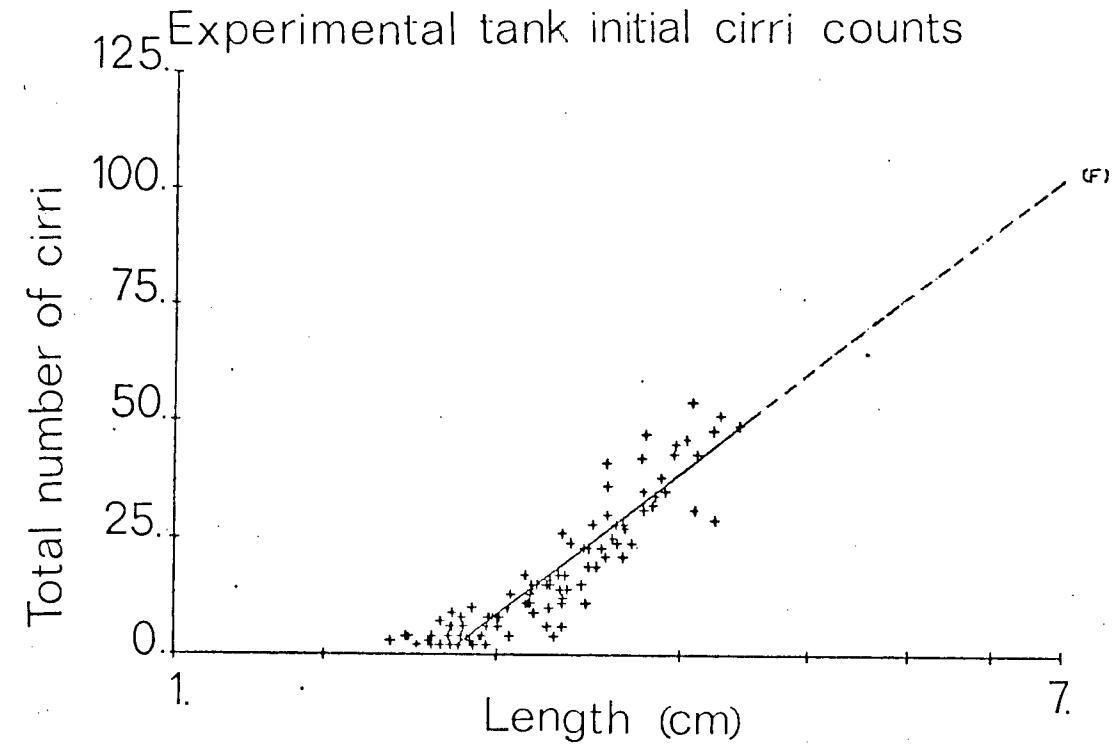


Figure 20 Total cirri-length regressions from O. maculosus introduced into experimental tank and from First Beach

Table 25

Experimental manipulation of cirri in Oligocottus maculosus
 Functional regression statistics (total cirri number - length)
 for initial and final samples and First Beach
 $\log x$ vs y : $y = u + v \log x$

Statistic	First Beach	Initial cirri number	Calm side	Wave side
u	-95.91	-43.27	-154.9	-99.24
v	246.7	172.3	333.0	242.9
Lower 95% confidence limit of v	221.1	157.6	278.3	183.2
Upper 95% confidence limit of v	271.4	186.9	387.7	302.6
N	101	102	23	16

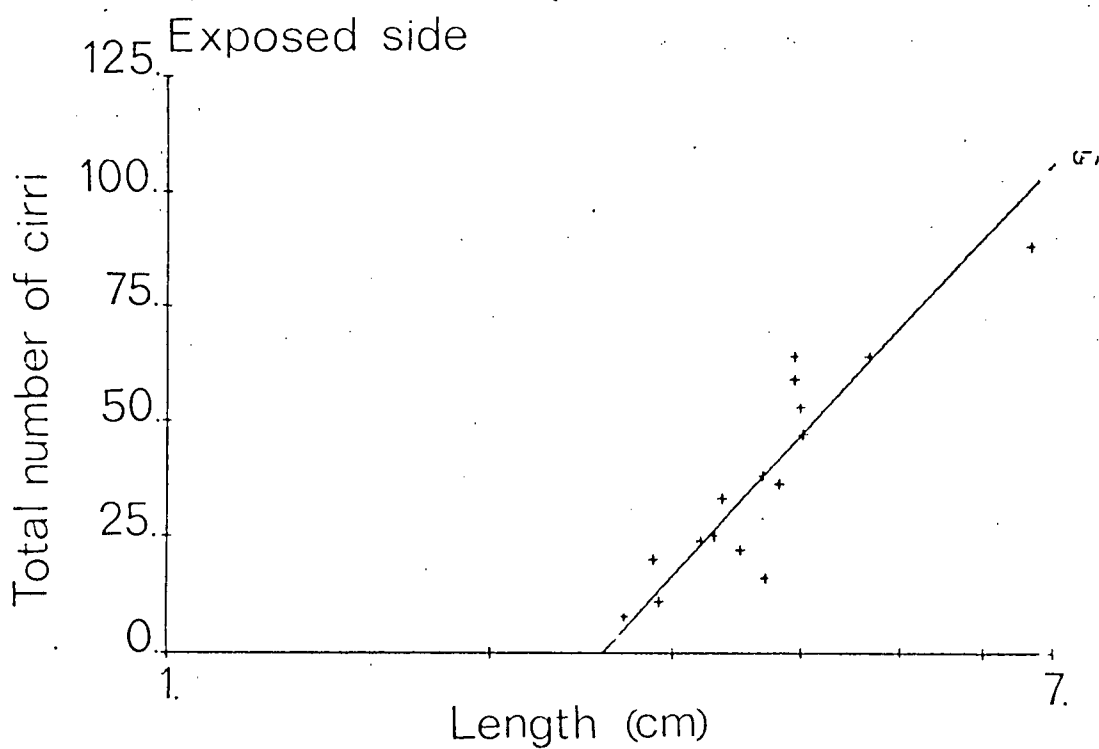
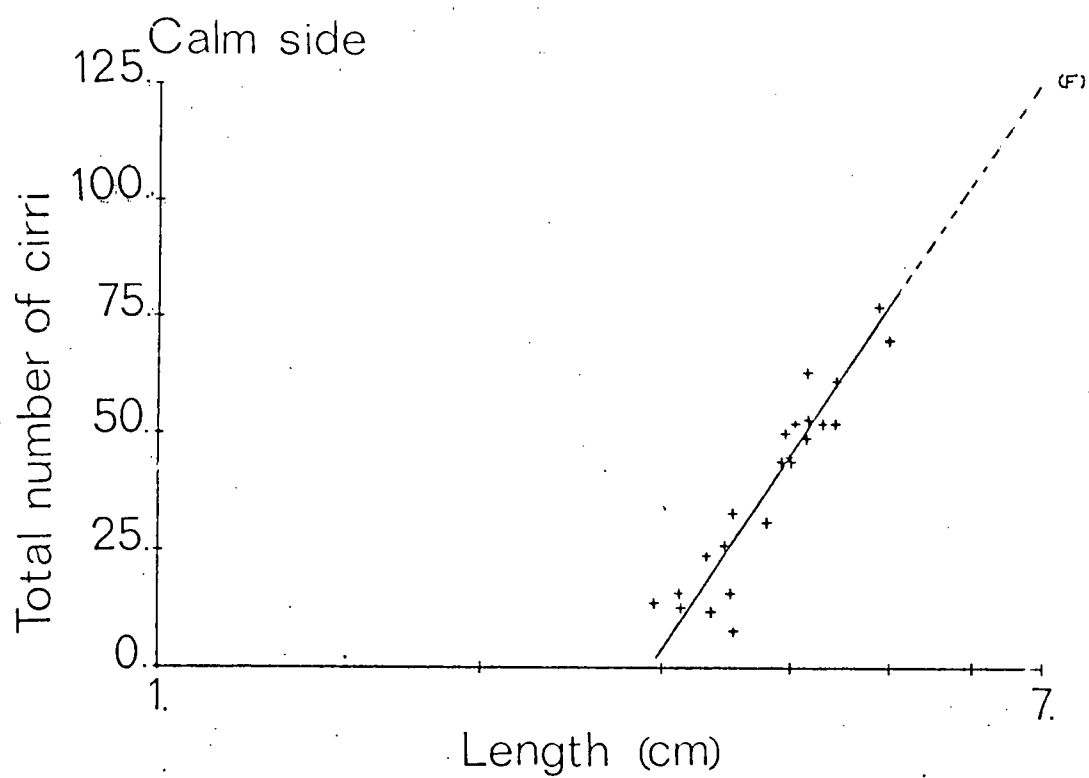


Figure 21 Total cirri-length regressions from O. maculosus in the calm and exposed sides of experimental tank

Comparison of these regressions with the regression of initial cirri counts appears to show that placing the juvenile fish in the experimental tank delayed cirri formation, in both the calm and exposed sides. The prediction that O. maculosus in the exposed side of the tank would produce greater numbers of cirri than in the calm side of the tank is not borne out by the results. Inspection of the 95% confidence limits of v (slope) results in rejection of the null hypothesis. It is interesting to note that the relationship between total cirri number and length shown by fish in the exposed side of the tank bears much closer resemblance to that shown by fish from First Beach than does the relationship shown by fish from the calm side of the tank.

Thus while the exposure of the exposed side of the tank can only be regarded as moderate, and the pattern of cirri formation appears to have been altered somewhat by the experiment, the numbers of cirri found on the small percentages of surviving fish suggest that while wave action may have some influence on the production of cirri, there is not a direct relationship between the degree of wave action and the number of cirri produced.

4. Histological examination of cirri

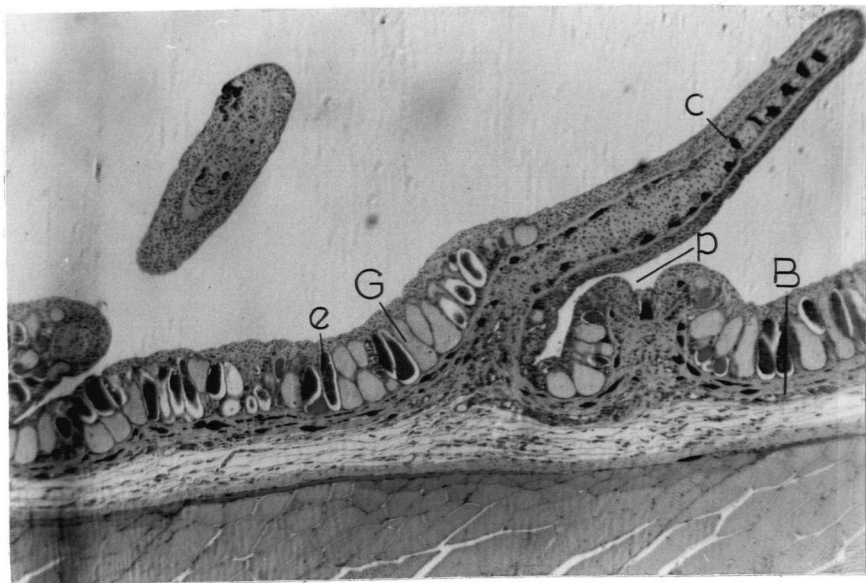
To determine whether cirri contain any sensory receptors such as taste buds, sections of cirri were examined.

Methods

Small pieces of skin bearing cirri were taken from the lateral lines and heads of ten male and female O. maculosus (3.9 to 6.3 cm total length) from First Beach, sectioned and stained with eosin-haemotoxylin and examined. Five of the fish had been kept in 5 ppm Triton-X-100 for seven days in an attempt to destroy chemoreceptors, if any were present.

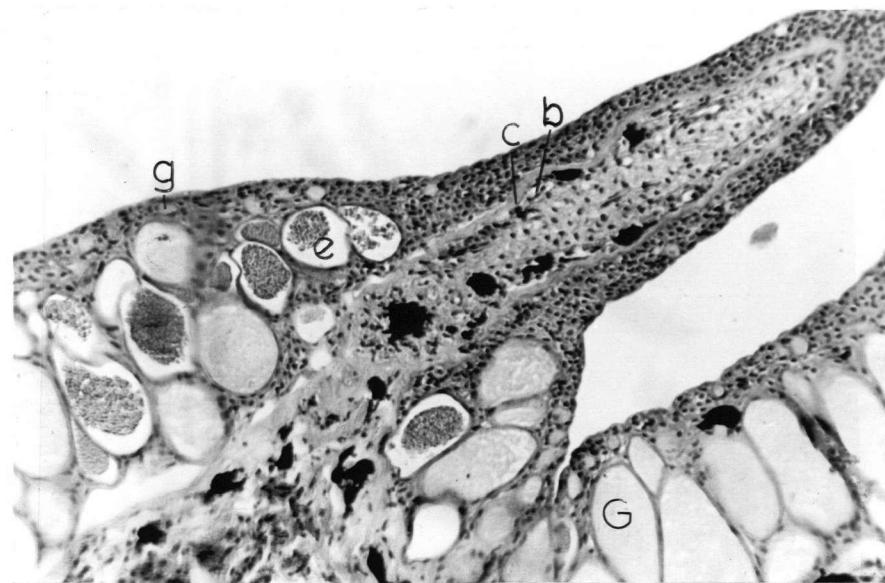
Results

There is no evidence from any of the sections (Figure 22) to suggest the presence of chemoreceptors in the cirri. They seem to be composed of some sort of elastic cartilage (W.S. Marshall, personal communication) surrounded by a layer of chromatophores and the basement membrane of the epithelium. Blood vessels are present in the cartilage. While the epithelium of the skin contains eosinophilic granular cells, large goblet cells and small goblet cells the epithelium of the cirri appears to contain only a few small, scattered goblet



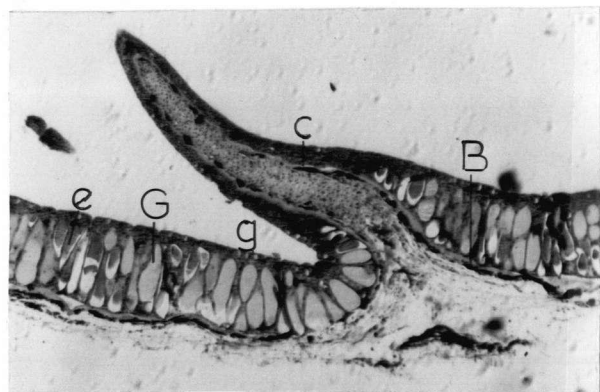
a

0.5mm



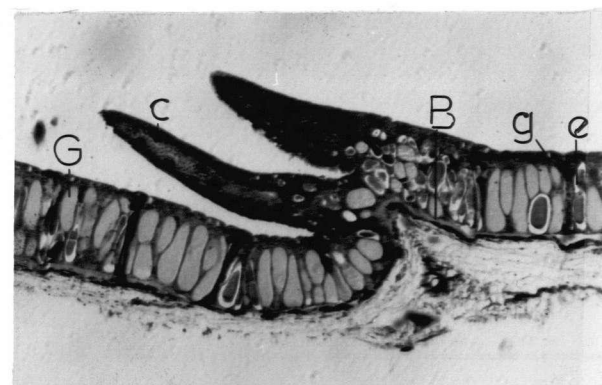
b

0.5 mm



c

0.5 mm



d

0.5 mm

Figure 22 Sections of cirri from lateral line (a, b) and head (c, d) showing small (g) and large (G) goblet cells, eosinophilic granular cells (e), chromatophores (c), blood vessels (b), lateral line pore (p), basement membrane of epithelium (B)

cells, and these seem to occur only towards the base of the cirri. Since the eosinophilic granular cells and the goblet cells are mucous secreting cells (Marshall, 1977) their absence in the cirri epithelium suggests that the cirri may remain uncovered by a mucous coat although the rest of the skin is covered with mucous. Since there appear to be no sensory receptors in the cirri, their function remains unknown.

5. Discussion

The investigation of morphological differences between fish in areas of different exposures produced no evidence to suggest that there are any morphological differences between fish that can be related to exposure. In particular, there appears to be no evidence that there is a greater number of cirri on O. maculosus in more exposed areas. This appeared to be confirmed by the failure of the attempt to manipulate the number of cirri, in the desired direction, by wave action in the laboratory.

The absence of any differences in meristic and morphometric characters between areas was not altogether surprising. Even if the relative placement of sensory receptors is important with respect to homing, selection acts on the totality of attributes possessed by an organism and homing is presumably only one of these attributes. Any relative

differences in the placement of sensory receptors would be small and may have little effect on the perception of clues.

While latitudinal differences in meristic characters have been demonstrated (Hubbs and Hubbs, 1953; Taning, 1952), the difference involved in the study areas on Vancouver Island is less than half a degree. The importance of temperature in determining numbers in meristic characters has been demonstrated (Taning, 1952), but the temperature differences involved here are probably small. Decreased oxygen pressure and increased carbon dioxide pressure, and in some cases, salinity, have been shown to influence meristic characters (Taning, 1952). However, since meristic and morphometric characters are largely determined before hatching, and the larvae are pelagic, differences would not be expected over such a small change in latitude.

Although there were differences in the relationship between cirri and length with different amounts of wave action, the relationship does not take the form of a simple increase in number of cirri with increasing wave action. No record was made of any environmental parameters other than wave action, although one temperature recording in July showed little difference between the sides of the tank (calm side: 9.3-10.2°C, wave side: 9.2-10.2°C). The high mortality observed in both sides of the tank may, however, obscure any possible relationship which may be valid in the field.

There is an increase in the number of cirri with length and age. However, there do not appear to be any obvious differences in the relationship between number of cirri and age by year-classes. The increase in cirri number and branching with length and age has been noted before (Bolin, 1944). In this respect, cirri differ from the majority of morphological characteristics investigated in fish populations where constant proportions or ranges of values are found throughout the length distribution of the species. This study has provided no evidence for (or against) genetic differences in number of cirri, since the members of one year-class may have parents belonging to several year-classes.

The function of the cirri remains unknown. While the presence of structures similar to taste buds in the tentacles and cirri-like structures of other fish, for example, Blennius tentacularis (Schulte and Holl, 1972) and the chemoreceptive sensitivity of catfish barbels (Hoagland, 1933; Bardach et al., 1967) suggested that such a function was likely for the cirri of O. maculosus, this does not appear to be the case. The presence of similar structures on other intertidal and subtidal cottids, for example, Oligocottus snyderi Greeley, O. rimensis (Greeley), Clinocottus embryum (Jordan and Starks), C. globiceps, Dasycottus setiger Bean, Asemichthys taylori Gilbert, Artedius lateralis, A. harringtoni, A. fenestralis Jordan and Gilbert, and agonids, for example, Agonus acipenserinus Tilesius, Asterotheca pentacanthus (Gilbert), A. infraspinata (Gilbert),

Bothragonus swani (Steindachner) (Hart, 1973) makes it interesting to speculate on their function. The most plausible function seems to be some kind of water movement (or possibly pressure) detection. The cirri are flexible structures and on live O. maculosus stand out from the body, such that the movement of water might cause deflections of these appendages. Hoagland (1933) showed that catfish Ameiurus [= Ictalurus] nebulosus (Lesueur) barbels responded to minimal touch or water currents and Bayliss (1914) suggested that the head tentacles of Blennius gattorugine Linnaeus were particularly sensitive to touch. However, further investigation is required to determine the true function of these structures.

