A COMPARATIVE STUDY OF THE MOVEMENT HABITS AND THEIR RELATIONSHIP TO BUOYANCY COMPENSATION IN TWO SPECIES OF SHALLOW REEF ROCKFISH (PISCES, SCORPAENIDAE)

by

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MASTER OF SCIENCE

in the Department of Biology

We accept this thesis as conforming
to the required standard

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ABSTRACT

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An assessment was made of the potential for restricted vertical movement in two species of shallow reef rockfish caused by concurrent changes in buoyancy. Movement habits of a schooling form, *Sebastes melanops*, were compared with those of a benthic crevice dweller, *Sebastes nebulosus*, on a moderate exposure rock-reef in Barkley Sound, British Columbia. Through multiple observations of tagged fish against a geographically fixed landmark system, distribution and movement of individuals was determined. Tagged *S. melanops* remained on the study reef for periods of about three weeks; but, while present, were distributed in the water column at select locations. Movements in this species occurred during 46 percent of successive observations with distances frequently greater than 15 meters, extending as much as 10 meters vertically. The solitary *S. nebulosus* were resident for most of the field study period (2 months) having a more limited distribution, apparently territorial. Their movements are less frequent (26 percent of successive observations involved movement) and usually less than 10 meters horizontally with little of no vertical aspect.

In the laboratory, *S. melanops* had a much greater capacity to use their swimbladder as a buoyancy device under changing pressure situations than *S. nebulosus*. Although nearly identical in general swimbladder morphology, measurements of the secretory epithelium showed that *S. melanops* have over twice the secretory area than *S. nebulosus* of similar body weight. In a simulated descent from the surface to 20 meters depth *S. melanops* required 90 hours to restore neutral buoyancy while *S. nebulosus* required 450 hours. Ascending from this depth using a stepwise decompression procedure to avoid damage through overexpansion, *S. melanops* could achieve neutral buoyancy in about 5 hours while it took *S. nebulosus* at least 20 hours.

Despite the comparatively faster rates of buoyancy adjustment in *S. melanops* it was clear that short term vertical movement in this species was not accommodated by buoyancy adjustment through secretion or resorption of swimbladder gas. Instead, vertical movement results in periods of non-neutral buoyancy. A survey was made of the various buoyancy strategies that facilitate vertical movement in other fish species; the relationship of those species to the two study species is discussed.

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ACKNOWLEDGMENTS

I would like to thank Dr. J. E. McInerney for his assistance in setting the stage for this study, including technical, financial, and theoretical aspects. Discussions with S. J. Westrheim, Dr. J. Hayward, B. M. Leaman, and Dr. G. J. S. Craik provided useful advice. Dr. L. Haldorson and B. M. Leaman read the manuscript and offered suggestions.

A major portion of the field work was done while diving with S.C.U.B.A. which required, for safety reasons, another diver. To avoid problems of trying to find people with time to help out, dives were combined with a concurrent study by V. E. Fletcher. Needless to say, the field work could not have been done without this support. However, his generally positive attitude and enthusiasm made the diving an especially enjoyable experience. I am also grateful to A. Lindwall and J. S. von Carolsfeld for their diving assistance.

Technical assistance with the pressure tank system was generously provided by G. Davies and P. Smith. P. Frank prepared the drawings and helped invaluably in the final preparation of this thesis.

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available the use of facilities at the Bamfield Marine Station.

Chapter I

INTRODUCTION

Many different groups of fish inhabit the open water spaces of the aquatic environment. Despite their wide distribution and diverse morphology these groups all share a common problem, that of counteracting gravity. Among bony fish, the most common means is a visceral air sac called the swimbladder. This organ is present in two general forms, physostomous and physoclistous. Physostomes have a duct connecting the swimbladder with the pharynx and are able to increase buoyancy by gulping air from the surface and decrease it by expelling air. In more advanced groups a closed or physoclistous swimbladder is common. These fish have no external duct and adjust swimbladder volume by physiological secretion or resorption of gas. This design has the advantage of allowing buoyancy adjustments to be made without coming to with the surface.

The swimbladder operates well as a hydrostatic organ in a constant pressure but is less suited for varying pressure situations such as fish encounter during vertical movement. In such cases, the ambient pressure changes, and the swimbladder, acting much like a bubble, changes in approximately an inverse relation to absolute pressure (Boyle's Law). As other variables such as fish volume and water density remain essentially constant the change in swimbladder size creates a net floating or sinking force. In moving from a depth of equilibrium, vertical position is maintained by compensatory swimming activity until neutral buoyancy is restored. This situation compounds itself in shallow depths where a small change in vertical position results in large changes in buoyancy. The volume of a gas bubble expands twice its original size while ascending from 10 meters to the surface. Similar expansion from a depth of 100 meters corresponds to a vertical ascent of 55 meters.

Fish which live in shallow water reef habitats are seemingly limited by having a closed swimbladder for a buoyancy apparatus. Because of the rapid change in volume with depth, neutral buoyancy exists in a narrow vertical zone. When moving from this depth, compensatory swimming becomes an essential part of maintaining vertical position, particularly while ascending. While the energy required to oppose negative and slight positive buoyancy may be more economical than having no swimbladder at all, furthered degrees of positive buoyancy require vigorous compensatory swimming. Consequently, depending upon the depth of neutral buoyancy, there exists a ceiling where further ascent requires much energy through swimming or a rapid means of buoyancy reduction through gas transport. Despite this apparent limitation, nearly all neritic and suprabenthic fish species in the shallow reef habitat have a closed type swimbladder and to some degree, are faced with this situation.

Part of the problem in determining the importance of buoyancy as a restricting feature in the movements of shallow reef fish lies in a general lack of information on movement habits. Many studies exist which consider distribution and movement patterns of populations, but few concentrate on movements of individuals and apparently none examine movement in such a way that information concerning buoyancy imposed restriction is evident. With the recent widespread use of radio telemetry for tracking fish, more information will likely be available. A second area which has received little attention concerns the response of fish to a pressure gradient. Some information is available on the time required to restore neutral buoyancy after artificial displacement and also swimming capabilities of fish at different buoyancy states. Studies by Jones (1951, 1952) are unique in providing both types of information on a single species, _Perca flavescens_ and presenting a concise view of restrictions to movement imposed by changes in buoyancy. However, his studies are primarily laboratory based and do not include direct information about movements in natural habitats.

The objectives of this study were to examine the relationship between movement habits and possible limitations imposed by the buoyancy system and to evaluate the importance of the swimbladder as a buoyancy device in a few species. A combined approach was used obtaining information on what buoyancy conditions fish naturally encounter versus that which they are capable of dealing with. These two categories correspond to the following general tasks:

1. An examination of temporal and spatial distribution of individuals in order to characterize movement habits.

2. An examination of physiological and behavioral aspects of buoyancy which relate to a fishes' ability to deal with different buoyancy states.

Members of the family Scorpaenidae present a unique situation well suited for this type of study. Often, as many as 10 rockfish species (genus, *Sebastes*) inhabit a rock reef-kelp bed habitat. Many of these species have distinctly different space requirements and social behavior but generally fall within one of two ecological groups. The first group consists of schooling fish which occur in the water space above the reef. Some representatives of this group are *Sebastes melanops*, *S. mystinus*, *S. flavidus*, *S. pinniger*, *S. miniatus*, and *S. entomelas*. A second species complex, usually solitary and occasionally territorial, inhabits the reef surface and enclosed spaces. Common members of this group are *S. caurinus*, *S. maliger*, *S. nebulosus*, and *S. nigrocinctus*. Despite their divergence in behavior patterns, all species of this genus are very similar morphologically (Chen, 1971).

A representative of each group was selected for this study. The black rockfish, *Sebastes melanops* (Girard), is an active water column dweller and the china rockfish, *Sebastes nebulosus* (Ayres), is a benthic crevice dweller. For convenience these species will be referred to by their common names only.

Chapter II

MATERIALS AND METHODS

2.1 FIELD STUDY

This study was conducted at the Bamfield Marine Station located in Barkley Sound along the outer coast of Vancouver Island, British Columbia, during the period May 1976 to February 1978. The majority of the field work was concentrated on a single study reef at Ohiat Islet (48°51.6N 125°11.2W). Since laboratory studies required the collection of many animals, dives were made at a variety of locations within southeastern Barkley Sound. More than 300 dives were made throughout the year, forming the basis for observations of distribution and behavior of the fish; half of the dives were made on the Ohiat site.

At the field site, efforts were directed towards determining mobility habits of individual fish. This demanded diver distinction of different parts of the reef as well as individual fish. The entire study reef was mapped and landmarks were placed to enable rapid underwater identification of specific places on the reef surface. After the mapping was completed, fish were captured using a variety of techniques and marked with individually specific tags. Both site preparation and tagging were carried out during the winter and spring months so that the summer could be used entirely for observations.

2.1.1 Description of the Study Site

Ohiat is a small islet (0.6 ha) located in the Deer Group, a chain of islands separating Trevor Channel from Imperial Eagle Channel in southeastern Barkley Sound (Figures 1 and 2). The north and west sides of the Islet have very rugose rock reef surfaces rising from a sand bottom approximately 25 meters deep. Solid and broken rock make up the reef terrain. The steep slope leads into a shallow flat region where the kelp, *Nereocystis leutkeana*, develops seasonally. The large and diverse fish populations present as well as the steep vertical profile, made this area particularly useful for space utilization studies.

2.1.2 Site Preparation

2.1.2.1 Mapping Techniques

The site was mapped using methods shown in Figure 3. A base line was laid out along the sand bottom directly adjacent to the sand-rock interface. Transects perpendicular from the base line were made at 7 meter intervals, measuring the vertical and diagonal components of the reef slope. Reef orientation with respect to shoreline was established by measuring compass bearings along the base line and above water at the shoreline. Information collected from all

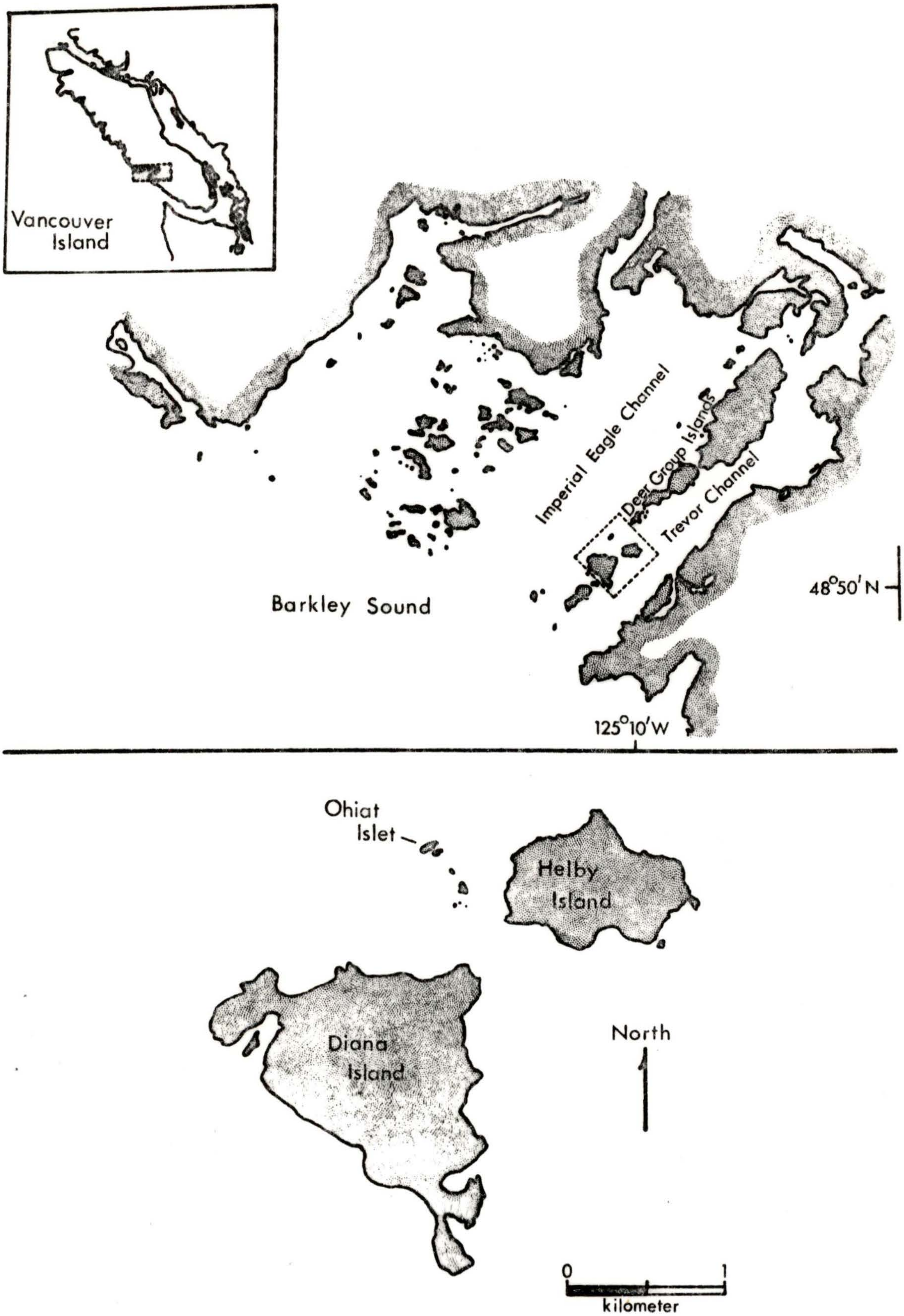


Figure 1. The general location of the study area.

Figure 2: Aerial photograph showing the location of the study site at Ohiat and neighboring islands.


study site
Ohiat Islet
Diana Island

transects was transferred to scale on graph paper and used in constructing a topographic map. Subsequent dives using a water resistant copy of the map enabled verification of the general reef geography as well as allowing the incorporation of more specific reef detail such as the location of crevices, boulders and ledges.

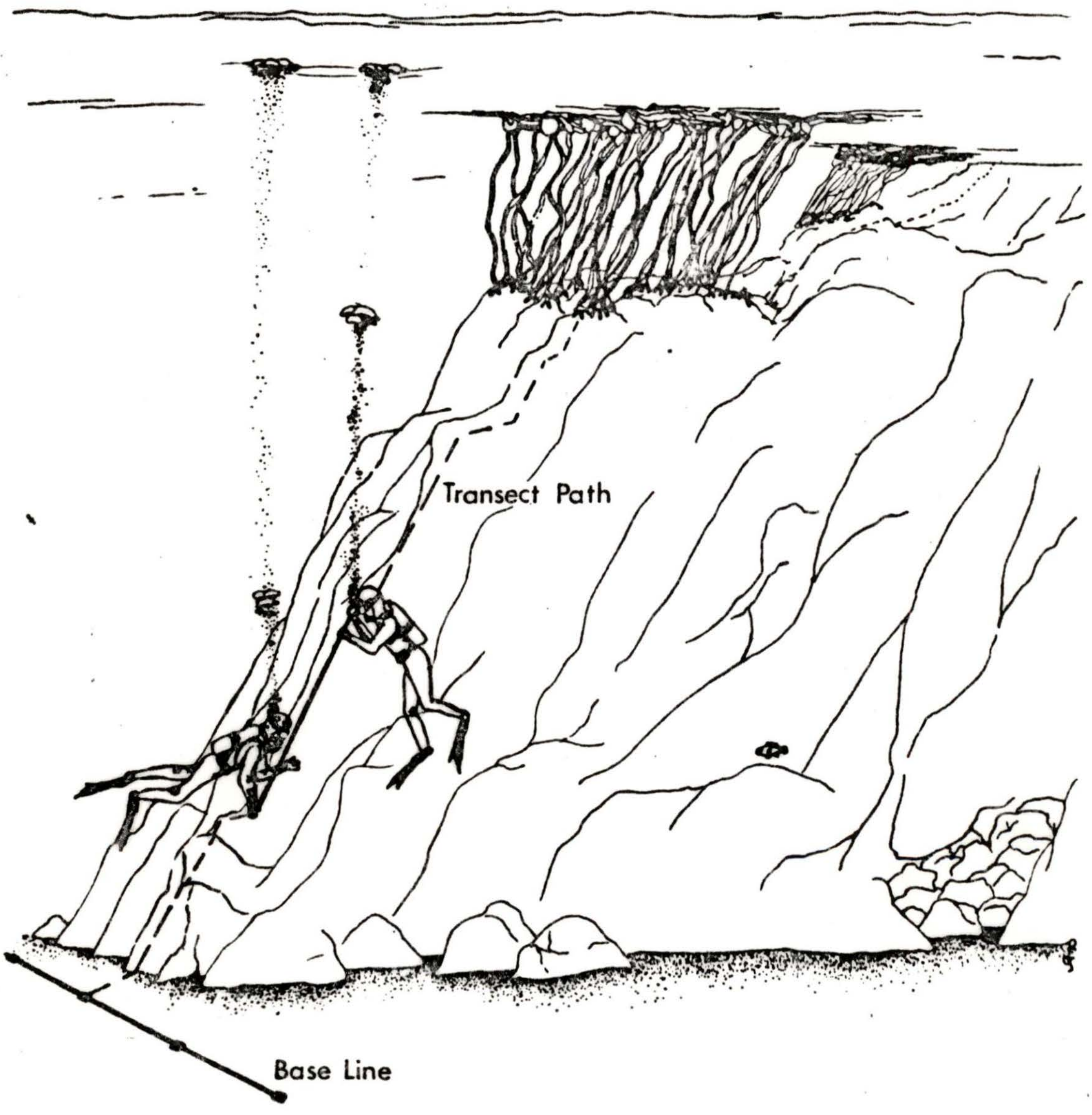


Figure 3: View of survey techniques used for mapping. Shown are divers approximating the reef slope by measuring the distance between different depths.

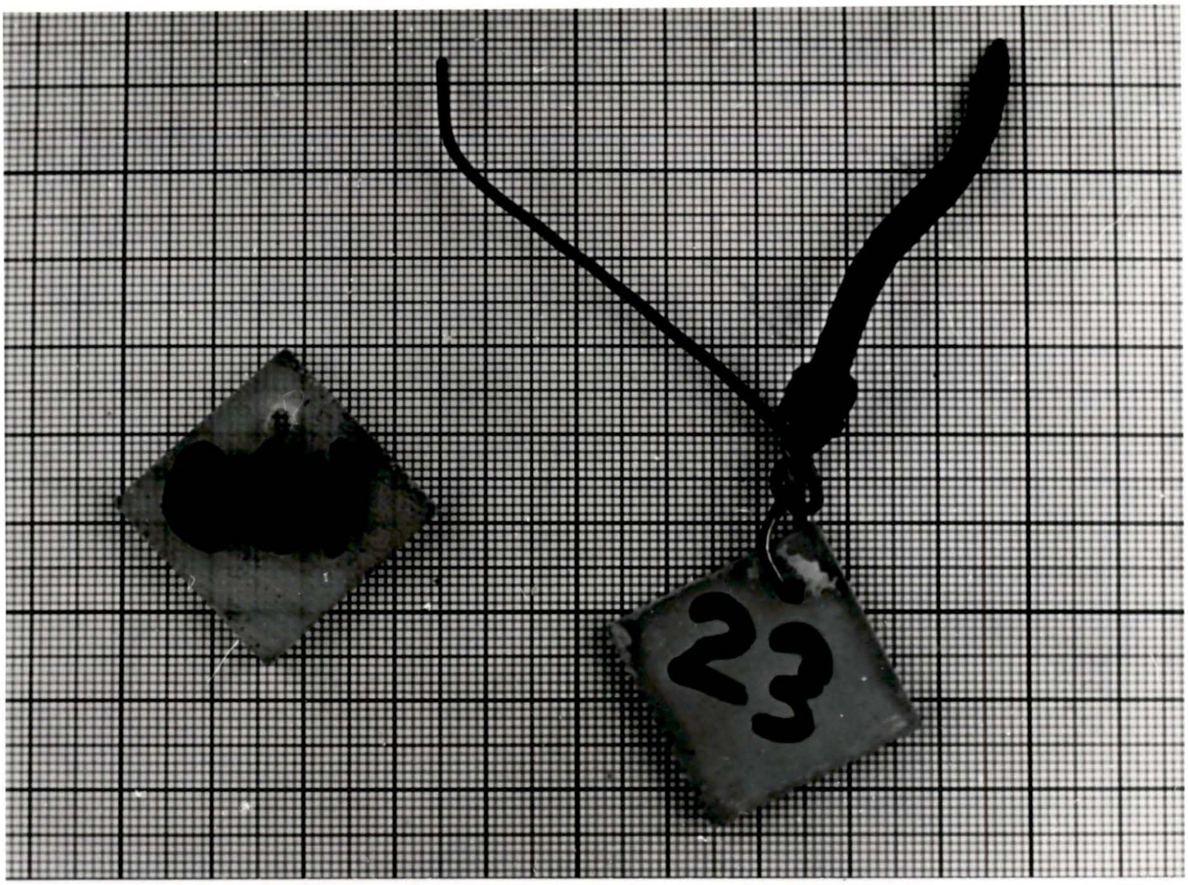
Equipment used for mapping were a depth gauge (U.S. Divers Depth Master II), tape measure, and an underwater compass (AMF, model DC-300). Using pressure (depth gauge) as a measure of depth has inherent problems as a consequence of depth gauge sensitivity and temporal fluctuations in water level due to tides, weather conditions, and passing swells. Depth gauges were good quality, oil filled, and had a guaranteed maximum error of 1 meter. Accuracy of gauges was periodically checked using laboratory pressure tanks (see section 2.2.2.1) and was within 0.3 meters. Variation in water depth between survey dives was corrected by recording the depth at a reference marker located in the deep water sand portion of the site. During periods of large swells, survey dives were not made. When variations due to passing waves occurred, true depth was taken to be the median gauge reading.

2.1.2.2 Reef Markers

After making several visits to the study reef, I had explored it thoroughly and was familiar with most of the complex reef geography. However, during low light conditions or high water turbidity, one can become easily disoriented and markers serve useful points of bearing. Numbered markers can be recorded rapidly and represent an exact position that can be easily relocated. Markers were placed throughout the dive site, primarily along 3.3 meter (10 foot) horizontal contours. These were spaced at a variety of intervals according to the complexity of the reef. The major criteria in spacing of markers were that each marker could be easily observed from neighboring markers and that the distribution of markers was descriptive of the terrain complexity. Consequently, markers were placed at prominent locations along contours such that neighboring markers could be seen during reasonable water clarity (3 meters or better). In areas where there were crevices, boulders or other conspicuous features, more markers were placed to make points within this area distinguishable. No markers were placed within the kelp bed since they could not be easily distinguished. Also, the microgeography of this area was variable such that different areas were distinctive without markers.

Markers were constructed from 4 cm squares of 4 mm thick plexiglass shown in Figure 4. On the back surface of each square was painted a number (painted backwards) and overlaid with a thick protective coat of brightly colored enamel. From the unpainted side of the square, the number appears in the normal orientation over a contrasting background. A small hole was drilled in the corner of each marker such that a wire could be threaded through for use in anchoring to the substrate. Pieces of surveyor flag tape were tied around the wire to ensure the tags were conspicous when placed on the reef.

Figure 4: Stages of marker construction (upper) with finished marker shown in position on the reef surface (lower).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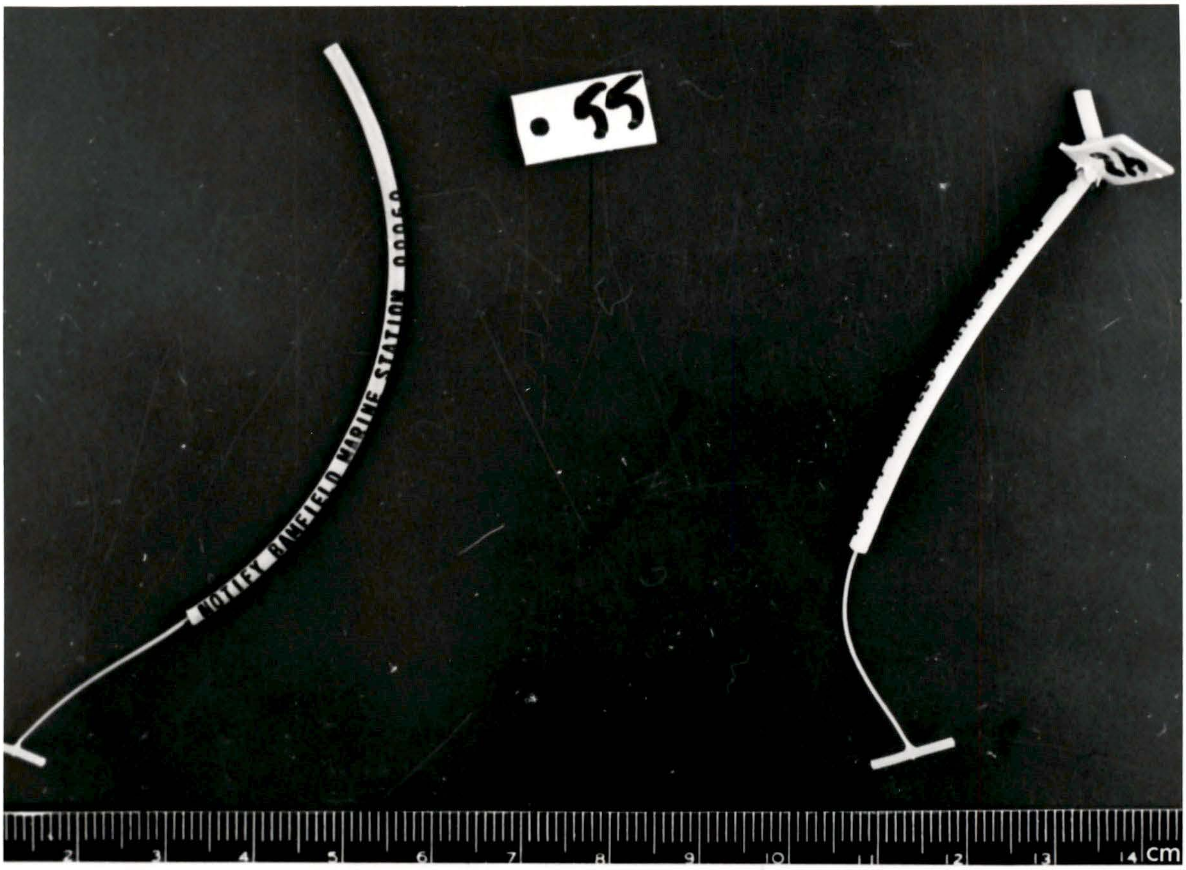
Markers were attached to the reef surface with tempered steel concrete nails. These nails become wedged in surface cracks much like a mountain climber's piton. The markers were attached with several wraps of wire around the nail head. In areas where the reef surface was not suitable for driving nails, markers were attached to red-clay bricks and placed in position. The lateral boundaries of the site were marked with flourescent-orange colored bricks.

2.1.2.3 Fish Collection and Tagging

The requirements for fish tags were that they distinguish individual fish, be visible from a distance, and not impair the swimming ability of a fish. Floy anchor tags (Floy Tag and Mfg. Co., model FD-67) meet these requirements, however the observer must be very close to distinguish the different numbers on similarly colored tags. Each tag was therefore modified by attaching a small numbered piece of thin plastic (6mm x 12mm x 1mm) as shown in Figure 5. Fish implanted with these tags could be discerned at distances of up to 4 meters during clear water conditions.

Tags were placed in the dorsal musculature at the base of the spinous dorsal fin, using a tagging gun (Floy Tag and Mfg. Co., model FDM-68) with the anchor set approximately 1 cm subdermally. After inserting, each tag was gently pulled to ensure that it had become firmly lodged.

Figure 5: Modification procedure for Floy anchor tags (upper) and a tag in place on a china rockfish (lower).


NOTIFY BAMFIELD MARINE STATION
• 55
26
2
3
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8
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10
11
12
13
14 cm

An effort was made to tag as many fish as possible without subjecting them to pressure stress. Fish taken to the surface from depths showed signs of bladder damage due to overexpansion of the swimbladder (see section 2.2.2.2.). In order to prevent damage, fish caught in the deeper regions of the site (> 5 meters) were tagged at depth. Fish caught in shallow water were taken to the surface for tagging. Standard length, tag number, and catch location were recorded prior to release. All fish were released at their point of capture except shallow-caught fish which were released from the surface directly above the point of capture. There were 3 techniques used in collection: gill nets, anesthetics, and lures. Black rockfish were collected primarily with gill nets while the latter two methods were more useful in catching china rockfish.

Fish which inhabit the water space above the reef surface were captured using gill nets. Various sized nets, ranging from 3.8 cm to 7.6 cm (stretched mesh dimensions), were deployed by divers in areas where fish were abundant. Nets set in shallow water were recovered from a boat while fish caught from the deeper nets were removed at depth and transferred to 'goody' bags prior to tagging. Depending upon the number of fish being caught, nets were left in place for intervals of up to 2 hours. While rockfish have tough external surfaces which resist damage by the nets, continuous monitoring is necessary to prevent asphyxiation.

The use of anesthetics to capture crevice dwelling fish was preferred because of the ineffectiveness of entangling nets and traps. Anesthetics used were Quinaldine (2-methylquinoline; Eastman Kodak) and MS-222 (Tricaine methanesulfonate; Sandoz). While not harmful when used in the appropriate dosage (Bell, 1964), anesthetized fish are still subject to injury caused by abrasion on sharp reef surfaces from water motion as well as direct predation from other marine animals. For this reason anesthetics were applied sparingly on individual fish (as opposed to general application over a broader area) and fish were allowed to fully recover prior to release.

Solutions of Quinaldine (10 percent in 2-propanol) or MS-222 (2 grams per liter of seawater) were carried in applicators designed for easy use by divers (Figure 6). The applicator consisted either of a squeeze or pump design connected to a long hose, tipped with a glass nozzle. Using this tool, small quantities of anesthetic could be directed at the fish while remaining at sufficient distance to prevent alarm. By carefully watching respiratory movements of the fish and timing the release just prior to inspiration, use of the anesthetic was optimized. Two or three doses in this manner usually dulled the sensory motor reflexes enough to coax the fish away from the crevice where it could be scooped into a 'goody' bag. Once captured, fish were tagged and confined in the bags until normal orientation and reflexes returned.

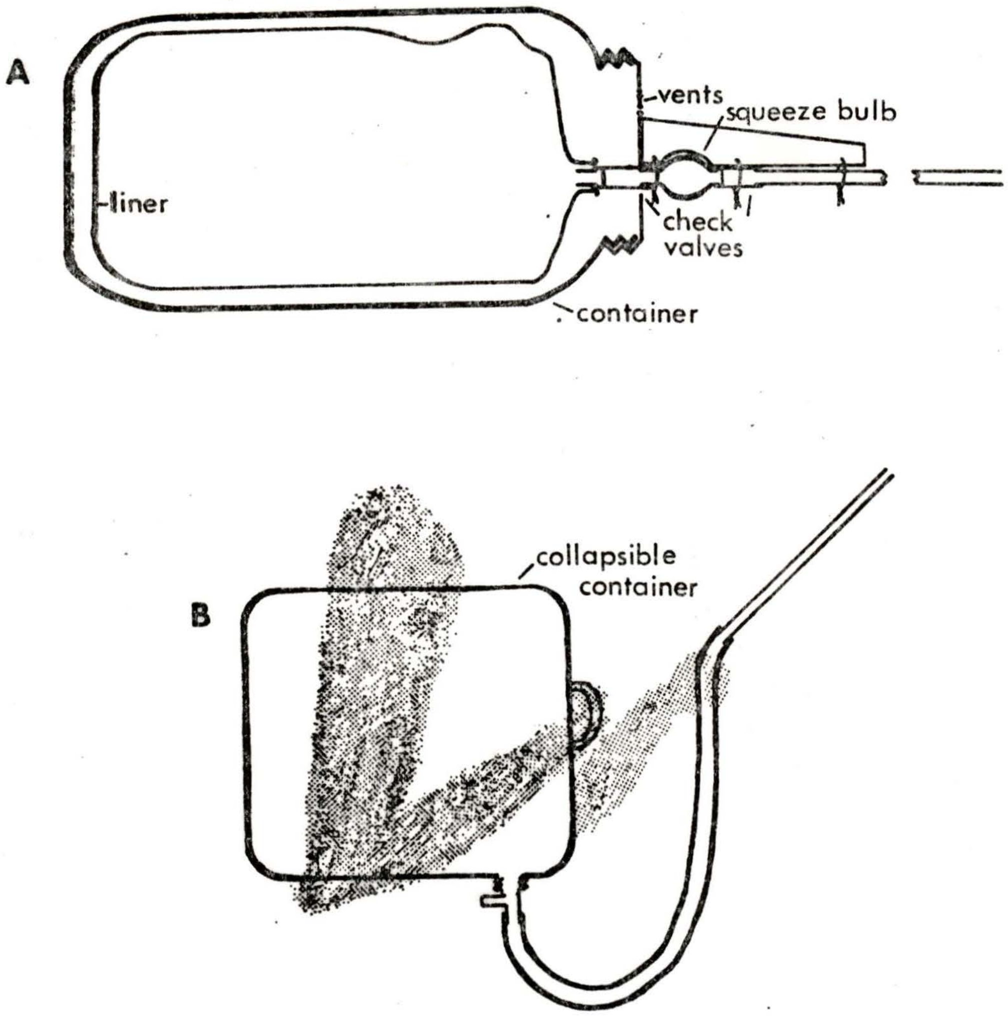


Figure 6: Anesthetic applicators used to narcotize fish. A, hand pump; B, squeeze bottle.

After discovering the success of jigging for rockfish from a boat and suggestions by Leaman (pers. comm.), a small diver held fishing pole was developed. The pole consisted of a light-weight PVC pipe to which a short line and fishing lure were attached. Artificial lures were tried and proved extremely effective in catching china rockfish. A lure was dangled in front of an inhabited crevice making slight jigging motions to attract the occupant. Response was vigorous, fish often bit 2 or 3 times if not hooked on the first try. Once captured, fish were tagged on location and immediately released. Interestingly, black rockfish showed little interest in these or any other lures and were rarely caught in this manner.

A problem arose with the tag design making individual identification increasingly difficult over time. The shaft and numbered portion of the tags became overgrown with algae and bryozoans, resulting in an indistinct feathery mass trailing from the fish's side. Within one month after tagging, fish became increasingly difficult to identify. It should be noted that this fouling did not develop on tags of china rockfish or other benthic fish, even after several months but was a constant feature of suprabenthic fish. A second tagging effort was initiated late in July to compensate for the reduced numbers of identifiable black rockfish. Over a period of 24 hours gill nets were continually set in the kelp bed region and tended periodically by divers. Previously tagged fish were retagged and untagged fish were measured and tagged as before. At the end of this period the number of tagged black rockfish was increased by 37. Observation dives were resumed after a 3 day period in which fish were left undisturbed. The rockfish tagged during this period were designated as group 2, differentiating them from group 1, tagged initially.

2.1.3 Field Observations

To reduce diver caused physical damage, the reef was only visited by Mr. Fletcher and myself, occasionally accompanied by experienced divers. During the observation period the only dives made on the site were for observation purposes except for a one week period when observations were postponed in order to tag more fish.

Each dive lasted approximately 35 minutes but varied depending upon the amount of time spent in the deep reef sections. Dives were separated by up to 24 hours except in 10 instances where there was greater than a 24 hour break. The observation period for group 1 black rockfish and china rockfish consisted of 65 dives while the period for group 2 black rockfish consisted of 38 dives. Dives were conducted primarily during daylight hours when the best observation conditions prevailed. However; dawn, dusk and night dives represented a substantial proportion of the observation effort.

