A FIELD STUDY OF THE DISTRIBUTION AND BEHAVIOR OF OLIGOCOTTUS MACULOSUS GIRARD, A TIDEPOOL COTTID OF THE NORTHEAST PACIFIC OCEAN

by

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ABSTRACT

The study was concerned first of all with the distribution pattern at low tide of <u>Oligocottus maculosus</u> Girard and other cottid fishes inhabiting tidepools on the west coast of Vancouver Island, B.C. Five species (<u>O. maculosus</u>, <u>O. remensis</u>, <u>Clinocottus acuticeps</u>, <u>C.</u> <u>embryum</u> and <u>C. globiceps</u>) have their centers of distribution in the intertidal zone. Seven species (<u>Hemilepidotus hemilepidotus</u>, <u>Artedius</u> <u>lateralis</u>, <u>A. fenestralis</u>, <u>Ascelichthys rhodorus</u>, <u>O snyderi</u>, <u>Enophrys</u> <u>bison</u> and <u>Leptocottus armatus</u>) inhabit tidepools but are most abundant in the subtidal zone.

O. maculosus is the most abundant and widely distributed tidepool cottid in the intertidal zone. Only three other species (<u>C. acuticeps</u>, <u>C. embryum</u> and <u>C. globiceps</u>) regularly inhabit tidepools above LLHW (lowest lower high water). The primary environmental factor correlated with the distribution of <u>O. maculosus</u> is exposure to wave action. In exposed transects this species is restricted to the upper intertidal zone, while in sheltered transects it inhabits tidepools throughout the intertidal zone. Observations show that <u>O. maculosus</u> responds to water turbulence by retreating to cover. It is concluded that to inhabit a given tidepool <u>O. maculosus</u> must have a minimum period of low turbulent conditions. This species has 'capitalized' on the tidepool habitat to invade the open coast environment.

The study's second concern was to determine the fidelity of

individual <u>O. maculosus</u> to the tidepool in which they are found. <u>O</u>. <u>maculosus</u> shows fidelity to specific tidepools and will return to these pools when displaced from them. The results indicate that the navigational ability of <u>O. maculosus</u> is not solely dependent upon familiarity with geographical features of the intertidal zone. It is suggested that homing behavior functions as a mechanism stabilizing the spatial distribution of this species.

Thirdly, the study was concerned with determining what factors affect the field activity such as feeding and spawning of <u>O. maculosus</u>, and a comparison of its field activity to that under controlled conditions. In the natural habitat its activity is dependent primarily upon such factors as turbulence, temperature and light. Field observations on feeding behavior support Morris' (1960) conclusion, drawn from physiological studies, that approximately the 16^oC isotherm is the limiting environmental factor in the southward distribution of this species.

Under constant conditions <u>O. maculosus</u> exhibits a tidal rhythm of locomotor activity. The characteristics of the rhythm indicate that it is entrained directly by the tide. Hydrostatic pressure is suggested as the possible synchronizer. The rhythm is not directly related to the field activity of <u>O. maculosus</u>. It is concluded that it represents the coupling of an avoidance or escape response to a biological clock. Such a mechanism would function with, and be partially responsible

for, the homing behavior.

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GENERAL INTRODUCTION

Much descriptive and experimental work has been published during recent years concerning the intertidal and subtidal distribution of plants, primarily algae, and invertebrate animals. Relatively little work of a similar nature, however, has been published on the fishes of these shore zones. Whereas workers in the fields of marine phycology and marine invertebrate ecology are at the stage where they are directing attention towards the dynamic aspects of intertidal biological phenomena, investigators interested in the littoral fish fauna are still lacking adequate descriptions of these phenomena.

A possible reason for the limited attention given to the ecology and behavior of littoral fishes is the difficulty encountered when trying to study them. Unlike plants and many intertidal invertebrates, fishes are typically very mobile once they complete embryological development. Also, except for a relatively few species which can pass through periods of tidal emergence under moist but nonsubmerged conditions, most littoral fishes must remain submerged throughout the tidal cycle. Therefore, diving apparatus is usually required if observations and measurements of environmental parameters are to be made. Aside from the telemetry difficulties involved, such studies can be hazardous at best, even when working in relatively sheltered areas. A physical feature of the shore which tends to concentrate and isolate intertidal fishes is the tidepool. Tidepools along the Pacific Coast of North America usually contain, when they are isolated at low tide, a varied and often abundant assemblage of fishes. Along the west coast of Vancouver Island, British Columbia, about 26 species of fish are commonly found in tidepools. The family Cottidae accounts for the majority of species (about 14) and individuals. The remaining species are primarily blennioid fishes of the families Stichaeidae and Pholidae. Because these fishes are readily accessible when the pools are isolated, and because tidepool parameters can be monitored relatively easily, the tidepool is an ideal unit to focus attention upon in order to increase our fundamental understanding of the ecology and behavior of littoral fishes.

Despite their relative accessibility, the tidepool fishes of the northeastern Pacific have received very little attention except for their systematics. The present investigation of the tidepool fishes of the west coast of Vancouver Island, British Columbia, was undertaken in hopes that at least partial answers to the following questions could be obtained: What is the local distribution pattern of the tidepool fish fauna and how stable is this pattern? How are specific environmental factors correlated with this pattern? What is the relationship between individual fish and the tidepool in which they are found? What are

some of the behavioral mechanisms which lead to the observed distribution pattern and in what way can they be considered as being adaptive?

It became apparent early in the study that it would not be feasible to work with the entire tidepool fish fauna. Consequently, the cottid fishes were selected for study because of their relative abundance in species and numbers, their apparent greater dependence upon the tidepool environment than the blennioid fishes and because their taxonomy has been well established (Bolin, 1944). Similarly, <u>Oligocottus maculosus</u> Girard received more intensive study than any of the other cottids because of its presence and abundance in relatively high, readily accessible tidepools.

The thesis consists of three major sections: Part I describes the local low tide distribution of <u>O. maculosus</u>, the associated tidepool cottids and seasonal population fluctuations in the former species. Part II describes the high tide movements and homing behavior of <u>O.</u> <u>maculosus</u>. Part III describes aspects of the activity of <u>O. maculosus</u> under natural and controlled conditions. A final discussion relates the various aspects of the study.

I. LOCATION OF STUDY AREA

The intertidal area selected for the present investigation is located on the southwest coast of Vancouver Island, British Columbia. It is approximately 5 km southwest of the logging community of Port Renfrew and 400 m southeast of the entrance to San Juan Inlet, in latitude $48^{\circ}32$ 'N and longitude $124^{\circ}27$ 'W (Fig. 1). The site is located on the Strait of Juan de Fuca, but is an open coast with a westerly and northwesterly exposure to the Pacific Ocean.

The region was selected, firstly, because the shore is ideally suited both geologically and biologically for the study of tidepool organisms, and, secondly, because it is undisturbed yet relatively accessible. It was possible to construct research and living quarters at the site. This made it feasible and convenient to carry out <u>in situ</u> experiments and observations throughout the year.

It is of historical interest that the location of the research laboratory was 75 m west of the old site of the Minnesota Seaside Station. This station was operated as a summer marine and terrestrial biological laboratory by the University of Minnesota from 1900 to 1909. In recognition of its early use as a biological research site the shore region is now called Botanical Beach. Despite this early recognition of the uniqueness of the site for the marine investigations, the present study, and others associated with it, represent the

Fig. 1.

Chart showing the southwestern coast of Vancouver Island, B.C., the mouth of the Strait of Juan de Fuca and the northern part of the Olympic Peninsula, Washington. The study site is located at Botanical Beach.



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first time since 1979 that intensive investigations have been conducted there.

II. GENERAL ENVIRONMENTAL CONDITIONS

Geological Features

The geological feature dominating Botanical Beach is a Tertiary sandstone and conglomerate formation. This formation is apparently a remnant of a once extensive coastal plain of Oligocene or early Miocene sedimentary rocks which, according to Holland (1964), probably existed all along the southwest coast of Vancouver Island. Where the formation extends into the intertidal zone benches exist which are several hundred feet long and extend out a similar distance from the high water mark. Local variations in the texture and hardness of the formation have resulted in very irregular surfaces and a large number of tidepools of various shapes and sizes. The following description from the 1906 Annual Announcement of the Minnesota Seaside Station (Anon., 1906) is a rather picturesque but factual account of these pools:

> At mid and low tides a great sandstone shelf is uncovered in which boulders have ground innumerable cistern-like potholes varying in size from mere teacups to great wells, twenty feet across, and thirty or more in depth. These act as natural aquaria and serve to segregate the plants and animal populations, to the very great convenience and instruction of students and collectors. Nothing like this natural formation is known to exist in connection with other

seaside stations.... A great advantage is gained by the extraordinary accessibility of the rich marine flora and fauna.

Where the Tertiary formation has been completely eroded, harder rocks of the Vancouver Group (cf. Hull, 1906 and Clapp, 1917) are exposed. Relatively few tidepools occur in these slate and shale formations, and where they do occur they are usually long, relatively shallow pools which follow the lines of stratification (Fig. 33). A further description of the physiography of the tidepools in the vicinity of the study site is given by Henkel (1906).

The aerial photographs in Figs. 2 and 3, taken during a low water spring tide, show the physical features of the intertidal zone in the vicinity of the field laboratory. In many places the intertidal rock formations end abruptly and drop vertically into ten to twenty feet of water at extreme low tide. In adjacent locations the intertidal zone has an even slope of approximately 20 degrees which continues in the subtidal.

The sandstone benches are mostly free of unconsolidated material but immediately in front of the field laboratory a stretch of the shore approximately 30 m wide is littered with glacially deposited boulders and cobbles. In this same area coarse sand and gravel occur above the 9' tide level.



Fig. 2. Aerial view of the study site during a low water spring tide. Nearly the entire rock formation shown is Tertiary sandstone. The shore facing to the left of the photograph is exposed to Pacific swells. The research facility is located in about the middle of this shore.



Fig. 3. Aerial view of the intertidal zone in front of the research facility (note the position of the tree shadows in Fig. 2). Boulders can be seen littering the intertidal zone in the left side of the photograph. This shore faces westerly with open exposure to Pacific swells.

Temperature of the Sea Water

Almost weekly temperature and salinity readings for the surface sea water at Botanical Beach were made from November 1965 to March 1967. An inductive salinometer (Model RS52, Industrial Instruments Inc., New Jersey) was used for these measurements.

The mean monthly temperature of the surface water for 1966 is shown in Fig. 4. Two features are characteristic. The average temperature is relatively low and the amplitude of variation is comparatively small. The highest temperature (11.8°C) occurred during August and the lowest (6.7°C) during February.

The most southern station on the west coast of Vancouver Island where daily records of surface sea water temperature are kept, is Amphitrite Point (see Fig. 1). For comparison the average mean monthly, surface sea-water temperatures at Amphitrite Point for the period 1935 to 1964 (Hollister, 1966) also are shown in Fig. 4.

Sea water temperature data collected at stations off the mouth of San Juan Inlet by the Pacific Oceanographic Group from October 1951 to October 1952 (Anon., 1955) indicate that there is little temperature variation between the off-shore and on-shore surface sea water in the vicinity of the study site (Table 1).



Fig. 4. Mean monthly temperature of the surface water at Botanical Beach (o-o) for 1966, and the average mean monthly temperature of the surface water at Amphitrite Point (o···o), B.C., for the period 1935-1964 (Hollister, 1966).



Fig. 5. Mean monthly salinity of the surface water at Botanical Beach (o-o) for 1966, and the average mean monthly salinity of the surface water at Amphitrite Point (o···o), B.C., for the period 1935-1964 (Hollister, 1966).

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TABLE I

Surface sea water temperature and salinity data collected at a station near the mouth of San Juan Inlet and at a station approximately 4 km off-shore (Anon., 1955).

	Temperature °C		Salinity /oo	
October 6, 1951	11.17	11.31	29.54	31.10
November 5, 1951	8.85	10.65	31.55	31.95
March 6, 1952	7.20	7.80	31.00	31.30
April 25, 1952	7.85	8.33	31.79	31.91
June 3, 1952	9. 19	9.38	31.52	31.57
August 13, 1952	9.35	9.78	32.09	31.83
September 23, 1952	2 10.25	10.31	31.56	31.44

Salinity of the Sea Water

The mean menthly salinity of the surface water at Botanical Beach for 1966 is shown in Fig. 5. There was a seasonal variation in the salinity of the shore water of approximately 3.0%. The highest salinity (32.35%) occurred during the comparatively dry summer months and the lowest salinity (28.35%) occurred during the wet winter months. This seasonal variation is typical of the west coast of Vancouver Island as shown in Fig. 5 by the average (1935-1964) mean monthly salinity at Amphitrite Point (Hollister, 1966). As with the temperature of the shore water, there appears to be little variation between the salinity of the on-shore and offshore surface sea-water in the vicinity of the study site (Table I).

Meteorological Conditions

Records of maximum and minimum air temperatures at Botanical Beach were kept from October 1965 to January 1967. The mean monthly maximum and minimum air temperatures are shown in Fig. 6. The daily range in temperature is small, the summer being cool and the winter mild. During December 1965 and January and February 1966 minimum temperatures of below freezing were recorded on only eleven days. The lowest temperature was -2.2°C. Temperatures above 18°C were recorded on only five days during the summer of 1966. The highest temperature was 22.2°C.





No continuous records of rainfall were kept at Botanical Beach, but such records are kept at Port Renfrew by British Columbia Forest Products Ltd., who kindly made them available to me. These records for 1965 are presented in Fig. 7. Daily rainfall data are collected at Pachena Point (Fig. 1) and for comparison the average monthly rainfall at this station for 1931-1960 is also shown in Fig. 7.

Annual precipitation all along the west coast of Vancouver Island is high, usually over 85 in. (216 cm) and is characterized by marked seasonality. During the spring and summer the prevailing flow of air from the northwesterly direction is cool, relatively dry and stable. In the fall and winter the high pressure center over the North Pacific weakens and moves south to be replaced by a low pressure center. The prevailing flow of moist winter air is from the southwest on the west coast of Vancouver Island, often easterly in the Strait of Juan de Fuca.

Dense fog is characteristic of the summer months and during July, August and September 1966 it was on shore for at least half the day on an average of ten days per month.

Sea State Conditions

Sea state data were recorded on a semi-daily basis from November 1965 to December 1966 at all times that the study site



Fig. 7. Total monthly precipitation at Port Renfrew (---) for 1965, and average monthly precipitation at Pachena Point, B.C. (---) for the period 1931-1960 (Anon., 1965).

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was occupied. All observations were made from the shore. The height of the swell was measured with a stadia rod graduated in tenths of feet using the horizon as a reference level. These data are presented in Fig. 8 as the percent of the total number of observations made each month that had sea swells of 0-lft., 2-3 ft., and greater than 6 ft.

It is apparent that the sea is considerably rougher in the winter and early spring than in the summer and early fall. These observations correspond with sea state data recorded on a semidaily basis during 1956 by the light ships Swiftsure and Relief (Anon., 1958) at Swiftsure Bank (Fig. 1) off the mouth of Juan de Fuca Strait (Fig. 9).

<u>Tidal Features</u>

At Botanical Beach the tides are of the mixed semi-diurnal type. There is about equal inequality in both the high and low water. Consecutive high tides and consecutive low tides are comparatively equal only during the new moon periods. These features of the tides are evident in the 14-day cycles shown in Figs. 10 and 11.

The two tides of each tidal day depart from a 12.4 hour periodicity by as much as 2.6 hours. The time interval between the lower low water and the higher high water is almost always longer than the time interval between the higher low water and lower high



for 1966 with swells of \geq 6 ft., (o), 2-3 ft. (•) and 0-1 ft. (\checkmark).