VI. OTHER FACTORS AFFECTING VARIABILITY IN HOMING BEHAVIOUR

Since homing ability may change over the life of O. maculosus and it is possible that there may be genetic differences in homing ability, age, length and year-class differences were examined. Particular emphasis was placed on juvenile O. maculosus, since examination of behaviour at the time they first begin to show evidence of area fidelity and homing might be more revealing than examination of the relatively well developed homing behaviour of larger fish.

1. Age

To determine whether the variability in homing behaviour is a function of age the homing performance of untreated fish was examined with respect to age and sex.

Methods

Data on homing behaviour of untreated Oligocottus maculosus used in ten homing experiments over 60 m at First Beach were used for this analysis. Using the age-length regression calculated previously, the ages of fish were determined from the known lengths and the data classified by age and initially by sex. Since it was apparent that there were no differences between sexes, only the combined data were used.

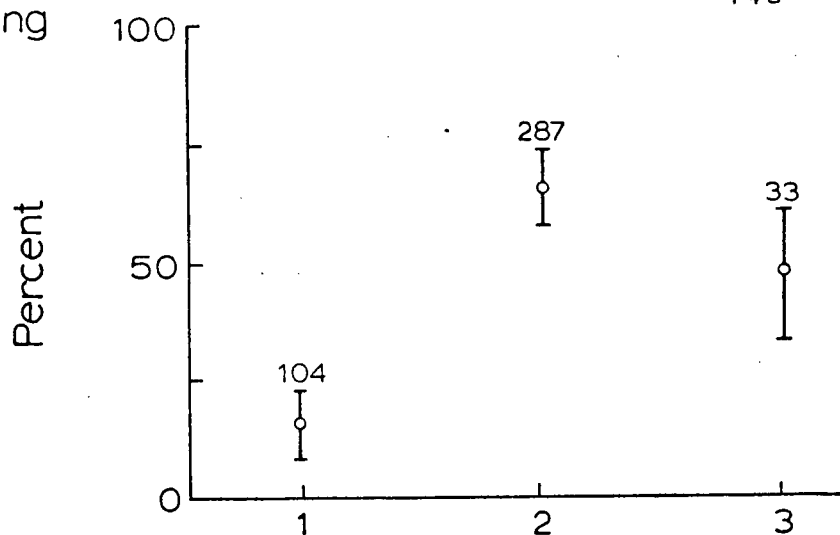
Three analyses were conducted on homing performance for each age group in each experiment: the percentage successfully homing, the percentage remaining in the transplant area and the percentage of successful homers returning to the home pool. To facilitate presentation of the data, the mean percentages and standard errors of the means (Snedecor and Cochran, 1967) were calculated for each analysis in each age group. The mean values are used merely to reflect what is apparent from the individually tabulated percentages, but in a more straightforward manner.

Results

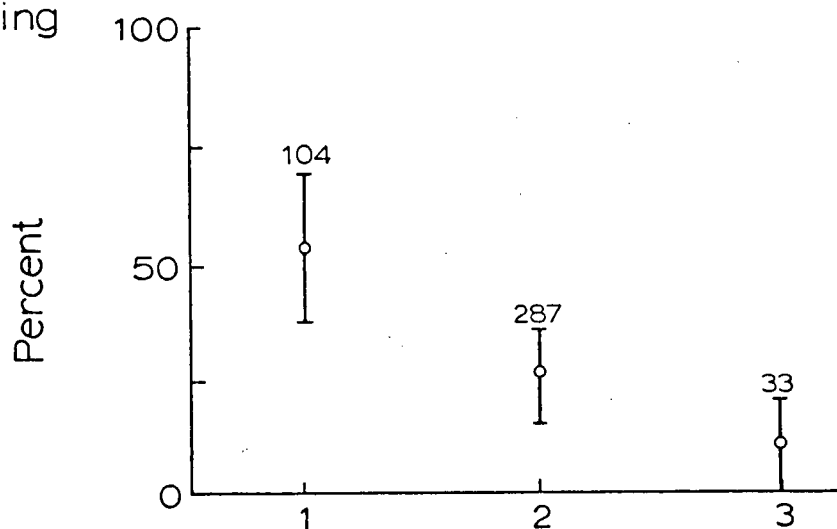
While there is considerable variability between experiments and within age groups (Figure 23 and Table 26), it is evident that one year old fish are relatively poor homers compared with two year old fish, and to a lesser extent, three year old fish. However, of those fish which do home, all age groups appear to show equivalent percentages returning to the home pool, that is equal precision. With respect to O. maculosus remaining in the transplant area, it appears that there is a decline with age in the percentage remaining in the area to which they were transplanted.

These results suggest that at least some of the variability in homing performance is related to the age of the fish under consideration. It is possible that "learning" of

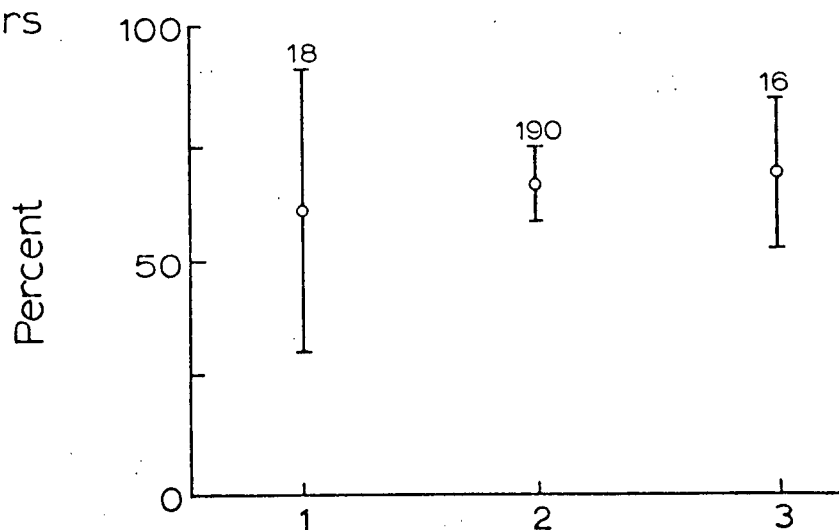
Mean Percentage Homing by Age



Mean Percentage Remaining in the Transplant Area by Age



Mean Percentage of Homers Returning to Home Pool by Age



Age (Years)

Figure 23 Homing performance by age (mean \pm 2 s. e.)

Table 26

Homing performance by age

Date released	26 May 1975	11 Aug 1975	4 Sept 1975	21 Sept 1975	23 Aug 1976	15 Sept 1976	4 July 1977	16 July 1977	5 Aug 1977	9 Aug 1977
Percentage successfully homing										
Age 1										
Number released	13	1	1		13	2	21	15	38	
Percent homed	8	100	100		31	0	19	20	11	
Age 2										
Number released	21	44	59	30	18	17	38	30		30
Percent homed	48	59	78	77	61	82	68	53		60
Age 3										
Number released	8	9	9	3		1	1			2
Percent homed	50	33	56	33		0	100			100
Percentage remaining in transplant area										
Age 1										
Percent remaining	15	0	0		31	50	67	67	66	
Age 2										
Percent remaining	14	14	29	7	22	18	34	53		47
Age 3										
Percent remaining	13	22	0	33		0	0			0
Percentage of homers returning to home pool										
Age 1										
Percent homing to home pool	100	100	100		25		50	33	100	
Age 2										
Percent homing to home pool	60	88	72	57	73	64	69	44		61
Age 3										
Percent homing to home pool	100	67	60	100			0			50

some kind is involved in homing, but divisions of the fish tested simply into age groups are obviously too gross to either account for a great deal of the observed variability or to elucidate the time at which this learning of the area might take place.

2. Year-class

To determine whether the variability in homing behaviour is a result of genetic differences and specifically a function of year-class, the homing performance of untreated fish was examined with respect to year-class and sex.

Methods

Data on homing performance of untreated O. maculosus used in ten displacement experiments over 60 m at First Beach were used in this analysis. Using the ages calculated from age-length regressions, and the year in which the experiment was conducted, a year-class was assigned to each fish. The data on homing behaviour were then analyzed by year-class, and initially, by sex. Again, since there were no sex differences, the data were combined.

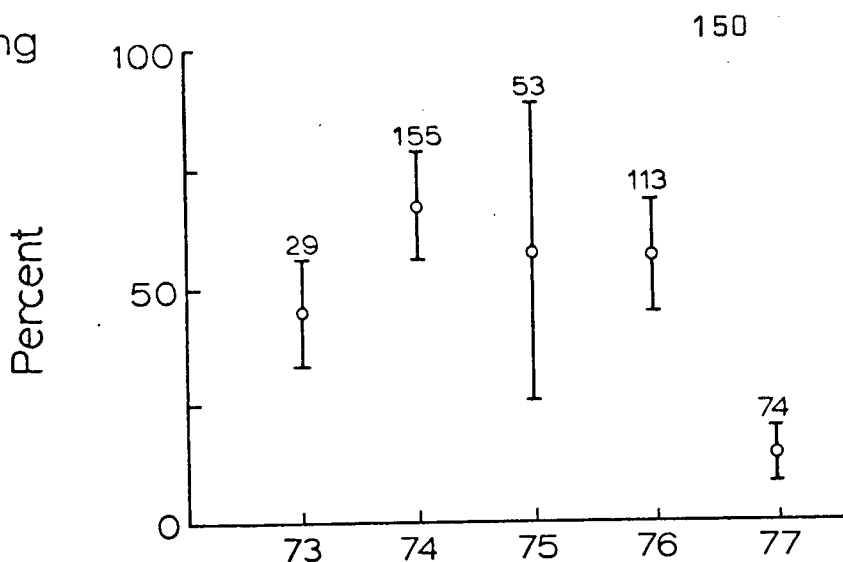
The subsequent analysis conducted on the data was identical to that for the examination of homing performance by

age, except that in this case, the analyses were performed by year-class.

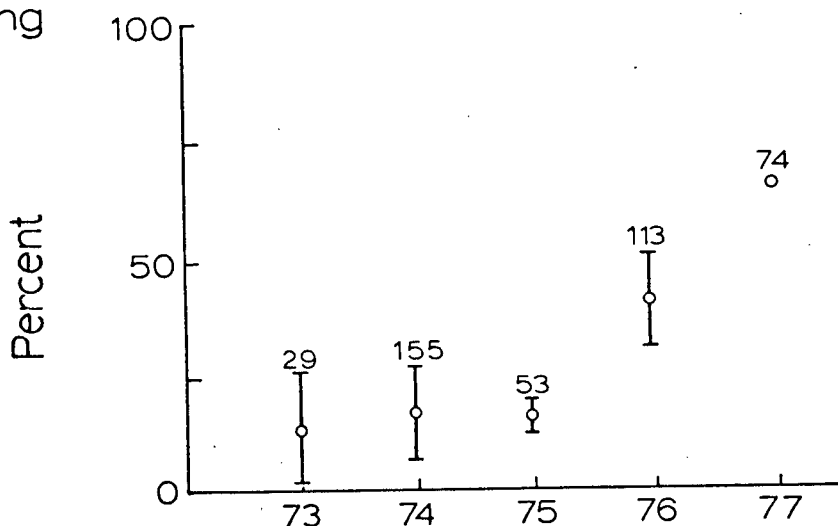
Results

While again there is considerable variability within year-classes and between experiments (Figure 24 and Table 27), it is evident that the only apparent year-class differences in homing performance are a reflection of the age related differences in homing performance. Thus for example, the 1977 year-class which consists of only one year old fish, shows lower percentages homing and greater percentages remaining in the transplant area than the other year-classes. Only two of the year-classes examined (1974 and 1975) contain fish from all three age groups. Thus, in general, there appear to be no year-class differences in homing performance with respect to the three factors examined.

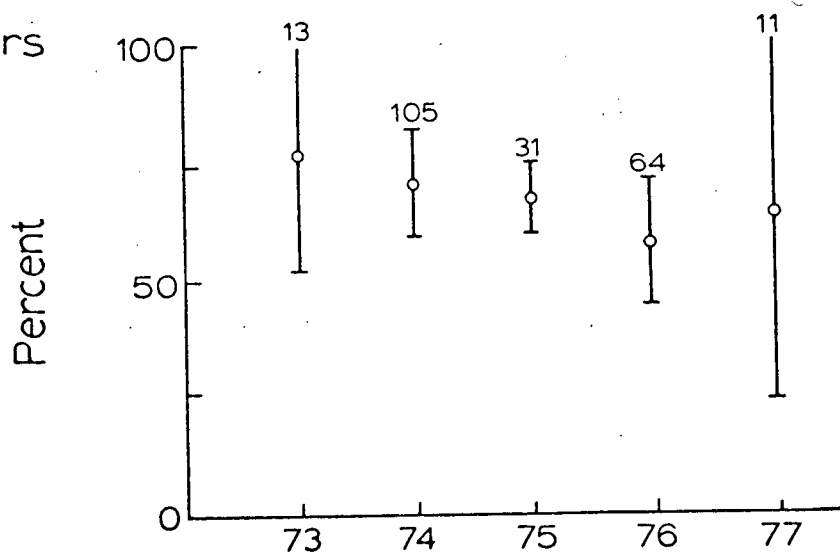
Mean Percentage Homing by Year Class



Mean Percentage Remaining in the Transplant Area by Year Class



Mean Percentage of Homers Returning to Home Pool by Year Class



Year Class

Figure 24 Homing performance by year-class (mean \pm 2 s. e.)

Table 27

a. Homing performance by year-class
(percentages successfully homing)

Date released	26 May 1975	11 Aug 1975	4 Sept 1975	21 Sept 1975	23 Aug 1976	15 Sept 1976	4 July 1977	16 July 1977	5 Aug 1977	9 Aug 1977
Year-class 1977										
Number released							21	15	38	
Percent homed							19	20	11	
Year-class 1976										
Percent released					13	2	38	30		30
Percent homed					31	0	68	53		60
Year-class 1975										
Number released	13	1	1		18	17	1			2
Percent homed	8	100	100		61	82	100			100
Year-class 1974										
Number released	21	44	59	30		1				
Percent homed	48	59	78	77		0				
Year-class 1973										
Number released	8	9	9	3						
Percent homed	50	33	56	33						

Table 27 (continued)

b. Homing performance by year-class
(percentage remaining in transplant area)

Date released	26 May 1975	11 Aug 1975	4 Sept 1975	21 Sept 1975	23 Aug 1976	15 Sept 1976	4 July 1977	16 July 1977	5 Aug 1977	9 Aug 1977
Year-class 1977										
Number released							21	15	38	
Percent stayed							67	67	66	
Year-class 1976										
Percent released					13	2	38	30		30
Percent stayed					31	50	34	53		47
Year-class 1975										
Number released	13	1	1		18	17	1			2
Percent stayed	15	0	0		22	18	0			0
Year-class 1974										
Number released	21	44	59	30		1				
Percent stayed	14	14	29	7		0				
Year-class 1973										
Number released	8	9	9	3						
Percent stayed	13	22	0	33						

Table 27 (continued)

c. Homing performance by year-class
(percentage of homers homing to home pool)

Date released	26 May 1975	11 Aug 1975	4 Sept 1975	21 Sept 1975	23 Aug 1976	15 Sept 1976	4 July 1977	16 July 1977	5 Aug 1977	9 Aug 1977
Year-class 1977										
Number released							21	15	38	
Percent homing to home pool							50	33	100	
Year-class 1976										
Number released					13	2	38	30		30
Percent homing to home pool					25	0	69	44		61
Year-class 1975										
Number released	13	1	1		18	17	1			2
Percent homing to home pool	100	100	100		73	64	0			50
Year-class 1974										
Number released	21	44	59	30		1				
Percent homing to home pool	60	88	72	57		0				
Year-class 1973										
Number released	8	9	9	3						
Percent homing to home pool	100	67	60	100						

3. Length

Since there appears to be an improvement in homing performance with age, homing performance was examined in smaller size classes than are encompassed by one year age groups. This was done to elucidate more precisely the size (and age) at which juvenile fish commence homing, the size classes over which improvement appears to occur and the sizes at which homing is best expressed. Analysis of experiments conducted in the enclosure in Grappler Inlet and homing performance by size classes at First Beach was undertaken. In addition, several experiments at First Beach investigating homing in juvenile fish were conducted. One of these involved removing from the field juvenile O. maculosus which had just moved into lower pools and determining whether on replacement, they showed similar homing capabilities to juveniles which had been in the field for that period of time. Inferior homing ability of the removed fish might imply that "learning" had begun to occur at this time.

Methods

A number of experiments involving the introduction of tagged and untagged O. maculosus into the enclosure were conducted. 172 tagged fish were introduced in seven experiments where attempts were made to examine pool fidelity and homing

behaviour, concentrating on juvenile fish. About another 100 tagged and untagged O. maculosus of all sizes were introduced at varying times to try to establish pool residents, which if untagged but recognizable by individual markings, could later be tagged and experiments conducted on them.

The majority of fish used in the enclosure were collected at First Beach, although a number of juveniles were collected in the bay in Grappler Inlet. Fish used in experiments were measured, sexed where possible, tagged and introduced into various pools in the enclosure. In all but one of the experiments reported, introductions were made with a view to the fish taking up residence in the available pools, determining the size at which they did this and then displacing them to determine at what length they homed. Consequent on this, various investigations of homing behaviour were to be undertaken. One experiment was conducted to determine if survival was affected by residence in the pools; tagged fish were put in a pool and the pool covered with fibreglass window screening. In two experiments juveniles were introduced into the highest pool in the enclosure which would not be covered by high tides for several days. This was undertaken to enhance the chances of fish returning to that pool after several uninterrupted days of residence in it.

Regular monitoring (usually daily and sometimes twice daily at low tides and less frequently at high tides) of pools was conducted to determine the location of introduced fish. The

trough at the front of the enclosure was also examined to determine which fish had followed the receding water line without moving into a pool.

Analysis of homing performance by length classes at First Beach was also undertaken. The data on homing performance from ten displacement experiments over 60 m at First Beach were used in this analysis. Emphasis was placed on fish less than 4.0 cm (total length). This size group was divided into three classes - 2.5 to 2.9 cm, 3.0 to 3.4 cm and 3.5 to 3.9 cm. Larger size classes were examined in 1.0 cm size intervals. In addition to calculating percentages by length class successfully homing, remaining in the transplant area and of homers returning to the home pool for each experiment, the mean percentages and standard errors of the means (Snedecor and Cochran, 1967) were also calculated for each length class. The relationship between size and pool fidelity was investigated by analyzing the data from the three replacement experiments at First Beach by length classes. Percentages found only in the home pool, in the home and nearby pools, in the home range and in distant pools were calculated.

One of the homing experiments included in the above analysis was specifically conducted to examine homing performance of juvenile fish. A total of 38 O. maculosus juveniles (less than 3.4 cm total length) were transplanted to pools approximately 60 m away. Data were collected for five weeks. Percentages homing and remaining in the transplant area

were calculated.