Dives were usually scheduled 2 per 24 hour period, covering all phases of the light-dark cycle. The daily pair of dives usually covered contrasting states such as day-night or dawn-day, etc. When visited in low light conditions a variety of lights were used, these included: Darrel-Allen Bug Diver 400, Ikelite C-light, and a US Divers Aqualung dive light. The latter two are nearly identical while the former is considerably brighter.

During each observational dive Mr. Fletcher and I covered separate portions of the reef recording the tag number and location of marked fish. Other data such as visibility, water current, dive time, and miscellaneous observations were also recorded. During the dives data were recorded by pencil on plastic slates with a roughened surface, information was later transcribed from the slate to a more permanent record. The pattern of swimming over the site varied from dive to dive to eliminate possible systematic bias due to 'herding' of fish. Fish were always observed from a maximum distance, determined by water clarity. We found that fish became noticeably disturbed if followed for any period of time as evidenced by their tendency to swim faster and return to crevices or areas where there were other fish. Consequently, fish observations were discrete rather than continuous, although multiple observations of the same fish within a dive were recorded.

2.2 LABORATORY STUDIES

2.2.1 Morphology

2.2.1.1 Specific Gravity

The specific gravity of a neutrally buoyant fish is the same as the surrounding water since the mass to volume ratio has been adjusted with the addition or removal of bladder gas. In the absence of a swimbladder, the specific gravity is usually greater than water and is dependent upon the proportion of different tissue components such as bone, protein and fat. By measuring the specific gravity of a fish, the buoyant force or volume of gas required to create a neutrally buoyant state can be determmined.

Using Archimedes' principle, density was determined as follows:

$$\mathrm{DENSITY}=\left[((\mathrm{Wair}-\mathrm{Wwater}/(A))/(\mathrm{Wair}\right]^{-1}$$

where Wair is the weight in air, Wwater is the weight of the fish when immersed in seawater, and A is the density of seawater.

Recently-killed animals were blot dried with paper towels and weighed on a top loading balance (Metler, model P1200). Animals were then opened ventrally and the swimbladder was punctured with scissors. All the gas was removed by immersing fish in a seawater bath and pressing down on the gas bladder. The weight in water was determined with a hanging pan triple-beam balance (Ohaus, model 310) set up over an aquarium so that a fish could be suspended from the scale by fine string without contacting the glass aquarium walls. Density of the seawater bath was determined by measuring the temperature and salinity and derivation from tables (U.S. Navy Hydrographic Office, 1952).

2.2.1.2 Blood Analysis

Hematocrit samples were taken from field fresh, recently dead, specimens. Blood samples were drawn in 1.2 mm I.D.

heparinized hematocrit tubes (Fisher Scientific Co.) and sealed with an oil-base clay (Plasticene). Samples were spun at 12,500 rpm for 3 minutes in a hematocrit centrifuge (IEC, model 5-040) and the proportion of red blood cells versus plasma was obtained by measurement to the nearest millimeter. Initially, as many as 10 samples from each fish were taken but due to the highly consistent results, only 2 samples were subsequently taken.

2.2.1.3 Secretory Center Morphology

The secretory center (ie, rete mirabile and associated secretory epithelium) was removed from freshly killed specimens and photographed for later examination. The tunica internus, on which the secretory center is located, was removed by peeling it free from the outer tissue layers. Once removed the tunica internus was cut such that the secretory center could be laid flat on a sheet of heavy-weight paper. The preparations were photographed using a close-up lens or, in the case of very small fish, photographs were taken through a dissecting microscope. Photographs were subsequently enlarged on 8 by 10 (20 x 25 cm) photographic paper for morphological and meristic analysis.

A variety of observations were made from the secretory center preparations. Surface area of the secretory epithelia was measured using a zero-compensating polar planimeter. The length of the rete mirabile was measured to the nearest 0.1 mm using a vernier caliper.

2.2.1.4 Swimbladder Wall Resistance to Overexpansion

The swimbladder wall forms an envelope which entirely encloses a gas space. When ambient pressure changes rapidly, the swimbladder gas responds accordingly with a change in volume. With depressurization, this organ expands to a point where the elastic wall has stretched to its maximum size. Further depressurization results in a build up of internal bladder pressure and finally, rupture of the wall. The percent reduction from atmospheric pressure represents the theoretical instantaneous maximum pressure reduction a fish could undertake without rupture of the swimbladder.

A collection of animals was made while diving. Black rockfish were collected in a gill net set along the bottom and china rockfish were caught using underwater angling. Precautions were taken to minimize bladder damage upon ascent (sec. 2.2.2.2). Once in the laboratory, fish were contained in a shallow aquarium approximately 15 cm depth for an adjustment period of one week. During this time buoyancy was restored with the fish coming to equilibrium at the aquarium depth which was equivalent to a pressure of 1.015 ata (sec. 2.2.2). Fish were killed with a high concentration of Quinaldine, ventrally dissected, and placed within the evacuation apparatus shown in Figure 7. Pressure was slowly reduced using a vacuum pump (VacTorr, model D-25) to a point where the expanded gas bladder ruptured. Burst pressure was determined by comparing the barometric pressure and the pressure within the chamber as indicated by a mercury column.

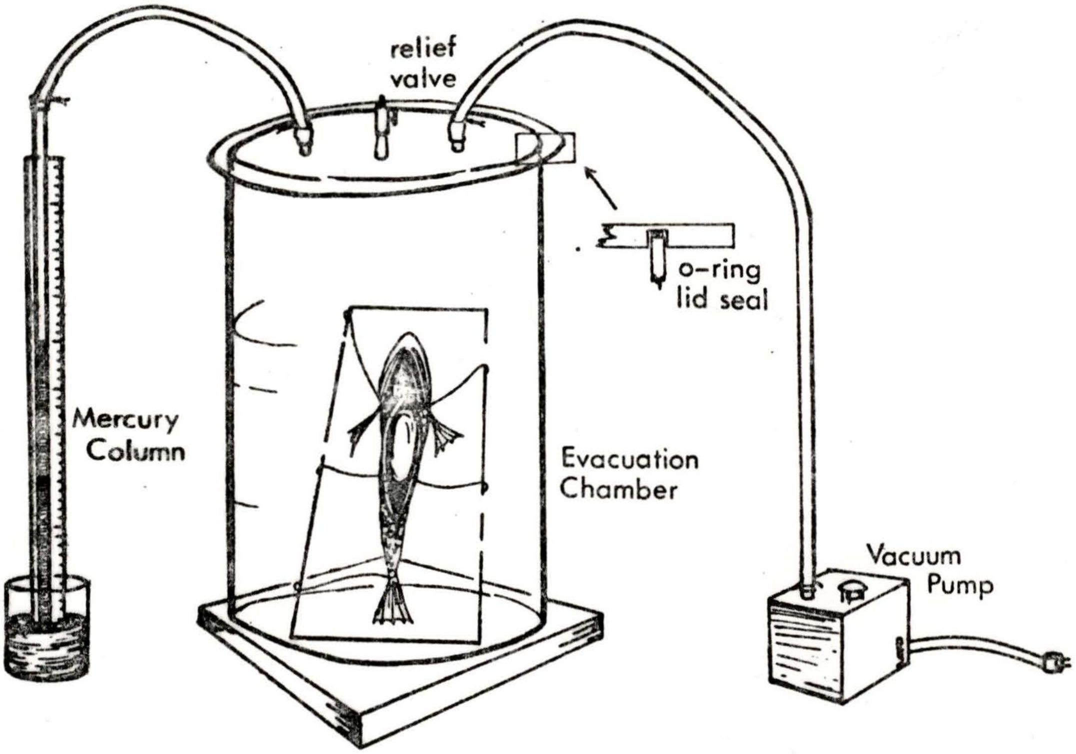


Figure 7: View of vacuum chamber used in swimbladder burst experiments.

2.2.2 Buoyancy Adjustment

Pressure aquaria were developed to study the characteristics of rockfish buoyancy adjustment. Variable pressure aquaria simulate vertical depth gradients, since a change in pressure causes expansion or shrinkage of the swimbladder such as a fish would experience moving vertically in the water column.

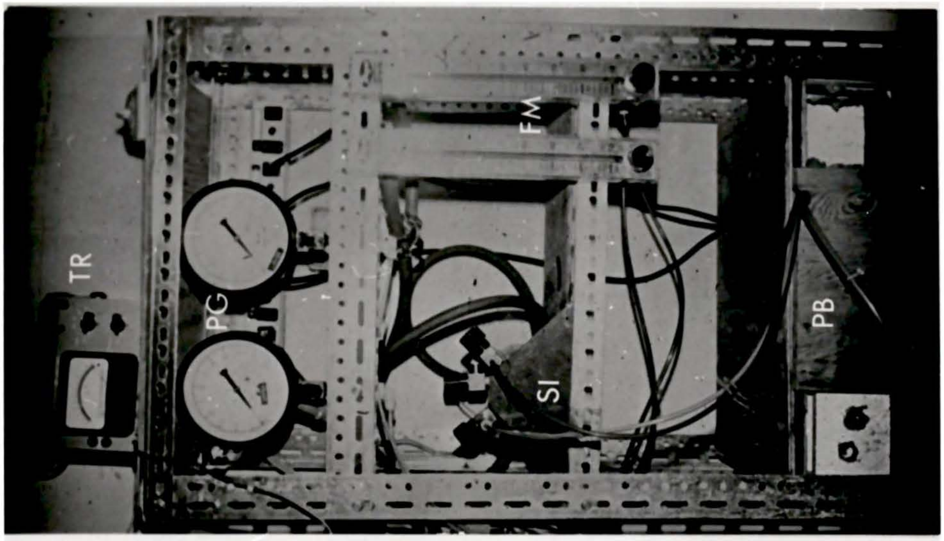
All values of pressure in this study were given in atmospheric units. One atmosphere pressure is equivalent to 10 meters seawater, 76 cm mercury, or 14.7 pounds per square inch. Measurements of ambient pressure are expressed relative to zero pressure and are therefore absolute atmospheric pressure units or, ata. When expressing a pressure difference, atmospheric pressure units are used or atm. The former is a unit of total pressure while the latter applies to a pressure increment.

2.2.2.1 Aspects of the Pressure Tank System

The pressure system consisted of two 85 liter tanks capable of simulating depths up to 40 meters. The two tanks were entirely independent as each could operate over the full pressure range without disturbing the other. A flow through water system continually replaced tank water to provide adequate life-support conditions. The system design provided stable pressures such that animals can be maintained in a simulated deep water environment for as long as 4 weeks. The aquarium itself was designed and constructed by Mr. Gordon Davies at the University of Victoria and is shown in Figure 8 while the general pattern of operation is shown in Figure 9.

The pressure tank was a 1.3 cm thick acrylic cylinder measuring 1.2 meters by 0.3 meters in diameter. The ends of the tank were constructed of 2.0 cm plexiglass secured in position with bolts and sealed by an O-ring. During normal operation the end plates were tightened into position and

Figure 8: Pressure tank system used in buoyancy experiments. Shown are the two tanks within their plastic enclosure (right) and the console containing support instruments (left). Right photograph: FM, flow meter; PB, box containing pumps; PG, pressure gauges; SI, seawater inlet; TR, temperature recorder. Left photograph: B, bypass; BV, pressure bleed valve; RV, over pressure relief valve; TD, trap door.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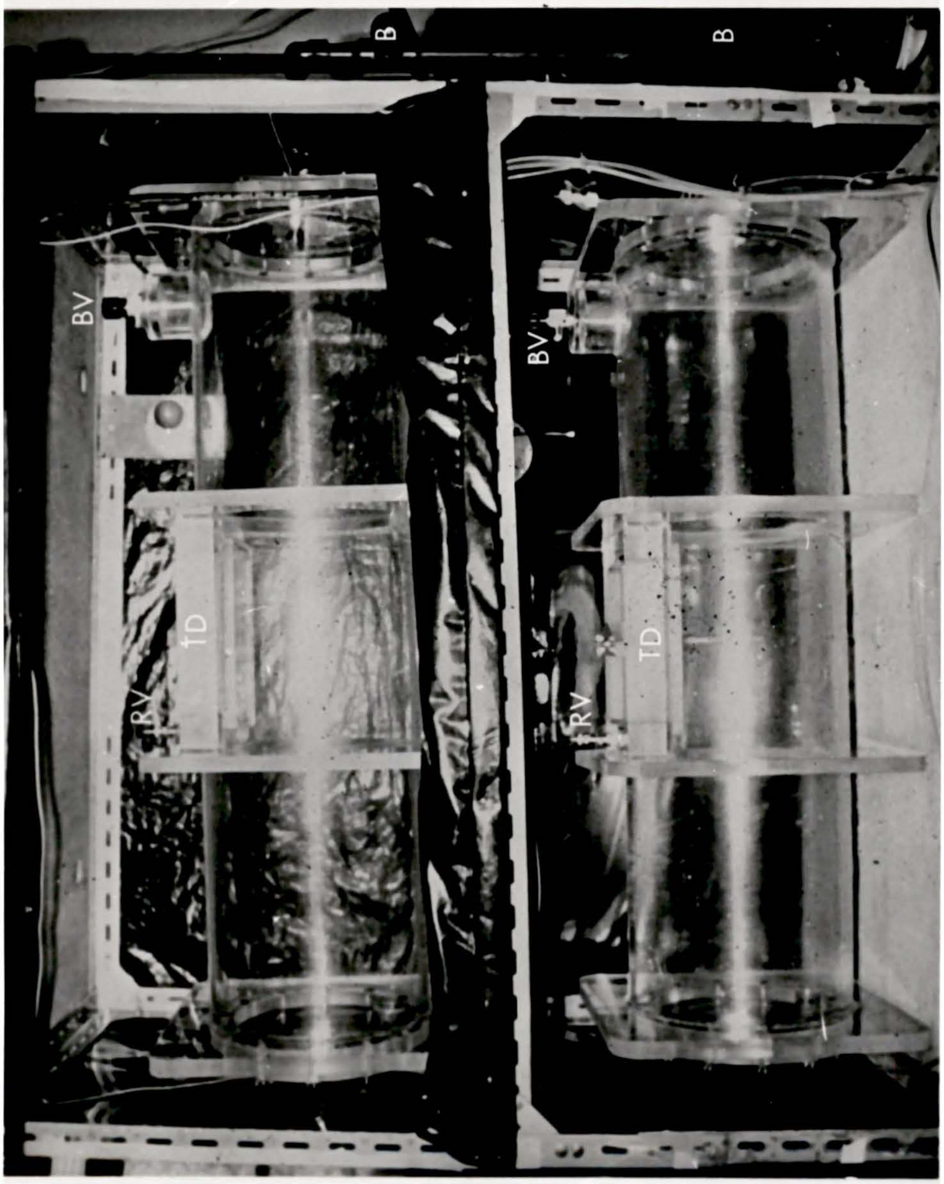
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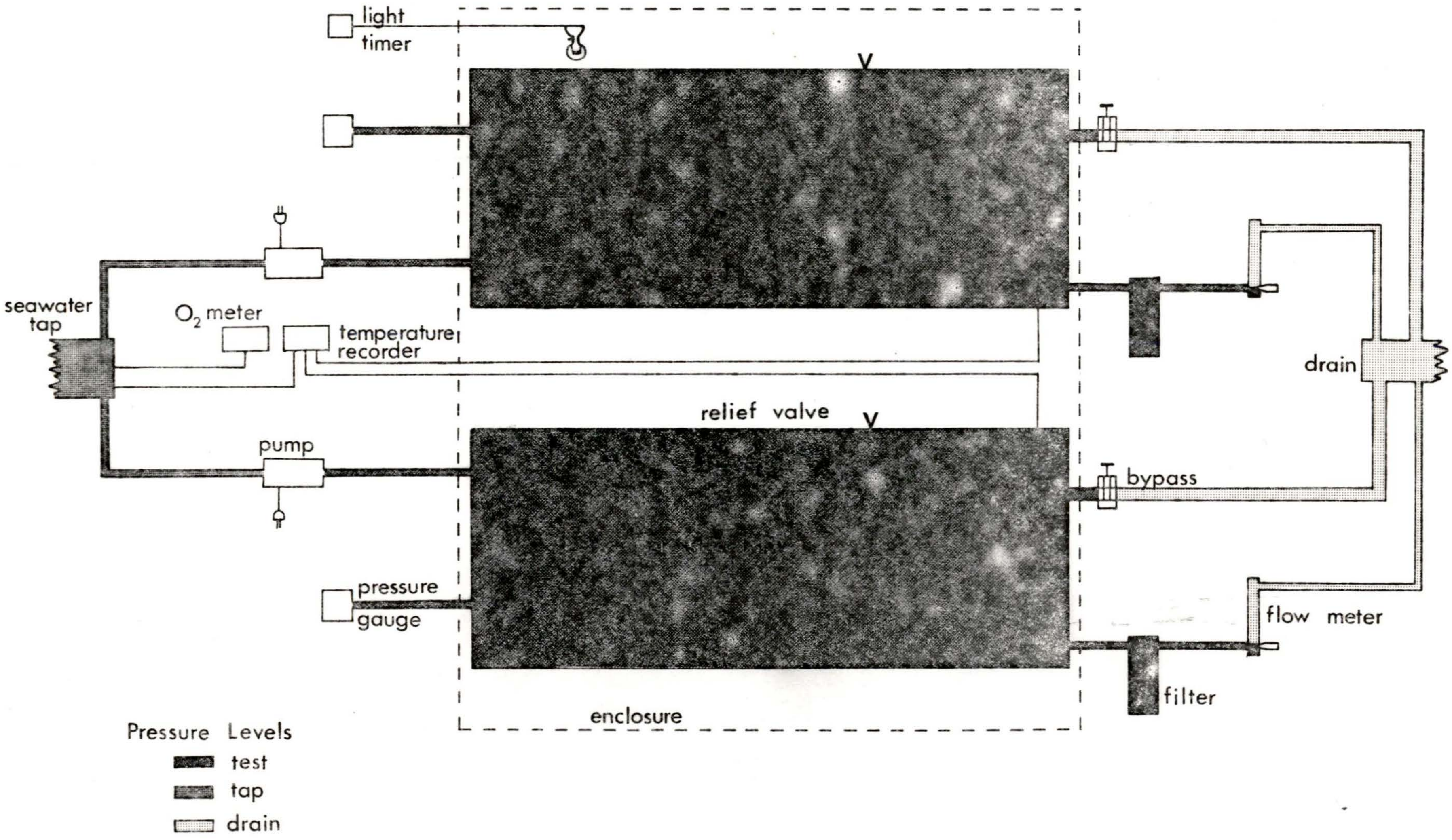


Figure 9. Schematic diagram of pressure tank construction.

access to the tank was made through a one-way pressure sealing trap door situated at the top.

Each tank was separately housed so that animals were isolated from the rest of the laboratory. The enclosures consisted of an opaque tent constructed of 4 mil black plastic taped to an aluminum frame. Inside, the tank space was illuminated with a 15 watt incandescent bulb set on a light-dark cycle equivalent to outside conditions. Observations of fish were made through small peek holes in the plastic cover. Pressure tank support equipment (pumps, flowmeters, etc.) were positioned outside the enclosures on a separate cart reducing the noise level and freeing the fish from disturbance during equipment maintenance and adjustment.

Pressure was established by pumping water into the tank and regulating the flow of outgoing water. A gear pump connected directly to the seawater tap created a maximum blocked-flow pressure capacity in excess of 5.8 ata. The rate of water flow was primarily controlled with a flow meter at the tank discharge, although fine adjustments could be made by regulating an internal bypass within the pump itself. To prevent the flow meter from becoming clogged with debris, discharge water was filtered through a 50 to 125 micron inline filter. Tank pressure was stable within 0.13 atm when supplies of electricity and water remained stable.

The water system for the pressure tanks was open circuit with fresh, cool seawater continually replenishing the tanks during operation. Inlet and outlet lines were situated at opposite ends of the tank to promote thorough circulation. This was confirmed by injecting colored dye (methylene blue) into the inlet line and observing the pattern of dispersion throughout the tank. The colored water entered the tank and passed toward the opposite end along the bottom, gradually mixing into the upper part of the tank. As a consequence of system design, the flow rate through the tank is inversely proportional to the tank pressure. Therefore, maximum tank pressure levels produced diminished flow while high flow rates occurred when pressure was low. Over the operating pressure range the flow rates varied from 1.9 to 3.2 liters per minute corresponding to total tank water replacement times of 45 to 26 minutes, respectively.

A bypass arrangement alleviating water flow through the normal tank discharge system provided a rapid means of lowering tank pressure without interfering with the finely metered system. When open, the bypass port accommodated all outgoing water and the tank pressure was low. As the bypass valve was closed, more and more water was forced through the flowmeter, causing tank pressure to rise until finally, all water was passing through the flowmeter and tank pressure was at the preset level. The bypass system was useful in making short duration pressure changes such as those needed for buoyancy observations. At other times it was left closed since debris collected in the valve causing unstable tank pressures.

During early phases of the system design, the quality of the tank habitat was checked. An oxygen electrode placed through the tank end plate indicated minimum dissolved oxygen levels of 85 percent saturation at all operating pressures. This compared favorably with field values. Using a telethermometer (YSI, model 46:6), incoming and outgoing water temperatures were recorded. The temperatures observed were comparable to the range of temperatures at which fish were observed in the field. The temperature difference between incoming and outgoing water was usually less than 1°C. indicating that the turnover rate was sufficiently high. Following the use of a pressure tank, algal and fecal matter were removed to prevent contamination. It was concluded that the pressure tank environment was at least as good, if not better, than a well kept aquarium system.

2.2.2.2 Collection of Fish

Animals used in buoyancy adjustment experiments were required to be in generally healthy condition and apparently free from bladder damage. Consideration was given to the manner in which fish were collected. Damage associated with rapid pressure reduction was assessed by post mortem examination to insure that collection techniques were suitable. One method used was simply fishing the animals from shallow reefs. Black rockfish were not damaged coming to the surface from 10 meters and recovered rapidly from the resulting positive buoyancy. These specimens showed no indication of hemorrhaging or stretching of the bladder wall and it was concluded that pressure reductions from 10 meters depth and less were safe. Fishing resulted in considerable bladder damage in china rockfish as these animals generally inhabit depths greater than 10 meters. Often, the outer layers of the swimbladder wall tore forcing the inner lining through. This condition was usually followed by a buildup of fluid and infection which may have permanently damaged the organ. To prevent this damage, techniques developed at the Ohiat site were used to catch china rockfish at depth so that their swimbladders could be partially deflated by inserting a sterile 12-gauge syringe needle through the lateral musculature and orienting fish so that gas drained passively; fish were taken slowly to the surface and transported in buckets to the laboratory.

2.2.2.3 Experimental Procedure

All experiments followed the same general time sequence shown in Figure 10. After collection, fish were kept in 50-gallon aquaria for approximately 3 days during which buoyancy came to equilibrium at the new pressure (ie, atmospheric plus the 40 cm depth of the aquaria, or 1.04 ata). Individuals were then transfered to pressure tanks and acclimated at minimal operating pressures of 1.1 ata for a period of 24 hours. The experiment began with slow eleva-

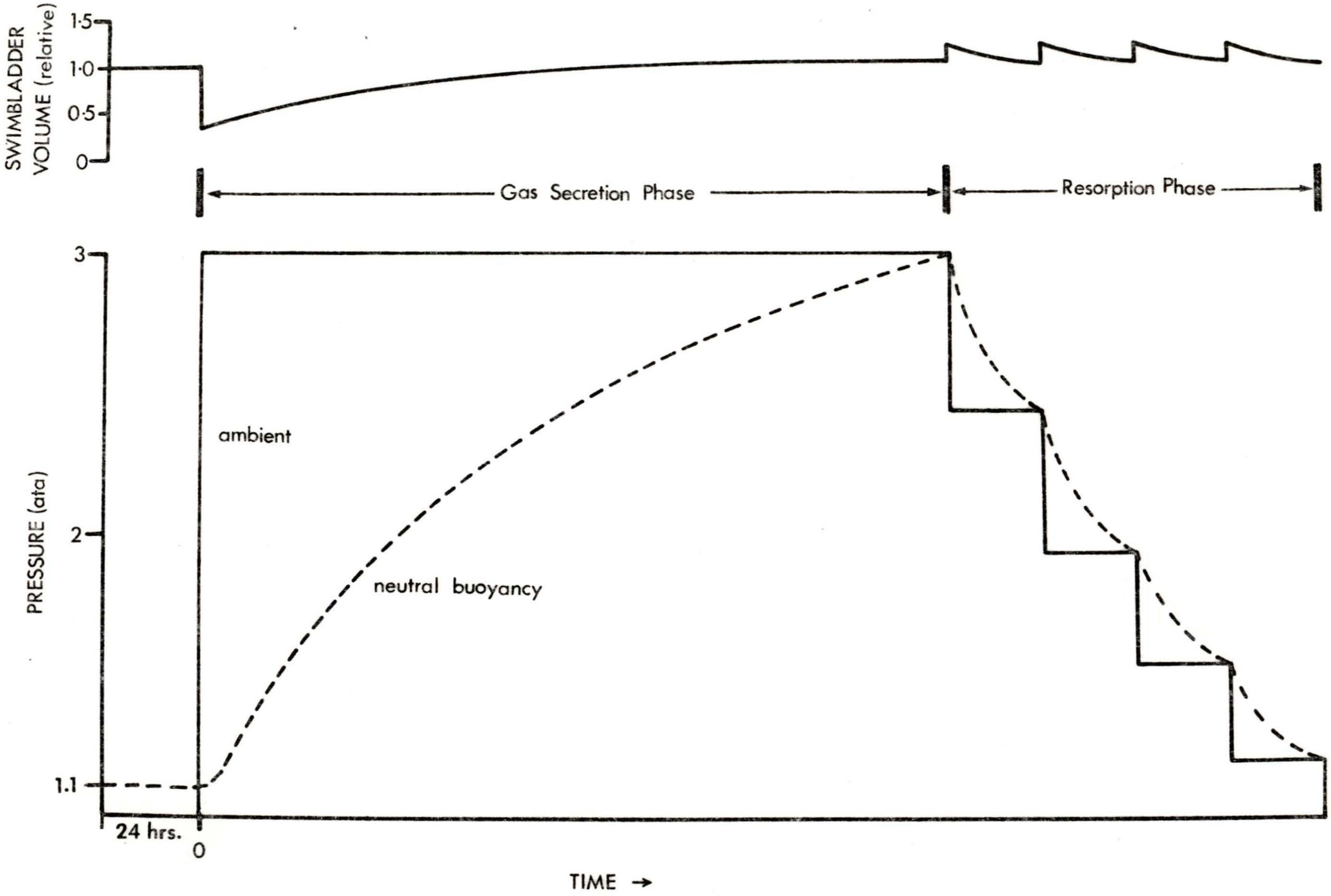


Figure 10. Time sequence showing the pattern of operation during pressure experiments.

tion of tank pressure (1 atm per minute) to the operating level. The normal operating pressure was 3 ata, however, additional experiments were conducted at 2 and 4 ata with black rockfish. Operating pressure remained constant until neutral buoyancy had been achieved at the elevated pressure. During this period, progress toward increased buoyancy was determined with neutral buoyancy measurements. Once fish had established neutral buoyancy at the operating pressure, tank pressure was lowered in a stepwise fashion allowing the fish to adjust at each pressure level before proceeding with the next pressure reduction. Again, the progress toward adjustment was periodically measured with neutral buoyancy measurements. The increment of pressure drop was determined from Boyle's law allowing for a known expansion of 10, 20, or 30 percent and used to calculate the pressure reduction increment. Once fish had come to equilibrium with atmospheric pressure on the last step, equipment was shut down and the fish were removed. Animals were killed using a lethal dose of Quinaldine. The fish were then measured, dissected, and examined for signs of bladder damage such as tissue rupture of hemorrhage.

Response of animals to pressure changes was measured by determining the neutral buoyancy pressure, employing a method originally described by Evans and Damant in 1928 (Brown, 1939). Specifically, this is the pressure at which bladder volume precisely compensates for the weight of the fish. Neutral buoyancy pressure was determined by manipulating tank pressure with the bypass valve while observing the swimming behavior of the fish through a small hole in the chamber cover. Fish were considered neutrally buoyant when hovering was achieved without compensatory activity of the pectoral fins. Through practice, these measurements were made rapidly and the time from test pressure was minimal (<5 minutes).

Chapter III

RESULTS

3.1 FIELD STUDY

3.1.1 Description of the Study Site

The general characteristics of the Ohiat study reef are shown in Figure 11 which provides information on both bathymetry (topography) and terrain characteristics. Below 10 meters the reef was generally steep sloped, flattening out appreciably in shallow water. The reef rose to a mound which emerged at one point during minus tides. The mound was separated from shore by a narrow, boulder-filled trench. The steeply inclining portions of the reef were generally composed of solid rock sparsely laced with crevices. Much of the more gradual sloping reef surfaces consisted of broken angular rock which was large (25 to 75 cm) in shallow water and decreased in size (5 to 10 cm) with depth. These bouldered areas were the result of gradual erosion of the solid rock in areas of weakness, such as along fracture planes. Thus, most of the boulder areas occurred within a broadly rounded trough of solid rock. Below 25 meters, the reef confronted a clear, low sloping, sand bottom. As far as could be determined from hydrographic charts and visual examination, the bottom descended gradually toward Sattelite Channel changing to a mud substrate with depth. There did

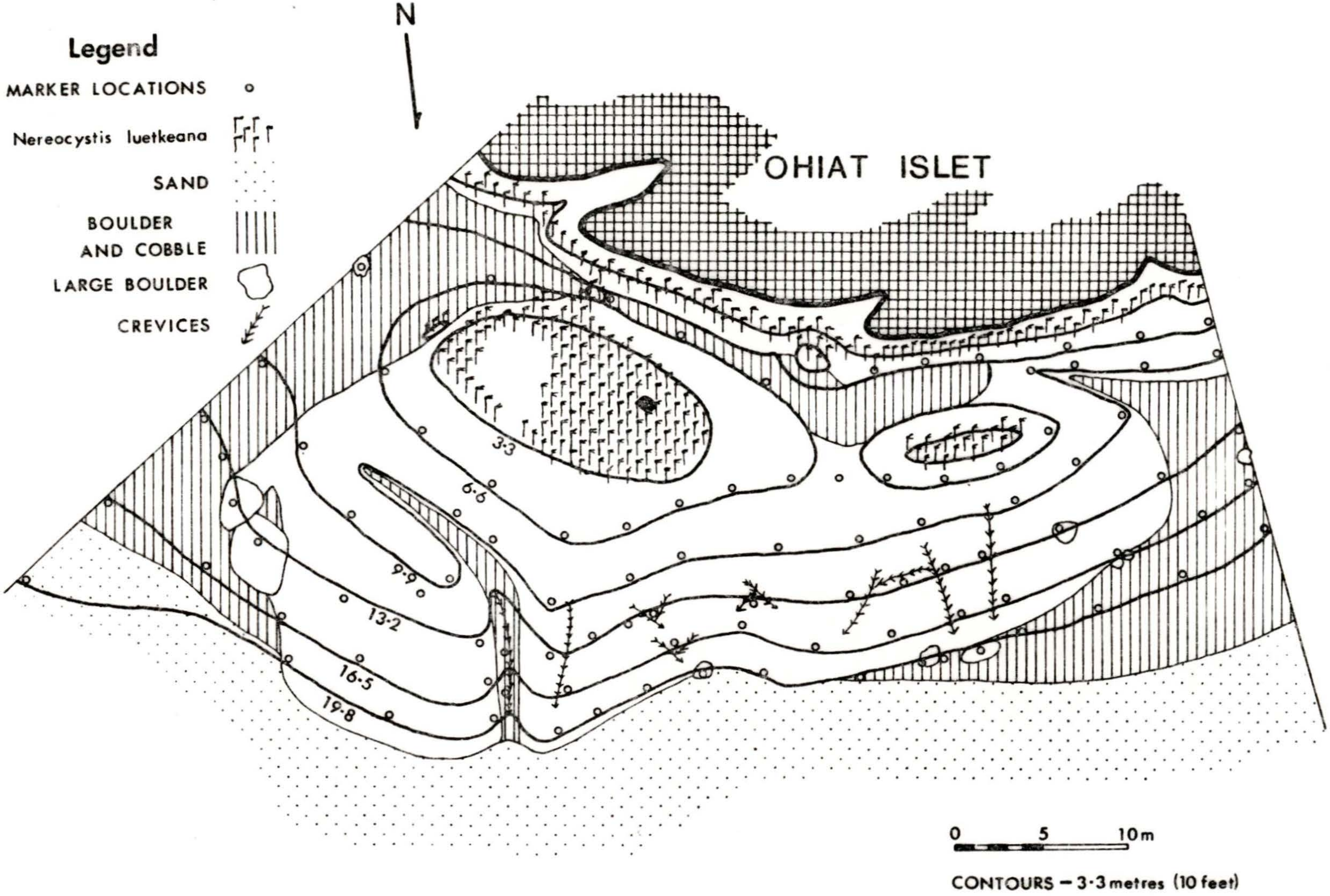


Figure 11. Bathymetric relief of the study site.

not appear to be any solid substrate below 25 meters in the vicinity of the study reef.

The position of Ohiat is such that it receives moderate to severe exposure from wave activity during nearly all seasons of the year. Except during the winter ocean swells are of less significance as compared to waves generated by local winds. Ohiat Islet directly faces Imperial Eagle Channel and Sattelite Channel, affording little protection from two major wind patterns. The summer onshore breezes, or Westerlies, generate rough conditions at Ohiat on the side opposite the study area. While there was little turbulence felt at the study site, Westerly winds usually created reduced water clarity and a slight surface current. During the fall, nocturnal offshore winds, apparently funneling through Alberni Inlet, blow directly at the study site from Trevor Channel. These winds, which I call Northerlies, cause a considerable amount of wave activity as well as strong west flowing currents.

One of the most significant aspects of the reef in terms of terrain complexity was the presence of rock crevices. These provided protected enclosures which were inhabited by a tremendous assortment of marine life. Crevices are formed by eroded fractures in the solid rock resulting in long, narrow, and occasionally deep openings. The largest crevice on the site (shown near left-center in Figure 11) was 0.25 meters wide, 6 meters high, penetrating the reef at least 5 meters. This crevice was occupied by a large (15 kg) octopus, *Octopus dophleini*, during most of the study. Most other crevices were only a few meters long and less than a meter deep. Elsewhere on the site there were a variety of crevices formed by overlying boulders. Most of these were like a labyrinth with many openings and passageways. One exceptionally large crevice was formed by two large boulders (4 meter diameter) overlying a solid rock portion of the reef (shown to the left in figure 11).

The biota at the Ohiat site are characteristic of exposed tidal and subtidal habitats. The most striking floral characteristic was the kelp forest formed by the bull kelp, *Nereocystis leutkeana*. The bed was seasonal, entirely absent in the winter, becoming noticeable as small plants on the shallow rock surfaces by the end of March. Later in May, the kelp had reached their full size. Over the summer the plants matured and the kelp bed gradually began thinning out towards fall. During peak developement, the kelp covers a major portion of the reef at depths less than 4 meters. In one area on the east end of the kelp bed there was a mysterious clearing devoid of plants which had never developed growth and remained clear over the season. During the winter the turbulence in shallow reef sections was severe and the rock appeared very barren.