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ig. 9. Percent of total observations of sea state at Swiftsure Bank for 1956 with swells of ≥ 6 ft. (o), 2-3 ft. (\bullet), and 0-1 ft. (Δ), (Anon., 1958).




Fig. 11. Computer plotted curve of the tide at Port Renfrew for the period December 19, 1966 to January 2, 1967. First quarter moon is represented by Φ and full moon is represented by O.

water. The tidal day departs from a 24.8-hour periodicity usually by less than 20 minutes and never by more than approximately 48 minutes. The variations in tidal periods and tidal day periods for June and July, 1966 are shown in Fig. 12.

The amplitude of extreme tides is approximately 12.0 feet. A summary of all the tidal features at Port Renfrew is presented in Fig. 13. Curves showing the duration of maximum single emergences and submergences as a function of height in the intertidal zone for the period May 1 to June 14, 1966 were prepared from six-minute tidal predictions for Port Renfrew (Fig. 14). It is apparent that there are definite steps in these curves which are related to particular tidal factors. Fig. 15 shows the percent of the year that various heights in the intertidal zone are covered.

Seasonally there is a change in the time of day at which extreme high and low tides occur. From mid September to mid March the lowest low tides occur in the late afternoon and evening while the highest high tides occur near mid day. From mid March to mid September the lowest low tides occur during the early morning and the highest high tides occur near midnight.

Fig. 12. Diagram showing the relatively small changes in the lengths of the daily tidal periods, i.e., High High Water to Low High Water and Low High Water to Low High Water (upper part of the diagram) as compared with the relatively large changes in the lengths of the semi-daily tidal periods, i.e., High High Water to Low High Water (lower part of the diagram). Times of the high tide are from six minute tidal predictions for Port Renfrew (Canadian Hydrographic Office, Ottawa).



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Fig. 13.

. Tidal factors at Port Renfrew for the period May 1 to June 14, 1966. HHLW equals Highest Higher Low Water, MHHW equals Mean Higher High Water, etc. From six minute tidal predictions for Port Renfrew (Canadian Hydrographic Office, Ottawa).



Fig. 14. Maximum duration of single submergence (o---o) and emergence (o---o)
for various heights in the intertidal zone at Port Renfrew for the period
May 1 to June 14, 1966. From six minute tidal predictions for Port
Renfrew (Canadian Hydrographic Office, Ottawa).



Fig. 15. Percent of the year that various heights in the intertidal zone at Port Renfrew are covered by the sea. From 15 minute predictions of the tide at Port Renfrew for 1966.

III. SPECIFIC ENVIRONMENTAL FEATURES

Methods

Surveying and Levelling

The intertidal zone at the study site was extensively surveyed and levelled during the summer of 1965. Additional surveying and levelling was completed in the spring and summer of 1966. A K&E Paragon transit, Zeiss Self-Levelling level, steel 100 ft. measuring tape and a stadia rod graduated in tenths of a foot were used in these operations.

Fifteen permanent bench marks were established on the shore. They were located from near the lowest water spring tides to above highest water spring tides. As no previously established bench mark was present at this site the heights of the bench marks relative to mean tide level were determined from six minute tidal predictions for Port Renfrew obtained from the Canadian Hydrographic Office, Ottawa. Over a period of several months in the summer of 1966 the times of submergence and emergence of one of the more sheltered bench marks were recorded on days when sea swells were less than one foot. The average of the heights determined in this way was taken as being the height of the bench mark relative to the mean tide level at Port Renfrew.

During the initial and subsequent levelling and surveying operations a large number of tidepools were given identifying numbers and the vertical height of each relative to one of the bench marks was determined. These data were recorded along with notes describing the general physical features, maximum depth and surface dimensions of each tidepool. Maps were also prepared showing the horizontal relationships of many of these tidepools.

Determination of Tidepool Volumes

The volumes of 50 tidepools which had been surveyed and levelled were determined by fluorescene dilution. A known amount of concentrated fluorescene solution was injected into a tidepool with a 50 ml syringe. The pool was then thoroughly mixed with a wooden oar after which a 100 ml sample was taken. The samples were kept in tightly scaled glass jars until they were analyzed. All samples were analyzed within one week after they were taken with a Model 111 Fluorometer, Turner Associates, Palo Alto, California. Values obtained with the dilution technique were found to be within 3% of values obtained by manually emptying pools and directly measuring the volume of the water removed.

Determination of Temperature and Salinity

The same inductive salinometer that was used to measure the temperature and salinity of the shore water was used to monitor temperature and sclinity changes in tidepools. Often, however, when only temperature observations were being made a glass mercury thermometer was used.

A submersible Ry. n 15-day recording thermometer, Ryan Recording Thermometer Company, Seattle, Washington, was used during the summer and fall of 1966 to monitor on a nearly continuous basis the temperature fluctuations in a single tidepool. Another Ryan recording thermometer, an 8-day model, was used several times in conjunction with the above model to compare the temperature characteristics of tidepools at different levels and tidepools of different depths. Each of these thermometers was secured with wire to the bottom of the tidepool in which it was placed.

Determination of Oxygen and pH

Water samples to be analyzed for dissolved oxygen were obtained by siphoning water directly from tidepools into B O D (biological oxygen demand) bottles. The modified Winkler method of oxygen analysis was used (Strickland and Parsons, 1960).

Hydrogen ion determinations were made with a Beckman Model N-2 pH meter, Scientific Instruments Division, Fullerton, California.

Exposure of Tidepools

The degree of exposure of tidepools was determined with a device referred to by Green and Druchl (in preparation) as a surf sensor. The sensor consists of two 13 cm long, 0.6 cm diameter brass rods mounted horizontally 3.8 cm above a 1.3 cm thick, 7.6 cm x 12.7 cm plexiglass plate (Fig. 16). When in operation, a sensor is attached to the substratum at a known vertical height in the intertidal zone by a 1/2 in. bolt through the center of its base. The bolt is screwed into an anchored 1/2 in. diameter Philip shield.

The rods are connected by rubber insulated telephone dropline to a Rustrak Model 91, six volt recorder situated above high water. The gap separating the free ends of the rods is adjusted so that the recorder circuit is completed causing a maximum deflection of the chart stylus when the rods are submerged by the surf or the flooding tide. Conversely, with each emergence of the rods the stylus falls to zero.

By running two or more sensors in conjunction with one another, the relative exposure of different pools or locations in the intertidal zone was determined by comparing the actual time at which a sensor became submerged or emerged with the predicted time of submergence or emergence for that vertical height. The predicted submergence and emergence times were based on six minute tidal



Fig. 16. Surf sensor bolted to the substratum at the 7 ft. tide level. Wires leading to the recorder are at the top of the photograph. Note the abundance of Littorina, Balanus and Acmaea. predictions for Port Renfrew provided by the Canadian Hydrographic Office, Ottawa.

Surf sensor data were used to place pools into one of four exposure categories: sheltered, moderately sheltered, moderately exposed, or exposed. With a 3 ft. on-shore swell, actual flooding of pools in these classes preceded the predicted time of flooding by approximately 1/2, 1-1/2, 2-1/2, and 3-1/2 hours respectively.

Determination of Flora and Fauna

Observations were made throughout the year to assess the dominant flora and fauna of tidepools at different heights and with different exposures. Such observations were generally made at low tide from above the surface of the pool, but in some cases a face mask was used in particularly deep or well-shaded pools. On the basis of all the tidepools observed, organisms were classified as being abundant, common, rare or absent.

The vertical distributions of the dominant exposed benthic algae and invertebrates were determined in the same way as the vertical heights of the tidepools.

Results

Physical and Chemical Features of the Tidepool Environment

In common with organisms living in the subtidal region, tidepool inhabitants are not exposed to periodic intervals of desiccation. In many other respects, however, tidepool environmental factors vary considerably more than do the same factors below the intertidal zone. The rhythmical changes which occur in the physical and chemical properties of tidepools have previously been investigated by a number of workers, notably Klugh (1924), Johnson and Skutch (1928), Gersbacher and Dennison (1930), Humphrey and Macy (1930), Stephenson, Zoond and Fyre (1934), Pyefinch (1943) and Naylor and Sinns (1958).

1. Temperature

Temperature is one of the most obvious and important environmental parameters which shows large fluctuations in tidepools. The temperature range encountered in a particular pool depends primarily upon the degree of isolation of the pool from the sea (Table II). This factor is in turn determined by the vertical position of the pool, its exposure and the sea state. Therefore, just as the maximum length of single emergences is critical in determining the amount of desiccation of the open rock habitat, it is also of direct

TABLE II

Maximum surface temperatures recorded in a series of tidepools on August 15, 1966 in relation to the time of flooding of each pool. The sea surface temperature was 10.66°C.

Tidepool Number	Tide Height of Pool (feet)	Maximum Surface Temperature (°C)	Flooding Time (PDLST)
2005	4.0	11.72	1100
15	5.0	11.96	1200
932	8.5	14.60	1300
102	9.0	17.08	1330
103	8.5	24.00	1500
97	10.0	24.16	1500

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importance relating to the temperature variability of the tidepool habitat.

It is usual, however, that two tidepools equally isolated from the sea will have different temperature characteristics because of differences in factors such as depth and degree of shading. This is evident in Fig. 17 in which simultaneous 6 day continuous records of the bottom temperatures of two pools at the 9 ft. tide level with the same exposure but with different depths are shown. Shading may be due either to plants or other cover within the pool or to obstructions above the pool. Temperatures at the same depth in shaded and nonshaded portions of a single pool have differed by as much as $3^{\circ}C$ when the surface of the pool reached its maximum temperature.

Continuous records of the bottom temperature of a 30 cm deep, moderately sheltered tidepool at the 9 ft. level were obtained for much of the summer and early fall of 1966 (Fig. 18 and 19). These records show the effect of both the daily tidal cycle and the lunar fortnightly tidal cycle on the temperature fluctuations of the pool.

2. Salinity

The salinity of tidepools can differ from the salinity of the sea either as a result of evaporation or of the inflow of water of higher or lower salinity. Evaporation was found to be insignificant



Fig. 17. Comparison of the bottom temperatures of two tidepools with the same exposure and vertical height, but with different depths. The upper chart was in a pool with a depth of 36cm and the lower chart was in a pool with a depth of 94cm.

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Fig. 18. Records from a recording thermometer in a 36cm deep tidepool at the 9 ft. tide level covering parts of June, July and August, 1966. The variations caused by the daily and fortnightly tidal cycles can be seen.





ω L in raising the salinity of tidepools unless the pools were isolated from the sea for weeks at a time. In tidepools completely isolated throughout summy summer days maximum daily increases in salinity of less than 0.4‰ were recorded.

Precipitation can significantly alter the salinity characteristics of tidepools. Table III shows the extent to which the surface salinity of pools is lowered even when there is little or no surface drainage into them. Table IV shows the surface and bottom salinities of pools which have extensive run off entering them. It is evident from both tables that in the absence of active mixing, pools can become strongly stratified with respect to salinity. Because of the heavy rains and subsequent run off which occur, particularly during the winter, some pools and surge channels even at the lowest tide levels may have very low salinities at low tide. Salinities of less than 4.0% were frequently recorded at the 2 ft. level in several surge channels which, at high tide, had salinities of over 28.0 %

3. Chemical Features

Oxygen and pH were not extensively investigated at the study site but sufficient data were collected to substantiate the findings of Klugh (1924), Pyefinch (1943) and Stephenson, Zoond and Fyre (1934). These workers investigated diurnal and tidal changes in dissolved oxygen and hydrogen ion concentration of the tidepool environment

TABLE III

Effect of rain on the salinity of tidepools subject to little surface run off. Pools emerged for less than eight hours.

	Depth of Pool		0.2m	0.5m	<u>l. lm</u>	<u>0.7m</u>	<u>l.5m</u>
· · · · · · · · · · · · · · · · · · ·	Temperature	°C	8,28	8,20	8.00	9. 84	9.56
Surface	Salinity	%00	8.64	6.60	27.24	26.04	9.40
Bottom	Temperature	°C	8.40	8.36	8.08	8.92	9.36
	Salinity	%。	29.20	30,52	31.28	29,56	28.12

TABLE IV

Effect of rain on the salinity of tidepools subject to surface run off. Pools emerged for less than eight hours.

	Depth of Pool		 0.3m	0.3m	<u>0.3m</u>	0.3m
Surface	Temperature	°C	8.96	6.24	7.92	8.60
	Salinity	%.	3.16	16.56	5.88	3.24
Bottom	Temperature	°C	 8,32	7.81	8.86	8.60
	Salinity	700	 27.80	29.08	29.68	28.24

and concluded that the range of variation of these factors is primarily dependent upon the density of the flora. In tidepools in which the ratio of plants to animals is large, dissolved oxygen and pH variations are greater than in pools in which this ratio is small.

Most of the tidepools above the 3 ft. tide level have sparse algal floras, but some tidepools at all tide levels have dense growths of eel grass (<u>Phyllospadix scouleri</u>). Thus, at all levels in the intertidal zone there are pools at any one time with different dissolved oxygen and pH characteristics.

In an attempt to determine whether dissolved oxygen might be a limiting factor in certain tidepools, oxygen determinations were made in several high tidepools which contained large growths of <u>Phyllospadix</u>. Determinations were made during the phase of the monthly tide cycle when the pools were isolated for maximum periods of darkness. The lowest concentrations obtained approximated 15% saturation.

General Features of the Benthic Biota

Very little information has been published concerning the vertical distribution of the intertidal benthic flora and fauna of the west coast of Vancouver Island. The most comprehensive study relating to the site at Botanical Beach is the investigation by Rigg and Miller (1949) in the vicinity of Neah Bay, Washington (see Fig. 1). Widdowson (1965) investigated the vertical and horizontal distributions of a number of intertidal algae and invertebrates along the southwest coast between Port Renfrew and Victoria. Green and Druehl (in preparation) determined the vertical distributions of dominant benthic organisms in three vertical transects at Botanical Beach. These authors were able to relate differences between transects to quantitatively evaluated differences in the exposure of the transects to surf.

The benthic biota at Botanical Beach is that of an open coastal environment. This is typified by the presence of <u>Postelsia palmaeformis</u>, a kelp which is restricted to rocky shores with exposure to heavy surf (Smith, 1944). Few qualitative differences were found during the summer of 1966 between the intertidal flora and fauna at Botanical Beach and at such fully exposed shore sites as Pachena Point on the west coast of Vancouver Island and the west coast of Cape Flattery on the northwestern tip of the Olympic Peninsula, Washington. The transition from open coast to sheltered coast along the southwest coast of Vancouver Island between Port Renfrew and Victoria is exemplified by the shoreward boundaries of open coastal forms and the seaward boundaries of sheltered forms (Widdowson, 1965).

The more conspicuous biotic features of the intertidal zone at the study site are shown in Fig. 20. The division of the shore into the upper intertidal zone and the lower intertidal zone is



Fig. 20. Dominant features of the distribution of the intertidal benthic flora and fauna at Botanical Beach.

arbitrary but useful. The lower intertidal zone is characterized by a cover of kelp which has its upper limit at about the 6 ft. tide level. This height corresponds with several tide factors as can be seen in Fig. 11. <u>Hedophyllum</u> dominates the lower intertidal zone except in very exposed transects where it is largely replaced by <u>Alaria nana</u> and <u>Lessoniopsis</u> (Fig. 23).

The upper intertidal zone, on the other hand, is mostly devoid of algal cover (Figs. 21 and 22). Only in very exposed transects, where <u>Postelsia</u> occurs (Fig. 23), and in sheltered transects where <u>Fucus</u> occurs, is algal cover present. The upper intertidal zone is characterized primarily by three invertebrate genera: <u>Acmaea</u>, <u>Littorina and Balanus</u> (Fig. 20).