To examine whether "learning" may take place when juvenile fish have just moved into lower pools, three collections of juvenile fish were made from study pools at First Beach. Pools from which collections were made spanned the vertical distribution of study pools at the site. The first two collections involved 24 and 14 O. maculosus between 2.3 and 2.7 cm (total length). These fish were kept in the laboratory for seven and five weeks, respectively, prior to release. The third collection involved 42 O. maculosus between 2.7 and 3.3 cm (total length) which were kept in the laboratory for three weeks prior to release. The second collection initially involved over 30 O. maculosus but a number of these died. The fish in the laboratory were fed almost daily with small pieces of mussel (Mytilus californianus) and chopped mussel was left in the tanks between feeding times. Following tagging, the fish were transplanted about 60 m. Data were collected for four weeks. Percentages homing and remaining in the transplant areas were calculated.

Results

In each of the seven experiments conducted in the enclosure, the movements of the fish were monitored until no tagged fish could be found. It is evident that in all cases few fish were seen after introduction for any length of time (Table

28). It is apparent that there is little difference in the results whether the fish were introduced into high or low tidepools.

In experiments 1 and 4 relatively high percentages of juvenile fish moved from the pool of introduction to the trough at the seaward end of the enclosure prior to disappearing. Only in two experiments (6 and 7) where fish were introduced into the highest tidepool was there any evidence of pool fidelity. However once the pool was well flooded by higher tides, the fish left the pool and enclosure very rapidly.

Results not included in this table from tagged and untagged fish introduced and observed in the enclosure present much the same pattern. Larger fish were rarely found after release and if they were located it was in the trough at the front. Only one introduced adult fish was found on several successive days in one pool. A number of untagged juveniles (recognized by individual markings) were observed for several successive days in various pools, but never for longer than three days.

From these results it is evident that nothing can be concluded about the length at which juvenile fish adopt and home to a tidepool.

The results of the analysis of homing experiments at First Beach (Figure 25 and Table 29) show that while there is considerable variability within and overlap between size

Table 28

Summary of experimental introductions
into tidepool enclosure

Experiment 1					
Date released		19 September 1975			
Length classes(cm)	<3.0	3.0-3.4	3.5-3.9	≥4.0	Total
Number released	6	15	13	0	34
Percent found in release pool	0	7	8		6
Percent found in other pools	0	13	8		9
Percent moved to more seaward pools	0	7	8		6
Percent found in trough	67	53	69		62

1. Fish introduced into all tidepools
 2. No fish seen after 6 days
 3. 2 fish found in bay outside enclosure for 13 days
-

Experiment 2					
Date released		7 October 1975			
Length classes(cm)	<3.0	3.0-3.4	3.5-3.9	≥4.0	Total
Number released	10	23	14	0	47
Percent found in release pool	0	9	0		4
Percent found in other pools	0	9	0		4
Percent moved to more seaward pools	0	9	0		4
Percent found in trough	0	0	7		2

1. Fish introduced into one relatively high pool
 2. No fish seen after 8 days
 3. 2 fish seen in bay once after 8 days
-

Table 28 (continued)

Experiment 3

Date released

2 October 1975

Length classes(cm)	<3.0	3.0-3.4	3.5-3.9	≥4.0	Total
--------------------	------	---------	---------	------	-------

Number released	8	4	3	0	15
-----------------	---	---	---	---	----

Percent found in

release pool

Percent found in

other pools

Percent moved to

more seaward pools

Percent found in

trough

-
1. All fish introduced as controls into one covered pool
 2. All fish survived up to 21 days
 3. After 21 days storm destroyed pool cover and enclosure
-

Experiment 4

Date released

8 July 1976

Length classes(cm)	<3.0	3.0-3.4	3.5-3.9	≥4.0	Total
--------------------	------	---------	---------	------	-------

Number released	10	4	3	8	25
-----------------	----	---	---	---	----

Percent found in release pool	40	25	33	0	24
-------------------------------	----	----	----	---	----

Percent found in other pools	30	0	0	0	8
------------------------------	----	---	---	---	---

Percent moved to more seaward pools	10	0	0	0	4
-------------------------------------	----	---	---	---	---

Percent found in trough	70	50	0	0	36
-------------------------	----	----	---	---	----

-
1. Fish introduced into highest pool
 2. No fish seen after 7 days
-

Table 28 (continued)

Experiment 5

Date released

19 July 1976

Length classes(cm)	<3.0	3.0-3.4	3.5-3.9	≥4.0	Total
Number released	0	2	1	8	11
Percent found in release pool		0	0	0	0
Percent found in other pools		0	0	25	18
Percent moved to more seaward pools		0	0	25	18
Percent found in trough		0	0	25	18

1. Fish introduced into second highest tidepool
 2. No fish seen after 14 days
-

Experiment 6

Date released

24 July 1976

Length classes(cm)	<3.0	3.0-3.4	3.5-3.9	≥4.0	Total
Number released	8	12	0	0	20
Percent found in release pool	100	75			85
Percent found in other pools	0	8			5
Percent moved to more seaward pools	0	8			5
Percent found in trough	0	0			0

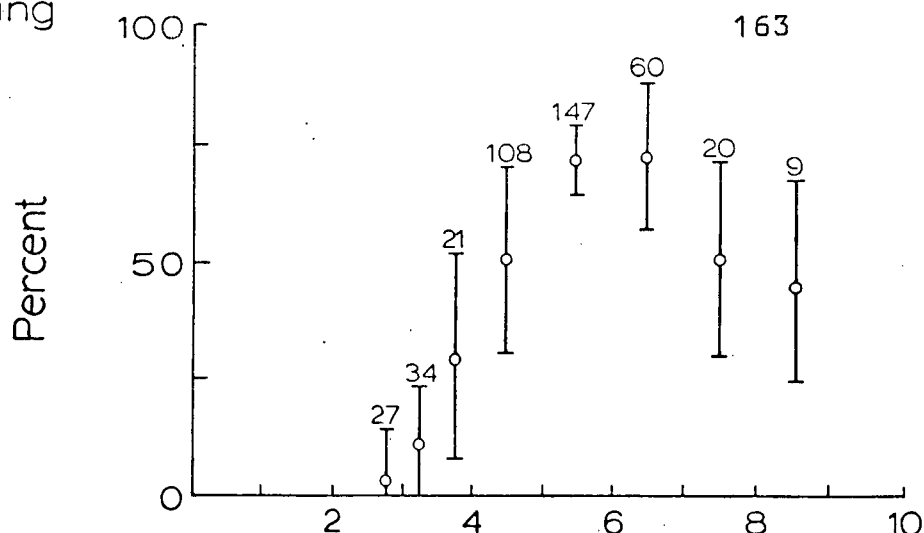
1. Fish introduced into highest pool
 2. No fish seen after 14 days
-

Table 28 (continued)

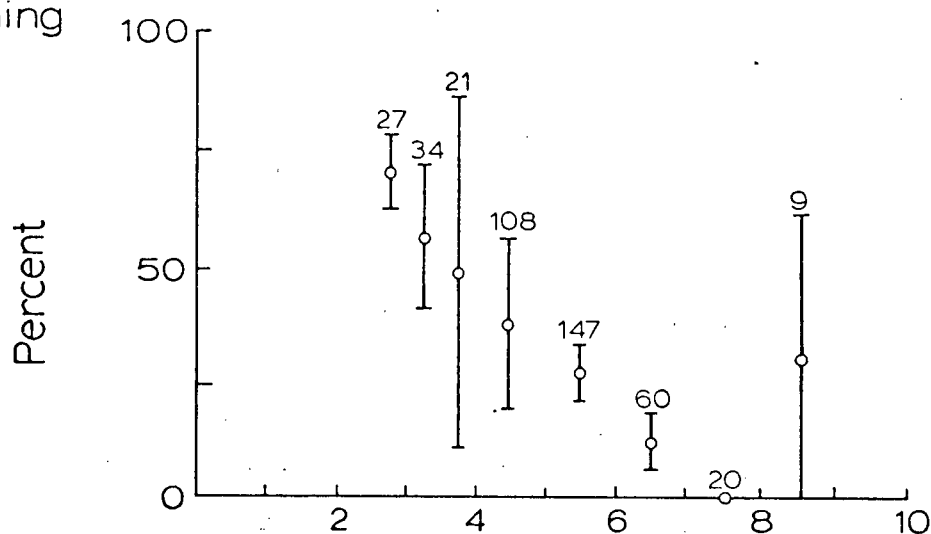
Experiment 7					
Date released	10 August 1976				
Length classes (cm)	<3.0	3.0-3.4	3.5-3.9	≥4.0	Total
Number released	6	9	5	0	20
Percent found in release pool	100	100	100		100
Percent found in other pools	0	0	0		0
Percent moved to more seaward pools	0	0	0		0
Percent found in trough	0	0	0		0

1. Fish introduced into highest tidepool
 2. No fish seen after 3 days
-

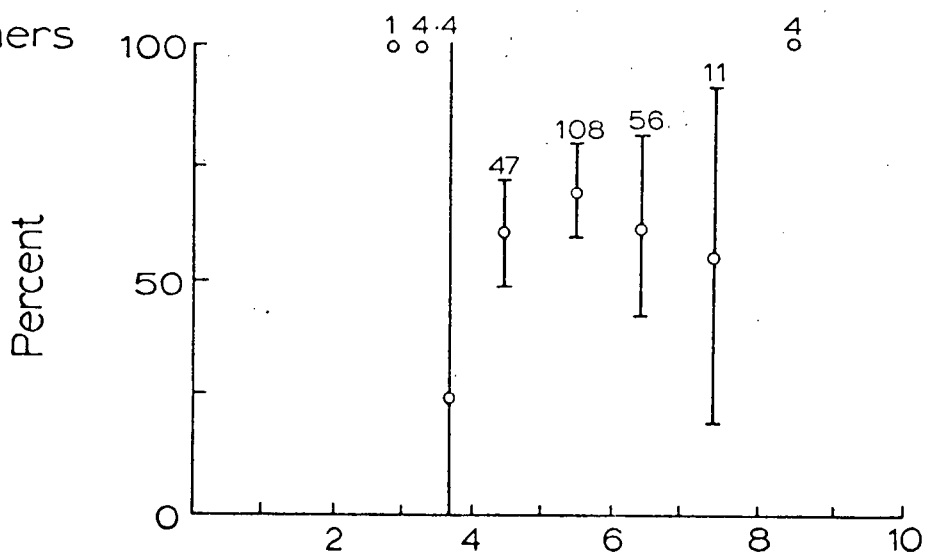
Mean Percentage Homing by Length Class



Mean Percentage Remaining in the Transplant Area by Length Class



Mean Percentage of Homers Returning to Home Pool by Length Class



Length (cm)

Figure 25 Homing performance by size classes (mean \pm 2 s. e.)

Table 29

a. Homing performance by length classes
(percentage successfully homing)

Date released		26 May 1975	11 Aug 1975	4 Sept 1975	21 Sept 1975	23 Aug 1976	15 Sept 1976	4 July 1976	16 July 1977	5 Aug 1977	9 Aug 1977
Length class (cm)											
2.5 - 2.9	Number released	1	0	0	0	0	0	5	4	17	0
	Percent homed	0						0	25	0	
3.0 - 3.4	Number released	0	0	0	0	5	0	6	2	21	0
	Percent homed					0		0	0	19	
3.5 - 3.9	Number released	5	0	0	0	6	0	5	5	0	0
	Percent homed	0				50		20	40		
4.0 - 4.9	Number released	18	9	16	3	3	2	25	24	0	6
	Percent homed	17	78	93	100	33	0	56	38		33
5.0 - 5.9	Number released	4	31	26	21	13	7	13	8	0	24
	Percent homed	100	61	69	76	62	86	92	75		67
6.0 - 6.9	Number released	6	7	18	7	4	10	6	2	0	0
	Percent homed	67	29	89	71	75	80	67	50		
7.0 - 7.9	Number released	4	6	6	1	0	1	0	0	0	2
	Percent homed	50	33	67	0		0				100
8.0 - 8.9	Number released	4	1	3	1	0	0	0	0	0	0
	Percent homed	50	100	33	0						

Table 29 (continued)

b. Homing performance by length classes
(percentage remaining in transplant area)

Date released		26 May 1975	11 Aug 1975	4 Sept 1975	21 Sept 1975	23 Aug 1976	15 Sept 1976	4 July 1976	16 July 1977	5 Aug 1977	9 Aug 1977
Length class (cm)											
2.5 - 2.9	Number released	1	0	0	0	0	0	5	4	17	0
	Percent stayed	0						80	75	71	
3.0 - 3.4	Number released	0	0	0	0	5	0	6	2	21	0
	Percent stayed					20		67	50	62	
3.5 - 3.9	Number released	5	0	0	0	6	0	5	5	0	0
	Percent stayed	0				33		80	80		
4.0 - 4.9	Number released	18	9	16	3	3	2	25	24	0	6
	Percent stayed	17	0	31	0	33	50	48	63		50
5.0 - 5.9	Number released	4	31	26	21	13	7	13	8	0	24
	Percent stayed	25	19	35	48	31	14	23	25		46
6.0 - 6.9	Number released	6	7	18	7	4	10	6	2	0	0
	Percent stayed	17	14	17	0	0	20	67	50		
7.0 - 7.9	Number released	4	6	6	1	0	1	0	0	0	2
	Percent stayed	0	0	0	0		0				0
8.0 - 8.9	Number released	4	1	3	1	0	0	0	0	0	0
	Percent stayed	25	100	0	100						

Table 29 (continued)

c. Homing performance by length classes
(percentage of homers homing to home pool)

Date released		26 May 1975	11 Aug 1975	4 Sept 1975	21 Sept 1975	23 Aug 1976	15 Sept 1976	4 July 1976	16 July 1977	5 Aug 1977	9 Aug 1977
Length class (cm)											
2.5 - 2.9	Number released	1	0	0	0	0	0	5	4	17	0
	Percent homing to home pool								100		
3.0 - 3.4	Number released	0	0	0	0	5	0	6	2	21	0
	Percent homing to home pool									100	
3.5 - 3.9	Number released	5	0	0	0	6	0	5	5	0	0
	Percent homing to home pool					0		100	0		
4.0 - 4.9	Number released	18	9	16	3	3	2	25	24	0	6
	Percent homing to home pool	33	71	60	33	100		71	50		50
5.0 - 5.9	Number released	4	31	26	21	13	7	13	8	0	24
	Percent homing to home pool	75	89	61	63	88	83	58	50		63
6.0 - 6.9	Number released	6	7	18	7	4	10	6	2	0	0
	Percent homing to home pool	75	100	88	100	33	50	50	0		
7.0 - 7.9	Number released	4	6	6	1	0	1	0	0	0	2
	Percent homing to home pool	100	50	50							50
8.0 - 8.9	Number released	4	1	3	1	0	0	0	0	0	0
	Percent homing to home pool	100	100	100							

classes, there is a definite improvement in homing performance with size from about 2.5 to 5.0 cm. Between 5.0 and 7.0 cm homing is best exhibited. Older fish (7.0 to 9.0 cm) appear to show some decline in homing performance. Despite the small sample sizes for smaller fish, it generally appears to be true that of those fish which home, all size classes show about the same ability to return to a small area from a considerable distance.

The mean percentages remaining in the transplant area by length show a smaller percentages of fish remaining in the transplant areas with increasing size, except for the largest size class found at First Beach. Again, these data show considerable variation within and between length classes, but the relatively greater variability shown in the 3.5 to 3.9 cm size class, the size at which any sizeable percentage of fish are beginning to home, may reflect the differing stages of development of homing ability within this length range.

Analysis of the data, by length classes, from replacement experiments (Table 30) suggests that home range fidelity is not well developed in juvenile fish compared with large fish.

From Table 31 it is evident that the percentage of successful juvenile fish homing is small and that while the majority of fish remain in the transplant area for some period of time, many subsequently move elsewhere. The results appear

Table 30

Analysis of replacement experiments by length

Date released	28 May & 2 June 1975				30 June 1977				9 August 1977																		
Length class (cm)																											
3.0 - 3.4	Number released				9																						
	Percent found in home pool only					44																					
	Percent found in home and near pools						11																				
	Percent found in home range							56																			
	Percent found in distant pools								0																		
3.5 - 3.9	Number released				4				18																		
	Percent found in home pool only				25				28																		
	Percent found in home and near pools					0				56																	
	Percent found in home range					25					83																
	Percent found in distant pools					0						11															
4.0 - 4.9	Number released				17				34				15														
	Percent found in home pool only					35				38					40												
	Percent found in home and near pools						24					59					33										
	Percent found in home range							59						97					73								
	Percent found in distant pools							6							0												
5.0 - 5.9	Number released				4				13				25														
	Percent found in home pool only					0				38					40												
	Percent found in home and near pools						100					54					44										
	Percent found in home range							100						92					84								
	Percent found in distant pools							0							0												
6.0 - 6.9	Number released				3				1				4														
	Percent found in home pool only					33					0					25											
	Percent found in home and near pools						0						100					50									
	Percent found in home range							33						100					75								
	Percent found in distant pools							33							0												
7.0 - 7.9	Number released				4				1																		
	Percent found in home pool only					75					0																
	Percent found in home and near pools						0						100														
	Percent found in home range							75							100												
	Percent found in distant pools							0								0											
8.0 - 8.9	Number released				1																						
	Percent found in home pool only					0																					
	Percent found in home and near pools						100																				
	Percent found in home range							100																			
	Percent found in distant pools							0																			

Table 31.

Homing performance of juvenile Oligocottus maculosus.

Length class (cm)	2.5 - 2.9	3.0 - 3.4	Total
-------------------	-----------	-----------	-------

Date released	5 August 1977		
---------------	---------------	--	--

Number released	17	21	38
-----------------	----	----	----

Number homed	0	4	4
--------------	---	---	---

Percent homed	0	19	11
---------------	---	----	----

Number staying in transplant area	12	13	25
--------------------------------------	----	----	----

Percent staying in transplant area	71	62	66
---------------------------------------	----	----	----

Days staying in
transplant area

a. homers

1, 4, 6, 6

b. non-homers

1, 1, 1, 1,

1, 1, 2, 2,

1, 1, 1, 2,

6, 7, 7, 12,

5, 7, 12, 16

39

Percent of homers
homing to home
pool

100

100

to suggest that homing behaviour is not possible for fish less than about 3.0 cm, at which length a small percentage are beginning to show homing behaviour. Taken in conjunction with the analysis of pool fidelity data by length classes, the apparent inability of small O. maculosus to home may be associated with the absence of home range fidelity, that is, homing behaviour is not demonstrated until a home range has been established.

Table 32 shows that O. maculosus which were between 2.3 and 2.7 cm when collected were unable to home after being kept in the laboratory for five and seven weeks. Fish between 2.7 and 3.3 cm when collected and kept in the laboratory for three weeks showed some evidence of being able to home.

The number of fish seen after release given the small percentage homing was surprisingly high, in view of the fact that if homing was not undertaken, presumably the fish were moving around between tidepools and could have moved almost anywhere on the beach. Of the fish seen after release more than once in the transplant area the majority moved around widely between pools in the transplant area rather than remaining in the one pool. The amount of movement was comparable to that of adults from high tidepools, that is they showed a wider range of movement than the residents of the pools into which they were introduced. Of all the fish released only seven (all of which were 2.9 cm or greater in size) showed any evidence of strict pool fidelity.

