

A COMPARATIVE ANALYSIS OF THE BEHAVIOURAL ECOLOGY,
AGONISTIC BEHAVIOUR AND SOUND PRODUCTION IN
TWO SPECIES OF INSHORE EASTERN PACIFIC ROCKFISH
(GENUS SEBASTES)

by

VAL EDWARD FLETCHER

B.Sc., University of Victoria, 1969

A THESIS SUBMITTED IN PARTIAL FULFILLMENT
OF THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in the Department

of

Biology

ACCEPTED
FACULTY OF GRADUATE STUDIES

DATE

5 Feb 82

DEAN

We accept this thesis as conforming
to the required standard

J.E. McInerney

P.T. Gregory

K. Groot

C.W. Tolman

© VAL EDWARD FLETCHER, 1981

UNIVERSITY OF VICTORIA

JUNE 1981

*All rights reserved. This thesis may not be reproduced
in whole or in part, by mimeograph or other means,
without the permission of the author.*

Supervisor: Dr. J. E. McInerney

ABSTRACT

The relationship between ecology and social organization was examined in two species of rockfish inhabiting a shallow, semi-exposed rock reef on the west coast of Vancouver Island. The distribution and social behaviour of a schooling species, the black rockfish (Sebastes melanops) was compared to that of a benthic, solitary dweller, the china rockfish (S. nebulosus). Survey data were collected during a series of observational SCUBA dives on the study reef in which the position of tagged fish relative to reef markers was recorded. Laboratory studies involved a comparative analyses (between species) of agonistic behaviour and associated sound production. Behavioural and sound data were recorded during conspecific, pairwise, aggressive encounters.

Black rockfish primarily form egalitarian, non-polarized schools that show a certain degree of site attachment to particular regions of the reef. In contrast, china rockfish are exclusively solitary crevice dwellers, showing strong site attachment to a particular spot or home site on the reef. Limited evidence suggests they are territorial defending the home site and immediate area against conspecific intruders.

Black rockfish exhibit a greater tendency towards threat displays and intention movements during agonistic encounters than china rockfish. Multivariate statistical

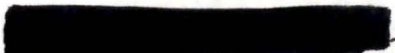
techniques applied to behavioural sequence data indicate that agonistic behaviour of both species can be adequately described as the relative strengths of two independent tendencies: attack and escape.

Sounds associated with various aggressive activities probably function to inhibit aggressive tendencies in the recipient fish. An analysis of selected temporal parameters of agonistic sounds indicate they are not likely to code for species specificity. Sound characteristics are rather variable and appear related to the level of motivation of the animal.

EXAMINERS:


J.E. McInerney


P.T. Gregory


K. Groot

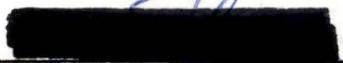

C.W. Tolman

TABLE OF CONTENTS

	Page No.
ABSTRACT	ii
TABLE OF CONTENTS	iv
LIST OF TABLES	viii
LIST OF FIGURES	ix
LIST OF APPENDICES	xii
ACKNOWLEDGEMENTS	xiii
DEDICATION	xv
INTRODUCTION	1
MATERIALS AND METHODS	3
FIELD STUDY	3
I. <u>Location and Description of Study Site</u> ...	3
II. <u>Study Site Preparation</u>	9
(i) Detailed Mapping of Study Site	9
(ii) Reef Position Markers	10
(iii) Fish Capture and Tagging	11
III. <u>Survey Methods</u>	12
LABORATORY STUDIES	14
I. <u>Capture, Transport and Holding of</u> <u>Experimental Animals</u>	14
II. <u>General Experimental Procedure</u>	16
III. <u>Behavioural Data Collection and</u> <u>Analysis</u>	18
IV. <u>Sound Recording and Analysis</u>	21
RESULTS	25
FIELD STUDY	25

I. <u>Distribution and Social Behaviour</u>	25
II. <u>Agonistic Behaviour</u>	32
LABORATORY STUDIES	33
AGONISTIC BEHAVIOUR	33
I. <u>Description of Behavioural Responses Exhibited During Pairwise Agonistic Encounters</u>	33
II. <u>Description of a Typical Agonistic Encounter</u>	57
(i) China Rockfish	58
(ii) Black Rockfish	59
III. <u>Observations on Factors Affecting the Outcome of an Encounter - Both Species Combined</u>	60
(i) Precedence (Initiator/Responder)	60
(ii) Size	60
(iii) Prior Residency	60
IV. <u>Comparison of Aggressive Behaviour Between Species</u>	61
(i) Bout Length	61
(ii) Threat Display and Overt Aggression	61
(iii) Relative Frequency of the Behaviour Components	63
(iv) Behavioural Sequences Analysis - Kinematic Graphs	66
V. <u>Causal Analysis</u>	72
(i) Temporal Associations of the Agonistic Behavioural Elements	72
(ii) Orientation of the Agonistic Activities	89

(iii) Models of Agonistic Behaviour	94
SOUND PRODUCTION	99
I. <u>Context of Sound Production</u>	99
II. <u>Agonistic Behaviour Patterns Associated With Sound Production</u>	99
III. <u>Description of Sounds - Both Species</u>	101
IV. <u>Comparison of Temporal Characteristics in the Two Species</u>	112
(i) Sound Burst Duration	112
(ii) Number of Pulses per Sound Burst	112
(iii) Pulse Interval	115
DISCUSSION	123
FIELD STUDY	123
I. <u>Behavioural Ecology of Reef Fishes</u>	123
II. <u>Social Behaviour and Reef Association</u>	126
(i) Black Rockfish	126
(ii) China Rockfish	127
III. <u>Agonistic Behaviour</u>	128
LABORATORY STUDIES	132
AGONISTIC BEHAVIOUR	132
I. <u>Interpretation and Function of the Agonistic Behaviour Patterns</u>	132
II. <u>Factors Affecting the Outcome of an Agonistic Encounter</u>	135
III. <u>Causation of Agonistic Behaviour</u>	136
IV. <u>Comparative Aspects of Agonistic Behaviour and its Relation to Behavioural Ecology in Both Species</u>	140

SOUND PRODUCTION	144
I. <u>Comparative Anatomy of the Swim Bladder - Sonic Muscle Complex</u>	144
II. <u>Mechanics and Acoustics of Sound Production and Reception in Rockfish</u>	147
III. <u>Relation Between Information Content, Biological Significance and Sound Characteristics</u>	150
(i) Amplitude	150
(ii) Duration	151
(iii) Repetition Rate	152
(iv) Number of Pulses per Burst	154
(v) Frequency	154
IV. <u>Species Specificity of Sounds</u>	155
V. <u>The Role of Sound Production in Agonistic Behaviour</u>	161
SUMMARY	164
LITERATURE CITED	166
APPENDICES	174

LIST OF TABLES

Table	Page No.
I. Rockfish species observed at the Ohia Island study site with information regarding their behaviour, abundance, distribution, and recapture during the tagging studies	26
II. Ranking of characteristics of the dominant fish in 30 agonistic encounters	62
III. Comparison between major groups of agonistic behaviour based on temporal associations using the techniques of cluster analysis, maximum spanning trees and factor analysis on identical data	88
IV. Summary of sound duration characteristics in two species of rockfish. Sounds were produced during agonistic encounters between conspecifics, or an individual and its mirror image	113
V. Summary of the number of pulses per sound burst in two species of rockfish	114

LIST OF FIGURES

Figure	Page No.
1. Location of Ohlat Islet study site	4
2. Topographic map of the study site	6
3. Study site showing the distribution of the combined tagged population of A. Black Rockfish B. China rockfish	28
4. Lateral view of dominant china rockfish opercular displaying, submissive fish on left is tilting	39
5. Lateral and frontal views of a china rockfish in full display	42
6. Two black rockfish carouselling	46
7. Two china rockfish engaged in a mouth fight	49
8. Percentage frequency of performance for individual elements of agonistic behaviour in two species of rockfish	64
9. Kinematic graph depicting the sequence of agonistic behaviour components in dominant black rockfish	67
10. Kinematic graph depicting the sequence of agonistic behaviour components in dominant china rockfish	69
11. Dendrogram showing the temporal relationship between aggressive behaviour elements during black rockfish encounters	73
12. Dendrogram showing the temporal relationship between aggressive behaviour elements during china rockfish encounters	75
13. Maximum spanning trees for rockfish aggressive behaviour constructed from preceding/following matrices. A. Black rockfish B. China rockfish	78
14. Cosine vector model - black rockfish behaviour	83

Figure	Page No.
15. Cosine vector model - china rockfish behaviour	85
16. Scattergram showing the relationship between the attack (ordinate) and escape (abscissa) tendencies over a 30 min period for 27 black rockfish encounters	90
17. Scattergram showing the relationship between the attack (ordinate) and escape (abscissa) tendencies over a 30 min period for 23 china rockfish encounters	92
18. Diagrammatic model of the agonistic behaviour of black rockfish	95
19. Diagrammatic model of the agonistic behaviour of china rockfish	97
20. Oscillograms of sound bursts emitted by the same china rockfish during two successive tail beats	102
21. A. Oscillogram of a higher amplitude secondary burst within a primary burst of sound recorded from a china rockfish during a mirror image interaction. B. Oscillogram of a black rockfish sound burst followed by three single pulses or "pops". C. Oscillogram depicting short initial rise time of amplitude envelope followed by a gradual decrease in amplitude near end of china rockfish sound burst	105
22. A. Oscillogram of a secondary burst recorded from a china rockfish showing several changes in amplitude and pulse interval. B. Oscillogram of a portion of a long duration sound produced during a black rockfish opercular display	107
23. A. Oscillogram of a china rockfish sound consisting of relatively low amplitude, lightly damped pulses. B. Oscillogram of a segment of the same sound depicted in A, at a later point in time. C. Oscillogram showing a change in amplitude and damping characteristics of a china rockfish avoidance sound	110

Figure

Page No.

24.	A. Comparison diagram of the pulse interval in seven aggressive sounds of black rockfish individual MEL-2. B. Comparison diagram of the pulse interval in ten aggressive sounds of china rockfish individual NEB-4	116
25.	Comparison diagram of the pulse interval in four avoidance sounds of china rockfish individual NEB-4	119
26.	Comparison diagram of the pulse interval in aggressive sounds among four black rockfish (top) and nine china rockfish (bottom)	121
27.	A. Morphology of the extrinsic swim bladder musculature in the black rockfish. B. Morphology of the extrinsic swim bladder musculature in the china rockfish	145

LIST OF APPENDICES

Appendix	Page No.
I. Listing of sex, weight, and standard length for individual fish used in agonistic encounters	174
II. Preceding/following matrix for black rockfish aggressive behaviour	176
III. Preceding/following matrix for china rockfish aggressive behaviour	178
IV. Factor loadings for each of 20 black rockfish behavioural elements on 3 factors	180
V. Factor loadings for each of 24 china rockfish behavioural elements on 5 factors	182
VI. Summary of sound data used for analysis	184
VII. Computer printout of a power spectral density derived from a china rockfish aggressive sound	186

ACKNOWLEDGEMENTS

I would like to express my sincere appreciation to my supervisor Dr. John E. McInerney for his support and inspirational attitude maintained throughout this study. Despite the fact I entered the biological field "through the back door", his confidence in my abilities was gratifying. Drs. Patrick T. Gregory, Kees Groot and Charles W. Tolman kindly read the manuscript and offered constructive criticism as well as useful suggestions during personal consultations.

The field work conducted at Ohiat Islet was part of a combined study with Howard McElderry who was interested in movement habits and buoyancy compensation in the same species of rockfish. I am greatly indebted to Howard for introducing me to the operational techniques required for all phases of the field work. Also, I would like to thank him for allowing me to use his excellent map of the study site. I will not forget his friendship and our many pleasurable dives together on Ohiat. Several other people deserve thanks for assistance on collection or observation dives: Kathleen Cole, Joachim von Carolsfeld, Philip Mladenov, William Roland and Mark Williams.

I would also like to acknowledge the use of the Bamfield Marine Station facilities provided through the auspices of the Western Canadian Universities Marine Biological Society. All the staff at B.M.S. were most helpful, especially Phill Smith, who freely provided technical assistance.

Craig Dickson, of the Department of Linguistics, University of Victoria, deserves special mention for his invaluable help in the analysis and interpretation of rockfish sounds and also for the many hours of theoretical explanations and discussions. Murray Fletcher also provided valuable counsel on the physical characteristics of sound and their analysis.

Thanks are also due Judi Fletcher for typing the final copy of this thesis. Finally, I would like to thank my wife Jeanne for typing the rough draft and especially for her patient support and encouragement.

DEDICATION

To Father

INTRODUCTION

Rockfish (genus Sebastes) comprise a significant fish group in terms of abundance and diversity in eastern North Pacific waters. Hart (1973) describes 37 species off the British Columbia coast. Rockfish maintain a high degree of congeneric syntopy with up to 10 species recorded at a sampling site (pers. obs.).

Nearshore habitats (depths < 45 m) include the kelp bed canopy, areas of rock rubble, deeply creviced solid rock and mixed sand shell bottom. Two broad assemblages may be identified within this group based on social behaviour and habitat utilization. The first includes schooling, suprabenthic species that occupy the water column adjacent to rock reefs, space in and around the kelp canopy, or regions of open water above a sand shell substrate. The second consists of solitary, benthic species that inhabit crevices and interstitial spaces of rock rubble or hover in close proximity to solid rock substrate.

The objective of the present study, comprised of both field and laboratory aspects, was to elucidate the relationship between ecology and social behaviour (socio-ecology) in representative species from each assemblage: the black rockfish, Sebastes melanops (Girard) from the schooling species and the china rockfish, S. nebulosus, from the solitary species. Field work focussed on a qualitative description of the behavioural ecology of both species. Since agonistic

behaviour is a major factor in mediating social spacing and hence social organization in fishes, the purposes of the laboratory study were to: (a) document agonistic behaviour in both species through the preparation of an agonistic ethogram or behavioural catalogue, (b) develop a model of agonistic behaviour for both species in terms of underlying causal mechanisms, and (c) describe the relationship between sound production and agonistic behaviour and determine if sounds are species specific.

MATERIALS AND METHODS

FIELD STUDY

I. Location and Description of Study Site

The study site was a rock reef on the north side of Ohlat Islet ($48^{\circ} 51'N$; $125^{\circ} 11'W$), one of the Deer Group of islands in Barkley Sound on the west coast of Vancouver Island, British Columbia (Fig. 1). Ohlat Islet was about 1.5 ha in area and above mean high water the topography consisted mainly of sloping, creviced bedrock rising to a dense crown of coniferous forest.

Figure 2 illustrates reef topography. Below mean high water, the solid rock slope levelled out to form a broad shelf at about 3 m in depth. The shelf extended to a width of about 15 m and gradually sloped to a depth of 10 m before dropping off to form a rock wall. Several plateaus rose from the shelf each supporting a seasonal growth of bull kelp (Nereocystis luetkeana). The largest plateau also featured a small rock outcrop, visible above the water's surface only during minus tides. A boulder strewn trench ran almost the entire length of the juncture between shelf and shoreline.

Below the shelf the nearly vertical rock wall ended abruptly at about 20 m in a gently sloping mixed sand shell bottom. The wall face was composed of deeply creviced solid rock with numerous ledges, overhangs and pockets of

Figure 1. Location of Ohlat Islet study site. Inset map shows location of Barkley Sound on the west coast of Vancouver Island.

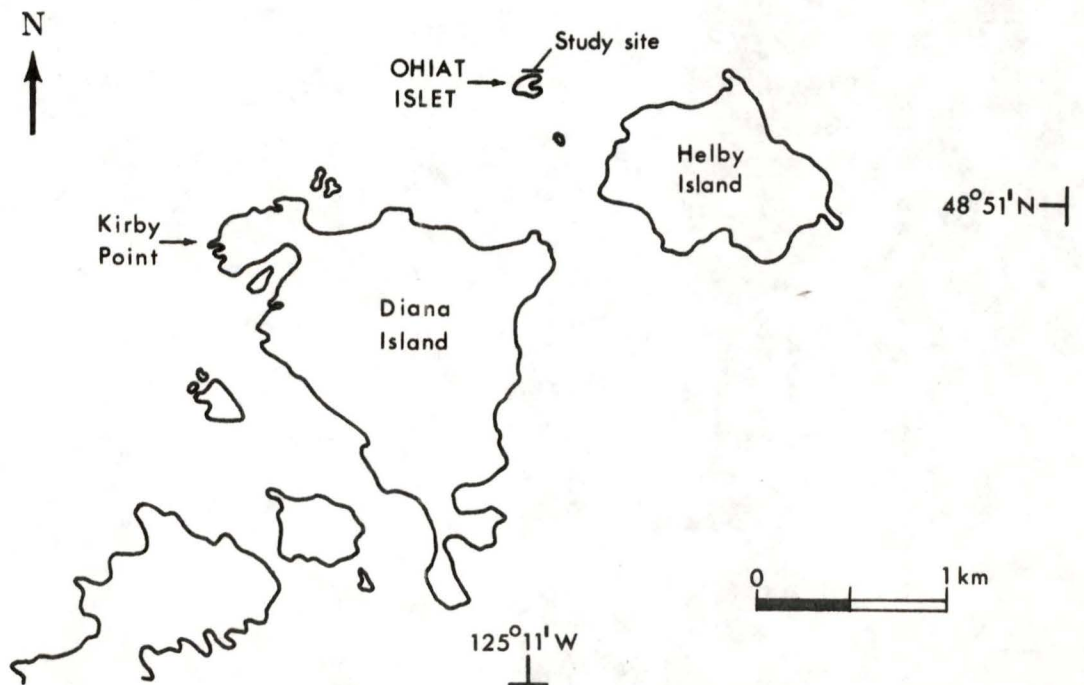
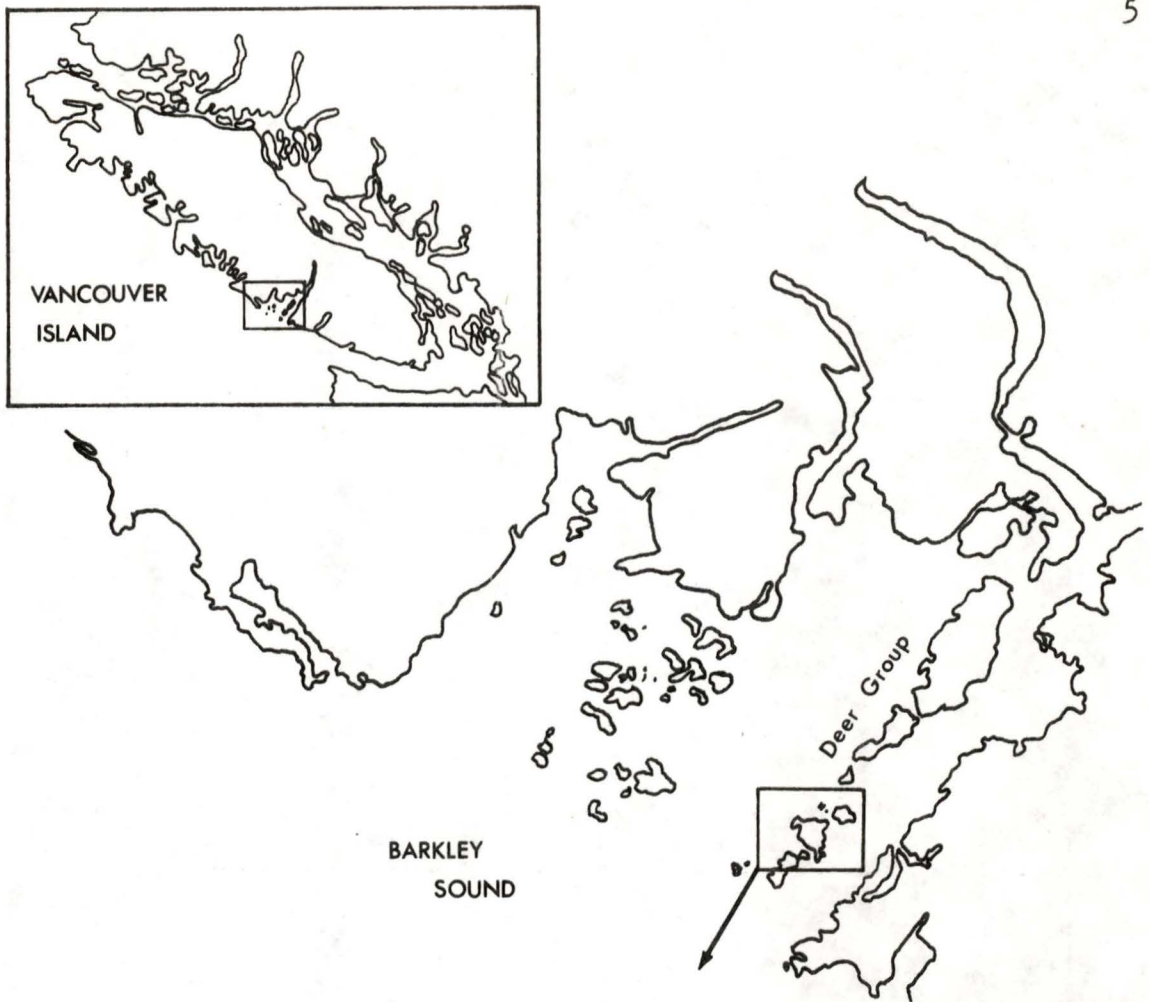
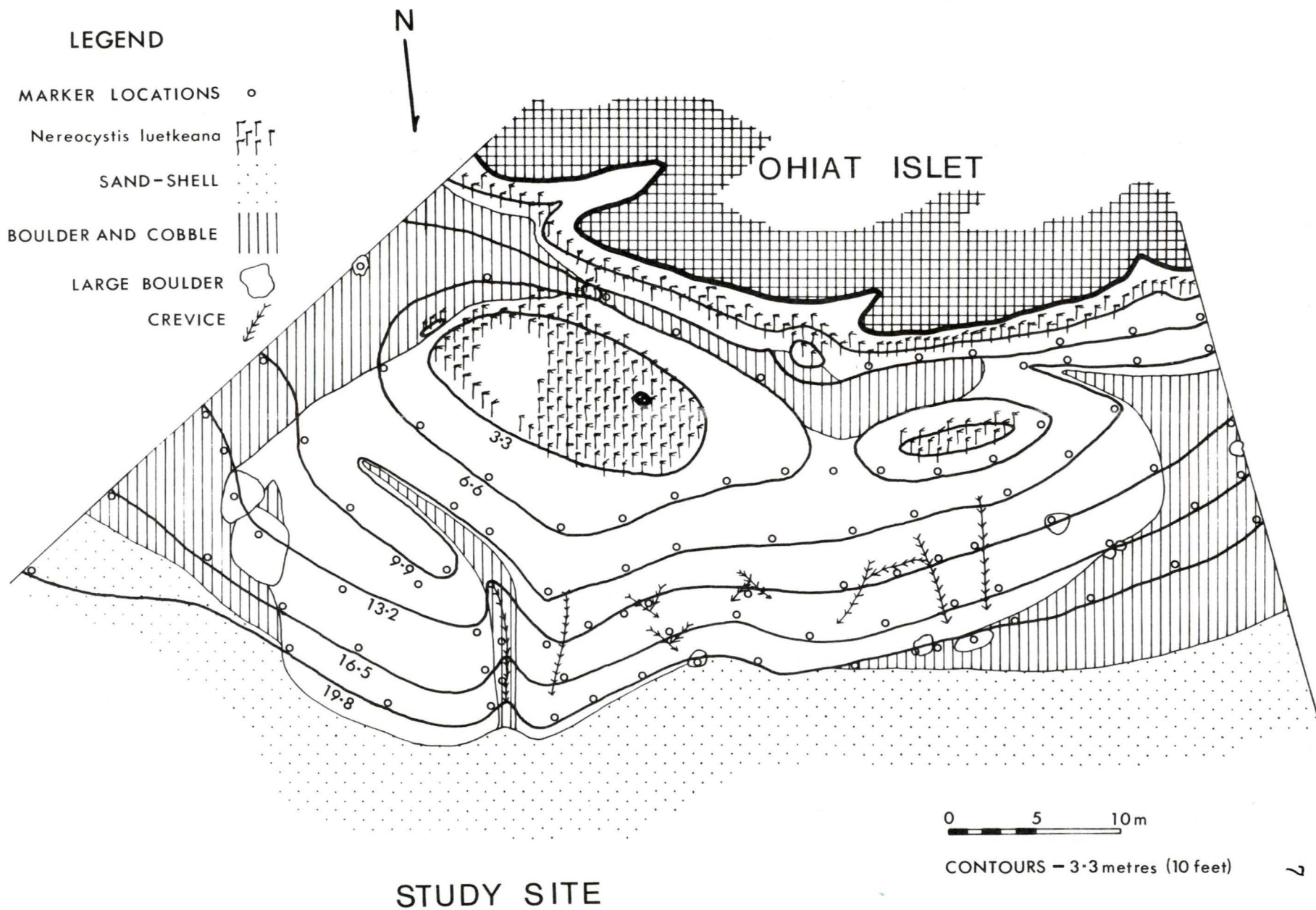


Figure 2. Topographic map of the study site.



coarse sand and boulders. Flanking the solid rock portions of the reef were slide-like areas of cobble with occasional piles of boulders. Two noteworthy features of reef topography were located on the west side of the study area: a large crevice extending from 13 m to 20 m in depth and a particularly deep overhang (3 m) formed by two large boulders.

The bull kelp Nereocystis luetkeana dominated shallow areas of the reef during summer months. The kelp forest began development as small plants in late March, formed a thick canopy by July and reached maturity in early August. Because of natural die off and the impact of waves generated by storms, plants were progressively broken up and dislodged from the substrate throughout the fall and winter months, leaving barren rock by late February. Other large brown algae (Laminaria species) were also common, growing among the Nereocystis plants.

Below the algal zone large numbers of invertebrates were found, including the sea urchins Strongylocentrotus franciscanus and S. drobrachiensis, the abalone Haliotis kamtschatkana, the cup coral Balanophyllia elegans, the starfish Pycnopodia helianthoides, the plumerose anemone Metridium senile and the scallop Hinnites multirugosus. Several octopi, Octopus dophleini, were present on the reef, residing in various crevices and small caves.

Water movement in the form of open ocean swells, wind generated waves (chop) and tidal currents were present at Ohia Islet. The study site was afforded limited protection

from the direct impact of incoming swells from the southwest, as the reef had a northerly exposure. Also, Kirby Point, located on Diana Island to the south (Fig. 1) likely served to dissipate and deflect swell action. Currents were caused by a combination of factors. Tidal currents, predominant at deeper areas of the reef (depths > 6 m), were typically moderate to weak and flowed in an easterly or westerly direction, depending upon tide cycle (mixed semi-diurnal). Surface currents (depths < 6 m) were primarily caused by wind generated waves. Winds, usually blowing from the southwest during summer months generated surface currents flowing towards the northeast. Similarly, northerly winds occurring during winter months produced south flowing currents. The shallow shelf area of the study site can be considered a high energy area in terms of water movement, as the effects of all three forces (swell, wind and tide) were expressed in this zone. Along the dropoff and rock wall areas, tidal action was the major contributor to water movement. However, on one occasion during a winter storm, swell action was present to a depth of 18 m.

II. Study Site Preparation

(i) Detailed Mapping of Study Site

Elementary survey techniques were used to prepare a topographic map of the site. A base line of nylon cord was established near the rock wall and sand shell bottom interface. Transects were swum at right angles from the base

line to the shore, at 7 meter intervals along the base line using a submersible compass. While ascending a transect, the reef slope was determined by measuring diagonal and vertical distances using a tape measure and an oil-filled depth gauge. A topographic map of the reef was then drawn, using basic trigonometry to calculate reef contours. Subsequent dives allowed additional details regarding small crevices, overhangs, boulders, kelp beds, etc. to be incorporated.

(ii) Reef Position Markers

To facilitate diver recognition of particular areas of the study reef, a system of markers was established. Square plexiglass markers (2.5 cm x 4 mm thick) were numbered on their rear surface with enamel and a contrasting background colour was then applied. A small hole drilled in a corner and threaded with a short length of copper wire allowed each marker to be attached to concrete piercing nails hammered into hairline fissures on the reef. In areas unsuitable for concrete nails, such as rock rubble, markers were attached to bricks painted fluorescent orange. Markers were attached at 3.3 m contour intervals from 6 m to 18 m in depth. Horizontal spacing was governed by reef complexity and water clarity: a greater number of markers were placed in rock rubble and highly creviced areas rather than on regions of smooth rock. In any case, markers were not placed more than 3 m apart, the minimum discernible distance during poor visibility conditions. Subsequent to preliminary data

collection dives, "home site" markers were placed at particular locations frequented by individually identified (tagged) fish.