Several species of subtidal algae such as <u>Laminaria setchellii</u>, <u>L. ephemera</u>, <u>Pterygophora californica</u> and <u>Pleurophycus</u> have upper levels at about the 1 ft. to 2 ft. tide levels. Because of the essentially subtidal character of the flora and fauna at these levels, they are considered as part of the subtidal zone. It is not justified, as Lewis (1964) points out, to extend the intertidal zone to the limits of the extreme low tides.

The benthic biota surrounding a particular tidepool depends upon the location of the pool. Tidepools in the upper and lower intertidal zone typically contain little algal cover aside from that



Fig. 21. Moderately exposed to moderately sheltered transect showing upper and lower parts of the intertidal zone. The band of kelp is primarily <u>Hedophyllum</u>. It marks the upper limit of the lower part of the intertidal zone.



Fig. 22. The lower part of the intertidal zone is characterized by a dense cover of kelp. The upper part of the intertidal zone has little or no algal cover. Transect in Fig. 21 is in the center of the photograph beyond the sandstone shelf.



Fig. 23. Exposed transect. The band of Hedophyllum is replaced by Alaria and Lessoniopsis, and Postelsia occurs in the upper intertidal zone. The highest point in the transect is at the 9 ft. tide level. Water is at about the 2 ft. tide level. afforded by calcareous genera such as <u>Corallina</u>, <u>Calliarthron</u> and <u>Bossea</u> (Figs. 25 and 27-31). A tidepool at any location may, however, contain large growths of ell grass (<u>Phyllospadix scouleri</u>) (Figs. 24, 26 and 30-32). It is only in some lower intertidal, moderately sheltered to sheltered tidepools (Fig. 24) that relatively dense algal cover occurs.

Despite the fact that <u>Hedophyllum</u> is dominant throughout much of the lower intertidal zone, it is present only in the shallowest parts of tidepools, if present at all (Figs. 25 and 27). In contrast to pools above approximately the 2 ft. to 3 ft. tide levels, lower pools often contain extensive algal cover afforded by such predominantly subtidal algae as <u>Laminaria</u>, <u>Costaria</u> and <u>Pleurophycus</u> and a variety of bladed and filamentous reds and greens.

The upper limits of subtidal and lower intertidal invertebrates are generally pushed upwards by tidepools. Thus, such species as <u>Mytilus californianus</u>, <u>Katherina tunicata</u>, <u>Calliostoma costatum</u>, <u>Acmaea mitra</u>, <u>Strongylocentrotus purpuratus</u> and <u>Anthopleura</u> <u>xanthogrammica</u> occur at conspicuously higher tide levels in pools than they do in the open rock habitat. Conversely, many of the upper intertidal invertebrates such as <u>Acmaea digitalis</u>, <u>Thais emarginata</u>, <u>Balanus</u> and <u>Littorina</u> do not regularly inhabit the deeper tidepools of the upper intertidal zone.



Fig. 24. A moderately sheltered tidepool at the 3.5 ft. tide level. Hedophyllum and Egregia are abundant outside of the pool. Odonthalia, Iredaea and Phyllospadix are abundant in the pool.



Fig. 25. An exposed tidepool at the 4 ft. tide level. Hedophyllum surrounds the pool but is not as abundant as in Fig. 24. There is little vegetation in the pool aside from calcareous algae. Mytilus is abundant at levels just above the pool.



Fig. 26. A moderately exposed tidepool at the 6 ft. tide level. Hedophyllum is abundant at tide levels below the pool but not above it. The dominant vegetation in the pool is Phyllospadix.



Fig. 27. An exposed tidepool at the 5 ft. tide level. Some Hedophyllum is around the pool and in its shallowest parts. Mytilus is abundant in and above the pool. Clumps of Mitella also are attached above the pool.

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Fig. 28. An exposed tidepool at the 8 ft. tide level. The surface of the pool corresponds with the upper limit of Mytilus in this location. Clumps of Mitella can be seen with the Mytilus below the pool, and around the edge of the pool. Coralline algae are the only conspicuous vegetation in the pool.



Fig. 29. An exposed tidepool at the 8 ft. tide level with a wire minnow trap at its bottom. Corallina and Mytilus are conspicuous in the pool. Note the loose rock at the bottom and the absence of crustose algae around it.

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Fig. 30. A moderately sheltered tidepool at the 7.5 ft. tide level. <u>Corallina</u>, <u>Phyllospadix</u>, <u>Mytilus</u> and <u>Anthopleura</u> are <u>conspicuous</u> in the pool.



Fig. 31. A moderately sheltered tidepool at the 8.5 ft. tide level. <u>Corallina and Phyllospadix grow in the deeper parts of</u> <u>pool while Odonthalia and Spongomorpha grow in its</u> <u>shallower parts.</u>



Fig. 32. Tidepools of intermediate exposure at the 9.5 ft. tide level. Note the absence of macroscopic vegetation outside the pools.



Fig. 33. A tidepool at the 10 ft. tide level showing the general physical features of pools in the shale and slate formations. Phyllospadix is conspicuous in the pool.

LOCAL DISTRIBUTION OF TIDEPOOL COTTIDS

The objective of this part of the present study was to define some of the factors in the environment of tidepool cottids along the west coast of Vancouver Island, B.C., and to relate certain factors to the local distribution and abundance of these fish. Particular emphasis has been given to <u>Oligocottus maculosus</u>, the most abundant and widely distributed of the intertidal cottids in this area.

In the past various workers have noted that species of northeastern Pacific cottids inhabit, and may be restricted to, the tidepool habitat (Greeley 1899, Bolin 1944, Clemens and Wilby 1961, and MacPhee and Clemens 1963). Greeley (1899) also reported that some tidepool cottids occur only in tidepools with a particular flora, and that some species occupy pools at definite heights in the intertidal zone.

The only recent contributions to knowledge of the local distribution of northeastern Pacific tidepool cottids are the studies by Morris (1960, 1962). These studies are primarily concerned with temperature and salinity as possible factors determining the geographical distribution of several species, but he also comments (Morris, 1962) upon the local distribution along the Oregon coast of <u>O. maculosus</u>, <u>O. snyderi, Clinocottus globiceps</u> and <u>Leptocottus armatus</u>. His data indicate that the 16^oC isotherm is the limiting factor in the southward

distribution of <u>O. maculosus</u> and <u>C. globiceps</u> (Morris, 1960). He also suggests that a low Q_{10} is responsible for the ability of <u>O. maculosus</u> to inhabit high tidepools (Morris, 1962).

Methods

Quantitative and Qualitative Collections

The distribution of species at low tide is based primarily upon poison collections made in tidepools and at subtidal stations. Chem Fish Collector, a rotenone-base chemical manufactured by Chemical Insecticides Corporation, Metuchen, New Jersey, was used as a fish toxicant. It was found to be better suited for making quantitative and qualitative collections of the tidepool fish fauna than a variety of other fish toxicants and anesthetics such as cresol, quinaldine, chloral hydrate, 2-phenoxyethanol, and tricaine methanesulfonate.

The typical reaction of northeastern Pacific tidepool fish to Chem Fish Collector is an initial period of activity during which they leave the seclusion of rocks and crevices, followed by a short period of immobility that preceeds death. The initial activity usually takes them to the surface or edge of the tidepool where they can be easily captured with a hand net or forceps. The response to other toxicants and anesthetics is not as general. Many species become immobilized
before they leave the seclusion of rocks and crevices. This makes it difficult or impossible to recover them. Gibson (1965a) has reported that he was able to make quantitative collections of British tidepool fishes with quinaldine. The tidepool fishes with which he worked either respond differently to quinaldine than the fishes investigated in the present study, or the tidepools in which he made his collection were much better suited for being thoroughly searched.

Cresol is an effective fish toxicant and causes a response similar to Chem Fish Collector. It is a more corosive chemical, however, and is much more injurious to the invertebrate fauna than rotenone. Other rotenone-base fish toxicants have the same general effect upon the fish fauna as Chem Fish Collector. But because of its greater potency, and composition, Chem Fish Collector is effective, unlike the others, at concentrations that do not alter the clarity of the water. It is therefore possible to make a thorough search of the pool following the application of the toxicant.

Precise quantities to add to pools were not determined. If the fish did not respond to the initial dosage within ten to fifteen minutes, more was added. It was never necessary to add a quantity of toxicant which interfered with the clarity of the water. After the toxicant was mixed into the tidepool, small dip nets and forceps were used to retrieve the fish and transfer them to 10% formalin.

From May 1964 to May 1967, 87 tidepool or subtidal collections were made, mostly in the vicinity of Botanical Beach; 20 were made between Pachena Point and Triangle Island, which is located just off the northwestern tip of Vancouver Island. During the summer of 1965, 36 collections were made between Prince Rupert, B.C., and Cape St. Elias, Alaska.

Periodic Trapping and Poisoning of Tidepools

Two series of tidepools with a combined volume of approximately 3,800 litres were trapped with wire minnow traps (Fig. 29) bimonthly or monthly from December 1965 to September 1967. The purpose of the trapping was to assess changes in the fish populations of the pools and to obtain data on growth for the species present. The pools were moderately sheltered to moderately exposed and were situated between the 8.5 ft. and 9.2 ft. tide levels. The traps were baited with broken pieces of <u>Mytilus californianus</u>. The usual trapping period was four hours. On some occasions, however, high surf necessitated an early removal of the traps from the pools. Trapping was usually confined to the daylight hours. When trapping was necessary at night, the tidepools were artificially illuminated during the trapping period.

The trapping of several pools just previous to poisoning them revealed that a very high proportion of the total number of

O. maculosus and C. globiceps over 55mm in length were taken in the traps. For example, in one pool 14 O. maculosus and 2 C. globiceps were taken after two hours of trapping. Subsequent poisoning took one additional O. maculosus. In another pool two hours of trapping took 5 O. maculosus and 7 C. globiceps, while subsequent poisoning took 2 additional C. globiceps.

One tidepool at the 9.4 ft. tide level was poisoned on a monthly basis or as close to a monthly basis as surf and weather conditions permitted. The pool had a maximum depth of 36cm and a volume of 42 litres. The purpose of the monthly poisoning was to obtain growth data for the fish present and to determine any seasonal differences in the degree of repopulation, or in the species which repopulated the pool.

All measurements of live fish were made to the nearest mm. No anesthetic was used and the fish were released immediately after being measured into the pool from which they had been taken. Preserved fish were measured with dial calipers to the nearest tenth of a mm. All measurements represent total length.

Results

General Distribution Patterns

On the basis of poison collections 16 species of littoral cottids common to the west coast of Vancouver Island can be placed into one of three categories: (1) those primarily restricted to tidepools, (2) those primarily restricted to the subtidal zone, and (3) those which occur both in tidepools and subtidally. The species placed in each of these categories are listed in Table V under the respective headings: primary tidepool cottids, subtidal cottids, and secondary tidepool cottids. Table VI summarizes all the collections made at Botanical Beach and the number in which the various cottid species were taken. Table VII summarizes the collections made between Botanical Beach and Cape St. Elias, Alaska.

The most obvious feature of the local distribution of the tidepool cottids is that at any given site the species characteristic of one tide level are different from those at other tide levels. In this respect the tidepool cottids exhibit vertical zonation just as does the intertidal benthic flora and fauna. The details of this zonation as it occurs at Pachena Point is shown in Table VIII.

Like the vertical distribution of species of benthic plants and invertebrates, the occurrence, abundance and vertical ranges of the

Categories into which cottid species, taken at Botanical Beach, are placed with respect to their occurrence in tidepools.

Primary Tidepool Cottids	Subtidal Cottids	Secondary Tidepool Cottids				
Oligocottus maculosus	Jordania zonope	Hemilepidotus hemilepidotus				
O. remensis	Hemilepidotus spinosus	Artedius lateralis				
Clinocottus globiceps	Blepsias cirrhosus	A. fenestralis				
C. embryum	Artedius harringtoni	Ascelichthys rhodorus				
C. acuticeps		Oligocottus snyderi				
		Enophrys bison				

Leptocottus armatus

Summary of cottid species taken in 67 poison collections made at Botanical Beach from 1965 to 1967. The numeral in far left of each row is the total number of collections in which that species was taken. Other numbers show the number of collections in which any two species were taken together.

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TABLE VI

Summary of cottid species taken in 56 collections made between Pachena Point, B.C. and Cape St. Elias, Alaska, from 1965 to 1967. The numeral in far left of each row is the total number of collections in which that species was taken. Other numerals show the number of collections in which any two species were taken together.

· · · · · · · · · · · · · · · · · · ·	Clinocottus acuticeps Oligocottus maculosus	Clinocottus globiceps	Clinocott us embryum	Oligocottus snyderi	Artedius lateralis	Hernilepidotus hennilepidotus	Hemilepidotus spinosus	Ascelich thys rhodo rus	Oligocottus remensis	Artedius · fenestr alis	Artedius harringtoni	Jordania z onope	Enophrys bison	Leptocottus armatus	Blepsias cirrhosus
C. acuticeps	2 1	1	1								1				
O. maculosus	31	11	11	6	4	6		3			3		4		
C. globicep	S	15	6	6	2	4		2		1			2		
C. emb	oryum		22	4	2	8	1	1	2		3				
0.	snyderi			15	5	7	· 2	6	1	1	3		2		
	A. late	ralis			10	5	1	3		1	2	2	1	1	
	<u>H.</u>	hemi	lepic	lotus	_	20	2	5	1	1	7	2	3		
		H. :	spinc	osus			4	3			2	2	1 -		
			Α.	rhod	orus	-		10			5	3	3		
				0. :	reme	nsis			2		1				
					Α.	fenes	stral	is '		1	T				
						Α.	harr	ingto	ni		10	2	3	·	
							J. z	onop	e		<u> </u>	3			
								E. 1	oison				7	1	
									L. a	rma	tus			2],
•										<u>В.</u> с	irrho	osus			

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TABLE VII

TABLE VIII

Cottids taken from a vertical series of tidepools near Pachena Point, B. C., during July 1966.

Tide Height Feet	Dominant benthic Organism	Oligocottus maculosus	Clinocottus globiceps	Clinoc ottus embryum	Oligocottus snyderi	Artedius lateralis	Hemilepidotus hemilepidotus	Artedius fenestralis	Ascelichthys rhodorus
10	Corallina	207	43						
7	Mitella & Mytilus	3	14	3					
6	Mitella & Mytilus	3	24	23	: 1				
4.5	Hedophyllum				10	3	1		
3.5	Hedophyllum		1		52	8	8	5	
_ 2	Laminaria		1		·7		1		3

primary tidepool cottids vary from one vertical transect to another. For example, in some transects, as is shown in Table VIII, <u>O.</u> <u>maculosus</u> occurs only in the upper intertidal zone. In other transects it occurs from the upper intertidal zone to the lowest tide levels. <u>Clinocottus embryum</u>, on the other hand, is rarely abundant at tide levels other than those shown in Table VIII and in many transects it is absent. In some transects <u>C. globiceps</u> extends throughout the intertidal zone, whereas in others it is restricted to the upper intertidal zone or absent altogether. In transects where it occurs <u>C. acuticeps</u> is restricted to the upper intertidal zone, whereas <u>O. remensis</u> has been collected only in the lower intertidal zone.

The secondary tidepool cottids all have their lower limits in the subtidal zone and all of them have upper limits in the lower intertidal zone. <u>Artedius lateralis</u>, <u>O</u> snyderi and <u>Ascelichthys rhodorus</u> have occasionally been observed in tidepools in the upper intertidal zone but they do not regularly inhabit this part of the intertidal zone at the study site. These species do, however, regularly occur higher in the lower intertidal zone than other secondary tidepool cottids.