Table 32

Homing performance of juvenile Oligocottus maculosus kept in the laboratory for varying periods of time prior to release

Length class (cm) when released	2.5-2.9	3.0-3.4	3.5-3.9	Total
------------------------------------	---------	---------	---------	-------

Date released	19 August 1977
---------------	----------------

Group A

Number released	17	7	0	24
Percent homed	0	0		0
Percent stayed in transplant area	47	71		54

Group B

Number released	9	5	0	14
Percent homed	0	0		0
Percent stayed in transplant area	67	60		64

Group C

Number released	12	29	2	43
Percent homed	17	14	0	14
Percent stayed in transplant area	42	62	50	56

Time in laboratory

Size when collected

Group A	7 weeks	2.3 - 2.7 cm
Group B	5 weeks	2.3 - 2.7 cm
Group C	3 weeks	2.7 - 3.3 cm

Previous experiments showed that O. maculosus are beginning to show evidence of home range fidelity between 2.5 and 3.0 cm, and to a greater degree between 3.0 and 3.4 cm. Homing behaviour also begins to become evident in these size classes of fish (2.5 to 2.9 cm - one fish out of 27 (2.9 cm); 3.0 to 3.4 cm - four fish out of 34). Since removal of O. maculosus from the field at this time (Groups A and B) resulted in their being unable to home when replaced, whereas larger fish (Group C) were able to home when replaced, it appears that "learning" of the intertidal and adoption of a home range begins to occur during this period of time.

4. Discussion

Differences in homing behaviour between year-classes are not apparent. Atkinson (1939) suggested, on the basis of three distinct modes in the diameter frequencies of ova from a mature female, that O. maculosus may spawn more than once a year. If this is the case, and since O. maculosus probably spawn over several years, any genetically related differences in homing behaviour would be difficult to distinguish.

Age related differences in homing behaviour are apparent, although the division into only three age groups is too gross to provide much indication of the stage at which fish

are learning to display successful homing behaviour and pool fidelity. It is evident that there is an increase in the percentage of successful homers between age one and two and some decline in age three fish, although of the fish which do home, all age groups home with equal precision. There is a decline in the number of fish remaining in the transplant area with age.

Examination of homing behaviour by smaller size classes reveals the relationship between homing behaviour and age in much greater detail. Juvenile fish do not appear to adopt a home range or start homing to it until they are about 2.8 to 3.0 cm long. Between this size and about 5 cm they show increasingly better developed home range fidelity and homing performance. The highest percentages successfully homing occur in fish between 5.0 and 7.0 cm. There appears to be some decline in percentages homing with larger fish. All size classes appear to home with equal precision. Percentages remaining in the transplant area show a decline with length, except for the largest size class.

It appears that juvenile fish (greater than about 2 cm), having moved into lower pools from the high tidepools in which they settle, show fairly extensive movement between tidepools, prior to adopting a home range and demonstrating homing behaviour. "Learning" and "memorizing" the area appear to begin when the fish are about 2.3 to 2.7 cm long. Removal from the field of O. maculosus which are greater than 2.7 cm does not appear to affect homing performance, relative to fish

of the same size which have always been in the field. It is suggested that juveniles move extensively between pools up to about 3 cm, and to a lesser extent, up to about 4 cm.

Although the low tide distribution of juvenile O. maculosus provides evidence of extensive movement between pools, Green's (1971b) work suggests that high tide movements may be even more extensive in some cases. He found that fish less than 5.5 cm in some sheltered and moderately sheltered areas were the only group to show an almost complete tidal shift in their vertical distribution, moving shorewards with the advancing tide and seawards with the falling tide. If this is the case, information acquisition, at least for fish in sheltered areas, may continue to occur until the fish are quite large.

The decline in the percentage successfully homing and increase in the percentage remaining in the transplant area in the largest size classes of fish may be due to the small sample sizes, impaired "memory", reduced swimming abilities, or some combination of these factors. Gerking (1957) found that faster growing fish tend to mature earlier and also become senile and die earlier than slower growing fish of the same brood. Since Port Renfrew O. maculosus do not appear to show any decline in the percentage of successful homers in the largest size classes (Green, 1967; Khoo, 1971) and since the data from this study suggests that they grow more slowly, perhaps the earlier onset of senility is a factor in the decline in homing performance in

the largest fish at First Beach.

A reduced rate of growth in Port Renfrew fish relative to First Beach fish may also account for the absence of any difference in homing performance in the smaller size classes. Since age or time is presumably more important with respect to learning information than actual length, it is probable that by the time O. maculosus at Port Renfrew are 4 cm long the majority have had sufficient time to acquire the information to home with ability comparable to that of larger First Beach fish. Thus examination of homing performance of smaller size classes of fish (less than 4 cm) may be necessary to determine the size and age at which Port Renfrew fish adopt a home pool and start homing to it. Another factor which may be of relevance here is the topography of the two areas, and its apparent effect on pool fidelity discussed earlier. Port Renfrew O. maculosus move more freely between pools than First Beach O. maculosus and may acquire information earlier since the beach is less irregular.

Investigation of the homing performance of another cottid, Clinocottus globiceps, by size classes showed no differences (Green, 1973). A similar situation was found to exist in the homing performance of Tautogolabrus adspersus (Green, 1975). Gibson (1967) showed that juvenile Blennius pholis (less than 5 cm) display the same degree of pool fidelity as adults but that juvenile Acanthocottus [= Enophrys] bubalis (less than 5 cm) appeared to show less pool fidelity than adults. Williams (1957) found no size differences (between 36

and 100+ mm) in pool fidelity of Clinocottus analis, although analysis of his data shows an increase in the percentage disappearing after tagging, with size. This was also true for Girella nigricans. Although he did not tag any C. analis less than 36 mm, fin clipping showed that fish as small as 11 mm were found in the same pools. Although Williams provides some evidence to suggest short term pool fidelity occurs in small Girella nigricans (23 to 28 mm long), long term pool fidelity of this size group was not exhibited. Both these fish move to deeper subtidal water as they increase in size, which suggests that pool fidelity changes over the life of the fish.

In freshwater fish, Larimore (1952) showed that smallmouth bass Micropterus dolomieu Lacepede larger than 25.4 cm showed higher rates of return than smaller fish. Complementary evidence was provided by Funk (1957) who found that bass up to 33 cm were increasingly mobile but the number of mobile individuals declined sharply in larger fish. Funk also showed different degrees of mobility according to size in rock bass, Ambloplites rupestris (Rafinesque) and channel catfish Ictalurus punctatus (Rafinesque), greatest mobility being shown by intermediate size classes in both species.

VII. SENSORY MECHANISMS INVOLVED IN HOMING BEHAVIOUR

1. Sensory impairment methods

Vision

Fish were blinded according to the method used by Khoo (1971). A slit was made in the cornea of the eyeball with a sharp scalpel and the sides of the eyeball were pressed with forceps until the lens emerged. The lens was then removed. Although perception of light and dark is possible shortly after lens removal, both the retina and the optic nerve ultimately degenerate (Rasquin, 1949).

When this operation was performed in 1976, fish were anaesthetized in quinaldine (1 ml per 4.5 litres). Recovery from the operation seemed good as indicated by survival in both the field and laboratory. As experience was gained in the technique, use of anaesthetic only increased handling time; no difference in recovery from the operation was observed between anaesthetized fish and those which were not anaesthetized. In experiments conducted in 1977 no anaesthetic was used.

Olfaction

Several methods were attempted to make fish anosmic. Initially heat cauterization was used (Khoo, 1971). A red hot needle was inserted into the anterior nares and moved into the position of the olfactory rosette. Fish were anaesthetized in quinaldine prior to the operation.

Recovery from the operation appeared to be satisfactory, as indicated by survival both in the field and laboratory. Examination of olfactory rosettes of six O. maculosus which had undergone this treatment showed destruction of the rosette. However, since it is impossible to examine each fish in this regard prior to release, it is possible that not all released fish were fully anosmic after treatment.

To overcome the problem of the uncertainty of the total destruction of the olfactory rosettes, several other methods were attempted to make the fish anosmic. Cutting of the olfactory nerve was attempted but was unsuccessful. Injection of latex proved impossible because of the small size of the nares. Covering the nares with vinyl acetate was unsatisfactory because of the irritating nature of the fumes and because it peeled off when it hardened. Orafix Special Plastic Denture Adhesive (Norcliff Products) and Lepage's Plastic Model Cement either dissolved or failed to adhere.

In one experiment the nares were blocked with Kodak Eastman 910 Adhesive which adhered satisfactorily for about three days in the laboratory. After this time it peeled off.

Finally, a dental glue, Durelon Carboxylate Cement (ESPE Fabrik Pharmazeutische Praparate GMBH) was used to block the nares. This adhered extremely well in the laboratory from seven days to two weeks, but again after this period it peeled off. No anesthetic was used when either of these treatments was applied.

Taste

The possibility that the cirri of O. maculosus contained taste buds, similar to those found in the tentacles of Blennius tentacularis Brunn (Schulte and Holl, 1972) and that these and other chemosensory receptors might be involved in homing, resulted in using the method of Bardach et al. (1965) in an attempt to destroy any such taste buds. Detergents reduce surface tension and act as fat solvents thus making all membranes of fish that come into contact with detergents susceptible to damage. Bardach et al. (1965) examined the effect of low concentrations of detergents (1 to 5 ppm) on Ictalurus natalis (Lesueur) and found that observable histological disintegration of taste buds occurred (after three to ten days). Behavioural observations suggested that damage to

the olfactory epithelium and gills may have occurred although histological examination did not support this. Recovery of the taste buds was not observed even after four to six weeks in clean water.

This technique was used initially in attempts to eliminate the sense of taste in O. maculosus. Ten O. maculosus individuals were put in low salinity water (5 ppt) containing 5 ppm household detergent. The water and detergent were changed daily. However, all fish died within three days. Whether this was due to the freshwater or to the detergent was unknown. Nakamura (1970) found that O. maculosus exposed to two ppt salinity survived from 88 to 102 hours and at a salinity of 7.5 ppt to 192 hours, when the experiment was terminated. This suggests that the complete mortality recorded here was a result of the combined effect of low salinity water and detergent.

A second attempt to eliminate chemosensory cells was made using octylphenoxypolyethoxyethanol (Triton-X-100), a non-ionic detergent which was found to induce involuntary convulsive effects on the mollusc, Buccinum undatum, similar to the effect induced by saponins from the starfish Asterias rubens and Marthasterias glacialis (Mackie et al., 1968). This escape response is suggested by the authors to be caused by saponins reacting with, or causing damage to, chemosensory cells of nervous origin in or near the surface epithelium of the foot muscle. Damage is caused by the detergent or surface active properties of the saponins.

Ten O. maculosus were put in seawater containing 5 ppm Triton-X-100. Another ten O. maculosus were run as controls in the same volume of seawater (10 l) only. The water and Triton-X-100 were changed daily. The fish were kept under these conditions for seven days, at which time five of the experimental fish and all the control fish were fixed separately in 10% formalin. The remaining five experimental fish were returned to clean seawater to determine the period of recovery of chemosensory cells (if they were destroyed).

Although, subsequent to the homing experiments in which the effect of 7 days immersion in Triton-X-100 was examined, no evidence was found to show that the cirri of O. maculosus contain any taste buds, it is possible that taste buds may be located elsewhere on the body and may be affected by detergent.

Fin Removal

Pectoral and pelvic fins were removed from O. maculosus individuals by cutting with sharp scissors. Removal of one set of paired fins appeared to have no effect on the survival of fish. Moring (1976) reported that O. maculosus whose pectoral and caudal fins were partially clipped showed "no unusual mortalities or loss of movement over an extended period" in the laboratory. Although none was kept in the laboratory for

any period of time in this study, field observations of O. maculosus which had pelvic fins removed were made up to seven months after release, by which time the fins appeared to be fully regenerated. Fish which had had pectoral fins removed were observed up to five months later, by which time these fins also appeared to be fully regenerated. Moring (1976) reported partial fin regeneration in O. maculosus and Gibson (1967) reported full fin regeneration after clipping in Blennius pholis and Acanthocottus [=Enophrys] bubalis.

Removal of both sets of paired fins (as was undertaken in one experiment) resulted in an obvious loss of manoeuvrability and control of movement. O. maculosus individuals treated in this manner tended to lie on one side. One O. maculosus with both sets of paired fins removed was seen in the field 81 days after release.

2. Interactions between resident and introduced fish

This experiment was designed to determine whether a behavioural or other interaction between the resident and introduced O. maculosus in a tidepool results in the introduced fish departing from the transplant pool and possibly returning to their home pool.

Methods

A total of 36 Oligocottus maculosus were collected from two nearby pools and transplanted to two other pools about 100 m away. The transplant pools were bailed out and the resident fish collected and returned to the lab. The pools were refilled by bucketing water in from other pools prior to introducing the transplanted fish. From the two transplant pools 11 and 21 fish were removed and 10 and 26 were replaced, respectively. Data were collected for two months.

Results

While the percentage of O. maculosus successfully homing is relatively small it is evident that the percentage of fish remaining in the transplant pool is not significantly larger than in many of the other homing experiments (Table 33). In addition, all of the fish observed in the transplant pools after release subsequently homed.

The small percentage of fish successfully homing may be partially a function of the distance between the home and transplant pools which was greater than in the other homing experiments. However it was still well within the range of 300 m from which distance Khoo (1971) found that O. maculosus can home.

Table 33

Homing performance after transplant pools
cleared of resident fish

Date released	12 October 1976
Number released	36
Number homed	14
Percent homed	39
Number remaining in transplant area	3
Percent remaining in transplant area	8
Days remaining in transplant area	
a. homers	1,1,1
b. non-homers	
Percent of homers returning to home pool	86

This experiment and the data from untreated O. maculosus in other homing experiments suggest that while some increase in the percentage of fish remaining in the transplant pool for some period of time may occur, because of the removal of some of the transplant pool residents, there is no evidence to suggest that behavioural interactions between resident and introduced fish are responsible for the majority of fish leaving the transplant pool and homing.

Since bailing out a tidepool does not remove all traces of water from the pool, it still remains a possibility that there is some pheromonal influence (from the resident fish) which, although diluted after bailing and refilling the pool, is still detectable by the introduced fish and results in their departure from the pool. Although this problem might be overcome by delaying the introduction of transplanted fish for several tide cycles, to allow tidal flushing of the pool, it is possible that other fish may have moved into the pool over this period.

3. Nature of movement between release and home pool

One experiment was conducted to determine whether homing O. maculosus showed any evidence of directed movement as revealed by their low tide distribution. The locations, between the release and the home pools, of two groups of fish transplanted to a central pool were analyzed with respect to angular direction.

Methods

A total of 66 fish from two groups of pools (29 from one group and 37 from the other group) were transplanted to a pool about midway between the home pool areas (27 and 33 m from the home pools). As far as the tide height permitted, pools in all directions between the release and home pools were searched for transplanted fish. When a fish was located, the angle of that pool relative to the release pool was recorded. Data from each of the first three days following release and, because the sample sizes were small, from the first three days combined, were plotted on circles, similar to diagrams of vanishing points used for birds in orientation analysis. In the case of the combined data, all except one fish had been seen only once, or more than once in the same pool in the area under consideration. For the one fish seen in pools in different directions from the

release pool, the initial sighting, in the direction opposite its home pool was used, to avoid bias.

Two kinds of analysis were conducted. For each day's records and for the combined records, sign tests were used to compare the home directions (85° and 235°) with the mean directions of each of the two samples to determine whether the mean direction taken by each sample could be considered as the home direction (Batschelet, 1965). To determine whether the two samples for each day and for the combined data were significantly different, the Watson nonparametric two sample test, based on a mean square deviation was used (Watson, 1961; 1962; Batschelet, 1965).

Results

For all but one of the samples from each day where there are sufficient data, it is evident that the mean directions taken by fish located between the release and home pools were the home directions. However, for only the first day, does the Watson test show a significant difference between samples (Figure 26). This may be due to the small sample sizes.

The combined data for the first three days, in which each fish is considered only once, shows that the mean directions taken are the home directions, and further that the samples are significantly different (Figure 26). Since the samples may be significantly different in angular deviation or

Is mean direction ($\bar{\theta}$) home direction (θ_o)?
 $\bar{\theta} = 235^\circ$ $\theta_o = 85^\circ$

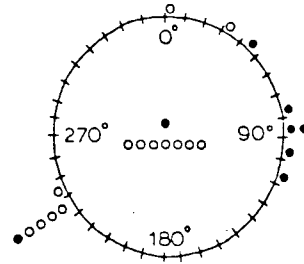
$N=7, n_1=2$
 $p=.454 > .05$
 $\bar{\theta} = \theta_o$

$N=7, n_1=2$
 $p=.454 > .05$
 $\bar{\theta} = \theta_o$

Samples significantly different (mean dir'n):
 $U_{7,7}^2 = .348 \quad p < .05$ (Burr, 1964)

Day 1

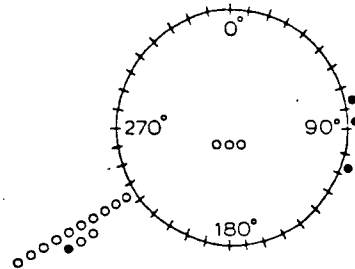
homepools (235°)



homepools (85°)

Day 2

homepools (235°)



homepools (85°)

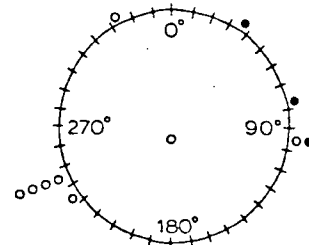
$N=12, n_1=2$
 $p=.038 < .05$
 $\bar{\theta} \neq \theta_o$

$N=4$
 insufficient data

Samples not significantly different:
 $U_{12,4}^2 = .0994 \quad p > .05$ (Burr, 1964)

Day 3

homepools (235°)
 oooooo



homepools (85°)

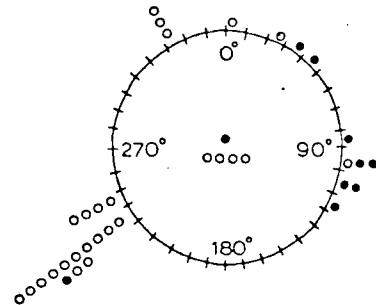
$N=7, n_1=3$
 $p=1.0 > .05$
 $\bar{\theta} = \theta_o$

$N=3$
 insufficient data

No tables available for $U_{7,3}^2 = .2019$

Day 1 + Day 2 + Day 3

homepools (235°)
 oo(oooo)



homepools (85°)

 (..)

$N=22, n_1=8$
 $p=.286 > .05$
 $\bar{\theta} = \theta_o$

$N=9, n_1=3$
 $p=.508 > .05$
 $\bar{\theta} = \theta_o$

Samples significantly different:
 $U_{22,9}^2 = .2787 \quad p < .05$ (Stephens, 1965)

Figure 26 Circular plots of direction over first 3 days taken by two samples of fish displaced to central pool (successful homers shown under home pools; those in parentheses found between release and home pools)

mean direction (Batschelet, 1965) (although the data suggest mean direction), 150° was added to the angular directions of the smaller sample (so that the home directions were identical for both samples) and the test statistic was recalculated (Watson, 1962). This resulted in $U^2_{22,9} = .1168$, showing no significant difference between the samples ($p > .05$). Thus the difference between the samples lies in the mean direction.