Other flora common to the study reef were the laminarian type algae of the genera *Laminaria*, *Costaria*, and *Pterygo-*

phora which were found along the shoreline at levels below 0 m tide level. These plants provided a dense undergrowth among shallow growing *Nereocystis* kelp. There were a variety of other plants but generally these did not provide significant cover and habitat for fish.

The most conspicuous intertidal fauna were the mussel, *Mytelus californianus*, and, in more shaded areas, the goose-neck barnacle, *Pollicipes polymerus*. Subtidally, below the laminarian algal belt, the purple and red sea urchins, *Strongylocentrotus purpuratus* and *S. franciscanus*, were locally abundant. Other invertebrates such as the purple-hinged scallop, *Hinnites multirugosus*, the abalone, *Haliotes kamchatkana*, the anemone, *Metridium senile*, the starfish, *Pycnopodia helianthoides*, and the cup coral, *Balanophylla elegans*, were common and conspicuous inhabitants of the subtidal region. There were 4 known dens of octopus, *Octopus dophleini*, and other miscellaneous observations indicated that the population may have been much larger. Along the prominent rock faces where the current was stronger the rock surface was densely overgrown with many tiny anemones and tube-dwelling polychaete worms.

The fish observed at Ohiat site are listed in Table 1. This list includes visually conspicuous species but omits those which were difficult to identify in situ (e.g. small cottids) or were obtainable only through chemical collections. Most of the fish were reef associated. Where tag-

Family	Reef Association	Abundance	Region
Squalidae			
Squalus acanthias	T	SA	N
Chimeridae			
Hydrolagus colliei	T	C	SB
Clupeidae			
Clupea harengus pallasi	T	C	N
Engraulidae			
Engraulus mordax	T	C	N
Salmonidae			
Onchorynchus keta	T	SA	N
Ophidiidae			
Brosmophycis marginata	R	U	C
Embiotocidae			
Brachyistius frenata	A	U	K
Cymatogaster aggregata	A	C	K
Embiotoca lateralis	A	C	K
Rhacochilus vacca	A	C	SB-K
Hexagrammidae			
Hexagrammos decagrammus	R	A	B-K
H. lagocephalus	A	C	B
Ophiodon elongatus	A	C	B
Oxylebius pictus	A	C	B
Scorpaenidae			
Sebastes caurinus	R	C	SB
S. elongatus	R	R	C-SB
S. flavidus	R	C	SB-N
S. maliger	R	C	C-SB
S. miniatus	R	U	SB
S. melanops	R	A	K-SB
S. nigrocinctus	R	U	C
S. nebulosus	R	C	C
S. pinniger	R	U	SB
Cottidae			
Enophrys bison	-	U	B
Hemilepidotus hemilepidotus	R	U	B
H. spinosus	A	U	B
Jordania zonope	A	A	B
Scorpaenichthys marmoratus	A	U	B
Aulorynchidae			
Aulorynchus flavidus	A	C	K
Gobiidae			
Coryphopterus nicholsii	R (probably)	C	B
Annarichidae			
Anarrhichthys ocellatus	R	C	C
Schichaeidae			
Chirolophis nugator	R	U	B-C
Pholidae			
Apodichthys flavidus	A	-	K-C
Gobiesocidae			
Rimicola muscarum	A	-	K

Key:			
	T - Transcient	SA - Seasonally abundant	N - Neritic
	A - Associated	C - Common	SB - Suprabenthic
	R - Resident	A - Abundant	C - Crevices
		U - Uncommon	B - Benthic
		R - Rare	K - Kelp

Table 1. List of species observed at the study site and information concerning their association, abundance, and distribution.

ging or direct observations indicated that a species resided specifically at the study site, a resident designation was assigned. Where there was no direct evidence of residency, fish were classed as reef associated only. Fish species which generally occur in other areas, periodically making excursions onto the reef, were considered transients.

Also present at the Ohiat site was a harbor seal (Pinnipedia; _Phoca vitulina_). While frequently seen basking on rocks on the other side of the Islet, it was occasionally observed at the study reef.

3.1.2 Observations of Fish

During the fish tagging operations, 104 fish were tagged and released of which 90 were black and 14 were china rockfish. Based on counts made of the tagged versus untagged fish, the tagged group corresponded to approximately 30 and 80 percent of the former and latter species' population, respectively. This large difference in abundance is a general pattern; usually, black rockfish far outnumber china rockfish apparently as a consequence of their respective social and solitary life styles. The population of china rockfish was smaller than other reefs where there were as many as a hundred over a similar area.

Over the observation period, sitings of tagged fish represent a major portion of the initial tagged group (Table 2). Thirteen of the 14 china rockfish tagged were seen at one time or another on the site. The corresponding value for the combined groups of black rockfish was 61 out of 90 tagged.

Table 2

Sitings of tagged fish.

Species	No. Tagged	No. Sited	Percent
Black Rockfish	90	61	67
1.	53	32	60
2.	37	29	78
China Rockfish	14	13	93

Many of the tagged black rockfish were observed for a limited number of times as indicated by observation frequencies shown in Figure 12. The two black rockfish groups reflect a similar pattern, with a greater tendency in individuals to be seen a few times. One fish, designated by tag pattern as Orange-20, was unusual as it was seen much more often than other conspecifics. In contrast, many china rockfish were seen more than 20 times.

The number of tagged fish observed over time is shown in Figure 13. Most black rockfish do not remain on the site long, as indicated by the decline in observations of both

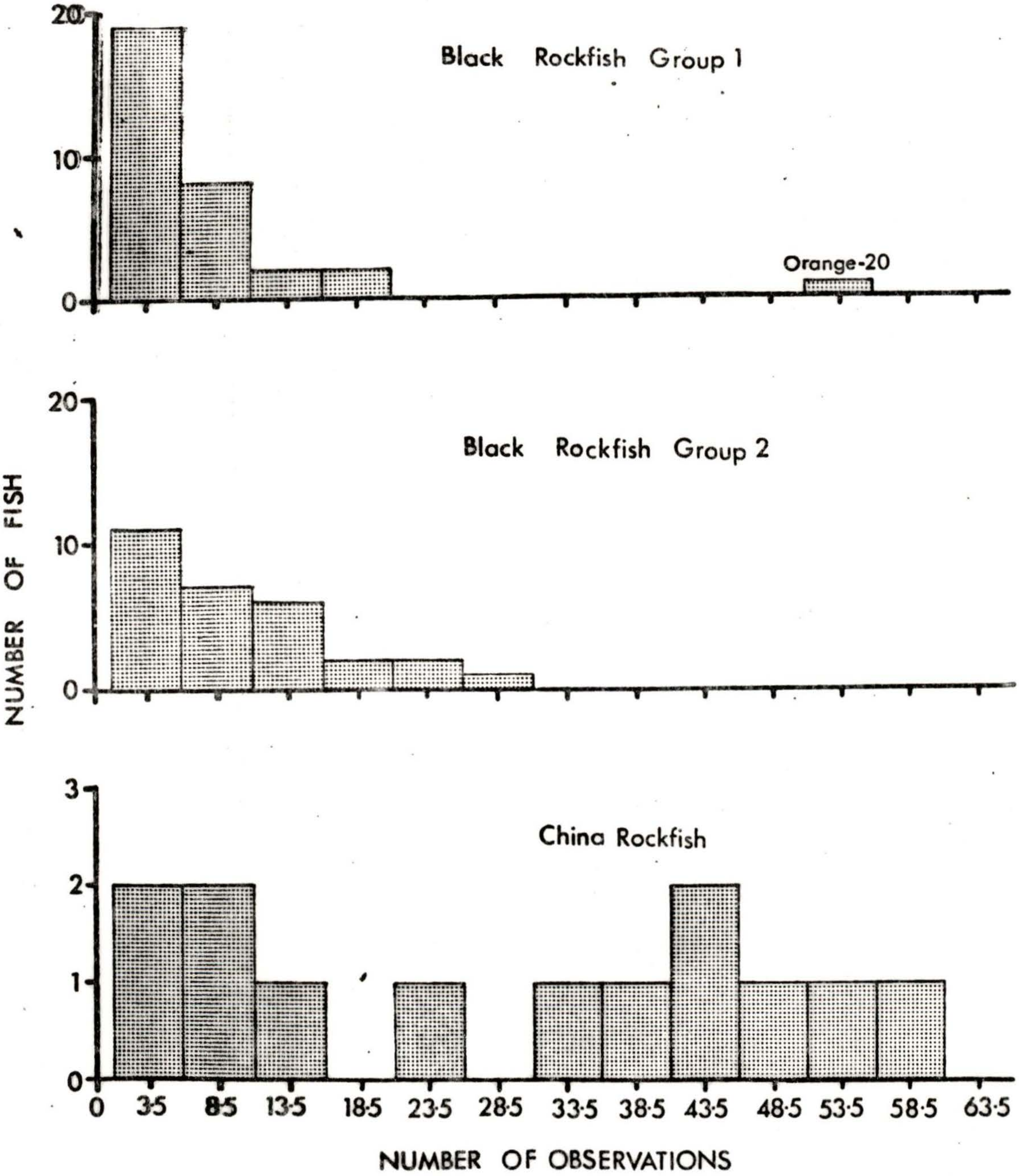


Figure 12: Frequency of observation of individuals of different tag groups.

groups through respective dive sequences. The wide fluctuation in numbers of black rockfish seen between related dives indicates an important observation limitation for this species. Black rockfish occupy a three-dimensional space that can not always be thoroughly checked. Often, schools of fish were approached from a variety of angles, each time revealing different tagged fish. While poor visibility and reduced light also reduce fish observability, it is unlikely that all the tagged black rockfish could ever be recorded on the site even under ideal conditions. China rockfish however, were consistently observed over the 65 dive sequence. Individuals associated with a particular area of the reef surface which could be revisited under the poorest of observation conditions. Consequently, observation success in this species increased with observer familiarity with the reef as reflected by the general increase in tagged china rockfish seen over time.

3.1.3 Distribution of Fish

Distributional observations of black rockfish were based on limited observations on many tagged fish, numerous observations of a few tagged fish, and observations of many untagged fish. In general, these three separate lines of observation show the same results. Black rockfish as a group, occupy a limited portion of the reef. This pattern is shown for commonly seen individuals (Figure 14A through E) and for the combined tagged population (Figure 14F).

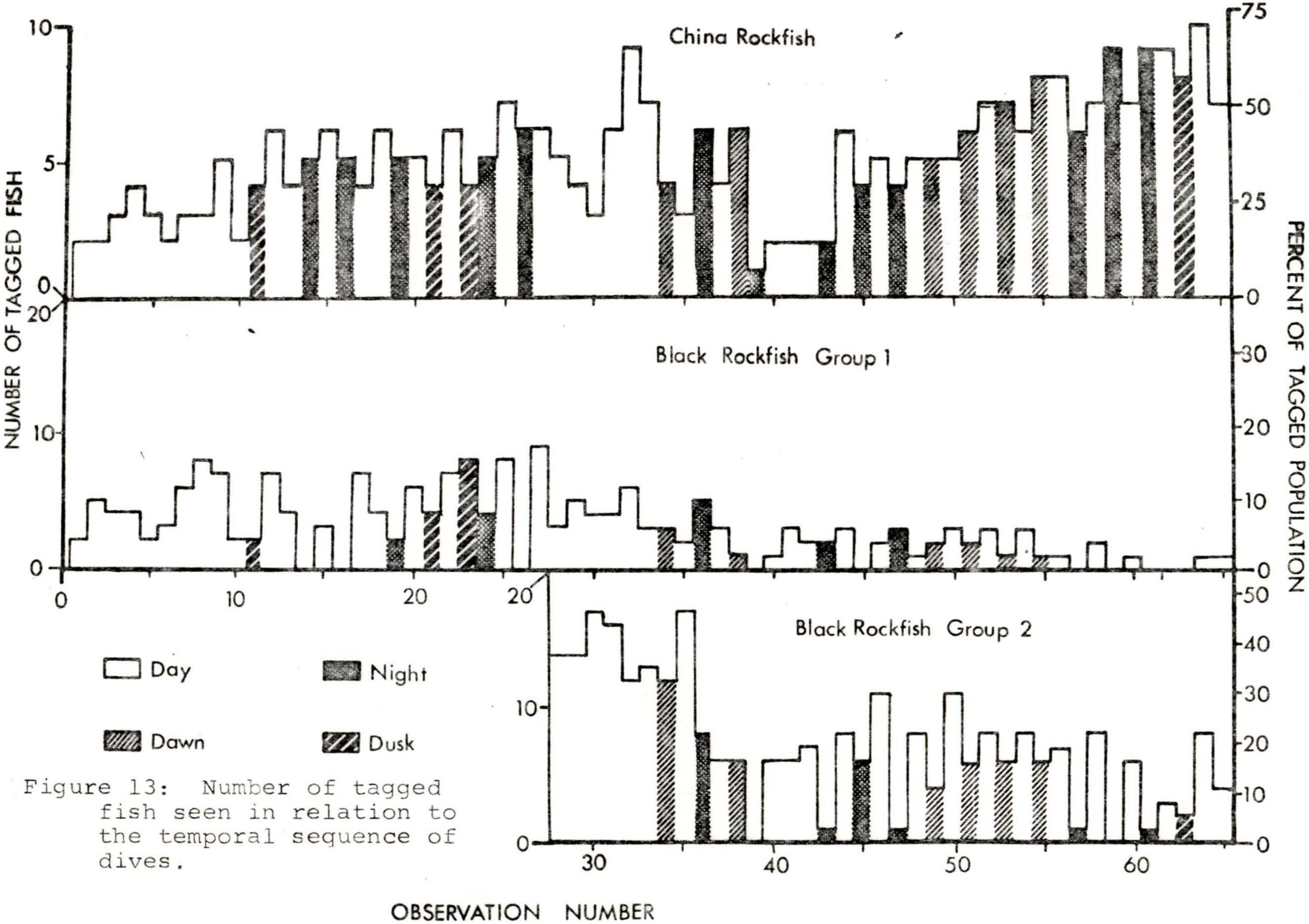


Figure 13: Number of tagged fish seen in relation to the temporal sequence of dives.

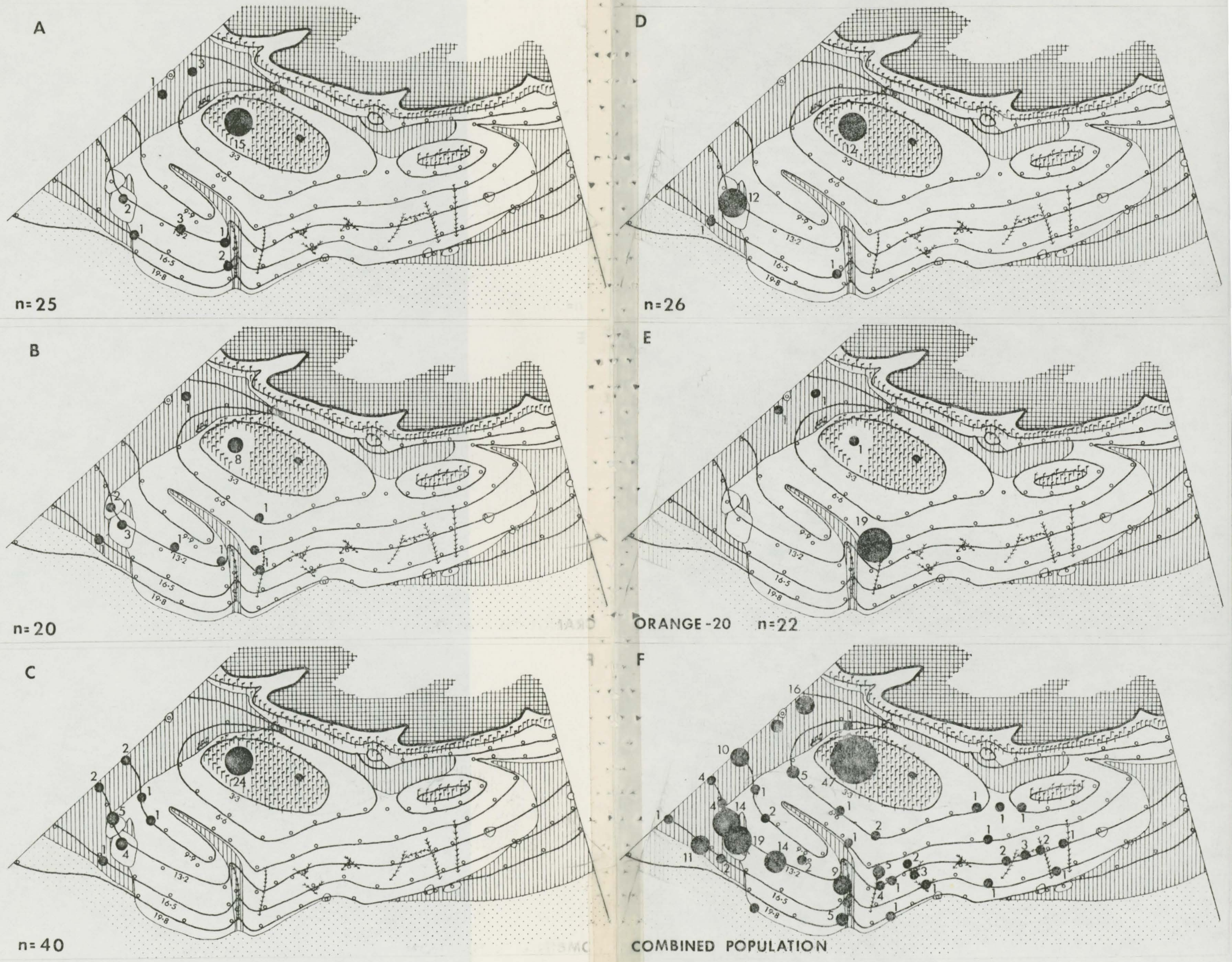

A
n=25
B
n=20
C
n=40
D
n=26
E
ORANGE-20 n=22
F
COMBINED POPULATION
3·3
6·6
9·9
13·2
16·5
19·8

Figure 14: Distribution of tagged black rockfish. A through E shows the distribution of individuals where dot size and adjacent numbers reflect the frequency of observations at each station. In F the number adjacent to each dot shows the number of different individuals recorded at that station.

There existed two behavioral modes in black rockfish which were related to their distribution. Most pronounced was schooling behavior where large numbers of black rockfish in addition to blue rockfish (*S. mystinus*) and occasionally yellowtail rockfish (*S. flavidus*) came together in loosely formed aggregations at specific locations a few meters above the reef surface. The second behavioral pattern occurred less frequently when individual fish separated from the school and settled on the reef surface or within crevices in an apparent inactive phase. Although many tagged fish showed this behavior, there was no consistancy of location, timing, or duration of inactivity. Part of the problem in understanding this behavior stemed from its instability. Fish resting on the open reef surface usually swam up and rejoined the school when approached whereas fish within crevices usually remained there.

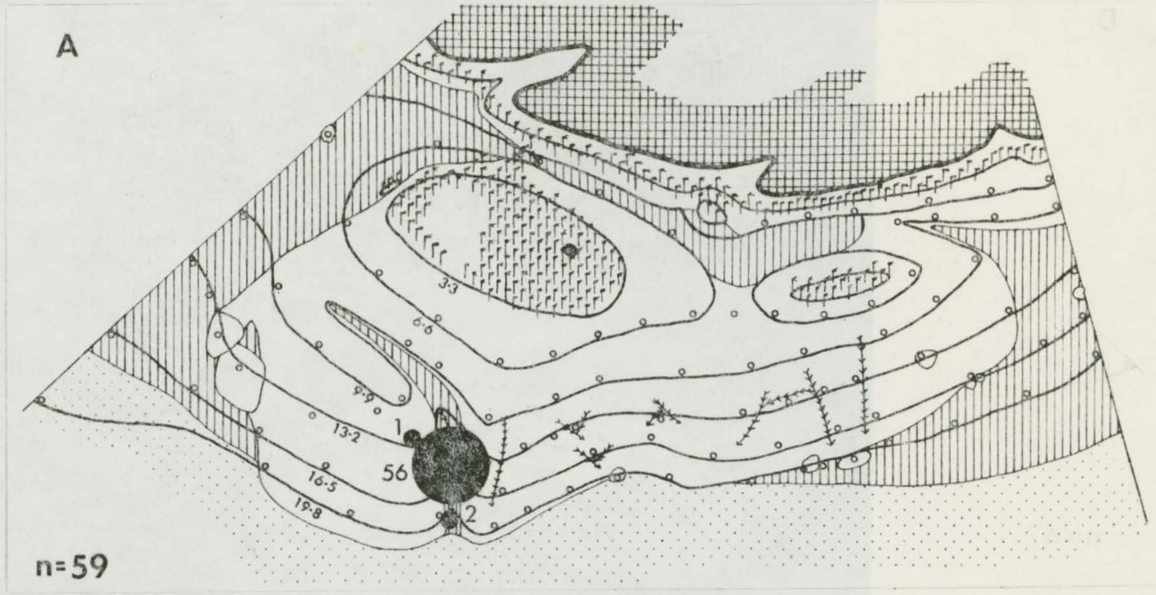
A primary feature in the distribution of schooling black rockfish was an association with specific reef topography. The kelp bed was a common focal point; schools were commonly seen within an open area in the center of the kelp bed and to a lesser extent within the more dense surrounding fronds. In deeper water, the large boulder was a site where schools congregated. Generally, smaller schools than those in the kelp bed clustered around the steep face on the seaward side and in the water space directly above the steep face.

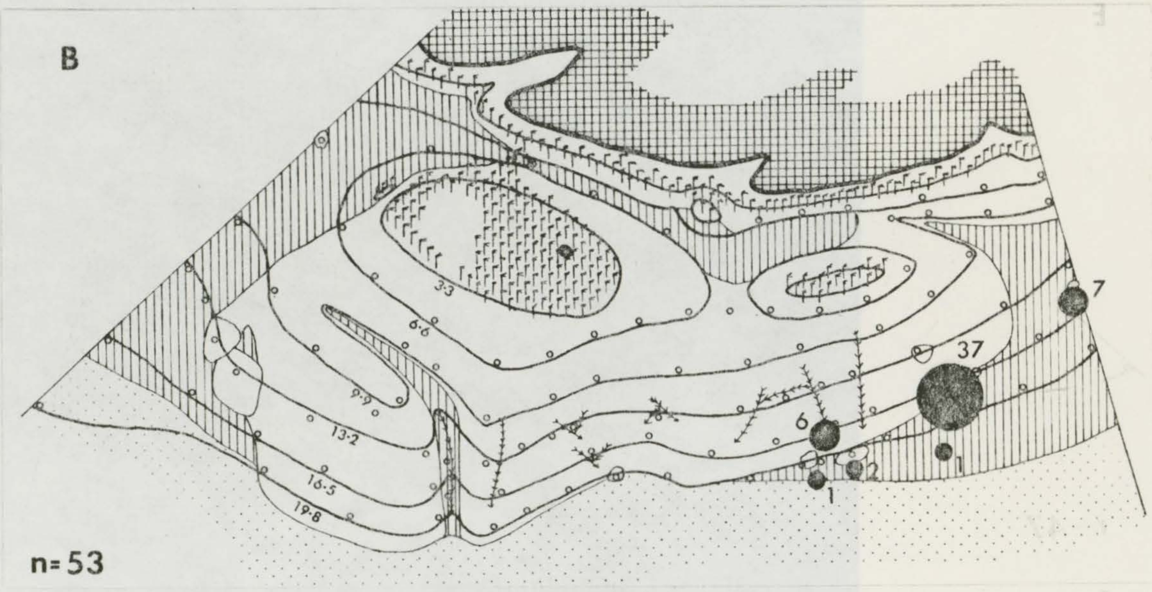
One individual (Orange-20) showed a pattern of distribution entirely different from other black rockfish (Figure 14E). Usually during the day this fish was seen sitting in the same place where the reef descends rapidly. Unlike the benthic style displayed by other black rockfish, the location for sitting was constant, varying only slightly over the two month study period. This pattern observed was strikingly similar to some juvenile rockfish on the site. Rather than sitting on the reef surface, young yellowtail rockfish (_S._ _flavidus_) and bocaccio (_S._ _paucispinis_) were found within crevices during the day. Like Orange-20, their selection of locations was constant usually within a 0.5 meter diameter area for several weeks.

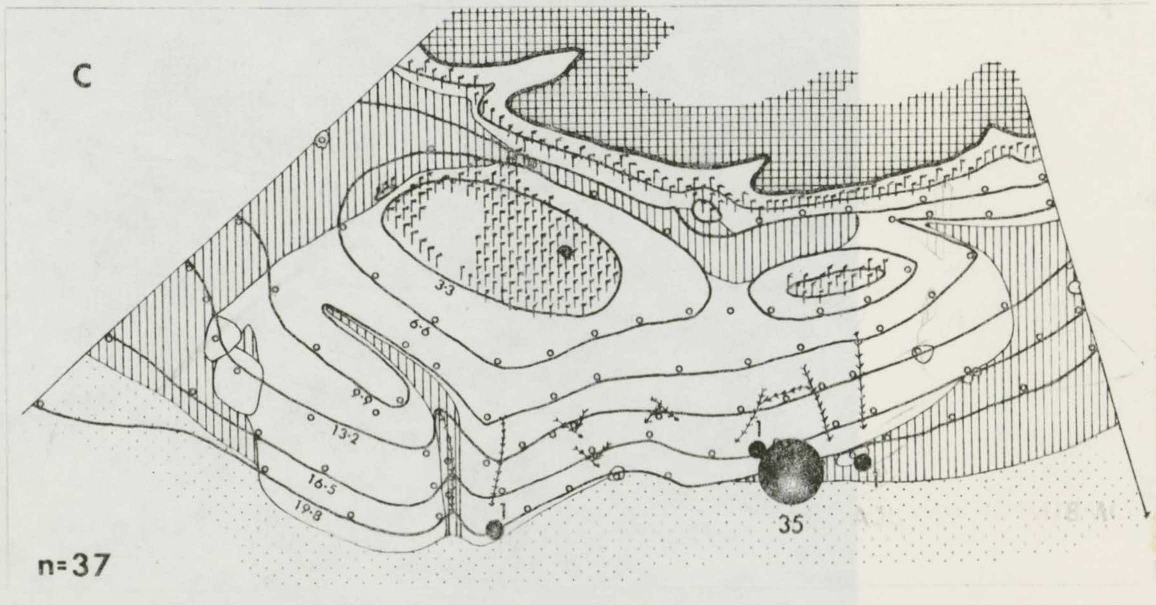
The distribution of several tagged China rockfish is shown in Figure 15. Five of the more commonly seen individuals are shown in 15A through E while 15F shows the combined distribution for the population. Each fish was solitary, having a range distinctly different from other conspecifics. Locations where more than one fish was present indicates situations where different individuals occurred at different times.

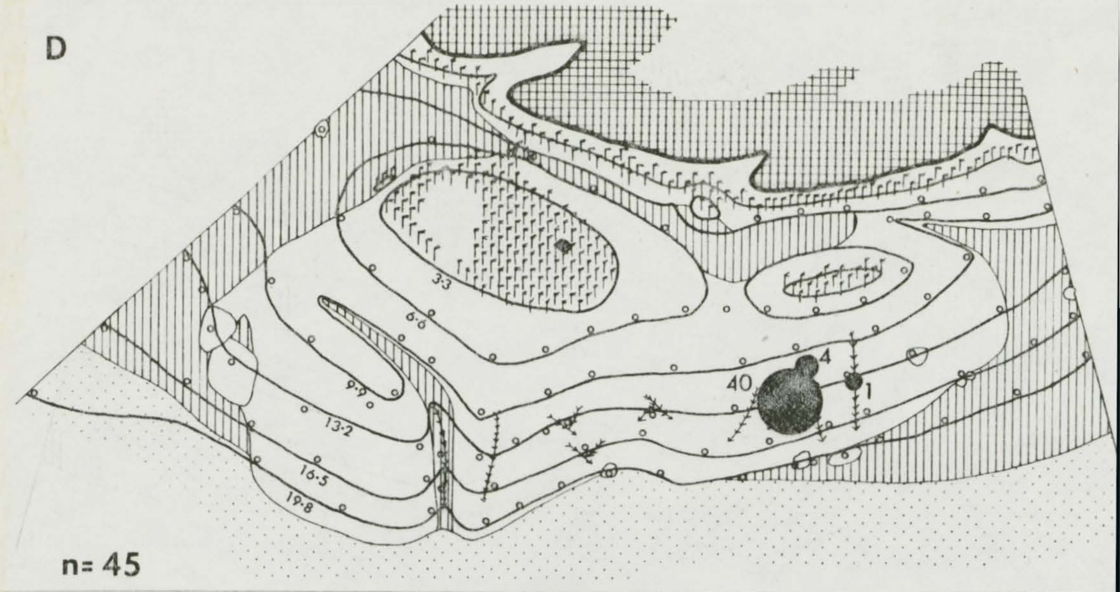
Each fish occupied a particular crevice for long periods of time. On most occasions, upon approaching an area, the resident fish was present in the crevice oriented in a head out position. At other times the same fish was observed just outside the crevice on the reef surface. Upon ap-

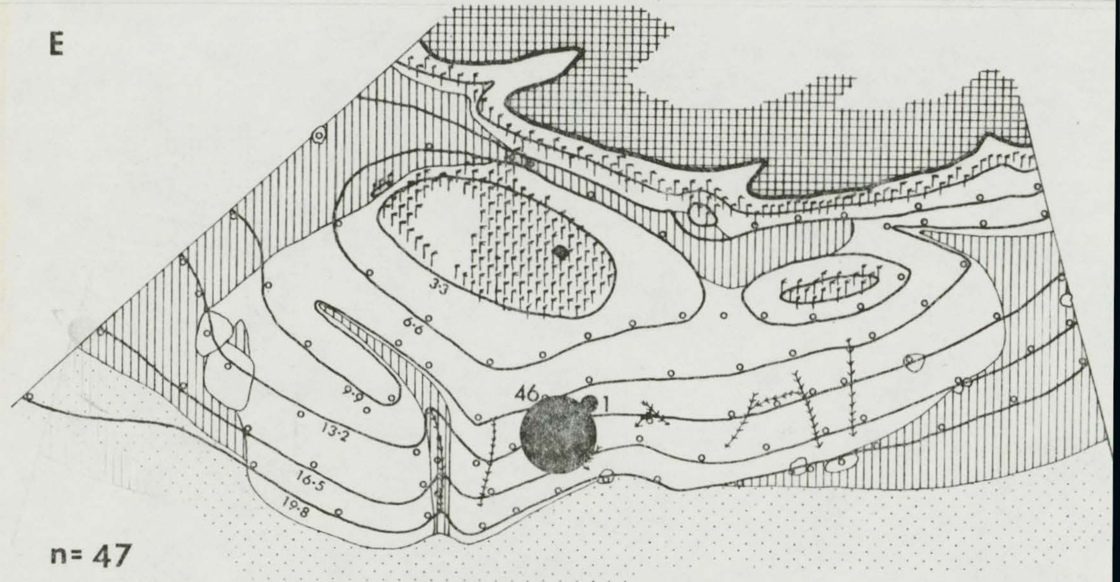
Figure 15: Distribution of tagged china rockfish. A through E shows the distribution of individuals where dot size and adjacent numbers reflect the frequency of observations at each station. In F the number adjacent to each dot shows the number of different individuals recorded at that station.

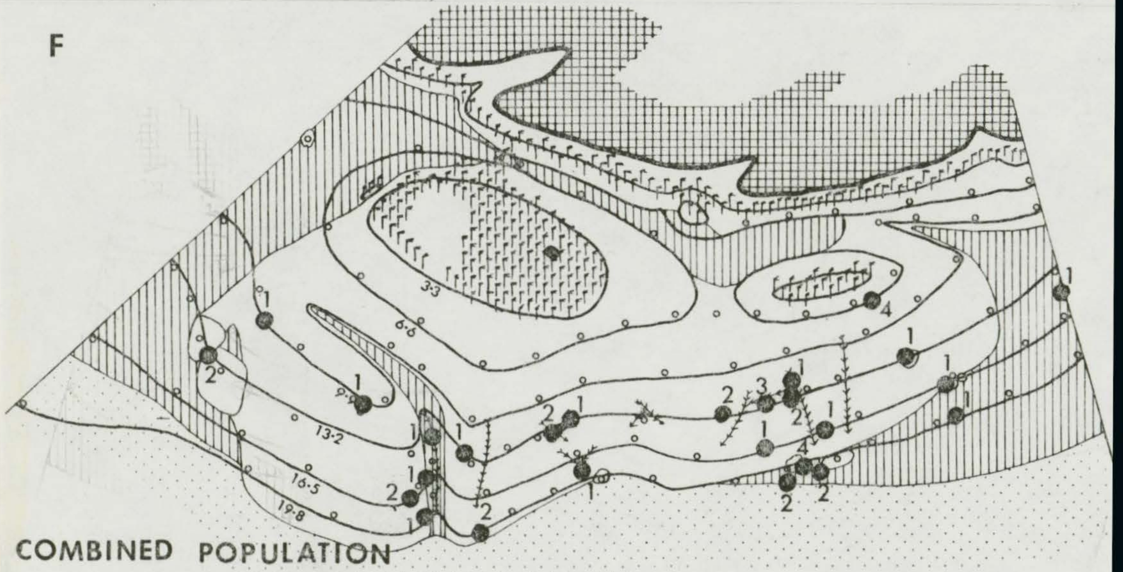












COMBINED POPULATION

proach, the fish usually fled to the home crevice or another nearby crevice.

On a few occasions interactions were observed between neighboring china rockfish who seemed very aware of the presence of an approaching conspecific and responded vigorously. In these observations, the encounters were brief, initiated by rapid approach of the resident and terminated with the intruder fleeing. The level of aggression displayed never became more intense than a chase.

During the observation period, there were 4 cases where china rockfish were displaced from their homesite by other reef animals. In the first case, a juvenile wolf eel, *Anarrhichthys ocellatus*, was observed at a variety of places on the reef prior to entering a homesite. The resident china rockfish disappeared for the duration of the wolf eel's occupancy (48 hours) but later reappeared after the wolf eel had left. In the remaining cases, china rockfish disappeared from their home crevice coincident with occupation by octopus, *Octopus dophleini* (ranging 10 to 20 kg). The resident china rockfish, occasionally seen elsewhere during this period (1 to 7 days), returned after the octopus had left.

Black and china rockfish showed distinctly different patterns of reef distribution (Figures 14 and 15). Black rockfish occurred over a wide depth range on the reef and concentrated in groups around high relief topography. China rockfish were strictly solitary benthic residents and, as a group, occupied crevices in the deeper parts of the reef. Individuals remained within a limited range near the primary home site. The much smaller range size in china rockfish is shown in Figure 16. As the distribution of reef markers was generally uniform over the site, the number of observations versus the number of locations for individuals reflects the relative range size. The lines drawn represent the limits of distributions when using discrete observations. On one extreme, fish were found in the same location on every observation indicating an very limited range. On the other extreme, an unlimited range occurs when, upon each new observation, a new location is inhabited. Individual china rockfish usually occurred at less than 3 locations whereas black rockfish locations increased in number with increasing observation frequency.