Environmental Factors and Distributions

Physical and Chemical Tidepool Factors

It has been shown that the physical and chemical conditions in tidepools vary considerably depending upon such factors as the depth of the pool, its flora and fauna, weather conditions, and the extent to which the pool is isolated from the sea. The latter factor determines the effects that the other factors have and it in turn depends primarily upon the height of the pool, and secondarily upon the pool's exposure and the sea state.

Pools below LLHW (Fig. 11) will flood twice in each lunar day. Pools above this height will flood no more than once per lunar day during the neap period of the monthly tidal cycle. Pools located above LHHW (Fig. 11) will be isolated for at least two consecutive tidal days each lunar month. These relationships between vertical height, length of emergence and tidal factors are illustrated in Fig. 12.

The upper limits of most of the tidepool cottids are situated below LLHW. Three of the four species (<u>O. maculosus</u>, <u>C. globiceps</u>, <u>C. embryum</u> and <u>C. acuticeps</u>) which regularly inhabit pools above this level also inhabit pools above LHHW. Only <u>C. embryum</u> inhabits pools above LLHW but does not occur above LHHW. This means that all the tidepool cottids except <u>O. maculosus</u>, <u>C. globiceps</u> and <u>C. acuticeps</u> have upper distributions correlated with daily, tidallyrelated, changes in environmental conditions. All the secondary tidepool cottids have upper limits correlated with semi-daily, tidally-related, changes in environmental conditions.

Because of the effects and possibly interactive effects of factors other than the vertical position of a tidepool, it is very difficult to determine what single factor, if any, in a pool is limiting the vertical distribution of a species. Tidepools of the same shape and size unfortunately do not occur in neat vertical transects. In this respect the tidepool environment is more difficult to evaluate than the open rock environment.

If temperature were limiting the upper distribution of a species, that species would be expected to be found higher in the intertidal zone in deep shaded pools than in shallow open pools. It has not been possible, on the basis of poison collections and trap catches, to correlate vertical distributions with depth or other physiographic characteristics of tidepools for any of the cottids which do not occur above LLHW.

It might also be expected that seasonally, vertical distributions would change in response to more favorable temperatures in tidepools above LLHW. But again such shifts have not been observed in the cottids which occur only below this tide level. The fact that seasonal changes in distribution patterns in these cottids do not occur even in transects where heavy run off at low tide causes the salinity to be much lower than that of the sea, indicates the ineffectiveness of salinity as a factor affecting the local distributions of these species.

For all three of the species which inhabit tidepools above LHHW seasonal shifts in distributions with respect to specific pools do occur (see below). In several of these cases the changes in distribution appear to be related to seasonal changes in temperature characteristics of the pools. Fig. 34 shows the number of <u>O. maculosus</u> and <u>C.</u> <u>globiceps</u> taken in a shallow pool at the 9.5 ft. tide level during 1966 and 1967. It is obvious that the pool is a more favorable habitat during the fall than during the summer despite the fact that it receives heavy run off during the former period.

Although these data suggest that high temperatures can restrict the distributions of <u>O. maculosus</u> and <u>C. globiceps</u>, temperature can not be used to explain the horizontal distributions of these species. In sheltered and moderately sheltered transects <u>C. globiceps</u> does not occur in pools which have less extreme temperature fluctuations than those in higher moderately exposed and exposed pools where the species does occur. This is also true for the distribution of <u>C. embryum</u>.

<u>O. maculosus</u> inhabits tidepools throughout the intertidal zone in sheltered and moderately sheltered transects, but has a high lower vertical distribution in exposed transects. Clearly the horizontal differences in the vertical distribution of <u>O. maculosus</u> can not be related to tidal fluctuations in physical and chemical factors within tidepools.



Fig. 34. Total number of O. maculosus (0...0) and C. globiceps (0-0) taken in poison collections in the same tidepool poisoned at different times of the year. The tidepool was located at the 9.5 ft. tide level, had a maximum depth of 36cm and a volume of 42 litres.

Exposure

The vertical distribution of <u>O. maculosus</u> at Botanical Beach is correlated with the degree to which the intertidal zone is exposed to surf. Where there is no protection from open sea swells, this species occurs only in tidepools in the upper intertidal zone. In sheltered transects, however, it occurs in tidepools and surge channels to as low as the extreme lowest tides. It has never been taken in a completely subtidal collection.

The relationship between exposure and the percent of the total cottid fauna represented by <u>O. maculosus</u>, as determined on the basis of surf sensor data and poison collections, is shown in Fig. 35. Fig. 36 shows that the density of <u>O. maculosus</u> per litre of tidepool volume is also correlated with exposure. It is apparent from the former figure that the factor(s) which limits the lower vertical range of the species does not exclude it from the lowest tide levels in either sheltered or moderately sheltered transects.

The vertical distributions of the other two abundant primary tidepool cottids at Botanical Beach are also correlated with exposure. Fig. 37 shows that the relationship between the vertical range of <u>C. globiceps</u> and exposure is nearly the reciprocal of that of <u>O. maculosus</u>. The vertical range of <u>C. embryum</u> (Fig. 38) tends to be related to exposure in the same way as that of <u>C. globiceps</u> but this

Fig. 35.

Percent of the total cottid fauna of tidepools represented by O. maculosus as a function of exposure and tide height. Exposure categories are (E) exposed, (ME) moderately exposed, (MS) moderately sheltered, and (S) sheltered. See text for explanation of exposure scale. Collections were made during July and August 1966.







Density of O. maculosus over 55mm in total length per litre of tidepool volume as a function of tide height in exposed (Δ) and moderately exposed (O) tidepools. Collections were made during July 1966.

Fig. 37.

Percent of the total cottid fauna of tidepools represented by <u>C. globiceps</u> as a function of exposure and tide height. Exposure categories are (E) exposed, (ME) moderately exposed, (MS) moderately sheltered, and (S) sheltered. See text for explanation of exposure scale. Collections were made during July and August 1966.



Fig. 38.

Percent of the total cottid fauna of tidepools represented by <u>C. embryum</u> as a function of exposure and tide height. Exposure categories are (E) exposed, (ME) moderately exposed, (MS) moderately sheltered, and (S) sheltered. See text for explanation of exposure scale. Collections were made during July and August 1966.



species is completely absent from sheltered and moderately sheltered tidepools.

Because of the relatively few collections which contained <u>O</u> remensis and <u>C</u>. acuticeps it is difficult to determine the relationship between the distributions of these species and exposure. At the study site, however, <u>O</u>. remensis has only been taken in moderately exposed to moderately sheltered tidepools in the lower intertidal zone. <u>C</u>. acuticeps, on the other hand, has only been taken in moderately sheltered tidepools in the upper intertidal zone.

The upper limits of the vertical distribution of the secondary tidepool cottids do not appear to be as markedly correlated with exposure as are those of the primary tidepool cottids. Poison collections do indicate though that most of these species are more abundant and tend to have slightly higher vertical distributions in areas with intermediate exposures.

Biotic Factors

The conspicuous vertical and horizontal variations in the benthic fauna and flora have been referred to in an earlier section of the paper. Since these variations are correlated with tidal factors in the same way as are the distributions of those tidepool cottids which only occur below LHHW, the distribution of these cottids is also correlated with the benthic biota. Only <u>O. snyderi</u>, however, has a sufficiently discontinuous distribution below the upper limits of its vertical range that a specific biotic factor can be correlated with its distribution. This species has rarely been collected at the study site, or at other collecting sites, where eel grass was not abundant.

The local distribution of <u>O. maculosus</u> is not correlated with conspicuous biotic features of the environment. Its occurrence at the lowest and highest tide levels in moderately sheltered and sheltered transects and in tidepools above the 3 ft. to 6 ft. tide levels in moderately exposed to exposed transects means that it inhabits pools with the widest possible range of biotic features. It inhabits tidepools with all other tidepool cottids. Often the only cottids in lower intertidal, moderately exposed to exposed pools where it does not occur are <u>C. embryum</u> and <u>C. globiceps</u>. Yet it commonly inhabits higher pools in which both <u>C. embryum</u> and <u>C. globiceps</u> have higher densities.

One can suggest that biotic factors may be important in relation to the distributions of <u>C. embryum</u> and <u>C. globiceps</u>. Both species do not inhabit pools in transects where physical and chemical environmental conditions are less variable than conditions in pools inhabited by these species in other transects. There is no basis,

however, to suggest what factor(s) may be important.

<u>Size</u>

The vertical range inhabited by <u>O. maculosus</u> depends upon the size of the fish. 0-year fish (≤ 55 mm) do not occur as low in any vertical transect as do older fish. Even in sheltered transects few 0-year fish inhabit tidepools below the upper intertidal zone. Larger fish inhabit pools as high as those inhabited by juveniles provided that the pools are deep enough. These features of the distribution of <u>O. maculosus</u> are shown in Fig. 39.

Specimens less than 45mm in length often inhabit tidepools less than 10cm deep, and specimens smaller than 15mm in length can be taken in shallow depressions no more than several cm deep. Fish larger than 55mm do not usually inhabit tidepools less than 10cm deep.

For most other tidepool cottids 0-year fish tend to be more abundant near the upper limit of the species' vertical distribution. But only for <u>C. globiceps</u> do 0-year fish inhabit pools not generally inhabited by larger fish of the species. The disparity between the distributions in the upper intertidal zone in sheltered and moderately sheltered transects of <u>C. globiceps</u> and <u>C. embryum</u> (Figs. 37 and 38) is due largely to the occurrence of juvenile <u>C. globiceps</u> in sheltered



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to moderately sheltered upper intertidal pools. Juvenile <u>C. globiceps</u> also tend to move to lower pools at a smaller size than do juvenile <u>O.</u> maculosus.

Seasonal Changes

There do not appear to be significant seasonal shifts in the upper or lower vertical limits of <u>O. maculosus</u>. There are, however, seasonally related changes in the occurrence of this species in particular tidepools. In some moderately sheltered to exposed pools in the upper intertidal zone few, if any, <u>O. maculosus</u> occur except during the summer months. Apparently these pools become uninhabitable during the winter months because of surf-induced abrasive action of cobbles and boulders which litter their bottoms. Such pools are typically devoid of any biota during the winter months except for possibly a belt of coralline algae around their upper edge.

Other tidepools at the study site become completely filled with sand or gravel during the summer and therefore fish are absent during this period. With the off-shore movement of sand which occurs during the fall and winter, these pools become populated with juvenile <u>O</u>. <u>maculosus</u>. Temperature has been mentioned above as possibly having a seasonal effect in some pools.

A storm during January 1967 dislodged two boulders from a tidepool at the 8 ft. tide level which was being trapped on a monthly

basis. Each boulder weighed about 10kg and they were the only cover in the pool. Whereas trap catches previous to the storm indicated a population of about 20 <u>O. maculosus</u>, no fish were caught or observed in the pool after the storm. Similar declines in other tidepool populations of <u>O. maculosus</u> following the disruption of the pools by storms have been observed.

None of the other primary or secondary tidepool cottids appear to have distributions patterns which vary seasonally. Only <u>C. globiceps</u> and <u>C. acuticeps</u>, because of their occurrence in the upper intertidal zone, are usually affected by the conditions mentioned above.

Population Fluctuations and Growth

Over the two years that populations of <u>O. maculosus</u> in several series of tidepools were monitored by periodic trapping, significant seasonal fluctuations in these populations occured. The results of the monthly trapping of two series of tidepools is shown in Fig. 40. It is evident from this graph that the population declined sharply during the winter and early spring and built up again over the summer and early fall. Length frequency analysis of the trap catches shows that the build up resulted from the recruitment of 1-year and 0-year class fish rather than a re-invasion of the pools by larger fish.



Fig. 40. Total numbers of O. maculosus over 55mm in total length (0...o) and C. globiceps over 60mm in total length (0---o) trapped in two series of tidepools at different times of the year.

This decrease in the population of <u>O. maculosus</u> during the winter and spring occurs throughout the vertical and horizontal range of the species at the study site. Thus, by February and March many pools at the lower vertical range of the species have few, if any, <u>O. maculosus</u> in them. In this way the lower limits of the species do tend to be pushed upwards over the winter, but it does not appear to be due to active emigration of fish from the pools.

The only other tidepool cottid for which similar data are available is <u>C. globiceps</u> (Fig. 40). This species also shows a population decline during the winter and early spring.

The growth of <u>O. maculosus</u> will be treated in detail in a later paper. However, in connection with the seasonal aspects of the distribution and population fluctuations of this species, it is useful to include data regarding seasonal aspects of growth. Fig. 41 shows monthly length frequencies of <u>O. maculosus</u> from poison and trap collections. It is apparent that the species grows little if at all during the winter months, and that growth was most rapid during late spring and summer.



Fig. 41. Length frequency diagrams of O. maculosus captured with wire minnow traps from the same series of tidepools at different times of the year.

HIGH TIDE MOVEMENTS AND HOMING BEHAVIOR

Basic to the understanding of the ecology and behavior of any mobile species of animal is a knowledge of the movements of individuals of the species. It is important to know the area covered by the individual in its normal activities of feeding and reproduction, whether or not special migrations for reproduction or other purposes occur, and if the individual tends to stay in a particular area for a considerable period of time. Previous studies on fishes have shown that a large number of marine and freshwater species have restricted movements, and that many species during reproductive and non-reproductive periods will return to a formerly occupied site, if they are displaced to another location (see review by Gerking, 1959).

Certain tidepool fishes have been investigated in regard to their movements and apparent homing behavior. Beebe (1934) and Aronson (1951) found that <u>Bathygobius soporator</u> returned, after being released in other tidepools, to the pools in which they had been captured. Williams (1957) concluded from returns of marked specimens of <u>Clinocottus analis</u> and <u>Girella nigricans</u>, which were released into the same pools in which they were captured, that both species homed to particular pools. On the basis of one experiment in which 10 of 35 specimens were still in the same pool 10 days after

being marked, Gerbacher and Denison (1930) suggested that <u>Oligocottus maculosus</u> shows fidelity to individual pools. Observations by Hubbs (1921) indicated that <u>Amphigonepterus aurora</u> also occupied the same tidepool on successive low tides. More recently Gibson (1967b)investigated the range of movements of two British tidepool species, <u>Blennius pholis</u> and <u>Acanthocottus bubalis</u> (=<u>Enophrys bubalis</u>). He concluded that both species move over limited areas and that at least the former species moves over a "home range" which includes several tidepools.

In all the above studies it was assumed that the species under investigation leaves the tidepool at high tide to make an on-shore feeding migration and subsequently retreats to the tidepool as the tide ebbs. Such movements away from the pool are crucial to the homing hypothesis in studies which do not involve displacement of specimens to other pools. Even so, the evidence concerning high tide movements has been primarily circumstantial. Only Williams (1957) attempted to directly observe the movements at high tide of the species he investigated. He concluded that the assumption that fish did not remain in the pool for the interval between consecutive low tides was undoubtedly true for <u>Girella nigricans</u>. The data were not so obvious for <u>Glinocottus analis</u>, even though at one shore location he observed an apparent complete upward shift in the vertical

distribution of this species during the flooding. He observed tagged specimens of <u>C. analis</u> only about 12 times, and although each of these fish was "at a considerable distance from the pool in which it was last observed" it is not mentioned if all these fish were ever seen in the home pool again.

Gibson (1967b) made no direct observations on the movements at high tide of either of the species studied. But he concluded that <u>Blennius pholis probably leaves the tidepool in that it feeds to some</u> extent on barnacles, which are not common in pools, and the fact that the species has a tidal rhythm of activity in which its locomotory activity is enhanced for 4 hours around high tide.

The first stage of this phase of the study was to make direct observations on the movements at high tide of <u>O</u>. <u>maculosus</u> at a variety of shore sites with respect to exposure to surf, and during different seasons of the year. The second purpose was to determine, through tagging experiments, the relationship of individual fish to particular tidepools. Attempts were also made to determine some of the factors which affect the tendency and ability of <u>O</u>. <u>maculosus</u> to return to specific pools after being displaced from them.