It may be concluded, therefore, that for the fish seen between the release pool and the home pools within the first three days following release, the mean direction taken, as revealed by their presence in tidepools, by the groups from each side of the release pool was the home direction and that the mean directions taken by each sample were significantly different. Of the 31 fish seen between the release and home pools, 24 or 77% homed. In total, 80% of the fish released homed.

While this experiment appears to provide evidence to show that homing O. maculosus display directed movement towards the home pool, two qualifications must be made. In the first three days only 31 out of the 66 O. maculosus released were found between the release and home pools. (Another five fish remained in the release pool and 12 fish which were not seen in the area under consideration had homed.) Since no fish were found in truly landward pools, the fish not seen may well have been in pools lower than those uncovered by the tide. More importantly, while the low tide distribution of fish supports

the idea of directed homeward movement, nothing can be concluded about their behaviour at high tide. However, if some kind of random search is involved in homing, greater numbers of fish than were observed might be expected to be found in pools in the "wrong" direction from the home pool.

4. Touch and/or chemosensory clues

A number of fish, for example, Urophycis chuss (Walbaum), Prionitus carolinus (Linnaeus), P. evolans (Linnaeus) (Bardach and Case, 1965) and Ictalurus sp. (Bardach, et al., 1967) have been shown to possess sensory receptors (taste buds) on their fins, barbels and body surfaces. Given that the paired fins of O. maculosus are in constant contact with the sea floor, Khoo (1971) conducted several homing experiments involving removal of pectoral or pelvic fins to determine whether detection of sea bottom clues is used as a method of homing. Since the results he obtained were inconclusive, several experiments were conducted in this study involving the removal of paired fins.

Methods

Three experiments investigating the homing ability of O. maculosus without either pectoral or pelvic fins were conducted. A total of 134 O. maculosus were transplanted, 65 with pelvic fins removed and 69 as untreated controls. (In this and subsequent experiments, untreated O. maculosus are referred to as control fish, even though they were not sham operated.) In the second experiment a total of 66 fish were transplanted, 33 with both pectoral fins removed and 33 as controls. In the third experiment a total of 113 fish were transplanted, 38 with both pelvic fins removed, 37 with both pectoral fins removed and 38 as controls.

In all three experiments reciprocal transplants were made as far as possible between two groups of four pools each about 60 m apart. Data were collected for four months in each experiment.

As a further examination of the ability of the paired fins to detect chemosensory (or touch) clues, histological examination was made of the pectoral and pelvic fins of six O. maculosus. Sections stained with eosin-haemotoxylin were examined to determine whether there is any evidence of sensory receptors.

Results

Compared with untreated O. maculosus, the removal of paired fins appears to have little effect on homing ability (Table 34). The percentages of O. maculosus remaining in the transplant area following release are all relatively high, although it is not possible to detect any major differences in percentages staying between control and treated fish. In all three cases the percentages of successfully homing fish returning to the home pool exceeded the percentages returning to the home range.

None of the sections of pectoral and pelvic fins examined showed any evidence of sensory receptors (Figure 27). In this connection, it is interesting to note that, from examination of Scorpaenichthys marmoratus, Freihofer (1963) suggested the fibres of the ramus lateralis accessorius (the main branches of which carry taste or gustatory fibres) are distributed to the pectoral and pelvic fins in cottids.

The transplant experiments and the histological studies provide no evidence to suggest that sensory receptors detecting chemosensory or touch clues in the paired fins are involved in the homing of O. maculosus.

Table 34

Homing performance after removal of paired fins

	Pect Cont		Pelv Cont		Pect Pelv Cont		
Date released	21 September 1975		4 September 1975		16 May 1976		
Number released	33	33	65	69	38	37	38
Number homed	23	24	41	52	21	18	20
Percent homed	70	73	63	75	55	49	53
Number staying in transplant area	4	3	19	17	10	5	8
Percent staying in transplant area	12	9	29	25	26	14	21
Days staying in transplant area							
a. homers	13	4	1,1,1, 1,5,5, 6,7	1,1,1, 1,1,4, 6,6,7, 17,18,	1,1,2		2,27
b. non-homers	2,2,2	3,78	1,4, 6,6,7, 12,32, 42,43, 49,50	6,6, 22,43, 13,17	1,1, 1,2, 27, 85, 123	1,2, 2,56, 56	2,2 73,73, 83, 110
Percent of homers returning to home pool	65	67	88	73	81	61	80

Pect: both pectoral fins removed

Pelv: both pelvic fins removed

Cont: untreated



Figure 27 Sections of tips of pectoral fin (above) and pelvic fin (below)

5. Relative importance of different senses

To determine the relative effect of different sensory impairments on homing ability an experiment was conducted in which homing performance was compared between groups of O. maculosus, each group of which was subjected to a different treatment involving destruction of sensory receptors. This experiment was designed to show whether homing performance was significantly more adversely affected by any one treatment.

To determine whether there is redundancy in the sensory systems involved in homing, the homing performance of a group of O. maculosus which had undergone all four sensory impairment treatments was compared with that of untreated fish.

Methods

In the first experiment, a total of 150 O. maculosus were reciprocally transplanted between two groups of four pools each about 60 m apart. Five equal sized groups of O. maculosus were involved having been treated as follows: blinded, made anosmic, one set of paired fins removed, immersion in Triton-X-100 for seven days and untreated.

Ten blind fish and five anosmic fish were held in the laboratory to investigate the effect of treatment on survival.

Data were collected for three and a half months.

In the experiment examining simultaneous sensory impairment of the same four senses, a total of 46 O. maculosus were reciprocally transplanted between two groups of pools about 60 m apart. A group of 20 fish were untreated controls and 26 were subjected to all four impairments. Following treatment, the fish were kept in the laboratory for several days before release. One mortality occurred in this period. Another ten treated fish were kept in the laboratory to investigate survival over the same period as the experiment. Data were collected for two and a half months. In these and the two subsequent experiments, tests of significance were conducted using the two factor G test of independence (Sokal and Rohlf, 1969).

Results

Given the low percentage of untreated fish which successfully homed it appears that no single sensory impairment treatment has any significant effect on the percentage of successfully homing O. maculosus ($p > .05$) (Table 35). Although the differences are not significant ($p > .05$), the percentages of successfully homing fish returning to the home pool are lower for blind and anosmic groups than for any other treatment suggesting that there may be a slight effect of these treatments on the precision with which the home pool can be located.

The percentages of O. maculosus remaining in the

Table 35

Relative homing performance after four
different impairment treatments

Blind Anosmic Finless* 7 days in Control Triton-X -100					
Date released	23 August 1976				
Number released	30	29	30	30	31
Number homed	21	12	15	22	15
Percent homed	70	41	50	73	48
Number remaining in transplant area	5	10	9	6	8
Percent remaining in transplant area	17	34	30	20	26
Days staying in transplant area					
a. homers	1,1,2	1	1,11	1,1,1,1, 11,24	2
b. non-homers	24,31	1,2,2,2, 11,49,73, 74,104	1,1,2, 8,24, 74,101		1,2,10, 11,46, 80,104
Percent of homers homing to home pool	48	42	53	59	60

*: one set of paired fins removed

transplant area are high particularly in the cases of the anosmic, finless and control groups. The fact that the control group shows an equally high percentage of fish remaining in the transplant area as the treated groups suggests little effect of the treatments themselves in this regard. Mortality of treated fish held in the laboratory was low, until a blockage in the seawater system caused total mortality after two and a half months. Until then no anosmic and one blind fish died. Mortality in the field was unknown, although blind, anosmic and control fish were observed in the field until the experiment was terminated.

From this experiment no single sensory impairment can be shown to have a significantly more adverse effect on homing ability compared with that of untreated controls.

Despite the small numbers of control fish used in the simultaneous impairment experiment, it is evident that the homing performance of treated fish is substantially affected by the treatments (Table 36). The difference in the percentages successfully homing is significant ($p < .05$). Two explanations or a combination of both may account for this. Homing ability may have been impaired because alternative sensory mechanisms were destroyed so that no system was available for homing. The two fish which successfully homed may have employed additional mechanisms or complete destruction of one of the sensory systems may not have been effected.

Table 36

Homing performance after four
simultaneous sensory impairment treatments

	Impaired	Control
Date released	15 September 1976	
Number released	26	20
Number homed	2	14
Percent homed	8	70
Number remaining in transplant area	4	4
Percent remaining in transplant area	15	20
Days staying in transplant area		
a. homers		1, 1
b. non-homers	10, 10, 23, 28	10, 26
Percent of homers returning to home pool	50	64

The alternative explanation may be that treated O. maculosus were unable to survive, regardless of being able to home, after such drastic treatment. The significantly higher percentage ($p < .05$) of treated fish which were not located at any time during the experiment (77% compared with 20% for controls) suggests that the majority of fish either moved out of the area, were subject to heavy predation or died. Specific predators of O. maculosus are unknown, but possible candidates include mink, gulls, crows, garter snakes, diving birds and fish. However, the majority of mink observed in this study were collecting crabs, no garter snakes were observed in tidepools, crows were seen at the study areas in the intertidal but never in a pool, and gut content analysis of Sebastes spp., hexagrammids and inshore cottids suggests that perhaps only Artedius spp. are the major fish predators of O. maculosus (Bruce Leaman, David Zittin, personal communications; personal observation). Gut content analysis of diving birds suggests that pelagic cormorants and pigeon guillemots are probably the only diving birds likely to eat O. maculosus and if they do, it is only as incidental catch (Ian Robertson, personal communication). Although gulls are the final host for a parasitic trematode (Cryptocotyle lingua) for which O. maculosus can act as an intermediate host (Ching, 1978), observations of gulls in tidepool areas suggests that only fish in high tidepools may be vulnerable and even for these fish, it seems unlikely that predation of this kind is very severe. Certainly, the fish which had undergone four sensory impairment treatments

appeared more vulnerable to predation by their behaviour in tidepools. Known mortality of treated fish held in the laboratory was relatively low (one death and one escape) until failure of the seawater system after two months. Behaviour of treated fish in the lab was noticeably different from that of untreated fish. The former tended to group in corners of the tank and rarely moved about in comparison with untreated fish. Treated fish exhibited no interest in mussel pieces dropped into the tank. This can be contrasted with the relative activity of untreated O. maculosus and the almost instant response to mussel pieces.

When treated fish were released into tidepools at First Beach their initial swimming was highly erratic compared with untreated fish, showing rolling and unsteadiness in their movements. Untreated fish immediately swam away from the release point to shelter underneath or at the side of rocks, stones or algae. Treated fish merely sat in the open in the pool occasionally swimming back and forward. If they swam into a solid object they remained beside or under it. By comparison the treated fish moved very little and for the most part sat in the open area of the pool into which they were released or to which they swam during their erratic movements.

It appears therefore that while the cumulative effect of these four sensory impairment treatments may have a considerable effect on the survival of O. maculosus, homing ability is definitely impaired. The results of other sensory

impairment homing experiments suggest that it is a combination of blindness and anosmia which together prevent homing, since the homing performance of fish without paired fins or after seven days immersion in Triton-X-100 appears to be relatively unaffected.

6. Simultaneous impairment of vision and smell

To explore further the suggestion that both vision and smell are involved in homing, two experiments were conducted to determine the effect of simultaneous impairment of these senses on homing performance.

In one experiment, the relative homing performance of a group of both blind and anosmic fish was compared with that of groups of blind, anosmic and untreated fish. In this experiment the effect of such treatments on juvenile fish was investigated with a view to determining whether these senses, and in particular, vision, are used to acquire the information required to home. If singly impaired adult O. maculosus can home, but juveniles cannot, it is possible that insufficient information or experience is available to them to use alternative mechanisms to home.

In the second experiment, a different method of making fish anosmic was used to compare the homing performance of simultaneously blind and anosmic fish with that of untreated

controls. Only adult fish were used in this experiment.

Methods

A total of 180 O. maculosus were reciprocally transplanted between two groups of pools about 60 m apart. One group of 45 fish were untreated controls, 46 fish were blinded, 44 were made anosmic using Kodak Eastman 910 Adhesive and a group of 45 fish were made blind and anosmic. In each group, about 25% of the fish were less than 4.0 cm, to investigate the effect of the impairment treatments on juveniles. A group of 10 O. maculosus which were both blind and anosmic were kept in the laboratory to examine survival. Data were collected for two months.

In the second experiment, a total of 72 fish were reciprocally transplanted between two groups of pools approximately 60 m apart. One group of 32 fish consisted of untreated controls and the other group of 40 fish were made blind and anosmic, the latter by blocking the nares with Durelon dental glue. A group of 10 fish which were blind and anosmic were kept in the laboratory. Data were collected for five weeks.

Results

In the first experiment (Table 37) in which anosmia was effected by blocking the nares with Kodak Eastman adhesive, it was evident that the adhesive came off the nares after one or two days in the field. Thus while the fish were certainly anosmic when released, it cannot be said with any certainty how long the condition persisted after release. In the second experiment (Table 38) Durelon dental glue was used. In the laboratory it remained in and around the nares for a considerably longer period than the Eastman adhesive. However the blind and anosmic fish released into tidepools exhibited unusual behaviour, swimming rapidly towards the surface and back towards the bottom of the pool "nose diving" into the gravel and rocks in the pool. In this manner several fish succeeded in knocking the coverings off the nares. It was evident, since the Durelon is pink, that none of the exterior applications of it remained on the fish longer than three days. Thus again, although some of the Durelon may have remained inside the nares, the period of anosmia cannot be stated with any certainty.

The results certainly suggest that simultaneous blinding and "anosmia" impair homing performance compared with that of untreated controls and either blind or "anosmic" fish. In both experiments the percentage of successfully homing blind and anosmic fish was significantly lower than the percentages

Table 37

Relative importance of blindness and anosmia

	Blind	Anosmic	Blind and Anosmic	Control
<hr/>				
Date released	16 July 1977			
Number released	46	44	45	45
Number homed	23	18	9	19
Percent homed	50	41	20	42
Number found in transplant area	28	27	20	26
Percent found in transplant area	61	61	44	58
Days spent in transplant area				
a. homers	1, 1, 2, 2, 2, 6, 9, 18, 35	1, 1, 1, 1, 1, 2, 5, 6, 6, 6, 14	1, 2, 2, 5, 9, 10	2, 2, 2, 2, 5, 42
b. non-homers	1, 1, 1, 1, 2, 2, 2, 5, 5, 6, 6, 6, 10, 10, 14, 18, 32, 36, 42	1, 1, 1, 1, 2, 2, 2, 5, 5, 10, 42, 45, 45, 59, 59, 59,	1, 1, 2, 5, 9, 10, 11, 22, 26, 26, 27, 59, 59, 59	1, 1, 1, 2, 2, 5, 6, 6, 6, 13, 14, 14, 14, 27, 27, 32, 55, 55, 59, 59
Percent of homers homed to home pool	22	39	44	42
Percent of fish seen after release	91	77	51	87

Table 38

Homing performance after
simultaneous blinding and anosmia

	Impaired	Control
Date released	9 August 1977	
Number released	40	32
Number homed	8	20
Percent homed	20	63
Number remaining in transplant area	18	14
Percent remaining in transplant area	45	44
Days staying in transplant area		
a. homers	3,3,3,3, 9,14,17	3,3,8, 18
b. non-homers	1,2,2,2, 3,3,3,14, 14,14,20	1,3,3,3, 8,8,11, 11,18,30
Percent of homers returning to home pool	38	60
Percent of fish seen after release	48	94

homing in the other groups employed in each experiment ($p < .05$). However the results must be treated with caution because of the uncertainty concerning the anosmic fish and because the percentages of fish seen after release are significantly lower ($p < .05$) for the simultaneously blind and anosmic groups (51% and 48%) than for any other groups (77% to 94%), suggesting that this treatment may have some impact on survival.

Consideration of the time to home in the differently impaired groups in the first experiment showed little difference between treatments, although the percentages of homers observed in the transplant area do - control: 32%, blind: 39%, anosmic: 61%, blind and anosmic: 67%. In the second experiment, the time taken to home was in general considerably longer for blind and anosmic fish than for controls; 60% of the controls which homed did so before any blind and anosmic fish homed. Furthermore only 20% of the successfully homing control fish were observed in the transplant area while 88% of the blind and anosmic fish were. This might suggest that the anosmic fish were unable to home until the dental glue was removed from the nares, and the sense of smell was again present.

The analysis of homing performance by length in the first experiment (Table 39) appears to show that by the time the fish are 3.5 cm long some of them have acquired sufficient information to use alternate senses to home; at least they do not require vision. Until that size is reached however, any impairment appears to be sufficient to prevent homing.

Table 39

Relative homing performance (percentage successfully homing)
following blindness and anosmia by length

Length class (cm)	2.5-2.9	3.0-3.4	3.5-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	Total
<hr/>								
Date released	16 July 1977							
Elind								
Number released	3	5	4	25	7	1	1	46
Number homed	0	0	2	13	7	1	0	23
Percent homed	0	0	50	52	100	100	0	50
Anosmic								
Number released	5	2	3	21	12	1	0	44
Number homed	0	0	0	12	6	0		18
Percent homed	0	0	0	57	50	0		41
Elind and Anosmic								
Number released	4	3	3	21	11	3	0	45
Number homed	0	0	0	3	4	2		9
Percent homed	0	0	0	14	36	67		20
Control								
Number released	4	2	5	24	8	2	0	45
Number homed	1	0	2	9	6	1		19
Percent homed	25	0	40	38	75	50		42

Table 39 (continued)

Relative homing performance (percentage remaining in transplant area)
following blindness and anosmia, by length

Length class (cm)	2.5-2.9	3.0-3.4	3.5-3.9	4.0-4.9	5.0-5.9	6.0-6.9	7.0-7.9	Total
<hr/>								
Date released	16 July 1977							
Blind								
Number released	3	5	4	25	7	1	1	46
Number stayed	3	3	3	15	3	0	1	27
Percent stayed	100	60	75	60	43	0	100	59
Anosmic								
Number released	5	2	3	21	12	1	0	44
Number stayed	3	1	1	14	8	0		27
Percent stayed	60	50	33	67	67	0		61
Blind and Anosmic								
Number released	4	3	3	21	11	3	0	45
Number stayed	1	0	2	11	7	1		20
Percent stayed	25	0	67	52	64	33		44
Control								
Number released	4	2	5	24	8	2	0	45
Number stayed	3	1	4	15	5	1		26
Percent stayed	75	50	80	63	25	50		58

Laboratory survival of both groups of blind and anosmic fish was good up to four weeks, although the fish were far less active than untreated fish. Until about seven days after the Eastman adhesive and the dental glue had come off the nares, the fish would not respond to mussel pieces. Even though they would feed desultorily after this time, the Durelon treated fish began to die after four weeks and the Eastman adhesive treated fish after six weeks.

7. Visual and olfactory tidepool clues

Since both vision and olfaction appear to be involved in homing, the role of visual and olfactory clues in tidepool recognition was investigated. To determine whether homing O. maculosus recognize pools by "landmarks", two kinds of conspicuous artificial landmarks were installed in tidepools and then exchanged to determine whether homing O. maculosus individuals would home to the pool of capture or to the pool with the familiar landmark. To investigate the role of olfactory clues emanating from the tidepool a choice experiment was conducted to determine whether O. maculosus individuals could distinguish water from the tidepool in which they were captured from seawater pumped into the Bamfield Marine Station from a depth of 20 m.