3.1.3.1 Movement of Fish

Movement magnitude was estimated by comparing the locations of repetitive observations of individuals over time. These spot observations provide estimates since they utilize only the geometric distance between two points whereas it is likely that the fish wandered, traveling a greater distance. Two time bases were used; short, successive observations within a dive period (35 minutes) and long, observations between consecutive dives. These dives ranged in time from a few hours separation to no more than 24 hours (12 hours

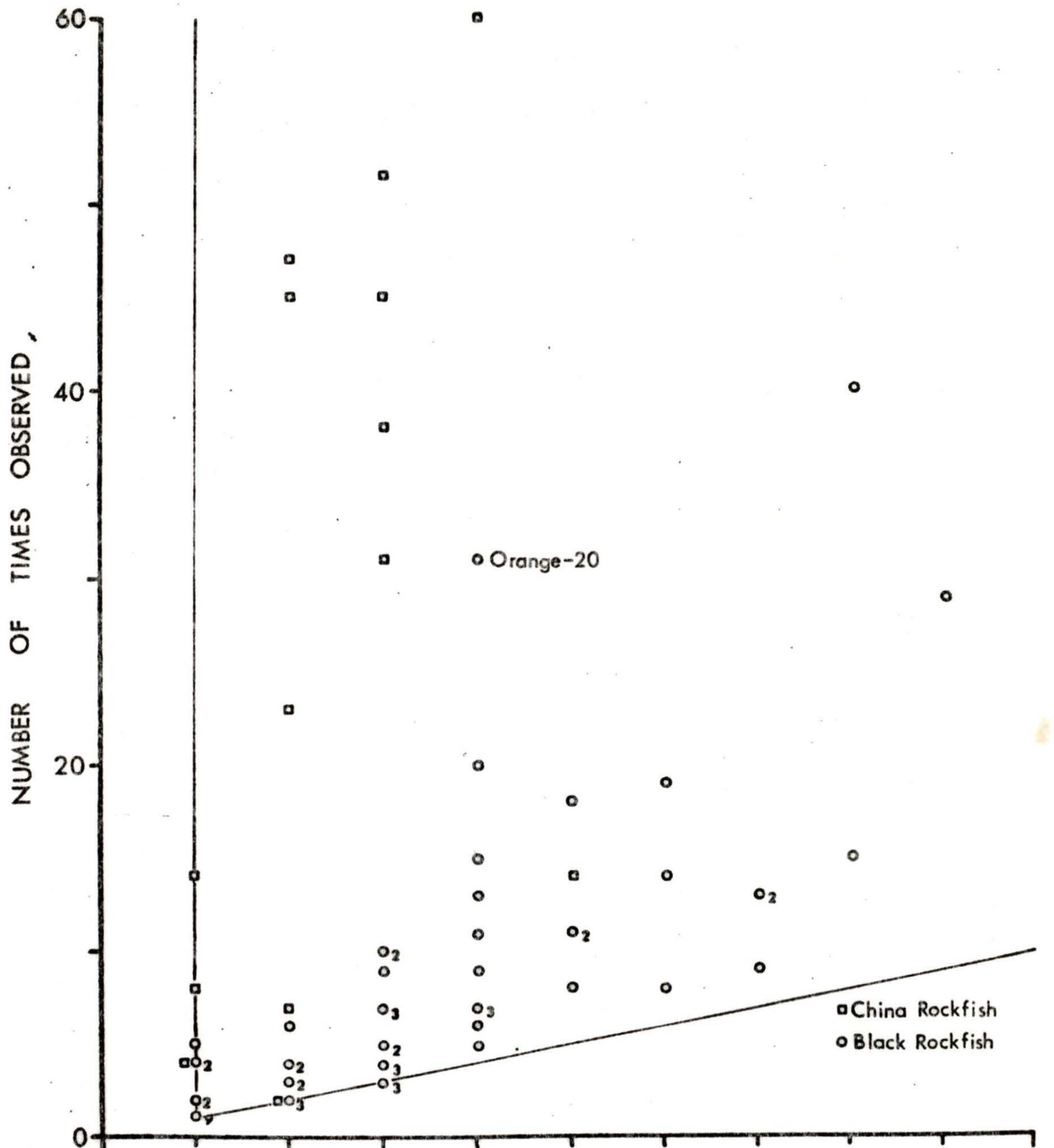


Figure 16: Relative range size for the two species at the study site in terms of the number of different landmarks where tagged fish were observed.

average). Over the 65 dive period there were 10 breaks of longer than 24 hours (usually less than 50 hours) leaving 54 dive pairs for consecutive dive movements. For brevity, these two movements are referred to as Within and Between, respectively.

The frequency of observed movement is shown in Table 3. For both species Within dive movement constituted only 9 percent of successive observations indicating that the tendency for fish to remain in one position was high. The frequency of movement for Between dive periods was considerably greater for both species: 49 percent for black rockfish suggesting that there was about an equal tendency to move as there was to remain stationary; 26 percent for china rockfish indicating that they were mostly stationary.

Table 3

Frequency of movement shown by tagged fish.

Time Interval	Species	No. of Total Observations	No. of Observations of Movement	%
Within	Black Rockfish	520	44	8.5
	China Rockfish	377	33	8.8
Between	Black Rockfish	117	57	48.7
	China Rockfish	215	56	26.0

Directionality of movement was recorded in three categories (Table 4). The first and second types were movements to shallower or deeper water, respectively. The third type was movement between positions at the same depth.

Chi-square tests for homogeneity indicated that black rockfish undertook more vertical than horizontal movements while the reverse is true for china rockfish. Secondly, the pattern of movement was the same, independent of time. The type of movement observed during a dive was consistant with those over longer time intervals.

The magnitudes of all movements are shown in Table 5 and differences for time periods, distances and species were tested as before. Distances are rounded to the nearest 3.3 meters since the site was laid out using a foot measuring system with 10 foot contours.

Chi-square tests for homogeneity showed that there was a significant difference in movement distances for the two species. Black rockfish frequently moved as far as 19.8 meters commonly move less than 13.2 meters. These tests also showed similarities in the time periods for each species. Despite the difference in duration of time for Within and Between categories, the difference in movement distances for these groups was not significant.

Table 6 indicates the vertical magnitudes of movements in the two species. The range is not as great as those in Ta-

Movement Type	Vertical Up	Vertical Down	Percent	Horizontal Only	Percent	Total	Chi-Square
Black Rockfish							
Within	16	17	84	8	13	41	4.71NS
Between	32	20		5		57	
China Rockfish							42.7**
Within	6	3	42	24	58	33	4.83NS
Between	16	12		28		56	

Table 4. Directionality of Movement. Chi-square test for homogeneity values are shown. NS, Not Significant; ** $p < 0.01$.

Movement Group	Distance of All Movements (Meters)						TOTAL	Chi-square values
	3.3	6.6	9.9	13.2	16.5	≥19.8		
Black Rockfish								
Within	2	9	2	2	7	22	44	3.13NS
Between	2	11	6	1	5	32	57	
TOTAL	4	20	8	3	12	54	101	74.37**
China Rockfish								
Within	8	8	6	11	0	0	33	4.80NS
Between	12	12	13	13	1	5	56	
TOTAL	20	20	19	24	1	5	89	

Table 5. Frequencies of movement in relation to distance. Results of chi-square tests for homogeneity are shown. NS not significant ** $p < 0.01$.

ble 5 indicating that the horizontal movements are more extensive. The same method was employed as before to test the time element for up, down, and species patterns. Black rockfish tend to make large movements and china rockfish appear to make very limited vertical movements (ie, few were greater than 3.3 meters). The magnitude of vertical movement was the same irrespective of time as well as direction.

Table 7 summarizes movement characteristics of the two species based on the previous four tables. The following patterns were evident.

1. While the frequency of movement during a short time base (Within dives) was similar in both species, black rockfish showed more movement during a longer time base (Between dives).

2. Movement in black rockfish was primarily up and down the reef slope while lateral reef movement was pronounced in china rockfish.

3. Black rockfish moved greater distances over the reef surface than china rockfish. Their movements also incorporated a broad vertical spectrum while china rockfish utilized a very limited vertical range.

Type of Movement	Magnitude (m)			
	3.3	6.6	9.9	13.2
Black Rockfish				
UP within	10	0	6	0
between	10	6	16	0
DOWN within	5	3	7	2
between	5	2	13	0
China Rockfish				
UP within	5	1	0	0
between	10	6	0	0
DOWN within	1	2	0	0
between	10	2	0	0

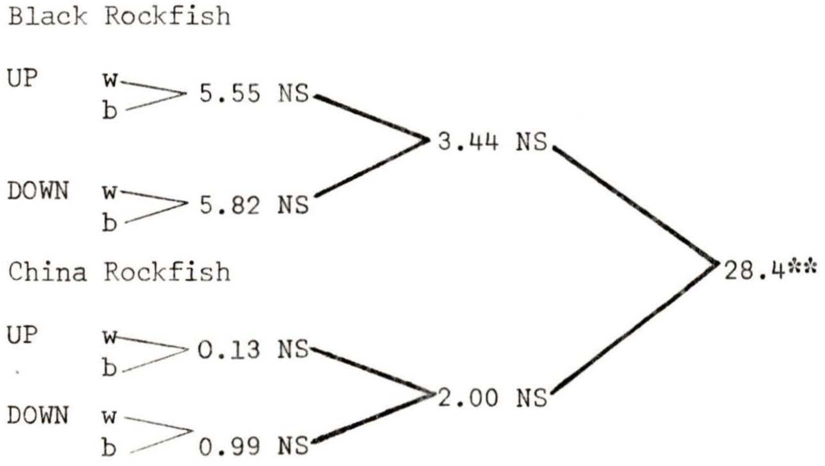


Table 6. Magnitude of vertical movement. Below, the pattern of analysis using chi-square test for homogeneity is shown. NS, not significant. **, p <0.01.

	1. Frequency (% Total Observations)		2. Direction (% Total Movements)		3. Distance			
					Percent All Movements		Percent Vertical	
	Within	Between	Vertical	Horizontal	<15 m	>15 m	<9 m	>9 m
Black Rockfish	9	49	84	13	35	65	54	46
China Rockfish	9	26	42	58	93	7	100	0

Table 7. Summary of movement patterns in Black and China Rockfish.

3.1.4 Diel Behavior

Unlike the kelp greenling, Hexagrammos decagrammus, which are day active seeking shelter at night, both study species seemed to change little. Diel patterns were not immediately apparent so a variety of comparisons were made. In this testing, an inherent bias deserves mention. Using lights to find tagged fish resulted in a greatly reduced field of view. Table 8 underscores this point showing consistently lower night totals for both groups of black rockfish. While this may represent a diel behavior pattern, I believe the difference was an artifact largely attributable to changes in diver ability to locate tagged fish at night. A different pattern occurred in tagged china rockfish which were seen at the same frequency both day and night. Observations of this species, because of its limited distribution and the observer's ability to locate specific areas on the reef surface, did not change with light.

The distribution plot for black rockfish was compared for day and night periods. In general, the population remained in the same place, irrespective of light, but close examination showed there was one major difference in the shallow reef sections. During the day, tagged fish remained within the kelp clearing area but at night there were comparatively more tagged fish seen in the nearby shallow areas to the east. Using a presence-absence scheme for the non-kelp shallow regions versus day and night in a chi-square matrix,

Table 8

Mean and variance for the number of tagged fish observed for dives at different times of the day.

	Dusk	Dawn	Night	Day
Black Rockfish 1.	$\bar{x} - 3.5$ N = 4	$\bar{x} - 1.7$ N = 6	$\bar{x} - 1.23$ $S^2 = 3.19$ N = 13	$\bar{x} - 3.69$ $S^2 = 5.13$ N = 42
2.	$\bar{x} - 2$ N = 1	$\bar{x} - 6.7$ N = 6	$\bar{x} = 2.25$ $S^2 = 9.07$ N = 8	$\bar{x} = 9.39$ $S^2 = 15.89$ N = 23
China Rockfish	$\bar{x} - 5$ N = 4	$\bar{x} - 6$ N = 6	$\bar{x} - 5.15$ $S^2 = 5.14$ N = 13	$\bar{x} = 4.92$ $S^2 = 4.55$ N = 42

there is a significant difference ($p < 0.001$) in tagged fish seen at this location between day and night (Table 9A). The distribution of black rockfish appears to expand out from the kelp area into the surrounding shallow areas at night (Figure 17).

Another approach toward day-night differences is to examine the relationship of light change with movement. In-

Table 9

Chi-square contingency tables for light related habits in black rockfish.

A

	Present	Absent
Night	10	21
Day	15	161

$X_{(1)}^{2} = 10.39^{**}$

B

	Light Change	No Change
Movement	35	20
No Movement	34	29

$X_{(1)}^{2} = 1.16$ NS

C

	Day	Night
Present	23	0
Absent	6	10

$X_{(1)}^{2} = 16.9^{**}$

stances where the same fish was observed on successive dives were taken and subdivided into a presence-absence table. In this case, the presence or absence of movement was compared with dive pairs where light remained constant (day-day; night-night) and those where light changed (day-night; night-day). The interaction of light and movement is not significant ($p>0.25$, Table 9B), this agrees with previous evidence that tagged black rockfish do not have any major shift in distribution over the site.

Striking differences did occur however, in Orange-20 with light. During the day this fish was seen many times sitting in its usual place on the reef. At night Orange-20 was absent and on two occasions, was seen among the schooling

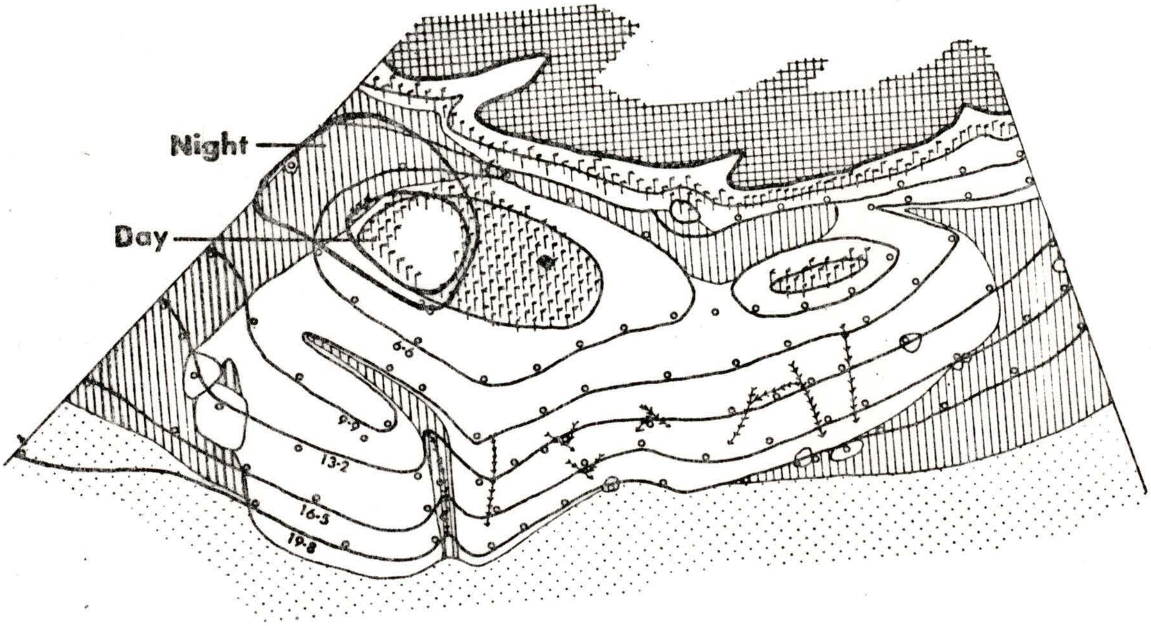


Figure 17: Day and night distribution of black rockfish in shallow areas.

black rockfish in the shallow reef areas. Using the same presence-absence scheme for the sitting location (Table 9C), the difference between day and night is significant ($p<0.001$).

Similar tests were conducted for the tagged china rockfish population. The frequency of observations of the tagged group remain essentially the same, irrespective of light (Table 8). Examining each individual separately, their presence or absence from the home site was unrelated to changes in light. Testing in another fashion, the coincidence of movement with light a transition was also not apparent indicating that china rockfish do not undergo a light related shift in distribution.

3.2 LABORATORY STUDIES

3.2.1 General Morphology

3.2.1.1 Specific Gravity

The specific gravity was measured in 109 individuals which are summarized in Table 10. The mean values of the two species were not significantly different ($p>0.05$). Within species, density remains constant with size over the range examined (>10 cm standard length). Using this value, the volume of gas required to neutrally buoy either species corresponds to 5.6 percent of body weight in air.

Table 10

Measurements of specific gravity in the two species.

Species	N	$\bar{x}$	s^2	t	Pooled Mean
Black Rockfish	59	1.087	3.0×10^{-6}	2.75 NS	1.087
China Rockfish	50	1.088	3.0×10^{-2}		

3.2.1.2 Red Blood Cell Proportions

The proportion of red blood cells (RBC) in plasma as determined by hematocrits was measured in 96 fish. The mean values for different size groups of the two species are shown in Figure 18. Black rockfish had significantly higher hematocrits than similar size groups of china rockfish. In both groups there is a direct size related RBC increase, although for china rockfish this is slight and not statistically significant. In black rockfish, the small group is significantly different from the more similar large size groups.

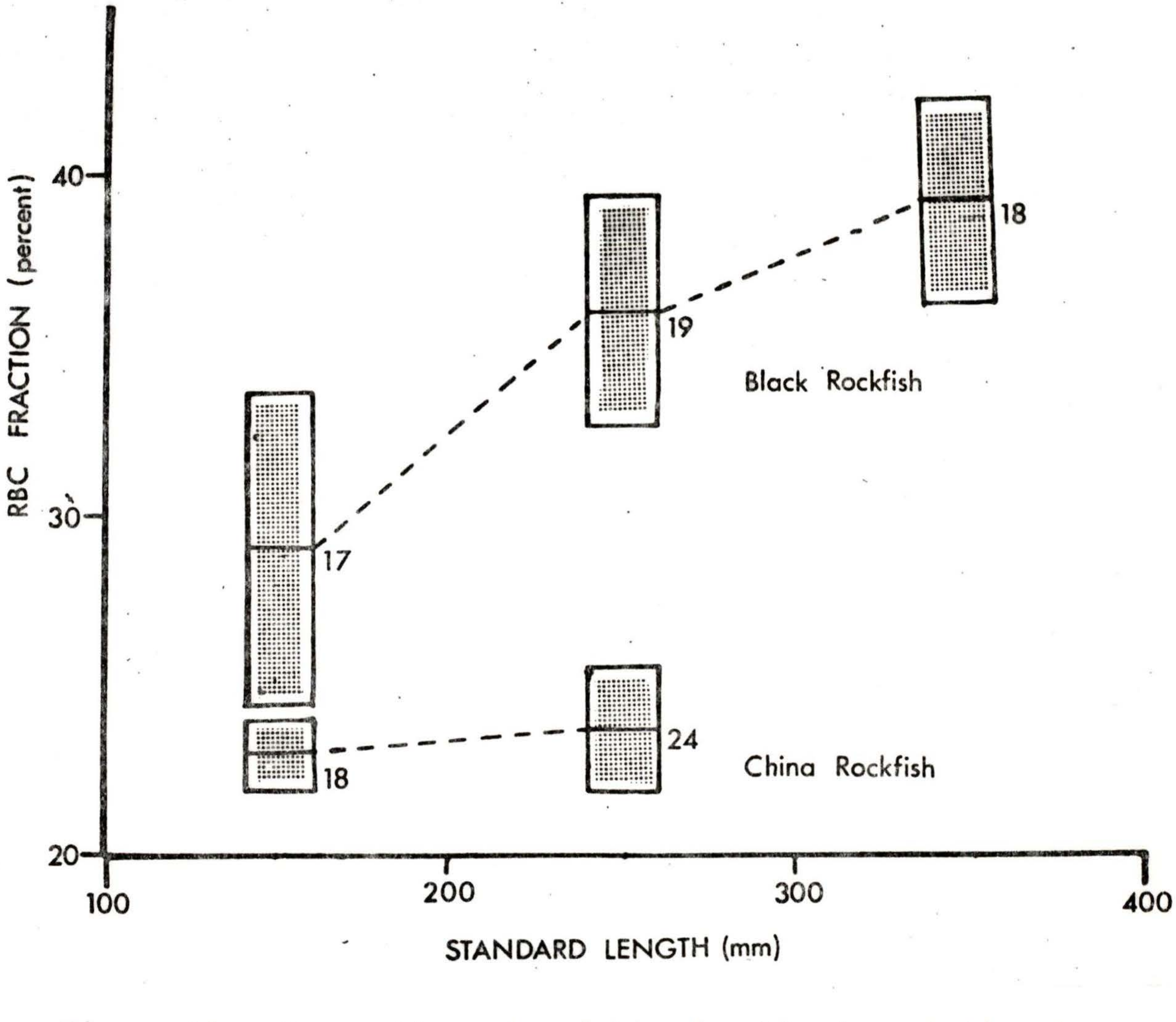


Figure 18: Proportion of red blood cells in relation to size in china and black rockfish. Shown are 95 percent confidence intervals for 100 mm size classes. Sample sizes are indicated for each size class.

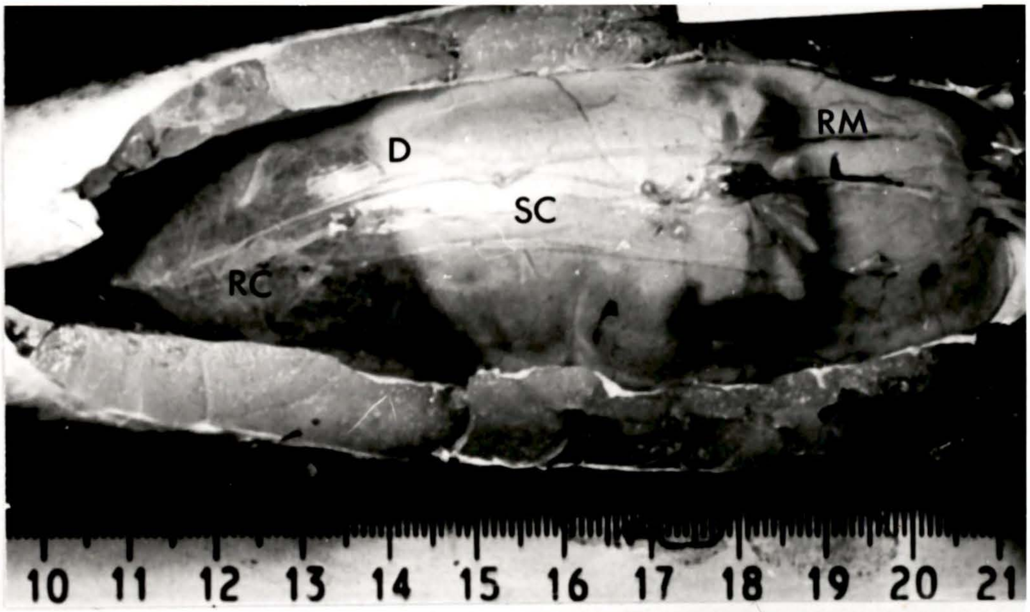
3.2.2 Swimbladder Morphology

Photographs of intact swimbladders of the two species are shown in Figure 19. The bladder is euphysoclist (see appendix A) situated directly ventral to the vertebral column occupying the dorsal surface of the coelomic cavity. From gross examination, most of the general anatomy can be identified. The outer connective tissue layer, the tunica externus, is quite thick providing support for the delicate internal tissue layer, the tunica internus. Within the tunica internus, there are two chambers, anterior and posterior, separated by a connective tissue diaphram (D) which interconnects the chambers when open. Both chambers are extremely thin and alternately distensible within their more rigid enclosure. The anterior chamber or the secretory chamber (SC) has the largest volume and contains the gas secretory center used in bladder filling. The posterior chamber or resorptive chamber (RC) is generally smaller and has highly vascularized walls that facilitate passive diffusion of gas from the bladder. Aside from the vascular and nerve tissue connections to these chambers there is apparently no other point of attachment. The two chambers glide freely on a gelatinous tissue, the serosa, within the tunica externus.

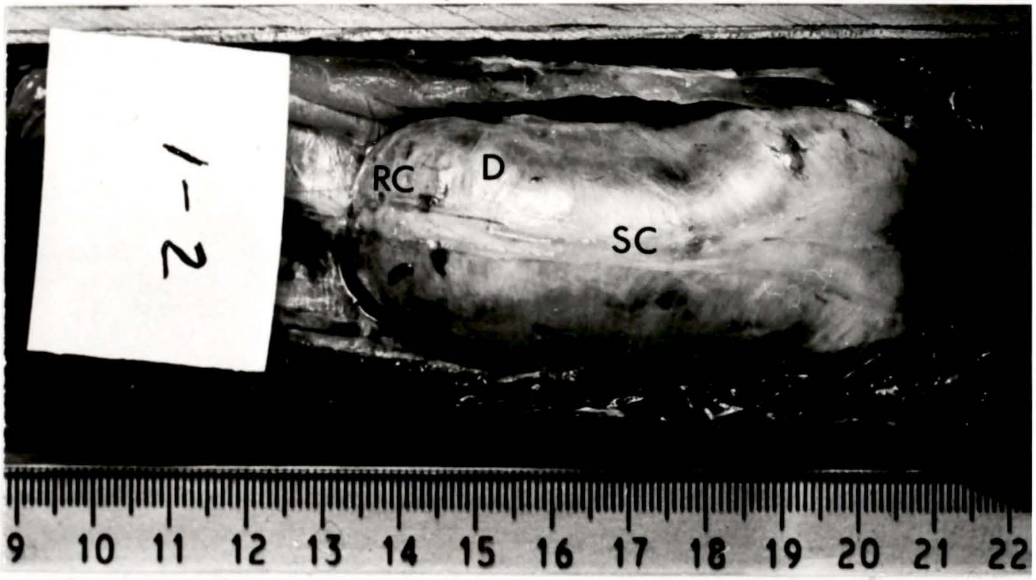
Figure 19C shows the swimbladder overexpansion in china rockfish when taken directly to the surface. The inner, tunica internus, is shown distended through a split in the outer, tunica externus. Upon further pressure reduction,

Figure 18: Ventrally dissected specimens showing the position of the swimbladder in the visceral cavity. A, black rockfish; B, china rockfish; C, china rockfish with ruptured tunica externus; D, diaphram; RC, resorption chamber; SC, secretion chamber; TE, tunica externus; TI, tunica internus.

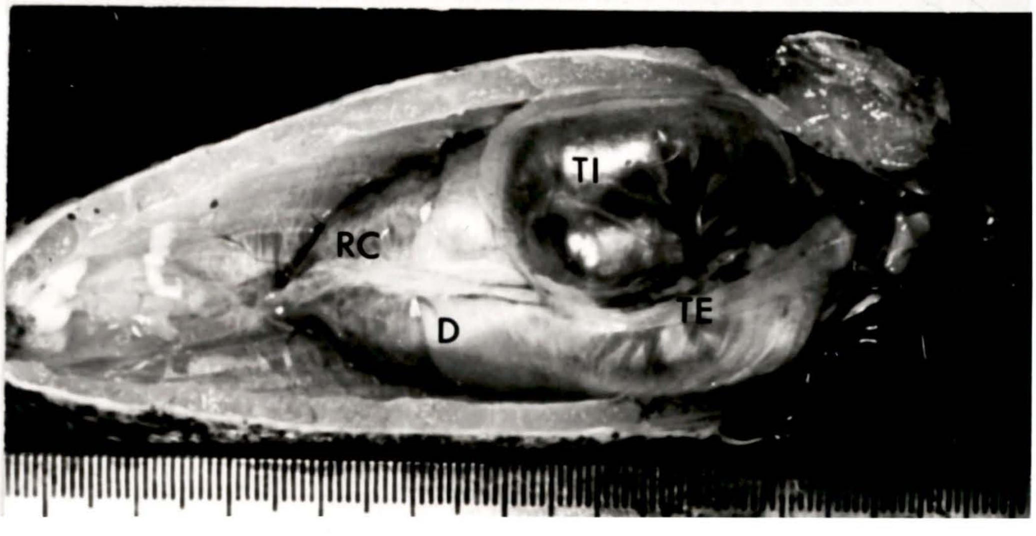
A


RM
D
SC
RC
10 11 12 13 14 15 16 17 18 19 20 21

B


1-2
RC
D
SC
9 10 11 12 13 14 15 16 17 18 19 20 21 22

C


TI
RC
TE
D

the inner layer usually ruptured, but its greater elasticity allowed much greater expansion than the tunica externus.

3.2.2.1 Secretory Center

The secretory center provides for transport of gas from the blood into the bladder against a concentration gradient. The functional units of this organ are shown in Figure 20. Blood enters through the celiacomesenteric artery (CA) and branches to one of several arterioles leading to the individual retia (R) of the rete mirabile (RM). Each retia is a counter-current multiplier where the partial pressure of gas is concentrated to a level in excess of that secretory chamber (not shown). Transport occurs at the secretory epithelium (SE) which radiate from the distal counter-current loops of the rete mirabile.

The rete mirabile of black and china rockfish is made up of as many as 10 individual retia which are shown for different size fish in Figures 21 and 22. During juvenile life stages these retia are separate and distinct but enlarge with growth. In 35 cm Black rockfish the retia become closely merged such that they appear as a single, horseshoe-shaped unit. In china rockfish many adults still have distinctly separate retia.

The pattern of rete mirabile growth with fish size is shown differently in Figure 23. Secretory area as measured

Figure 20: Preparations of tunica internus spread flat. A, china rockfish· B, black rockfish; CA, celiacomesenteric artery; D, diaphram; R, retia; RC, resorption center; SC, secretion center; SE, secretory epithelium.

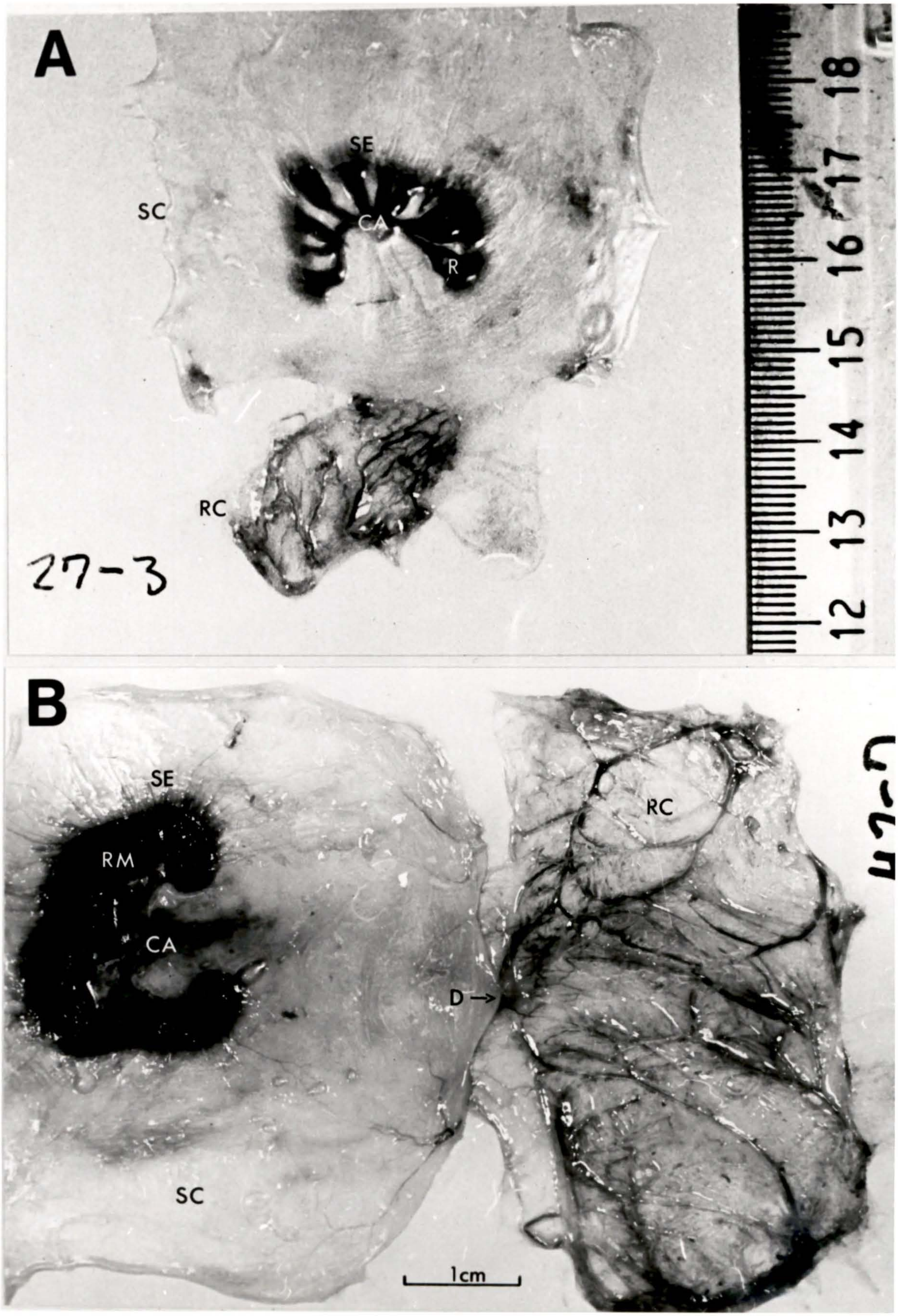
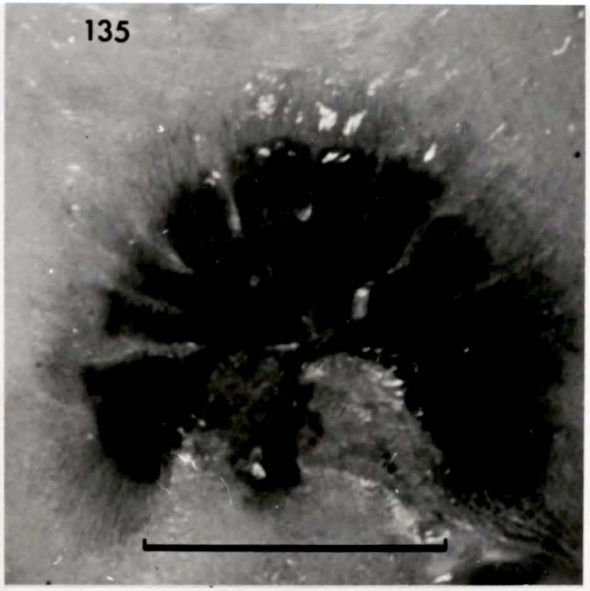

A
SE
SC
CA
R
RC
27-3
12
13
14
15
16
17
18
B
SE
RM
CA
D
RC
SC
1cm

Figure 21: Pattern of rete mirabile development with growth in black rockfish. Shown are standard body lengths (mm) and 1 cm scale.