Observations and homing experiments were also made on other tidepool cottids in the study area.

Methods

High Tide Distribution

The high tide distribution of <u>O. maculosus</u> was determined primarily by direct observations of tagged (see below) and untagged specimens. As a result of surf conditions, most of the observations had to be made from beneath the water surface. At times of calm seas, and in sheltered locations, however, it was possible to make observations on the distribution and movement of the species from above the sea surface. Under these conditions observations were made either from a vantage point, such as a rock or ledge, above the water or while standing in the water.

During most of the underwater observations a face mask and a snorkel were used, but SCUBA equipment was used on some occasions. Because of the roughness of the sea, particularly during the winter months, it was sometimes necessary to confine the observations to the more sheltered sites. Even during the winter months, however, there were periods of calm sea conditions which permitted observations to be made at the most exposed parts of the study site.

Notes concerning the distance and area covered by tagged specimens and the general distribution of tidepool populations were recorded on an underwater writing pad. In one moderately sheltered area monthly observations were made to determine the number of <u>O. maculosus</u> at high tide in an area of approximately $8m^2$ surrounding a single tidepool. This pool was also trapped on a monthly basis and it was therefore possible to calculate the number of fish in the area surrounding the tidepool as a percent of total population of the pool.

Monofilament gillnets of 1/2 in. mesh, knot to knot, placed at various depths and sites in the intertidal zone were also used to assess distributions at high tide. Each net was mounted on two, 61cm long, 13mm diameter, steel rods (Fig. 42). The rods were threaded at the bottom end so they could be screwed into 1/2 in. Philip shields anchored in the substratum. Three shields were placed 2m equidistant from one another at each gillnet site. Thus, all 3 sides of a triangle could be closed off with netting. The net was loosely hung between the rods and weighted so its bottom lay along the contour of the shore. Nets were examined for fish either just before or just after the ebbing tide exposed them.

Tagging

The principal type of tag used consisted of one or two colored embroidery beads attached to the fish's dorsal musculature midway between the anterior and posterior dorsal fins. The beads were attached with 3 lb. test monofilament nylon line inserted through the



Fig. 42. Gillnet site showing the three equidistant supporting rods anchored in the substratum. Research facility is in the background.
musculature with a #11 stainless steel sewing needle.

Previous to the actual tagging operation trgs consisting of a 10cm piece of line with a single bead securely tien to one end and a single loop in the line just below the bead were prepared. During the tagging operation the free end of the line was pushed through the fish's dorsal musculature about 3mm below the mid-dorsal surface and then through the loop below the bead. The loop was tightened and two knots in the free end were cinched tightly against it. When two beads were used, the procedure was the same except that the second bead was placed on the line just after it was passed through the fish.

Two other methods of marking fish were also used. Fin clipping was done extensively in conjunction with bead tags so that the individual fish could be identified. It was usually restricted to one or both pelvic fins, but in some instances anterior and posterior portions of the anal and dorsal fins were clipped.

Tags consisting of colored silk thread were used in a few experiments when the movement of marked fish was being observed from underwater. The thread was inserted in the same way and position as the bead tags and then knotted above the median dorsal surface. The free ends were cut so they were about the same length as the fish. The ends were then coated with vaseline so they would

float.

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Fish were caught for tagging with baited minnow traps or with small dip nets. No anesthetic was used during the marking of any fish, and each fish was sexed and measured after being tagged.

Two conditions were used to evaluate the effects of tagging on survival. Over a period of 18 months 25 bead-tagged <u>O. maculosus</u> (55mm to 70mm) were held in aquaria with 20 non-tagged <u>O. maculosus</u> (55mm to 70mm) for a minimum period of 6 months each. The water in the aquaria was not circulated or filtered and it was renewed only every week or 10 days. Daily temperature fluctuations in the aquaria corresponded to those which occur in tidepools in the upper intertidal zone. There were ne mortalities of either control or tagged fish.

In order to more accurately simulate natural conditions, 10 bead-tagged <u>O. maculosus</u> (60mm to 70mm) and 8 non-tagged <u>O.</u> <u>maculosus</u> (63mm to 71mm) were held in an 80 litre covered tidepool at the 9 ft. tide level. These fish were held in the pool from November 10, 1965 to June 9, 1966. One tagged and one non-tagged fish died between the 12th and 22nd of February, 1966, as a result of being caught under the screen cover. Another tagged fish lost its tag between the 25th and 30th of March, but was in healthy condition with the wound completely closed when the experiment was terminated. All 8 of the remaining tagged fish were in good physical condition at the termination of the experiment. The flesh surrounding the tags of all these fish, however, was to varying degrees worn away and the tags of several fish were about to be lost.

The latter observations indicated that tag loss could occur in the pool environment in a matter of months and perhaps weeks. The fact that there were no more hazards on which the tags could become snagged in the covered pool than in the aquaria, suggests that tag loss was probably due to the abrasive action of turbulent water. If this is true, one should expect to observe, as was the case, fewer tags lost during the summer than winter.

Tag loss does not result in increased mortality. Bead tags were forcefully removed from 10 <u>O. maculosus</u> one week after they had been attached. Five of these fish were held in an aquarium and five were held in the covered pool. At the end of 4 weeks no deaths had occured and the wounds of all the fish were healing.

Types of Tagging Experiments

Two types of tagging experiments were conducted: those involving transplant releases and those involving home pool releases. In the former experiments fish from one tidepool were tagged and subsequently released at a location other than the pool in which they were captured. Usually they were relased into another pool, but some were released directly into the sea. In the latter experiments tagged fish were released into the same pool in which they were captured. Data on the flooding history of the pools and surf conditions were recorded.

The primary means of obtaining recovery data were by extensive and intensive trapping of pools with minnow traps and from nocturnal observations of pools. The latter method proved to be an extremely effective and quick way of obtaining recovery data. Because tidepool cottids leave their hiding places at night and position themselves in the open, they can be easily observed and captured with a small hand net. In this way a large number of pools can be examined in a relatively short time.

Tagging studies were initially undertaken to determine the fidelity of individual fish to particular pools, and to what extent transplanted fish will return to a pool. Later, further studies were carried out to try and answer several questions about the observed homing instinct: how is homing affected by such factors as the season of the year, the distance to which specimens are transplanted from the home pool and the length of time fish are held in captivity?

Results

High Tide Distribution and Movements

Observations on the distribution of <u>O. maculosus</u> during high tides were concerned pilmarily with determining whether this species moves out of and away from the tidepools in which it is found at low tide. On the basis of diving observations and gillnet catches, it was found that the characteristics of the high tide distribution of this species depends upon both space and time factors at the study site.

Horizontally along the shore there is a difference between the high tide distribution of fish inhabiting tidepools in exposed transects as opposed to those inhabiting tidepools in sheltered transects. In the exposed habitat <u>O. maculosus</u> does not regularly leave the tidepool whereas in the sheltered habitat it does.

Seasonally there is a change in the high tide distribution of fish inhabiting tidepools of intermediate exposure. Fig. 43 shows the seasonal change in the average number of <u>O. maculosus</u>, as a percent of the total tidepool population, observed at high tide on a flat surrounding a moderately sheltered tidepool. It is apparent that the only time at which a significant percent of the pool population was out of the pool was during July, August and September.

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Percent of the total tidepool population of O. maculosus out of the tidepool at high tide during different months of the year. The value for each month represents the average for at least six high tides.

In transects where the high tide distribution encompasses a larger area than the low tide distribution, the species does not exhibit a complete upward shift in its vertical distribution. There are always fish which remain in the tidepool or at the same tide height as the pool regardless of how low in the intertidal zone it is located. The only specimens which tend to show a more or less complete tidal shift in their vertical distribution are 0-year fish in some sheltered and moderately sheltered areas. If there are no physical impediments to following the flooding tide to its highest levels, these fish migrate shoreward as their pools are flooded and then move off-shore again as the tide ebbs. This on-shore, off-shore migration can be seen particularly well at the study site in an area where a large sheltered tidepool at the 7 ft. tide level has only sand and gravel shoreward of it.

Tagged fish

According to the above observations, at least in certain tidepools and during certain months of the year, the same individuals of <u>O</u>. <u>maculosus</u> will be in particular tidepools on successive days and for successive weeks. Data from 117 <u>O. maculosus</u> that were tagged and subsequently released into the tidepools from which they were taken, show that this is so (Table IX).

TABLE IX

Summary of nine experiments involving home pool releases of O. maculosus. Recoveries within the first two weeks of tagging are not included.

Date	Number tagged	Number recovered	Number recovered in home pool	Percent resident of recovered	Percent resident of tagged
	⊈s o's	♀s ♂s	♀s o's		
22-X-65	9 13 22	6 12 18	6 12 18	100	82
23-X-65	·4 3 7	4 2 6	4 2 6	100	86
22-VI-66	3 1 4	3 1	2 1 3	75	75
18-VII-66	22 22 44	21 21 42	21 21 42	100	96
8-IX-66	3 4 7	3 4 7	3 4 7	100	100
8-IX-66	2 2 4	1 2 3	0 2 2 2	50	50
9-X-66	3 2 5	3 2 5	2 2 4	80	80
10-X-66	0 5 5	0 5 5	0 5 5	100	100
25-XI-66	12 7 19	10 3 13	i0 3 13	100	68
Totals	58 59 117	51 52 103	48 52 100	94 100 97	83 88 86

Aside from obtaining data by extensive and intensive trapping of tidepools, and night observations at low tide, high tide observations were also made on pools in which tagged fish were released. At times when sea conditions permitted, broken pieces offresh <u>Mytilus</u> were placed at the bottoms of tidepools at or near the time of high tide. This results in a convergence of the <u>O. maculosus</u> and other cottids in the pool to the <u>Mytilus</u>. In this manner it is possible to bring all the tagged fish in the pool into view. The number of observed tags can then be compared with the number of tagged fish released into the pool. Observations of this type confirmed that in exposed pools throughout the year, and in tidepools of intermediate exposure during most of the year, nearly all the <u>O. maculosus</u> remained in the pool the entire time that it was flooded.

Observations of tagged fish in tidepool areas of intermediate exposure also provided information on the distance away from the home pool that <u>O. maculosus</u> will travel during the season of the year when excursions from the pool are made. Very marked differences between individual fish were observed. Several tagged specimens which were observed at least three times a week for over a month were never seen more than 1 to 2m from the edge of their pool. The particular pool is located on a flat shelf with an area of over 250m². During observations on these fish, other tagged fish from pools on the same shelf but 3 to 5m away would frequently move into the vicinity of this tidepool. But even on this shelf where movement or vision was not restricted in any way, no tagged fish was ever seen more than 10m from its home pool and later observed again in its home pool.

Duration of Residence in Specific Tidepools

The length of time that individual fish spend in a single tidepool cannot be calculated from decreases in tag returns with time because tag loss is such a significant factor. It is also likely that tagged fish are more susceptible to predation, at least in certain pool areas, than non-tagged fish.

Duration of residence in specific tidepools was determined on the basis of data from fish which retained their tags for long periods, or remained identifiable as a result of clipped fins or other morphological characteristics which enabled positive identification. These data indicate that for the majority of <u>O. maculosus</u> over 55mm in length, inhabiting pools of intermediate exposure and exposed tidepools, the pool in which it was found was its permanent home pool. Forty <u>O. maculosus</u> have been observed in the same pool for over 6 months, and 10 have been followed in the same pool for more than a year.

Straying

Some <u>O. maculosus</u> have been observed over a period of time in two or more pools. Table IX shows that 3 fish that were released into the pool in which they were trapped were never taken again in that pool but were taken in another pool. Also, 10 fish which were still in the home pool at least two weeks after being tagged were later observed in other pools. All of these fish are referred to as strays.

Nine strays were observed in the second pool for at least one month before they disappeared and two of them were in the second pool for at least four months. Only 2 strays were observed in more than two pools. One of these was in the second pool for no more than a week, but was in the third pool for at least three months.

High Tide Distribution of Other Species

No cottid species other than <u>O. maculosus</u> were ever caught in gillnets situated in the upper intertidal zone. Two non-cottids, <u>Hexagrammos stelleri</u> and <u>Sebastodes melanops</u>, were frequently caught in gillnets in the upper intertidal zone. During diving observations these species have been observed at tide levels above 8 ft. Both species appear to follow the flooding tide on-shore, remain in the intertidal zone throughout the high tide and then retreat to lower levels as the tide ebbs.

Observations at high tide did not show that any of the secondary tidepool cottids have a tidal on-shore migration which carries them into the upper intertidal zone. <u>Artedius lateralis</u> and <u>O. snyderi</u> were frequently seen during the summer months feeding on open shelves between and away from tidepools, but usually they were never more than 5 to 7m from a pool. Two blennoid species, <u>Phytichthys chirus</u> and <u>Pholis ornata</u> were frequently seen feeding in eel grass beds 15 or more metres from the tidepools.

Homing Behavior

Definition

Williams (1957) in his study of homing behavior of rocky shore fishes defined homing as the presence of the same fish in the same pool on two successive observations of the fish during two different low tides. Homing should indicate that a species has navigational abilities rather than just fidelity to a particular geographical site. Consequently, on the basis of what has been stated about the high tide distribution of <u>O. maculosus</u>, the above definition of homing is clearly inadequate for this species. Homing must be defined in <u>O. maculosus</u>, and in other species with similar high tide distributions, in terms of the return of individual fish to tidepools from which they have been displaced. Homing experiments therefore consisted of tagging fish from specific pools and releasing them at sites other than the pool in

which they were caught. Only the initial recapture of such a fish in the pool in which it was originally caught was considered as an instance of homing.

Homing success

Transplant experiments were run in the same general area of the study site as the home pool release experiments and in many experiments the same pools were used. Twenty-one transplant experiments involving 149 <u>O. maculosus</u> are summarized in Table X. It is apparent from the results of most of the individual experiments and certainly from the grand totals, that this species possesses strong homing behavior. It is also apparent that <u>O. maculosus</u> has the ability to return to the home pool after being displaced over relatively long distances.

The data show that there is no difference in the homing behavior between males and females. Also over the range that was investigated, homing behavior is apparently not dependent upon age (Table XI).

Behavior of transplants

Often it was not possible due to unfavorable tide or surf conditions, to thoroughly search the home pool on the low tides immediately following the release of transplanted fish. Because of this it could not always be established in what time span successful

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Summary of 21 experiments involving transplant releases of - O. maculosus.

						-	Nu	mbe	r re-	- Percent	Percent
	Nu	ml)er	Nu	unbe	er	COV	/ere	d in -	homed of	homed of
Date	tag	gge	d	re	cov	ered	hor	ne p	oool	recovered	tagged
•	₽s		oʻs	₽ s		os	₽s		ດ ຣ		
22- X-65	6	12	6	5	11	6	5	10	5	91	83
22-1-66	9	11	2	6	7	1	5	6	1	. 86	55
20- II-66	3	6	3	3	6	3	3	6	3	- 100	100
2-I II-66	2	5	3	1	3	2	1	3	2	100	60
30-IV-66	0	7	7	. 0	7	7	0	7	7	100	100
2-V-66	7	16	9	5	11	6	5	11	6	100	69
10-VI-66	4	6	2	4	6	2	3	5	2	83	83
16-VI-66	3	7	4	3	7	4	2	5	3	71	71
16-VI-66	3	9	6	1	7	6	1	6	4	71	56
22-VI-66	0	2	2	0	1	1	0	1	1	100	50
24- VIII-66	5	9	4	.5	8	3	5	8	3	100	89
2-IX-66	2	3	1	2	3	1]	2	1	67	67
2-IX-66	3	3	0	1	1	0	1	1	0	100 .	33
25-IX-66	7	8	1	5	6	1	3	3	0	50	38
27-IX-66	3	.4	1	2	2	0	- 2	2	0	100	50
-27-IX-66	2	5	3	2.	2	0	1	1	0	50	20
1-XI-66	. 2	4	2	2	4	2	2.	4	2	100	100

TABLE X (continued)

Date	Nurr tagg	iber ed	Num	ber vered	Num cove home	ber re- red in e pool	Percent homed of recovered	Percent homed of tagged
	Ŷs	៤ ន	♀ s	്ട	₽s	o's		
9-XI-66	3	2	3	1 4	3	0	75	60
9-XI-66	0	5	0	4	0	4 4	100	80
9-XI-66	2	3	2	0 2	2	0	100	40
9-XI-66	5	5)	4	3 7	4	3 7	100	70
Totals	71	71	56 10	53 9	49 9	47 6	88 89 88	69 66 68

TABLE XI

Summary of 20 transplant experiments of O. maculosus showing the homing success of different size groups.