(iii) Fish Capture and Tagging

A tagging program was conducted to allow individual recognition of fish associated with the reef. Species, standard length, capture location (to the nearest reef marker) and tag number were recorded underwater on plastic slates. Where feasible, fish were released at or near the point of capture to minimize stress caused by pressure changes.

Various techniques were used to capture different species. Black rockfish were caught with gill nets of 5 cm to 10 cm stretched mesh. Nets were set in locations known to be regularly traversed by schools of black rockfish, either at the surface on the fringes of the kelp bed or at depths of up to 10 m. Nets were deployed for up to 2 hours depending upon the number of nets involved, their location, and capture rate.

The crevice dwelling china rockfish were captured using anaesthetics and an underwater angling technique. Two fish anaesthetics were employed: Quinaldine (2-Methylquinoline; Eastman Kodak) mixed at 0.5 g/l of 2 Propanol, and MS-222 (Tricane Methanesulfonate; Sandoz) mixed at 2 g/l of seawater. Anaesthetic solutions were held in pliable, 9 l plastic water containers to which a 1 m delivery tube (9 mm ID) was attached with a small length of flexible plastic tubing. By

squeezing the container between the arm and body a controlled volume of anaesthetic was directed at the mouth of the fish. This release was synchronized with inspiration movements of the fish to achieve efficient delivery of anaesthetic. Two or three doses applied in this manner would incapacitate the fish and allow capture by hand or net bag.

An alternative method of capture suggested by McElderry (1979) consisted of a simple underwater fishing pole (a short length of nylon line attached to a 1 m length of PVC pipe) and a small lure with barbless hook. Jiggling the lure at the entrance of an inhabited crevice usually resulted in capture. The struggling fish was then subdued by the diver running a free hand down the line and grasping the fish around the mouth and gill area.

Fish were tagged using a modified, brightly coloured "spaghetti" anchor tag (Floy Tag and Mfg. Co., Model FD-67). The Floy tag was modified by attaching a thin piece of numbered plastic (6 mm x 12 mm) at its trailing end. This allowed the numbers to be read at distances of up to 4 m under optimal light and water clarity conditions. Tags were inserted with a tagging gun (Floy Tag and Mfg. Co., Model FDM-68) into the musculature at the base of the spinous portion of the dorsal fin.

III. Survey Methods

Observations on the social behaviour of both species were based on 224 SCUBA dives from October 1976 to February

1978 and May to August 1978. The average dive length was 33 minutes, with a total observation time of about 123 hours. Ohlat Islet was the primary diving location with 144 dives; 80 additional dives were made at various regions in south-east Barkley Sound.

Normally, 2 dives were conducted within any 24 hour period. Dives were scheduled to allow study of behavioural changes among the dawn, daytime, dusk and night periods. However, the majority of dives took place during daylight hours under ideal observational conditions. Ideally, dives should have been made on a randomly chosen time schedule within each of the four periods. Various constraints including daily wind patterns (affecting access to the dive site and conditions underwater) and decompression limits made this strategy impractical, although some degree of variability was present. Lights were required during low-light and night dives, and may have biased results through a tendency to attract fish.

Initially, data collection dives consisted of swimming randomly chosen depth contours and recording on plastic slates the location (nearest reef marker), number of individuals (whether a schooling or solitary species) and position in water column (open water, hovering near bottom, perched on substrate, etc.) for both tagged and untagged fish. Once enough information was available on movement and distribution patterns, sighting efficiency was increased by searching only areas of the reef known to have large

concentrations of tagged and untagged fish. Such regions included the kelp bed and outer shelf area for the schooling black rockfish, and selected crevices, overhangs and caves for solitary china rockfish.

Successive search patterns were varied between dives to eliminate any herding effects on the fish. Disturbance was minimized by observing fish from as great a distance as possible while still obtaining the required information. This procedure was hindered during periods of low visibility such as plankton blooms or stirred up bottom sediments during storms. Environmental data, pertinent to fish movement, was also recorded for each dive: visibility, direction and speed of current, tide height, and wave conditions.

Observations during the additional dives outside the study area were more casual, as the primary purpose was the collection of fish for experimental work. However, useful information on species sighted, substrate type and social behaviour, was recorded.

LABORATORY STUDIES

I. Capture, Transport and Holding of Experimental Animals

Periodically, throughout 1976-1978, china and black rockfish were collected from a number of sites in Barkley Sound, using capture techniques described previously for the tagging program. Precautions were taken to prevent the

over expansion and subsequent damage to swim bladders in china rockfish when brought to the surface. At depths greater than 10 m, following suggestions by Gotshall (1964), an 18-gauge hypodermic needle was inserted through the abdominal wall and into the swim bladder. The fish was then oriented in a head-down position to allow escape of gases and partial deflation of the bladder. Black rockfish were caught at depths of less than 4 m, and thus could readily adapt to surface pressures. Fish were transported by boat to the Bamfield Marine Station in large plastic buckets and placed in holding tanks for acclimatization. After several weeks, and once fish were on a regular feeding regime, they were transferred to aquarium facilities at the University of Victoria. For the 3 1/2 hour road trip the fish were first placed in large, heavy gauge polyethylene bags with just enough sea water added to submerge them. The rest of the bag was filled with oxygen, creating a tent-like dome over the fish. The bag was tied off and placed in a styro-foam cooler and the lid securely fastened. Halfway through the trip the oxygen supply was replenished.

At the university, fish were maintained in 6 mm thick plate glass aquaria measuring 91 x 46 x 46 cm, holding 192 l of seawater. Two fish were housed in each aquarium, separated by a partition of opaque plexiglass. Walls of adjacent aquaria were also covered with black polyethylene so that all fish were kept in visual isolation. Aquaria were devoid of cover of any type, except for an airstone

supplied for each fish. Sea water at 10 °C was supplied at 151 l per minute to each aquarium via a closed, recirculating sea water system of 20,000 l capacity. Natural photoperiods were established using artificial lighting (cool white fluorescent) controlled by a photo cell placed outdoors. Fish were fed twice weekly to satiation on a diet of thawed shrimp or fresh water smelt, depending upon availability.

II. General Experimental Procedure

Experimental studies on aspects of agonistic behaviour and associated sound production were conducted from December 1977 to March 1980. Experiments were scheduled during the same daily time period (early afternoon) at a point midway between the twice weekly feeding regime. This may have lessened the effects of diel fluctuations or hunger on aggressive level. Seasonal variations were not controlled for, due to time limitations.

Several precautions were taken to minimize disturbance before and during an experiment. At least one hour prior to the starting of an experiment, a hydrophone was suspended in the aquarium and air stones, if present, turned off. Next, a blind, constructed from a large sheet of polyethylene, was set up 2 m from the aquarium to shield the observer. Finally, audio and video recording equipment was set up behind the blind and additional overhead lighting (one 400 W incandescent bulb) directed towards the aquarium to supplement room light.

An experiment was begun by removal of the opaque plastic partition separating the two fish. Subsequent agonistic behaviour was recorded using a portable video tape recorder (Sony, Model AV 3400). Initially, sounds associated with the various behaviour patterns were recorded on the audio track of the video tape. Later, higher quality sound recordings were obtained with a separate tape recorder (Section IV). Synchrony between the audio and video signals was maintained by an audible "countdown", coupled with a visual signal at the start of an encounter. Each encounter was allowed to proceed for 30 minutes and terminated with the replacement of the partition, once again isolating the fish. Immediately following the completion of a series of experiments, selected fish were transferred to different aquaria in order to face a new opponent for the next agonistic interaction.

A total of 50 agonistic encounters were staged between conspecifics. Twenty-four black rockfish were involved in 27 interactions and 21 china rockfish in 23 encounters. Both sexes were represented among china rockfish. Sexing black rockfish was difficult, since most were immature, although several larger fish were identified as males. Appendix I lists sex, weight and standard length for all experimental animals. Each fish took part in 1 to 4 encounters, depending upon the availability of replacement animals. The minimum time span between experiments for fish used more than once, was 4 weeks, in all but three instances.

Freshly killed experimental animals were blot dried with paper towels and weighed to the nearest 0.1 g on a triple beam balance (Ohaus Model 700). Standard length was then measured to the nearest 0.1 cm. Finally, specimens were opened ventrally with a longitudinal cut and the gonads examined to determine sex.

III. Behavioural Data Collection and Analysis

Thirty-six mutually exclusive behaviour patterns were recognized during each encounter. The behaviour of the dominant fish in each pair was subsequently transferred from the video tape to a written record, using a 20-channel Esterline-Angus operations recorder with a chart speed of 7.62 cm (3 inches) per minute, coupled to a keyboard. When sufficient (statistically meaningful) records of the frequency, duration and sequence patterning of behavioural elements were obtained in this manner, a later series of experiments (numbers 35 to 50) were conducted to obtain sequential and sound production data only. Behavioural sequences were recorded by code words spoken into a portable cassette tape recorder and subsequently transcribed into written records.

Sequential data from all encounters were pooled for each species and recoded into number sequences. A computer program was then written to summarize these data in a preceding/following matrix with 31 rows and columns, each corresponding to one behaviour pattern of the dominant fish.

The initial (preceding) acts were listed in the rows and the subsequent (following) acts in the columns. Thus, each entry in the column of the matrix represented the number of times each response followed any other, and similarly, each row entry represented the number of times each response immediately preceded another.

Multivariate analysis provides several methods for the treatment of ethological data cast in a preceding/following matrix. These methods primarily aid in the interpretation of data through grouping and visual representation, since the raw data matrix is often difficult to assimilate and explain. Because of this process, multivariate techniques also help generate more refined hypotheses concerning the data. Two such techniques, cluster analysis and factor analysis, were applied to the data matrices.

Cluster analysis is one technique that is often used in the analysis of multivariate data summarized in a two-way table. It is a general term for a variety of analytic techniques that seek to discover the inherent relationships that exist within the data, without reference to any externally imposed classification (De Gheet, 1978). Following methods outlined in Morgan et al. (1976), a triangular "similarity" table was constructed from the raw data matrix. The similarity between two elements of the table was a measure of their proximity or temporal association in a behavioural sequence. The similarity table was then

transformed into a dendrogram (a 2-dimensional pictorial representation of the similarities) using single link cluster analysis (Morgan et al., 1976).

One limitation of the single linkage method is the phenomenon of chaining, which is related to a loss of information when transforming the preceding/following data into a dendrogram. Another method of representing the data, a maximum spanning tree (MST), was used in the present study. It alleviates some of the problems associated with chaining. The MST provides more information than a dendrogram, as it is a kind of "half-way house" between data and dendrogram (Morgan et al., 1976). Morgan et al. (1976) present more complete details on the theory and construction of maximum spanning trees.

The technique of factor analysis is another multivariate method which can aid in identifying common casual factors in behaviour. Again, factor analysis begins with a preceding/following matrix, calculates an array of correlation coefficients among these elements, and attempts to determine whether the interrelations in the data can be expressed in terms of a smaller set of factors. If so, these new variables are associated with two or more of the behavioural elements, and can be said to "explain" the original correlations (Hinde, 1970). Kim (1975) points out the most distinctive characteristic of factor analysis is its data-reduction capability, and mentions one common application of the

technique is "the exploration and detection of patterning of variables with a view to the discovery of new concepts".

IV. Sound Recording and Analysis

Sounds for both species were recorded during intra-specific agonistic encounters. Initial recordings were made with an individual interacting with its mirror image. One half hour before an experiment, a large mirror covered with an opaque plexiglass shield was placed at one end of the aquarium. A hydrophone was then positioned centrally, 15 cm below the water surface. Subsequently, the shield was removed, and after several seconds the fish would produce sound concurrent with an aggressive response towards the "intruder". Although this technique produced high quality sounds in terms of duration and amplitude, later experiments involved interactions between two fish of similar size (Section II). Each fish was now reacting to normal behavioural feedback from its opponent, not simply its mirror image. Also, sounds emitted by both the submissive and dominant fish could be monitored.

Recordings were made with a Uher 4000 Report-L tape recorder at a tape speed of 19 cm/s connected directly to a Bio-Acoustik Model 901 hydrophone. The recorder's frequency response at 19 cm/s was 40 - 20,000 Hz. The hydrophone had a frequency response of 10 - 10,000 Hz and a sensitivity of -90 db (relative to a pressure of 1 microbar). Preliminary sound analysis involving amplitude and temporal parameters

was conducted using a direct-writing oscillograph (Honeywell Visicorder Model 1806A) running at a chart speed of 25 cm/s. Maximum frequency resolved at this chart speed was 500 Hz. A dual beam storage oscilloscope (Tektronix Model 5113) fitted with a dual trace amplifier (Tektronix Model 15A18N) and time base amplifier (Tektronix Model 5B10N) was used for more detailed study. A Tektronix Model C-5B oscilloscope camera was used to obtain permanent records of the oscilloscope traces. Occasionally, low level sounds were masked somewhat by high frequency background noise, likely tape hiss and amplifier noise. These sounds were fed through a low-pass filter (350 Hz) to remove high frequency components prior to analysis.

Several temporal and enumerative parameters of the recorded sounds were measured for each species: (1) the duration of sound bursts, (2) the number of pulses within a burst (a burst consisted of a series of pulses), and (3) the pulse interval (duration between the onset of successive pulses). Pulse interval was measured for randomly chosen pulses using a scale with an estimated precision of ± 1 ms. Successive pulses slowly decreased in amplitude and this, combined with signal damping, made the end point of the burst difficult to determine. The duration of a burst was standardized by measuring from the start of the first pulse to a point after the last recognizable pulse equal to the time between the penultimate and last pulses. This gave a

measurement somewhat shorter than the actual duration of the burst.

Although emphasis was placed on a study of specific temporal sound characteristics, limited analyses of spectral parameters were also conducted. Four samples of high quality sounds recorded from one particular china rockfish interacting with its mirror image were selected for study. Sound spectrum analysis produces a power spectral density, a three dimensional picture of the signal with frequency, time and intensity displayed simultaneously. Basically, the process involved two steps. First, the analog signal (amplitude or voltage as a function of time) from the tape recorder was converted to digital form. The second step involved transformation of the time-series data into a power spectral density representation, using a fast Fourier transform algorithm. Both steps were carried out on a Digital LSI 11 minicomputer; the resulting power spectra were then transferred to an IBM System 370/Model 3031 computer main frame for storage and printout. Fourier's theorem simply represented, states that any complex, periodic wave form can be represented as the sum of a number of sinusoidal waves of different frequencies, amplitudes and phases (Simpson, 1974). The spectrum of a sound wave specifies these three parameters of the wave's sinusoidal components. The basic pattern of the complex wave repeats with the same periodicity as the lowest frequency sine wave component, called the fundamental

frequency. For periodic waves, the higher frequency components are integer multiples of the fundamental frequency. Aperiodic waves may have components at all frequencies, not just those at multiples of the fundamental frequency (Denes and Pinson, 1963).

RESULTS

FIELD STUDY

I. Distribution and Social Behaviour

Rockfish formed a major group of fishes on Ohiat both in biomass and diversity. Table I shows the species of rockfish observed together with abundance, behaviour, distribution and tagging information. Two distinct groups emerged in relation to spatial distribution and social behaviour: (a) pelagic schoolers that maintain visual contact with the reef, e.g. the black rockfish (S. melanops) and (b) solitary bottom dwellers, e.g. the china rockfish (S. nebulosus).

A total of 90 black rockfish were tagged with 61 (68%) observed on subsequent dives. Seventy-five percent of these re-sightings were recorded from 1 to 10 times with the remainder seen more often. Population size was about 300 fish, based on visual estimates of the relative proportions of tagged versus untagged fish. A steady decline in observations of tagged fish occurred throughout the dive sequence, presumably due to emigration and mortality. Considerable variations were also recorded between numbers of tagged fish seen on successive dives. This reflects one of the difficulties in observing a dynamic group of fish moving in 3 dimensions: it was virtually impossible to see all members of the group from any one position.

The general pattern of distribution of tagged black rockfish, based on observations of the combined tagged

Table I. Rockfish species observed at the Ohiat Islet study site with information regarding their behaviour, abundance distribution, and recapture during the tagging studies.

Species	Social Behaviour	Abundance	Distribution	No. Tagged	No. Inds. Recaptured*
<u>S. flavidus</u>	Schooling	C	K,SB	10	5
<u>S. melanops</u>	Schooling	C	K,SB	90	61
<u>S. miniatus</u>	Schooling	U	SB	--	--
<u>S. mystinus</u>	Schooling	U	SB	1	1
<u>S. pinniger</u>	Schooling	U	SB	--	--
<u>S. caurinus</u>	Solitary	C	B	8	4
<u>S. maliger</u>	Solitary	C	B	20	15
<u>S. nebulosus</u>	Solitary	C	B	24	20
<u>S. nigrocinctus</u>	Solitary	R	B	--	--
<u>S. paucispinis</u>	Solitary	U	B	--	--

* Number of tagged fish observed on subsequent dives. Recapture data were collected on 65 dives during the period June - September 1977 for all species except the china rockfish (S. nebulosus); an additional tag - recapture study was undertaken during July - August 1978 with 10 data collection dives.

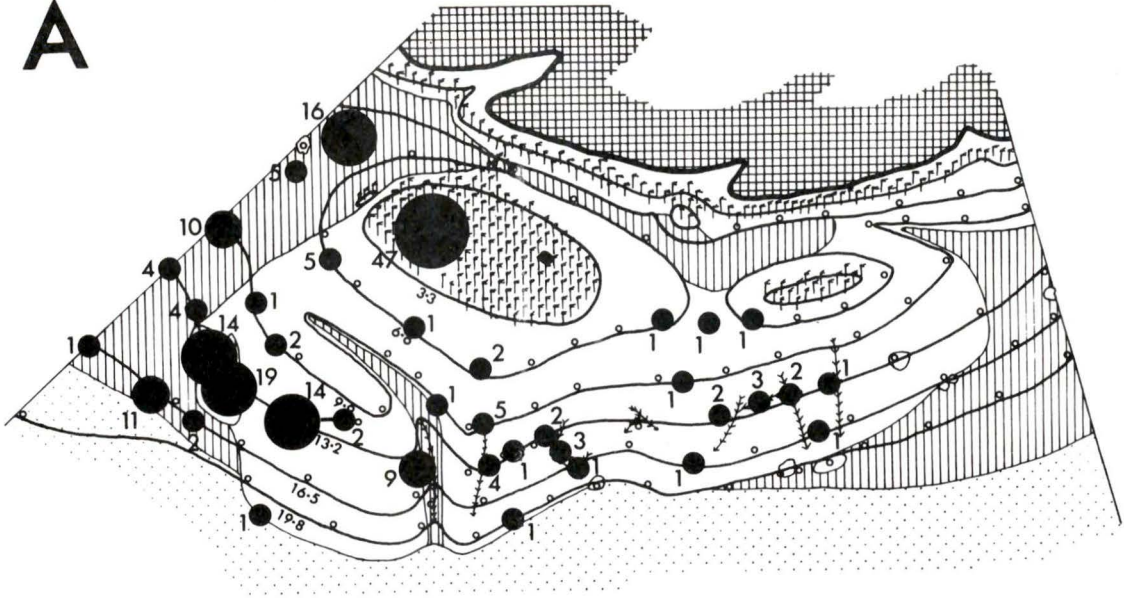
Key: C - Common: seen on every dive
 U - Uncommon: not seen on every dive, but often found
 R - Rare: seen once or twice for all dives
 B - Benthic: hover near or contact substrate
 SB - Suprabenthic: occur in water column but maintain visual contact with substrate
 K - Kelp Bed: found inside and on fringes of kelp bed

population, is shown in Fig. 3A. This pattern was followed closely by the population as a whole because of their schooling tendencies.

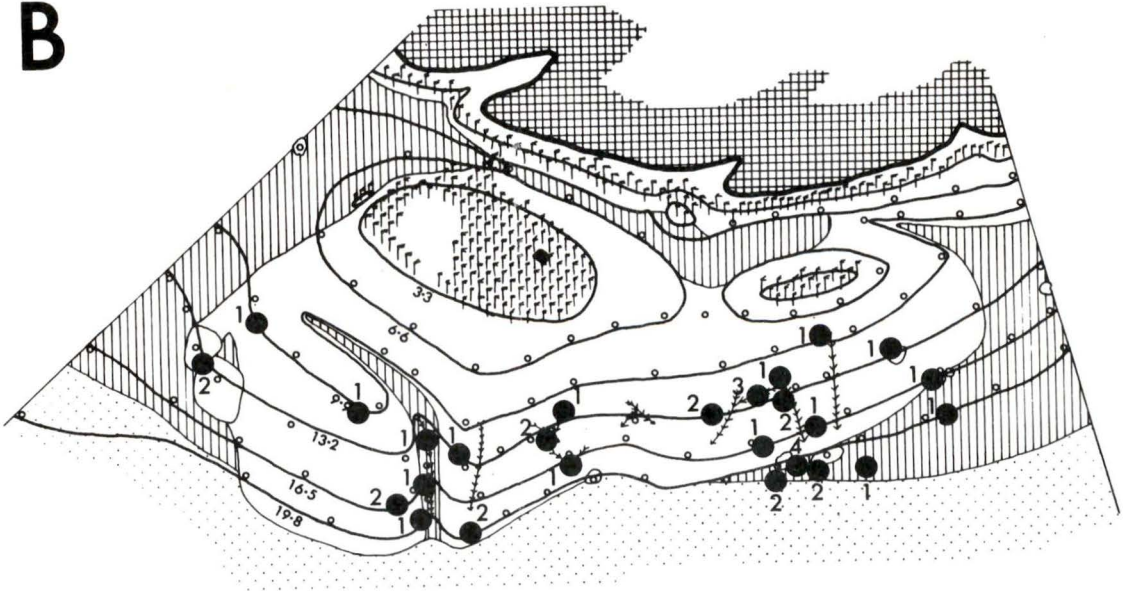
Black rockfish showed two behaviour patterns closely related to their distribution. The most common behaviour was schooling, in which large numbers of fish formed loosely organized aggregations above particular reef sites. These schools were occasionally heterotypic, with small numbers of congeners such as yellowtail rockfish (S. flavidus) and blue rockfish (S. mystinus) present. Two areas on the Ohia site provided focal points for schooling activity: an open area within the largest kelp bed and, in deeper water, two large rocks on the east side of the reef (Fig. 3A). Some exchange or movement of schools between these locations was observed. In addition, smaller schools than those noted above occurred sporadically in areas of current adjacent to rocky points and in the water column directly above regions of steep vertical relief. The second, less frequent behaviour pattern was an inactive phase in which fish settled out from a school and either perched on rock shelves or hovered within crevices. Although both behaviours were observed throughout the 24 hour period, sitting and schooling behaviour were commonly associated with day and night time periods respectively. Thus, black rockfish primarily formed mobile schools that were associated with particular types of reef topography, rock promontories, or other areas of rugged relief, and within and on the fringes of the kelp bed.

Figure 3. A. Study site showing the distribution of the combined tagged population of black rockfish. Size of solid circle related to the number of individual tagged fish seen at each location during the entire dive schedule (actual number written adjacent to the solid circle). B. Distribution of the combined tagged population of china rockfish. The number adjacent to the solid circle indicates the number of tagged fish seen at that location. Locations depicted with several fish present were those in which different fish occupied the site at different times.

A



B



Of 24 china rockfish tagged in two groups, 20 (83%) were observed on later dives. Population size was estimated at 18 fish during the first tagging effort (1977) and 14 fish during the second tagging effort the following summer (1978). Most individuals were recorded 20 or more times, and the number of sightings increased throughout the dive schedule. The difference in re-sighting success between the two species is, in part, due to the strong association of individual china rockfish with specific reef locations. Another factor was visibility; observations of china rockfish were rarely hindered by poor water clarity. The combined distribution of tagged china rockfish over the study area is presented in Fig. 3B. Each fish occupied its own very limited space or home site on the reef. Home sites included crevices, overhangs, small caves and the interstitial spaces of rock rubble or boulder piles (Fig. 3B). An individual normally positioned itself in the home site facing outwards, or hovered nearby just off the bottom. When disturbed, the resident would retreat deep into the home site, usually out of view. China rockfish tended to stray farther (several meters) from their home location during the night. When approached, they fled quickly to the home site, unless the diver blocked its retreat, whereupon the fish chose another nearby crevice as temporary refuge.

Three china rockfish frequented more than one specific site on the reef. Multiple dwellings were termed the primary and secondary home sites based upon their frequency

of use. Normally, a fish occupied the primary site unless disturbed by the close approach of a diver, at which time it sought refuge in the secondary site. The distance between home sites ranged from 4 m to 7 m depending upon substrate. Longer distances were associated with areas of smooth rock having few crevices as compared to areas of rock rubble. In two instances, the primary home site afforded less protection than the more enclosed secondary home site, but a better vantage point for viewing the surrounding reef area. One primary home site in particular consisted of nothing more than a depression in the rock with a cluster of plumerose anemones providing concealment for the resident fish.

China rockfish were temporarily displaced from their home sites on several occasions by other reef inhabitants. An adult wolf eel, Anarrhichthys ocellatus, occupied one home site for a period of two days after which the resident rockfish reappeared. Several fully grown octopi forced various fish to vacate home crevices for periods of up to 10 days. One fish, which inhabited a particularly deep and narrow crevice, was displaced first by an octopus and later by a wolf eel. In both cases the rockfish occupied a shallower crevice 2 m distant from its preferred home site.

In summary, china rockfish were exclusively a solitary, bottom dwelling species; each individual occupied a specific site on the reef. Limited movement from the home site was observed, rarely exceeding several meters.

II. Agonistic Behaviour

Agonistic behaviour occurred rarely between china rockfish and was never observed between black rockfish. Only three agonistic encounters were observed, each apparently caused by the approach of a diver. While fleeing from the diver, the fish would intrude into another occupied area and face a challenge from the resident fish.

Two of the interactions occurred on the Ohlat study site and involved the same two (tagged) individuals. Fish A occupied a primary home site under a shallow overhang. When disturbed, it fled to its secondary home site (a much deeper overhang), swimming directly across the opening in which fish B was located. On both occasions, B charged towards A with the spinous portion of its dorsal fin erect and flared opercular covers. At this point, A raised its dorsal fin and noticeably increased its swimming speed with vigorous swimming movements. Several meters from its home crevice, B abandoned its pursuit of A and quickly returned to its home site. Both encounters showed marked similarities in timing and position of actions, as well as form of postures.

The third agonistic encounter was observed during a dive off site for laboratory specimens. China rockfish C was hovering at the entrance to a small cave, formed by the juncture of a hollow in a large rock and the coarse gravel sea floor. When fish D sought refuge in the cave, fish C remained stationary, but oriented itself towards the intruder

with opercular covers extended. Fish D attempted to enter the cave on three occasions, each time turning away when confronted by C. Finally D swam over and then behind the rock, out of view. A few seconds later a black rockfish appeared from behind the rock and swam in full view of the resident fish, but elicited no response.

A degree of mutual tolerance between china rockfish of disparate size was evident in an area of rock rubble. The rock pile was frequented by at least three fish on any one occasion. Two fish would momentarily occupy the same interstitial space with only the briefest show of agonistic behaviour by the smaller fish, a momentary raising of the dorsal fin. This behaviour also occurred when two fish passed one another at the entrance to a cave.

Territoriality was another aspect of the solitary benthic habit of china rockfish. A specific home site and surrounding area was defended against (at least) conspecific intruders.

LABORATORY STUDIES

AGONISTIC BEHAVIOUR

I. Description of Behavioural Responses Exhibited During Pairwise Agonistic Encounters

The following are operational definitions of the 36 mutually exclusive behaviour patterns observed in the present study. They are listed in three groups: (a) non-interactive responses in which there was no direct interaction apparent

between the subject fish, (b) aggressive responses in which one individual clearly interacted or responded aggressively in some manner to the presence of the other individual, and (c) submissive responses in which an individual attempted to avoid or appease the aggressive acts or displays of an opponent. The three letter code in parentheses after each behaviour is the shorthand form used in figures and tables.