75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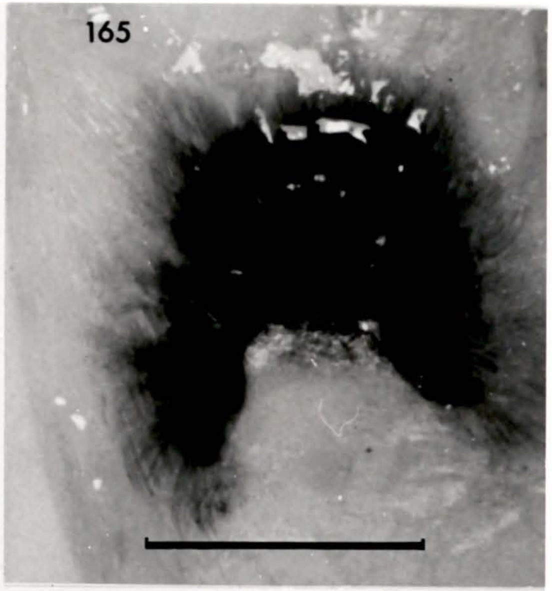
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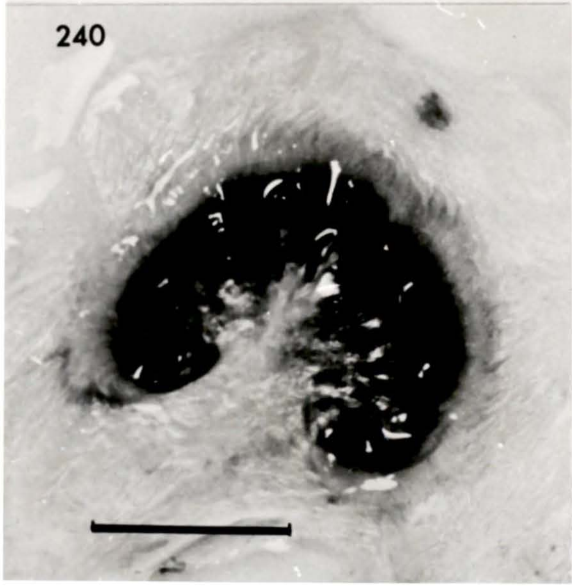
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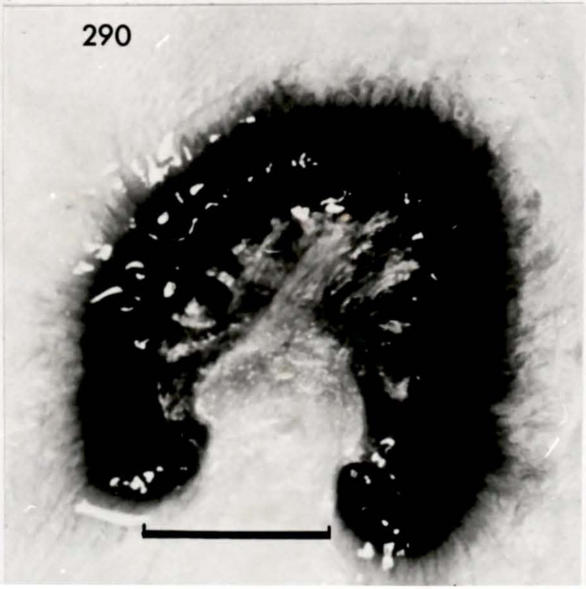
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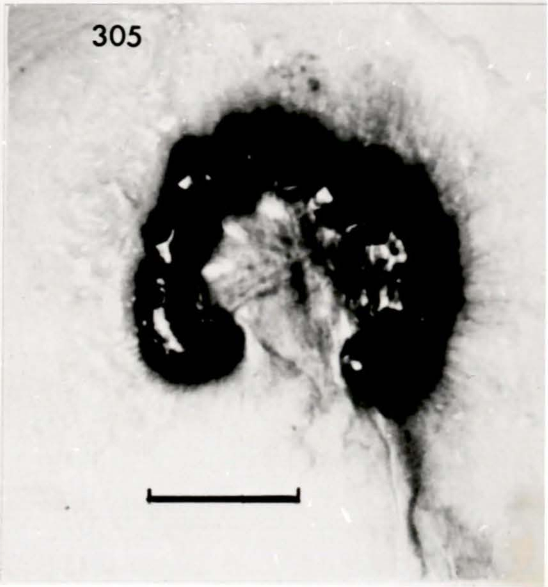
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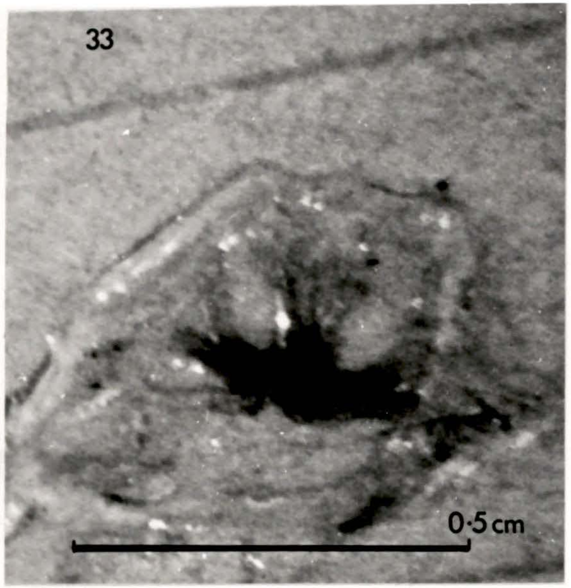
Figure 22: Pattern of rete mirabile development with growth in china rockfish. Shown are standard body lengths (mm) and 1 cm scale except as noted.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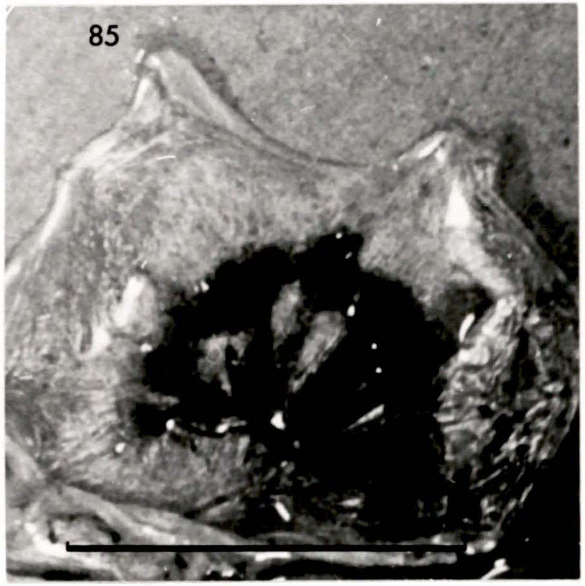
0·5cm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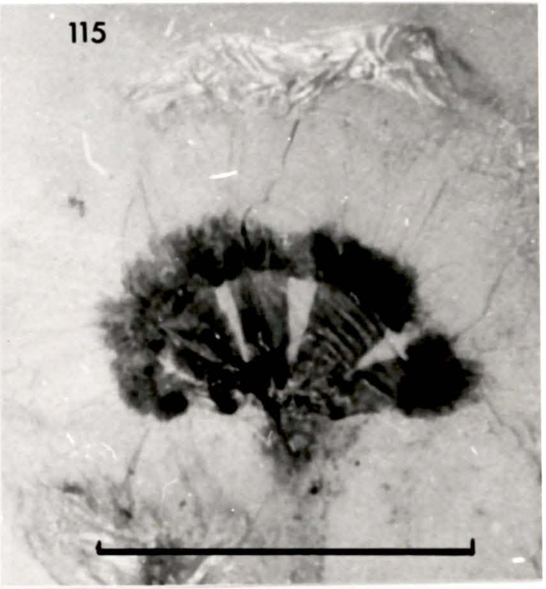
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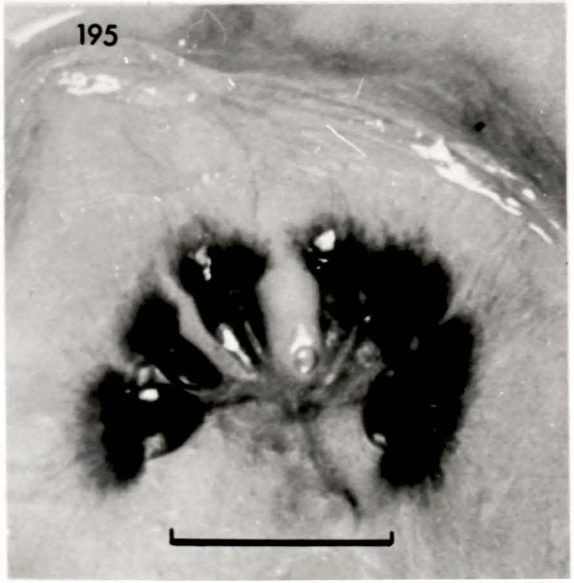
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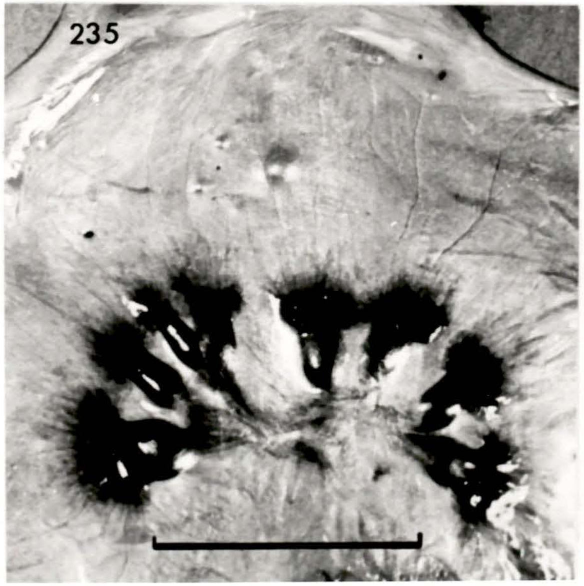
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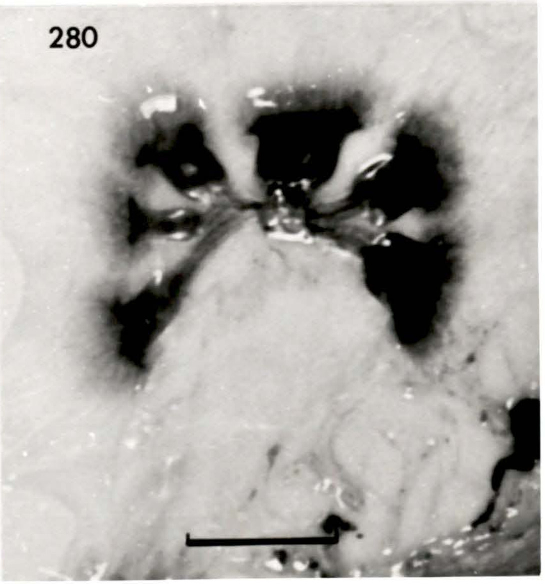
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from spread out preparations is shown in relation to body weight. In both species the correlation was significant ($p<0.01$) and regression coefficients (r) were 0.68 and 0.87 for china rockfish, respectively. Comparatively, the secretory epithelium in black rockfish was about twice that china rockfish.

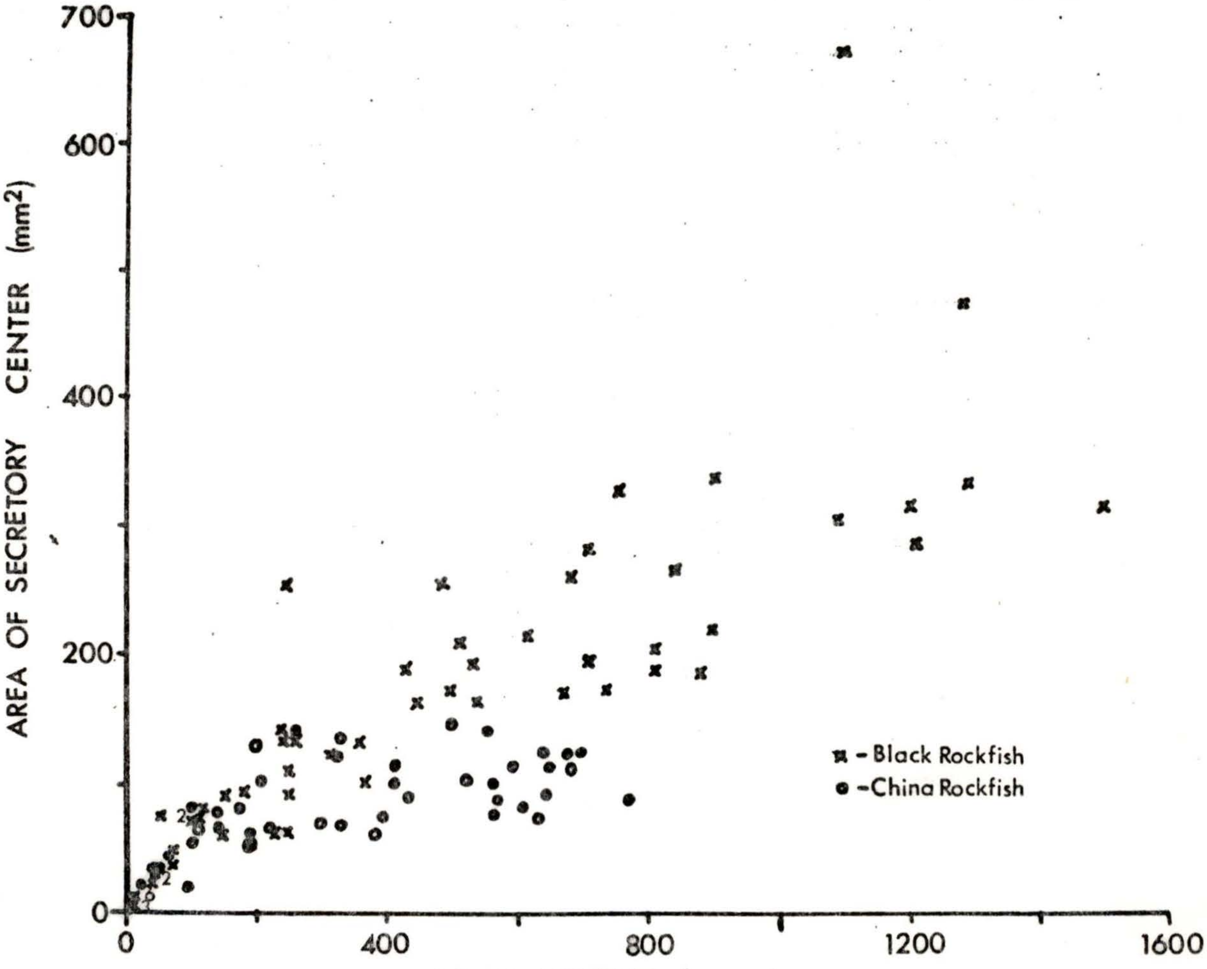

Figure 23: Surface area of the secretory center in relation to body weight in the two species.

A scatterplot comparing rete length with standard body length is shown in Figure 24. While the rete in both species reached a similar length, the correlation with body length was high in black rockfish (r=0.84) but not in china rockfish (r=0.59).

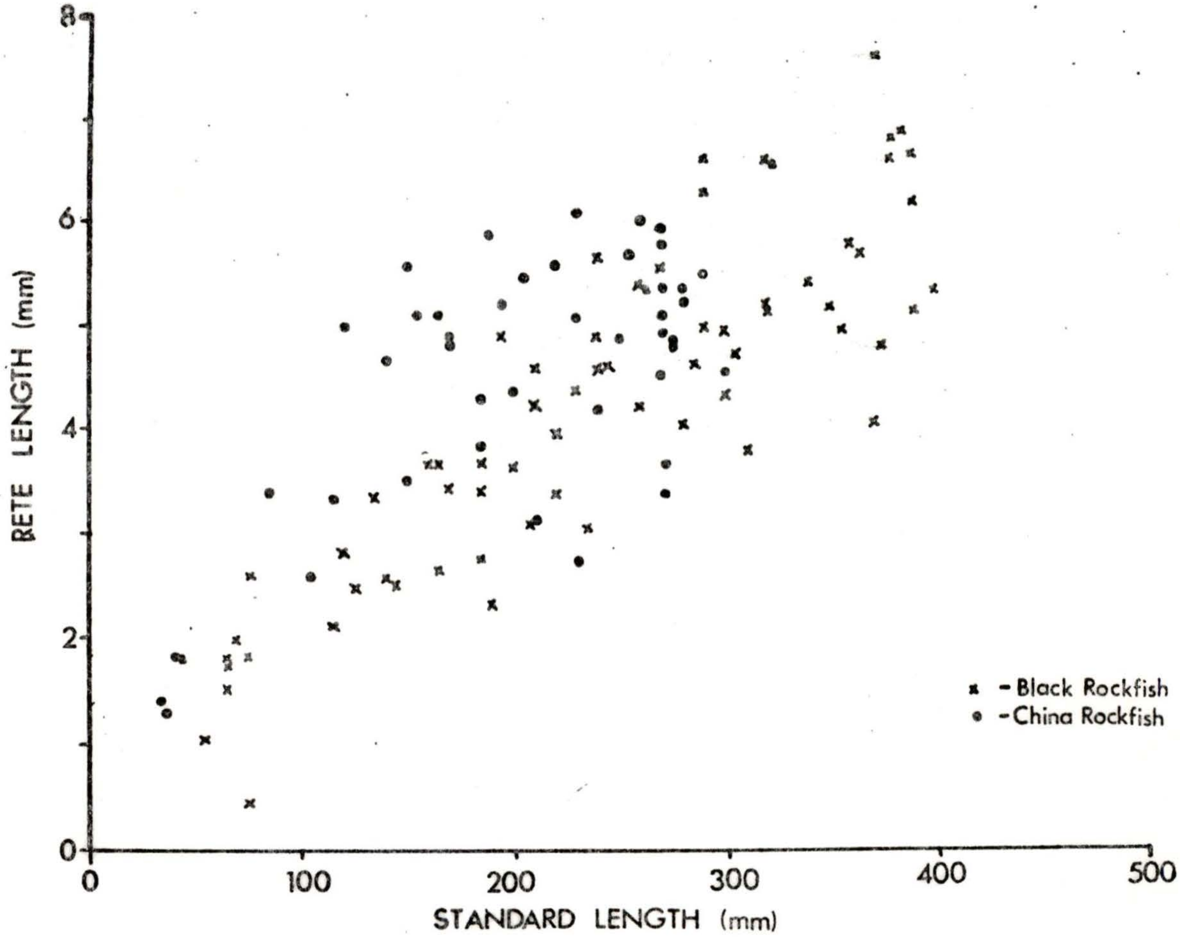

Figure 24: Relationship of rete length to standard body length in the two species.

3.2.2.2 Swimbladder Resistance to Overexpansion

The strength of the swimbladder wall was estimated by measurements of the resistance to swimbladder overexpansion during pressure reduction is shown in Table 11. When pressure was reduced by 70 percent, the swimbladder in black rockfish ruptured in the posteroventral region overlying the resorption chamber. During pressure reductions of 59 percent, the gas bladder of china rockfish ruptured laterally where the tunica externus attaches to the body wall. The sample sizes were small and high variability within china rockfish did not allow statistical comparison between species ($p>0.05$; F-test). It was apparent, however, that china rockfish consistently required less pressure expansion to cause damage and thus, black rockfish may be more tolerant of pressure reductions.

During periods of pressure tank experiments, there were occasions of equipment malfunction due to power failure, pump breakdown, etc. in which tanks lost pressure and forced the termination of an experiment. In many cases prior to the breakdown, neutral buoyancy pressure was known and consequently, the resulting pressure drop could be calculated. Assessment of bladder damage associated with pressure reduction provide a comparison between in vivo and ventrally dissected preparations. Results of these observations shown in Table 10B, compare well with the ventrally dissected measurements. The body wall seemed to pro-

Species	N	% Reduction $\bar{x}$	S^2	Remarks
A. Black Rockfish	5	70.4	0.24	
China Rockfish	6	58.3	36.8	
B. Black Rockfish		75		rupture
		75		rupture
		75		rupture
		75		rupture
		66.7		no damage
		66.7		no damage
		66.7		no damage
China Rockfish		60		rupture
		55		t.e. only
		66		t.e. only
		52		no damage

Table 11. Measurements of swimbladder burst characteristics. (a) pressure reduction required to burst the swimbladded ventrally dissected specimens using an evacuation chamber. (b) effects of rapid pressure reduction on live specimens in pressure tanks. t.e.: tunica externus.

vide little support in preventing expansion and rupture in the tunica externus but may help to resist rupture of the tunica internus.

3.2.3 Buoyancy Adjustment

3.2.3.1 Gas Secretion

When exposed to an increase in pressure, fish responded by increasing their buoyancy. In all cases, fish sat motionless within the tank when increasing their buoyancy. After a period of time, neutral or near neutral buoyancy was achieved and both species became more noticeably active. Black rockfish assumed a hovering position while china rockfish remained in contact with the tank bottom but frequently changed positions. The response curve in terms of neutral buoyancy pressure versus time was sinusoidal in shape becoming asymptotic with the test pressure level. Examples of this adjustment curve for a pressure change of 2 atm are shown in Figure 25 and 26 for black and china rockfish, respectively. Using the time for 50 percent adjustment as a comparative measure, the values within each species are generally consistent and apparently unrelated to size, weight,and sex over the range (>10 cm standard length) examined. A better comparison can be made from summary Figure 27 where the mean response curves and the range of 50 percent adjustment values are shown. In both cases, the time to adjust to a 2 atm increase in pressure was considerable and there was a large species difference. After approximately 90 hours, black rockfish had fully compensated for the change in buoyancy resulting from a two atm pressure increase. Two hundred and fifty hours were required for the same process in china rockfish. Also shown are buoyancy response curves for pressure changes of 1 and 3 atm for black rockfish. These two curves plus the 2 atm curve vary only slightly showing a generally consistent rate of buoyancy increase over the 3 atm pressure range.

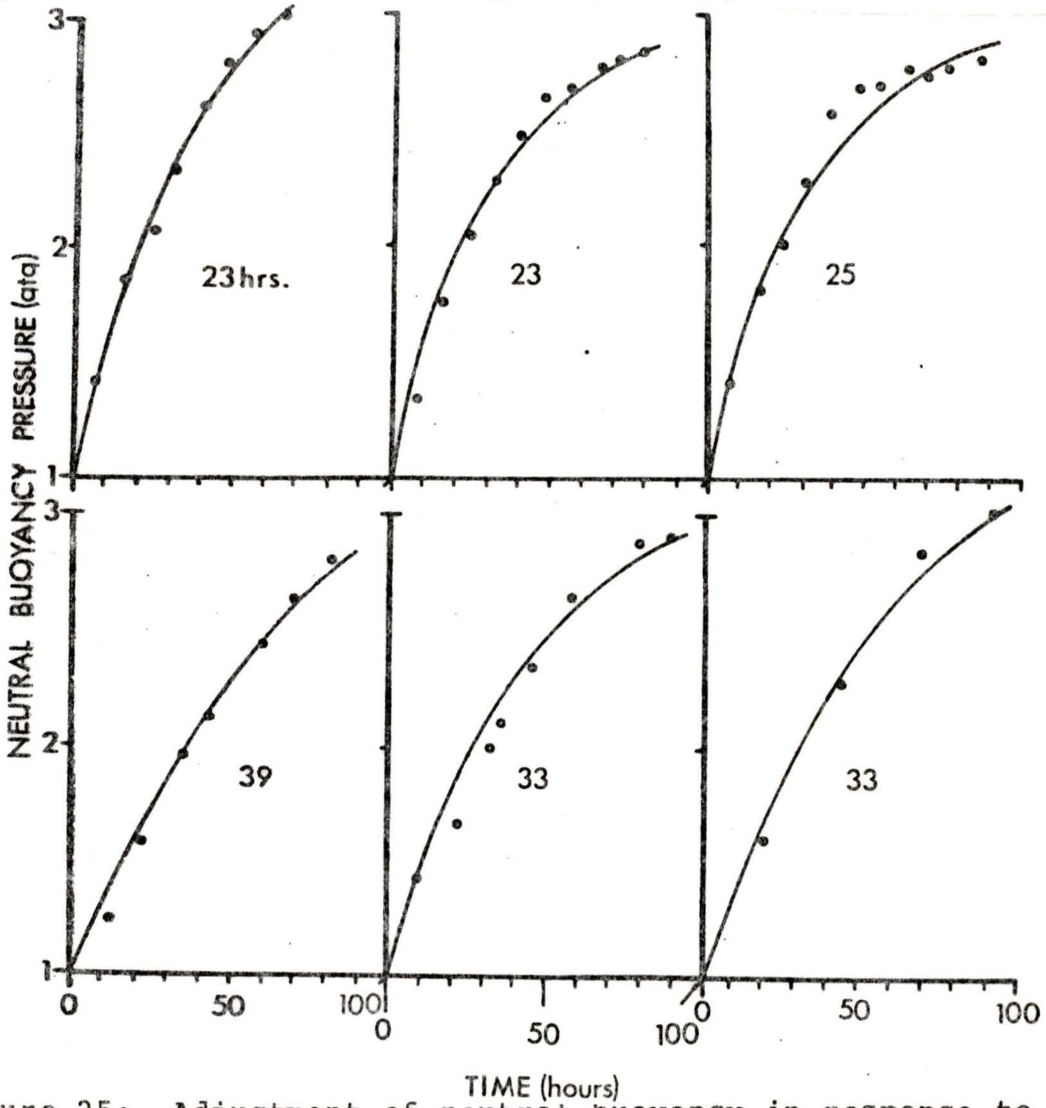

Figure 25: Adjustment of neutral buoyancy in response to a 2 atm pressure increase in 6 black rockfish. Time required for 50 percent adjustment is shown in each experiment for comparison.

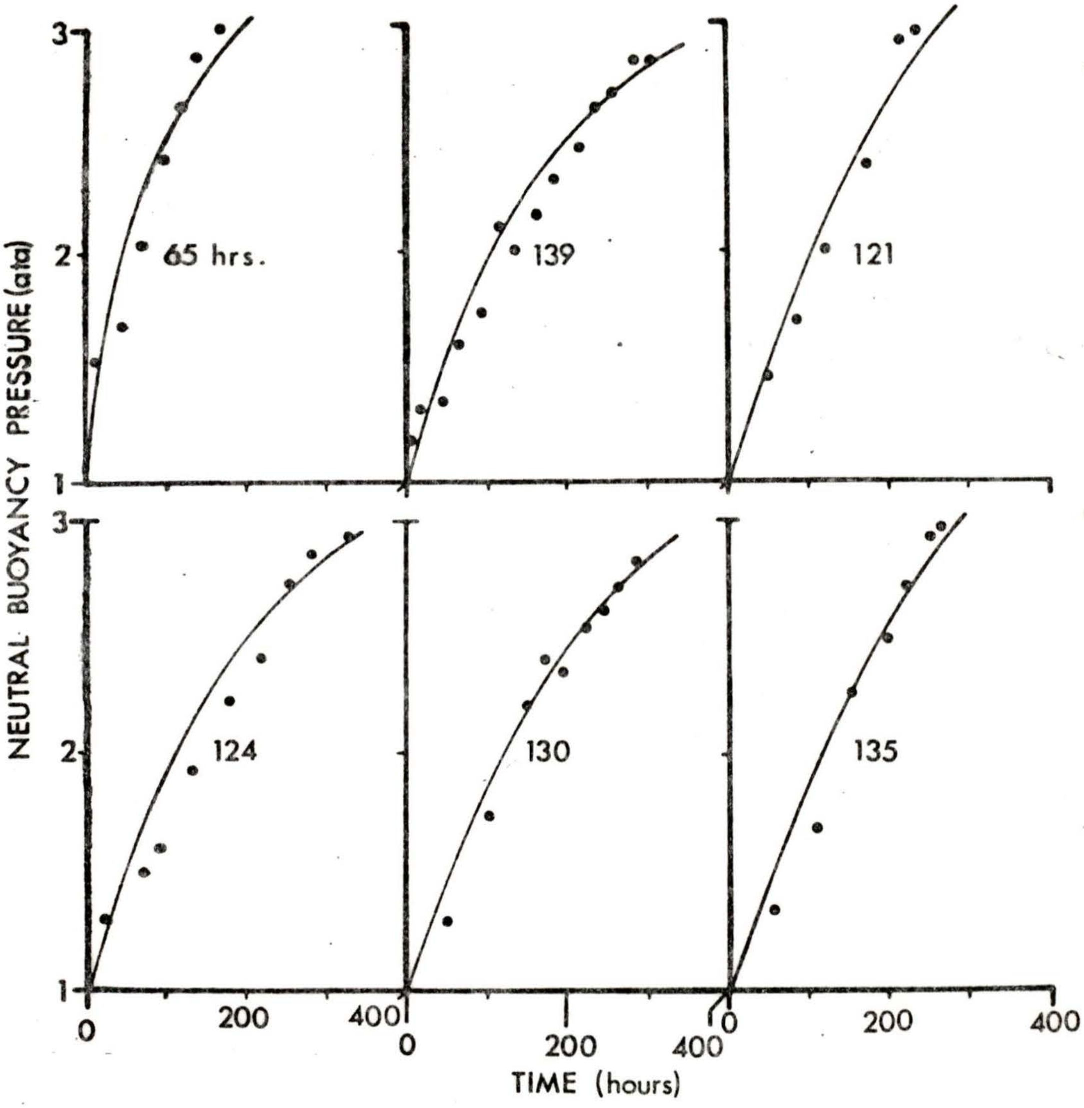

Figure 26: Adjustment of neutral buoyancy in response to a 2 atm pressure increase in 6 china rockfish. Fifty percent adjustment times are shown for comparative purposes.

3.2.3.2 Gas Resorption

Pressure reduction and subsequent positive buoyancy elicited vigorous swimming in both species. Animals passively lifted from their normal position and began actively opposing the tendency to rise. In most cases the tail inclined

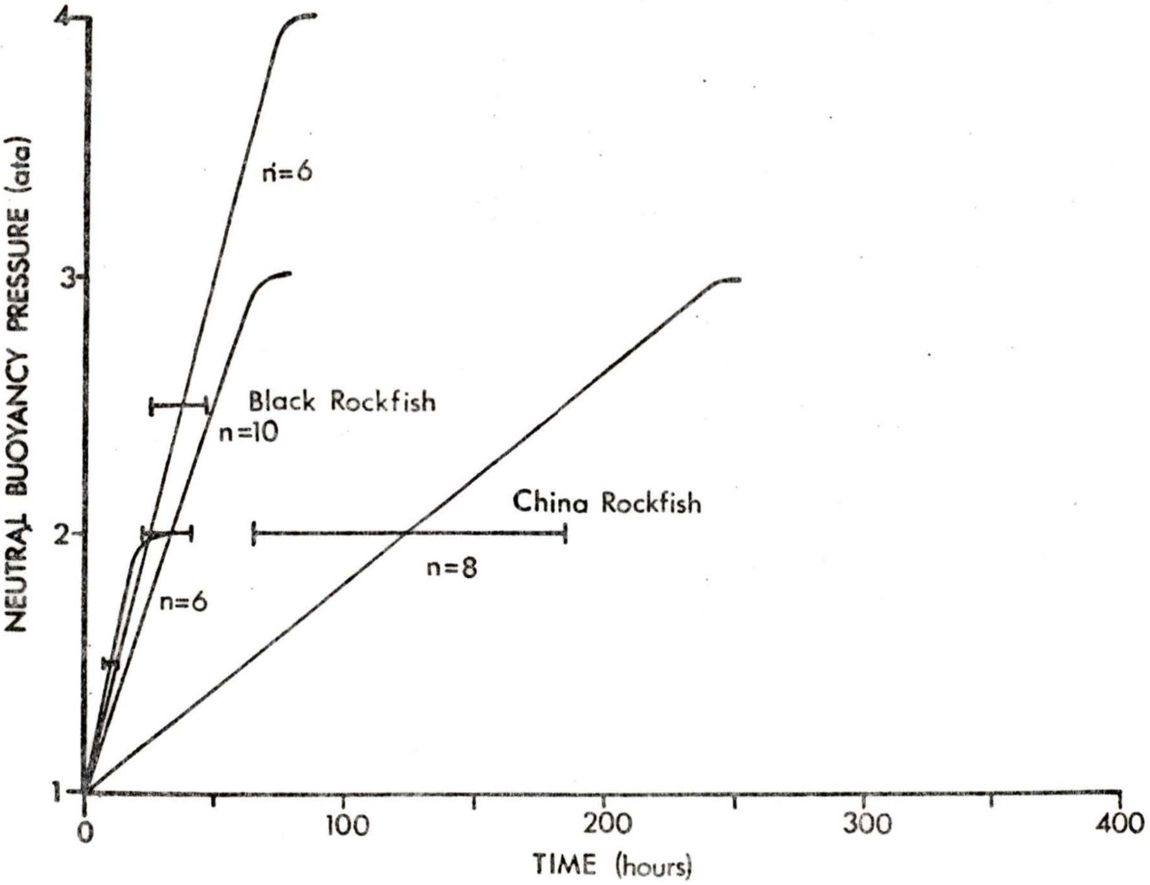

Figure 27: Summary diagram for buoyancy increase rate experiments. Shown are the range and mean 50 percent adjustment values for pressure increases of 1, 2, and 3 atm in black rockfish and 2 atm in china rockfish.

upwards to supplement compensatory pectoral fin beats. Under greater buoyancy states, the body inclination became increasingly vertical and pectoral fin beats also became more vigorous. Black rockfish usually broke from this position after a period of time and swam lengthwise through the tank with the pectoral fins projected laterally in a hydrofoil planing motion. This alternative method seemed to work well but was limited by the available swimming space. Upon reaching the tank end, the previous posture resumed while turning around to plane again. This swimming behaviour was not observed in China rockfish which were usually seen tail up, using the pectoral fins in a sculling motion. Usually within 30 minutes, both species stopped trying to compensate by swimming and and sought the support on irregular surfaces at the tank ends and on the upper surface of the tank.

Gas resorption began very soon after pressure was reduced. Black rockfish normally responded immediately by quickly restoring neutral buoyancy. China rockfish did not always respond to pressure reduction, often no adjustment was measureable after several hours of positive buoyancy. At other times, resorption began almost immediately and it appeared that this response was in some way related to swimming activity.