Methods

To investigate visual landmarks, two pairs of somewhat similar tidepools at First Beach were selected. Because of the difficulty of finding similar tidepools low in the intertidal, the pools selected were high relatively shallow pools. Two pairs of conspicuous landmarks were made and one landmark was anchored with cod line and cement nails in each pool, so that each pair of pools contained one pair of landmarks. The landmarks consisted of fireplace bricks painted fluorescent orange and inverted dish pans painted green (Figure 28).

After the landmarks had been installed for nine days, O. maculosus were collected and tagged. The height of the pools resulted in a large number of small O. maculosus (less than 4.0 cm) being collected. It was anticipated that if the pool to which the fish homed was influenced by landmarks, juvenile fish would be more readily influenced than adult fish. A total of 154 fish from the four pools were released into a pool about 65 m away, 11 days after the landmarks were initially installed. Prior to high tide, the landmarks from one pool pair were exchanged. The landmarks in the other pool pair were left unchanged to provide data on pool fidelity. Data were collected for almost two months. Percentages homing to each pool were calculated.

To investigate olfactory clues, ten O. maculosus were



Figure 28 "Landmarks" installed in pools at First Beach

collected from First Beach at varying intervals over a period of several months. At the time a fish was caught, about 4 l of water from the capture pool was collected and returned to the lab. Testing of each fish began within several hours of returning to the lab.

A Y-shaped choice tank similar to that used by Khoo (1971) was constructed of plexiglass and painted black to reduce the effect of exterior disturbance (Figure 29). Station seawater was run through the inlets at the ends of the choice arms. Burettes were placed so as to drip test (tidepool) or control (station) seawater into each arm of the tank at a rate of 40 to 50 ml per minute, slightly higher than the rate of flow in Khoo's (1971) experiments. The outer 12.7 cm of the non-choice arm was a holding chamber with a sliding gate.

Fish were placed in the holding chamber and allowed to acclimate for two hours before testing. Tests were run as a series of 20 or 40 test and control trials in the following sequence: half test trials, all control trials, half test trials. A break of at least ten minutes was allowed between trials to permit flushing out of the choice tank.

Control trials consisted of running station seawater through both burettes. In test trials home tidepool water was run through one burette and station water through the other. The burette through which tidepool water was run was changed throughout the test trials for all fish. In each trial the

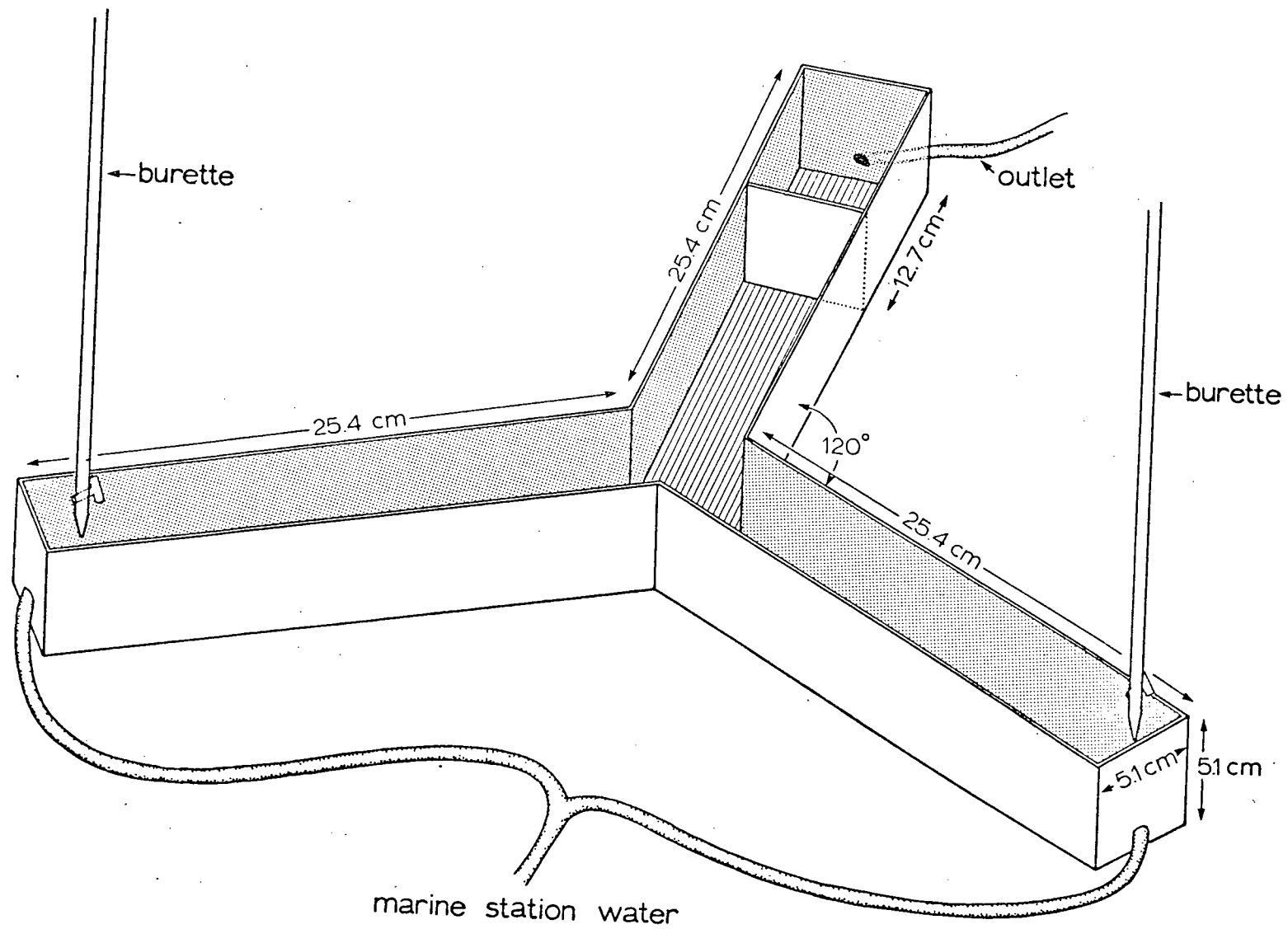


Figure 29 Y shaped choice tank

appropriate water was run through the burettes and the gate raised to allow the fish to swim out and make a choice. For the first six fish tested each trial was continued until the fish made a choice either right or left. This proved to be so time consuming that for the remaining four fish each trial was terminated after a period of 30 minutes and 'no choice' was recorded. On completion of the testing seven of the fish were tagged and released about 60 m away from their home pool to determine whether they were able to home.

The proportions of left and right choices made in the control trials were calculated and compared with the respective proportions of correct left and right choices in the test trials. A correct choice in a test trial was one in which the fish chose the arm containing home tidepool water. In the comparison of control and correct test choices for each arm of the choice tank, a 'negative' denoted that the proportion of control choices in that arm was greater than the proportion of correct test choices in that arm. A 'positive' denoted that the proportion of correct test choices was greater than the number of control choices in that arm. Even if a fish being tested showed a bias towards a particular arm in the control tests, a preference for home tidepool water would be shown as a greater proportion of test choices in that arm.

Results

Table 40 clearly shows that the exchange of landmarks (Pair 1) had no effect on the homing behaviour of the O. maculosus individuals from the first pair of pools. Of the relatively small percentages of fish which homed, only two fish returned to the alternate pool. Of those fish which did home, the majority displayed little fidelity to the pool of capture, moving between a wide range of pools, although infrequently moving to the alternate pool in the pair. The data from the "control" pools (Pair 2) support the evidence of transience of the O. maculosus individuals from these high tidepools. No fish homed to one pool in the pair and only a few to the other pool in the pair.

While most of the tagged fish were seen after release, it was evident that they moved to pools in the direction of the capture pools, and moved about amongst pools in between the release and capture pools more than the resident fish from these pools. It is possible that this experiment may have been more successful if conducted in lower pools, where pool fidelity is apparently considerably greater, however, the total failure of the experiment may be due to the brevity of the period for which the landmarks were installed. The apparent lack of effect of the landmarks could also be interpreted as meaning that a landmark conspicuous to the human eye is not so conspicuous to a

Table 40

Homing performance after pool "landmarks" exchanged

	Pair 1		Pair 2	
	Initial placement		Initial & final placement	
	Brick	Pan	Brick	Pan

Date released	20 July 1977			
Number released	42	37	21	54
Number homed to "brick"	19	0	0	0
Percent homed to "brick"	45	0	0	0
Number homed to "pan"	2	16	0	18
Percent homed to "pan"	5	43	0	33
Number staying in transplant area	18	9	8	33
Percent staying in transplant area	43	24	38	61
Number found in distant pools	2	0	6	1
Percent found in distant pools	5	0	29	2

fish in a tidepool or that the pool is not solely recognized by a conspicuous visual landmark.

In the choice tank experiments, if O. maculosus individuals demonstrated a distinct preference for home tidepool water over station water, a predominance of plus signs would be expected. This is not shown (Table 41). The distribution of plus and minus signs provides no evidence to suggest that O. maculosus individuals distinguish home pool water from water pumped into the marine station.

These results would appear to suggest that olfactory clues emanating from home tidepool water at low tide are not a significant factor in guiding the fish back to their home tidepool. This does not necessarily eliminate olfaction as a possible homing mechanism, for two reasons. If olfactory clues emanate from the tidepool at high tide (when the fish are homing) mixing with other water may alter their nature. Recognition of olfactory clues from tidepool water taken at low tide presumably need not be of great significance to the fish. Further, if the substance or substances producing olfactory clues are of a volatile nature, the time delays involved between collecting the water and testing the fish might be sufficient to eliminate any chance of the substance being detected.

Although these results suggest that neither conspicuous landmarks nor olfactory clues emanating from the tidepool are very important in the homing of O. maculosus, a

Table 41

Choice tank tests of arm preference

Fish	Control choices percent L	Test choices percent correct L	Sign	Control choices percent R	Test choices percent correct R	Sign	Total number of trials
<hr/>							
1	60	50	-	40	50	+	40
2	90	70	-	10	30	+	40
3	80	60	-	20	0	-	20
4*	70	100	+	30	60	+	20
5*	80	40	-	20	100	+	20
6'	90	60	-	10	80	+	20
7'	10	20	+	0	20	+	20
8'	0	20	+	0	40	+	20
9'	30	20	-	60	0	-	20
10'	10	0	-	10	0	-	20

-: percent control choices > percent correct test choices

+: percent control choices < percent correct test choices

': tagged and released

*: homed

small amount of evidence was obtained from the behaviour of one recognizable adult O. maculosus which had taken up residence in the enclosure in Grappler Inlet, suggesting that it is some attribute(s) of the pool itself to which the fish homes, rather than the position of the pool. On the three occasions when the fish was moved to pools other than the one in which it was regularly found in the enclosure, it had always returned to the home pool by the following low tide. When the home pool was exchanged with another pool in the enclosure, and the fish displaced, it returned to the relocated home pool. Further displacement of the fish and pools resulted in the fish disappearing.

8. Discussion

A number of senses and behavioural responses were examined to determine how O. maculosus finds its way back to its home range. No evidence was found to show that touch and/or chemosensory clues detected by the paired fins are involved in homing and immersion for seven days in a detergent-like substance which was designed to destroy chemosensory cells had no effect on homing ability. Behavioural interactions between resident and introduced fish and "space" or density in the transplant pool do not appear to be implicated in homing.

Evidence that homing is a directed movement was

suggested by the low tide distribution of transplanted fish. Comparison of observed percentages homing with calculated percentages homing and the ratio of predicted distance to be travelled with the direct distance, using various search patterns described by Griffin (1952) supports the concept of directed movement. With simple radial scattering along straight lines, a rectangular search pattern or an expanded rectangular search pattern over a direct distance of 60 m, the predicted percentages homing are less than 30% and there is a two to three fold increase in the predicted distance to be travelled. A spiral exploration involving more than one turn requires travelling about 12 times the direct distance.

Khoo (1974) showed that blind or anosmic fish were significantly less faithful to their home ranges than control fish at Port Renfrew and that the homing success of blind or anosmic fish was significantly less than for control fish, anosmic fish being significantly less successful than blind fish. Unilaterally blind or anosmic fish homed as well as control fish (Khoo, 1971). These results suggested to Khoo that while vision appears to be important in maintaining home range, it is not as important as olfaction in homing.

The results of this study generally support Khoo's conclusions although the importance of olfaction, by itself, does not appear to be as great for First Beach fish as for Port Renfrew fish. Bilateral blindness resulted in higher percentages homing than control fish, and had little effect on

the percentage remaining in the transplant area. However, conspicuous visual landmarks do not appear to be the pool characteristics recognized by the fish.

Anosmia resulted in low percentages homing (41% in each experiment), but these were similar to the percentages of control fish homing (48% and 42%). The percentages of anosmic fish homing in these experiments were higher than those generally observed by Khoo (0 to 20%). The percentages of fish remaining in the transplant area and the percentages of homers returning to the home pool do not seem to be affected by anosmia. While the period of anosmia remains doubtful in the experiments using adhesives, heat cautery, the method used by Khoo, did not appear to produce very different results. The amount of water mixing which accompanies high tide suggests that olfaction may be more important in recognizing the home pool (and possibly other pools) than in guiding the fish home by means of an odour stream. Although Khoo found that O. maculosus kept in an aquarium for three months showed a preference for aquarium over general source water, O. maculosus tested in this study showed no preference for water from tidepools in which they were captured, compared with water pumped into the Bamfield Marine Station. Although this does not necessarily eliminate olfactory clues emanating from the tidepool as a means of guiding the fish home or at least recognizing the home pool, for the reasons discussed earlier, it does cast some doubt on the olfactory hypothesis.

A combination of blindness and anosmia was shown to be the most effective method of reducing homing success to about 20% of released fish at First Beach. Additional treatment (removal of paired fins and immersion in detergent for seven days) appears to reduce homing success even further, but the lack of effect of these treatments individually suggests that although laboratory survival is good, survival in the field may be rather drastically affected. The difficulties in keeping the nares blocked with adhesives was mentioned earlier. However, the percentages of simultaneously blind and anosmic fish found in the transplant areas prior to homing (67% and 88% compared with 28% and 20% for controls) suggest that at least in the latter experiment the treated fish may have been unable to home until the nares were freed from obstructions. In this experiment the percentage of homers returning to the home pool was very low relative to control fish. Although laboratory survival was satisfactory for almost the entire duration of the experiment, the relatively small percentages of blind and anosmic fish seen after release (51% and 48% compared with 87% and 94% respectively) suggests that either survival in the field was affected or that straying is much more likely in fish treated in this way.

Both vision and olfaction appear to be essential for the homing of fish less than about 3.5 cm. Vision appears to become unnecessary before olfaction but it does not appear to be sufficient (without olfaction) to enable the fish to home until

they are larger. Homing performance of blind and anosmic fish shows an increase in the percentage successfully homing with length. Simultaneous blindness and anosmia seems to result in straying (or death) in a greater percentage of fish less than 3.5 cm than the other treatments.

These results suggest that both vision and olfaction are important in acquiring the information necessary for homing and that both are involved to some extent in homing, although olfaction appears to be of greater importance. If a technique which definitely precludes the perception of olfactory clues can be found (e.g. cutting the olfactory nerve) conclusive experiments can be conducted.

These results indicate that there are at least two mechanisms available for homing, the relative importance varying between areas. Thus it appears possible that when O. maculosus is unable to smell, but can see, homing performance is better in areas of more irregular topography. This might suggest that olfaction is more important in topographically regular areas.

The relative importance and kinds of visual clues used in homing and orientation behaviour have been shown to differ in homing and orientation behaviour in different fish occupying different areas, e.g. ponds, streams, reefs etc.. The possession of a topographic memory (presumably at least partly visually acquired) has been suggested for a number of littoral fish: Blennius ocellaris Linnaeus (Pieron, 1914), Fundulus

(Mast, 1915) and perhaps the best documented, Bathygobius soporator (Aronson, 1951, 1971). The jumping goby is believed to acquire knowledge of the local topography by swimming over the area at high tide, allowing it to orient its jumps correctly at low tide. The importance of small landmarks in the learned orientation of Phoxinus phoxinus (Linnaeus) was demonstrated by Hasler (1956).

Vision (and olfaction) appear to be important in the homing of reef fishes Epinephelus guttata and E. striatus (Bardach, 1958) and Carlson and Haight (1972) suggested that the inability of Sebastes flavidus to home over deep water might be due to loss of visual contact with the bottom.

In essentially still water, vision seems to be more important than olfaction. Hasler and Wisby (1958) suggested that the green sunfish, Lepomis megalotis used visual clues to home and Gunning (1959) reported that when Hasler made the fish anosmic, they homed as readily as controls. Experiments on various species of fish in the Kiev reservoir (bream, Abramis brama (Linnaeus), A. ballerus (Linnaeus) and Blicca bjorkna (Linnaeus); roach, Rutilus rutilus (Linnaeus); pike, Esox lucius Linnaeus; and perch, Perca fluviatilis Linnaeus) showed that blindness, anosmia, lateral line anaesthesia, simultaneous blindness and anosmia and simultaneous anosmia and lateral line anaesthesia resulted in little difference in initial azimuth of orientation and final orientation determined by tracking floats, between treated fish and controls (Abrosimova, 1975).

Simultaneous blindness and lateral line anaesthesia resulted in different orientation from control fish, but correct orientation was established faster when eye caps were removed than when the novocaine wore off (Abrosimova, 1976). Neither vision nor olfaction, taken singly, was shown to be essential for the homing of cutthroat trout, Salmo clarki Richardson in Yellowstone Lake, although blind fish took longer to home than anosmic or control fish (McCleave and LaBar, 1972). The authors believed that as many blind trout reached the home area as other fish but were unable to locate the trap.

Perception of visual clues other than landmarks has been demonstrated as possible in a number of fish: white bass, Roccus chrysops (Rafinesque), pumpkinseeds, Lepomis gibbosus (Linnaeus), bluegills, Lepomis macrochirus Rafinesque, (Hasler et al., 1958), parrot fishes, Scarus guacamaia Cuvier, S. coelestinus Valenciennes (Winn et al., 1964) and mosquitofish, Gambusia affinis (Baird and Girard) (Goodyear and Ferguson, 1969) (orientation to the sun); salmonids (Groot, 1965) cichlids (Waterman, 1958-1959, cited in Waterman, 1972) and halfbeaks (Waterman, 1972) (orientation to polarized light). However, it does not seem feasible that celestial bodies or polarized light are important in the homing of O. maculosus, since they can home from any direction and circumnavigate obstacles, and since they can home on cloudy days and nights (Khoo, 1971), the frequency of which is high. In any case, other information is required for the fish to recognize the home

pool or range. The role of vision therefore, would appear to be in the recognition of landmarks. Given the possible turbidity and turbulence of the intertidal, it is difficult to appreciate how this sense could be used over any distance.