Size groups (mm)	Number tagged	Number recovered	Number recovered in home pool	Percent homed of tagged
50-54	5	5 .	4	80
55-59	9	6	6	67
60-64	22	16	15	68
65-69	28	25	22	79
70-74	27	22	19	70
75-79	17	13	11	65
80-84	19	- 16	16	84
85-90	5	4	. <u>3</u>	60
70-74 75-79 80-84 85-90	27 17 19 5	22 13 16 4	19 11 16 3	70 65 84 60

homing was accomplished. However, in all nine of such instances when it was possible to make observations, all the fish which successfully homed were in the home pool by the second low tide. These observations, along with incomplete observations from other experiments, suggest that most successful homing is accomplished within the first one or two high tides following release.

Frequently it was possible to thoroughly search and observe the pool in which the transplants were released. In three instances the latter pool was poisoned during the first low tide following the release of transplanted fish. These observations showed that even if transplanted fish were not successful at returning to the home pool, they did not remain in the pool into which they were transplanted. Only four of over 100 transplanted fish for which such observations were made were still in the transplant pool following the first high tide. Two of these fish remained in the transplant pools for about two weeks and then returned to their respective home pools. A third fish remained in the transplant pool four weeks and then it also returned to its home pool. The fourth fish was taken with poison in the transplant pool on the first low tide following its release.

This immediate movement away from the transplant pool was shown not to be related to the density of <u>O. maculosus</u> or other cottids in the transplant pool. Neither the removal by poisoning of the entire

fish fauna or the removal by trapping of most of the cottid fauna several days prior to transplanting fish into a pool resulted in the transplanted fish remaining a longer time in that pool. Reciprocal transplants in which the same number of tagged fish were interchanged between two pools also did not modify this behavior.

Possible Influencing Factors

Position of pools

The transplant experiments in Table X involved transplanting fish to pools which had a variety of spatial relationships to the home pools. In some experiments the two pools were at about the same tide level while in other experiments the two pools encompassed nearly the entire vertical distribution of <u>O. maculosus</u>. In still other experiments the two pools were both vertically and horizontally separated from each other. Comparisons of the results of individual experiments indicate that the vertical and horizontal positions of the pool relative to one another do not influence homing success.

Distance from home pool

The transplant experiments summarized in Table X involved the transplanting of fish by as much as 102m from their home pool. The relationship between homing success and distance for these experiments is shown in Fig. 44. Even the greatest distance over which fish were



Fig. 44. Homing success of transplanted O. maculosus as a function of the distance away from the home pool that they were released.

transplanted was within the homing ability of the species. The fish in experiments involving distances of over 50m do tend to have a lower homing success than fish released at a shorter distance from the home pool, but this may reflect the effects of complexities and irregularities of the substratum rather than the effects of distance alone. The experiment in which high homing success was obtained over a distance of 102m involved the return of fish across a relatively level and non-dissected portion of the shore.

The fact that <u>O. maculosus</u> will move considerable distances in search of the home pool is indicated by three transplant experiments which are not included in Table X. In each of two experiments, 20 <u>O. maculosus</u> were tagged and transplanted to a pool in the area of the study site where the homing studies were being conducted from a large pool approximately 240m away. In the third experiment 10 <u>O. maculosus</u> were similarly treated. Extensive trapping and night observations of pools within 60 to 90m of the pools in which these fish were released indicated that all transplanted fish moved completely out of the study area. Unfortunately, it was not possible to determine if any of these fish successfully homed.

Time of year

Homing success as a function of the time of year is shown in Fig. 45. It is important to note that during all seasons of the year





O. maculosus exhibits homing behavior. The fact that all these experiments were conducted in intermediately exposed to exposed parts of the study site means that homing occurs at those times of the year when the fish are seldom, if ever, normally out of the home pool.

Captivity

Nearly all the transplanted fish were held in captivity over at least one tide cycle before being released. In five experiments transplanted fish were held in aquaria over three tide cycles. Homing success in these five experiments was no lower than the average success of all the other experiments.

In one instance a tagged fish which was being held in a covered pool escaped after being in the pool for six months. This fish was subsequently trapped in the pool from which it was originally taken. It remained in this pool for at least two months before disappearing.

The movement of fish out of an unfamiliar pool on the first tide that floods the pool appears to occur regardless of how long the fish have been held in captivity. In one of the two experiments described above in which 20 <u>O. maculosus</u> were transplanted from a pool 200m from the study area, the fish were held for two weeks before being released. Still they left the transplant pool on the first tide that flooded it. Similar results were obtained in another experiment involving six tagged fish from a single pool which had been held for six months in an aquarium with six tagged fish from another part of the study area. At the end of six months all 12 fish were released into the home pool of the first six. Intensive trapping a week later showed that all six of the original fish from that pool were still in the pool, but that none of the other six fish were.

Tagging of Other Species

The only tidepool cottid besides <u>O. maculosus</u> that was frequently tagged was <u>C. globiceps</u>. Tables XII and XIII show the results of home pool and transplant releases. Like <u>O. maculosus</u> this species shows fidelity to specific tidepools and will home to these pools when displaced from them. Table XIII shows that, unlike the former species, there was a greater tendency for transplanted male <u>C. globiceps</u> to disappear than transplanted females. Table XIV also indicates that the smallest size groups that were tagged show a stronger tendency to home to specific pools than larger size groups.

A total of 7 <u>C. embryum</u> (4 males and 3 females) were fin clipped and returned to the pools in which they were taken. After a period of one month, five of these fish (3 males and 2 females) were taken in the same pools into which they had been released.

TABLE XII

Summary of four experiments involving home pool releases of <u>C. globiceps.</u>

	Number tagged	Number recovered	Number recovered in home pool	Percent resident of recovered	Percent resident of tagged
Males	11	11	9	82	82
Females	28	25	25	100	89
Males & Females	39	36	34	94	87

TABLE XIII

Summary of nine experiments involving transplant releases of <u>C. globiceps.</u>

	Number tagged	Number recovered	Number recovered in home pool	Percent homed of recovered	Percent homed of tagged
Males	28	17	16	94	57
Females	19	15	14	93	74
Males & Females	47	30	30	94	64

TABLE XIV

Summary of nine transplant experiments of <u>C. globiceps</u> showing the homing success of different size groups.

Size groups (mm)	Number tagged	Number recovered	Number recovered in home pool	Percent homed of tagged
50-54	11	9	9	82
55-59	6	6	5	83
60-64	3	2	2	67
65-69	3	2	2	67
70-74	4	3	2	50
75-79	4	3	3	75
80-84	5	. 3	3	60
85-90	1	0	0	0

ACTIVITY STUDIES

Rhythmic locomotor activity which persists under 'constant' conditions has been investigated in a wide variety of organisms (see Sollberger, 1965). Such rhythmic activity has been found to be in phase with solar and lunar (tidal) cycles. The only studies of activity rhythms under 'constant' conditions in intertidal fish, however, are the investigations by Gibson (1965b, 1967b) on intertidal fish of the British Isles. He found that <u>Blennius pholis</u> and <u>Acanthocottus bubalis</u> (=Enophrys bubalis) exhibit rhythmic locomotor activity when held under 'constant' conditions. Both species show enhanced locomotor activity for several hours around high tide and this behavior persists in the laboratory for several days.

The only other tidal rhythms which have been reported in fishes are tidal rhythms of oxygen consumption. Gompel (1938) described such a rhythm in <u>Pleuronectes platessa</u> and Schwartz and Robinson (1963) suggested that a similar rhythm is present in <u>Opsanus tau.</u>

Despite the current emphasis on rhythm research, very few studies have been concerned with the ecological aspects of rhythmic locomotor activity which persists under 'constant' conditions. It is generally accepted that a behavior pattern which retains its periodicity in the absence of obvious time cues, i.e., the sun and the moon, is

adaptive. But it cannot be assumed that the environmental factor(s) with which the rhythm is synchronized is (are) directly related to the rhythm's adaptive functions (Cloudsley-Thompson 1961). Also it cannot be assumed, as Gibson (1967b) did, that the rhythm has special significance during the normal daily existence of the organism.

The purpose of this aspect of the present study was to investigate the activity of <u>O. maculosus</u> under both natural and controlled conditions. It was hoped that if this species showed rhythmic locomotor activity under 'constant' conditions, it would be possible to relate this activity to its field behavior. By this approach it was thought that information relating to the adaptive function(s) of the rhythm might be brought to light.

Methods

Field Observations

In order to make observations on the behavior and to assess the activity of tidepool fishes under natural conditions, field observations covering all months of the year were conducted from October 1965 to March 1967. Observations were made from both above and below the surface of the water, at all times of the day and night and at all phases of the daily and monthly tidal cycle.

For the purpose of making low tide observations from above the surface of tidepools, several pools were selected which permitted the observer to sit almost directly above the pool with an unobstructed view of its interior. Low tide observations made from below the surface of a pool were made with a face mask and snorkel, the observer lying prone either in or beside the pool. Snorkeling equipment was used during most of the observations made on submerged pools. On a few occasions SCUBA gear was used.

Observations were made to attempt to determine the influence of temperature, light, salinity, surf, and inter- and intraspecific associations on the behavior of <u>O. maculosus.</u>

Activity Apparatus

In the past, a variety of methods have been used to monitor

fish activity under laboratory conditions. Following Bohun and Winn (1966) such techniques can be broadly grouped as consisting of: direct observations; the measurement of a physiological parameter, such as oxygen consumption; the direct attachment of the fish to a recorder; the use of a mechanical device between the fish and recorder; or, the use of electronic sensor devices.

In the present study activity apparatus was designed of a mechanical type similar to that used by Harder and Hemple (1954) to monitor diurnal locomotor rhythms in pleuronectids and later by Kruuk (1963) in a behavioral study of <u>Solea vulgaris</u>. More recently the same technique was used by Gibson (1965b, 1967a) in his studies of tidal rhythms of locomotor activity in blennioid and cottid fish of the British Isles. The functioning of the apparatus depends upon the mechanical disturbance of a false aquarium bottom as the fish rises from the bottom to swim or change its position. This disturbance is then relayed by mechanical or electrical means to a recording device. Most littoral fishes are well suited for this type of apparatus because of their negative buoyancy and demersal habit. Because of this and its relative simplicity which makes its use in the field feasible, this technique was used in the activity chambers designed for this study.

The activity chambers (20cm x 20cm x 25cm) were constructed of 0.6cm plexiglass (Fig. 46). Holes of 0.6cm diameter located in the sides of the chamber permitted circulation of water through the



Fig. 46. Activity apparatus: a. recorder; b. plexiglass wall; c. counter-weight; d. clamp used as positive terminal; e. slide weight for sensitivity adjustment; f. balance arm; g. false bottom.

chamber. The false bottom of 0.6cm galvanized wire screen was attached to a balance arm by a 1.0cm diameter stainless steel rod. The balance arm was counter-weighted at the opposite end, and a slide weight enabled sensitive adjustment of the system for various sized fish.

The recording system consisted of a two-channel Rustrak model 91 recorder powered from a 6 volt wet cell. The apparatus was constructed so that any vertical movement of the false bottom activated the recorder circuit and resulted in a mark on the chart paper. Chart speeds of 1 in. per 30 min. and 1 in. per 10 min. were used.

All experiments were run at the study site and all fish, except those which had been held for particular reasons, were placed in chambers within 5 to 10 minutes after they were taken from the natural environment. Most of the fish were caught with a small hand net, both at night and during the day. Some were captured by baited and non-baited minnow traps. Specimens were transferred from the pools to the chambers in plastic buckets containing pool water.

The chambers were rinsed and filled with fresh seawater before each fish was introduced. Temperature was maintained as nearly constant as possible by insulating the chambers and water bath. A Ryan continuous recording thermometer in the water bath showed a maximum temperature fluctuation during a run of usually less than 1.5° C. The temperature of the water bath was usually kept within a degree or two of the shore water (7° to 11°C), but runs were made at temperatures from 4° to 17°C.

Chambers were operated under three light regimes: natural light, continuous and complete darkness, and continuous light. No quantitative or qualitative analysis of the continuously light condition was attempted. A 60 watt bulb was kept burning 2m above the chamber which was covered by a 3mm sheet of green fibreglass. No attempt was made to shut out natural light other than to shade the chambers from direct sunlight. When runs were made under natural light conditions the chambers were shielded from the light except for the green fibreglass cover. The chambers were always shaded from direct sun or moonlight. Continuous complete darkness was provided by placing the chambers and water bath in a light proof 3800 litre wooden stave tank.

Specimens were taken from pools of different heights and exposures. Usually specimens were placed in the chambers at approximately low tide, but some were placed in the chambers immediately following high tide and others at various intervals between successive high tides. Data were recorded concerning flooding history of the pools from which fish were taken. In many cases a surf sensor located at the pool from which the fish was taken, or at a known height in the intertidal zone, was connected to the same recorder as the activity chamber. In this way it was possible to directly compare the flooding of the pool, or a known vertical height, and the time of high tide with the activity of the fish. When a surf sensor was not used, tidal periods and heights were determined from six minute tidal predictions for Port Renfrew.

Some specimens were run in a chamber for four or five days, but most specimens were in the chamber for 48 hours or less. None of the specimens were fed during a run, and each was sexed and measured on its removal from the chamber.

Because the activity studies were conducted at the study site, the specimens were minimally disturbed as a result of handling. Also, due to the isolation of the site there were no periodic disturbances or background noise associated with the experimental facilities.

Results

Activity Under Natural Conditions

To determine the effects of some environmental factors on the activity of <u>O. maculosus</u> under natural conditions, observations were conducted on a series of tidepools at the 8.5 ft. tide level which consisted of deep central pools surrounded by shallow water 5 to 10cm in depth (Fig. 31). Under favorable conditions <u>O. maculosus</u> moves out of the deeper parts of these pools to feed in the beds of <u>Odonthalia</u> and <u>Spongomorpha</u> which grow in their shallow parts. During unfavorable conditions the fish retreat to or remain in the deeper water where they seek the seclusion of rocks and other cover. Throughout 1966 and parts of 1965 and 1967 observations were made to try and determine what factors cause the fish to be in the deeper parts of the pools.

Temperature

Temperature was one of the factors that was frequently monitored on a continuous or periodic basis during low tide in the shallow parts of the pools. At the same time that temperature was being monitored observations were made at periodic intervals to determine what percent of the total pool population of <u>O. maculosus</u> were in the shallow part of the pool.

Fig. 47 shows that at temperatures above approximately 15° C the fish either retreat to or remain in the deeper water. Because the time of day at which this temperature is reached varies considerably from day to day, depending on the state of the sea and the weather as well as the tidal cycle, it can be shown that there are no daily or tidal rhythmic responses involved.