A general buoyancy response curve for black rockfish is shown in Figure 28. As pressure decreased, the process of gas resorption began. Response was initially fast but slowed as buoyancy approached neutral. In nearly all of the resorption experiments, the fish became negatively buoyant with respect to the the test pressure. However, neutral buoyancy returned presumably through gas secretion when left at the test pressure for a period of about 2 hours. Detailed data for stepwise decompression of 11 black and 10 china rockfish are shown in Table 12. Resorption times were measured over a variety of percent expansion values ranging

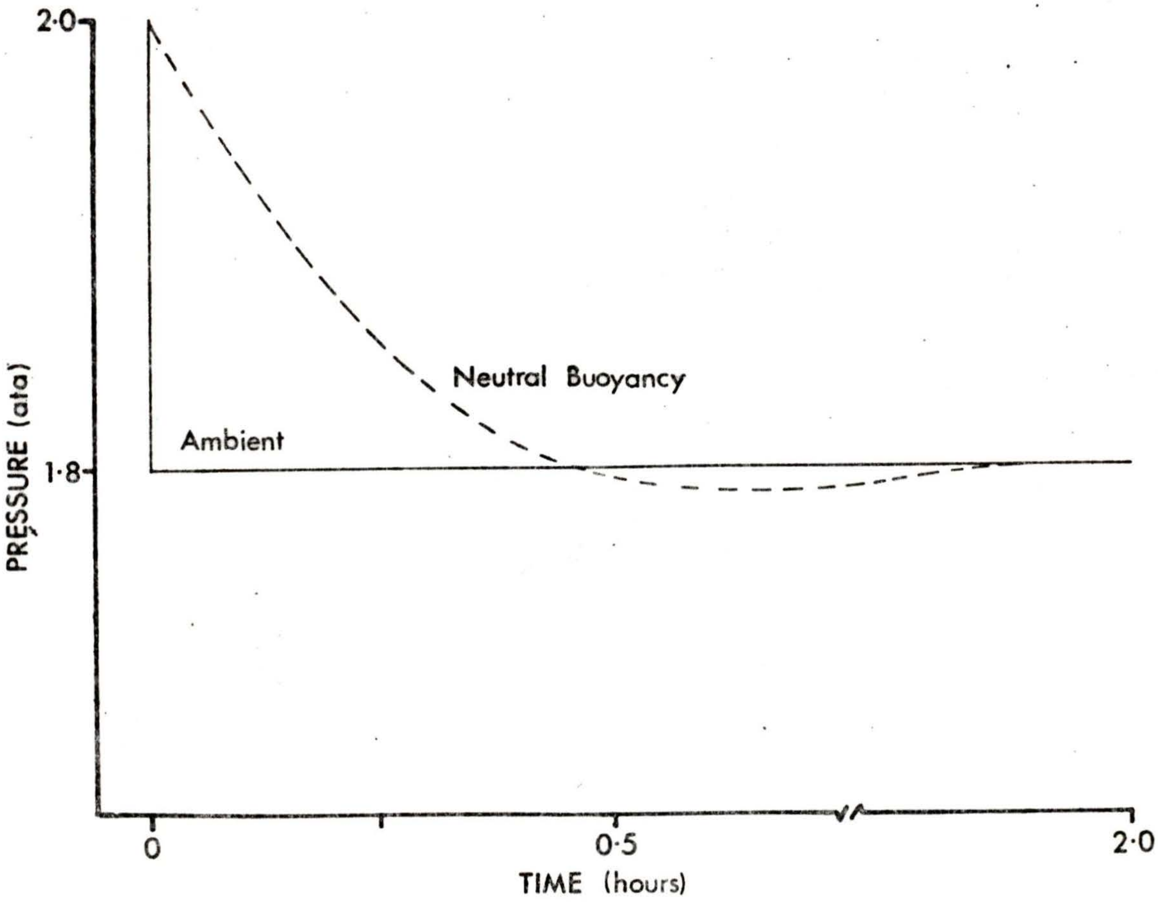

Figure 28: Generalized adjustment curve of black rockfish in response to a 10 percent decrease in pressure.

from 10 to 30 percent. In general, black rockfish decreased volume quickly, making a 10 percent reduction of buoyancy in less than 30 minutes and a 30 percent adjustment in about 1.7 hours. There was an extremely large range in values for similar adjustments in china rockfish which were probably due to long periods of time during which no adjustment occurred. During experiments where continual resorption appeared to have taken place, the rates for 10 and 30 percent reduction were 2.0 and 12.0 hours, respectively.

Table 12: Rates of buoyancy reduction.

Species	Fish No.	% Reduction	Time (Hours)	Fish No.	% Reduction	Time
Black Rockfish	1	11	0.5	4	10	1.0
		10	0.5	5	15	1.0
		10	0.5		15	1.0
		10	0.5		20	1.5
		10	0.5	6	14	0.5
		10	0.75		12	0.7
	2	10	0.75		32	2.2
		10	0.75	7	14	0.5
		10	0.5		8	0.7
		10	0.55		27	3.2
		10	0.5	8	30	2.6
		10	0.5		30	2.4
		10	0.45		20	1.9
		10	0.5	9	30	1.7
		10	0.75		30	5.7
	3	10	0.5	10	20	2.5
		10	0.55		30	2.6
		10	0.75		36	4.2
		10	0.5	11	8	1.0
		10	0.5		14	1.5
		10	0.5		20	1.0
		10	0.9		22	1.0
		10	1.2			
China Rockfish	1	10	8.0	4	10	30.0
		10	13.0		10	8.0
	2	10	19.0		10	2.0
		10	3.0		10	2.0
		10	2.0		10	3.0
		10	2.2		10	3.0
		10	2.7		10	6.5
		10	4.0		8	9.9
	3	10	1.0	5	10	1.5
		10	0.92		20	9.0
		10	18.5		30	80.0
		10	4.0		9	152.0
		7	0.92	6	30	21.5
		8	3.0		20	17.5
		10	6.5		30	12.5
		6	8.0	7	29	19.0
				8	36	19.0
				9	28	24.0
					28	15.5
				10	34	574.0

The stepwise drop procedure used in decompressing from a large pressure differential yielded a series of adjustment times. Analysis of variance was made on 3 samples from each species to test the null hypotheses that there was no difference between the range of values between the two species and that there were no temporal changes in resorption rates. The results (Table 13) show that the first hypothesis was rejected with a very low probability. While the range in values for china rockfish was high, even the fastest times were much slower than black rockfish. The second hypothesis was also rejected as the variability as the variability between samples was not significantly different from that within samples. Consequently, there is no evidence that the rate increased with 'practice' or decreased with fatigue.

Table 13

Analysis of variance summary table comparing the time sequence of rates measured from black rockfish numbers 1, 2, and 3 with china rockfish numbers 2, 3, and 4 (Table 11).

Source	SS	df	MS	F
Between subjects	401.52	5	80.34	
A	343.88	1	343.88	23.88**
Subjects within groups	57.63	4	14.40	
Within subjects	1077.74	39	22.45	
B	225.40	8	28.18	1.468 NS
AB	238.16	8	29.77	1.551 NS
B x subjects within groups	614.19	23	26.7	
TOTAL	1479.26	44		

Chapter IV

DISCUSSION

4.1 ECOLOGICAL ASPECTS

4.1.1 Species Distribution

4.1.1.1 Black Rockfish

Sebastes melanops (Girard) occupies a comparatively large range of the northeastern Pacific Ocean extending from Paradise Cove in southern California (34°02N 118°42W) north, turning west along the coastline to Amchitka Island in the western Aleutian Archipelago (51°30N 170°00E; Miller and Lea, 1972:96). The bathymetric range extends from the surface to 366 meters (200 fathoms; Hart 1973:427). In an offshore trawl survey, Alverson et al. (1964) found this fish commonly at deep stations (greater than 50 fathoms) off California northward to southeast Alaska. Despite the implication that the distribution centers in deep water (between 100-150 fathoms) a review by Leaman (1976a) points out contrary evidence indicating a shallow water coastal center of distribution, extending to the upper continental shelf. In the inshore waters of northern Washington (Puget Sound), there is an active sports fishery, over 24,000 black rockfish landed in 1978 (M. G. Pedersen, unpub. data, Washington Dept. of Fisheries). The absence of a similar fishery in

British Columbia is probably attributed to the comparatively higher economic and sport value of salmon not to a lower stock size.

Juvenile black rockfish, as with many other rockfish species such as, S. pinniger, S. miniatus, and S. flavidus, utilize the inshore marine habitat prior to an adult life offshore. Within Barkley Sound the size range of fish present is related to reef characteristics. Shallow, low profile reefs are generally inhabited by smaller fish while large fish occur on moderate and high relief reefs in exposed areas. Leaman (1976a), in part, showed this pattern with length data for fish caught while trolling from central toward seaward parts of Barkley Sound. Diving and angling observations made in the present study indicate that the pattern exists at different locations of varying characteristics. In areas such as the kelp beds along the Marine Station foreshore in Bamfield Inlet, schools are dominated by black rockfish 15 cm and smaller. Similarly, the black rockfish in the Macrocystis bed studied by Leaman at the Deer Group Islands were small, 25 cm and less. Typical reefs for subadult and adult fish are those of moderate to high relief having exposure either from currents or the ocean. As the intensity of these features increase, the size of fish present also increases. Accordingly, the fish at Ohiat which is of moderate exposure and high relief, were large; reaching lengths of 30 cm. Outer coast and occasional reefs within Barkley Sound typically have black rockfish in excess of 38 cm. Adult lengths of up to 60 cm are reached in deeper water (based on troller catch sample, M. G. Pedersen, unpub. data).

Since adults primarily inhabit the outer coast regions, the free swimming larvae also originate there. Their absence on many of the subadult and adult reefs may result from several causes. There are large differences in physical characteristics such as temperature and water motion. Warmer waters may facilitate the rapid growth phase that is characteristic of the early life stages in many of the large rockfish species including black rockfish (Chen,1971; Appendix B). The small size may be a disadvantage in more exposed areas limiting the efficiency in obtaining adequate food and space. Finally, the greater abundance of large fish probably pose a greater predation potential compared to the shallow inshore areas.

4.1.1.2 China Rockfish

Sebastes nebulosus (Ayres) is similarly a broad ranging coastal fish. Love (1974) extended the southern limit (previously recorded by Phillips, 1957) to San Miguel Island in southern California (34°03N 120°21W). Likewise, Alverson et al. (1964) extended the northern limit from southeast Alaska (Phillips, 1957) to the Gulf of Alaska (no coordinates given). The bathymetric range as reported by Hart

(1973:433) extends from the surface to 126 m (69 fathoms), but more commonly 92 m (50 fathoms). Miller and Gotshall (1965:114) report the range from 3.3 m (10 feet) to 36 m (120 feet). In this study china rockfish usually occurred at depths greater than 10 meters and uncommonly at depths shallower than 8 m. This difference may be due to the greater wave activity characteristic of the British Columbia coast. The geographic pattern of species abundance generally parallels that of the black rockfish except for the northern range. The general abundance in northern California described from a sportfishing perspective by Miller and Gotshall (1965:114) is fitting for British Columbia:. . . (china rockfish) . . 'are nowhere abundant, always an incidental part of the catch but still not uncommon'.

A unique aspect of china rockfish distribution is their restriction to moderate and extreme exposed coast habitats. Along Vancouver Island they occur along the west and north coastline and as far south on the eastern side as Port Hardy (Dr. A. Peden, pers. comm.). It has not been recorded from Georgia Strait and the Gulf Islands, but there have been siteings from San Juan Island on the United States side of the Gulf Island system (Delacy et al., 1972; Moulton, 1977) and at Race Rocks in Jaun de Fuca Strait (V. Fletcher, pers. comm.).

The exposed coast distribution was also observed on a smaller scale within Barkley Sound itself. China rockfish are found along exposed reefs facing Imperial Eagle Channel and on the seaward reaches within Trevor Channel. Reefs which appear to receive lower exposure from waves and current as evidenced by the less diverse encrusting fauna and a fine film of silt are usually not inhabited by china rockfish. This pattern was further apparent in observations during an extensive dive survey made within Clayoquot Sound, 40 km north of Barkley Sound (McElderry and Fletcher, unpublished data).

4.1.2 Reef Association

Tropical coral reefs as well as rock and kelp reefs contain a variety of fish having differing habitat associations. This has been shown best in studies which deal with the fish assemblage as a community (Hobson, 1968, 1974; Hiatt and Strasburg, 1960; Smith and Tyler, 1973) as opposed to single species studies which are far too numerous to mention. Many of these studies identify species distributions limited to a portion of the reef space over time. This may exist as a home range in which a fish simply limits its movements within a undefended area over time (Reese, 1973; Sale, 1971; Gerking, 1959). Alternatively, many territorial species defend a reef space both interspecifically (Myreberg and Thresher 1974, Low 1971) and more generally, intraspecifically (Keenleyside, 1972; Clarke, 1970). Following the terminology of Gooding and Magnuson (1967), other behavioral categories which apply to reef fishes are visitors and transients. Visitors are species that remain on the reef for a few hours or a few days and then move on. Examples of this at Ohiat are lingcod, *Ophiodon elongatus*, tube snout, *Aulorhynchus flavidus*, and some embiotocids, notably *Embiotoca lateralis*. Transients move through a reef without seeming to be affected by it or responding to it in any obvious way. This category applies to fish such as pacific herring, *Clupea harengus*, salmon, *Onchorhynchus* sp. and dogfish, *Squalus acanthias*.

4.1.2.1 China Rockfish

The type of reef association shown by china rockfish is clearly residential and probably territorial. Each tagged fish occupied a unique space, the home crevice, that was separate from home crevices of conspecifics. The locations were well established as residence in most cases lasted the duration of the study. As with other territorial reef fish (Sale, 1975), china rockfish positioned themselves so as to view their surroundings and accordingly respond to intruders or food. This was the most common position held although very few agonistic interactions were observed. The territory defended may not be fixed geographically since these fish moved to secondary points of distribution, termed secondary home sites. While the behavior at the new location was consistent with that at the home site, these areas were cooperatively occupied by other fish at other times. Often the secondary homesites were separated such that while fish were present, defense of the primary home site was impossible. Perhaps the low expression of territoriality observed was the result of low species density and the abundance of apparently suitable but unoccupied crevices.

With china rockfish, the crevice probably serves as a means of protection in addition to a source of food. The crevice provides a protected vantage point with which to view the surrounding reef. Potential predators which are probably pinnipeds, lingcod (Miller and Giebel, 1973:72) and to a lesser extent dogfish (Bonham, 1954) are unable to approach within the confined walls of most crevices. Small lithoid and _Cancer_ crabs, both major diet items (appendix C), also seek protection of rock crevices during inactivity. China rockfish are ambush feeders, sitting motionless and seizing small prey as they come into view. Most of this activity is probably initiated from the crevice.

4.1.2.2 Black Rockfish

Residence on the study site. The black rockfish population had a less defined relationship with the study reef. After a few weeks, much of the first tag group was no longer present. Reduced recognition from tag fouling in part explains this, although this number was usually less than those fish with recognizable tags. Including unrecognizable tags, the number of tagged fish after the first and second month was, at best, 10 and 20 percent for group 1 and 2 (Figure 13), respectively, indicating that the majority of fish had dispersed. The pattern shown by tagged fish is similar to that of Bermuda Serranids observed by Bardach (1958): 'Most of the tagged Serranids stayed on the reef for about a month. After two months considerable exchange of fish between the reefs seems to have taken place and after a year a virtually new group appears to be present.' Miller and Giebel (1973:28) studied residence and movement patterns in the blue rockfish, _Sebastes mystinus_, on a kelp-reef in Monterey Bay, California. Several thousand fish were tagged and released at one of the three stations from which they were caught. While the stations were separated by 350 meters, these three groups remained essentially distinct for over two years. In another study, Carlson and Haight (1972) demonstrated that adult yellowtail fockfish, _Sebastes flavidus_, have a homing ability and were capable of returning over distances of 21 kilometers. In very limited homing experiments with juvenile black rockfish, only two out of thirty individuals returned (Leaman, 1976a) which is not statistically different from random movement. My experience with the three aformentioned species is that they show strikingly similar behavior, at least during their preadult life stages. The apparent differences presented between black and both yellowtail and blue rockfish are probably not real.

The size of the home range may not be rigid but rather, a reflection of terrain characteristics. Reefs can be viewed as having a variety of structures, some of which promote association, some not. In a reef system with patchy regions suitable for association separated by broad regions of unsuitable nature, fish may be expected to show restricted movement. Alternatively, over homogeneously desirable terrain the potential for straying may be stronger. Such varying conditions might mistakenly lead to widely divergent species characterizations as to visitor or home ranging status. Such a situation is possible at Ohiat and may have accounted for the exchange of fish to and from the study reef. While normally resident, the uniformity of apparently suitable substrate along the shoreline could promote straying. Some evidence for this stems from observations of two tagged fish among schools around the opposite side of Ohiat from the site. While off-site observations were limited, I believe that many tagged fish were present spread sparsley among the other reefs on the Islet.

Gerking (1959) cautioned that the size of a study area bears a strong relationship to the conclusions that may be drawn about fish associations studied. Too small a study area may result in an apparently large straying estimate. Within tropical reef systems, surrounding sand areas are important feeding grounds for many nocturnal feeders (Hobson, 1968; Bardach, 1958). Focusing a study on the reef alone overlooks a very important trophic resource as well as mobility habits of the fish using it. At Ohiat, the great fluctuation in numbers of tagged fish seen over short time periods (Figure 13) could be an indication of off-reef movement. Black rockfish may move out of the reef away from shore at night although an alternative conclusion that the variability in numbers is attributed to changing observer efficiency is equally valid. Short of using nets or continuous monitoring methods (eg, radio tags) the extent of movement into these areas can not be determined. Over a longer time period the observed movement did not support the idea that the study reef is part of a larger home range. Even though black rockfish limit their movements while on the site, there was a continual decline in tagged fish present over time. Once fish left the site, they seldom returned.

Terrain selection. In many schooling reef fish, including black rockfish, high profile areas serve as points of aggregation (Quast, 1968a). Prominent reef features such as rock outcroppings, steep rock faces, and other strongly vertical features seem to attract schooling fish. These principles also apply to artificial reef such as offshore drilling platforms, shipwrecks and other introduced solid structures (Carlisle et al., 1964). Fishermen also realize this and concentrate their fishing efforts near such regions. There seem to be two reasons for which fish associate with strongly vertical areas. Quast (1968a) points out that these areas serve as landmarks whereby a fish can maintain both a fixed spatial orientation and their schooling habit. A second possible reason is the protection from predators (Hobson, 1968). Fish close to the vertical faces may blend into the general features and escape notice or they may discourage predators because of limited maneuvering space. As predator size increases, the area required to effectively home in on prey also expands making it difficult to operate around confining reef spaces.

In a similar fashion, kelp beds provide a vertical extension of the reef surface. The kelp bed is not an essential requirement for many associated fish but provides a pronounced vertical dimension to which they are attracted. Two large scale studies conducted on the larger, deeper growing California species, Macrocystis pyrifera, and associated fish were undertaken because of the conflicting interests between fishermen and kelp harvesters (North and Hubbs, 1968; Limbaugh, 1955). These studies indicated that few fish depend upon kelp as a direct food resource but often non-essential intermediate food links occur such as the isopod, Idothea. Both studies (summarized in Quast, 1968b) concluded that kelp harvesting as practiced was compatible with fishing interests and kelp cutting had no measurable effect on the fish populations. Leaman (1976a) examined the interaction of juvenile black rockfish with the smaller, British Columbia kelp, *Macrocystis integrifolia*. His findings showed no apparent food relationship and that fish use the kelp for shelter. Moulton (1977) made similar observations of food habits among subadult black rockfish. The hypothesis that *Macrocystis* beds serve as a shelter received support from observations of this species in relation to an artificial kelp stand (Leaman 1976a). Groups of fish were observed within the framework of plastic strips supported by wire. Upon changing the density of 'kelp blades', the number of fish present changed accordingly.

The distribution of black rockfish at Ohiat was primarily centered in areas of high vertical relief. Throughout the summer, the distribution was limited to two general regions although there were many other apparently suitable areas across the site. Most important was a small region on the eastern end of the kelp bed probably selected because the clearing provided an open space for the school to congregate while also enclosing it with a curtain of kelp. The faunal richness that occurs in relation to the kelp bed edge as well as within open spaces has been documented elsewhere (Leaman 1976b; Feder et al., 1974; Limbaugh, 1955). Ebeling and Bray (1976) observed that many fish seemed to be attracted to the sunlit open spots and avoided the shaded areas on the reef. Their interpretation was that this behavior was feeding related since food was more readily seen in bright light. A second area of major distribution was the deep water boulder area. Much like the kelp bed, groups of fish congregated around the upper and seaward sides of the boulder. There were also many fish within a large crevice as well as sitting on the rock surface in the surrounding area.

The function of various parts of the reef that black rockfish associated with remains unclear. The kelp bed appeared to serve a dual purpose, concealing occupants from predators and providing access to the productive shallow water where prey are most abundant. The function of the deep water region was not obvious though many of the fish sitting and those within crevices appeared to be in an inactive state. The fish in deep positioned schools however, appeared similar to those in shallow schools except for the smaller numbers of fish. The two areas were physically different in many respects including light, temperature, and water clarity and the boulder area may have been more suitable for non-feeding groups of fish.

4.1.3 Reef Seasonality

An important feature of kelp bed and rock reefs in Barkley Sound is that they are distinctly seasonal. A reef may completely change its apparent shape with the onset of winter and many fish will leave. A most striking change was the decline of the kelp canopy occurring late in summer. Concurrent with this, was a pronounced increase in water motion as large ocean swells pounded the outer coast and penetrated farther into the Sound. The reduced day length, low sun angle, and cooler temperatures reduced phytoplankton production generally increasing visibility.

During the winter, many reefs of this latitude experience a decline or complete loss of summer fish populations (Leaman, 1976a; Moulton, 1977) while in the more moderate conditions of southern California, little seasonal change is apparent (Ebeling and Bray, 1976). Based on personal observations, seasonality varied at different reefs. A relatioship was apparent between the physical change and fish loss, especially black rockfish. Low profile reefs, which derive considerable vertical structure from macrophytes, experienced the greatest loss of fish. Alternatively, high profile rock reefs supported large winter populations because much of the basic reef structure was permanent. Despite this relationship all reefs seemed to have fewer fish during the winter. Whether this decline was due to fish leaving or reducing their activity and moving among the rocks is not known. Moulton (1977) felt that many rockfish species move to deeper parts of the reef and others like the longfin sculpin, Jordania zonope, modify their behavior and move within crevices. The current state of knowledge on the winter habits of many reef fish needs improvement.

The Ohiat site experienced moderate seasonal changes. Subjective estimates of the winter fish population indicated that it was at least half that of summer (based on 30 winter dives). Shallow reef sections which became devoid of *Nereocystis*, lost their large summer black rockfish populations. Instead, most black rockfish were found in deep water along the rock slope on the eastern side. Occasionally, with high visibility, schools of black rockfish were seen in shallow water directly above the rock slope, well away from shore. China rockfish underwent a similar apparent decline in population. Many of the homesites seemed vacant although others were occupied by the same residents. Why this occurred is unknown since many of the habitat features were unaffected by season.

4.1.4 Movement Habits

Movement about the reef can be viewed as an interplay between intrinsic requirements of a fish balanced by extrinsic environmental characteristics. Fish probably limit their activities to those necessary, such as feeding, predator avoidance and rest. The potential of an area to fulfill these needs may regulate range size accordingly. Area suitability depends on both spatial aspects such as reef terrain and temporally changing elements like daylight, current and water clarity. These extrinsic factors function to modify behavior. For example, feeding drive may be diminished or enhanced by habitat characteristics such as reduced visibility. Different reefs undoubtedly have slightly different characteristics, consequently it is unlikely that movement patterns remain consistent from reef to reef. In defining movement patterns for the study species it is important to place structural features of Ohiat into perspective with other reef systems and define the functional response of the fish to variation in spatial and temporal environmental factors.

4.1.4.1 Spatial Features

At Ohiat, the china rockfish population was probably not greater than twenty. Many were broadly separated in distance even though there were many apparently suitable uninhabited crevices. On other more exposed reefs, typified by very rough surfaces with many crevices, china rockfish are much more numerous and are often found in crevices that are within a meter of each other. The varying density of fish on reefs results in a broad spectrum potential range size. At Ohiat, movements were as large as 13.2 meters but usually less (Table 5). The range of movement is probably lower on reefs of high fish density and expanded on sparsely populated reefs. Range limits are probably a function of prey density and level of aggression.

Black rockfish probably have a similarly fluctuating range size pattern which is primarily a function of reef topography. Fish on reefs with large vertical relief probably exhibit reduced horizontal movement. On reefs with low vertical relief, fish will travel greater distances to reach a depth over the expanded horizontal dimension. At some point the horizontal distance becomes too great and fish will not inhabit the reef.

4.1.4.2 Temporal Features

Diel behavior. In tropical fish communities striking differences appear between day and night (Domm and Domm, 1973; Hobson, 1972,1965). Light is apparently a timing cue used by fish in permitting species complexes to use the same resources with reduced competition. The complement of diurnal species is usually quite different from their nocturnal counterparts. The transition is most pronounced in the water column and reef surface as fish move from an active, suprabenthic phase to an inactive, sedentary phase. Pisciverous fish are known to take advantage of this succession, feeding most actively during twilight periods of dawn and dusk (crepuscular habits). The two groups remain temporally separate in their activities although diurnal species may emerge on bright moonlit nights (Hobson, 1968). Day and night differences also occur in the patterns of space use. As mentioned previously, featureless sand flats that surround many reefs are very active at night but devoid of fish diurnally.

Such a pattern results from a high diversity community utilizing a limited environment. While food and space are limiting, food is in greater supply (Smith and Tyler, 1972) posing a geometric problem of species packing. Hobson (1968) has emphasized the importance of predation as a selective pressure in moulding the different patterns of distribution of many fish. Thus diurnally, formation of schools and concentration around relief is a compromise between predator avoidance and feeding. With darkness the lower predation pressure allows free use of the reef without limiting movement to areas of strong profile. These patterns may be genetically ingrained as Hobson (1972) has suggested in explaining the persistence of such behavior in tropical fish families which live in areas such as Hawaii where large piscivorous fish are few.

Temperate and boreal(1) kelp bed and rock reefs do not have clear patterns of light related activity. Nighttime is usually a period when most fish are generally lethargic (Ebeling and Bray, 1976; Moulton, 1977). Many fish show little or no change in distribution with exceptions such as the kelp greenling, *Hexagrammos decagrammus* (Moulton, 1977; this study), and tropical derivatives (e.g., Pomacentrids; Ebeling and Bray, 1976). Black rockfish in the present study showed no diel difference in overall distribution although a general dispersion of fish from the kelp bed occurred at night. China rockfish also have a nondistinct diel

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(1)Geographic divisions as given by Quast (1968a).

pattern. Their distribution remains constant irrespective of daylight and similarly their behavior was unchanging.

Kelp bed fish communities have a high degree of intraspecific variability in behavior and movement. Ebeling and Bray (1976) noted that often in schooling species (Embiotocids) individuals break away and assume solitary foraging behavior, rejoining later. They concluded that behavior patterns in temperate fish communities are 'loosely programmed' as compared with tropical systems. Black rockfish had a similar variability as the population was mixed between the kelp bed, the deep water boulder region and the adjacent reef with no apparent short term temporal pattern. The aberrent nocturnal behavior of Orange-20 emphasizes the lack of intraspecific congruity.

The expression of diel behavior seems to vary between reefs. Leaman (1976a) demonstrated a movement of juvenile black rockfish into the kelp at night while they generally were more abundant outside diurnally. Further, visual observations indicated that the fish descended to the reef surface at night. Fish at Ohiat remained in the water column showing a weak expression of movement outward from the kelp bed to the surrounding shallow areas. Moulton (1977) observed that juvenile yellowtail rockfish, _S. flavidus_, behaved differently at the reefs used for his study. On two separate reefs, fish were hidden during the day emerging and becoming active after dark. On other reefs, they were apparently diurnally active.

Bray and Ebeling (1976) proposed that the relative absence of predators in California kelp beds does not create strong selective pressure for a nocturnally active assemblage of fish. Moulton (1977) agreed, adding that predation vulnerability modifies behavior differently at different reefs. Inactive fish which are unable to derive protection by schooling may seek shelter on the reef bottom. Consequently, there exists a behavioral difference between tropical fish communities and those of temperate and boreal reef systems. While tropical fish have more highly specialized behavior patterns, their northern counterparts have a lower degree of niche specialization and a limited capacity to modify this in relation to their surroundings.

A different approach may be used to determine the activity schedule of benthic fish. Many species, including china rockfish, which feed on benthic cryptofauna time their activity in relation to that of their prey (Hobson,1968; Vivean and Peyrot-Clausade, 1974). While many crustaceans are active at night, china rockfish may follow suit. To this end, studies of stomach fullness at different periods of the day would be useful.

Water clarity. Water clarity seemed important to all reef fish, particularly suprabenthic and water column fish which were much less abundant during low visibility, even when reduced observer efficiency is considered. Quillback rockfish, *S. maliger*, and diurnal crevice inhabiting juvenile yellowtail rockfish, S. flavidus, move from the reef surface to the nearby water column when visibility is high. China rockfish did not move, although changes in the water clarity do change the reactive distances to prey. Black rockfish did change their distribution in relation to clarity. The water space used by these fish is comparable to similar California species which maintain their schools within visible limits of the reef (Quast, 1968c). This was most apparent from the large movements away from the reef surface made in the winter but not in the more turbid summer period. While admittedly, the open areas of the reef can not be visually censused easily in low visibility, the varying distance of fish from the reef surface indicates that they respond to changes in clarity.

In most cases varying water clarity had little effect on mobility during the summer. Movements of fish were generally from shallow to deep across the reef surface. While visibility may influence the distance maintained from reef objects, movement still persists between different reef areas. Presumably at some very low visibility, movement about the reef may be restricted by the lack of visual reference. However conditions such as these are probably uncommon.

Water current. Periods of strong current may also influence fish movement. Wind-driven currents at Ohiat build with the afternoon Westerlies in the summer and, more pronounced, the North winds in the fall. Both wind patterns are diel in nature, Westerlies in the afternoon and Northerlies at night. While their influence depends on reef orientation, wind produced currents are primarily a surface phenomenon, dissipating with depth. Black rockfish showed a strong positive response as is indicated by their distribution pattern (Delacy et al., 1972; McElderry and Fletcher, unpublished data) as well as in laboratory experiments (Leaman, 1976a). This species may move into shallow water in response to wind developed currents, however, this behavior was not studied.

4.2 VERTICAL MOBILITY AND BUOYANCY

4.2.1 Pressure and Bladder Expansion

Borelli (1680) and Delaroche (1809) were probably the first to suggest that the gas bladder could act independently of ambient pressure (see Reyer, 1977). Borelli suggested that changes in muscular tension would alter gas bladder volume thus producing vertical movement. Alternatively, Delaroche believed that changes caqused by vertical movement could be corrected by the application of muscular compression once at the new depth. In both cases the swimbladder was considered to maintain a bladder pressure different from ambient pressure as a result of either intrinsic or extrinsic muscular actions regulating bladder volume. A unique study by Peters (1951) lends support to Borelli's view; the seahorse, Hippocampus brevirostris, immobilized with an anesthetic (MS-222), demonstrated the ability to move vertically in an aquarium without any apparent fin motion. As MS-222 acts on skeletal muscle tissue, the movements were claimed to be caused by intrinsic smooth muscles constricting the bladder wall. A variety of other studies have shown that the capacity to correct buoyancy changes as hypothesized by Delaroche is present in many fish but to a limited degree. The potential for muscular compression as an accessory to vertical mobility deserves review.

Upon pressure reduction, some fish show an ability to limit the resulting buoyancy increase. Magnuson (1973) observed that the swimbladder walls of some large scombroid and xiphoid fishes were thickened. He speculated that this morphology was adaptive in limiting expansion, thus providing a consistent buoyancy over a variety of pressures in which these active pelagic fish are known to move. Such thickening is absent in many inshore fishes including rockfish and therefore is probably not a wide spread means of buoyancy control.

McCutcheon (1958) described a yawn reflex that, by extrinsic compression, reduces buoyancy. The yawn, which involves gaping of the mouth and flexing of the fins is stimulated by positive buoyancy. This reflex can restore neutral buoyancy against pressures of 0.1 to 10 cm water (0.0001 to 0.01 atm) for 5 to 10 minutes. Vigorous thrusts have been observed to momentarily produce internal pressures of 30 cm water (0.03 atm) above ambient (McCutcheon, 1962). Yawning has been observed in 13 species and it is probably prevalent elsewhere (McCutcheon, 1966). In fact, this was observed during this study both in the field and particularly during buoyancy experiments. However, buoyancy reduction as a result of yawning could not be detected within the pressure tank sensitivity (0.03 atm) and therefore must be comparable in magnitude to values of McCutcheon (1958). From a theoretical point of view, extrinsic compression controlling bladder volume has limited value because, to be of use, pressure must be applied equally over the swimbladder surface. Such a capability is doubtful in view of the general morphology of most fish. Containment of an expanded gas bladder within the body walls places pressure on visceral organs and the vascular system. In view of the low blood pressures characteristic of fish (Mott, 1957), pressure applied by sandwiching vascular tissue between the rigid body musculature and expanding bladder would undoubtedly impair blood flow. Other evidence comes from bladder expansion with reduced pressure. Jones (1951) and Reyer (1977) found the body wall has little effect in reducing expansion. Comparisons between live and ventrally dissected preparations in this study also indicate that the body wall provides little support. Therefore, the process of swimbladder compression by extrinsic muscles may be widespread as McCutcheon claims but undoubtedly functions as a limited fine tuning mechanism.

Under increased pressure the problems posed by decreased buoyancy are slight, although the energy saved through neutral buoyancy as compared to that lost through swimming is considerable (Alexander, 1970). Sundnes and Gytre (1972) showed that during increased pressure a resistance to bladder compression could be developed and even increased by *Gadus morhua*. Internal bladder pressure as much as 0.08 atm below ambient were established when the fishes body became rigid. The difference was lost, however, upon yawning. Excess internal bladder pressure is a constant feature in the swimbladders of cypriniforms (Alexander, 1959a; Gee, 1977). This has the potential to broaden the neutral buoyancy range before ambient pressure exceeds internal pressure, causing compression. Alexander (1959b) examined this in 32 species outside the order of cypriniforms and found no excess internal pressure. He concluded that internal pressure is probably essential for the function of Weberian ossicles. Other investigations finding internal pressure in the swimbladder of stream-fish (Gee, 1977; Gee et al. 1974) suggest that this may be a means for expanding the range of neutral buoyancy in shallow water.

While the ideas of Delaroche and Borelli are supported to a limited extent, vertical movement for most fish coincides with a change in buoyancy. A variety of work shows that the swimbladder behaves very much as predicted by Boyle's gas law. Jones (1951) found that the swimbladder of *Perca fla-*

vescens expanded to 80 percent of that predicted at pressures 60 percent below ambient. The discrepancy he attributed to limited elasticity of tissues. Similar experiments on four marine and one fresh water species showed that the bladder expanded to within 89 percent of that predicted for a 31 percent reduction in pressure (Alexander 1959b). Reyer (1977) found a similar pattern in cichlids but not in salmonid or cyprinid species. China and black rockfish probably also provide little resistance to changing pressure. This was evidenced by changes in bladder volume upon pressure reduction in ventrally dissected specimens. Similarly, live animals also experienced a change in bladder volume with pressure changes as was evidenced by their changed swimming attitude.

An alternative strategy employed by many fish is to maintain negative buoyancy through reduced bladder size. While not alleviating excess density, this may adaptive in expanding the vertical range. Laboratory and field observations indicate that this is not so for either china and black rockfish. Both species filled their swimbladders to a level close to neutral buoyancy in a constant pressure situation, such as in experimental pressure tanks. In the field, direct observations of this were difficult to obtain. China rockfish usually stay on the reef surface revealing little hydrostatic information. When they swam, a negetive buoyancy was not apparent. An indirect approach using anesthetics and observing the behavior of narcotized fish was tried.

China rockfish immobilized in such a manner tend to remain on the bottom and sink very slowly when manually placed above the reef surface. Black rockfish occupy a wide depth range and it was difficult to visually assess buoyancy condition. After several attempts, obscuring events such as water current, the absence of a suitable background frame of reference, and fish becoming disturbed and swimming away, no conclusions were drawn except that fish appeared to be close to neutral buoyancy. Upon bringing these fish to the surface as was the case when they were tagged, all fish were positively bouyant and experienced difficulty in maintaining position when confined in the buckets.

4.2.2 Restrictions to Vertical Movement

Changes in buoyancy through vertical movement are accommodated by compensatory swimming and gas transport. Jones (1952) made this observation in separating restrictions imposed on fish during rapid and slow vertical movement. Rapid movement, such as during feeding forays and territorial defense, cause changes in buoyancy that can not be corrected physiologically. Ascending movement is a more serious problem than descending since the expanding gas can reduce density to many times lighter than that of water. While descending, increased pressure diminishes bladder volume to a size where most of its effect is lost. Rapid ascent is limited to a distance determined by the compensatory swimming ability and degree of expansion without damage to which the swimbladder is capable. Slow vertical movement results in minimum energy expenditures on vertical positioning and is compensated by physiological gas transport, which is limited primarily by time.