In streams, the role of olfaction in homing seems to be more important than vision. Gunning (1959) showed this to be the case for homing longear sunfish Lepomis megalotis megalotis (Rafinesque). That vision must play a role however, was shown by the failure of simultaneously blind and anosmic fish to home. The importance of olfaction in the homing of salmonids to particular streams seems to be fairly well established. In the homing of chinook salmon, Oncorhynchus tshawytscha (Walbaum), olfaction was shown to be more important than vision, although simultaneous blindness and anosmia almost completely eliminated homing (Groves et al., 1968). The return to appropriately scented streams of coho salmon Oncorhynchus kisutch (Walbaum) and rainbow trout Salmo gairdneri Richardson, imprinted to an organic chemical (morpholine or phenethyl alcohol) as smolts or fingerlings, and electrophysiological studies of olfactory bulb responses to morpholine scented water, by homing imprinted and control fish, appear to confirm the importance of olfaction (Cooper et al., 1976; Cooper and Scholz, 1976; Scholz et al., 1976; Cooper and Hasler, 1976). The involvement of long term memory in the olfactory discrimination of home and other stream waters has been demonstrated electrophysiologically (Oshima et al., 1969). However Bodznick (1975) has suggested caution be

exercised in the interpretation of electrophysiological results relying on the amplitude of olfactory bulb discriminations.

The ability of fish other than salmonids to discriminate between odours has been shown. Bluntnose minnows Hyborhynchus notatus Rafinesque were trained to discriminate between the waters of two different streams (Hasler, 1966) and between rinses of natural plants (Walker and Hasler, 1949). Previously trained blind fish could make these discriminations but anosmic fish could not. Anguilla vulgaris (Turton) = Anguilla anguilla (Linnaeus) elvers have been shown to be able to discriminate between ebb and flood tide water using additions of natural inland water, presumably through olfaction. Simply changing the salinity did not produce the same response (Creutzberg, 1959). The ability to locate the source of an odour in a circular tank divided into compartments was shown by Kleerekoper (1967) to depend on an increased rate of flow in the odour releasing compartment relative to the other compartments.

The importance of olfaction in the homing of O. maculosus has been demonstrated and it appears necessary to postulate the existence of discrete odour streams in the turbulent intertidal, or the existence of discrete odours associated with particular pools. Since vision appears to be involved in the acquisition of information, a topographic memory may be established which is associated with the perception of clues from other senses, e.g. the lateral line, and olfaction may be used to assist in recognizing the particular pools. When

both vision and olfaction are eliminated the fish may be unable, using other senses, to determine where it is, in relation to the home range, thus being unable to home. The fact that blind fish can home coupled with the difficulty of appreciating how the olfactory sense can be used over any distance in the mixed intertidal, suggests the auxilliary involvement of another sense (or senses) when only vision or olfaction is eliminated.

Since this study has not eliminated the possibility that additional mechanisms are involved in homing, some consideration of them must be made. The acoustico-lateralis system seems to be the most likely auxilliary mechanism (if there is one) involved in homing.

Acoustic energy is present in two forms: displacement and pressure. Displacement is particularly evident at close range to the source and the phenomenon has been termed the "near-field" effect and is chiefly detected by the array of displacement receptors in the lateral line. Pressure, on the other hand, is regarded as a "far-field" effect and the inner ear-swim bladder complex is believed to be primarily sensitive to compression waves (Tavolga, 1971a) although the near-field effect can stimulate the acoustical and vestibular apparatus (Harris and van Bergeijk, 1962).

The lateral line can detect currents and other near-field movements of water produced when a fish approaches an obstacle (or vice versa) (Dijkgraaf, 1962) and possibly other

hydrographic phenomena produced by the locomotion of the fish in the vicinity of obstacles (Tavolga, 1971b). Lowenstein (1957) suggested that the lateral line could give a "fairly accurate three-dimensional representation of the immediate environment". In addition, the lateral line appears to be able to detect low frequency vibrations within the near-field (Harris and van Bergeijk, 1962) defined as being within one sixth of a wavelength (van Bergeijk, 1962). Low frequency sounds of 50 to 100 Hz provide an effective near-field range of about 50 to 3 m, respectively (Tavolga, 1971a). Because the lateral line is an array of displacement receptors the fish should be able to get range and bearing information quite readily (Tavolga, 1971b). Localization of far field sounds by fishes appears to be more open to dispute (Popper and Fay, 1973).

While it seems highly improbable that homing O. maculosus are responding to far field sound sources, near field effects may be of greater importance. Whether information received by the lateral line can do more than prevent the fish swimming into obstacles and being swept out to sea, that is, maintaining the general movement of the animal, is difficult to assess. It is possible that tidepools have specific characteristic water movements which can be detected and discriminated by O. maculosus. Whether areas between tidepools have specific recognizable water movement characteristics, given weather and sea state changes seems more doubtful, although if at least general direction (perpendicular to tidal flow) and

general area can be perceived, the use of vision or olfaction to recognize specific pools may be involved. Although to my knowledge, this has not been investigated, it has been suggested that tidepools may have "sounds" which are pool specific (Norman Wilimovsky, personal communication) or specific harmonics (Bruce Leaman, personal communication). If this is the case and if this information can be detected and used by O. maculosus, a further means of recognition of specific pools is available to the fish.

The possibility that O. maculosus may use some kind of crude echo-location to find its way home has not been investigated, but it seems unlikely. It is not known whether this species is capable of sound production although another cottid, Myoxocephalus octodecimspinosus (Mitchill), is known to produce sounds (Barber and Mowbray, 1956). However, Tavalga (1971b) found no evidence to suggest that the sea catfish Galeichthys [=Arius] felis (Linnaeus) was using information from reflections and reverberations of emitted sound to orient itself. However, the ambient level of shallow water noise (Wenz, 1962) and the amount of water movement and degree of turbulence in the intertidal may reduce the effectiveness of any clues perceived by the acoustico-lateralis system.

Investigations of the role of the lateral line are difficult to conduct. A major problem seems to be to find a way of eliminating the perceptiveness of the lateral line. Heat cautery of the lateral line pores and cutting nerves are

difficult on such small fish, and to date, no adhesive has been found which will adhere to the skin of O. maculosus for any period of time. The effects of anaesthetics, such as novocaine, wear off too soon (Abrosimova, 1975, 1976). Even if a satisfactory method could be found to eliminate the sensory perceptiveness of the lateral line, and if this resulted in poor homing performance, it might be difficult to conclude that the lateral line was involved in homing since the perception of water movements must be relatively important to a fish living in the intertidal zone. Eliminating the ability to perceive these movements might result in the fish being unable to maintain itself at all in such an environment.

Since intertidal fish live in an area where pressure changes can be considerable and depth detection may be of some importance, the possibility that these factors are involved in the homing of O. maculosus cannot be excluded. In a brief examination of response to pressure, six fish (from 1.2 to 5.0 cm) from First Beach were placed in a plexiglass tank in which the pressure could be adjusted, by manipulating by-pass valves connected to a mercury column and the pressure tank. After allowing the fish to acclimate for several minutes, the pressure was slowly increased from sea level to 1.8 atmospheres. The pressure was then rapidly raised and lowered providing pressure fluctuations of 4 m (simulating large waves). Both tests were performed under light and dark conditions. In none of the tests was there any overt reaction by the fish to pressure changes.

The majority of fish remained in their initial positions in the tank, and although a few fish occasionally moved, the movement did not immediately follow pressure changes.

O. maculosus in the laboratory have been shown to display a tidal rhythm of locomotor activity the peak and midpoint of which coincide with high tide (Green, 1971c). He suggested that the possible synchronizer of the activity rhythm was hydrostatic pressure, since temperature, turbulence and salinity are too dependent on sea and weather conditions to be reliable synchronizers. Gibson (1971) found that experimental pressure cycles were capable of entraining a tidal activity rhythm in arrhythmic Blennius pholis individuals as well as altering the phase of an existing rhythm.

Thus while there is some circumstantial evidence, from Green's work, to suggest that O. maculosus perceives pressure changes, the nature of the mechanism is not clear. While detection of pressure changes is possible in fish with swim bladders, O. maculosus like all cottids, does not possess a swim bladder. However at least two larval teleosts lacking swim bladders have been shown to respond to pressure changes, Pleuronectes platessa Linnaeus and Centronotus gunnellus (Linnaeus), although they do not appear to be as sensitive as larvae possessing swim bladders, for example, Blennius pholis (Qasim et al., 1966). Pressure responses in invertebrates lacking gas-filled organs are well known (Knight-Jones and Morgan, 1966). Green (1971c) points out that Morris and

Kittleman (1967) reported two species of fish which have piezoelectric otoliths¹ which they suggest may be a mechanism of pressure reception. Further, Shamos and Lavine (1967) suggest that piezoelectricity may be a universal property of all living tissue.

Although the role of pressure and depth detection in homing cannot be evaluated from this study, other clues would be required to home since no account is taken of direction and since pools at the same vertical height will be at the same depth at high tide.

The possibility that inertial navigation might be implicated in the homing of O. maculosus seems unlikely. According to this hypothesis, the animal keeps track of all outward movements (directly recording acceleration, integrating acceleration with respect to time to obtain velocity, and integrating again with respect to time to obtain distance) in order to either retrace precisely the outward journey back home or to calculate the course back home (Barlow, 1963; Keeton, 1974).

The former possibility (precisely retracing the outward journey) can easily be ruled out for O. maculosus. Animals collected at First Beach (and at the majority of other

¹Otoliths with a crystalline arrangement such that when a mechanical stress (pressure) is applied, an electromotive force is generated.

sites) were transported to and from the laboratory by foot and by boat, taking either of two possible routes. The fish were kept at least overnight in the laboratory and were moved around for tagging and other purposes.

The second alternative (calculating the course back home) requires that the fish "know" or calculate the geographical coordinates of the home and release sites and "compute" a path, not necessarily direct, home. The majority of investigations of this possibility have been conducted with birds and although the available evidence is largely negative, the possibility cannot be eliminated (Schmidt-Koenig, 1965; Keeton, 1974). However birds carried to the release sites on turntables, in lightproof drums, under deep anaesthesia or with surgical lesions of the vestibular apparatus (the presumed principal detectors of acceleration) showed no difference in initial bearings or homing successs from controls (Keeton, 1974). Moreover, the threshold acceleration to which vertebrates respond ($.5^\circ/\text{sec}$ and $6 \text{ cm}/\text{sec}^2$) is three to four orders of magnitude greater than that which would be tolerated in a precision system (Harden Jones, 1968).

The possibility that fish may make use of such a system has not been examined. However, Kleerekoper et al. (1969) found that in the absence of directional cues, Carassius auratus (Linnaeus) maintains a nearly constant relationship between right and left turns (that is, cumulative left and right turns are nearly symmetric) over thousands of turns of varying

magnitude, direction and sequence. This suggests that once a direction is established continuous compensation of angle of turn occurs and the direction can be maintained for some period (11 hours). The authors suggest that this ability may be important in long range orientation if the initial direction was established by other clues.

However in the presence of tides and currents the position of the fish may be altered at a rate below the perception threshold of angular acceleration and the fish would soon be swimming on a different course. Other clues would be required to maintain position (Tesch, 1975). Since the movement of O. maculosus appears to be composed of short hops rather than long swims, and since tidal flow and currents would be present at times of homing, inertial navigation without the rather extensive use of other directional clues seems unlikely.

The possibility that O. maculosus uses an electric sensory mechanism in orientation is unlikely, since electric receptors have yet to be identified in the majority of teleosts. For the same reason and the short distances involved, as well as the absence of any evidence in favour of the hypothesis (McCleave et al., 1971), the possibility that information derived from the earth's magnetic field is used in orientation by O. maculosus is unlikely. In either case, other information is required to recognize the home pool.

VIII. GENERAL DISCUSSION

1. Variability in homing behaviour

This study has shown that homing behaviour of O. maculosus differs between areas and that this variability can be related to turbulence and the roughness of the topography. With decreasing turbulence and regularity of the terrain, fidelity is shown to an increasingly large area. Homing success increases and the percentage of fish remaining in the transplant area decreases with decreasing turbulence and topographical irregularity in tidepool areas, but in inlets, very few fish home or remain in the transplant area. The fish which do home in turbulent rough areas show the highest percentages returning to the home pool, compared with other tidepool areas. It does not seem unreasonable to extrapolate from this finding to suggest that at least some of the variability in homing behaviour observed within any one area is partly a function of the turbulence of particular pools and the nature of the topography surrounding the pools. In addition to the variability which appears to be related to turbulence and topography, size or age related variability in homing appears to exist, so that homing success increases with age up to about 2 years and then declines. The percentage of fish remaining in the transplant area decreases with age except for the oldest fish.

The variability in homing behaviour may be associated with the significance of such behaviour. Two major reasons have been put forward for the function of homing in intertidal fish. Williams (1957) suggested that homing serves to prevent the fish from being stranded at low tide in unfavourable situations such as on dry land or in pools that disappear through subsurface drainage. Green (1971b) and Khoo (1971) suggested that it may serve as a stabilizing mechanism for population distribution and balanced utilization of resources in the intertidal. Space or the availability of tidepools appears to be the main resource involved in the distribution of O. maculosus. If dispersal and establishment of home occur early in the life of the fish and if strict fidelity to the adopted home is maintained throughout adult life, these factors added to a homing mechanism would ensure an balanced exploitation of the environment. Conversely, an inflexible homing mechanism would be disadvantageous to the species, since turbulent conditions may result in complete annihilation of the population. However, the 'non-homers' which may provide the adult recruits in tidepools may serve a dispersal and repopulation function.

Both suggested reasons have some validity. However, selection against the kind of mistake suggested by Williams would seem to be severe. Knowledge of those characteristics of a pool which make it an acceptable place at low tide, would seem to be all that is required, and homing to a particular pool for

this reason would seem to subject the fish to unnecessary risk. In inlet areas, a restricted home range and inflexible homing behaviour conceivably could result in stranding, unless the home range encompassed a vertical transect which allowed the fish to move seawards with the falling tide.

With regard to the second reason, it appears that pool fidelity and homing behaviour is very closely associated with the degree of risk involved in movement around a particular area. In rough areas, where movement between pools at high tide may result in population reduction, such movement is not shown, and displacement to other pools appears to result in adoption of the new pool as the home area. Only where the danger of being lost from the population by movement between pools is reduced, is there an increasing amount of movement and homing behaviour. Thus in each area, the kind of homing behaviour shown can be related to the maintenance of the local population, and because it results in a balanced distribution of fish throughout the intertidal, allows the even utilization of resources.

Although the question of 'non-homing' fish in tidepool areas was not directly addressed, information from this study provides a number of suggestions concerning their derivation and function. There appear to be several categories of non-homing fish: those in turbulent, rough areas which adopt the new pool when displaced, those from sheltered (frequently high) tidepools which appear to show little area fidelity or homing behaviour but move extensively between pools, those fish which are never

seen again after displacement, and juvenile fish which move relatively widely around the intertidal before adopting a home range.

Since there appears to be a "space" factor of some sort involved in the determination of pool numbers of O. maculosus (John Green, personal communication; personal observation) the relatively extensive movements of juvenile fish prior to the adoption of a home range may permit the "balancing" of pool population numbers over relatively wide areas. Those fish which adopt the transplant pool as the new home pool provide a dispersal and repopulation mechanism in turbulent rough areas, and those from sheltered pools which show extensive movement presumably serve a similar function in less rough areas. However, the limited data from this study suggest that this latter category of fish continue to move around widely even when they encounter more exposed pools. If these fish are accidentally displaced or move to a lower pool and are caught and used in a homing experiment, they may be the fish which do not show homing behaviour, possibly moving elsewhere on the beach or being subject to mortality by moving out of a tidepool during turbulent conditions. The fate of fish which are never seen again is unknown; mortality, dispersal out of the study area or predation appear to be the alternatives.

In inlets, little area fidelity and homing behaviour are shown. The relative absence of turbulence and the topographical regularity of such areas allows relatively

unrestricted lateral movement and a considerable amount of vertical movement. It is suggested that these factors and the seasonal instability of inlet populations (believed to be largely a result of the seasonal turbulence and instability of food and shelter resources) contribute to the relative absence of home range fidelity and homing behaviour in such areas. In addition to the possibility of being stranded at low tide, the fact that movement is both possible and and subject to little risk of being swept away for a large part of the year, suggests that the adoption of a small home range and homing behaviour serve little purpose. When food and shelter resources disappear at the most turbulent times of year, the maintenance of a home range would subject the fish to unnecessary risk. This may be the reason for the winter dispersal of many inlet fish (presumably to deeper water). Another factor which may contribute to the absence of homing behaviour in inlets is that of predation, which is believed to be much more important in inlet areas than tidepool areas. Herons, gulls, kingfishers and other birds have frequently been observed feeding in such areas and presumably at least some of the prey is O. maculosus. Possible fish predators, Artedius fenestralis and Leptocottus armatus, have been caught (sometimes in greater numbers than O. maculosus) in all the sheltered areas studied. The adoption of a small home range and inflexible homing behaviour might well disadvantageous for the avoidance of predators.

Thus the kinds of movement shown by O. maculosus may

be closely related to the demands for survival imposed by a particular area, and in this way determine a balanced population distribution and resource utilization.

2. Sensory mechanisms involved in homing behaviour

The mechanism(s) used by O. maculosus to home are still unclear. Movement from the release to the home pool appears to be directed, rather than involving some kind of expanded search process, and there is a suggestion that attributes of the pool are recognized by the fish, rather than the position of the pool. Olfaction and vision are known to be involved in homing behaviour, particularly in its acquisition. However, in adults neither appears to be essential for successful return to the home range.

The turbulence of the intertidal suggests that olfaction (and possibly also vision) cannot be used over any distance. Thus it seems that the use of olfaction may be restricted to recognition of the home pool, and possibly other pools also. Presumably vision is concerned with the recognition of landmarks of some sort, although whether this is confined to home range recognition or involves wider areas is unclear. Although this study failed to show that either visual home pool landmarks, or olfactory clues from the home pool were recognized by the fish, neither can be eliminated as possible, for the

reasons discussed earlier. A "memory" of the odours and landmarks of particular pools and their relative positions in the intertidal may be established during the period of extensive juvenile movement. Specific water movement characteristics of pools and areas between pools may also be learned. In addition, detection of when the transplant pool, as opposed to the home pool, is flooded may provide an indication of the relative height of the transplant pool in the intertidal, and the fish, using directional information from tidal flow currents, may be able to swim from "pool" to "pool" to return to the home pool.

Although no evidence has been found implicating other senses, the possibility cannot be ruled out. The work on homing pigeons has demonstrated that a number of mechanisms are available for homing, and most importantly, that different mechanisms may be used under different conditions (Keeton, 1974). Further, there may be differences between individual animals at any one time, regardless of changes over time or in conditions, in the mechanisms used in homing. The variability in homing behaviour between areas due to turbulence and topography, suggests that the relative importance of different senses may be very different between areas. Certainly, the results of Khoo's (1971) work and this study suggest that olfaction is more important to homing at Port Renfrew than at First Beach.

Emlen and Keeton (Adler, 1971; Keeton, 1974) have pointed out that cues which may be essential in the ontogenetic

development of orientation and homing behaviour may not be essential to adults, and even if the same set of cues is being used, the relative importance of the cues may differ for juveniles and adults. This study has shown that both vision and olfaction are essential to the homing of juvenile O. maculosus but vision and subsequently olfaction apparently become unnecessary, at least at First Beach. This does suggest that these senses may be essential to "learning" the area, but once other senses have acquired sufficient information, they can be used quite successfully in the absence of either vision or olfaction. Associated with this are the differences in homing behaviour between areas and the apparently different sizes (ages) at which fish begin to show homing behaviour in different areas. The relative importance of different senses may be very different in the ontogenetic development of homing behaviour in areas of differing turbulence.