Some of the observation pools were situated in such a manner that it was possible to siphon water into them from a higher pool. The pool that was siphoned from was deep enough so that water near its bottom never reached a temperature much above that of the surface sea water. Thus, by siphoning from different depths it was possible to add water of the same temperature or a lower temperature to the observation pools.

If the water in the shallow parts of a pool is cooled after it has warmed to a temperature above 15-17^oC the fish immediately move out into the cooled part of the pool. This is the same reaction that occurs when the tide first floods one or part of one of these pools. If, on the other hand, water of the same temperature is added to the pool, the fish become active for several minutes and make brief excursions out of the deeper water, but they then move back to the deeper parts of the pool.






Percent of the total tidepool population of O. maculosus (---) in the shallow parts of a tidepool in relation to the temperature (---) in that part of the pool. The effects of rain and flooding on the temperature are shown. In the absence of tidal flooding the fish will move into the shallow parts of the pool again if convective cooling lowers the temperature of these parts of the pool below the temperature of the deeper water.

In the winter months temperatures of less than $5^{\circ}C$ appear also to keep the fish from moving out into the shallow parts of the pool.

Salinity

Variations in salinity, at least over a wide range, do not apparently affect the natural activity of <u>O. maculosus</u>. Following periods of heavy rainfall it was not uncommon for the shallow parts of the observation pools to have salinities as low as 10.00% Under these conditions the fish move into the shallow parts of the pools and feed as long as the temperature is not too high.

In other tidepools in which the bottom salinities were as low as 3.00% as a result of run off, <u>O. maculosus</u> was observed feeding on food material that was being washed into the pools. When food material was artificially introduced into these pools, it was eaten readily also.

Turbulence

The fact that <u>O. maculosus</u> exhibits different behavior at high tide depending upon pool exposure and season of the year has been discussed in the section on high tide distribution and movements. Those data indicate that the behavior of this species is modified by turbulence. In areas where turbulence is usually great the species is inactive at high tide, whereas in areas where there is a minimum of turbulence the species is active at high tide. Also, at those times of the year when average conditions are most turbulent the species is inactive at high tide relative to those times of the year when average conditions are least turbulent.

Over the spring and summer months fish become conditioned to the general low level of turbulence to leave the pool as soon as it begins to flood. The result is that during summer periods when storms cause turbulent conditions the fish remain out of the pools despite the turbulence. During the winter months there are days when the sea is flat calm. Observations on tidepools of intermediate exposure during these days show that <u>O. maculosus</u> does not move out of the tidepools at these times. As soon as the pool begins to flood the fish retreat to cover and remain there until shortly before the pool becomes isolated again. The response to <u>O. maculosus</u> to turbulence, therefore, appears to be a response conditioned to the flooding of the pool rather than a response induced by the intensity of the immediate turbulence. Light

In the description of the methods used in obtaining recovery data for tagged fish, it was mentioned that it is characteristic of tidepool cottids at the study site to position themselves in the open during the period of darkness while the pool is isolated. Individual <u>O. maculosus</u> will often position themselves in exactly the same spot in a tidepool each night the pool is isolated for weeks and even months at a time. The fact that a fish can be seen in exactly the same spot from shortly after the pool becomes isolated to just before it floods again, indicates that there is a minimum of activity during this time. In the above mentioned observation pools most of the fish remained in the deeper parts of the pools when the pools were isolated at night.

Night observations at high tide show that <u>O. maculosus</u> has a distribution similar to that during daylight high tides. At night fish in sheltered areas, and during summer fish in areas of intermediate exposure, move out of the home pool at high tide. Stomach analyses and the fact that <u>O. maculosus</u> appears to be primarily a sight feeder, however, indicate that little food is taken in at low light intensities.

Inter- and Intraspecific Interactions

During all the field observations of <u>O. maculosus</u> no aggressive behavior was ever observed either towards other species or between individuals of the species. Copulation was frequently observed and in no instance did males exhibit threat responses to the presence of other males or females. It was not uncommon to see two males attempting to copulate simultaneously with the same female. In such cases the two males take up positions on either side of the female. If a female is unreceptive to a male, she simply swims away. In no instance did a female ever exhibit threat responses to a pursuing male.

The introduction of food into a tidepool never leads to threat displays between individual fish, and there is no indication of any dominance within tidepool populations. All the fish in a pool converge on food that is placed in the pool. If the food is a broken <u>Mytilus</u>, they simultaneously attempt to tear away pieces of it.

Activity Under Controlled Conditions

The Natural Rhythm

The typical activity rhythm observed when freshly caught O. maculosus are placed in an activity chamber is shown in Figs. 48 and 49. These Figures show several basic features of the rhythm: (1) the activity reflects the period parameters of the concurrent natural tide cycle; (2) the mid point of the activity period corresponds to the time of the concurrent high tide; (3) the mid point of the activity period is also the time of maximum activity; and (4) the activity period

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Fig. 48.

Record of the activity of a female <u>O. maculosus</u> (70mm) from a tidepool at the 7 ft. tide level under conditions of constant temperature $(10^{\circ}C)$ and natural light. The times of lower high water (LHW) and higher high water (HHW) are shown.



Fig. 49.

Record of the activity of a remale <u>O. maculosus</u> (65mm) from a tidepool at the 3 ft. tide level under conditions of constant temperature (10°C) and constant darkness. The record from a surf sensor located at the 9 ft. tide level is also shown. The times of lower high water and higher high water are indicated.

has a duration of 2 to 3 hours.

The rhythm usually remains overt for only 24 to 48 hours. In a few specimens, however, the rhythm has remained overt for 72 to 96 hours. Analysis of the activity of those specimens which have retained overt rhythmic activity for this length of time shows that under constant conditions the activity periods lose phase with the concurrent tide cycle.

Influence of the tide

The fact that O. maculosus inhabits tidepools throughout the intertidal zone means that it is possible on a given day to take specimens from tidepcols which have had very different flooding histories. Thus, paired experiments can be run in which one fish is from a low pool which floods twice in each lunar day and the other fish is from a high pool which may be flooding only once or not at all in each lunar day. Whereas specimens from the former tidepools always show two periods of locomotor activity per lunar day, specimens from the latter tidepools may show only one or no periods of activity. Usually if a tidepool has not flooded during a particular high tide (HHW or LHW) for two successive tide cycles specimens from that tidepool will not exhibit an activity period during that high tide. Under natural conditions, therefore, the rhythm is damped as rapidly as it is under constant controlled conditions. Specimens taken from tidepools which have not been isolated from the sea for at least four days show the same rhythmic activity typical of specimens taken from tidepools which are isolated and flooded twice per lunar day.

Entrainment under natural conditions

Once a specimen no longer shows rhythmic activity under controlled conditions, it is possible to entrain a rhythm to the tide cycle by placing a specimen back into the tidepool environment. The fact that <u>O. maculosus</u> inhabits home pools means that after a specimen has been run in an activity chamber it can be released into the natural environment and then be recaptured after it has been exposed to a specified number of high tides.

The following procedure was used to establish how many tide cycles a specimen must be exposed to before the overt rhythm is re-established. Six specimens were trapped from a pool and held in aquaria until they no longer showed rhythmic activity. After they had not shown rhythmic locomotor activity for two day, four of them were released into the home pool. The pool was then trapped on a daily basis and one of the marked fish was removed from the pool each day and run in an activity chamber with a specimen which had been in the pool until that day. The two control fish which were not replaced in the tidepool were run in an activity chamber after a returned fish showed overt rhythmic activity. In no instance did they show overt rhythmic activity.

Two of these series were run and in each case specimens which had been held in captivity did not show an over: tidal rhythm of locomotor activity until they had been re-exposed to at least two HHW tides. When specimens which exhibited no rhythmic activity were placed in tidepools which were flooded only once per lunar day, it was possible to establish a rhythm which showed only one peak per lunar day.

It is possible to duplicate these situations under completely natural conditions. Specimens can be taken from pools which have not flooded for three consecutive lunar days or three consecutive HHW tides, and then they can be compared with fish from the same pools run in the activity chamber, one, two and three days after the pool has started to flood again. When this was done the same results were obtained. Fish had to be exposed to at least two flooding tides before they showed rhythmic activity.

The natural light cycle

Each high tide moves through the solar day at an average rate of about 40 min. per day. Thus HHW tides and LHW tides both occur during variously illuminated parts of the solar day (Figs. 8 and 9). Activity data from freshly caught <u>O. maculosus</u> do not show that there is any difference in the lengths of the activity periods which normally occur during daylight periods as opposed to those which occur during periods of darkness.

Constant conditions

Regardless of the light regime (constant light, constant darkness or natural light) under which specimens are run in an activity chamber the rhythm maintains synchronization with the concurrent tide cycle over 24 to 36 hours. Because the rhythm is damped so quickly at this point, it has not been possible to determine if photoperiod or light intensity do affect period length or the level of activity.

Temperature

Specimens were run in activity chambers at several temperatures primarily to determine if rhythmic activity would be exhibited at different temperature extremes. No rhythmic activity was observed at temperatures below 4° C or above 17° C. Between $10-13^{\circ}$ C the rhythmic activity appears to be unaffected by temperature.

DISCUSSION AND CONCLUSIONS

Distribution

Local distribution

Rasmussen (1965) summarized the previous studies of the effects of increased exposure on the distribution of benthic intertidal organisms. In general, the presence or absence of some species and changes, usually upward shifts, in the vertical distribution of other species are associated with the degree of exposure of an intertidal transect. Several investigators have attempted with only limited success to devise relationships including such factors as wind, fetch, bottom topography, etc., which could be used to quantify the exposure of intertidal transects, i.e. Moore (1935) and Guiler (1950). The biological exposure scale devised by Ballantine (1961) for the comparative description of rocky shores was developed from the point of view that the organisms themselves are the best indicators of the exposure of a given shore. This scale is not quantitative and is unworkable at sites far afield from the region on which it is based. It has been possible in the present study to quantify by direct measurements of submergence and emergence with an automatic recording device (Green and Druchl, in preparation) the exposure of intertidal transects and tidepools. It is concluded from data obtained from these measurements at Botanical Beach that the exposure of a given transect is the

only environmental factor strongly correlated with the intertidal distribution of O. mapulosus.

According to Rasmussen (1965) exposure is more often associated with the absence of species than with their presence. Green and Druchl (in preparation) found this to be true at Botanical Beach. In comparing the attached biota of transects of different exposure they found that more intertidal species were lost than were gained in moving from more sheltered to more exposed conditions. Ecologically there are two important aspects of exposure. These can be referred to as (1) the durational (time) aspect, and (2) the intensity aspect. With reference to the durational aspect, as exposure increases the emergence curve (Fig. 14) for a particular transect is pushed upwards, and actual or "effective" tide levels become increasingly different from theoretical tide levels. The result, as far as physical and chemical conditions are concerned (i.e., temperature, salinity, oxygen), is less variable tidepool conditions at higher tide levels in exposed tidepools than in sheltered tidepools. With respect to the intensity aspect, the more exposed a vertical level is, the greater is the intensity with which breaking waves strike the substratum.

Except in the case of delicate species which are obviously not able to withstand the abrasive action and stress imposed by breaking waves, it is difficult to determine if it is the duration or intensity aspect of exposure, or a combination of both, which is causally related to the distribution of a particular species. The results of the present study suggest that the dominant characteristic of the intertidal distribution of <u>O. maculosus</u> can be most satisfactorily explained as an interactive effect of both aspects of exposure operating through the behavior of the species. The explanation which the data support is that turbulence from breaking waves causes anunfavorable condition which, if persisting for more than a critical duration, prevents the species from performing necessary functions such as feeding, copulation and spawning. <u>O. maculosus</u> is adapted for relatively non-turbulent conditions and consequently such conditions must be of a minimum duration for <u>O. maculosus</u> to inhabit a specific intertidal environment.

The behavioral observations show that <u>O. maculosus</u> reacts negatively to turbulence by retreating to cover and remaining inactive until conditions become calm again. This response is not seasonal as it is in evidence at all times of the year in those specimens inhabiting exposed tidepools. In the autumn the change from being active to inactive at high tide occurs first in those individuals inhabiting the more exposed of two otherwise similar tidepools, showing that their change in activity is directly associated with the degree of turbulence. In the most exposed transects at the study site <u>O. maculosus</u> is present at all times of the year in tidepools in the upper intertidal zone. The intensity with which waves break on a particular tidepool is not, therefore, in itself the reason for the absence of <u>O. maculosus</u> from lower less exposed or equally exposed tidepools. Rather, the intensity aspect of exposure is related to the distribution of <u>O. maculosus</u> through its direct effect upon the level of turbulence.

If turbulence has a marked negative effect upon the activity and behavior of O. maculosus, it would be expected that a decreased rate of growth and increased mortality would correspond with times of average high turbulence. At the study site both decreased rate of growth and increased mortality do occur during the months when average conditions in the intertidal zone are most turbulent. Nakamura (pers. comm.) in a study to determine if competition for food exists between O. maculosus and O. snyderi, concluded that such competition does not exist and that organisms comprising the food of both species are abundant and available throughout the year. A decreased amount of time for feeding due primarily to increased turbulence, and secondarily to decreased light, rather than a decreased amount of available food, would appear to be the most important factor for the seasonal growth characteristics of the species. A general decrease in the condition of individuals would contribute to increased mortality during times of continued high turbulence.

The above reference to a 'critical' duration of calm conditions for <u>O. maculosus</u> to be able to inhabit a given tidepool does not imply that its distribution can be defined in terms of the tide-factor hypothesis described by Doty (1946). It is not known in the case of <u>O. maculosus</u> what the characteristic of the time factor might be. The critical value could depend upon accumulated time within a certain, critical, longer period (e.g. a total of five active hours per week), or a maximum single period within a critical, longer period (e.g. at least one activity period per week with a minimum length of one hour) or some other relationship between what happens during every tidal cycle and what happens at some longer interval. It seems unlikely to determine the nature of the characteristics of the time factor until it is possible to measure and evaluate turbulence in the intertidal environment in terms relating directly to the fish.

Geographical distribution

The local distribution of <u>O. maculosus</u> at first appearance would not seem to support Morris' conclusion that its southward latitudinal distribution is related to the 16° C isotherm (Morris, 1960). The species regularly inhabits tidepools which consistently have temperatures well above 16° C for most of the day during summer months. Some of the tidepools inhabited by this species have temperatures higher than 16° C for several consecutive days. Observations on the effect of temperature on the behavior of <u>O. maculosus</u> do, however, give support to Morris' conclusion. The inflection in the temperature-salinity tolerance line at approximately $16^{\circ}C$ (Morrie, 1960) corresponds to the temperature at which, in the present study, <u>O. maculosus</u> was observed to cease normal feeding activity. Unless the species exhibits latitudinal temperature acclimatization, which Morris (1962) indicates it does not, the direct ecological significance of this temperature can be seen readily.

Other species

The upper vertical limits of the local distribution of the other tidepool cottids at Botanical Beach were not found to be correlated with a single environmental factor to the exclusion of other factors. Only <u>Clinocottus globiceps</u>, <u>C. embryum</u> and <u>C. acuticeps</u> have distribution patterns which suggest that biotic factors may be more important than physical or chemical factors in determining their distribution in some vertical transects. Within its vertical range the distribution of <u>O. snyderi</u> does appear to be related to the distribution of Phyllospadix scholeri.

Further conclusions concerning the local distributions of tidepool cottids at Botanical Beach will have to await more field and laboratory studies of their physiology, behavior and ecology. What has been learned about the distribution of O. maculosus should caution against concluding too much from laboratory studies which are not supported by field investigations. For example, <u>O. maculosus</u> inhabits tidepools in which the temperature is regularly well above its physiological optimum and certainly above the termperature that it would prefer if it could move to a lower temperature. The fact that a species inhabits only tidepools below a certain tide level may have little to do with the conditions in the pools above this level other than the fact that the species must experience flooding once or twice per lunar day. The wide occurrence of tidal rhythms among intertidal organisms makes this an intriguing and plausible possibility. Ideally, then, physiological and behavioral experimental situations which are being related to the distribution of an intertidal organism should have tidal fluctuations incorporated into them.