A. Non-interactive Responses:

Bottom sit (BST): Two expressions of this response were evident, here called resting and alert bottom sit, the distinction being the posture assumed by the individual.

The resting posture was characterized by the fish lying motionless with almost the entire ventral portion of its body in contact with the aquarium floor. Both the spinous and rayed portions of the dorsal fin, together with the pelvic and anal fins, were folded to the body. The caudal fin and pectoral fins were partially folded with the pectorals extended outwards from the body, providing lateral stability. Occasionally, one or both of the pectorals were fanned rhythmically for several seconds at a time, apparently as an aid in maintaining stability.

The alert posture featured partial or full erection of the rayed dorsal and partial erection of the caudal, anal, pelvic, and pectoral fins. The pectorals were also extended outwards and downwards so that they, together with the pelvic and caudal fins, formed a stable "tripod" structure supporting the individual in an elevated position.

Usually, the resting bottom sit was assumed by an individual facing into, and positioned at a corner of the aquarium. Frequently one side of its body was pressed against the aquarium wall. The alert bottom sit, however, was associated with a fish positioned more centrally in the aquarium, not in contact with any vertical surfaces.

Although the two forms of this response may indicate the degree of alertness or "readiness to act" of an individual, the alert posture occurred infrequently, and it is combined with the resting form in subsequent analyses.

Bottom sit was both the most frequent and longest in duration of all behaviour patterns observed for china rockfish. Durations ranged from several seconds to a maximum of over 27 min.

Bottom touch (BTT): The fish assumed a head up posture at an angle of 35° - 45° with its caudal fin touching the floor of the aquarium. The position was maintained by a slow sculling action of the pectorals. The rayed dorsal fin was partially erect and the spinous dorsal completely folded. Pelvic fins were also tucked in close to the body with the anal fin fully extended. The caudal fin was folded where it was in contact with the glass surface.

Bottom touch was a fairly common behaviour pattern in black rockfish, but rarely observed in china rockfish. It apparently served as an intermediate state between hovering and bottom sitting with durations from 3 s to 94 s.

Backward fin (BFN): During a backward fin the fish slowly moved backwards using fanning motions of the pectoral fins. All other fins were held closely to the body. Occasionally, the individual appeared to "walk" backwards on the aquarium floor. This was accomplished with pushing motions of the pectoral fins against the glass surface. Lateral body flexions and a forward curl in the caudal fin also accompanied the walking action. Backward fin had an interactive component in that it was usually associated with a movement back to a favoured area or corner of the aquarium after a tentative approach towards an opponent. The orientation of the fish allowed it to maintain visual contact with its opponent during a backward fin.

Backward fin was an uncommon occurrence during encounters for both species with durations of only a few seconds.

Drift (DFT): This response was characterized by the complete absence of fin or body movement. The fish, almost instantaneously, stopped all fin and body motion and gradually descended towards the bottom. All fins were partially spread except the pelvics, which were extended, probably in anticipation of contact with the glass surface, and perhaps to aid lateral stability.

China rockfish commonly drifted back to the aquarium floor and bottom sit after a bout of activity, whereas black rockfish normally maintained an active hovering state between bouts.

Hover (HOV): The individual maintained a fixed position in the water column by simultaneous, slow, regular movement of both the pectoral and caudal fins. All other fins were loosely folded except the rayed portion of the dorsal fin, which was erect.

Black rockfish maintained a slight head up attitude during a hover and were more active during this state than china rockfish. Activities included turns on the spot, lateral movements of the head and pitching motions of the body, all synchronized with pectoral and caudal fin beats.

Orientation of the fish with respect to its opponent during a hover depended upon the behavioural context. During an aggressive bout, in which it appeared to represent a "station keeping" behaviour prior to further aggressive acts or termination, the hovering fish faced directly towards the other fish. However, in a non-interactive context, the hovering fish may have faced directly away from or taken an intermediate position from the direction of the other fish.

Because of their schooling tendencies, hover was the most frequent of all black rockfish behaviour patterns shown. Durations varied from a few seconds to 6 min 52 s.

Free swim (FSW): This response involved directed movement of an individual from one area to another powered by lateral movements of the caudal peduncle and tail fin. Normally, the spinous dorsal was folded, all other fins being loosely spread. During a relatively slow free swim, however, the spinous dorsal was partially or fully erect.

The free swim lasted a few seconds and occurred most frequently in situations where china rockfish returned to a preferred position or "home" corner in the aquarium after being displaced by either aggressive or submissive movements on its part.

Restless swim (RSW): The fish swam forward with its lower jaw in contact with the aquarium wall. This action was undirected with the fish moving up and down or back and forth on a small area of wall. The spinous dorsal was fully erect with all other fins involved in normal swimming movements.

Durations ranged from 6 s to 2 min 32 s.

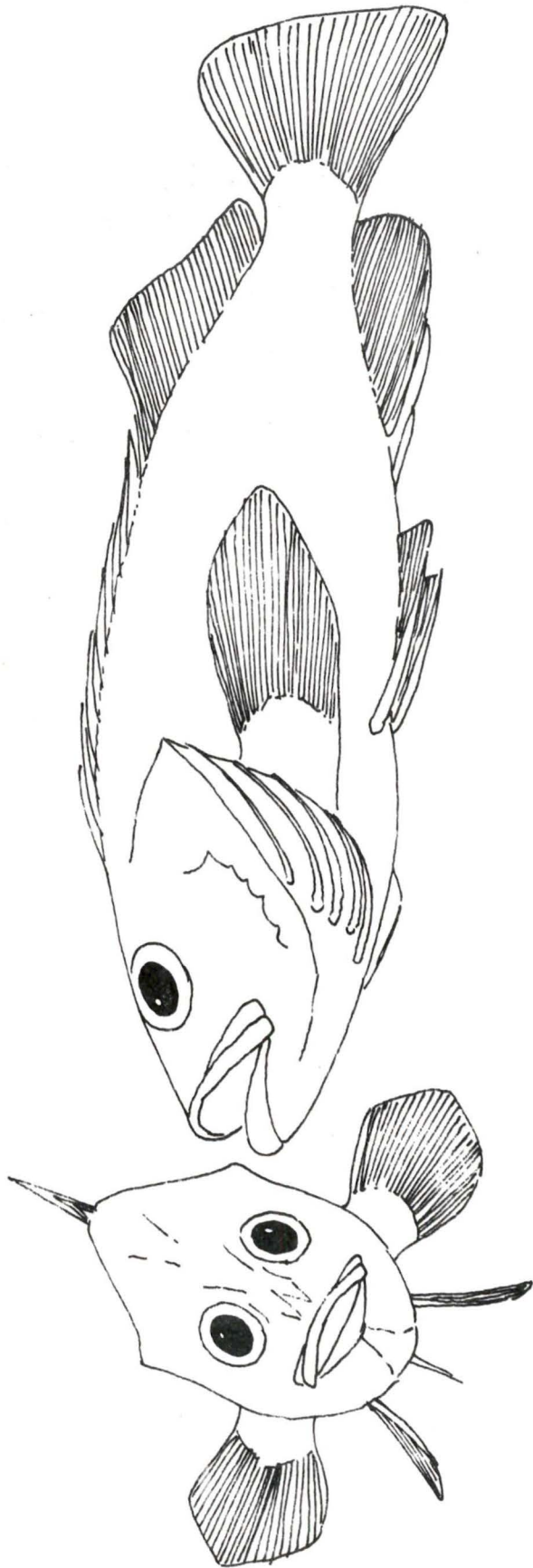
B. Aggressive Responses:

Two common displays, detailed below, facilitate the subsequent description of several aggressive responses, the latter comprised of both display and overt action components.

Opercular display (OPD): This display was characterized by a partially open mouth, extension of the branchiostegal membranes, and flaring of the opercula (Fig. 4). These actions increased the apparent size of the head, especially when viewed from the front. The position and movements of the median and paired fins were consistent with the orientation and actions of the fish, except that the spinous portion of the dorsal fin was folded closely to the body.

Opercular displaying was characterized by the displaying fish hovering in close proximity to its stationary opponent.

Figure 4. Lateral view of dominant china rockfish opercular displaying, submissive fish on left is tilting.



Four common orientations between the two fish were observed: (i) a head-to-head parallel formation, (ii) a head-to-head "V" formation, (iii) a head-to-head "L" formation, and (iv) a "T" formation in which the displaying fish faced the side of its opponent midway along the body. Sound production was frequently associated with opercular display in both species.

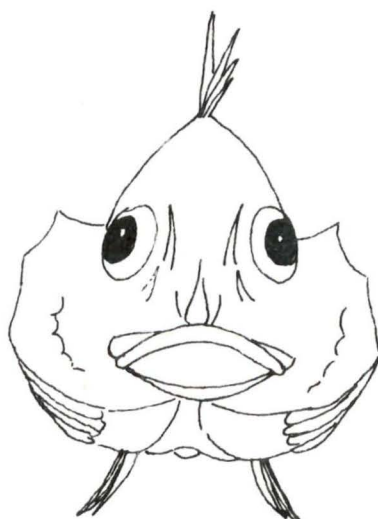
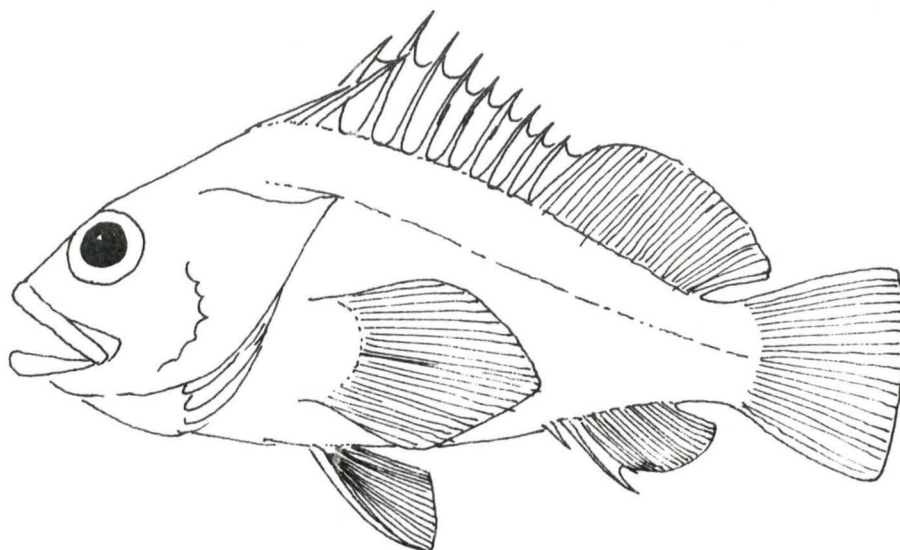
Opercular display was observed more frequently in black rockfish encounters and durations for both species ranged from 1 s to 62 s.

Full display (FLD): The same general characteristics were shown in this display as described for opercular display. Typically, however, the spinous dorsal was fully erect except for the first 2 or 3 anterior spines. The anterior spines were folded over to one side of the erect elements behind them (Fig. 5). Again, both fish were stationary during the display, with the displaying fish hovering in a head-to-head position in front of its opponent. Usually the longitudinal axes of both fish formed an angle of greater than 90 degrees. Sound production, by china rockfish only, occurred on rare occasions with this display.

Full display was a more frequent occurrence during china rockfish encounters and durations ranged from several seconds to 18 s.

Orient (ORT): For both species, orient was the most common act signalling the start of an aggressive bout. An individual, while in full display, turned to face directly

Figure 5. Lateral and frontal views of a china rockfish in full display.



towards its opponent. This response was usually followed by further aggressive responses, such as approach or charge. Occasionally, full display was not shown throughout orient, and a non-interactive response, usually hover, was maintained for a variable length of time before an approach was initiated. Infrequently, during china rockfish encounters, movement of subordinate individuals elicited an orient and subsequent response from the dominant.

Orient was observed many times for both species during agonistic encounters and was very short in duration, typically 1 - 2 s in length.

Approach (APP): One individual initiated a direct deliberate advance towards a stationary opponent. China rockfish usually exhibited full display during this response, but sometimes lowered the spinous dorsal (i.e. showed opercular display only) during the last phase of the approach, usually within a body length of the opponent. During the latter case, the approaching fish hovered facing the opponent with an opercular display. Black rockfish normally showed opercular display during an approach, with full display occurring less frequently. During an approach, both species usually produced low pitched growling sounds. Sounds were louder and more frequent during initial stages of an encounter until dominance was established by one fish over the other.

Duration of approach was variable (2 - 10 s) as some fish would hesitate slightly as they swam forward.

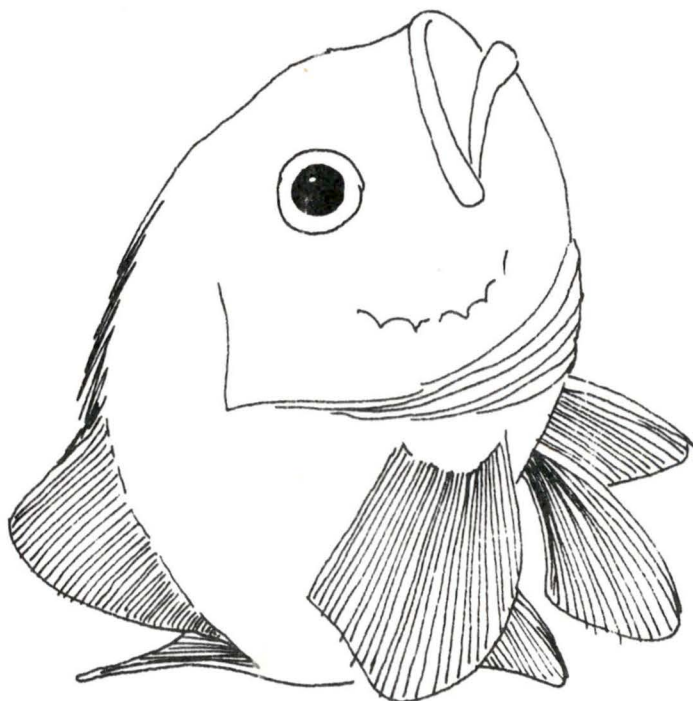
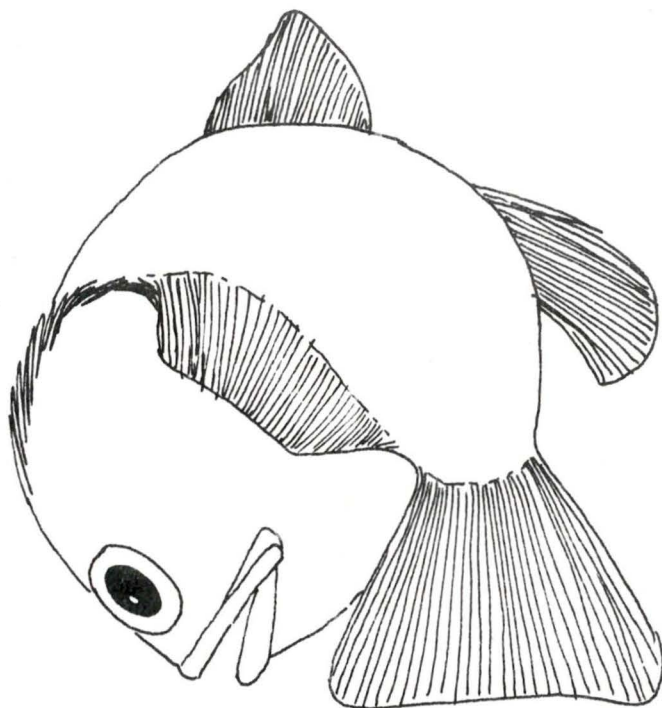
Charge (CHG): Charge was similar in action and posture to an approach, but occurred more swiftly (about 1 s in duration). Frequently, in both species, the spinous dorsal was completely erect with no anterior folding. Occasionally, the spinous dorsal would fold to the body at distances of less than one body length from the recipient fish. Growling sounds were always associated with a charge.

A charge was usually followed by more overt acts of aggression, including butts, chases and nips, and indicated a high level of motivation. Charges occurred rarely during black rockfish interactions.

Carousel (CAR): This occurred when two fish, both opercular displaying, slowly circled one another. Also, what appeared to be very shallow tailbeats were directed at each others' head (Fig. 6). Occasionally, short bursts of speed occurred, when a fish tried to nip its opponent, and the recipient simultaneously attempted to evade its attacker. Carousel lasted from 4 to 10 s and was always accompanied by sound production in china rockfish confrontations. No sounds were monitored during black rockfish encounters.

Mouth lock (MLK): Two fish seized each other firmly by the jaws. Except during the actual bite, there was very little movement, as both individuals bottom sat. Ventilation movements of the gill covers increased both in frequency (from 1 cycle in 2 s to 1 cycle in 1 s) and range of motion, presumably because the efficiency of the respiratory pumping action was impaired.

Figure 6. Two black rockfish carouselling.



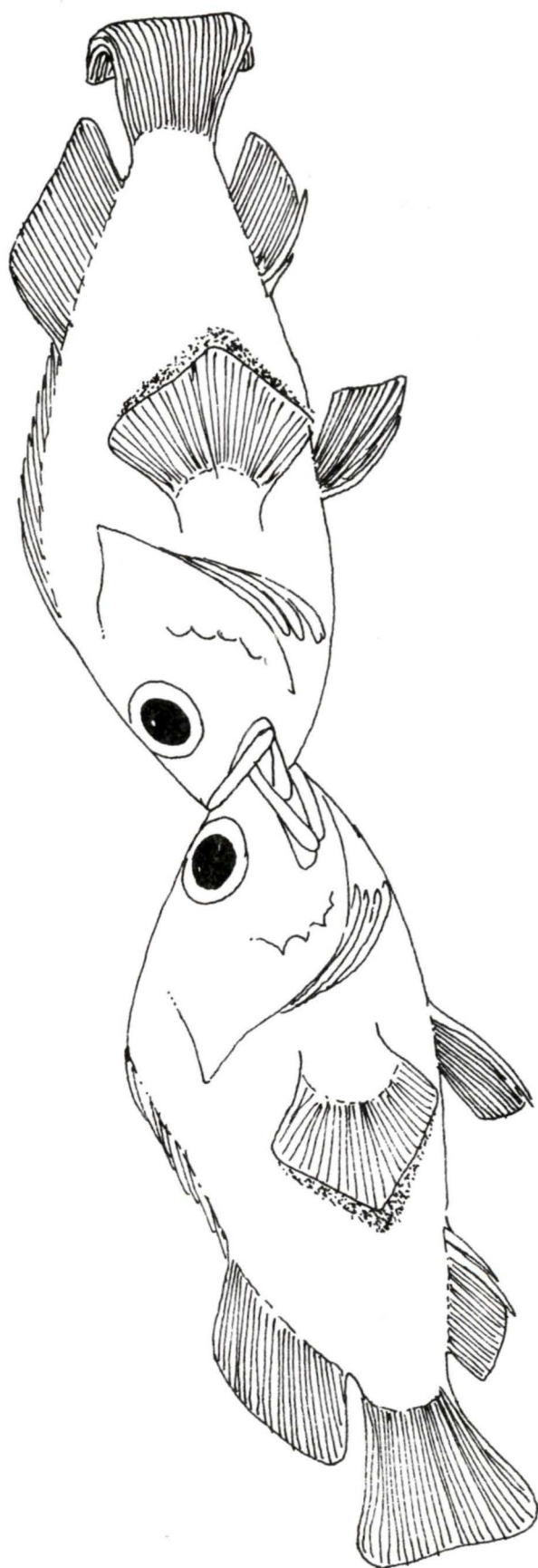
Durations ranged from 10 s to slightly over 5 min. This response was not observed during agonistic encounters between black rockfish.

Mouth fight (MFT): In this behaviour, both individuals with mouths locked and opercular displaying, engaged in violent, lateral head shaking and pulling motions (Fig. 7). The latter consisted of sustained, powerful backward swimming with occasional longitudinal jerking motions of the head. Sound production occurred with each vigorous body movement. Also, on rare occasions, one fish attempted to roll the other on its back, but the other thwarted this move by extending its dorsal fin. Occasionally, the mutual hold between fish was broken momentarily, only to be regained, allowing the conflict to continue. Mouth fight may have served as a test of comparative strength.

Mouth fights were exclusive to china rockfish conflicts, and they varied from 6 s to 16 s in duration.

Encircle (ENC): An individual, while exhibiting opercular display, swam in a tight circle (less than one body length in radius) around the other fish which was bottom sitting. This was an uncommon response in both species and appears closely related to carousel in action. Encircle was usually restricted to situations in which the recipient fish did not react with any overt submissive responses, but remained stationary and showed opercular display. Encircle may be a challenge to the recipient to engage in physical conflict (e.g. a mouth fight).

Figure 7. Two china rockfish engaged in a mouth fight.



Duration of encircling was from 4 s to 24 s.

Parallel run (PRN): This occurred when a dominant fish, showing an opercular display, swam side by side with a slowly moving subordinate for several seconds. The dominant fish appeared to impede the progress of the subordinate by assuming a head-to-head "V" position. This response was not observed during china rockfish encounters.

Circular swim (CSW): During this behaviour, the fish were oriented in a head-to-head "L" position, and the subordinate swam with a head up attitude, rotating on the spot, in its attempt to avoid the dominant fish. The dominant fish showed opercular display with its head within 1 or 2 cm of the subordinate, and slowly circled with the subordinate.

Circular swim was a rare occurrence, observed only during black rockfish encounters. It lasted from 9 s to 16 s.

Follow (FOL): Following is similar to parallel run, but the subordinate fish maintained a position just in front of the following dominant. The dominant trailed from one half a body length to a full body length behind the head of the subordinate. One instance of sound production accompanying this behaviour was noted for black rockfish.

Follow varied from 4 s to 12 s in duration and was an infrequent occurrence during encounters between both species.

Chase (CHS): A similar response to follow, except that swimming movements were noticeably more rapid and erratic in response to the evasive movements by the subordinate fish.

The chasing fish maintained a position quite close to the fleeing individual, usually less than one body length. Sound production was common during chases in china rockfish encounters.

Chase was a common response of short duration, typically of 2 s to 8 s.

Mouth threat (MTH): Mouth threats commonly occurred at the end of a chase and were characterized by a momentary enlargement in the opening of the mouth coupled with a noticeable increase in swimming speed towards the fleeing fish. This response appeared to indicate heightened aggression just prior to termination of the chase.

Tail beat opponent (TBO): Tail beats were delivered under a variety of circumstances. Normally the dominant fish was oriented parallel (head-to-head) to the subordinate fish. The aggressor showed full display and also emitted growling sounds while directing a series of slow, lateral undulations of its caudal peduncle and tail fin against the posterior regions of the submissive fish. Single tail beats were also observed. A short sound may be associated with one rapid tail movement given in an anti-parallel (head-to-tail) position, as an aggressive fish turned and swam away from its opponent. In this case the spinous dorsal was folded. Physical contact between the fish was not necessarily involved during single tail beats, but in any case, water currents were directed towards the opponent's head from the tail fin movements.

Tail beats were observed on one occasion (while carouselling) during all black rockfish encounters, and were uncommon occurrences in china rockfish interactions. Tail beats were short in duration with typical times of from 2 - 6 s.

Lateral push (LAP): Using the open mouth, an individual in full display pushed against a lateral body surface of another fish with slow, exaggerated swimming motions. The point of contact was usually just behind the gill. Sound production was always associated with this behaviour pattern.

This response was more commonly seen in china rockfish interactions and lasted from 2 s to 10 s.

Ventral push (VTP): Ventral pushing involved an aggressive individual showing opercular display and repeatedly pushing on the ventral surface of another fish between the pelvic and anal fins. The dominant fish was on its side and used the side of the mouth and gill cover to deliver a series of quick, upward thrusts using violent body flexions.

Ventral push was seen in one instance only for each species with durations of 12 s and 14 s for black and china rockfish interactions respectively.

Attempted butt (ABT): This response occurred when instantaneous evasive action by the recipient fish caused a butt to miss entirely or have little effect if contact was made. Some fish inadvertently struck the aquarium wall if the intended victim moved out of range quickly enough.

Butt (BTT): Here a fish, while charging, approaching or chasing, accelerated and rammed into the recipient fish at nearly full swimming speed. The action was quick (less than 1 s in duration), and it appeared that the mouth of the aggressor was closed at the moment of impact. Butts were primarily directed at the large lateral surface area of the trunk region, with occasional strikes on the opercular cover.

Both attempted butt and butt were uncommon events for both species.

Attempted nip (ANP): This behaviour occurred when an individual missed during an attempt to nip its opponent. It is not known whether this action was due to misjudgement on the part of the attacker, or was an intentional threatening response. Quite often the attacker did not pursue a fleeing opponent, even though the recipient remained within striking distance (less than one body length).

Nip (NIP): During an approach, charge or chase an individual momentarily accelerated towards, and bit, a fleeing adversary. Nips were usually directed at the pectoral fins, anal fins, caudal peduncle or caudal fins.

Attempted nip and nip were fairly common responses in both species, with a proportionately greater number of attempted nips observed in black rockfish.

Bite (BIT): An individual seized an appendage of an opponent between its jaws and retained its grip for an extended period. Bites were directed at two areas, the

(spinous) dorsal and pelvic fins. Occasionally, biting was accompanied by head shaking from the attacker and body jerking from the recipient. Intermittent body jerking appeared to be an attempt by the recipient to free itself from the grasp of the attacker.

On one occasion, an attacker, while grasping its opponent's spinous dorsal fin, attempted to overturn it with a backward fin (BFN).

Bites were a rare occurrence and were never observed during black rockfish encounters. Bites ranged from 30 s to 5 min 8 s in duration.

Turnaway (TRN): This response involved a quick change in direction during an approach or charge, or a change in orientation of a stationary individual after it had oriented towards another fish.

During a charge or approach, turnaway frequently occurred on the border of the aggressor's side of the aquarium in which case the spinous dorsal was fully erect. Often an aggressor, already facing an opponent less than one body length away, did not charge or approach directly; it first showed turnaway, then re-oriented and finally approached the opponent - all in one continuous movement.

Turnaway was a common response during interactions for both species.

Tail beat aquarium (TBA): Single tail beats, frequently accompanied by sound production, were also directed against

the aquarium floor, during encounters by both aggressive and submissive fish. Here the fish swam downwards, usually from a hover, turned on its side and delivered a quick, sharp strike of its tail to the bottom.

Tail beats were uncommon and usually occurred in series of 2 to 4 at a time.

C. Submissive Responses:

Although no analysis was done on behaviour exhibited by subordinate fish, the following responses are included to complete the agonistic behaviour catalogue.

Avoid: This response was characterized by a rapid swimming action to evade an advancing individual accompanied by a fully raised dorsal fin. Sound production may be associated with the sudden muscular action. Depending upon the position of the recipient in the aquarium, evasive action showed two general forms. Where the fish was near the aquarium floor and thus had a large volume of water above, it retreated upwards in one quick vertical swimming movement. In tighter situations such as corners, or nearer the water surface, the avoidance manoeuvre was slightly modified. At the moment of flight, the fish rolled on its side with the dorso-ventral axis parallel to the aquarium floor, and swam horizontally. Presumably this manoeuvre presented the spinous dorsal towards the advancing fish as well as decreasing target area.

Flee: This action was the same as Avoid, except that it extended over a longer period of time, since the attacker maintained the pursuit.

Tilt: This was a posture that occurred during bottom sit or hover in which the fish, with dorsal fin fully erect, rolled over sideways and presented its dorsal surface and fully erect dorsal fin to an advancing fish (Fig. 4). This appeared to be a protective posture, by presenting a raised spinous dorsal to the attacker rather than a lateral surface.

Attitude of inferiority: The subordinate individual maintained a "head up" attitude in the water with a completely raised dorsal fin. Normally the fish hovered well off the aquarium floor facing into a corner with the head just below the surface of the water.

Tail stand: This response was observed only once, during a china rockfish interaction. The individual supported itself with head up, vertically in a corner of the aquarium. The ventral body surface was pressed against the glass surface with lateral support provided by extended pectoral fins. The caudal fin, in contact with the floor of the aquarium, was folded to one side into a cup shape. The spinous dorsal was normally folded to the body and partially raised only when the dominant fish was in close proximity. This response appeared similar to the attitude of inferiority.

II. Description of a Typical Agonistic Encounter

Agonistic behaviour exhibited by both species of rockfish was complex. Variation in the sequence of behavioural responses are assumed to depend upon the interaction between endogenous and exogenous factors, which may vary throughout

the course of a conflict. However, given two fish of similar size and prior isolated residency, some degree of predictability in the course of events was possible.