IX. SUMMARY

Variability in homing behaviour in different areas

The majority of O. maculosus at First Beach showed evidence of home range fidelity, with equal proportions of fish showing fidelity to one particular pool as to a small group of pools. Of the latter group, the majority showed greater fidelity to one of the pools in the group than the other pools. The majority of O. maculosus displaced at First Beach showed evidence of homing behaviour, although variability in the percentages homing was observed. The majority of homing O. maculosus returned to the initial pool of capture. Variable but sometimes considerable percentages of transplanted O. maculosus remained in the transplant area, some for extensive periods of time.

In Grappler Inlet, O. maculosus displayed little evidence of restricted home range fidelity or homing behaviour. Variable but low percentages of fish remained in the transplant area. Homing across the deep water of the inlet was found to be impossible.

Differences in homing behaviour between O. maculosus at First Beach, Grappler Inlet and Port Renfrew were initially believed to be related to exposure, as determined by location and observation. Further examination of homing behaviour at different areas showed that differences in homing behaviour

could be related to wave action (turbulence) and the roughness of the terrain. With decreasing turbulence and increasing regularity of the terrain, fidelity is shown to an increasing number of pools or a wider area. In tidepool areas, increasing percentages of fish show homing behaviour. The fish which do home in turbulent rough areas show the highest percentages of homing fish returning to the home pool. In inlets, little homing behaviour is expressed. With decreasing turbulence and increasing regularity of the terrain, decreasing numbers of fish remain in the transplant area. These findings can be related to the reduced high tide activity of O. maculosus in turbulent areas shown by Green (1971b,c).

Age, length and year-class differences in homing behaviour

There is an increase in the percentage of O. maculosus successfully homing from age 1 to age 2 fish. Age 3 fish show a decline in the percentage successfully homing. All ages of fish show equal percentages of homing fish returning to the home pool. There is a decline in the percentage remaining in the transplant area with age. There do not appear to be any year class differences in homing behaviour.

Examination of the age related differences in homing behaviour by smaller size classes shows an increase in the percentage of fish successfully homing with length up to about 5 cm. Between 5 and 7 cm, homing is best expressed and there seems to be some decline in the percentage successfully homing

with the largest size classes of fish. All size classes appear to show equal percentages of homing fish returning to the home pool. There is a decline in the percentage remaining in the transplant area with length, except for the largest size classes. Juvenile fish (about 2.3 to 2.7 cm) which have just moved down into lower tidepools, show extensive movement between pools and it is suggested that at this time they begin to "learn" and "memorize" the area. By the time they are about 3 cm long, the fish are beginning to show some evidence of home range fidelity and homing behaviour.

Sensory mechanisms involved in homing behaviour

There is no evidence that touch or taste receptors in the paired fins and possibly taste receptors located elsewhere are involved in homing. There is no evidence that density, "space" or behavioural interactions in the transplant pool have any effect on homing performance. Limited evidence was found to suggest that homing is a directed movement from the release pool to the home pool.

Both vision and olfaction are involved in homing, a combination of blindness and anosmia being the most effective in reducing homing success to low levels. It is suggested that the fish are unable to home until one of these senses is available. Both senses are essential to the successful homing of juvenile fish but vision seems to become unnecessary before olfaction. Although it appears that the homing fish recognize some

attributes of the home pool, rather than the position of the pool, neither conspicuous visual landmarks in the pools nor olfactory clues emanating from home pool water were shown to be recognized by O. maculosus. It is suggested that the relative importance of sensory mechanisms may alter in both the ontogeny of homing behaviour and between areas.

Morphological differences between fish in different areas

There are no consistent differences in meristic or morphometric characters between O. maculosus in the areas studied, which can be related to exposure or homing behaviour. There is a variable increase in the number of cirri, on all parts of the body with length and age, but there are no apparent differences between year classes in the number of cirri. There are differences in the relationship between cirri and length and age from O. maculosus in different areas but these do not appear to be related to exposure. The function of the cirri is unknown. They do not possess any sensory receptors detectable by light microscopy.

Age determination in O. maculosus

Otoliths were shown to be a valid method of age determination in O. maculosus by comparison of results from vertebrae and length frequency analysis. Ageing studies revealed that at any one time there are two main age groups in the population with increasingly smaller numbers of age 3 and 4

fish. Age-length regressions for O. maculosus from different areas showed differences between areas, but these could not be related to a particular factor.

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XI. APPENDICES

Appendix 1Descriptions of study sites

Major study site: First Beach

At the south end of the beach there is a rocky shelf situated below a small steep gravel beach. In the lower intertidal Hedophyllum sessile is abundant. Moving up the intertidal, Ulva spp. and Porphyra perforata occur, giving way to the Fucus zone in which most of the study pools occur. Higher than the Fucus zone some patches of Enteromorpha sp. can be found.

In the tidepools, Prionitis sp. is most abundant. Also occurring are Iridaea spp., clumps of Phyllospadix scouleri (especially in the lower pools), Cladophora sp., coralline algae, particularly Corallina vancouverensis, and in the higher pools, Gigartina sp..

In the Fucus zone and lower, extensive beds of Mytilus californianus occur. M. californianus is also present in lower tidepools along with some M. edulis. Littorines and Tegula funebris are extremely numerous in most study pools. Limpets that are present include Notoacmaea persona, N. scutum,

Collisella digitalis and C. pelta. Balanus glandula is extremely common, and some B. cariosus can be found. Anthopleura xanthogrammica and A. elegantissima are very abundant, particularly in lower pools. The hermit crabs, Pagurus hirsutiusculus and P. granosimanus are common and Hemigrapsus nudus can also be found. Some Pisaster ochraceus, Strongylocentrotus purpuratus and occasionally S. droebachiensis occur in lower pools.

Along the west coast of Vancouver Island, about 26 species of fish are commonly found in tidepools, of which about 14 species belong to the family Cottidae, the remaining species being composed primarily of species from the families Stichaeidae and Pholidae, with a few representatives from the families Liparidae, Gobiesocidae and Hexagrammidae (Green, 1967; Chadwick, 1976; personal observation). The most abundant fish in all tidepool areas studied was O. maculosus. The only other fish at First Beach regularly trapped was Clinocottus globiceps but this species was not nearly as numerous. O. snyderi and Anoplarchus purpurescens Gill were captured occasionally.

Exposed study sites: Cape Beale, Port Renfrew, Benson Island, Pachena Point, Kirby Point

In all areas the lower intertidal is characterized by large beds of the California mussel, Mytilus californianus and the goose neck barnacle, Pollicipes polymerus. Hedophyllum sessile is abundant at these levels and Postelsia palmaeformis

occurs on exposed rocky outcrops, except at Kirby Point.

Moving up the intertidal, Fucus sp. (and at Pachena Point, Endocladia sp. and Cladophora sp.) surrounds the more seaward study pools, except at Cape Beale and Kirby Point where Mytilus californianus and Pollicipes polymerus cover the shelves. At higher levels, the study sites are bare or have a scattered covering of Enteromorpha spp. Littorines are numerous at these levels at both Pachena Point and Botanical Beach.

In the pools themselves, Phyllospadix scouleri, Codium fragile and Prionitis sp. are common in all areas. At Botanical Beach and Pachena Point, the pools are extensively covered with corallines. The pools at Kirby Point are comparatively bare except for clumps of Pollicipes polymerus.

Invertebrates typically found on exposed rocky shores which were found in pools in all areas include M. californianus, Strongylocentrotus purpuratus (particularly at Pachena Point), S. droebachiensis, Anthopleura xanthogrammica, A. elegantissima (except at Kirby Point), Collisella pelta, Katherina tunicata and Pisaster ochraceus. At higher levels in and around the pools, Balanus glandula and B. cariosus were present.

Again, O. maculosus was the most abundant fish species in the tidepools. Other fish trapped at the study sites included Clinocottus globiceps, C. embryum, O. snyderi and Aselichthys rhodorus Jordan and Gilbert.

Moderately exposed study sites: Helby Island, Haines Island (southeast side)

Both study sites lie in the Fucus zone. Amongst the Fucus, Cladophora sp. and Leathesia difformis are present. At Haines Island, patches of corallines, Halosaccion glandiforme and Ulva spp. also occur.

The pools in both areas are lined with gravel and mussel shells and the predominant algae at both sites is Prionitis spp. Corallines, Fucus spp., Phyllospadix scouleri and at Haines Island, Ulva spp. also occur. Invertebrates to be found in pools at both sites include Mytilus californianus, M. edulis, Anthopleura xanthogrammica, A. elegantissima, Notoacmaea persona, N. scutum, Collisella digitalis, Hemigrapsus nudus, Pagurus spp., Tegula funebris and Mopalia spp. and in a few of the lower pools at Haines Island, Strongylocentrotus purpuratus. At higher levels in both areas, Balanus glandula, B. cariosus and littorines are common.

Fish species caught or observed at these sites were similar to those at First Beach, except that on two occasions at Helby Island, Gasterosteus aculeatus Linnaeus were observed in several high shallow tidepools.

Sheltered study sites: Grappler Inlet (bay and mudflat), Rance Island, Dodger Channel, Haines Island (large tidepool)

The substrate in the bay in Grappler Inlet consists of

boulders and rocks of various sizes over a mixture of crushed shell, gravel and mud. Clumps of Mytilus edulis, Fucus sp., Polysiphonia collinsii, Leathesia difformis and Enteromorpha sp. are found on the rocks and stones. The area is somewhat similar to the channel behind Rance Island except that the Rance Island site is muddier and the predominant algae are Fucus sp., Rhodomela larex and Gracilaria sp. Balanus glandula, B. cariosus, Pagurus spp., Hemigrapsus sp., and Notoacmaea persona are common in both areas. Pycnopodia helianthodes is common in Grappler Inlet but not at Rance Island and the reverse is true for Thais lamellosa and shells of Tresus capax, Saxidomas giganteus and Crassostrea gigas.

The mudflat in Port Desire supports a considerable bed of eelgrass, Zostera marina, covered with Smithora naiadum. A beached fish boat and several waterlogged logs at the study site have outcroppings of Mytilus edulis, Fucus spp. and Balanus glandula. The other most obvious invertebrates are Hemigrapsus nudus, Pagurus sp., Mopalia sp., Thais lamellosa, Pisaster ochraceus, Pycnopodia helianthodes, Cucumaria miniata and Tresus capax.

The two sites on Haines Island have similar substrates of sand and mud with small stones and embedded rocks and rocky outcrops. There is a small eelgrass bed in the large tidepool and in summer months this and the extensive bed in Dodger Channel are covered with Smithora naiadum. Fucus sp. and Ulva sp. occur on rocky patches at both sites while Halosaccion

glandiforme is common in Dodger Channel and Enteromorpha sp. in the large tidepool. Mytilus edulis, Balanus glandula, B. cariosus and shells of Tresus capax, Saxidomus giganteus and Protothaca staminea are found in both areas. Notoacmaea scutum, Pagurus spp., Hemigrapsus sp. and Dermasterias imbricata are common in the tidepool while Anthopleura elegantissima is extremely numerous in Dodger Channel.

The pool at Rance Island is somewhat similar to the pool on Haines Island with a muddy, sandy substrate and large boulders scattered throughout. Fucus sp., Ulva sp., Mytilus edulis, Balanus glandula, Notoacmaea scutum, N. persona and Mopalia sp. occur in the rocky areas. Pagurus sp. and Hemigrapsus sp. are numerous.

While O. maculosus was the most numerous fish at certain times of year in all areas, relative to tidepool areas other fish were more abundant in sheltered areas. At the bay in Grappler Inlet, Artedius fenestralis, Coryphopterus nicholsi (Bean) and Nautichthys oculofasciatus (Girard) were frequently caught, although they were never as numerous as O. maculosus. Gasterosteus aculeatus and Aselichthys rhodorus were also trapped occasionally. At the mudflat in Grappler Inlet, G. aculeatus was sometimes numerous, and A. fenestralis, A. rhodorus and Isopsetta isolepis (Lockington) were occasionally caught. At Rance Island, Leptocottus armatus were sometimes trapped in greater numbers than O. maculosus. G. aculeatus were frequently caught there, and less frequently,

Pholis laeta (Cope), P. ornata (Girard), A. fenestralis and small Porichthys notatus Girard. In the large tidepool on Haines Island and at the eastern of the Dodger Channel eel grass bed, L. armatus was commonly trapped along with occasional Clinocottus globiceps. At the western end of the eel grass bed, Hexagrammos decagrammus (Pallas) was the only species caught.

Note: For descriptions and pictures of the invertebrates and algae referred to above, see any general reference on intertidal biology such as:

Carefoot, Thomas.

1977. Pacific Seashores. J. J. Douglas Ltd., Vancouver, B. C. 208 pp.

Kozloff, Eugene N.

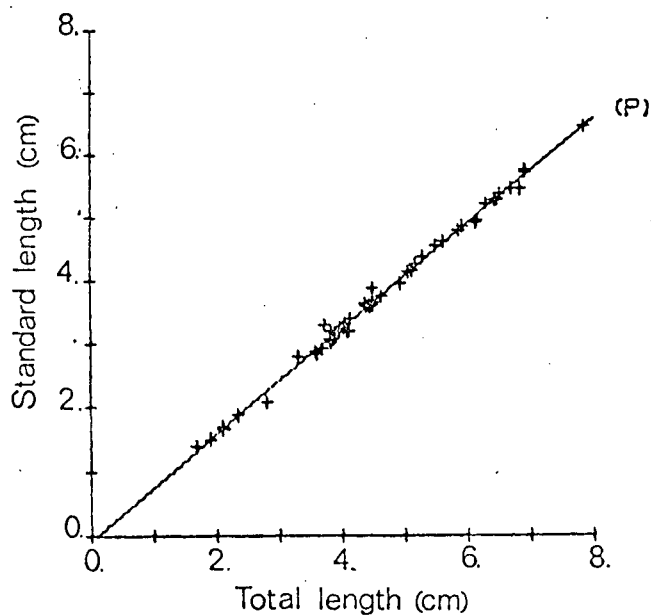
1973. Seashore life of Puget Sound, the Strait of Georgia and the San Juan Archipelago. J. J. Douglas Ltd., Vancouver, B. C. 282 pp.

Ricketts, Edward F. and Jack Calvin. Revised by Joel Hedgepeth.

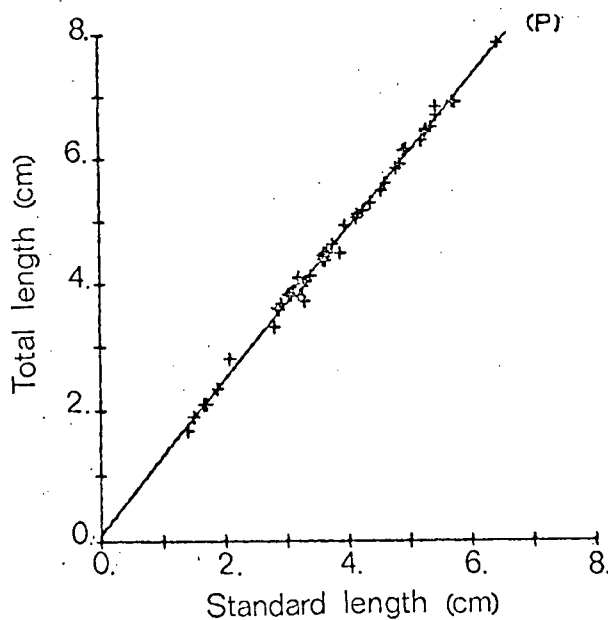
1968. Between Pacific Tides. Stanford University Press, Stanford, California. 614 pp.

Appendix 2Conversions of total length (TL) to and from standard length (SL)

TL to SL: $SL = -.08132 + .8343TL$ (N=58)



SL to TL: $TL = .1180 + 1.193SL$ (N=58)



Appendix 3

Algae and invertebrates from experimental tank

Exposed side

Chlorophyceae

Ulva expansa (Setchell) Setchell and Gardner
Enteromorpha linza (L.) C. Agardh
Proropsis plumosa (Hudson) C. Agardh
Spongomorpha saxatilis (Ruprecht) Collins

Phaeophyceae

Nereocystis luetkeana (Mertens) Postels and Ruprecht
Macrocystis integrifolia Pory
Egregia menziesii (Turner) Areschoug
Desmarestia ligulata var. ligulata (Lightfoot) Lamouroux
Laminaria ephemera Setchell
Laminaria saccharina (Linnaeus) Lamouroux
Eisenia arborea Areschoug
Agarum sp. (Bory) Postels and Ruprecht

Rhodophyceae

Antithamnion kylinii Gardner
Porphyra miniata (C. Agardh) C. Agardh
Rhodomenia pertusa (Postels and Ruprecht) J. Agardh
Callophyllis firma (Kylin) Norris
Iridea cordata (Turner) Bory
Fauchea laciniata J. G. Agardh
Antithamnionella glandulifera (Kylin) Wollaston
Platythamnion pectinatum Kylin

Cirripedia

Balanus cariosus (Pallas)
Balanus rostratus alaskensis Pilsbry

Gastropoda

Collisella pelta Rathke
Notoacmea parsona Rathke
Notoacmea scutum (Rathke)
Calliostoma ligatum Gould
Littorina scutulata Gould
Littorina egg masses
Lacuna carinata Gould
Lacuna egg masses
Margarites pupillus (Gould)
Lirularia lirulata (Carpenter)

Calm side

Chlorophyceae

Ulva expansa (Setchell) Setchell and Gardner
Enteromorpha sp. Link

Rhodophyceae

Callophyllis firma (Kylin) Norris

Cirripedia

Balanus cariosus (Pallas)
Balanus rostratus alaskensis Pilsbry

Gastropoda

Collisella pelta Rathke
Notoacmea parsona Rathke
Notoacmea scutum (Rathke)
Calliostoma ligatum Gould
Littorina scutulata Gould
Littorina egg masses
Lacuna carinata Gould
Lacuna egg masses
Margarites pupillus (Gould)
Lirularia lirulata (Carpenter)
Cerastostoma foliatum (Gmelin)
Velutina laevigata Linnaeus
Amphissa columbiana Dall

Ascidacea

Corella willmeriana Herdman

Bivalvia

Chlamys rubida Hinds

Mytilus edulis Linnaeus

Mytilus californianus Conrad

Holothuroidea

Cucuraria pseudocurata Deichmann

Calcarea

Scypha sp.

Bryozoa

Amphipoda

Caprellidae

Polychaeta

Nereis procera Ehlers

Spirorbis sp.

Platynereis bicanaliculata (Baird)

Ascidacea

Corella willmeriana Herdman

Bivalvia

Chlamys rubida Hinds

Mytilus edulis Linnaeus

Mytilus californianus Conrad

Anthozoa

Anthopleura elegantissima Brandt

Calcarea

Scypha sp.

Bryozoa

Amphipoda

Caprellidae

Polychaeta

Capitella capitata (Fabricius)

Spirorbis sp.

Platynereis bicanaliculata (Baird)

Nereis neoneanthes Hartman

Harmothoe imbricata (Linnaeus)

Oligochaeta

Enchytraeidae

Isopoda

Munna sp.