4.2.2.1 Rapid Vertical Movement

Jones (1952) attempted to classify the range of rapid movement that a fish might make by observing the behavior at different levels of positive buoyancy. Fish were 'quite at home' and could easily compensate when pressure was reduced within one-sixth their neutral buoyancy pressure. At pressure reductions of one-quarter and greater fish became thoroughly alarmed, initiating escape movements which would normally take the fish to deeper water. At pressure reductions greater than one-third, a fish could not compensate and floated helplessly upward. This experiment was conducted with *Perca flavescens* in fresh water. Marine fish have a smaller swimbladder, 5 as opposed to 8 percent of body volume (Aleev, 1969), associated with differences in salt and fresh water density. Correcting for this, values are one-fifth for the comfort range and one-half for loss of compensatory ability. In five marine species similarly measured pressure reductions of 32 percent covered at least the range of comfortable swimming (Alexander, 1959b).

Such a classification can not be applied to either rockfish species. During gas resorption rate experiments where the behavior during positive buoyancy was observed, both species were able to compensate at 30 percent pressure reductions but neither persisted for long. Black rockfish swam lengthwise in the tank using the pectoral fins as planes. In the pressure tank environment this species appeared alarmed upon a 30 percent reduction but judging by their capacity to compensate within the 1.3 meter swimming area, their 'comfort range' was probably much greater. Alternatively, china rockfish employed a head down sculling motion rather than compensating by horizontal swimming. After trying to swim against the floating tendency, china rockfish locked themselves in at the tank ends or allowed themselves to float against the the upper tank surface, resuming an apparent state of comfort.

Compensatory swimming ability in both species was not lost at 50 percent pressure reduction but persisted in excess of the pressure required to burst the swimbladder. This was observed on numerous occasions while angling for specimens. Fish caught at depths which, from experience, the swimbladder was known to have ruptured showed an ability to return to the bottom despite their distended appearance. These fish initially have difficulty because their overbuoyant condition makes them float on the surface. However, when held just below the surface they were able to descend.

Contrary to the 90 percent mortality in perch (Jones, 1951) rockfish may survive bladder rupture (Gotshall, 1964) but personal observations of laboratory held fish indicated that their swimbladders healed very slowly, if at all. This indicates that the range of rapid movement is not limited by the loss of swimming ability per se, but rather by that which causes damage from over-expansion.

The theoretical upper limit of rapid movement is a point just prior to swimbladder rupture. Measurements of burst pressure from the literature as well as those from this study are shown in Figure 29. Using these values, the maximum vertical ascent distance from a position of neutral buoyancy can be calculated for different depths of occurrence. The vertical distances between the bottom line and the upper line show the maximum vertical range for the different species. Surprisingly, the various values for the different species are quite similar, showing that a more resistant bladder does not increase vertical range at these depths. Therefore, it is hard to imagine for these fish that a stronger bladder wall affords greater vertical movement.

In trying to establish the ranges of rapid vertical movement for the study species, it is helpful to consider the vertical distance above the depth of neutral buoyancy as a gradient of decreasing probability. Based on field and laboratory observations of behavior it appears that both spe-

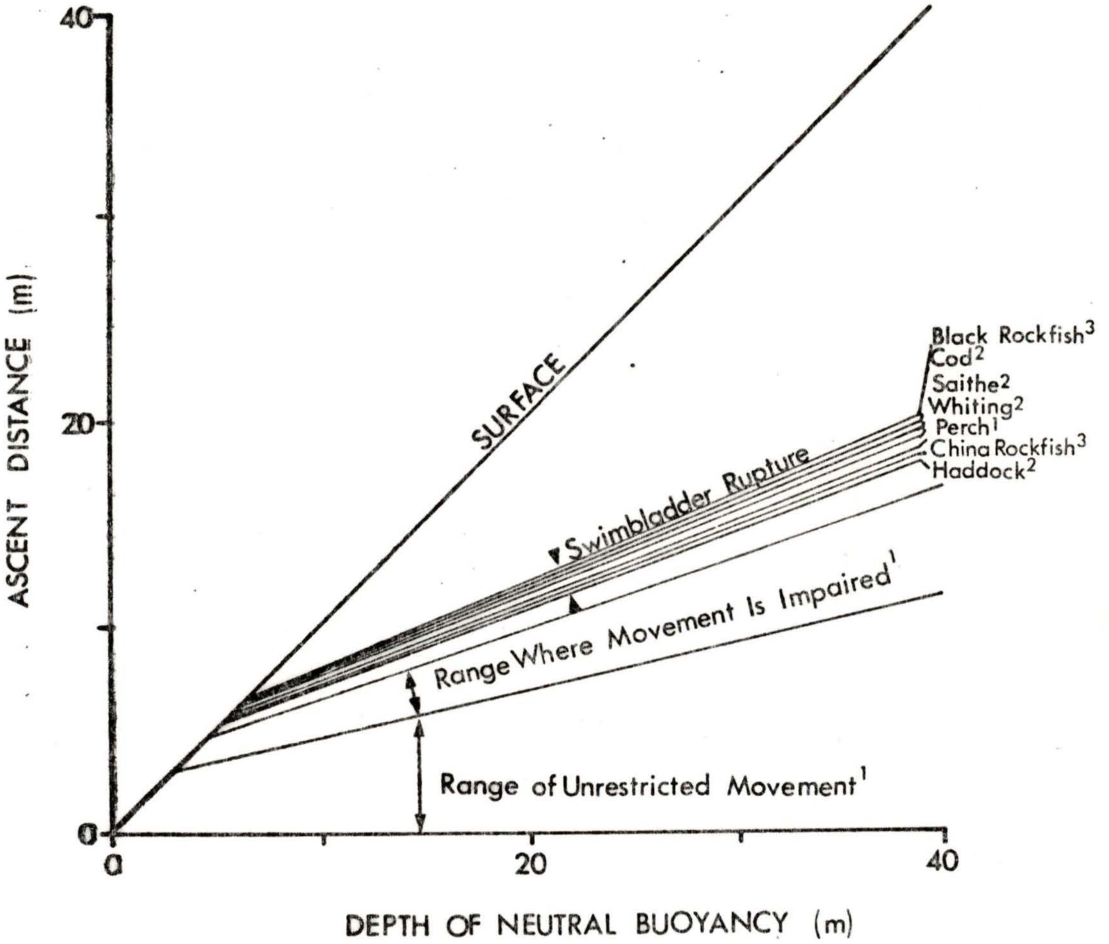

Figure 29: The consequences of vertical ascent from a depth of neutral buoyancy. 1-Jones (1952), 2-Tytler and Blaxter (1973), 3-This study.

cies use a sizable portion of their respective ascent ranges. States of slightly positive buoyancy are probably very frequent events as the fish move about the reef. Vertical movements resulting in states of high positive buoyancy are quite rare and are probably associated with unusual feeding or predator avoidance excursions. Rapid ascent for feeding purposes may not be common since most of the time visibility was reduced such that a deep fish could not see prey in shallow water. On one occasion on a steep-faced reef, I observed quillback rockfish, *S. maliger*, rapidly ascend from the reef surface to feed on an overhead school of herring, *Clupea harengus*. The ascent carried them to a level of pronounced positive buoyancy but swimming was very rapid and movement was not impaired. In most instances on a reef the motivation for deep neutrally buoyant fish to rapidly ascend does not exist.

4.2.2.2 Slow Vertical Movement

In moving vertically through the water column fish initially rely on swimming motions to remain oriented while physiological compensation catches up. The important aspect as far as a fish is concerned is the energetic choice between compensatory actions and gas transport functions. Comparative theoretical treatments indicate that the energy required to maintain vertical position without a swimbladder is greater than that needed to secrete gas based on both physiological energy cost (Kuhn et al., 1963) simple estimates of gas compression (Alexander 1975:147). In a situation of partial buoyancy, a portion of the fish's weight is compensated for by the swimbladder and the remainder comes from elsewhere. Evolutionarily, rockfish must adaptively 'decide' whether or not the energy cost of a complex buoyancy control organ system is worth the energy saved in reduced gas transport time. An insight comes from an analysis of morphology in relation to buoyancy adjustment capacity.

The buoyancy system in the study species was investigated morphologically to compare the degree of organ system development. There are three areas of buoyancy control: the secretory center, the resorptive center, and blood dynamics. Of these, the secretory center was chosen for study since it is a distinct organ and can be reliably measured. The resorption center received little attention because methodology to handle this delicate organ did not exist. Very basic blood measurements were also made. Clearly, the rockfish swimbladder morphology needs detailed investigation using more sophisticated techniques. However, information obtained showed the separate lines of development in the two species which correlate well with dynamic aspects of buoyancy adjustment.

Secretory surface area increases in relation to mass in species specific ways. In both species the organ consists of separate retia, 6 to 10 in number, located around a common vascular system. With growth, the retia in black rockfish merge forming a horseshoe shaped structure, while in china rockfish these remain distinct over the whole life phase. The area of the vascular portion consists basically of secretory epithelium and underlying rete mirabile, and increases linearly with mass. This would provide different sized fish with a similar rate of buoyancy adjustment capacity as was observed in pressure tank experiments. Black rockfish have much larger secretory area, about twice that of a similar sized china rockfish.

As pointed out by Kuhn et al. (1963) and Scholander (1954), rete length (counter current loop length) determines the pressure gradient against which the gas pump can be operated. Since both species have similar bathymetric ranges, differences in rete length are not expected. Marshall (1972) has studied these characteristics in mesopelagic fish in relation to their bathymetric distribution. He found that species from the upper mesopelagic region (150 - 600 meters) have retial lengths of 0.75 to 2.0 mm while fish in the lower mesopelagic zone (600 - 1000 meters) are 3.0 to 7.0 mm in length. Adult rockfish of both species which inhabit much shallower depths have rete lengths about 6 mm. Perhaps the discrepancy is influenced by rete efficiency which may depend on spatial organization of afferent and efferent retial capillaries or diameter of capillaries themselves (Scholander, 1954). Such variability may influence the ability to exchange gases across the counter current loop thus determining concentration gradient characteristics. Unfortunately, there are apparently no studies which compare rockfish morphology with other bathymetrically similar species.

Many studies of secretory ability in fish have concentrated specifically on the effects of pH on blood-gas solubilities. It has been shown that dissociation properties such as increased Bohr and Root shift per unit pH, augment gas secretion (Kuhn et al., 1963; Scholander, 1954; see Appendix A). Comparative studies of similar but bathymetrically separate species show increased dissociation properties with depth (Scholander and Van Dam, 1954). Baines (1976) studied blood properties in the shallow water rockfish assemblage of southern California. His findings were:

1. Species of the genus *Sebastes* have strong Bohr and Root effects while *Scorpaena gutatta*, also a scorpaenid but lacks a swimbladder, has a reduced Bohr and Root effect.

2. Species of *Sebastes* which inhabit greater depths have larger Bohr-Root effects than other *Sebastes* that live normally in shallow water.

3. Normally sluggish species have lesser Bohr-Root shifts than more active species.

While these species are taxonomically different, in many respects they are similar to the British Columbia rockfish assemblage both in general appearance (Gotshall, 1977) as well as ecologically (compare Moulton, 1977 with Quast, 1968a or Limbaugh, 1955). It is therefore reasonable to deduce the latter two conditions given by Baines apply as well. Thus black rockfish very likely have a greater Bohr-Root shift than china rockfish.

Measurements of red blood cell (RBC) fractions in the study species also showed marked differences. Black rockfish consistently had a greater RBC proportion than china rockfish while there was a proportional increase with size. This size trend was much less apparent in china rockfish. Increased oxygen capacity of the blood results from a variety of physiological demands, metabolic in origin. It is unlikely that increased RBC concentration is a direct response to greater secretory demand, although it would certainly facilitate it. Black rockfish spend time in the water column as opposed to the sedentary china rockfish; this probably accounts for the difference in RBC proportions.

Rates of buoyancy adjustment correlate with differences in secretory center morphology. China rockfish have a secretion rate at least half that of black rockfish. Within a species, secretion rates are not size dependent, although some preliminary information suggests that small (<6 cm) china rockfish secrete much faster than larger fish of the size range studied. However, further work is needed.

Rates of buoyancy adjustment in response to increased pressure have been studied in a few species (Table 14). Buoyancy increase can be produced by attaching weights, withdrawing gas, and increasing ambient pressure. A comparative study should be made testing the similarity of these methods. The variability in adjustment rates is extremely high. Some fish such as the blue fish, <u>Pomatomus</u> sp., can refill an emptied swimbladder in less than 4 hours. China rockfish are the slowest, requiring over 400 hours to re-

Table 14
Measurements of buoyancy increase in several species that are available from the literature.

Species	% Reduction in Swimbladder Volume	Time Required to Readjust	Ambient Pressure	Method	Reference
Lebistes reticulatus	28.6	8.0	1.4	pressure	Brown, 1939
	25.7	3.0	1.35		
Ambloplites rupestris	24.8	10.5	1.33	pressure	Rostorfer, 1942
	34.6	24.4	1.53		
	47.1	43.0	1.89		
	66.2	61.0	2.96		
Fundulus heteroclitus	100	48	1.01	gas removed	Copeland, 1952
Gadus morhua	100	10	1.0	gas removed/ Yohimbine	Scholander et al., 1956
Gadus morhua	50	23	2.2	pressure	Tytler & Blaxter, 1973
	76.7	48	4.3		
Pollachius virens	50	24-25	2.2	pressure	Tytler & Blaxter, 1973
	76.7	>48	4.3		
Lagodon romboides	100	4-9	1.05	pressure	McCutcheon, 1962
Pomatomus saltatrix	100	<4	1.0	gas removed	Wittenburg et al., 1964
Anquilla anquilla	100	10-18	1.0	gas removed	Wittenburg et al., 1964
Opsanus tau	100	18-24	1.0	gas removed	Wittenburg et al., 1964
Prionitis sp.	100	48	1.0	gas removed	Wittenburg et al., 1964
Tautoga onitis	100	4	1.0	gas removed	Wittenburg et al., 1964
Stenotomus chrysops	100	6-12	1.0	gas removed	Wittenburg et al., 1964
Lepomis macrochirus	50	<24	1.0	gas removed	McNabb & Mecham, 1971
	-25	3.0	1-1.16	implanting weights	Gallepp and Magnuson, 1972
Carrasius auratus	13.0	228	1.19	pressure	Reyer, 1977
Tilapia mariae	13.0	18	1.19	pressure	Reyer, 1977
Sebastes melanops	50	30	2	pressure	this study
	66	90	3		
	75	120	4		
S. nebulosus	66	450	2	pressure	this study

store a bladder volume reduction of two-thirds. Black rockfish are similarly slow when compared to other fish, requiring about 90 hours to replace two-thirds of their bladder volume.

A criticism of the pressure tank experiments is that they do not allow fish a choice in the pressure change. Experiments conducted in this study in effect forced fish to move to a new depth and there was no certainty that rates determined were the same as those for voluntary vertical movements. There are two different lines of evidence which treat this. In one study, McCutcheon (1966) placed pinfish, <u>Lagodon rhomboides</u>, within a 6 meter column which could be elevated from a horizontal position to an angle of 35 degrees. When placed in the column, fish maintained their position relative to column markings despite changes in hydrostatic pressure caused by moving the column to a more vertical position. Fish in McCutcheon's experiments chose to stay in one position despite the change in pressure. Alternatively, in experiments of Harvey and Bothern (1972) and Gallepp and Magnuson (1972), fish changed their position and attempted to remain in the same state of buoyancy as pressure changed.

Resorption values obtained for both species, but particularly china rockfish, were extremely variable, both within and between individual experiments. In most cases, stepwise pressure reductions were made and a sequence of values was obtained which showed no apparent pattern. In some cases resorption values were long, several times that of the fastest rates. However, many of these values are not true measures of resorption time since there are long periods with no adjustment. In china rockfish failure to reduce buoyancy is probably associated with their thigmotactic habits as was found by Jones (1952). China rockfish are always associated with reef crevices and in the pressure tank, try to wedge themselves among the irregular surface of the tank end. Thus, they may be initially disturbed by their inability to sit but later find places to wedge themselves in. Because of this, the best estimates of buoyancy reduction probably come from the most rapid rates.

Gas resorption rates measured in both species were much faster than gas secretion over a similar pressure intervals. Using repetitive stepwise measures, black rockfish required about 5 hours to ascend from 20 meters to the surface. The corresponding value for china rockfish is at least 40 hours. These values are considerably greater than similaly obtained values for other species (Table 15).

Table 15: Rates of buoyancy reduction measured from different fish.

Species	% Increase in Swimbladder Volume	Time Required to Readjust	Ambient Pressure	Method	Reference
Gadus morhua	50	5.0	1.0	pressure	Tytler & Blaxter, 1973
Pollachias virens	50	5.0	1.0	pressure	Tytler & Blaxter, 1973
Lebistes reticulatus	15	2.0	0.86	pressure	Brown, 1939
Perca flavescens	12.5	2.5	0.92	pressure	Jones, 1952
	25	9.0	1.0	movement in a water column	Jones, 1952
	33	16.0	1.0	movement in a water column	Jones, 1952
Ambloplites rupestris	30	23	0.70	pressure	Rostorfer, 1942
	2	6	0.98	pressure	Rostorfer, 1942
Sebastes melanops	10	0.5	variable	pressure	this study
	20	1.0			
	30	1.7			
Sebastes nebulosus	10	2	variable	pressure	this study
	20	9	variable		
	30	12	variable		

Chapter V

CONCLUSIONS

Over the time bases studied, vertical movements are apparently independent of buoyancy adjustment. The rates of buoyancy adjustment observed in pressure tanks were many times slower than would be required to accommodate vertical movement. Further, the magnitude of vertical movement (Table 6) observed in both species, particularly black rockfish, were the same over short and long periods indicating that time is not a factor in their normal vertical movements. Consequently, most of the vertical movements made by the two species probably occur without active buoyancy response to the pressure change.

5.1 BLACK ROCKFISH

Both the rates of gas transport and the pressure effects on bladder volume resulting from observed mobility patterns indicate that black rockfish are unable to maintain neutral buoyancy at all times. Clearly, these fish have a depth of neutral buoyancy and tolerate non-neutral states elsewhere. From an energetics standpoint, if these fish were able to select a depth for neutral buoyancy, it would be one that costs the least, considering the amount of time a fish spends at different depths versus the energy cost of being there. Short periods of time spent in a strongly positive state compare equivalently with long periods at deeper depths (negative buoyancy). Consequently, black rockfish at Ohiat would probably select neutral buoyancy at a shallow depth. For such fish the cost of negative buoyancy at the deeper boulder site is comparatively low, and may be further reduced by lowered activity in the deep areas.

An alternative approach to the energetics decision for a neutral buoyancy depth assumes that control of a buoyant state is passive. If buoyancy is a condition determined by the pressure to which a fish is exposed, vertical movement such as was observed may result in oscillation of the opposing swimbladder gas transport systems. While moving to a deeper position gas secretion begins and the benefit obtained is a function of the time spent and the of gas secretion. Alternatively, moving up to a positive state, gas resorption begins. Here again, the benefit in buoyancy reduction is related to the time and rate. Since the rate of gas secretion is many times slower than resorption, neutral buoyancy would settle at a shallow depth even if the fish were to spend an equal amount of time at all depths. Since black rockfish spend most of their time in the kelp bed, neutral buoyancy would undoubtedly reflect this depth.

The majority of the black rockfish population observed did not appear to have buoyancy restricted vertical mobility. Their presence in shallow water allows virtually unrestricted rapid movement throughout all depths of the reef without any imposed limitation caused by excess positive buoyancy. The potential for restricted movement in black rockfish is apparent in two instances, namely, the unusual benthic residing sub-adult, Orange-20, and juveniles which were seen within crevices during the day. These are two instances of fish which spend a considerable amount of time deep but move into the kelp bed at night. The amount of time spent deep is great enough for substancial buoyancy increase to occur. Also during the winter when black rockfish move to deeper places on the reef vertical movement which is undertaken during clear water periods was probably restricted by excess positive buoyancy.

5.2 CHINA ROCKFISH

The relationship between mobility and buoyancy in china rockfish is curious. Their strong association with crevices and reef substrate except for rapid assaults on prey, leave no doubt that the swimbladder serves little function as a hydrostatic organ. In view of the well developed sonic musculature (Hallacher, 1974) and increasing evidence that sound production is integrated with aggressive behaviour (V. E. Fletcher, pers. comm.), one must conclude that the swimbladder of china rockfish is primarily a sound organ. It remains unclear why this fish maintains buoyancy close to neutrality when it is benthic, not needing the hydrostatic support. Perhaps the larger size gained by filling the swimbladder to a neutral state increases intensity or frequency sound production.

In china rockfish the process of buoyancy adjustment is very slow but does not seem to be taxed heavily by movement patterns. In most instances china rockfish remain within, or in close proximity to, their home crevice. Temporary or permanent exclusion from the home crevice caused by space competitors such as octopus and wolf eels result in repositioning and perhaps readjustment of buoyancy. Otherwise, movements from the home crevice are mostly short term resulting in no buoyancy adjustment. The fact that individuals occupy a very small vertical range correlates well with a very limited buoyancy adjustment capacity.

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Appendix A

STRUCTURE AND FUNCTIONAL ASPECTS OF THE SWIMBLADDER

The swimbladder originated as a diverticula on the floor of the pharynx. It is generally accepted that this structure was primitively a lung although morphological evidence linking the two is poor (Goodrich, 1958). The swimbladder was first apparent in the Antiarchs, a group of placoderms from the Devonian (Romer, 1966). From what is understood of the early habitat of these fishes, an air-breathing organ provided a respiratory alternative in the sometimes oxygen-poor fresh water environment. Later, as bony fish radiated into regions where oxygen was not limiting, the lung lost its' respiratory function and was retained as simply an air bladder. Currently, the swimbladder occurs embryologically in all Osteichthys but in higher teleost groups it is sometimes lost in adults (Jones and Marshall, 1953; Goodrich, 1958).

Function of the Swimbladder

Although the morphology of the swimbladder is variable in most groups its primary function is as a buoyancy device or hydrostatic organ. Also associated with the swimbladder are sound production, auditory and respiratory functions.

As fish tissue is more dense than the surrounding medium, gas contained within the bladder neutralizes buoyancy of the fish by establishing an equivalent weight to volume distribution. In considering bladder volume, the buoyant force applied by a gas is equivalent to the weight of the water displaced minus the weight of the gas. The relative volume of the gas bladder in fresh or salt water fish can be estimated by comparing the fish density, D_f , with that of the medium, D_m , as follows:

$$\text{Bladder Volume (\% Body Volume)} = \left(1 - \frac{D_m}{D_f} \right) \text{X } 100 \; .$$

Using the following approximations, fish tissue density is about 1.076 g/cc, salt water has a density of 1.024 g/cc, and of course, the desity of fresh water is 1.000 g/cc (Taylor, 1921). It is apparent that neutrally buoyant fresh water fish should have a bladder volume of 7% and salt water fish 5% of the total body volume. Detailed bladder measurements encompassing 42 families of fish (Aleev, 1969) generally supported these estimates. Further agreement comes from work by Taylor (1921), Jones and Marshall (1953), and Harvey (1963). The hydrostatic function of the swimbladder is further evident from the theoretical energy savings of neutral buoyancy. Swimming fish are opposed by two forces, gravity (vertical) and drag (horizontal). In neutrally buoyant fishes, the vertical component is eliminated and only the horizontal force must be overcome whereas fish without a bladder must counteract gravitational force by producing lift. In the shark the pectoral planing surfaces and heterocercal tail provide the required lift. Alexander (1967) estimates that a 16.5 cm salmon (Oncorhynchus) without a swimbladder swimming at a speed of one length per second would have to increase its' metabolic rate by 7% to achieve the lift necessary to maintain a constant depth. Inactive fish which 'hover' achieve minimal energy expenditure at or near neutral buoyancy. Activity, in terms of pectoral fin beat frequency, in relation to the buoyant state of a surf-perch (Embiotocidae) is shown in figure 1. A level of activity just adequate to offset propulsion produced by branchial ventilation is maintained at neutral buoyancy. Under conditions of positive or negative buoyancy the fin beat frequency increases to offset

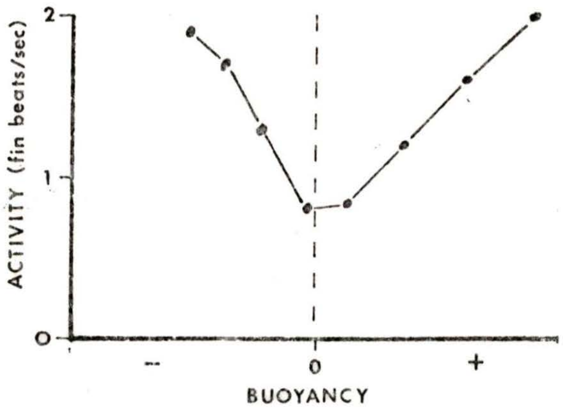

Figure 1.
Activity of Cymatogaster aggregata in relation to buoyant state.
(McElderry, unpublished data)

floating or sinking respectively.

The swimbladder may have a profound effect on the enhancement of a fishes acoustic environment, both in sound production and hearing. Sound is produced by musculature lying adjacent to the bladder wall. Muscles associated with sound production occur as either intrinsic or extrinsic in many fish groups (Marshall 1966; Tavolga, 1964). Rapid muscle contractions create vibrations of the bladder wall which propagate sound waves into the surrounding medium. Sound may also be produced by expulsion of gas from the bladder. In some fish such as the trigger fish, the swimbladder serves as a resonator for sounds produced by nearby organs. The quality of sound has been reported in some species (Sand et al, 1973; Evans, 1973; Fish, 1954, cited in Jones, 1957; Yearsley and McInerney, in press). Sound production serves as a means of communication between fish (Fish, 1954). In many species this is important in both breeding and agonistic interactions. Sound production is more behaviorally integrated in some fish which have dawn and dusk choruses (e.g. Sciaenidae) or use it as a navigational aid in echo-sounding (Griffin, 1950, cited in Jones, 1957).

Hearing in fish has been discussed by many authors (Jones and Marshall, 1953; Jones, 1957; Alexander, 1967; Tavolga, 1971). Offute (1970) points out that many fish are probably capable of sound wave reception due to the piezoelectric properties of the otolith alone. However, the swimbladder greatly enhances the auditory capacity both in quality and quantity. Sound waves traveling in water produce oscillations on the bladder surface which can be transmitted to the labyrinth by gas-filled forward extensions of the swimbladder (e.g. Clupeidae, Holocentridae) or by a series of bones called the Weberian apparatus (e.g. Ostariophysi). Chapman and Hawkins (1973) have shown that in Gadus morhua, which lacks the swimbladder connection with the auditory center, the presence of the swimbladder alone provides a source for sound reradiation. Vibrations from the bladder wall radiate through the tissue at a higher intensity than incoming sound. Enhancement of hearing by sound reradiation was also demonstrated in _Peuronectes platessa_ which lacks a swimbladder (Chapman and Sand, 1974). Hearing in this fish was increased when a reradiation source was provided by placing a small balloon near the fish. However, fish which have no bladder connection with the auditory center are less sensitive to high frequency (above 2,000 cps) and low intensity (Jones, 1957).

Finally, the swimbladder may serve as an accessory respiratory organ. This may occur either as a air-breathing device or simply as an oxygen store. Since the gills are dependent upon water flow to separate lamellae, such structures collapse in air and are ineffective for gas exchange. Several regions along the alimentary track have been shown to be structurally adapted for air breathing (Carter, 1957). In some fish the swimbladder is adapted to this function. However, air-breathing in fish occurs in oxygen poor environments which are generally absent in marine surface waters. Accordingly this function is of little importance to marine fish. Moreau (1976, cited in Hall, 1924) was probably the first to suggest that the swimbladder may serve as an oxygen reserve. Such a system would be an advantage to fish which move through oxygen minimum zones (e.g. mesopelagic fish). A reduction in oxygen levels within the swimbladder during anoxia has been noted in many species (Powers, 1932; Safford, 1940; Jones, 1957). However, Hall (1924) estimated that the amount of oxygen supplied by the swimbladder during anoxia would sustain a fish for only a fraction of an hour. Alexander (1967) points out that little respiratory advantage occurs since oxygen resorbed from the bladder passes directly to the heart and is equilibrated with water in the gills. Jones and Marshall (1952) suggest that the use of the swimbladder as an oxygen store may be more functional in deep water fish where the density and concentration of oxygen in the bladder is greater. In conclusion, it is doubted that the swimbladder has any respiratory function as far as most marine fish are concerned.

Although obviously useful the swimbladder has certain disadvantages. Swimbladder volume under changing pressure approximates Boyle's law, $P_1V_1 = P_2V_2$ as shown in Fig. 2 (Jones, 1951). As buoyancy is dependent upon bladder volume, vertical movement in the water column results in a change of

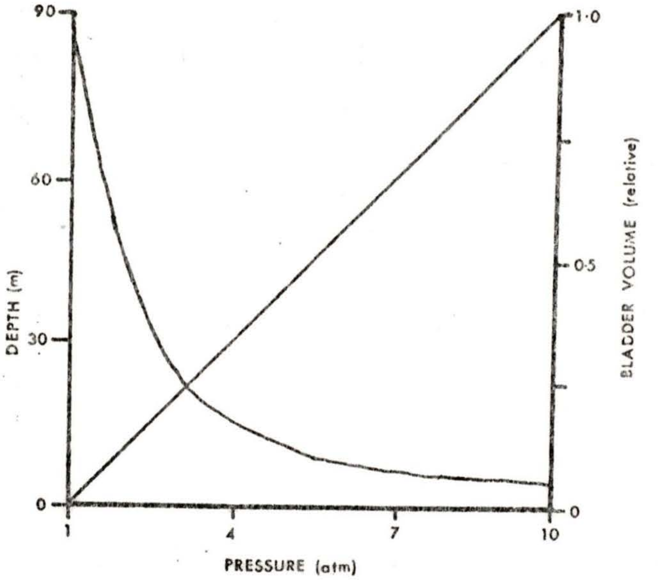

Figure 2.
The effects of pressure on bladder volume and the relationship between depth and pressure.

buoyant state. Clearly, there is a limit to positive buoyancy for which a fish can compensate. In shallow water, changes in pressure affect a greater change in volume than in deep water, Consequently, the potential vertical mobility of a species in terms of distance is more restricted in shallow water. Alexander (1967) suggests that the effect of pressure on buoyancy generates a selective pressure towards reduction in fish tissue density. Work by Aleev (1969) supports this hypothesis showing a trend in tissue density from 1.11 g/cc to 1.01 g/cc in fish ranging from benthic forms lacking swimbladders to pelagic types with swimbladders.

The additional body volume due to the swimbladder is a disadvantage to fish which are rapidly passing through water. The drag force on a swimming fish is a function of body volume and surface area. A decrease in body volume or surface area of a fish results in a reduced drag. Consequently, the energy expenditure for swimming increases with fish size. For Oncorhynchus swimming at 4 lengths/ second it is energetically cheaper to reduce total body volume by deflating the swimbladder than to reduce gravitational forces through neutral buoyancy

(Alexander, 1967). A similar situation is true for fish which live in areas of strong currents. Gee (1968) found a negative relationship between bladder volume and stream current velocity in *Rhinichthys cataractae*.

Pelagic fish which have swimbladders can be easily located through marine mammal echolocation. Since the swimbladder provides an excellent surface for reflection of sound waves. Such fish may thus fall easy prey to predators. This as well as other considerations discussed previously may have provided sufficient selective pressure for many of the active pelagic fish to loose the swimbladder entirely.

Structure of the Swimbladder

Swimbladders can be divided into two classes on the basis of their structure as shown in figure 3. The first type, termed physostomous, retains the tubular connection with the pharynx (pneumatic duct) while this duct is lost in physoclistous swimbladders. Evolutionarily, more primitive fish groups tend to be physostomes while the physoclist condition is more common in higher fish groups. However, the swimbladder is a poor systematic tool since specific variation is great (Goodrich, 1958). Embryologically, the physostomous condition prevails, although the pneumatic duct may degenerate at some period in developement

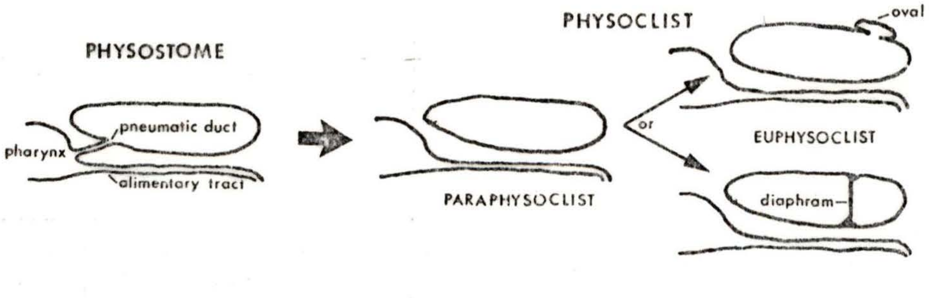

Figure 3.
Types of swimbladders showing the trend in development.

giving rise to a physoclist swimbladder. Organs of gas secretion and reabsorption may be present in both swimbladder types although they are more extensively developed in physoclists. Volume adjustment in physostomic fish more commonly occurs by passage of gas along the pneumatic duct. Within physoclistous fish, there is a tendency toward separation of the secretory and resorbent regions in more highly developed forms (see figure 3). This occurs with a postero-dorsally located evagination called the oval or with a posteriorly located chamber separated by a muscular diaphram. Swimbladders of this construction are termed euphysoclistous while swimbladders with a single chamber are called paraphysoclistous.

Essential to the operation of the physoclist swimbladder are the organs of gas secretion and resorption since these provide the only means of gas transfer in the closed swimbladder. The gas secretion center consists of the rete mirabile (wonderful net) and gas gland (see figure 4a). The rete is a countercurrent system which functions to elevate the partial pressure of gases in the blood passing through. A gradient is developed along the loop slightly in excess of pressure within the bladder. Steen (1970) provides some information on the size of exchange surfaces in the rete of Anguilla. Surface area of

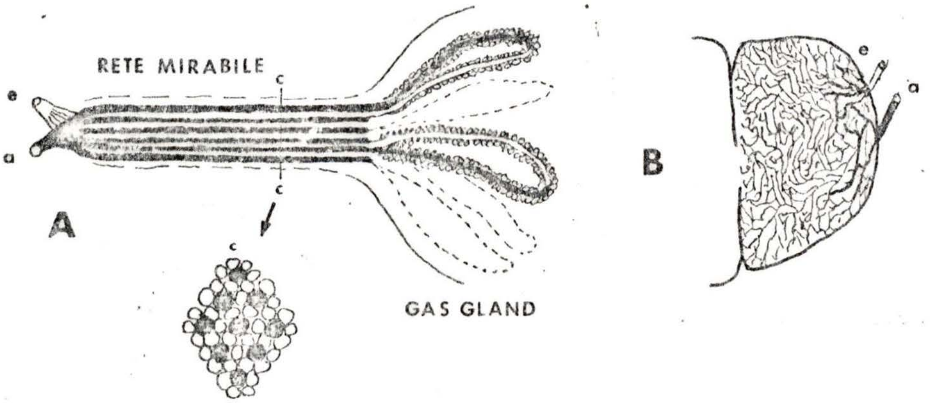

Figure 4.
Gas transfer regions of the swimbladder. (From Marshall, 1966)
A. Secretory center with cross section of rete mirable shown in c-c.
B. Resorption center. e and a denote efferent and afferent blood supply, repectively.

arterial and venous capillaries are estimated at 105 m^2 and 106 m^2, respectively. The exchange ratio in the rete is approximately 1700 cm^2/cm^3 in contrast to the human lung, 100 cm^2/cm^3. The gas gland, located along the vertex of the counter current loop, is the actual interface between rete blood and the bladder lumen. Secretions, primarily lactic acid and carbonic anhydrase, in the gas gland function in the development of a concentration gradient in the rete. The gas resorption center consists of a network of capillaries located in the posterior or dorso-posterior region of the bladder.(see figure 4b). In euphysoclists this structure is situated in the posterior chamber or the oval. Resorption of gas from the bladder occurs by passive diffusion.