(i) China rockfish:

Normally, before removal of the partition, both fish bottom sat facing into a corner of the aquarium. Several seconds after the divider was removed, one animal, called the initiator, began the encounter with an orient and approach towards its opponent. At this point the other fish, called the responder, now aware of the presence of an intruder, also oriented, and both animals hovered face-to-face in opercular display. This brief confrontation preceded carouselling, which was terminated by a vigorous mouth fight. Sound production in both fish was associated with all actions to this point except orient.

Often the responder did not immediately escalate the conflict into a carousel and mouth fight, but merely returned opercular display. In this case the responder was intimidated into physical conflict by a lateral push and/or tail beat delivered by the initiator, both actions accompanied by sound production. At the end of the mouth fight, one individual withdrew and consistently attempted to avoid the aggressive advances of its opponent. Thus, several minutes from the start of the interaction a dominant-subordinate relationship was established, and subsequently the level of sustained activity declined.

Numerous short bouts of activity, less than one minute in duration, occurred at irregular intervals throughout the remainder of the experimental period. Typical aggressive responses showed by the dominant were chase, nip and attempted nip; the subordinate fish responded with flee and avoid. During the latter stages of an encounter, overtly aggressive responses with concurrent sound production usually declined in frequency. An approach with no sound production followed by a mouth threat seemed adequate to elicit an escape response from the subordinate. Indeed, some mutual tolerance was evident at the close of the experimental period when both fish bottom sat, at extreme ends of the aquarium for increasingly longer periods of time.

(ii) Black rockfish:

A typical black rockfish encounter was similar in the general course of events to that described for china rockfish, with some exceptions. Although carouselling was seen during interactions, mouth fight or mouth lock was never observed. Black rockfish apparently resolved conflict situations with the less overtly aggressive responses of approach and opercular display in conjunction with sound production. Visual displays such as shown in follow, circular swim and parallel run were used more frequently to intimidate a submissive fish rather than physical acts of aggression. Similarly, near the end of an encounter, the approach of the dominant was usually terminated by the

submissive fish, now hovering in the attitude of inferiority, momentarily raising its spinous dorsal.

III. Observations on Factors Affecting the Outcome of an Encounter - Both Species Combined

(i) Precedence (Initiator/Responder)

Of 50 encounters, there were two occasions in which no clear dominant/subordinate relationship was established and two additional encounters in which the individuals initiated the conflict simultaneously. The initiator subsequently dominated its opponent in 34 of 46 (74%) encounters, whereas the responder dominated in the remainder (12 of 46 or 26%). The frequency of wins by the initiator was significantly different from chance (Binomial test, $p < 0.001$).

(ii) Size

Omitting encounters in which there was no clear winner (2 of 50) and those in which the size differential was less than 5% of the smaller fish (17 of 48), the larger fish won significantly more encounters (25 of 31 or 81%; Binomial test, $p < 0.001$). In 5 of the remaining 6 cases in which the smaller fish won, it was also the initiator.

(iii) Prior Residency

Excluding experiments in which the opponents had the same prior residency (26 of 48), 14 of 22 (64%) winners had a shorter prior residency and 8 of 22 (36%) winners had a longer prior residency than losers. This proportion was not significantly different from chance (Binomial test,

$0.20 < p < 0.50$).

The nature of the interaction between these three factors is unknown. Precedence or initiation of the conflict and relative size of the fish apparently play an important role in determining the outcome of an aggressive encounter, whereas prior residency appears to have no clear influence.

Since the data are nominal in nature no probability can be assigned a particular fish of winning an encounter, as the covariance of the two variables involved (precedence and relative size) cannot be calculated. However, Table II provides an indication of a "winning profile" showing that a winner was most likely to be the initiator of the encounter and also the larger of the two fish, and least likely to be the initiator and smaller of the two individuals.

IV. Comparison of Aggressive Behaviour Between Species

(i) Bout Length

A "bout" of aggressive behaviour was defined as a continuous series of interactive aggressive responses (threat displays or more overtly aggressive acts) punctuated by various non-interactive responses. Each bout had a clearly defined beginning (e.g. orient (ORT), approach (APP)) and end (turnaway (TRN), free swim (FSW), hover (HOV)). Bout lengths for china rockfish were significantly longer than those of black rockfish (Mann-Whitney U-test, $.005 < p < 0.0025$).

(ii) Threat Display and Overt Aggression

Two aggressive responses for each species were also

Table II. Ranking of characteristics of the dominant fish in 30 agonistic encounters.

Characteristics		Number of dominant fish with both characteristics
Precedence	Relative Size	
Initiator	Larger	15
Responder	Larger	9
Initiator	Smaller	6

chosen for comparison. One, opercular display (OPD), was a common threat display. The other, chase (CHS), was an overtly aggressive act. There was no significant difference in duration of opercular display (OPD) between species (Mann-Whitney U-test, $0.20 < p < 0.50$). However, the duration of chase (CHS) was significantly greater for china rockfish (Mann-Whitney U-test, $0.005 < p < 0.01$).

(iii) Relative Frequency of the Behaviour Components

Figure 8 shows the frequency of performance of the 31 elements of agonistic behaviour combined over all experiments for both species. Significant differences between species occurred in 27 of the behavioural categories (test of difference between proportions, Zar 1974, $p < 0.001$). No difference between proportions was observed in the carousel (CAR), mouth threat (MTH), butt (BUT) and tail beat aquarium (TBA) responses.

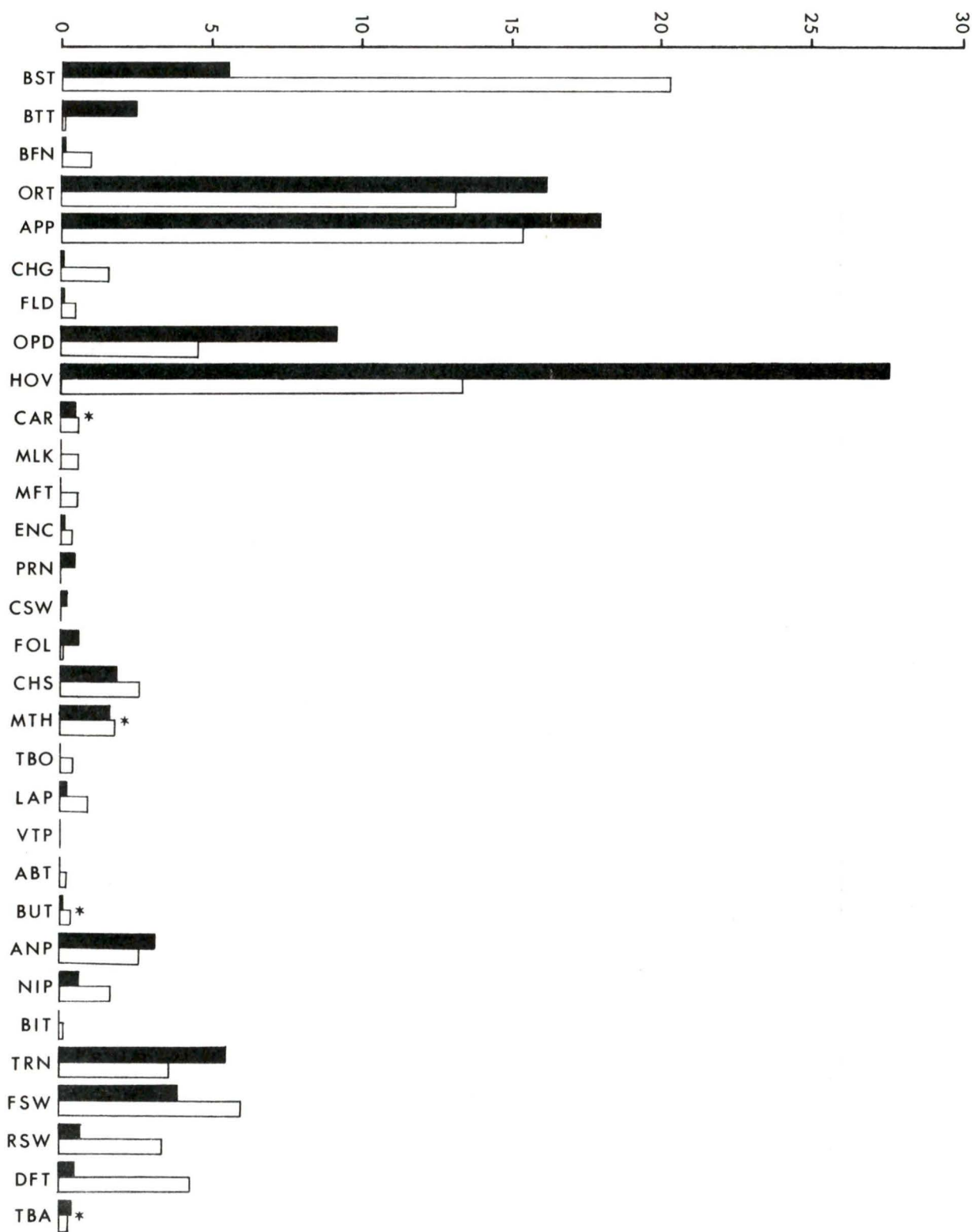
The ranking of the relative frequencies of the 31 behavioural elements was not significantly different between species (Spearman Rank Correlation Coeff, $r_s = 0.686$, $p < 0.001$). In both species non-interactive and threat responses generally occurred more frequently than overtly aggressive responses. No instances of backward fin (BFN), charge (CHG), encircling (ENC), tail beat opponent (TBO), ventral push (VTP) or butt (BUT) were observed for black rockfish, while only parallel running (PRN) was absent from the china rockfish repertoire.

Figure 8. Percentage frequency of performance for individual elements of agonistic behaviour in two species of rockfish. Black areas: Black rockfish. White areas: China rockfish. * denotes no significant difference in values (see text for explanation).

Key for behavioural codes:

BST - bottom sit	CHS - chase
BTT - bottom touch	MTH - mouth threat
BFN - backward fin	TBO - tail beat opponent
ORT - orient	LAP - lateral push
APP - approach	VTP - ventral push
CHG - charge	ABT - attempted butt
FLD - full display	BUT - butt
OPD - opercular display	ANP - attempted nip
HOV - hover	NIP - nip
CAR - carousel	BIT - bite
MLK - mouth lock	TRN - turnaway
MFT - mouth fight	FSW - free swim
ENC - encircle	RSW - restless swim
PRN - parallel run	DFT - drift
CSW - circular swim	TBA - tail beat aquarium
FOL - follow	

Percent total number of elements recorded



(iv) Behavioural Sequences Analysis - Kinematic Graphs

Figures 9 and 10 depict the sequence of agonistic behaviour components in dominant black rockfish and china rockfish respectively. Such a representation is termed a "kinematic graph" (Sustare, 1978). States or events are represented by circles, the size of which is proportional to the percentage frequency of the individual elements. An arrow joining two circles indicates that a transition may occur between those two states with its direction indicating the temporal sequence. The width of the arrows is proportional to the percentage frequency of the transitions. In order to simplify the kinematic graph and hence clarify the main transitions in both systems, states with frequencies less than 1% and transitions with frequencies less than 10% were omitted.

Simplified kinematic graphs present data that is difficult to assimilate in preceding/following matrix form; they serve to demonstrate the main sequence chains and their variations. The most frequent behaviour pattern observed during aggressive encounters was the hover (HOV) for black rockfish and the bottom sit (BST) for china rockfish. In Figures 9 and 10 respectively these behaviours are centrally located and may be considered the major non-interactive or neutral behaviour pattern in the behavioural repertoire. Virtually all behaviours shown in both kinematic graphs have arrows leading to the pivotal, neutral behaviour patterns.

Figure 9. Kinematic graph depicting the sequence of agonistic behaviour components in dominant black rockfish. See text for explanation of symbols.

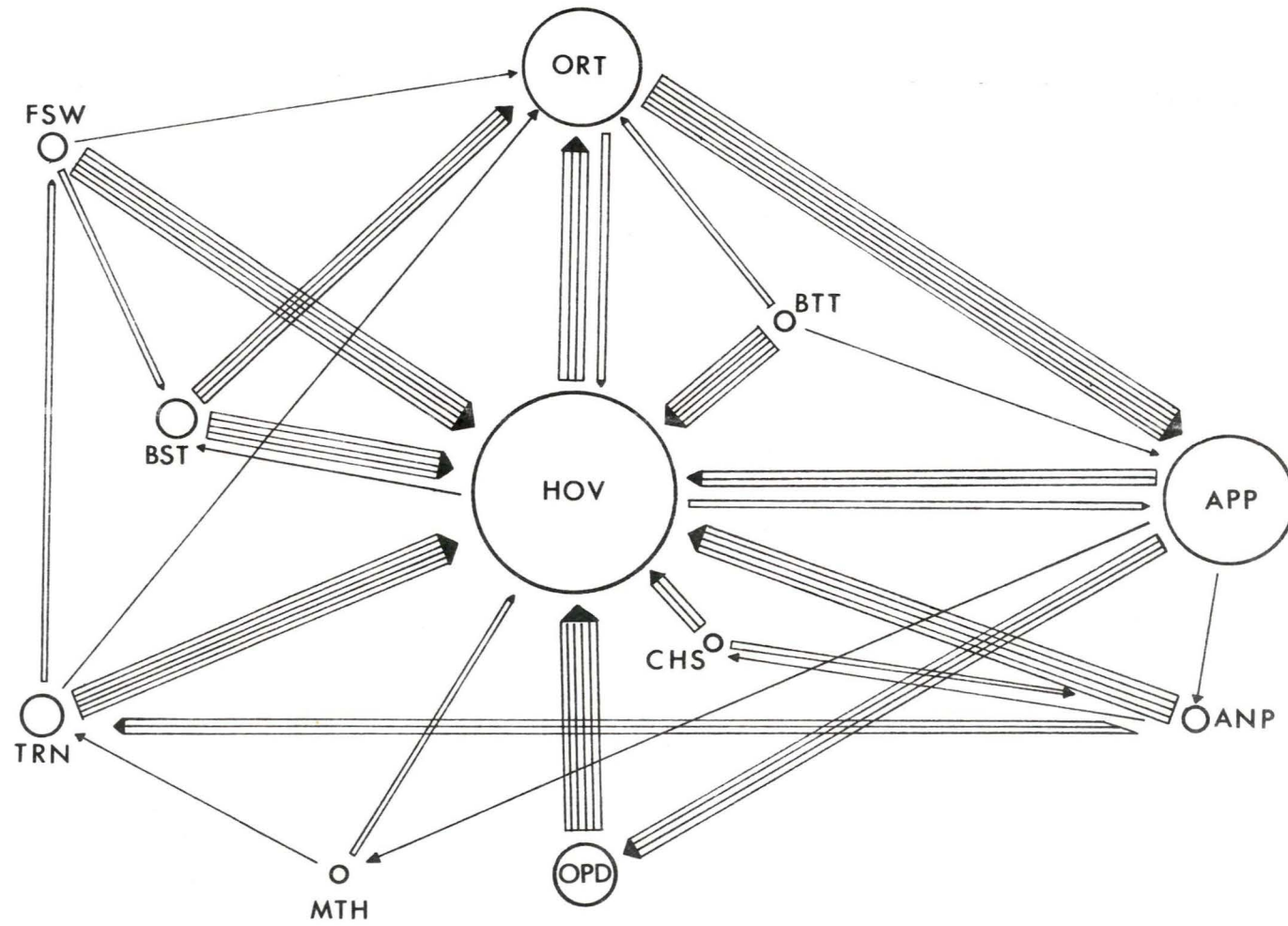


Figure 10. Kinematic graph depicting the sequence of agonistic behaviour components in dominant china rockfish. See text for explanation of symbols.

Figure 9 illustrates that the most probable sequence of aggressive behaviours in a black rockfish was as follows: hover (HOV) → orient (ORT) → approach (APP) → opercular display (OPD) → hover (HOV). During threat behaviour the individual can go from approach (APP) to mouth threat (MTH) or attempted nip (ANP), both relatively uncommon events. Instead, the fish usually showed opercular display (OPD), followed by hover (HOV). Attempted nip (ANP) may lead to chase (CHS) (which itself may precede attempted nip (ANP)), or, more likely lead to hover (HOV) or turnaway (TRN) then hover (HOV). For the most part, black rockfish behaviours occurred in a fairly well defined order, reflected in the high inter-element frequencies in Figure 9.

From Figure 10, the most probable china rockfish aggressive sequence consisted of the following elements: bottom sit (BST) → orient (ORT) → approach (APP) → hover (HOV) → bottom sit (BST). Although this was the most probable sequence observed, a further examination of Figure 10 shows this was only marginally so. China rockfish aggressive sequences were less structured than those of black rockfish. A large proportion of the behavioural elements had nearly equi-probable succeeding transitions. This is characterized in Figure 10 by the large number of alternative following behaviours with similar frequencies.

V. Causal Analysis

(i) Temporal Associations of the Agonistic Behaviour Elements

If the agonistic activities of a fish have no common causal factors, they would be expected to precede or follow each other randomly (Wiepkema, 1961). However, if one can demonstrate a temporal association between groups of activities (i.e. non-randomness) then it can be assumed common causal factors are present. The techniques of cluster analysis, maximum spanning trees and factor analysis were applied to the raw data in order to elucidate the temporal relationships among different activities.

Preceding/following matrices for black rockfish and china rockfish aggressive encounters are presented in Appendices II and III respectively. Prior to further analysis, and as an aid in clarity of presentation, behaviours occurring rarely (less than 10 observations) were eliminated.

Single linkage cluster analysis applied to these data resulted in the dendrograms depicted in Figures 11 and 12. The cluster structure for black rockfish aggressive behaviour (Fig. 11) show similarity levels of less than 0.5, indicative of relatively loosely knit clusters. Primary (two-element) clusters that emerged were chase (CHS)/attempted nip (ANP), drift (DFT)/bottom sit (BST), hover (HOV)/tail beat aquarium (TBA) and orient (ORT)/approach (APP). Secondary clusters of more than two elements are not well defined because of chaining. For example, from Fig. 11 the primary cluster

Figure 11. Dendrogram showing the temporal relationship between aggressive behaviour elements during black rockfish encounters.

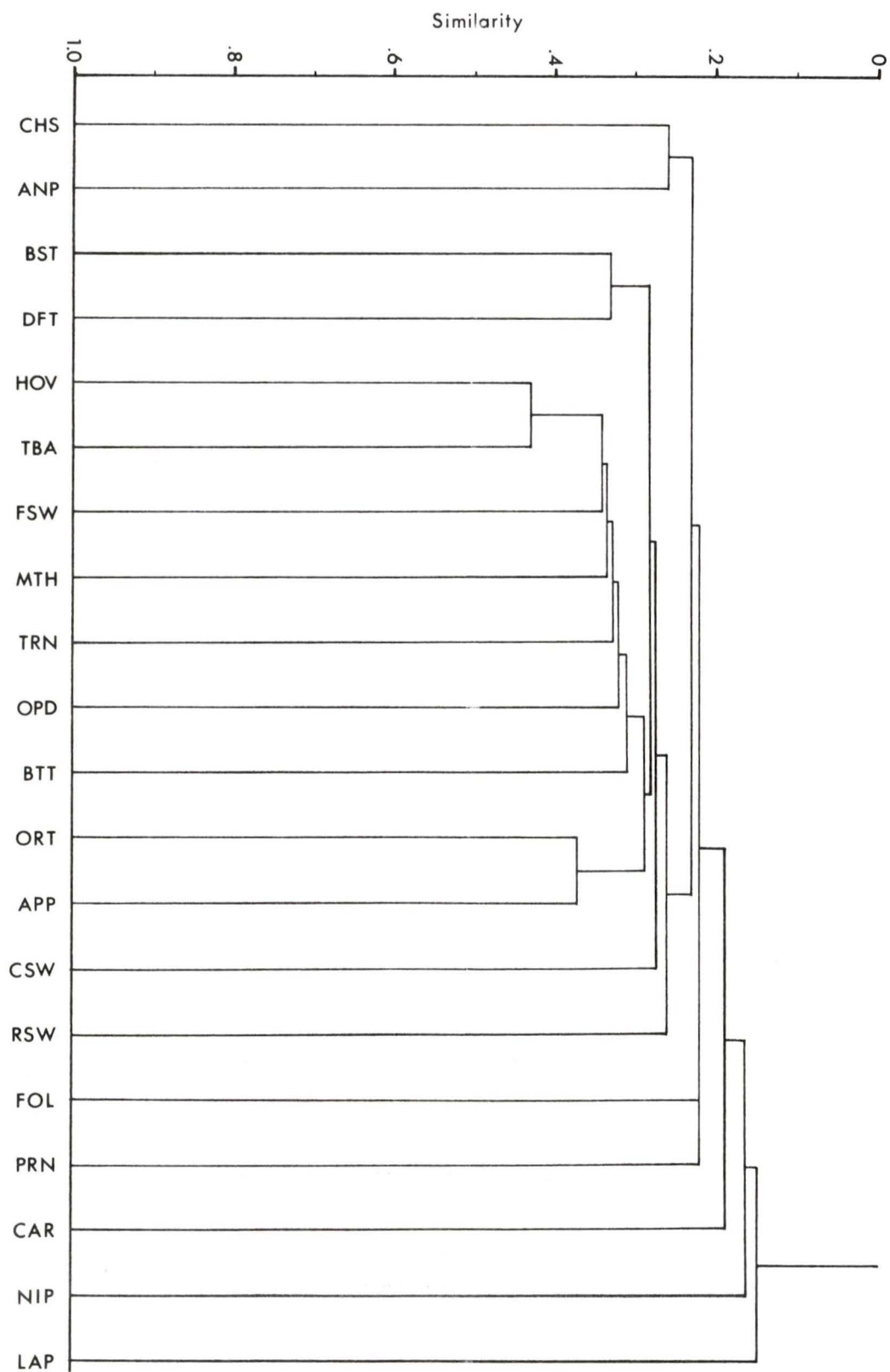
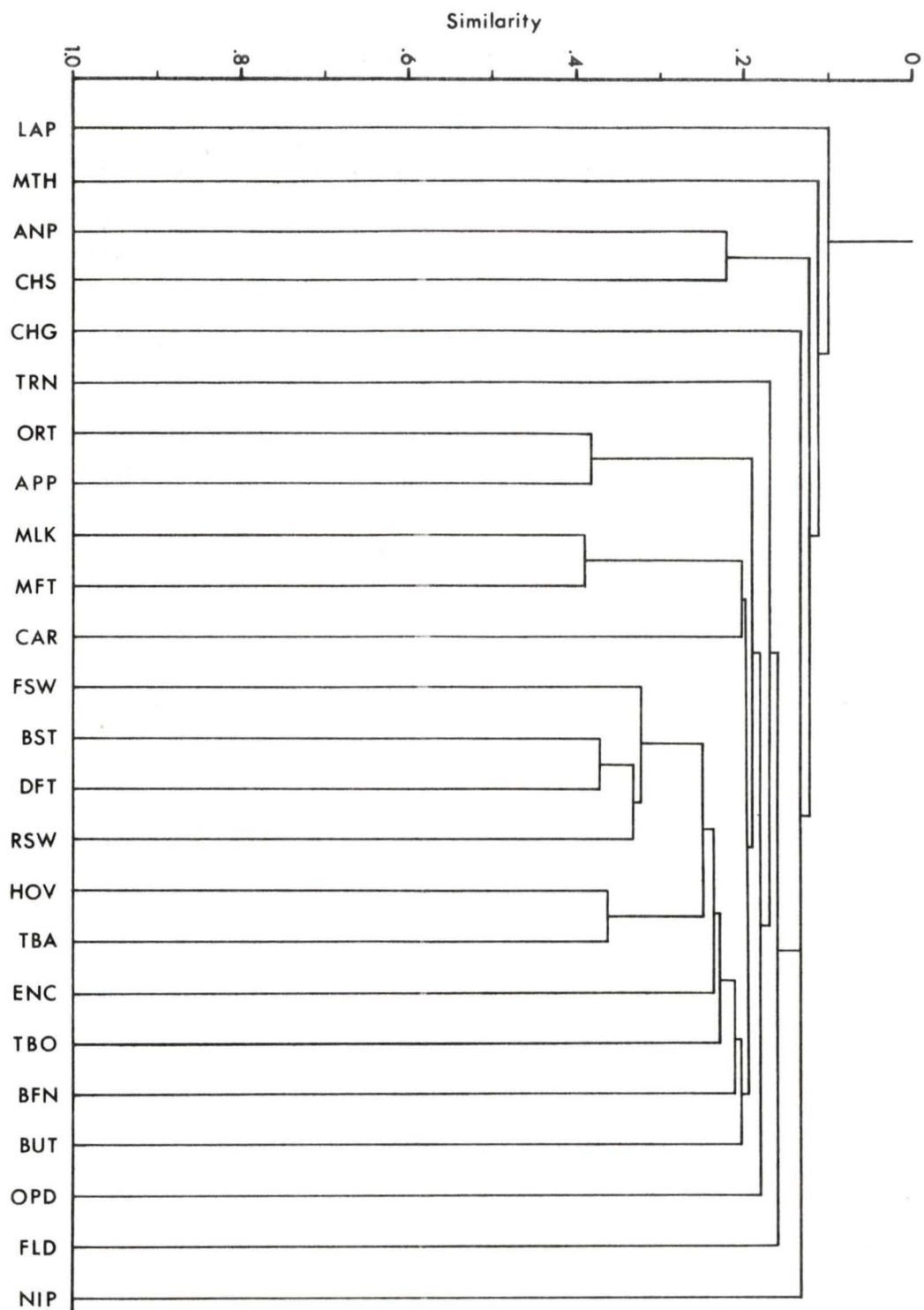


Figure 12. Dendrogram showing the temporal relationship between aggressive behaviour elements during china rockfish encounters.



orient (ORT)/approach (APP) joins another secondary cluster at similarity 0.288. However, without the original data (similarity matrix) it is impossible to determine whether this is due to orient (ORT) being similar (i.e. temporally associated) to hover (HOV), or approach (APP) similar to freeswim (FSW) and so on.