Movements and Homing

That <u>O. maculosus</u> shows fidelity to specific tidepools and will home to, or attempt to home to these pools when they are displaced from them, is concluded from the present study. It is also concluded that the high tide movements of this species are dependent upon quantitative characteristics of the exposure of the home pool. The latter factor may vary seasonally and when it does there is an accompanying change in the high tide movements of individuals inhabiting the pool. This feature of the movements at high tide of an intertidal fish has not been described, and possibly not considered, in previous investigations of movements and homing behavior (e.g. Williams, 1957 and Gibson, 1957b).

The consequence of restricted movements of a tidepool fish as the result of specific exposure characteristics of the home pool raisesdoubts about the validity of attributing homing behavior to a species only on the basis of the presence of the same fish in a pool on consecutive low tides, especially when the effects of exposure on the species have been evaluated. Although concluding the Clinocottus analis homes on the basis of marked fish released into their home pool, Williams (1957) showed that this species will not return to the home pool when displaced to pools a maximum of two meters away. He attributed this to the fact that disturbance of the fish during capture and marking causes a considerable portion to abandon their home pool, and that their bottom-dwelling habits provide a limited view of the surrounding areas. How this latter statement is reconciled with the conclusion that the species homes as a result of familiarity with geographical cues outside the pool is not clear. Disturbance during capture and tagging of O, maculosus does not appear to affect homing behavior or the fidelity of an individual to the home pool. O, maculosus is also a bottom-dwelling species but will return to the home pool over considerable distances.

In his investigations of the return to the home pool of displaced <u>Blennius pholis and Enophrys bubalis</u>, Gibson(1967b) concluded that "results of the displacement experiments do not give evidence for the presence of a directed movement back to the original pool...". He further stated that "until more evidence is available on this point, the best working hypothesis that can be put forward to explain the return of displaced fish is that although movements may be random within the limited area of the home range, the fish are able to recognize their home pool when they come across it by chance."

The present evidence indicates that <u>O. maculosus</u> does exhibit directed movements back to the home pool. The mechanism by which these movements are made is not known, but certainly homing is dependent upon a precise behavior mechanism inherent in the fish. It appears also that this mechanism does not necessitate a spatial familiarity with the area covered during homing. In some areas <u>O. maculosus</u> exhibits regular movements away from the home pool, but even these movements are restricted when compared with the distance over which the species will home. If individuals can recognize geographical features beyond the range of their daily movements they must have obtained this information at an age and size when they do not show strong fidelity to specific pools.

O. maculosus has been shown to home to and to show fidelity to specific pools after being held in an unnatural environment for periods as long as six months. This indicates that an image of the home pool is retained over long periods, and suggests that at some stage in the development of individual fish some specific characteristic(s) of a pool is(are) imprinted on the fish. Unless information relating to the geographical features of the surrounding area is similarly 'remembered' it is difficult to avoid the conclusion that this species has bicoordinate navigational ability. Orientation toward the home pool from an unfamiliar location would imply that the fish can perform the equivalent of fixing its present position on a grid of two coordinates, calculating the course to swim in order to regain the coordinates characteristic of the home pool and steering the course (Hinde, 1966). Whether O. maculosus does orientate more or less directly toward the home pool is not known. The transplant experiments indicate that it at least orientates in the proper direction relative to the position of the shore. Once an individual is swimming in the proper direction parallel to the shore, orientation to a specific depth of water or familiarity with a transect perpendicular to the shore would then provide the cues which would enable the individual to home.

Various species of littoral crustaceans have been shown to possess the ability to orientate themselves by the sun (see Pardi, 1960).

In these species this ability enables individuals to return to the water along a direct course perpendicular to the shore. Whether any such ability exists in <u>O. maculosus</u> remains to be learned. Hopefully, answers to some of the specific questions concerning orientation in this species will result from the current studies being conducted at Botanical Beach by Khoo (pers. comm.).

Ecological significance

According to Williams (1957) homing behavior in intertidal fish is "a mechanism by which shallow water fishes of rocky shore areas avoid being left by the tide in unfavorable situations, such as pools that disappear through subsurface drainage." If there is a danger of O. maculosus being left in unfavorable situations at low tide, the homing instinct would be a mechanism of survival to the species. One is left with the question whether or not such dangers were the primary cause for the development of homing and whether this is the primary function it now serves. It would appear, for example, that familiarization with the biotic features characteristic of tidepools, which retain water at low tide, would prevent the fish from being stranded in a non-tidepool location, and would mot necessitate the fish seeking out the home pool when displaced from it. Under conditions of high turbulence, the apparently inflexible homing behavior in O. maculosus would seem to be a liability rather than an asset.

The hypothesis which is suggested here is that homing behavior in <u>O maculosus</u> serves much the same purpose in this species that territoriality serves in other species. Gerking (1959) states that "territoriality is a stabilizing influence because it separates individuals from one another in a regular and orderly fashion in addition to making the fish intimately aware of its surroundings." Territoriality depends upon aggressive interaction among individuals in a population. As there is no aggressive interaction among individuals of <u>O. maculosus</u>, territoriality in the above sense does not exist in this species.

It would seem, however, that in a species like <u>O. maculosus</u> which inhabits an extremely variable and rigorous environment, a strong mechanism by which the species remains dispersed and stabilized would be of special importance and adaptiveness. In the absence of such a mechanism the species would tend to aggregate in only the most favorable habitats--the tidepools--within its range of distribution. Aggregated in this way the species as a whole would be more susceptible to the unpredictability of environmental conditions typical of an exposed coast. The imprinting of visual cues of the tidepool on an individual at an age when the juvenile population is relatively well distributed throughout the range of the species, coupled with homing behavior is visualized as serving this stabilizing function in O. maculosus.

Tidal Rhythm

The variations in tidal amplitude (Fig. 8) and tidal periods (Fig. 12) at Botanical Beach are not directly correlated with periodicities in lunar zenith and nadir. Under these conditions a biological rhythm cannot be well correlated continuously with both moon and tides (Enright, 1963). The tidal rhythm of locomotor activity in <u>O. maculosus</u> not only follows the period parameters of the concurrent tide accurately, but also responds directly to the flooding history of the pool from which the fish is taken. It is concluded, therefore, that the rhythmic tidal activity of <u>O. maculosus</u> is entrained in the field by the direct influence of the tide rather than by geophysical variables.

It has not been possible in the present study to experimentally establish what parameter associated with the tide operates as a synchronizer. The results strongly indicate though that none of the physical and chemical changes, i.e. temperature and salinity, associated with the initial flooding of individual tidepools, function as synchronizers. Such synchronizers would be very unreliable as a result of the direct influence of the state of the sea and weather conditions on the time when individual pools flood, and on the time when variations in these properties occur. Specimens taken from high pools exhibit the same rhythmic locomotor activity as fish taken from low tidepools as long as the higher pools are completely flooded during each high tide. The rhythm is the same despite the fact that the lower pool may flood four hours before the higher pool. Also, the rhythm remains entrained in fish inhabiting low pools which are in constant contact with the sea for several consecutive days. That factors such as temperature and salinity do not operate as synchronizers is further indicated by the fact that in those situations where a pool is flooded enough to completely change its physical and chemical conditions, but not enough to bring the pool into complete contact with the sea, the rhythm is not entrained.

Two other possible synchronizers would appear to be turbulence and hydrostatic pressure. Enright (1965) showed that the tidal rhythm of locomotor activity in the sand beach isopod, <u>Excirolana chiltoni</u>, can be entrained in the laboratory by a device designed to simulate wave action on a beach. The results suggest that mechanical stimuli arising from wave action on a beach may be the normal synchronizing factor for Excirolana and perhaps other similar organisms.

With respect to the tidepool habitat, turbulence would appear to be as unreliable a synchronizer as changes in factors such as temperature or salinity. Maximum turbulence is not always well correlated with the time of high tide. Also, the time at which there is a significant change in turbulence--the time at which the tidepool begins to flood--has the same limitations as a reliable synchronizer

as mentioned above for temperature or salinity.

Hydrostatic pressure would theoretically meet the requirements of a reliable synchronizer. It reaches an average maximum value, taking into consideration variations due to waves, at the time of high tide for any location on the flooded portion of the intertidal zone. The problem in postulating that pressure functions as the synchronizer for the tidal rhythm of <u>O. maculosus</u> is to show the mechanism by which pressure cures are perceived. The swimbladder is known to function as a pressure receptor (Jones and Marshall, 1953), but <u>O. maculosus</u> like other cottids does not have a swimbladder or other gas-filled structure.

Morris and Kittleman (1967) recently reported that two species of fish they investigated have otoliths which are piezoelectric. They suggest that this constitutes a mechanism for depth perception. If it can be demonstrated experimentally that pressure functions as the synchronizer of the tidal rhythm in <u>O. maculosus</u>, perhaps a similar or equally subtle pressure receptor will be involved.

Number of oscillators

Evidence for the existence of daily (circadian) and tidal components in the persistant rhythmic activity of intertidal organisms has been presented by various investigators (see Palmer, 1967). Neither Enright (1963) nor Gibson (1967) found evidence of other than tidal rhythms of locomotor activity in sand beach amphipods and intertidal fish. In the present study no evidence for rhythmic activity other than that associated with tidal cycles was found in <u>O. maculosus</u>.

. Enright (1963) discussed the possibility of two separate oscillators within the individual being responsible for the tidal rhythm in Synchelidium. Apparently his conclusion was that the results did not support the concept of a two-oscillator system any more strongly than they supported a single-oscillator system. Results of the present study do appear to support the concept of a two-oscillator interpretation of the rhythm in O. maculosus. The fact that a specimen can be entrained in the field to exhibit a single activity period each lunar day which is not different from the activity periods in fish which are entrained to exhibit two activity periods per lunar day, is not in agreement with what would be expected with a single-oscillator system. Also, when the rhythm is being entrained in the field under conditions of two tidal floodings per day, a specimen will only show one activity period if it is removed from the pool between the fifth and sixth floodings which, again, suggests that the two oscillations are independent of one another.

From the point of view of synchronization and timing, the advantages of a two-oscillator system over a single-oscillator system as far as being better adapted to the variations in the lengths of the tidal periods are clearly apparent. The tidal day periods (e.g. HHW-HHW) at Botanical Beach vary by a considerably smaller time interval from day to day, and have a much smaller total variation than do the semi-daily periods (e.g. HHW - LHW) as is shown in Fig. 12. Two oscillations each with a period of approximately 25 hours would have to undergo only slight rephasing to remain in phase with the natural tide cycle.

Ecological Significance

The activity of <u>O. maculosus</u> in its natural habitat is directly dependent upon such factors as turbulence, temperature and light. The tidal rhythm of locomotor activity which this species exhibits under controlled conditions, often is not associated with the time during the day when this species is active under matural conditions. It would appear, therefore, that the rhythm represents the functioning of a biological clock which is linked to an avoidance or escape response. Coupled with the homing behavior and an escape response to an unfamiliar habitat, such a clock would be of survival value to the species.

Were a fish displaced by one means or amother to a different tide level, or different location of the same level, such an internal clock and associated swimming activity would emable the fish to home, or attempt to home, at the time of highest water. The fact that displaced fish apparently remain in the pool into which they are transplanted at least until 1 to 2 hours before the time of high tide

regardless of when the transplant pool floods, supports this conclusion. It is clearly not valid to make inferences concerning the natural activity patterns or behavior of this species solely on the basis of a tidal rhythm of locomotor activity exhibited under constant conditions. Perhaps such errors in the ecological interpretations of rhythmic behavior are commonly made.

SUMMARY

1. On the basis of tidepool collections made on the west coast of Vancouver Island, B.C., five species of fish (<u>Oligocottus</u> <u>maculosus</u>, <u>O. remensis</u>, <u>Clinocottus acuticeps</u>, <u>C. embryum and</u> <u>C. globiceps</u>) are referred to as primary tidepool cottids. They have vertical distributions centered in the intertidal zone. <u>O. maculosus</u> is the most abundant and widely distributed in the intertidal zone of these species.

2. Seven species of fish (<u>Hemilepidotus hemilepidotus</u>, <u>Artedius</u> <u>lateralis</u>, <u>A. fenestralis</u>, <u>Ascelichthys rhodorus</u>, <u>Enophrys bison</u>, <u>Leptocottus armatus and O. snyderi</u>) are referred to as secondary tidepool cottids. They inhabit tidepools but are most abundant in the subtidal zone.

3. Evaluation of environmental factors show that the distribution of <u>O. maculosus</u> is correlated with exposure to wave action. In exposed transects this species is restricted to the upper intertidal zone, while in sheltered transects it inhabits tidepools throughout the intertidal zone. <u>C. embryum and C. globiceps</u> have wider vertical distributions in more exposed than in more sheltered transects. <u>C.</u> <u>acuticeps</u> is restricted to sheltered tidepools in the upper intertidal zone, while <u>O. remensis</u> inhabits intermediately exposed tidepools in the lower intertidal zone. 4. The upper vertical distributions of the secondary tidepool cottids are not correlated with a single environmental factor to the exclusion of other factors. None of them regularly inhabit pools above LLHW (lowest lower high water). Within its vertical range the distribution of <u>O. snyderi</u> appears to be related to the distribution of <u>Phyllospadix</u> scholeri.

5. Behavioral observations show that <u>O. maculosus</u> responds to water turbulence by retreating to cover. Depending upon the exposure of the tidepool, this response is always exhibited, or is exhibited only during the turbulent parts of the year. Decreased rate of growth and increased mortality are associated with that time of the year when conditions in the intertidal zone are most turbulent. It is concluded that in order to inhabit a given tidepool, <u>O. maculosus</u> must have a minimum duration of low turbulent conditions. <u>O. maculosus</u> has 'capitalized' on the tidepool habitat to invade the open coast environment.

6. <u>O. maculosus</u> shows fidelity to particular tidepools and will return to these pools when displace from them. Homing success does not appear to be related to time of year, sex or size above 55mm. Homing occurs regardless of the direction from the home pool that fish are released.

7. Individuals successfully homed from locations 102m from the home pool. Observations in the tidepool area where homing experiments were conducted show that <u>O. maculosus</u> moves a maximum of 15m from the home pool at high tide. This indicates that <u>O. maculosus</u> may have navigational ability not dependent solely upon familiarity with particular geographical features of the intertidal zone. It is suggested that homing behavior functions as a mechanism stabilizing the spatial distribution of this species.

8. <u>C. embryum and C. globiceps</u> also show fidelity to particular tidepools. <u>C. globiceps</u> was shown to home to the tidepools in which they were captured. No tagged C. embryum were transplanted.

9. In the natural habitat activity such as feeding and spawning in O. maculosus is dependent primarily upon turbulence, temperature and light. In relation to temperature, natural feeding activity ceases when the water temperature rises above $15-16^{\circ}$ C. This field observation supports Morris' (1960) conclusion, drawn from his physiological studies, that approximately the 16° C isotherm is the limiting environmental factor in the southward distribution of this species.

10. Under constant condition O. maculosus exhibits a tidal rhythm during which locomotor activity is enhanced for 2-3 hours at the time of high tide. The characteristics of the rhythm indicate that it is

entrained directly by the influence of the high tide, and that the system consists of two independent oscillators. Hydrostatic pressure could be the synchronizer.

11. The rhythm is not arrectly related to the field activity of <u>O. maculosus.</u> It is concluded that it represents the coupling of an avoidance or escape response to an unfamiliar habitat, to a biological clock. Such a mechanism would function with, and be partially responsible for, the homing behavior.

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