As the swimbladder is a derivative of the alimentary tract, similar endodermal and mesodermal components are evident. Nomenclature for the tissue layers of the bladder wall and their alimentary equivalents are shown in Table 1. The tunica externa has reduced muscle tissue and mostly consists of fibrous connective tissue. Occuring within this layer are guanine crystals and a special type of collagen which have a function in reducing gas permeability. The rate of gas diffusion across this layer is 0.01 % of that found in normal

Layers in the wall of the Alimentary Canal	Layers in the Wall of the Swimbladder	
	Description	Terminology Suggested by Fänge (1953)
Serosa	Peritoneum covering the swimbladder ventrally	Serosa
Muscularis externa	Dense collagenous connective tissue with smooth and striated muscles	Tunica externa
Submucosa	Loose, jelly-like layer of fibro-elastic tissue	Submucosa
Muscularis mucosa	Layers of Smooth Muscle Cells	Muscularis mucosa
Lamina propria	Collagenic connective tissue surrounding smooth muscles of the muscularis mucosa	Lamina propria
Inner epithelium	Inner epithelium	Inner epithelium

Table I. Relationship between swimbladder and alimentary canal walls. (From Jones, 1957).

connective and muscle tissue (Denton et al 1972). The loose jelly-like nature of the submucosa enables independent movement of the underlying tissue layers. The muscularis mucosa adjusts the tension on the inner bladder wall affecting the extent of exposure of gas to transport regions.

Vascular and nervous supplies to the swimbladder are similar to other visceral organs. Blood from the celiacomesentric artery supplies the gas secretory center while the resorption center recieves blood directly from the dorsal aorta. The oval of euphysoclists may additionaly be supplied by blood from the intercostal arteries. Venous return in the secretory center occurs by way of the hepatic system while blood from the resorption center returns through the posterior cardinal vein or the hepatic portal system. The parasympathetic-sympathetic antagonism typically occuring in visceral organs is also present in the swimbladder. A branch from the vagus nerve controls functions associated with gas secretion while sympathetic nerves control gas resorption activity.

Nerve Reflexes in the Swimbladder

Fänge (1966) suggests a means by which nervous control of volume adjustment occurs. The secretory reflex, activated by a reduction in bladder volume, produces vasodialation in the secretory vascular system, vasoconstriction in the resorbent vascular system, relaxation of the secretory chamber, and constriction of the resorbent chamber (see figure 5a). Conversly, the resorbent reflex, stimulated by an increase in bladder volume, produces vasodialation of the resorption vascular supply, vasoconstriction of the secretory vascular supply, relaxation of the resorbent chamber, and constriction of the secretory chamber (see figure 5b). Volume adjustment reflexes occur by enhancing operation of one center while inhibiting function of the opposing center. As with most physiological systems, neither system is completely inactivated. Consequently, volume adjustment occurs with one center operating to a greater degree than the other.

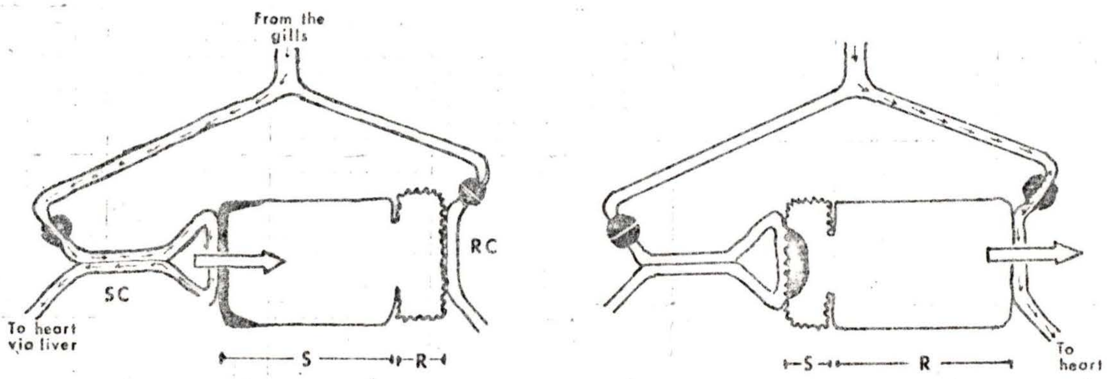

Figure 5.
Swimbladder volume adjustment reflexes.
A. Secretion reflex
B. Resorption reflex
(From Fänge, 1966)

Nature of Gases in the Swimbladder

Gases found in the swimbladder are similar to those found in the fishes' environment. Relative concentrations differ with oxygen, nitrogen, and carbon dioxide being the dominant gases found. Traces of argon are also apparent. The ratio of gases may vary with habitat and species. Generally, fresh water fish have a high nitrogen concentration in the swimbladder while oxygen is more prevalent in marine fish. There is a positive relationship between oxygen content and depth of occurrence in marine fish. Fish living near the surface tend to have a gas content similar to air while oxygen is predominant in deeper fish (Steen, 1970). Within species relative concentrations of gases in the swimbladder may vary with concentrations in the environment (Safford, 1940; Copeland, 1952; Wittenberg et al, 1964). During volume adjustment of the swimbladder, the ratio of gases changes. In all cases oxygen is the most rapidly transported gas (Copeland, 1952). Consequently, during secretion the oxygen level rises while a decline is seen during gas resorption. In some cases it may take weeks for the original ratio of gases to be re-established after volume adjustment.

Mechanism of Gas Secretion

The mechanism of gas transport into the swimbladder has intrigued physiologists for decades. Basically, the problem lies in finding a means for which a gas occurring at a low partial pressure in the blood can enter the bladder where the partial pressure is many times greater. Historical reviews of transport theories are given in Hall (1924), Fänge (1966), and Steen (1970). It was accepted early (≈ 1910) that gas secreted into the bladder arose from the blood. Hall (1924) points out that at that time there were basically three views as to how gas was transferred from blood into the bladder: 1) direct entry, 2) the gas gland served as a pumping organ which 'pumps' gas into the bladder, 3) gas is derived from cytoplasmic decomposition of gas gland cells. Currently, the second view is receiving the most experimental support. Much of the physiological work on the swimbladder in this century has been directed toward understanding the mechanism of this 'pump'. It has long been understood that dissociation of hemoglobin occurs in the presence of an acid (Hall, 1924). Later, as more specific characteristics of fish hemoglobin became known, the potential as a means for oxygen transport into the bladder was realized (Root, 1931; Powers, 1932). Koch (1932, cited in Fänge, 1966) suggested that secretion of salt or production of heat decreases the solubility of gases. Subsequently, the salt secretion principle, generally referred to as the 'salting out' effect, has received support and is believed to be a means by which inert gases can be transported (Kuhn et al, 1963; Wittenberg et al, 1964; Scholander, 1954). The idea that the rete mirabile functions as a counter current multiplier was suggested by Haldane (1922) and Koch (1932). This idea was generally accepted but did not receive rigorous examination until much later. A model developed by Scholander (1954), later revised by Kuhn et al (1963) demonstrated a mathematical basis for which secretion of gas could occur. Later, the mechanism received strong support through the experiments with Anguilla by Steen and coworkers (see Steen, 1970). At present, it is generally accepted that the three effects, oxygen dissociation, salting out, and counter current multiplication, form the basis for secretion of gas into the bladder although the extent to which the two former effects are important is still disputed (Prosser, 1973; Steen, 1970).

The gas concentrating mechanism of the secretory center depends upon the principle of altered gas solubility in relation to changing salt concentration. In this discussion, the term salt refers to ions in general. In the case of the swimbladder, salt refers specifically to the secretory products of the gas gland, namely, lactic acid and carbonic anhydrase. From Henry's law the equilibrium state of a gas in solution is directly proportional to the partial pressure P_o as follows

$$C_o = A_o P_o \qquad (1$$

where C_o is the concentration of gas in solution and A_o is the solubility coefficient (Henry's constant). The solubility coefficient varies with temperature and ion content. As temperature is constant, ion content modifies the solubility coefficient as follows

$$A_s = A_o(1 - E\Delta C_s) \qquad (2$$

where E is an interaction parameter (based on the electric properties of the ion) for the salt quantity ΔC_s. Thus for a given pressure, the concentration of gas in solution is affected by the salt concentration.

Even with a low solubility, oxygen is carried in the blood in appreciable quantities. This is due to the carrier molecule, hemoglobin. Fish hemoglobin can normally carry about 10 cc/100 cc of blood while plasma will carry about 4 cc of oxygen per atmosphere of pressure (Alexander, 1975). A similar effect on the solubility of oxygen with hemoglobin occurs with changing ion concentration. Oxygen bound to hemoglobin (oxyhemoglobin) dissociates reversibly in the presence of H^+ ions as follows

$$HbO_2 + H^+ \rightleftharpoons Hb + O_2$$

This characteristic of hemoglobin produces two effects in oxygen loading characteristics of fish blood. The first, typical of all vertebrates and some invertebrates is called the Bohr effect. In the presence of an acid the binding capacity of hemoglobin is reduced. The oxygen dissociation curve shown in figure 6a undergoes a shift to the right (Bohr effect) with an increase in H^+ion content. The tencency to bind with oxygen is reduced but can occur at a higher pressure. This quality is very similar to the dependency of gas solubility on salt concentration seen earlier (equations 1 and 2). The Root effect, usually found only in fish with swimbladders, differs in that the maximum saturation capacity of the hemoglobin is affected. The Root off-shift occurs with a decrease in pH resulting in a reduction of bound oxygen as shown in figure 6b. The Root effect completely blocks oxygen from part of the hemoglobin and has been shown in some fish to occur at pressures as high as 140 atm. (Scholander and Van Dam, 1954).

Following the model developed by Kuhn et al (1963), the mechanism of gas secretion can be demonstrated. The schematic diagram shown in figure 7 represents one loop of the counter current system in the rete mirable. Blood flowing in the afferent limb, with a gas concentration, C_a , enters the loop

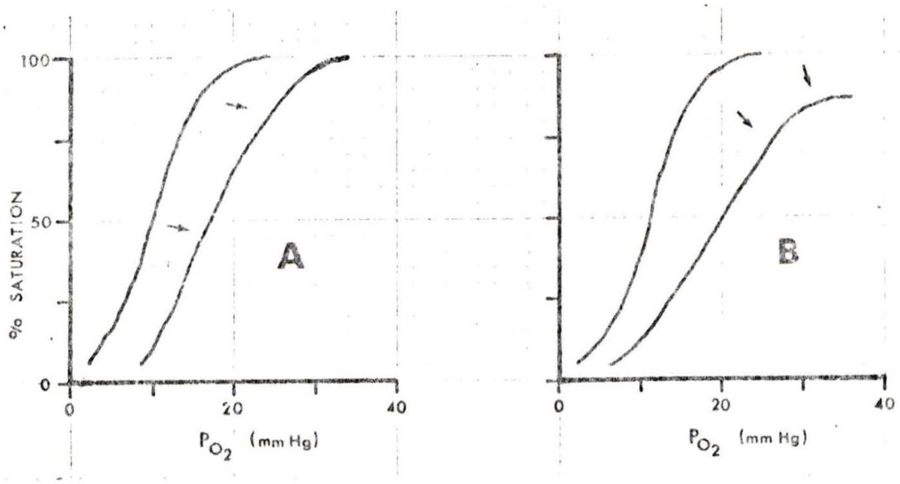

Figure 6.
Dissociation characteristics of fish hemoglobin with reduced pH.
A. Bohr effect. B. Root effect.

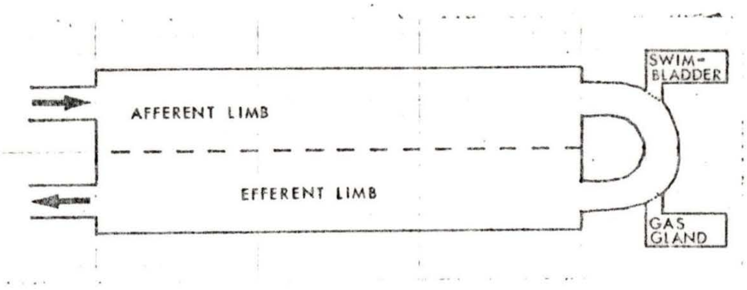

Figure 7.

Schematic diagram of secretory center.
See text for explanation.
(From Kuhn et al, 1963)

passing the bladder, gas gland, continues along into the efferent limb with a gas concentration, C_e , and passes out of the rete. The two limbs are separated by a membrane which is relatively impermeable to salt and water and permeable to gas. At this point there is no concentration gradient within the loop consequently $C_{\alpha} = C_e$ and the afferent partial pressure, P_{α} , is equal to the efferent partial pressure, P_e . Now suppose blood flows into the afferent limb with afferent blood passing through the loop, receiving salt secretion, ΔC_s , and emerges in the efferent limb. From equation 1 the equilibrium concentration of gas in the afferent limb is

$$C_{\alpha} = A_{\alpha} P_{\alpha} \tag*{(3}$$

From equation 2 the efferent solubility coefficient is modified as follows

$$A_e = A_{\alpha}(1-E\Delta C_s) \tag*{(4}$$

Therefore, the equilibrium gas concentration in the efferent limb is

$$C_e = A_{\alpha}(1-E\Delta C_s)P_e \tag*{(5}$$

Dividing equation 3 by 5

$$\frac{C_a}{C_e} = \frac{P_a}{P_e}(1-E\Delta C_s) \qquad (6$$

From the initial assumption, $C_a = C_e$, it is apparent that

$$P_e = P_a(1-E\Delta C_s) \qquad (7$$

That is, $P_e > P_a$ which results in a diffusion of gas across the membrane to achieve equilibrium conditions. Having done this, $P_e = P_a$. From equation 6 the following condition exists

$$C_a = C_e(1-E\Delta C_s) \qquad (8$$

That is, the concentration of gas in the afferent limb exceeds that in the efferent limb.

This single concentrating effect just demonstrated is multiplied by virtue of the fact that salt is continually secreted into blood passing the gas gland. With the passage of blood through the loop, a steady diffusion of gas into the afferent limb of the counter current system occurs. As the partial pressure of gas in the vertex of the loop exceeds that found in the bladder, diffusion of gas into the bladder occurs.

The concentration of gas in the loop can develop reaching a maximum end state. This occurs in a situation where the ambient pressure exceeds the maximum concentrating capacity of the secretory center. The end state occurs primarily as a result of the time needed for diffusion to occur across the membrane. Since a specific time is required for equilibrium to occur across the membrane, the concentration gradient along the loop toward the vertex can only develop at a certain rate.

This model is based on the assumption that the rete is impermeable to acid and water. Steen (1970) however, found that the rete is highly permeable to acid. It was then reasoned that the basis for concentration was unrelated to membrane permeability but, rather, to the differential rate of response of hemoglobin to a change in H^+ions (Steen, 1970). The $T_{1/2}$ (half completion time) of the Root off-shift occurs in 50 msec allowing for immediate dissociation. The Root on-shift $T_{1/2}$ is much slower ranging from 10-20 sec. While flowing away from the vertex, the reduced oxygen affinity of blood in the efferent limb is maintained in spite of an increasing pH. Consequently, the difference in solubility in the afferent and efferent limb results in the same pressure differential shown in the Kuhn model.

Rate of Gas Transport

The rate of gas transport in general is very slow. When deflated, the time required for secretion of gas to refill the bladder ranges from about 4-48 hours. Data from several species are presented in table 2. The data for rate of gas resorption is more scarce. The time required for Perca to adapt from 3 m to the surface is about 9 hours (Jones, 1952). The rockfish, Sebastes melanops can adjust from 10 m to the surface in 6 hours while S. pinniger can adjust from 20 m to the surface in 16 hours (McElderry, unpublished data). These rates of resorption are not directly comparable since the rate is a function of initial and final pressure and other variables such as size.

Efficiency of Gas Transport

The efficiency of gas transport can be expressed in terms of gas concentrating capacity and the rate of gas transport. It is important that the secretory center is capable of generating pressure levels comparable to the pressure at

Species	Time required to fill drained swimbladder (hours)	Reference
Pomptomus saltatrix	4	Wittenberg et al, 1964
Stenotomus versicolor	6-12	"
Anguilla	10-18	"
Opsanus tau	18-24	"
Prionitis	48	"
Gadus morhua	10	"
Fundulus heteroclitus	48	"
Lagodon rhomboides	4-9	McCutcheon, 1962
Sebastes melanops	72*	McElderry, Unpub. data
Sebastes pinniger	72*	"
Sebastes nebulosus	660*	"

* calculated from filling time of partially deflated bladder

Table 2. Time required to fill drained swimbladder

which the fish lives. The concentrating ablitity of the secretory center is a function of the rete length, salt secretory effect ($E\Delta C_s$), and the carrying capacity of the blood. The length of the counter current loop has a profound effect on concentrating ability since the pressure gradient developes exponentially along the loop. It is estimated that in Anguilla a 0.5 cm rete can develop 300 atm pressure while a 1.0 cm rete can develop pressures in excess of 2000 atm (Kuhn et al, 1963). In a morphological study of swimbladders in deep sea fish Marshall (1960) points out that there is evidence that deeper living species have longer rete. From equation 2 it is evident that greater secretions of salt produce a greater pressure differential across the membrane resulting in a higher concentrating capacity. However, the quantity of salt secreted is limited by the osmotic tolerence of blood cells. Therefore, it is doubtful that this would serve as a useful means of elevating pressure capacity. An alternative approach would be to increase the magnitude of the Bohr and Root effects per unit salt secretion. Scholander and Van Dam (1954) pointed out that in some fish at pressures greater than 20-30 atm the oxygen dissociation curve is horizontal and therefore, the Root effect is responsible for differences in binding capacity. A positive relationship between depth of occurrence and magnitude of Root effect has been shown in some species of Sebastes (Baines, 1975). Finally, the amount of gas carried by the blood can enhance the concentrating ability of the rete. Variations in hemoglobin concentration have been shown to occur in a species seasonally (Powers, 1974) and under varying environmental conditions (Powers, 1932). It should be pointed out that the concentrating ability of the rete is impaired by changes in blood flow as time is required for equilibration to occur across the membrane. An increase in blood flow reduces the concentration effect since equilibrium does not occur across the membrane. Reduced blood flow results in degeneration of the concentration gradient since back diffusion along the loop away from the vertex becomes significant.

When considering both secretion and resorption, the rate of gas transfer is primarily determined by the size of the exchange surface. A larger area of exchange enables greater diffusion capacity. Enhancement of exchange surface in the secretory center usually occurs with an increase in the number of rete or capillaries within the rete while an increase in vascularization is found in the resorbtion center. Secondarily, the carrying capacity of the blood is important. This is a function of the binding efficiency of the blood and concentration of hemoglobin in the blood. The binding capacity of hemoglobin probably has little relation to gas resorption rate. As resorption of gas is a passive process, the rate T is dependent upon the differential pressure of gas in the bladder P_1 and in the medium P_2 as follows

$$T = B \ln \frac{P_1}{P_2} \qquad \text{(Jones, 1951)}$$

where B is a constant for the efficiency of gas resorption in a species. As the partial pressure of gas in the bladder is likely to be in excess of the maximum saturation of hemoglobin, a large part of the gas resorbed is carried in solution. As was pointed out earlier, there is an optimal rate of blood flow into the secretory center. Consequently, blood flow does not affect secretion rate enhancement. The rate of gas resorbtion is related to blood flow since the volume of blood for which gas can diffuse into is increased.

Energy Required for Gas Secretion

Since gas is secreted against a concentration gradient, the process essentially involves compression and requires energy. The energy E required to compress a gas from pressure P_1 to P_2 is

$$E = P_2 V \ln \frac{P_2}{P_1}$$

where V is the volume of gas at P_2. Alexander (1975) estimated the energy required to compress gas from an ambient partial pressure of 0.01 atm to pressure within the bladder of 100 atm. With an efficiency of 5 % the energy required to maintain a constant volume is about 1.5 % of the resting metabolic rate. Kuhn et al (1963) examined the problem differently by pointing out that the energy required to concentrate gas is a function of salt production. Since counter current multiplication operates on the free energy of the salt (i.e. the osmotic effect), the process of supplying salt to the system is essentially the work requirement. Although no data are presented, Kuhn et al (1963) feel that the energy requirement is low.

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Appendix B

AGE, LENGTH, AND WEIGHT RELATIONSHIPS

Information concerning growth patterns was collected from specimens dissected for swimbladder studies. Length (mm) and weight (g) measurements are shown in following tables for both species. Missing values are denoted by 999. and sex is indexed as 1 and 2 for male and female, respectively. The frequency of males was unusually high in black rockfish; however, it is unknown why. Regressions of length with weight were made and are significant in both cases ($p<0.01$). Predictive equations for S. melanops and S. nebulosus respectively, are:

$$\text{Log Weight} = -4.93 + 3.13 \text{Log Length} \quad (r=0.99, n=77)$$

$$\text{Log Weight} = -4.68 + 3.07 \text{Log Length} \quad (r=0.98, n=82)$$

Age was estimated from otoliths collected and stored in glycerol for a minimum of one month. While more sophisticated techniques are available (Westrheim, pers. comm.), age was estimated by simply counting otolith annuli. A total of four counts were made; one for practice, 2, 3, and 4 for screening and elimination of poorly resolved annuli. The following figure shows the mean lengths and 95 percent confidence intervals calculated for different age classes of both species. Data points are presented in cases where there are fewer than 4 samples per age class.

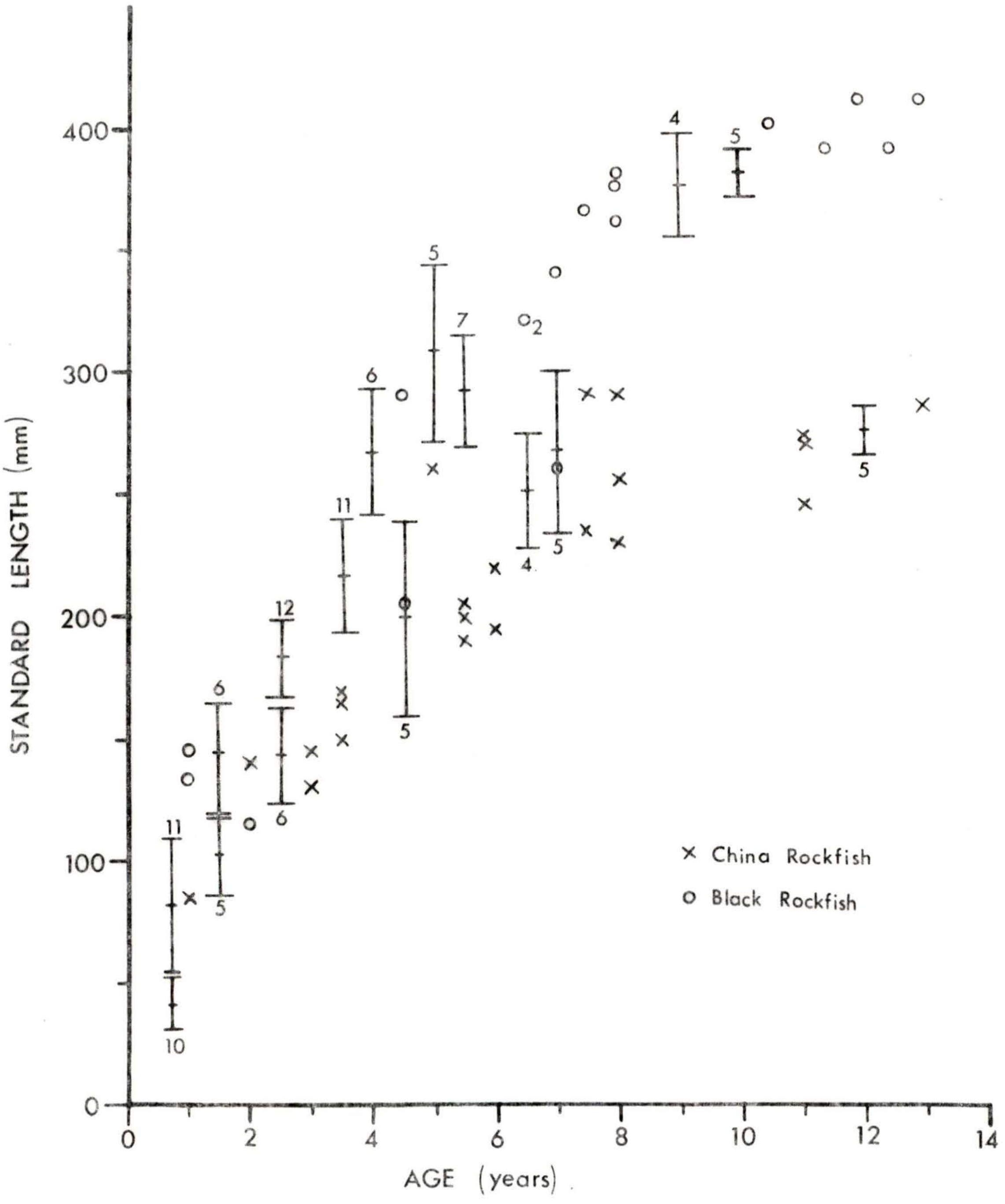
```
ROCKFISH MORPHOMETRICS      CHINA ROCKFISH

FILE    NONAME    (CREATION DATE = 04/25/79)

    CASE-N        SEX        AGE      LENGTH      WEIGHT

         1         2.        9.0        275.       714.6
         2         1.      999.0        275.       725.5
         3         1.      999.0        265.       582.1
         4         2.      999.0        240.       438.7
         5         2.        8.0        255.       600.2
         6         2.       13.0        285.       765.3
         7         2.        9.0        235.       420.4
         8         1.        7.0        280.       999.0
         9         1.        3.0        145.        77.4
        10         1.        9.5        220.       373.3
        11         2.        6.5        240.       400.1
        12         2.      999.0        255.       575.1
        13         1.       11.0        275.       608.5
        14         2.      999.0        270.       640.3
        15       999.        2.0        140.        88.1
        16         1.       11.0        245.       433.1
        17         1.        6.5        270.       591.7
        18         1.        6.5        255.       533.0
        19         1.       12.0        290.       741.2
        20       999.      999.0        270.       634.2
        21         1.        7.5        290.       782.8
        22         1.       11.0        270.       612.9
        23         1.        7.0        290.       740.0
        24         1.       17.0        280.       687.2
        25       999.        6.5        240.       387.7
        26         1.       12.0        270.       590.6
        27         2.       10.0        300.       775.7
        28         2.       12.0        270.       643.1
        29         2.        4.5        210.       296.7
        30         2.       12.0        270.       633.4
        31         2.       10.0        270.       565.4
        32         1.        9.0        270.       675.7
        33         1.        5.0        260.       557.9
        34         2.        9.5        270.       582.8
        35         1.      999.0        280.       679.7
        36         2.        7.0        280.       687.0
        37         1.        4.5        250.       525.6
        38         1.        8.0        290.       690.2
        39         1.        2.5        165.       138.2
        40         2.        5.5        205.       257.6
        41         2.        6.0        195.       204.5
        42         2.        3.5        170.       174.9
        43         1.      999.0        220.       384.2
        44         2.        7.0        230.       414.5
        45       999.        2.5        120.        64.9
        46         2.        2.5        120.        47.8
        47         2.        2.5        150.        99.8
        48         2.        8.0        230.       329.5
        49         2.        5.5        200.       217.6
        50         1.        4.5        185.       199.2
        51         2.       10.0        270.       522.5
        52         2.        7.0        255.       498.1
        53         2.       12.0        275.       651.1
```

```
ROCKFISH MORPHOMETRICS           CHINA ROCKFISH (cont.)

FILE    NONAME    (CREATION DATE = 04/25/79)

      CASE-N        SEX        AGE     LENGTH      WEIGHT

          54         2.        7.5       235.       374.7
          55         2.        3.5       165.       121.7
          56         1.        2.5       155.       113.9
          57         2.        4.5       170.       141.0
          58         2.        5.5       190.       188.5
          59         1.        4.5       185.       197.6
          60         2.        6.0       220.       322.3
          61         2.        1.5       115.        36.5
          62         1.        3.5       150.       106.9
          63       999.        0.0        35.         0.9
          64       999.      999.0        65.         7.2
          65       999.        0.0        35.         0.9
          66       999.        0.0        35.         0.9
          67       999.        0.0        40.         1.3
          68       999.        0.0        40.         1.3
          69       999.        0.0        33.         0.9
          70       999.        0.0        42.         1.6
          71       999.        0.0        40.       999.0
          72       999.        0.0        40.         1.2
          73         2.      999.0       230.       328.1
          74       999.        0.5        85.        15.2
          75       999.        1.0        85.        18.5
          76       999.        1.5       105.        31.1
          77         1.        2.5       150.        97.0
          78         2.        9.0       260.       507.0
          79         2.       10.0       255.       501.8
          80         2.        3.0       130.        52.4
          81         1.        9.0       235.       406.6
          82       999.        1.5        95.        22.4
          83       999.        1.5        90.        19.3
          84       999.        1.5       115.        39.4
```

```
ROCKFISH MORPHOMETRICS     BLACK ROCKFISH

FILE    NONAME    (CREATION DATE = 04/25/79)

     CASE-N         SEX          AGE      LENGTH      WEIGHT

          1          1.          4.0        235.       371.3
          2          2.         10.0        385.       999.0
          3          1.         10.0        370.      1210.0
          4          2.         13.0        410.       999.0
          5          1.          5.0        305.       712.0
          6          1.          5.5        305.       743.0
          7          1.          9.0        355.      1087.4
          8          1.          9.0        380.       999.0
          9          1.          9.0        385.       999.0
         10          1.          5.0        285.       539.0
         11          1.          5.5        255.       371.1
         12        999.          4.0        260.       421.9
         13          1.          4.0        250.       374.2
         14        999.          2.5        175.       135.4
         15        999.          3.5        185.       156.8
         16          1.         12.0        410.       999.0
         17          1.         16.0        400.       999.0
         18          1.          4.0        270.       496.8
         19          1.          5.5        300.       714.7
         20          1.          2.5        200.       228.7
         21        999.          8.0        360.       999.0
         22          1.          5.5        260.       434.7
         23          1.          4.0        290.       623.3
         24          1.          4.0        300.       674.2
         25        999.          2.0        115.        37.5
         26        999.          1.5        120.        42.2
         27          1.          1.0        140.        66.4
         28          1.          7.0        340.       908.8
         29          1.          3.5        240.       456.4
         30          1.          3.5        230.       246.7
         31          1.          7.0        260.       537.6
         32        999.          3.5        240.       360.8
         33          2.          5.0        350.       883.5
         34          1.          5.5        320.       811.7
         35          1.          3.5        240.       316.6
         36          1.          6.5        999.       815.0
         37          1.          3.5        215.       246.0
         38          1.         10.0        390.       999.0
         39          2.          5.5        290.       725.0
         40          1.          5.0        320.       897.0
         41          1.          4.5        290.       686.4
         42          1.        999.0        195.       193.6
         43          1.          6.5        320.       760.1
         44          1.          3.5        245.       331.4
         45          1.          1.5        185.       161.5
         46          1.          1.5        125.        44.8
         47          1.          3.5        260.       492.5
         48          1.         10.0        380.       999.0
         49          1.          2.5        220.       261.2
         50          1.          1.5        160.       107.6
         51          1.          2.5        140.        59.7
         52          1.          3.5        210.       244.6
         53          1.          5.5        310.       245.3
```

BLACK ROCKFISH (cont.)

```
ROCKFISH MORPHOMETRICS
FILE    NONAME    (CREATION DATE = 04/25/79)
     CASE-N          SEX          AGE       LENGTH        WEIGHT

       54             1.          6.5        320.          842.7
       55             1.          2.5        210.          247.5
       56             1.          5.0        280.          514.1
       57             1.         12.5        390.         1702.2
       58             1.         10.5        400.         1457.6
       59             1.         11.5        390.         1550.5
       60             1.          7.5        365.         1201.1
       61             2.          8.0        380.         1292.5
       62             1.         10.0        375.         1267.0
       63             2.          8.0        375.         1135.0
       64             1.          9.0        380.         1285.0
       65             1.          1.5        140.           64.6
       66             1.          1.5        135.           58.2
       67             1.          3.5        140.           66.8
       68             1.          2.5        160.          102.2
       69             1.          1.0        145.           72.6
       70             1.          2.5        165.          115.4
       71             1.          2.5        190.          196.5
       72             1.          3.5        185.          152.0
       73             1.          2.5        170.          119.9
       74             1.          4.5        205.          219.5
       75             1.          2.5        165.          107.7
       76             1.          2.5        185.          151.6
       77             2.          2.5        220.          243.8
       78           999.          0.0         75.            9.5
       79           999.          0.0         75.            7.9
       80           999.          0.0         75.            8.0
       81           999.          0.0         82.           11.2
       82           999.          0.0         65.            5.3
       83           999.          0.0         65.            5.9
       84           999.          0.0         68.            5.0
       85           999.          0.0         65.            4.4
       86           999.          0.0         65.            4.4
       87           999.          0.0         55.            3.1
```


STANDARD LENGTH (mm)
400
300
200
100
0
AGE (years)
0
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4
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12
14
× China Rockfish
o Black Rockfish
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Appendix C

FOOD HABITS

The following table lists items found in stomachs of field-caught specimens. Given are the fish standard length (mm), identity and number of items. Abbreviations used are: PC, *Petrolisthes* crab; CC, *Cancer* crab; SC, spider crab. In other instances contents were not distinguishable or identifications to genera were not made.

China Rockfish

Length	Contents
85	shrimp
85	PC claw; SC
90	2 PC; 2 crab legs
95	PC; crab
105	cottid; 3 crabs
115	empty
115	SC; shrimp
120	SC
120	bryozoans
130	empty
140	2 SC; PC; limpet
150	SC
150	PC claw
155	2 PC; CC
165	crab claw; fish
170	3 crabs; 2 caprellids
185	PC; crab claw
185	4 PC; CC
190	crab
200	SC
220	4 SC; CC; gastropod (3 mm)
222	8 PC; SC; CC
230	PC
230	3 SC
235	crab claw
235	6 crabs, bryozoan, shrimp, fish
250	2 SC; CC
255	10 crabs
260	4 crabs; CC
270	2 CC
270	PC, SC, CC, polychaete, gastropod
275	3 crabs; *Haplogurus*
280	SC; ophiuroids, bubble snail

Black Rockfish

Length	Contents
165	empty
170	crab larvae; caprellid
185	fish
190	herring
205	ctenophore; unid. plankton
365	50 ctenophores
375	herring; unid. plankton
375	herring
390	empty
390	*Idothea*; herring

VITA

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Date of Birth: 5 JUNE, 1953

Educational Institutions Attended, with dates of entering and leaving:

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Occidental College, California	1972 to 1975
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Publications: none

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A COMPARATIVE STUDY OF THE MOVEMENT HABITS
AND THEIR RELATIONSHIP TO BUOYANCY COMPENSATION
IN TWO SPECIES OF SHALLOW REEF ROCKFISH
(PISCES, SCORPAENIDAE)

Author [redacted]

Howard Ingram McElderry

October 1979