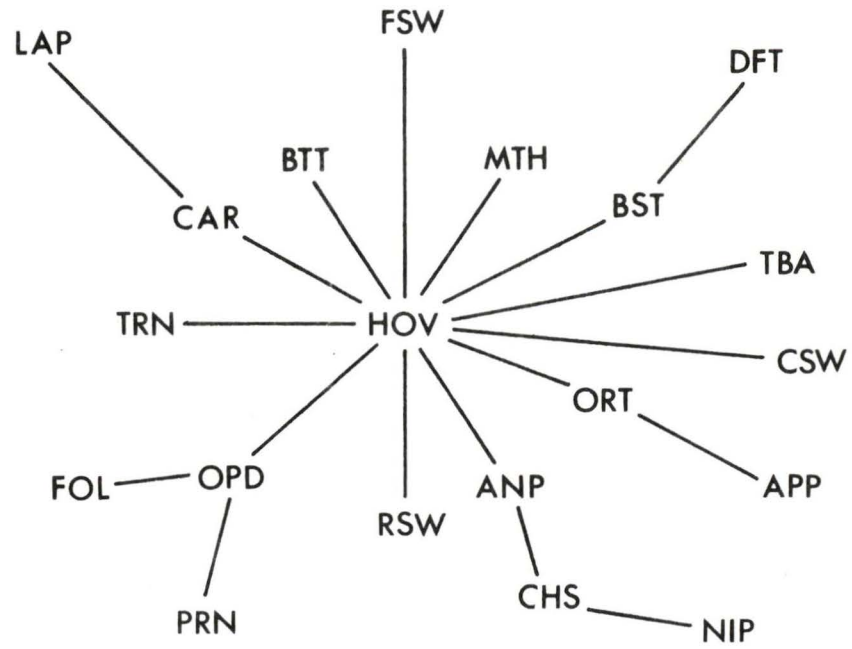
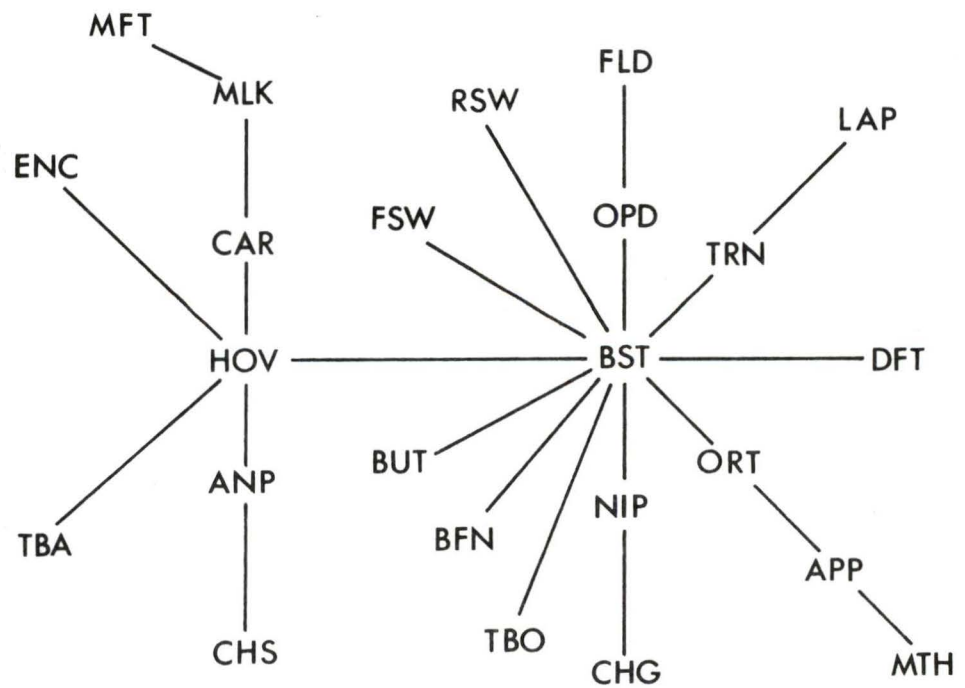
Figures 13A and 13B show the maximum spanning trees (MSTs) for black rockfish and china rockfish agonistic behaviour respectively. For black rockfish, Fig. 13A shows that two branches of the tree, namely orient (ORT)/approach (APP) and bottom sit (BST)/drift (DFT), coincide with two primary clusters in Figure 11. It is now apparent that the inclusion of the orient (ORT)/approach (APP) cluster into the larger secondary cluster (at similarity 0.288) is due to the similarity of orient (ORT) to hover (HOV). Additional branches are evident on the MST which break down the chaining of the cluster analysis at lower levels of similarity. Thus, the groups lateral push (LAP)/carousel (CAR), follow (FOL)/opercular display (OPD)/parallel run (PRN) and attempted nip (ANP)/chase (CHS)/nip (NIP) emerge from the MST analysis.

On the whole, the cluster structure for china rockfish (Fig. 12) agonistic behaviours is less compact than that for black rockfish. A large proportion of the elements do not enter the cluster structure until a similarity of 0.2, compared to 0.3 for black rockfish.

Primary clusters include: attempted nip (ANP)/chase

Figure 13. Maximum spanning trees for rockfish aggressive behaviour constructed from preceding/following matrices.

A. Black rockfish. B. China rockfish.

A**B**

(CHS), orient (ORT)/approach (APP), mouth lock (MLK)/mouth fight (MFT), bottom sit (BST)/drift (DFT) and hover (HOV)/tail beat aquarium (TBA). Secondary clusters (3 - 4 elements) consist of mouth lock (MLK)/mouth fight (MFT)/carousel (CAR), free swim (FSW)/bottom sit (BST)/drift (DFT)/restless swim (RSW). There also appears to be one fairly well defined tertiary (cluster of primary and secondary clusters) cluster of free swim (FSW)/bottom sit (BST)/drift (DFT)/restless swim (RSW)/hover (HOV)/tail beat aquarium (TBA). The MST (Figure 13B) not only shows several primary clusters but also has branches relating full display (FLD)/opercular display (OPD), turnaway (TRN)/lateral push (LAP), nip (NIP)/charge (CHG) and orient (ORT)/approach (APP)/mouth threat (MTH).

The following clusters of agonistic behaviour were common to both species: bottom sit (BST)/drift (DFT), orient (ORT)/approach (APP), hover (HOV)/tail beat aquarium (TBA) and chase (CHS)/attempted nip (ANP). Though a direct comparison of the results of cluster analysis and kinematic graphs may not be valid because of the differences in the number and class of elements involved, some agreement is apparent. Certainly, for both species, almost all major associations found in the kinematic graphs are represented by primary and secondary clusters.

The data were subjected to factor analysis by means of principle-component analysis and varimax rotation (Kim, 1975). For black rockfish, 100% of the total common variance among

the 20 behavioural elements was accounted for by 3 factors, with 84% explained by 2 factors. For china rockfish, 100% of the total common variance among the 24 behavioural elements was accounted for by 5 factors. However, since a relatively large part of the total variance (75%) can be explained by a 2 factor solution, the 3 additional factors were of no practical significance and have been omitted from further study. Thus, both solutions were easily visualized in a 2 factor (2 dimensional) geometric representation called a cosine-vector model. In this model each variable is represented by a vector with the correlation coefficient between any two elements equal to the cosine of the angle between them. Thus, acute angles indicate positive correlations (maximum at 0°), obtuse angles, negative correlations (maximum at 180°) and right angles, uncorrelated variables. Stated another way, the smaller the angles between vectors the higher their temporal association; the larger the angles, the less likely they are to precede or follow each other. The factors themselves have been chosen orthogonal to each other (i.e. uncorrelated), as this represents the least complex solution, and their position "rotated" so that each corresponds as nearly as possible to a group of vectors (varimax orthogonal rotation).

The length of each vector symbolizes the extent to which it can be explained with the aid of the common factors introduced. The projection of a vector onto each factor is its "factor loading" and indicates the degree to which that

factor is represented in it. Thus, important aspects in interpreting the cosine-vector model are the relative length and direction of a variable vector from the axes, the clustering of variables and the relative position of clusters to each other.

The cosine vector model for black rockfish aggressive behaviour is shown in Fig. 14 (Appendix IV lists the factor loadings for each variable). The vectors of five activities namely, opercular display (OPD), mouth threat (MTH), chase (CHS), attempted nip (ANP) and nip (NIP) are closely grouped around the positive side of factor 2. Since these movements, for the most part, indicate overt aggression, factor 2 will be called the aggressive factor. Factor 1 has high positive loadings for the vectors of bottom sit (BST), bottom touch (BTT), free swim (FSW), restless swim (RSW), drift (DFT), tail beat aquarium (TBA), orient (ORT), and turnaway (TRN), and can thus be described as the non-aggressive factor. The variables parallel running (PRN) and lateral push (LAP) are near the origin and therefore have small loadings on both factors, whereas carousel (CAR) and circular swim (CSW) have some loading on both factors. Several activities such as nip (NIP) and restless swim (RSW) are almost pure measures of their respective factors of aggression and non-aggression, as their loadings on the other factors are nearly zero.

Figure 15 depicts the two-dimensional vector model of the behaviour of the china rockfish (factor loadings for each variable are shown in Appendix V). Here, an obviously

Figure 14. Cosine vector model - black rockfish behaviour

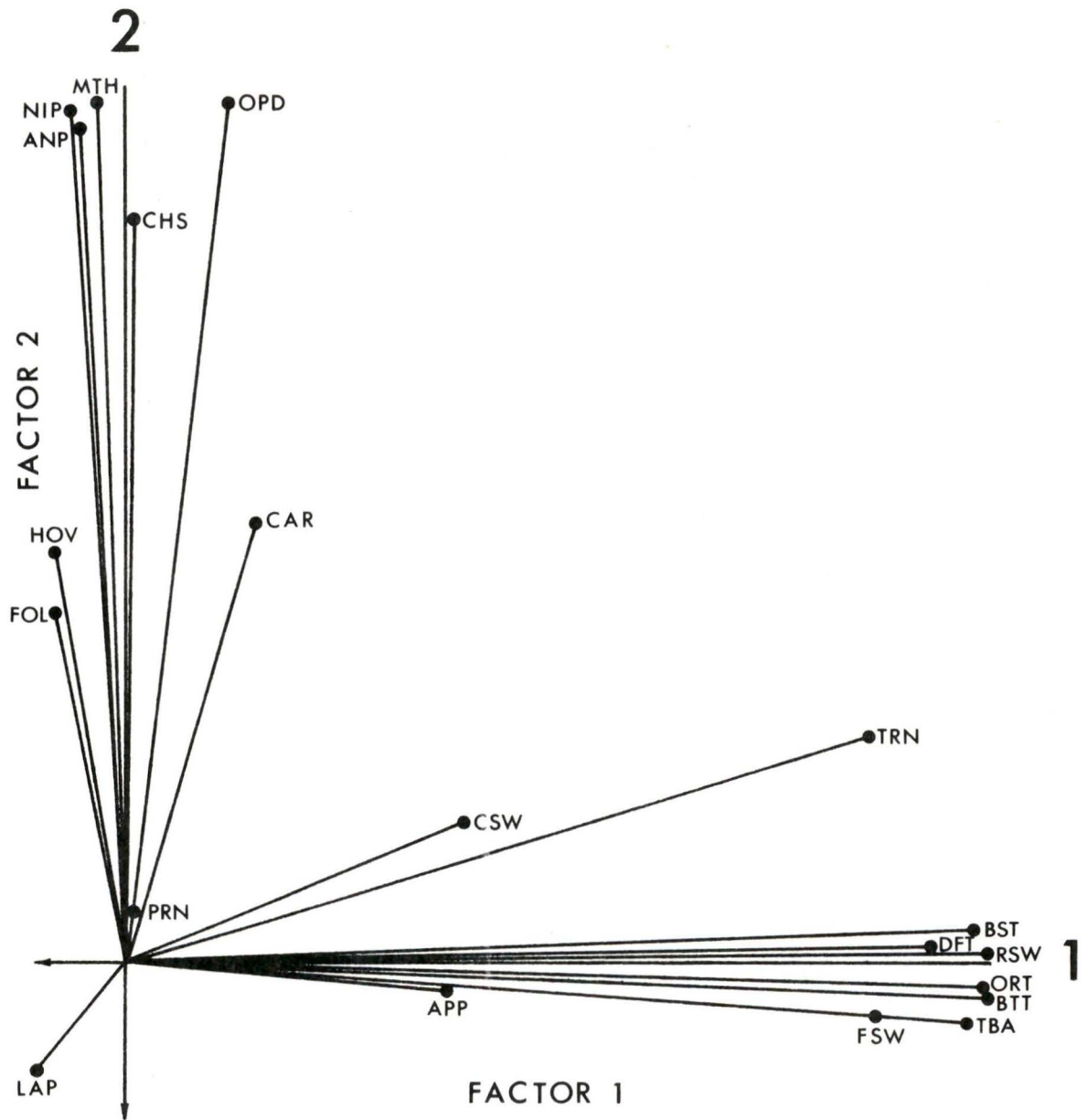
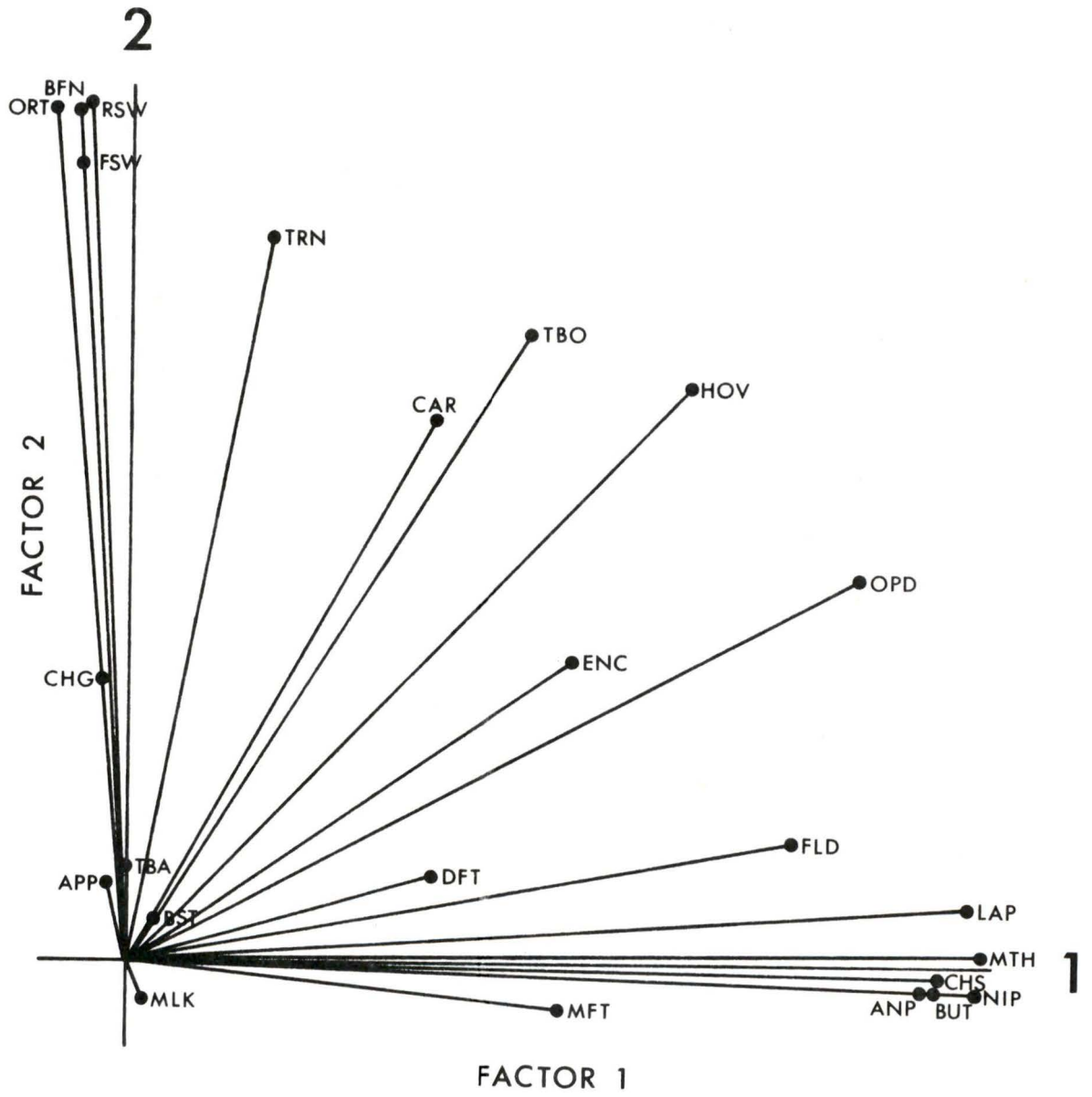


Figure 15. Cosine vector model - china rockfish behaviour



aggressive cluster of behaviours including lateral push (LAP), mouth threat (MTH), attempted nip (ANP) and nip (NIP) load high on factor 1 but low on factor 2. Factor 1 is thus labelled the aggressive factor. Similarly factor 2, comprising backward fin (BFN), orient (ORT), free swim (FSW), restless swim (RSW) and perhaps turnaway (TRN) may be called the non-aggressive factor. There are also a number of variables with loadings on both factors; these include carousel (CAR), tail beat opponent (TBO), hover (HOV), encircle (ENC), and opercular display (OPD), and thus may be regarded as expressing both aggressive and non-aggressive tendencies. Approach (APP), bottom sit (BST), mouth lock (MLK) and tail beat aquarium (TBA) are not well represented in this 2-factor dimensional model, as their loadings on both factors are rather small.

Table III presents a summary of the temporal associations between the activities of dominant individuals of both species based on cluster analysis, maximum spanning trees and factor analysis. As expected, there is generally good agreement amongst all three methods, since the data base was identical in each case. Although the first two methods are valuable techniques, factor analysis seemed to provide the most information for the greatest number of variables. In light of these results, it appears the agonistic movements expressed in pairwise encounters of both species express the relative strengths of two independent tendencies, namely the aggressive and non-aggressive tendencies (cf. attack and

Table III. Comparison between major groups of agonistic behaviour based on temporal associations using the techniques of cluster analysis, maximum spanning trees and factor analysis on identical data.

	Black Rockfish			China Rockfish			
Cluster Analysis	BST	ANP	LAP	ANP	ORT	MLK	
	DFT	CHS	CAR	CHS	APP	MFT	
	ORT	MLK			BST		
	APP	MFT			DFT		
					FSW		
					RSW		
Maximum Spanning Tree	BST	ANP	LAP	ANP	ORT	MLK	
	DFT	CHS	CAR	CHS	APP	MFT	
		NIP			MTH	CAR	
	ORT	OPD		NIP			
	APP	FOL		CHG			
		PRN		TRN			
				LAP			
				OPD			
				FLD			
Factor Analysis	Factor	1	2	Both	1	2	Both
	BST		ANP	CAR	ANP	ORT	CAR
	DFT		CHS	CSW	CHS	FSW	TBO
	ORT		NIP		NIP	RSW	ENC
	APP		OPD		LAP	TRN	HOV
	TRN		FOL		OPD		OPD
	FSW		MTH		FLD		
	BTT		HOV		MTH		
	TBA				BUT		

escape tendencies, Keenlyside and Yamamoto 1962; aggressive and flight tendencies, Wiepkema, 1961).

Although the common causal factors have been represented as independent of each other in the cosine vector model, there is some demonstration that the groups of activities mutually inhibit one another in the extreme. Figure 16 shows the relationships between the total frequencies of aggressive (attack) movements compared to the total frequencies of non-aggressive (escape) movements over the period of the experiment (30 min) for black rockfish. These data suggest that the attack and escape tendencies are negatively correlated at their extremes, implying an inhibitory relationship between the internal mechanisms underlying these tendencies. At lower values of these tendencies, there appears to be no correlation.

A similar plot for china rockfish (Fig. 17) is less convincing, but does indicate some degree of inhibition between the mechanisms underlying attack and escape at higher values.

(ii) Orientation of the Agonistic Activities

Wiepkema (1961) states that aggressive and non-aggressive (flight) tendencies express themselves in the orientation of agonistic activities. Thus, an aggressive act by an individual is characterized by movement/orientation directed towards the opponent and a non-aggressive act by movement/orientation away from the opponent.

Figure 16. Scattergram showing the relationship between the attack (ordinate) and escape (abscissa) tendencies over a 30 min period for 27 black rockfish encounters. Attack tendency is measured by the summed frequencies of NIP, MTH, CHS, and OPD. Escape tendency by the summed frequencies of TRN, RSW, BST, and BTT. Each ● indicates one 30 min period (experiment).

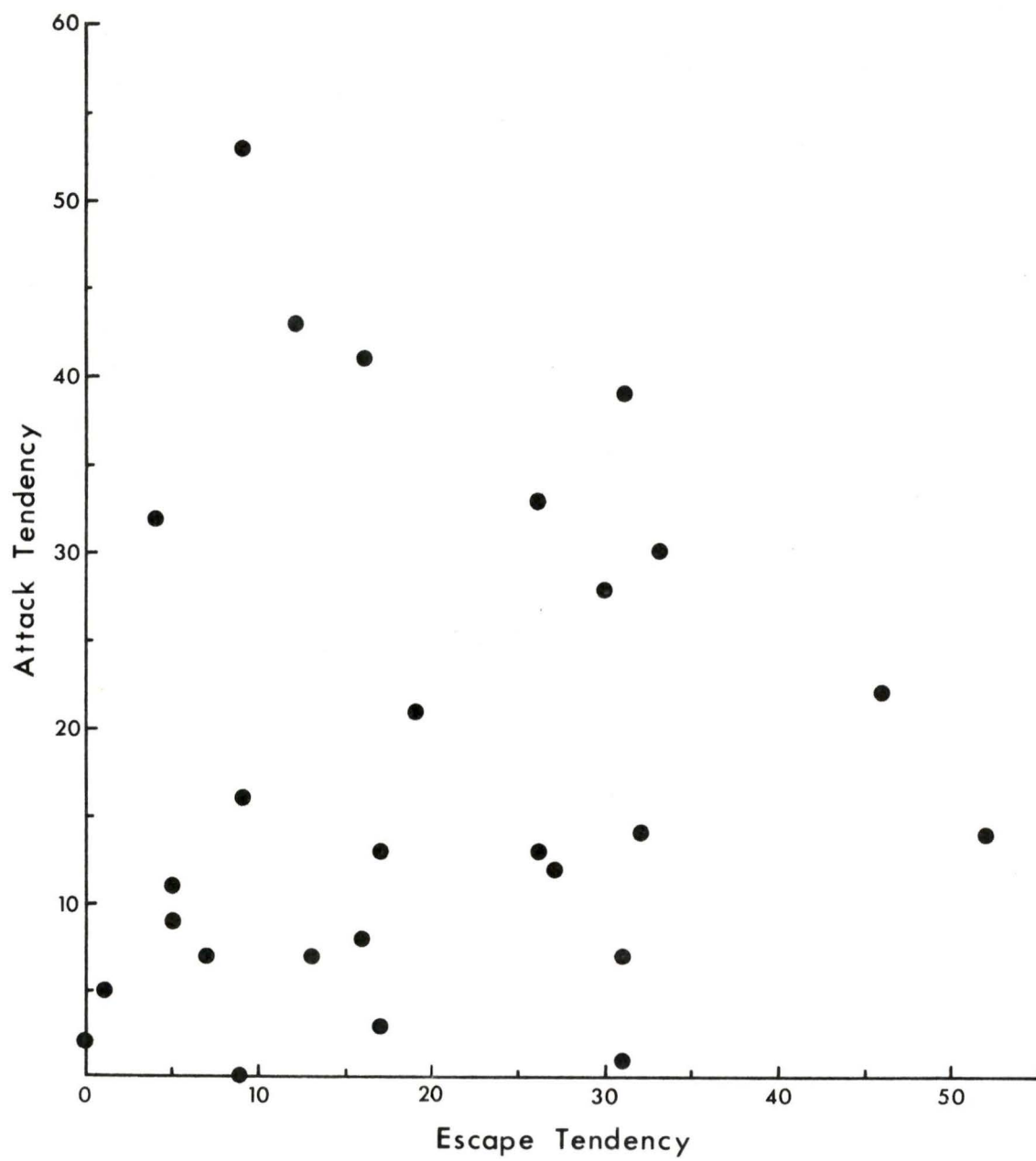
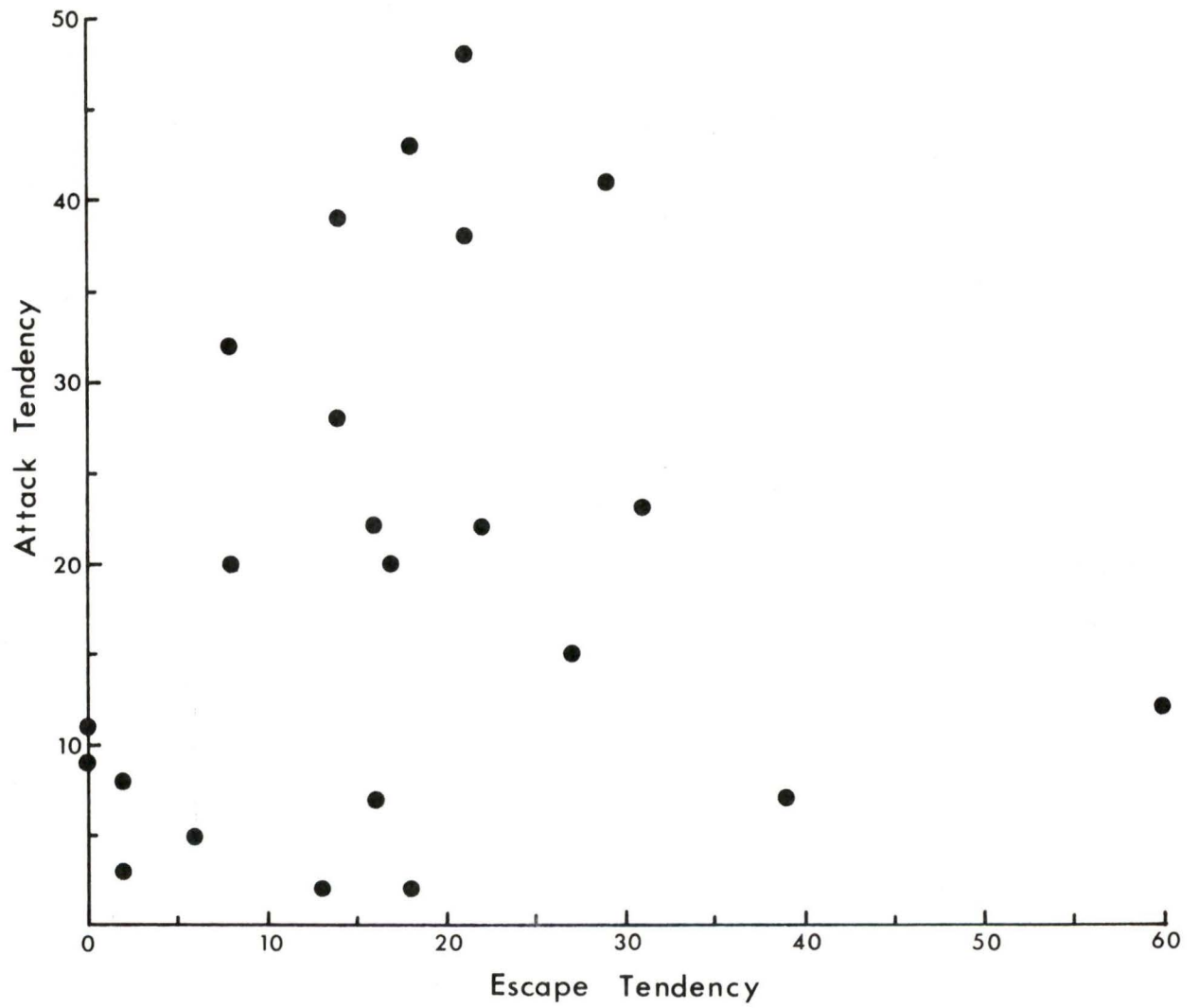


Figure 17. Scattergram showing the relationship between the attack (ordinate) and escape (abscissa) tendencies over a 30 min period for 23 china rockfish encounters. Attack tendency is measured by the summed frequencies of NIP, ANP, BUT, LAP, CHS, MTH, FLD and OPD. Escape tendency by the summed frequencies of TRN, FSW, BFN, and RSW. Each ● indicates one 30 min period (experiment).



The movements and orientations of chase (CHS), lateral push (LAP), nip (NIP) and attempted nip (ANP) clearly imply strong aggressive tendencies, while turnaway (TRN) and backward fin (BFN) are the purest examples of flight tendencies. Several behaviours show evidence of both tendencies since an individual assumes an orientation neither facing the opponent nor facing away. Such actions include carousel (CAR), encircle (ENC) and opercular display (OPD). Qualitative observations on the orientation and movements of the various agonistic activities are thus consistent with the results obtained by factor analysis.

(iii) Models of Agonistic Behaviour

Figures 18 and 19 represent generalized models of agonistic behaviour for black and china rockfish respectively. These models incorporate the salient features obtained from the application of cluster analysis, maximum spanning trees and factor analysis to the data matrices. In both figures the internal attack and flee mechanisms are symbolized with A and F respectively. The relative influence of both mechanisms on each behaviour element is represented by the width of the line connecting attack or flee to each element. The arrows pointing to A and F depict external stimuli that modify the relative influence of these mechanisms and inhibitive relationships between the internal mechanisms when either tendency is high.

Figure 18. Diagrammatic model of the agonistic behaviour of black rockfish.

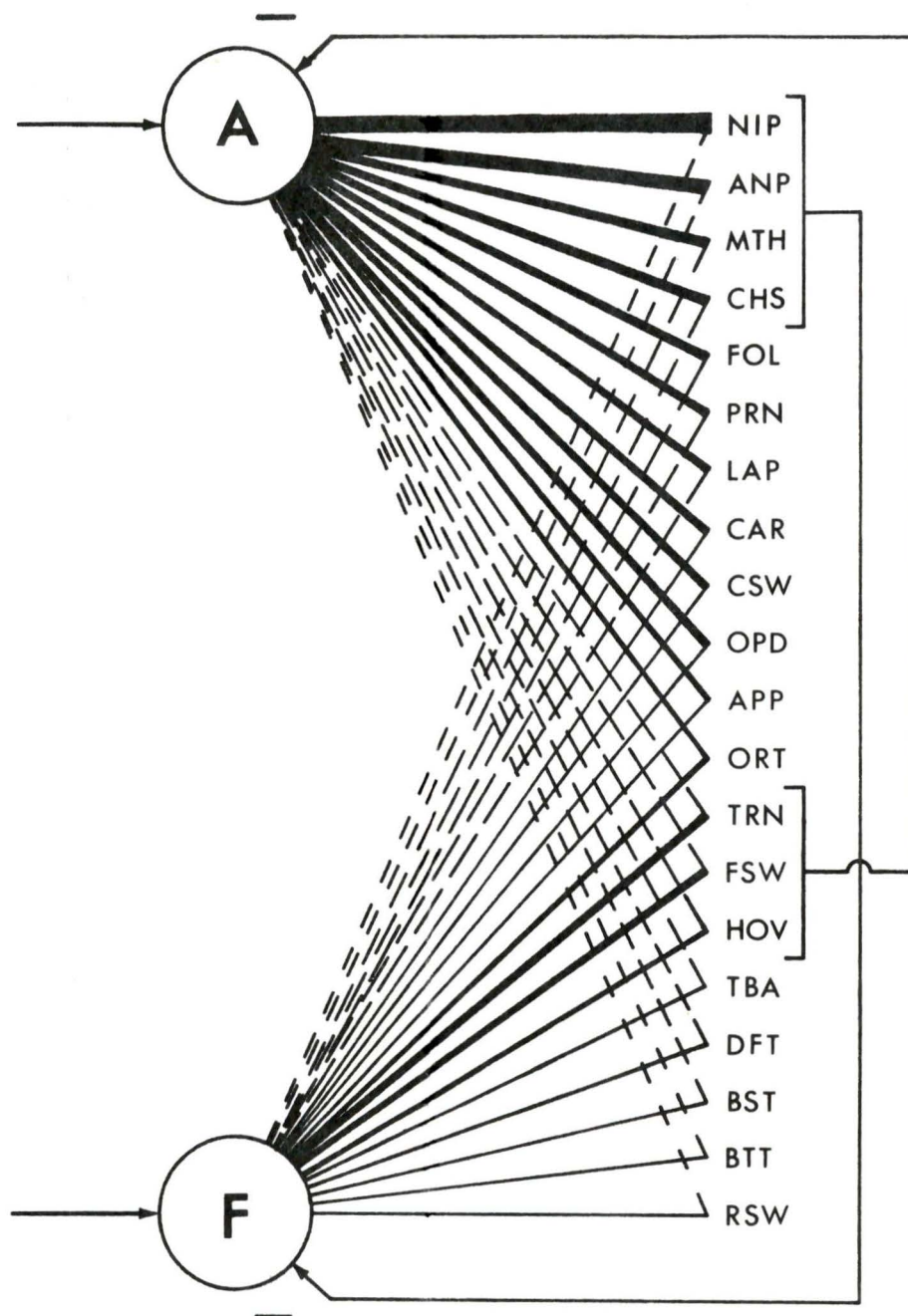
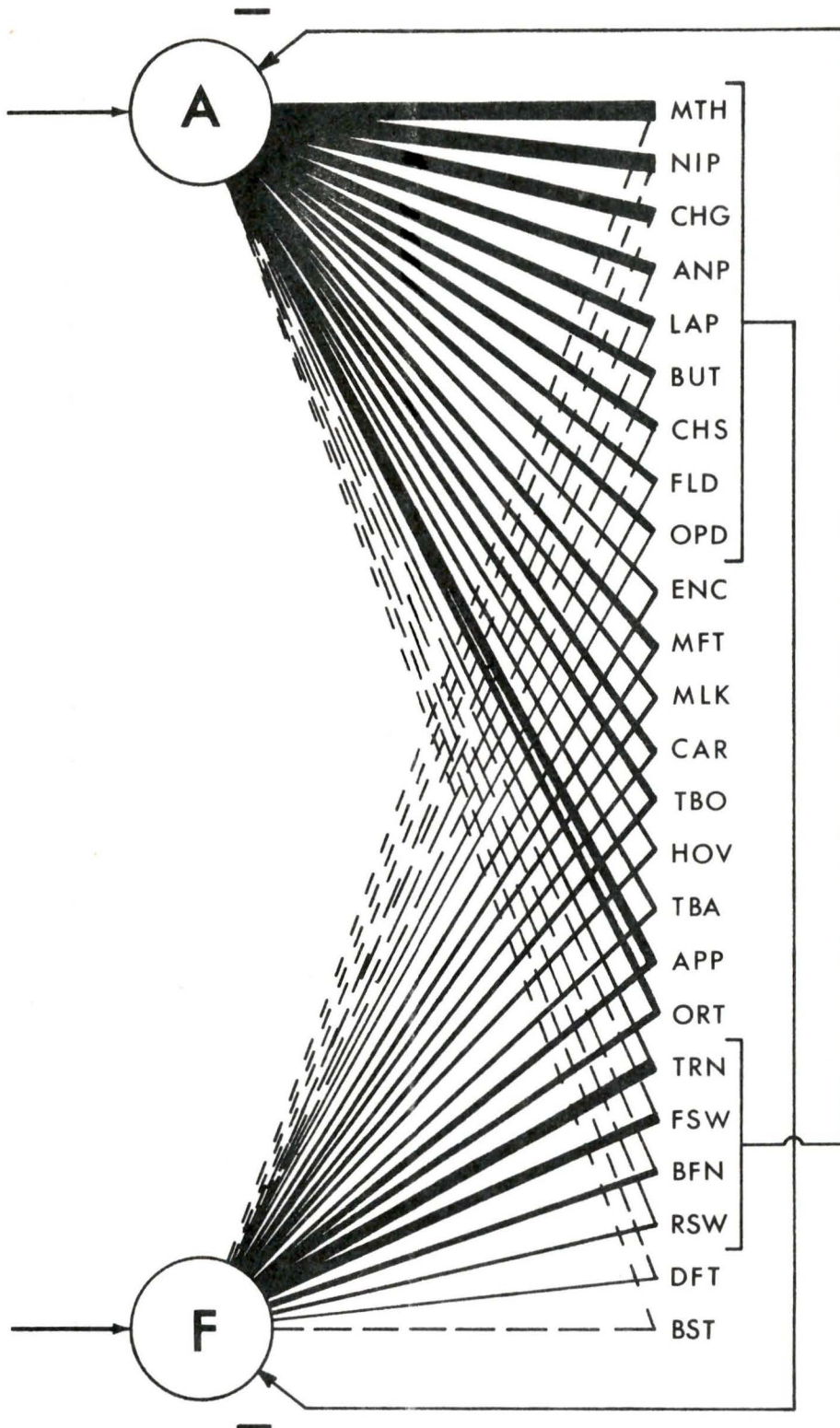


Figure 19. Diagrammatic model of the agonistic behaviour of china rockfish.



SOUND PRODUCTION

I. Context of Sound Production

Sounds were emitted by dominant and subordinate fish of both species during staged agonistic encounters. Both sexes of china rockfish produced sounds. Of all black rockfish producing sounds, only one large individual was identified as male; the rest were immature (Appendix I). Although sounds were recorded during many encounters, only loud sounds were suitable for analysis. A summary of sounds analysed together with their behavioural context is presented for each individual fish in Appendix VI.

Even though submissive behaviour was evident during encounters between black rockfish, only sounds associated with the aggressor were picked up by the hydrophone. In general, the number of sounds produced and their amplitudes were related to the intensity of the conflict. Black rockfish showed a lower level of aggressive motivation when compared to china rockfish, and this was reflected in the production of fewer and much fainter sounds. Thus the apparent lack of sound production by submissive black rockfish may have been due to the low sensitivity of the hydrophone, or a masking of the signal by background noise.

II. Agonistic Behaviour Patterns Associated With Sound Production

Approach was the aggressive response most commonly associated with sound production for both species. Low

frequency growling sounds were produced during the approach, and often continued for several seconds while the fish hovered in opercular display. Frequently, during an approach, the sound increased in loudness as the aggressor neared its opponent. Often, it appeared speed of approach was related to sound production; sounds rarely accompanied slow approaches, whereas sounds were usually associated with quick approaches. A very fast approach, i.e. charge, was always accompanied by sound production.

Other common aggressive responses associated with sound production were follow and chase for black rockfish and full display, charge, chase, tail beats, carousel and lateral push for china rockfish. During a tail beat aquarium, a short burst of sound was emitted at the moment of contact, associated with the sudden movement of the fish's body and tail.

A single fish interacting with the mirror would produce continuous sounds while swimming with its snout pressed against the mirror in an attempt to approach its "opponent". Periodically, while in this position, the fish thrust itself against the aquarium wall with violent sweeping motions of its tail, at the same time producing a much louder sound.

Submissive fish usually avoided the close approach of the dominant fish with a quick, darting escape movement, at the same time displaying a fully erect dorsal fin. Again,

sound production was frequently linked with sudden lateral body motion of the fish. Avoidance sounds were of short duration and were the only sounds produced by submissive fish.

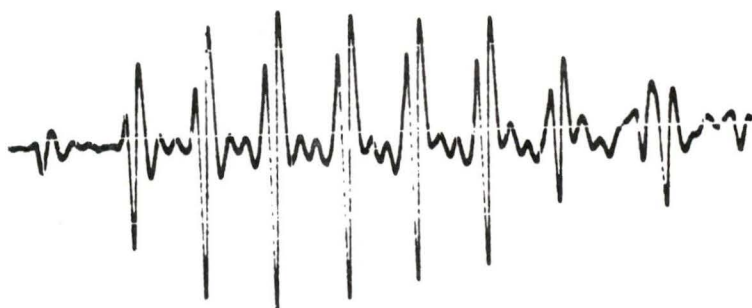
III. Description of Sounds - Both Species

Each sound complex associated with a bout of activity was made up of one or more bursts of sound. The number of bursts and the time interval between them were so variable that they could not be readily characterized. For example, during an approach towards a stationary opponent, a single sound of long duration was often produced. Subsequently a series of shorter bursts were emitted by the same fish while repeatedly approaching a fleeing opponent. For convenience, I will consider each of these bursts of sound as the basic sound element, and the terms sound and sound burst as synonymous.

Sound bursts consisted of a series of brief, damped pulses. Fig. 20A shows a typical sound burst emitted by a china rockfish during a tail beat directed against the aquarium floor. A slight decrease in pulse interval is associated with an increase in amplitude of the pulses and vice versa. Correspondingly, a sound burst made up of equal amplitude pulses tends to have a constant pulse interval (Fig. 20B).

The relationship between amplitude and pulse interval was particularly evident in sounds of long duration, about

Figure 20. Oscillograms of sound bursts emitted by the same china rockfish during two successive tail beats. A. Note relationship between pulse interval and amplitude of signal at terminal portion of sound. Time bar 20 ms. B. Note relatively constant pulse interval associated with constant amplitude. Time bar 20 ms.

A**B**

6 seconds (s), produced during mirror image interactions. These bursts were comprised of a very low amplitude, long pulse interval sound, frequently changing into a high amplitude, short pulse interval sound, of typically 300 milliseconds (ms) duration. These secondary bursts, (Fig. 21A), within the primary burst of sound coincided with violent, momentary swimming actions of the fish thrusting itself against the mirror. Pulse repetition rates were characteristically about 42 pulses per second (pps) during the low amplitude phase, rising to an average of about 47 pps during a secondary burst.

On several occasions black rockfish produced sounds that showed a wide range in pulse interval and amplitude. The sounds were characterized by a normal burst followed by from one to several "pops" (after McInerney and Yearsley, in press). Pops were single pulses, easily recognized as such by the human ear, because of the long pulse interval. Pulse interval was typically on the order of 100 ms. In addition to the longer pulse interval, pops were much higher in amplitude than the preceding burst of pulses (Fig. 21B).

The shape of the amplitude envelope of the sound was usually dependent upon its duration. Brief sounds initially showed a rapid increase in amplitude to a maximum value, then decreased at a slower rate during the last few pulses (Fig. 21C). Long sounds contained many significant changes in amplitude (i.e. secondary bursts) or remained relatively constant throughout (Fig. 22A and 22B respectively). This

Figure 21. A. Oscillogram of a higher amplitude secondary burst within a primary burst of sound recorded from a china rockfish during a mirror image interaction. Arrows mark low amplitude primary pulses preceding secondary pulses. Time bar 50 ms.

B. Oscillogram of a black rockfish sound burst followed by three single pulses or "pops". Note increase in pulse interval and amplitude. Time bar 50 ms.

C. Oscillogram depicting short initial rise time of amplitude envelope followed by a gradual decrease in amplitude near end of china rockfish sound burst. Time bar 50 ms.

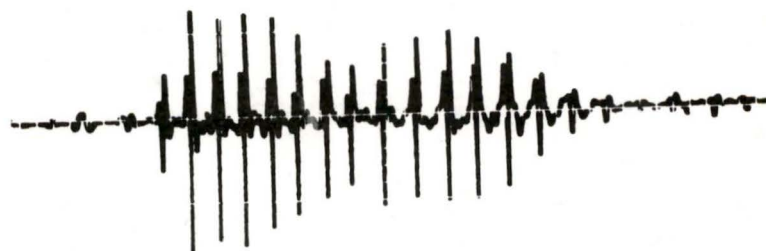
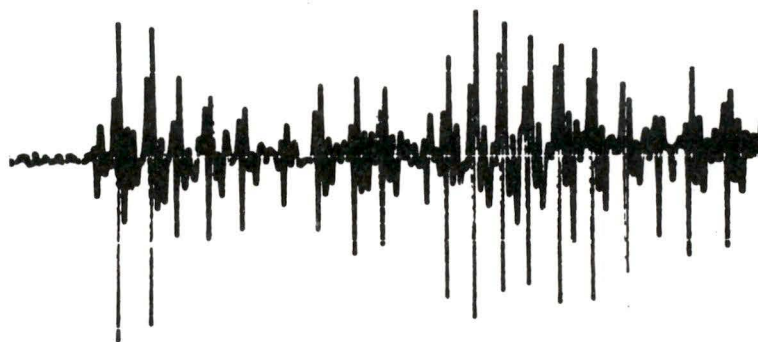
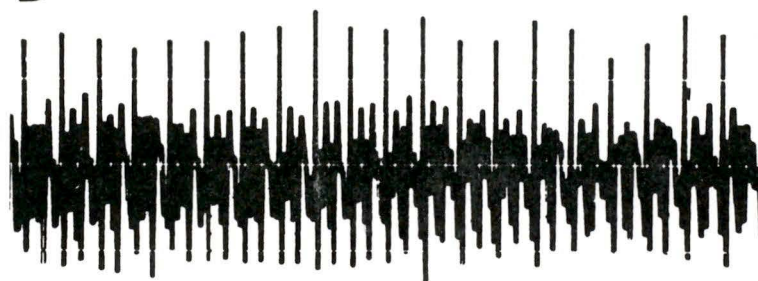
A**B****C**

Figure 22. A. Oscillogram of a secondary burst recorded from a china rockfish showing several changes in amplitude and pulse interval. Time bar 50 ms. B. Oscillogram of a portion of a long duration sound produced during a black rockfish opercular display. Note the relatively constant amplitude and pulse interval. Time bar 100 ms.

A**B**

latter character was commonly related to sounds produced during display behaviour, in which the fish was stationary.

A power spectral density display of a sound produced during a mirror image interaction is presented in Appendix VII. Oscillographic analysis of the identical sound indicated a mean fundamental pulse repetition rate of 47 pps and a range of 27 to 83 pps. High frequency components were also present in the sound but could not be resolved at the chart speed utilized. Correspondingly, the power spectral density showed a fundamental frequency in the 39 - 59 Hz range with harmonics present up to a maximum of about 2500 Hz depending upon amplitude of the signal. The number of harmonics present was influenced by the amplitude of the sound, with more harmonics evident at higher amplitudes. The greatest proportion of acoustical energy occurred consistently under 400 Hz.

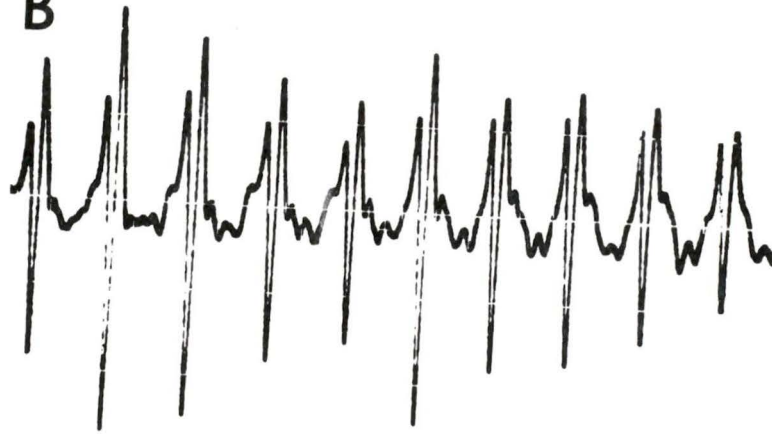
Several sound bursts emitted by china rockfish changed character dramatically within a burst. Initially, the sound had a muffled, indistinct quality, then suddenly took on the louder, more distinct character of a typical growl. This change in quality, apparent to the human ear, was confirmed by oscillographic analysis. Figures 23A and 23B show portions of the indistinct and distinct sounds respectively. The difference between oscillograms appears in the amplitude of the pulse and the degree of signal damping (attenuation) occurring after the pulse. The distinct growl is characterized by a high amplitude, highly damped pulse as

Figure 23. A. Oscillogram of a china rockfish sound consisting of relatively low amplitude, lightly damped pulses. Time bar 20 ms. B. Oscillogram of a segment of the same sound depicted in A, at a later point in time. Note high amplitude, heavily damped pulses. Time bar 20 ms. C. Oscillogram showing a change in amplitude and damping characteristics of a china rockfish avoidance sound. Time bar 20 ms.

A



B



C



compared to a lower amplitude, less damped pulse for the muffled sound. A similar, nearly instantaneous change in sound character also occurred in shorter avoidance sounds (Fig. 23C). In this case the lower amplitude, less damped pulses were associated with the terminal portion of the sound.

IV. Comparison of Temporal Characteristics in the Two Species

(i) Sound Burst Duration

Table IV indicates that the duration of sounds produced by both species were variable in character. Generally, sounds associated with brief activities by the fish, such as avoidance movements or tail beats, appeared less variable and of shorter duration than those produced during longer activities involving opercular displays. Sounds elicited during mirror image interactions also tended to last for a longer period of time than those produced during interactions with another individual.

(ii) Number of Pulses per Sound Burst

Since the number of pulses within a burst of sound was closely related to the sound duration, Table V shows results similar in character to Table IV. The number of pulses per sound burst was highly variable in both species and again, mean number of pulses per burst bore some relationship to the behavioural context of the sound.

Table IV. Summary of sound duration characteristics in two species of rockfish. Sounds were produced during agonistic encounters between conspecifics, or an individual and its mirror image.

Species	Associated Behaviour	Duration (ms)				
		Mean	Range	S.D.	C.V.	n
Black Rockfish	Approach/Chase	715	236-1560	407	0.57	18
China Rockfish	Approach (mirror image)	716	64-9560	1784	2.49	52
	Approach/Chase	536	108-2272	440	0.82	34
	Tail beat	136	100-172	51	0.38	2
	Avoidance Movements	250	48-900	199	0.80	15

Key: S.D. - Standard deviation

C.V. - Coefficient of variation defined as: $S.D./Mean$

n - Number of observations, all fish combined (see Appendix VI)

Table V. Summary of the number of pulses per sound burst in two species of rockfish.

Species	Associated Behaviour	Number of Pulses				
		Mean	Range	S.D.	C.V.	n
Black Rockfish	Approach/Chase	40.8	3-99	30.7	0.75	18
China Rockfish	Approach (mirror image)	39.6	2-339	86.1	2.17	46
	Approach/Chase	27.8	4-96	23.3	0.84	30
	Tail beat	8.5	7-10	2.1	0.25	2
	Avoidance Movements	13.0	9-16	5.0	0.38	13

Key: S.D. - Standard deviation

C.V. - Coefficient of variation defined as: $S.D./Mean$

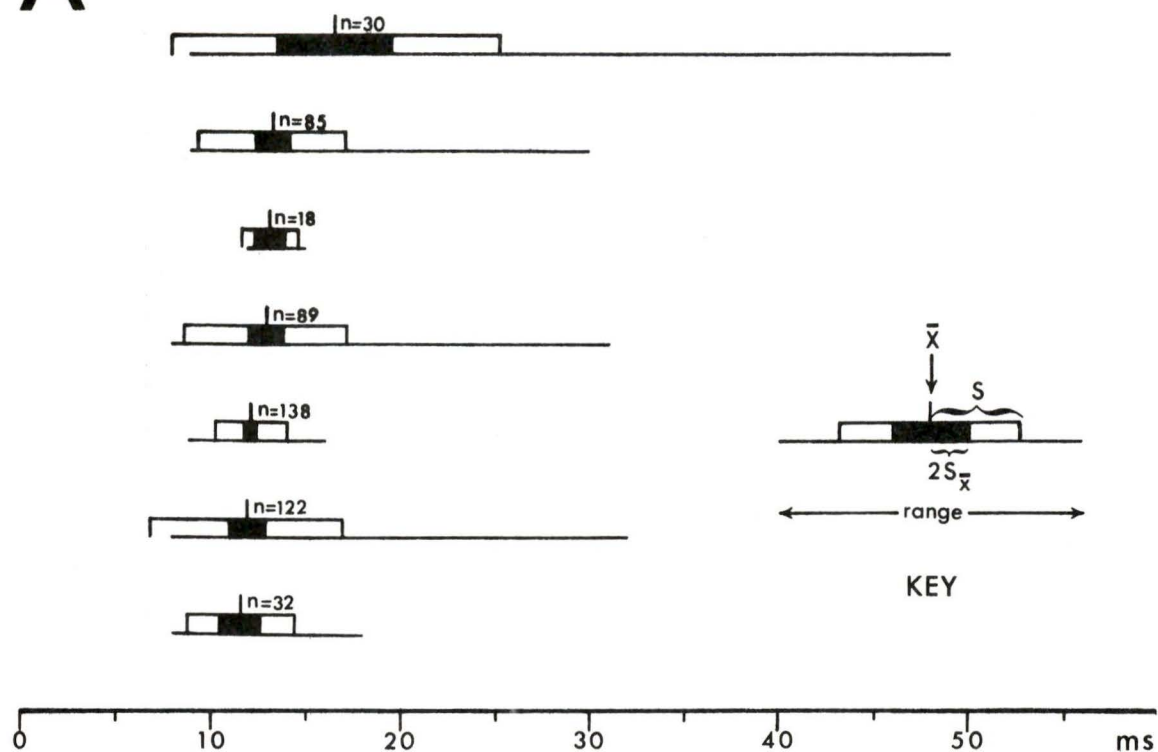
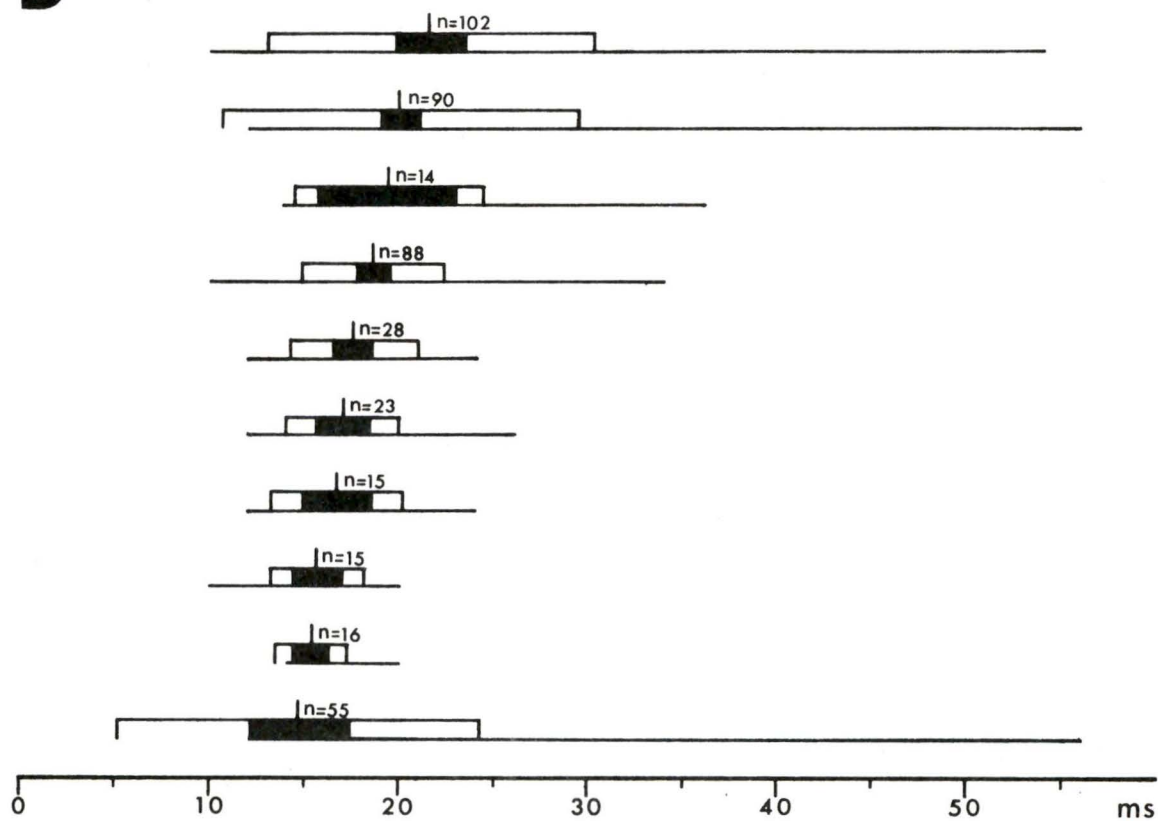
n - Number of observations, all fish combined (see Appendix VI)

(iii) Pulse Interval

The remaining temporal property, pulse interval, was examined within individuals of each species and compared both among members of the same species and interspecifically. Since sample sizes were small in terms of number of individuals and the number of sounds recorded from each (Appendix VI), a rigorous statistical analysis of pulse interval data was not possible. However, some measure of variation in pulse interval was obtained and is presented in pictorial form as a comparison diagram (e.g. Fig. 24).

Figures 24A and 24B show the variation in pulse interval for several sounds produced by individual black and china rockfish respectively. Mean pulse interval appears relatively constant among the sounds sampled for black rockfish individual MEL-2, ranging from about 12 ms to 17 ms (Fig. 24A). The sound at the top of Fig. 24A showed the highest mean value and greatest variation, due to a marked increase in the pulse interval (i.e. a series of "pops") during the terminal phase of the sound. Results for china rockfish individual NEB-4 indicate a slightly more variable mean pulse interval among sounds (Fig. 24B). All sounds depicted were recorded during a mirror image interaction which usually evoked a wide repertoire of sound characteristics because of the physical activity of the fish directed towards the mirror. Mean pulse interval ranged from about 15 ms to 22 ms. A plot of the mean pulse intervals of four

Figure 24. A. Comparison diagram of the pulse interval in seven aggressive sounds of black rockfish individual MEL-2. Mean represented by the vertical line; black bar indicates plus and minus two standard errors of the mean (95% confidence limits); distance from the mean to the end of white bar is one standard deviation; range of values represented by the horizontal line; sample size given as n. B. Comparison diagram of the pulse interval in ten aggressive sounds of china rockfish individual NEB-4. Descriptive key as in Fig. 24A.

A**B**

avoidance sounds produced by NEB-4 is presented in Fig. 25. These sounds showed more consistency, with a range of about 14 ms to 16 ms.

Figure 26 shows combined results of pulse interval analysis among individuals of both species (4 black rockfish and 9 china rockfish). Mean pulse interval appeared to vary among individuals of the same species, as a result considerable overlap was evident between species.

Figure 25. Comparison diagram of the pulse interval in four avoidance sounds of china rockfish individual NEB-4.
Descriptive key as in Fig. 24A.

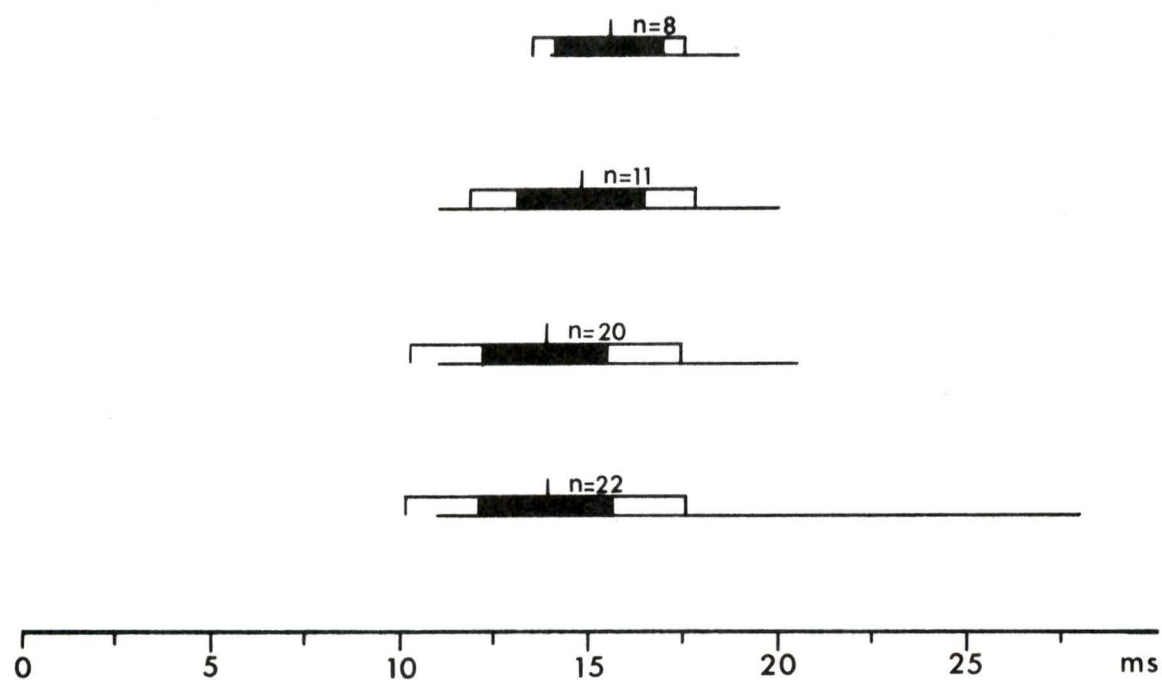
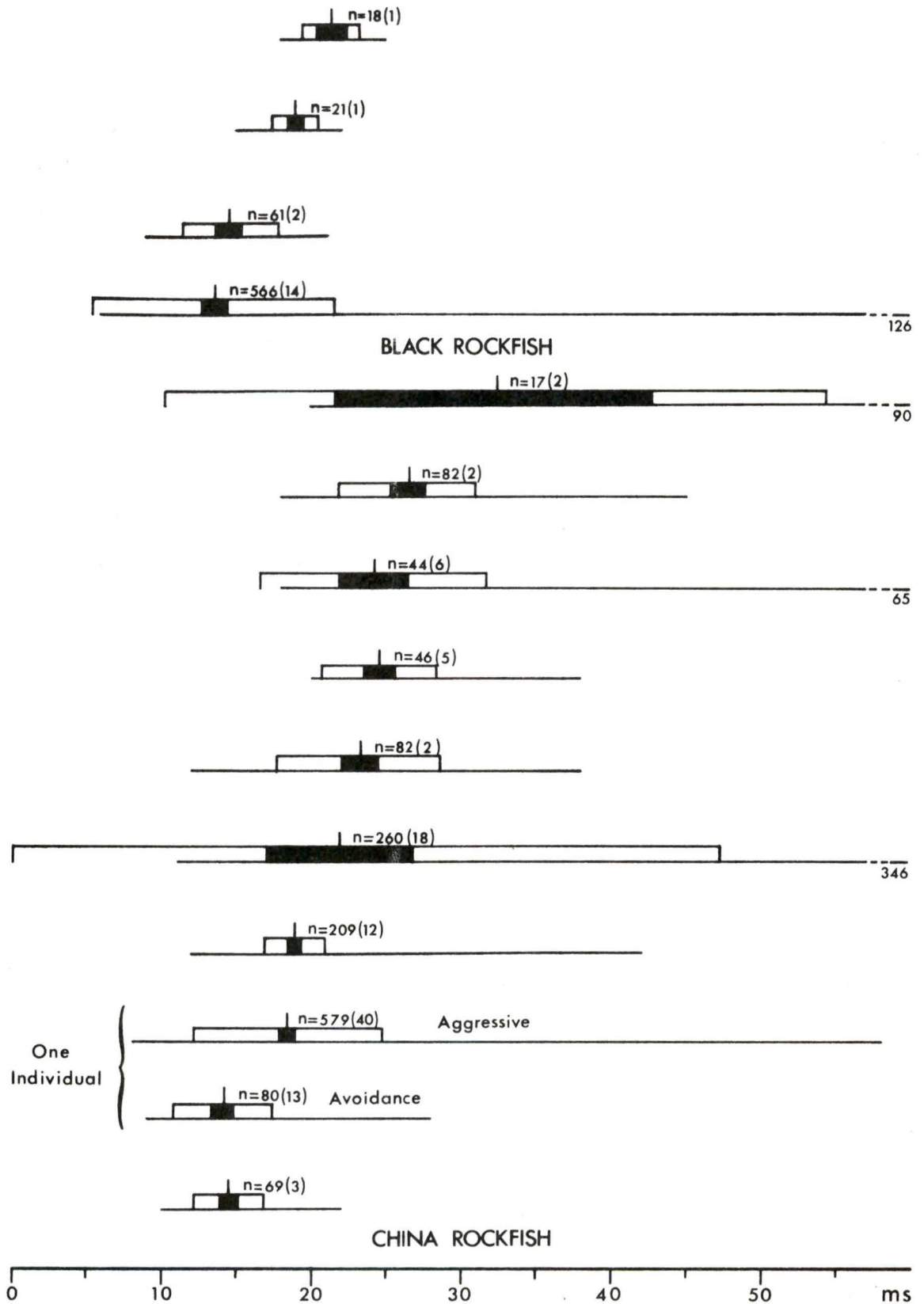


Figure 26. Comparison diagram of the pulse interval in aggressive sounds among four black rockfish (top) and nine china rockfish (bottom). Brace indicates avoidance sounds were also recorded for one china rockfish individual. Number in parentheses following n indicates the number of sounds sampled for each individual, otherwise descriptive key same as in Fig. 24A.



DISCUSSION

FIELD STUDY

I. Behavioural Ecology of Reef Fishes

A limited amount of information has been published on the behavioural ecology of rock reef fishes. Studies by Clarke (1970), Gibson (1969), and Hobson (1965, 1968, 1971) on various rocky shore fishes suggest similar patterns, in terms of habitat associations and site attachment to those of coral reef fishes.

Sale (1978) distinguishes between two major groups of coral reef fishes, transients and residents. The distinction applies equally well to temperate rocky shore fishes. Transients are fish of the water column who do not associate with the reef in any special manner. Salmon Onchoryhynchus spp. and dogfish Squalus acanthias are two examples found at Ohia Islet. The resident group show a close reef association, exploiting it for food and/or shelter from predators. Both china and black rockfish are included in this latter category. Some species observed at Ohia apparently belong to an intermediate group. The lingcod Ophiodon elongatus and several perch species occupy the reef area for short periods of time, up to several days, and then move on. These visitors (Gooding and Magnuson, 1967), represent a group behaviourally midway between transient and resident groups.

Rosenthal (1980) recognized three distinct groups of fish in his study of spatial distribution and habitat

utilization of inshore fish fauna in the Gulf of Alaska: the bottom dwellers, near bottom dwellers and pelagic schoolers. Bottom dwellers include fish that rarely leave the sea floor except in pursuit of prey or when startled; the wolf-eel, Pacific halibut and several small sculpins are members of this group. The china rockfish is an example of a near bottom dweller, a sedentary bottom fish that seldom moves beyond the protection of the substrate. Solitary species typically hover 0.5 to 3 m above the bottom during the day and seek shelter in rock crevices and caves. Finally, pelagic schoolers are a group of mobile, schooling fishes found higher in the water column in areas of kelp forest, around rock promontories and above rugged terrain. Black rockfish are a prominent member of this group.

Typically, coral reef fish are sedentary (i.e. resident), site specific and to a limited degree habitat specialists (Erhlich, 1975; Sale, 1978). The limits of restricted movement over an area of reef may define a home range or territory. The home range of an animal is the undefended area over which it normally travels (Hayne, 1949). It can also be mutually shared by members of a cohesive social group (Wilson, 1975).

Although black rockfish exhibit a degree of site attachment as a home range on Ohiat, the exact nature of this association is unclear. After several weeks of observations, a large proportion of the tagged fish were not seen again. Several factors may have contributed to this

decline. They include reduction in visibility of tags because of algal growth and increased mortality of tagged fish from handling stress or their greater attraction to predators. An alternative explanation is emigration. Movement of black rockfish into deeper water during the winter months may be related to spawning activity or the loss of the kelp bed (Moulton, 1977). Summer movement of the tagged population may simply be to adjacent areas of Ohia Islet. Regions of uniform substrate near the shoreline may function as corridors for the transfer of fish between different areas of a home range larger than the study site (Gerking, 1959). Indeed, two tagged fish were evident among schools observed on the opposite side of the islet from the study site. However, the nature of this movement remains unknown because of limited off site observations.

A territory is any area defended against intruders (Nice, 1941). Territorial fish show both intra- and interspecific hostility in defense of a reef area (Gerking, 1959; Myrberg and Thresher, 1974; Reese, 1975). Observations on china rockfish indicate the home site and immediate area is defended against conspecifics and hence is a territory. Two main types of territories exist among fishes, breeding and feeding territories. Breeding territories commonly include space for egg-laying, nesting and rearing of young. Since china rockfish are ovoviviparous, giving birth to free swimming larva (Hart, 1973; Delacy et al., 1964), territoriality is likely related to defense of a feeding

area. Territoriality serves to disperse individuals throughout suitable habitat, optimizing use of food resources.

II. Social Behaviour and Reef Association

(i) Black Rockfish

A school of fish, i.e. a group of fish that show mutual attraction, may show a polarized or nonpolarized internal structure (Shaw, 1978). Polarized schools are those in which members take up precise positions and move, as one, in a highly organized group. Black rockfish primarily formed nonpolarized schools in which members faced random directions, either as a stationary group or one slowly milling around a particular reef location, such as the perimeter of the kelp bed. Some degree of polarization was evident where fish faced into the current or showed directed movement between two areas of the site. In both cases, there was a tendency for individuals located at the margin of the school to stray, and then rejoin the group, in an apparently random manner. Although black rockfish schools were not highly organized, individual distances of 2 - 3 body lengths were maintained during daylight hours. This distance was not fixed and appeared to diminish at night and during periods of poor visibility.

Polarized schools are rare in coral reef fishes also, perhaps because they are strongly site-attached (Sale, 1978). The maintenance of close visual contact with the substrate may not be compatible with a rigid system of orientation

amongst other members of the school. Ogden and Buckman (1973) observed a degree of polarization in mobile foraging aggregations of the striped parrot fish when moving between two areas of a coral reef. This behaviour is similar to that shown by the schools of black rockfish moving between the kelp bed and the two large boulders on the eastern end of the study site.

Schooling species are commonly attracted to high relief areas on rock reefs (Quast, 1968). These regions include boulder piles, sheer rock faces and the kelp bed. These areas may serve as landmarks to aid in orientation of the school in the water column (Quast, 1968). The kelp may act as a vertical extension of the surface of the reef, thus providing a visual anchor with the substrate. The association may also provide limited protection from predators, either through concealment or reduced manoeuvring space for the predator. Leaman (1976) examined the relationship between the giant kelp Macrocystis integrifolia and juvenile black rockfish and showed that while black rockfish seek shelter in the kelp bed, they do not depend upon it as a foraging area.

(ii) China Rockfish

China rockfish are solitary bottom dwellers. Every tagged fish showed strong site attachment, each occupying its unique home site. Mobility was restricted to movement between primary and secondary home sites and localized forays, probably in search of prey. The home site itself probably

serves a dual purpose, providing both a source of food and a means of protection. Benthic crustaceans, a major diet item, are vulnerable, as they seek refuge in crevices during periods of inactivity (McElderry, 1979; Moulton, 1977). Predators such as the lingcod and dogfish would be unable to pursue and capture a china rockfish seeking shelter deep within a crevice. Familiarity with local topography allows an animal to escape quickly to adequate cover and also promotes more efficient use of food resources in an area (Tinbergen, 1957).

The dispersion pattern of china rockfish is directly related to the spatial distribution of appropriate home sites. Greater densities of fish were present in regions of large rock rubble. Assuming an adequate food supply, areas of high interstitial volume provide more potential home sites than other locations on the reef. Although no study was undertaken to determine the size of the defended area, presumably it would decrease as the population density increased in a homogeneous environment. Secondary home sites were found only in low population density regions on the reef and it appears the reef, as a whole, has the potential to support a larger china rockfish population.

III. Agonistic Behaviour

Agonistic behaviour is a class of activities which include attacking, threatening, submissive and fleeing behaviours (Hinde, 1970). King (1973) associates agonistic

behaviour with a contest or struggle between individuals. Conflict situations may occur over competition for space or resources, and are normally intraspecific (Miller, 1978). Agonistic behaviour was rarely observed on the study reef. No black rockfish agonistic behaviour was seen either in the schooling or resting phase, although in both cases an "individual distance" was maintained. This distance tended to increase during the resting phase, when the fish were perched on rock shelves. It is not known whether this change was due to behavioural factors or merely availability of suitable terrain. Perhaps close association with the substrate tends to emphasize individual rather than group tendencies, as when schooling.

China rockfish agonistic behaviour was observed on only 3 occasions. Indeed, in the absence of the disturbing influence of divers, agonistic encounters may have been very rare. A number of factors may account for this. Territorial size is usually related in some way to population density and/or prey availability. On portions of the reef with low population densities, territorial boundaries may not share a common border or be ill-defined. In either case, there appears to be a limit to the area an animal will attempt to control (Wilson, 1975). In high density areas, such as the rock rubble piles, individuals are not in constant conflict with each other. Even though territories may be contiguous, it is energetically wasteful for neighbours to fight continuously (Miller, 1978). Wilson (1975) terms this the

"Dear Enemy" phenomenon, made possible primarily through the mechanism of habituation. Sale (1978) states some territorial coral reef fish may show individual recognition of neighbours, but this may simply be a result of repeated observations of a neighbour at a familiar site. Finally, territorial defense may vary seasonally, either related to the reproductive cycle or changes in food resources.

Agonistic behaviour in all cases was of a low intensity. Typical aggressive postures included full extension of the branchiostegal membranes and partial erection of the spinous portion of the dorsal fin. The resident fish rapidly approached and pursued the fleeing intruder, turning back and swimming to the home site after a certain limit was reached. Typical submissive behaviour included various avoidance movements ranging from turning away, to fleeing an area entirely. The intruder normally showed full erection of the spinous portion of the dorsal fin during the confrontation and subsequent flight.

Haaker (1978) describes the agonistic behaviour he observed between two treefish, S. serriceps, while diving at Santa Catalina Island off the California coast. Treefish are similar in habit to china rockfish in that they are territorial and seek shelter in rocky crevices (Feder et al., 1974). The encounter occurred between the defender of a cave and a smaller intruder. The defender approached with erect dorsal fin and gaping mouth. The intruder responded in a like manner, and both fish attempted to grasp one

another by the jaw during a series of darting motions. A mouth fight ensued, during which each fish would grasp the other's jaw and hold it for several minutes while moving back and forth. Hallacher (in Haaker, 1978) has observed similar displays and actions in the gopher rockfish (S. carnatus), but considers these rare occurrences.

Although black rockfish did occasionally pass within "striking distance" of a china rockfish in or near its home site, no interspecific encounters were observed. Myrberg and Thresher (1974), describing territorial behaviour in a Caribbean damselfish, Eupomacentrus planifrons, concluded these fish differentiate among a variety of species and react differentially to each. Ecologically similar, and hence potential competitor species, were attacked further from the residence than noncompetitors. This may explain the lack of aggression shown towards the black rockfish by an ecologically dissimilar species, the china rockfish.

LABORATORY STUDIES

AGONISTIC BEHAVIOUR

I. Interpretation and Function of the Agonistic Behaviour Patterns

Both black and china rockfish exhibit, at least under aquarium conditions, "classic" aggressive behaviour patterns, similar in form and function to those described for many other species ranging from cichlids (Baerends and Baerends - van Roon, 1950) to blennies (Gibson, 1968). Any attempt to relate the agonistic displays and movements to the level of aggressive tendency of the fish must consider three elements: (i) the overt action as a whole, i.e. the behaviour which accompanies the display, (ii) the positions or posture of the fins or other body parts and (iii) the relative orientation of one fish towards the other. The development of aggressive behaviour in both species consists of increasingly complex behaviour from the initial orient and approach. The complexity probably depends upon steadily increasing motivational conflicts which in turn depend upon both internal and external factors. Thus a large fish proceeds directly to a much smaller (fleeing) opponent and butts it; a fleeing fish is attacked immediately.

During conflicts between equal sized fish, more elaborate displays and actions are evident. The direction of movement of the fish indicates which tendency is predominant at any point in time. Advancing movements such as approach or chase

are expressions of higher aggressive tendencies, whereas turnaway, flee or backward fin are the result of increasing flight or escape tendencies. A balance of these two tendencies can be seen in carousel, encircle and opercular display. The erection of gill covers together with full extension of the branchiostegal membrane is observed in both species, a common threat display in fish (e.g. the cod, Gadus callarias L., Brawn, 1961a; siamese fighting fish, Betta splendens, Simpson, 1968). This posture presumably serves to increase the apparent size of the fish, most noticeably from a frontal view and to a lesser extent laterally.

With two exceptions, the position (extension/contraction) and movements of the paired and median fins are principally involved in stability and locomotion. Changes in position of the spinous (anterior) portion of the dorsal fin and the motion of water produced by lateral motions of the caudal fin (tail beats) both serve a communicatory function. Complete erection of the dorsal fin spines is a typical defensive manoeuvre in spiny-rayed fishes, and appears in both species of rockfish during submissive acts. The tilt manoeuvre described under submissive behaviour, in which the fish rolls to one side presenting its raised dorsal fin to the superior fish is similar to "leaning" in the asian teleost Badis badis (Barlow, 1962). Full erection of the dorsal fin by submissive fish may provide additional stability required for a sudden avoidance manoeuvre.

Both species of rockfish also showed two other characteristics typical of appeasement behaviour among spiny-rayed fishes: reduction of motion and a head up posture (Barlow, 1962). Movements on the part of the submissive fish play an important role in interactions, usually precipitating an aggressive response from the other fish. Once approached, escape movements usually resulted in chase, attempted nip or nip. Similarly, Stringer and Hoar (1955) showed clearly that movement was a primary requisite eliciting nipping in kamloops trout.

The characteristic folding over of the anterior elements of the spinous dorsal fin and opercular flaring during full display was also observed by Barlow (1962) in Badis badis during what he called a "frontal approach". He also noted progressive folding of the leading dorsal spines as a fish moved forward towards its opponent, likely indicating a higher tendency to "ram". This could also apply to china rockfish, as high speed swimming seen during butting was accompanied by a completely folded dorsal fin, possibly to reduce drag. At first sight, the nearly erect dorsal fin observed during full display suggests a high flight tendency and as such should be ranked under opercular display. However, several observations indicate full display has a higher aggressive component than opercular display. Full displays were associated with frontal approaches towards an opponent, (i.e. head-to-head confrontations), lateral pushes

and multiple tail beats, whereas opercular displays usually occurred in conjunction with lateral orientation to the opponent, a position favourable to either attack or escape.

Mouth fighting, similar in form to that seen in china rockfish has been observed in two species of cichlids, Hemichromis bimaculatus (Baerends and Baerends - van Roon, 1950), Nannacara anomala (Jakobsson et al., 1979) and the centrarchid, Lepomis gibbosus (Keenlyside, 1965). Jakobsson et al. (1979) observes that mouth fights probably function as a test of relative strength between combatants. This appeared to be true for china rockfish encounters, for prior to a mouth fight both fish showed similar threat behaviour in the form of opercular display and carousel. However, subsequent to the mouth fight, one fish always emerged a clear winner and a dominant/subordinate relationship was established.

An agonistic encounter between two rockfish can now be understood in terms of a series of stereotyped displays and movements. Each of these behaviours can be broken down into various component elements that allow a functional and motivational significance to be assigned to the behaviour as a whole.

II. Factors Affecting the Outcome of an Agonistic Encounter

The outcome of an agonistic encounter was most likely decided in favour of the initiator of the conflict and/or the larger of the two fish, whereas the length of prior isolated residency seemed to have little or no influence. Many studies have shown that larger individuals normally dominate smaller

members of the same species (e.g. Baerends and Baerends - van Roon, 1950; Newman, 1956; Wiepkema, 1961). Also, as Sale (1977) points out for coral reef fish, prior residency gives a psychological advantage (and frequently a size advantage) to the home fish in any struggle with an intruder. The lack of significant influence of prior residency on the probability of a fish winning or losing is difficult to explain, perhaps the movement of fish from one aquarium to another during an experimental series was a disturbing influence. The decided advantage of initiating a conflict has implications in territorial defense. The advantage apparently is in favour of the defending fish, as presumably it would initiate any conflict between itself and an (accidental) intruder, at least near its home site. There is also some evidence to suggest that (within limits) smaller fish may successfully defend a home site against a larger intruder because of its role as "initiator".

III. Causation of Agonistic Behaviour

An understanding of "why an animal does what it does when it does" would ideally involve a study of what internal and external factors act and interact to cause the performance of a given behavioural pattern at a given time (Brockway, 1964). In the present study, causation was limited to a broad analysis of the motivation of various agonistic behaviours. Two methods commonly used in motivational analysis are: (i) the nature of the behaviour itself with

regard to posture, motor patterns and orientation (discussed in the previous section) and (ii) what the individual does immediately before and after a given behaviour pattern (Tinbergen, 1959). Method (ii) was achieved through the application of cluster analysis, maximum spanning trees and factor analysis to behavioural sequence data.

Factor analysis indicated that about 80% of the total common variance among the agonistic behavioural elements for both species of rockfish can be explained with the aid of two independent tendencies, the aggressive and escape tendencies. The agonistic activities of a dominant rockfish can be described in terms of the relative strength of these two tendencies. Some activities such as nip and attempted nip probably express one tendency only, or as Tinbergen (1959) states, possess single or unitary motivation. Other agonistic activities such as carousel, opercular display and encircle possess dual motivation.

Although the common factors were chosen to be statistically independent, this does not imply independent changes in the levels of the corresponding tendencies. There is evidence to suggest a negative correlation between major tendencies when they are high and this correlation is probably a function of the level of these major tendencies, with independence existing only at lower levels.

Observations from method (i) involving the study of postures, orientations and movements, are compatible with the model of aggressive behaviour developed for both species

of rockfish through the application of the three multivariate techniques. Similar analyses of complex behaviours have produced comparable results. Using factor analysis, Wiepkema (1961) analysed the reproductive behaviour of the male bitterling (Rhodeus amarus), which establishes a territory around a mussel. He found a 3-dimensional (3-factor) model accounted for about 90% of the total common variance among the 12 movements. Factor one, the "aggressive factor", was comprised of aggressive movements in defense of the mussel; the second "non-reproductive" factor was characterized by feeding, comfort and flight movements; the third "sexual" factor was comprised of movements intended to entice the female towards the mussel. The agonistic movements were shown to express two independent tendencies, that of aggression and flight. Wiepkema stated that real independence would probably only exist at the lower and middle levels of these tendencies, with an inhibitive relationship present at high levels.

Baerends et al. (1970) also used factor analysis in a study of the interruptive activities performed during incubation shifts of the herring gull. Their 3-factor solution explained 70% of the total common variance among variables, with two distinct groups emerging. One group comprised "building" activities. The two groups were almost diametrically opposite each other, indicating a high degree of negative correlation. Results indicated both preening and building are evoked by unsatisfactory feedback stimulation

(e.g. disarrangements of the plumage and nest structure respectively) and that both differed in their causation. Preening was associated with a tendency to break up incubation while building was associated with a tendency to continue incubation. Both these studies suggest that activities tend to occur in groups which appear to mutually inhibit one another.

Several investigators have questioned the use of factor analysis in ethological studies, and some confusion exists in recent literature. Morgan et al., (1976) recommend cluster analysis over other multivariate methods (e.g. factor analysis), as it requires fewer assumptions. However, Frey and Pimentel (1978) state that (principal component) factor analysis appears to be very robust to departures from the experimental assumptions of (i) multinormal (i.e. multivariate normal) distribution of the population being sampled and (ii) random sampling to ensure that samples are representative of the populations from which they are drawn. DeGhett (1978), on the other hand, proposes both factor analysis and hierarchical cluster analysis should be used as an aid in identifying common causal factors in behaviour, with neither acting as the sole criterion. Andrew (1972) points out a general problem with factor analysis: it assumes the usefulness of describing causation in terms of a few factors whose nature is questionable. Some behaviours may appear to be related because of constraints imposed on them by the environment or are included in a group because of close relations

between other acts. Andrew (1972) also comments on the fact that it is easy to explain behaviours with loadings on two factors in terms of a conflict theory of motivation, thus tending to confirm preconceived notions.

Multivariate techniques as applied in the present study have shown that agonistic activities in both species of rockfish can be understood in terms of two common tendencies: attack and escape tendencies. However, the model does not reveal the nature of the causal factors underlying these common tendencies. As Wiepkema (1961) points out, one can only state that they are comprised of external and internal factors. Further experimentation will be required to elucidate the relative influence of internal factors, i.e. the characteristic structure of the organizing network (Baerends, 1976), or external factors of the environment on the tendencies.

IV. Comparative Aspects of Agonistic Behaviour and its Relation to Behavioural Ecology in Both Species

Agonistic behaviour in black rockfish appears to be more ritualized than in china rockfish. Threat displays (e.g. opercular display) and intention movements (e.g. attempted nip) are characteristic of black rockfish encounters, whereas actual physical contact (e.g. lateral push, bite, nip) is commonly seen in china rockfish encounters. Obvious differences between the species appear in the frequencies of bottom sit and hover. These contrasts are directly related to the behavioural ecology of each species in its natural environment.

Black rockfish, which exhibit low frequency of bottom sit and relatively high frequency of hover, spend much of their time schooling. They also have a resting phase in which individuals sit on suitable rock shelves and outcroppings. In contrast, china rockfish show a high frequency of bottom sit and a relatively lower frequency of hover, consistent with their solitary benthic lifestyle.

Kinematic graphs reveal a more predictable pattern to the sequence of events during a black rockfish encounter, than that of china rockfish. This may indicate a greater complexity of the association between internal and external factors which affect aggressive tendencies, or simply be an artifact of the aquarium situation. An argument can be made for both points of view. Motivational analysis suggests that china rockfish are "finely tuned" to the subtleties of the external environment, whereas black rockfish aggression appears to be an "all or none" proposition.

Gibson (1968) points out that abnormal behaviour (i.e. behaviour not occurring in nature) may result if aquarium space available to the fish is too small compared to spatial requirements in the natural environment. Based on field observations, china rockfish were housed under rather crowded conditions. This, coupled with the fact that no cover was available, may have affected both the frequency and nature of observed agonistic activity, since a defeated fish would not be able to escape or seek cover as it would in nature.

Thus, further experimental studies on the agonistic behaviour of both species of rockfish require a habitat closely matched in available space and cover objects to that found in their natural environment. For china rockfish especially, this would allow the finer structure of threat displays and aggressive movements to be analysed more critically.

Interactions could be monitored over various distances (and hence, relative strengths of attack and escape tendencies) from the home site itself to the territorial boundaries. The aggressive activities observed during the present study may present only one facet of the entire agonistic repertoire.

The functional significance of aggressive behaviour between conspecifics of a territorial species such as china rockfish is easily understood. However, why do black rockfish, a social (schooling) species in the natural environment act aggressively towards conspecifics in the experimental environment? Agonistic behaviour in social groups may function in the establishment and maintenance of dominance hierarchies or mobile personal spaces (Sale, 1972). Dominance hierarchies have been documented among several species of coral reef fishes that occupy restricted areas and live in small stable groups. Sale (1977), for example, describes dominance hierarchies in the pomacentrid Dascyllus aruanus. Small groups, commonly of 2 to 5 individuals take shelter in one coral colony and restrict their movements to the water immediately surrounding it. However, dominance hierarchies do not appear to be a feature of large, mobile schools fully

exploiting available resources (Radakov, 1973; Sale, 1978). Typical schools of this nature include those of anchovies, herring and tuna. Shaw (1978) describes schooling fishes as an example of a "truly egalitarian state" in which all members of the group have equal influence and importance. Although black rockfish schools show limited site attachment some evidence that movement of schools off the reef does exist. This relative mobility over the reef coupled with the large size of black rockfish schools, typically numbering in the hundreds, probably rules out the formation of dominance hierarchies.

Individual distance, or the area around an animal in which it excludes members of the same species through threat, attack or retreat, may explain black rockfish aggressive behaviour. Brawn (1961a), in attempting to explain aggressive behaviour of captive cod, postulated the existence of an "invisible territory" around each aggressive fish. A zone in which the presence of another cod would not be tolerated. Lorenz (1966) considers the area around the individual, whose radius is the individual distance, as a small movable territory. He argues that the behavioural mechanisms maintaining the area are fundamentally similar to those which result in the concept of territoriality. A high level of aggressive motivation is associated with a large individual distance and vice versa. Gibson (1968) demonstrated in his studies on blennies that aggressive motivation was affected by total available space and size difference between fish. He observed

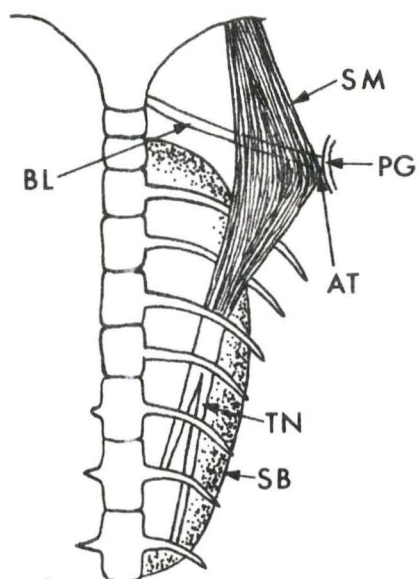
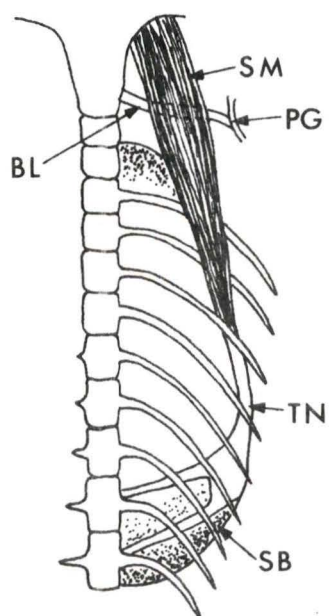
that the level of aggressive drive was generally lower under crowded conditions (see also Keenleyside and Yamamoto, 1962) and that the smaller fish was attacked more often in encounters with two fish of similar, rather than disparate, size. Finally, various studies in fish linking social-aggressive behaviour to short-term intervals of isolation indicate isolation from conspecifics increases aggression (Davis et al., 1974; Hinkel and Mair, 1974; Chizar et al., 1976; Thresher, 1978).

SOUND PRODUCTION

I. Comparative Anatomy of the Swim Bladder - Sonic Muscle Complex

Rockfish produce sound by rapid contraction of striated bilateral, extrinsic swim bladder or "sonic" muscles (Matsubara, 1943; McInerney and Yearsley, in press). They originate on the occipital region of the cranium and, extending posteriorly, insert on the swim bladder or vertebral parapophyses by means of tendons (Hallacher, 1974). Considerable variation in morphology and attachment occurs throughout the genus. Hallacher (1974) placed the black rockfish and china rockfish in distinct categories based on muscle arrangement and attachment. In the black rockfish the muscles also attach to the pectoral girdle from their origin on the cranium and then insert on ribs (Fig. 27A). There is no attachment to the swim bladder itself, although the muscles and tendons are in close association with the

Figure 27. A. Morphology of the extrinsic swim bladder musculature in the black rockfish. Dorsal view, right side showing (SM) striated muscle, (PG) pectoral girdle, (BL) Baudelot's ligament, (AT) attachment of muscle to pectoral girdle, (TN) tendon, (SB) swim bladder. Note lack of firm connection to swim bladder by tendons. B. Morphology of the extrinsic swim bladder musculature in the china rockfish. Descriptive key as in Fig. 27A. Note muscle does not attach to pectoral girdle but is firmly connected to swim bladder wall. (after Hallacher, 1974).

A**B**

bladder wall as they pass posteriorly. China rockfish sonic muscles do not connect to the pectoral girdle but are firmly attached to the swim bladder wall and then insert on vertebral parapophyses (Fig. 27B). Their muscles are thicker and more cylindrical in shape than those of the black rockfish. The swim bladder muscles in both species are pink in colour, indicative of a high degree of vascularization.

The rockfish swim bladder is a completely closed, gas filled, cylindrically shaped organ, broadly rounded at both ends. Internally, it is divided into anterior and posterior chambers by a thin membrane of connective tissue. This diaphragm has a small aperture, controlled by a sphincter which interconnects the chambers when open. The anterior chamber encloses the largest volume and contains the gas secretory centre used for filling the bladder. The posterior chamber has highly vascularized walls that allow diffusion of gas out of the bladder. Comparatively, the china rockfish swim bladder is less elongate in shape, more bulbous at the anterior end and has a thicker outer tissue layer than that of the black rockfish.

II. Mechanics and Acoustics of Sound Production and Reception in Rockfish

Contraction of the sonic muscles provide the driving force in sound production, causing a change in volume and pressure within the swim bladder. Vibrations (deformations) of the bladder are transmitted to the water by the surrounding

tissue. Contraction of the sonic muscles appears to decrease bladder volume and increase internal pressure in both species of rockfish (Fig. 27). The return of the muscles to their initial state is presumably dependent upon the elastic properties of associated connective tissues and skeletal components.

The swim bladder is a resonant structure and when disturbed, vibrates at its resonant frequency. After the last contraction, the amplitude of succeeding vibrations declines at a rate that depends upon the degree of damping of the system (Alexander, 1966). Various authors (Tavolga, 1965; Alexander, 1966; Weston, 1967) have suggested an analogy between the swim bladder and a free spherical bubble of gas in water. At a given pressure the resonant frequency is primarily a function of the radius of the bubble (Alexander, 1966). Sand and Hawkins (1973) state that the resonant frequency and damping of the fish swim bladder is affected by the shape of the organ and the restraining effects of surrounding tissue respectively, effects which must be considered when applying the resonance equation for a spherical gas bubble to the swim bladder. The resonant frequency will tend to increase for any shape other than a sphere, and surrounding tissue will heavily damp the resonance of the swim bladder in shallow water (less than 200 m). However, rough calculations indicate that the fundamental frequencies of rockfish swim bladder sounds are

of the same order of magnitude (about 100 Hz) as the resonant frequency of a gas bubble of equivalent volume. Thus it appears the sonic muscles drive the bladder at or near its resonant frequency, optimizing the efficiency of the system.

In order to assess the plausibility of a communicatory system in fish, something must be known about the ability of the receiver to detect sounds. The acoustic energy of a sound propagating underwater is present in two forms, a pressure wave and a displacement (Tavolga, 1965). The pressure wave, or far-field effect, is associated with the elastic propagating sound wave and declines in direct proportion to distance. The amplitude of the displacement (hydrodynamic motion) or near-field effect is inversely proportional to the square of the distance from the source (Fay, 1978). Thus the displacement is detectable only at small distances from the sound source, within 1 wavelength/2 or about 4 m for a 60 Hz signal (Popper and Fay, 1973).

The lateral line and inner ear of fish primarily function as near-field and far-field sensors respectively. In fishes with swim bladders the inner ear receives near-field displacements from the bladder (Tavolga, 1968). The acoustic impedance of fish tissue and water are very similar and a fish is virtually transparent to water-borne sounds (Griffin, 1955). However, the swim bladder represents an acoustical discontinuity and acts as a transducer for pressure waves, transforming them into a near-field effect (Harris and

van Bergeijk, 1962; van Bergeijk 1964). The swim bladder reradiates impinging acoustic energy to the inner ear via intervening tissue and bone. This process is probably enhanced in rockfish because the sonic muscles create a direct link between their origin on the otic region of the skull and insertion on the swim bladder.

Popper (1974) investigated the response of the swim bladder of the goldfish Carassius auratus, to acoustic stimuli and found it to be a "broadly tuned" system. Such a system has a broad resonance permitting sensitivity over a wide range of frequencies, and also responds quickly to impulsive sounds (Harris, 1967). Thus the rockfish swim bladder/sonic muscle complex seems well adapted for the reception and transfer to the ear of pulsed sounds.

III. Relation Between Information Content, Biological Significance and Sound Characteristics

Fine et al. (1977) categorized five basic ways, often related, in which a sound signal produced by a fish may be varied: amplitude, duration, repetition rate, number of pulses within a signal, and frequency. Each of these characteristics will be discussed in light of results, with emphasis on potential information content.

(i) Amplitude

Sounds produced by both species of rockfish showed a wide range in amplitude which appeared to be related to motivational state, or level of arousal, of a particular

fish. High amplitude sounds were evident during a charge, active pursuit or physical contact with an opponent. Relatively low amplitude sounds were produced during less active threatening displays, usually accompanied by opercular flaring. Black rockfish sounds were generally fainter than china rockfish sounds, apparently due to the low level of aggression shown towards conspecifics. Brawn (1961b) noted a similar variation in the loudness of "grunts" emitted by the cod Gadus callarias, during aggressive encounters. The grunt was loudest during a determined threat and became fainter at the end of the aggressive period. Also, the squirrelfish Myripristis berndti, emits grunts and staccato calls as warnings, with the louder staccato representing the most intense warning response (Salmon, 1967).

(ii) Duration

Sound duration is apparently associated with the amount of time the stimulus eliciting the sound and concurrent behaviour is present. The longest sounds were produced during mirror image interactions, a situation in which the "intruder" did not attempt to flee, and therefore, presented a nearly constant stimulus to the defender. Interactions involving another individual resulted in more variable sound durations that reflected the varied response of the opponent, whether "holding ground", with a threat display and sound production of its own, or fleeing. Similarly, the courtship grunt produced by a male damselfish Eupomacentrus partitus, was variable in both number of pulses and duration. Each

character was correlated with the period of time the male spent swimming near the female (Myrberg, 1972a; 1972b). Schneider (1964) found the tigerfish Therapon jarbua, produced two different agonistic calls depending upon the level of motivation. Drumming sounds were short and numerous, and the louder, threatening sounds were longer and occurred less often. Threatening sounds consisted of a rapid series of drumming sounds and the more intense the threat, the longer the fish produced the sound.

(iii) Repetition Rate

Pulse repetition rate (i.e. the reciprocal of pulse interval) was associated with amplitude to some degree, and thus was related to the motivational state of the fish. There is evidence to support the statement by Fine et al. (1977) that motivational states and their meanings can be graded by variation in repetition rate. Slightly higher pulse repetition rates than those related to aggressive growls, were associated with sudden avoidance movements in china rockfish. It is unclear whether these sounds were an expression of fear or merely the involuntary result of violent muscle action. I suspect the former, since a similar movement involving a vigorous sweep of the tail and change in direction, a tail beat, usually, but not exclusively, involved concurrent sound production. McInerney and Yearsley (in press) describe similar sounds produced by the subordinate fish in agonistic encounters. They called these sounds, associated with quick escape movements, "raised

pitch growls".

The significance of the pops or single pulses emitted at the end of several aggressive growls by one black rockfish is unknown. McInerney and Yearsley (in press) reported similar, rarely occurring sounds for several species of rockfish, including the black rockfish. They also reported popping sounds were commonly produced when individual fish were physically molested, implicating the sounds as a possible warning signifying danger. Apparently, a marked increase in amplitude is gained at the expense of a decreased pulse repetition rate, not surprising, considering the mechanical properties of the swim bladder/sonic muscle complex. Perhaps a bladder, being pulsed at high amplitude, would not equilibrate in time before the next pulse occurred at higher repetition rates. The change in pulse rate could be a function of intensity of threat, with pops signifying a low level of motivation. Also, since high amplitude sounds travel further, pops may be a means of further intimidating a fleeing opponent. Myrberg et al. (1965) found the louder "thump" sound produced during fights between male cichlids Hemichromis bimaculatus, had a pulse repetition rate about one third of that for the "brr" sound, produced before attack. Interestingly, the "thump" sound was heard in the early stages of a fight between conspecifics and probably had an intimidating effect on the opponent. Once the fight was decided, however, no sounds were heard as the victor followed and rammed the loser (Myrberg et al., 1965).

(iv) Number of Pulses per Burst

The number of pulses in each sound burst for both species was related to the duration of the burst and the pulse repetition rate. As a result, the number of pulses per burst was part of a continuum, reflecting the behavioural motivation of the animal.

(v) Frequency

The frequency spectrum of sounds produced by the swim bladder/muscle complex is probably a function of the sonic muscle contraction rate. Various workers (Packard, 1960; Skoglund, 1961; Schneider, 1964) have noted the correspondence between a single muscle contraction and the production of one pulse of sound in other fish. Power spectral density profiles confirmed this hypothesis, showing a fundamental frequency of about 60 Hz with harmonics at 60 Hz intervals. The number of harmonics present was related to the amplitude of the sound, with high intensity bursts showing harmonics up to 2500 Hz.

Although repeated muscle contractions produce harmonics, Tavalga (1962) has shown harmonic properties may also be influenced by the acoustic qualities of the environment. Winn (1972) demonstrated, through playback experiments to toadfish, a positive response to pure tones of 200 - 400 Hz containing no harmonics. Also, energy above the second harmonic within this frequency range is beyond the hearing range of the toadfish (Winn, 1972; Fish and Offutt, 1972). There is no firm evidence about the role harmonics play in

signal coding, and these higher frequencies may occur above the fishes' range of sensitivity.

The ability of china rockfish to alter the damping characteristics of the swim bladder in a fraction of a second may involve a change in tonus of the surrounding axial body musculature. Observations on the cod swim bladder by Sand and Hawkins (1973) showed that the stiffness of the tissues surrounding the organ may control the acoustic characteristics of the bladder. McCutcheon (1958) has suggested that fish maintain a slight muscle tonus at resting depth to aid in the control of bouyancy. A momentary relaxation of this tonus may account for the change in response of the bladder. No relationship between these unique, less damped sounds and a particular behaviour pattern was established, as mirror interactions were not video taped.

IV. Species Specificity of Sounds

Environmental characteristics must be considered of major importance when assessing the suitability of a particular sound property for species specific content. Frequency components of a sound can be dramatically altered by the physical environment. Bottom and surface reflections may cancel or enhance particular frequencies under certain conditions (Albers in Gerald, 1971; Parvaiescu, 1964). Rockfish inhabit a complex, physical environment ranging from the dense kelp forest in shallow water to deeper areas

of rock rubble, crevices and sand shell bottom. All of these surfaces have unique effects on the frequency components of reflected sounds because of their different densities. The underwater acoustical environment may also interfere with the transmission of information via frequency components. In shallow water, ambient noise due to turbulence created by waves breaking on the shoreline, or surface waves themselves, may mask or enhance the frequency characteristics of fish sounds. Added to this are the noise of tidal streams flowing over rough surfaces, distant storms, and surprisingly, ships at sea. Propellor turbulence and engine vibration apparently create a general background noise of 100 Hz (Haines, 1974). Finally, Winn (1964) contends that amplitude and frequency characteristics of fish sounds are unimportant in communication, as they do not seem to contain enough information. Consequently, the information-carrying part of the sound, if present, must involve temporal patterning in some manner.

Narins and Capranica (1977) note that animal vocalizations possessing a high degree of species specificity show a low degree of variability in signal structure. Schleidt (1971), among others, has noted that highly stereotyped signals result in a distribution with a coefficient of variation ≤ 0.1 . Thus, if one were to analyse the temporal parameters of sounds emitted by a particular species, the most stereotyped parameters are most likely to be species specific.

No temporal parameters for sounds produced by either species of rockfish satisfied Schleidt's (1971) criterion of stereotypy. Sound burst duration and number of pulses per burst were associated to some extent, and both showed a high degree of variability. Pulse interval showed marked variability both within an individual and among individuals of the same species. It is difficult to determine from the data whether the observed individual variability is a consequence of the small sample size (4 black rockfish and 9 china rockfish) or actual individual differences. Although Fig. 26 must be interpreted with caution because of the small sample sizes, pulse repetition rates for the two species appear to be indistinguishable. Variability in the temporal parameters of the sounds, together with the unsuitability of their frequency components as information carriers, suggests that the sounds are not species specific.

Species specific courtship sounds have been demonstrated for two groups of fish. Gerald (1971) studied male courtship grunts produced by six sympatric species of sunfish (Lepomis). He showed significant statistical differences in mean grunt duration and mean pulse rates among the species. Playback experiments indicated that the fish may respond to conspecific calls, but more data were required for conclusive evidence. More recently, Spanier (1979) analysed male courtship sounds in four sympatric species of damselfishes Eupomacentrus. These fish carry out reproductive activity

in the same shallow-water habitat at the same time of the year. Male courtship displays include sound production. Each sound, or "chirp", is made up of a number of short pulses. An analysis of five properties of the chirps indicated significant differences between species in pulse interval. Playback experiments showed that pulse interval and number of pulses within a chirp were the significant variables in sound recognition. Spanier (1979) felt that this acoustic discrimination, together with other sensory cues, was likely an effective ethological isolating mechanism, preventing interspecific mating.

Courtship and mating behaviour have not yet been described in rockfish and the role, if any, of sound production in reproductive behaviour remains unknown. On the assumption that sounds produced by sympatric species of rockfish are not species specific, their use as a reproductive isolating mechanism is severely limited. However, sounds produced by both males and females could function during reproductive behaviour in several ways. For example, the male cod uses the same grunt sounds for agonism and courtship; in the latter case stimulating the female to respond more effectively to the courting behaviour of the male (Brawn, 1961b). Also, the "brr" sound emitted by the female cichlid fish Hemichromis bimaculatus, seems to have an inhibiting effect during aggressive situations in the courtship period (Myrberg, et al., 1965). Thus, while the sounds

are not species specific, they may play an important role in the series of behavioural events comprising courtship and reproduction.

The need for additional comparative studies of rockfish sounds is clearly indicated. Mirror image interactions would be the most efficient method of obtaining the sample size necessary for meaningful statistical analysis. Even though a statistical difference may be shown in a particular temporal parameter among or between species, the difference or even the parameter itself may be meaningless to the fish. Playback experiments, in which recorded sounds are played back to the fish while observing responses, are a means of establishing the relevance or message content of a sound. For rockfish, the response to various agonistic and warning sounds of congeners could be an effective measure of species recognition. Similarly, the level of agonistic response to conspecific sounds, experimentally altered sounds, or artificially produced sounds could also be used for assessing information content in playback experiments. Studies on the auditory capabilities of rockfish regarding range of frequency sensitivity, frequency of greatest sensitivity, and sound pressure thresholds would also be useful in understanding the communicative potential of sounds.

Recording undistorted sounds within the confines of a glass walled aquarium is virtually impossible. Schneider (1974) found glass walled tanks to be completely unsuitable

because the original signals were substantially altered. Resonances and reflections in the tank masked the pulsed nature of tigerfish threatening sounds. After some experimentation a suitable aquarium, constructed of concrete and lined with foam rubber, was used for recording relatively clear and undistorted sounds. Parvulescu (1967) states that the oscillatory field in a small tank rarely resembles the field encountered by a fish in its normal habitat. Even in tanks with thick walls of dense material and fairly well damped (as Schneider's) problems remain serious. Parvulescu (1967) goes on to say that it is impossible to create an anechoic tank smaller than a wavelength (of sounds produced) by use of passive materials. Based on frequency of about 60 Hz it seems a study on rockfish sounds would require a foam rubber lined concrete aquarium at least 25 m in its shortest dimension, to avoid problems of resonance and reflection. Practical considerations aside, one cannot remain naive about the effects of aquaria size and material on sounds, and some attempt should be made to simulate natural conditions in the laboratory. One point to consider, however, is that fish live in a complicated acoustical environment and the method of information transfer in an efficient system must be unaffected by "noise" generated by the environment.

V. The Role of Sound Production in Agonistic Behaviour

Sound production by fishes during agonistic interactions is well documented (Brawn, 1961b; Schneider, 1964; Myrberg et al., 1965; Salmon, 1967; Schwarz, 1974a; McInerney and Yearsley, in press). Schwarz (1974b) suggests the wide-spread occurrence of this phenomenon implicates sound as an important means of underwater communication. However, for species such as the cod, in which the (apparently) same "grunt" is used for agonism, courtship and the cessation of courtship, sound may function as an alerting or display-enhancing device lacking a specific message content (Fine et al., 1977).

Growling sounds produced by both species of rockfish were associated with aggressive acts or displays closely associated (temporally) with overt aggression. Salmon (1967) found that a schooling, nonterritorial squirrelfish, Myripristis berndti, produced two calls during agonistic encounters. "Knocking" accompanied brief chases of a small fish by a larger and "growls" were produced during more intense interactions (nipping) between similar sized fish, both willing to fight. In the latter case, when one fish fled, knocks were produced by the attacking and possibly the fleeing fish. Salmon (1967) hypothesized that the actions and associated sounds function as a spacing mechanism within schools, minimizing the likelihood of more than one individual being caught by a predator, and also optimizing individual efficiency of predator detection. In the case

of black rockfish, aggressive behaviour and sound production is also consistent with the concept of individual distance discussed previously.

Schwarz (1974a), in her study of sound production and associated aggressive behaviour in a territorial cichlid fish Cichlasoma centrarchus, showed that responses to behaviours differed depending upon the presence or absence of sound. Aggressive displays accompanied by sounds usually caused the recipient to retreat, whereas silent acts usually elicited imitative responses, possibly reflecting an unwillingness to escalate a fight. Also, successive actions of a sound producing fish suggested it was advertising a high probability of attack and a low probability of retreat. Finally, Schwarz (1974a), postulated that acts accompanied by sounds may constitute separate displays, since she found that the recipient fish responded more to the acoustic mode of a display than the visual mode.

Results of an experiment in which sounds were played back to acoustically but not visually isolated pairs of Cichlasoma centrarchus (Schwarz, 1974b), indicate that sounds inhibit aggressive behaviour in the recipient, thus reducing the investment of time and energy in potentially injurious fighting.

Again, in order to establish or confirm a communicatory function in rockfish sounds, playback experiments involving observations of the effects of sound on behaviour under

controlled conditions are required. Additional studies could also focus on the analysis of recipient behaviour during agonistic encounters coupled with an informational analysis approach.

SUMMARY

1. The most common social pattern exhibited by black rockfish is the formation of non-polarized schools showing some degree of site attachment to particular areas on the reef.
2. China rockfish, in contrast, are a solitary, bottom dwelling species staying close to a preferred home site, usually a deep crevice or cave on the rock reef. Limited evidence suggests this species is territorial in defending its home site against conspecific intruders.
3. In the laboratory, china rockfish are more aggressive in terms of overt actions than black rockfish during conspecific aggressive encounters. Black rockfish tend to show more threat displays and intention movements during encounters. This may be related to the maintenance of an individual distance in schools, whereas the territorial china rockfish shows the potential for escalated conflict.
4. The various activities characteristic of agonistic encounters in both species can be interpreted in terms of the relative levels of two underlying, independent tendencies: attack and escape.
5. Sounds associated with various agonistic actions do not appear to be species specific, but probably inhibit aggressiveness in recipient fish. Sound characteristics

are more indicative of the level of aggressive motivation in a particular fish.

LITERATURE CITED

- Alexander, R.McN. 1966. Physical aspects of swim bladder function. *Biol. Rev.* 41:141-172.
- Andrew, R.J. 1972. The information potentially available in mammalian displays. *In* Non-verbal Communication. R.H. Hinde (ed.). Cambridge Univ. Press, Cambridge, pp. 179-204.
- Baerends, G.P. and J.M. Baerends - van Roon. 1950. An introduction to the study of the ethology of cichlid fishes. *Behaviour*, Supplement 1:1-242.
- Baerends, G.P., Drent, R.H., Glas, P., and H. Groenewold. 1970. An ethological analysis of incubation behaviour in the herring gull. *In* The Herring Gull and its Egg. G.P. Baerends and R.H. Drent (eds.). *Behaviour*, Suppl. 17:134-235.
- Baerends, G.P. 1976. On drive, conflict and instinct and the functional organization of behaviour. *In* Perspectives in Brain Research, Progress in Brain Research. M.A. Corner and D.F. Swaab (eds.). Elsevier/North-Holland Biomedical Press, Vol. 45, pp. 427-447.
- Barlow, G.W. 1962. Ethology of the asian teleost Badis badis. III. Aggressive Behaviour. *Z. Tierpsychol.* 19:29-55.
- Brawn, V.M. 1961a. Aggressive behaviour in the cod (Gadus callarias L.). *Behav.* 18:107-147.
- Brawn, V.M. 1961b. Sound production by the cod (Gadus callarias L.). *Behaviour* 18:239-255.
- Brockway, B.F. 1964. Ethological studies of the budgerigar (Melopsittacus unclulatus): non-reproductive behaviour. *Behaviour* 22:193-222.
- Chizar, D., Ashe, N., Seixas, S., and D. Henderson. 1976. Social-Aggressive behaviour after various intervals of social isolation in bluegill sunfish (Lepomis macrochirus Rafinesque) in different states of reproductive readiness. *Behav. Biol.* 16:475-487
- Clarke, T.A. 1970. Territorial behavior and population dynamics of a pomacentrid fish, the garibaldi, Hypsypops rubicunda. *Ecol. Monogr.* 40:189-212.

- Davis, R.E., Harris, C. and J. Shelby. 1974. Sex differences in aggressivity and the effects of social isolation in the anabantoid fish, Macropodus opercularis. Behav. Biol. 11:497-509.
- DeGhett, V.J. 1978. Hierarchical cluster analysis. In Quantitative Ethology. P. Colgan (ed.). John Wiley and Sons, New York. pp. 115-144.
- Delacy, A.C., C.R. Hitz and R.L. Dryfoos. 1964. Maturation, gestation, and birth of rockfish (Sebastes) from Washington and adjacent waters. Fish. Res. Papers. Wash. Dept. Fish. 2(3):51-67.
- Denes, P.B. and E.N. Pinson. 1963. The Speech Chain: The Physics and Biology of Spoken Language. Waverly Press, Inc., Baltimore, Md. 158 pp.
- Ehrlich, P.R. 1975. The population biology of coral reef fishes. Ann. Rev. Ecol. Syst. 6:211-247.
- Fay, R.R. 1978. Sound detection and sensory coding by the auditory systems of fishes. In The Behaviour of Fish and Other Aquatic Animals. D.I. Mostofsky (ed.). Academic Press, New York. pp. 197-231.
- Feder, H.M., C.H. Turner and C. Limbaugh. 1974. Observations on fishes associated with kelp beds in southern California. Calif. Dept. Fish and Game. Fish. Bull. 160:1-144.
- Fine, M.L., H.E. Winn and B. Olla. 1977. Communication in fishes. In How Animals Communicate. T. Sebeok (ed.). Indiana Univ. Press, Bloomington. pp. 472-518.
- Fish, J.F. and G.C. Offutt. 1972. Hearing thresholds from toadfish, Opsanus tau, measured in the laboratory and field. J. Acoust. Soc. Amer. 51:1318-1321.
- Frey, D.F. and R.A. Pimental. 1978. Principle Component analysis and factor analysis. In Quantitative Ethology. P. Colgan (ed.). John Wiley and Sons, New York. pp. 219-246.
- Gerald, J.W. 1971. Sound production during courtship in six species of sunfish (Centrarchidae). Evolution 25:75-87.
- Gerking, S.D. 1959. The restricted movements of fish populations. Biol. Rev. 34:221-242.

- Gibson, R.N. 1968. The agonistic behaviour of juvenile Blennius pholis L. (Teleostei). Behaviour 30:192-217.
- Gibson, R.N. 1969. The biology and behaviour of littoral fish. Oceanogr. Mar. Biol. Ann. Rev. 7:367-410.
- Gooding, R.M. and J.J. Magnuson. 1967. Ecological significance of a drifting object to pelagic fishes. Pac. Sci. 21:486-497.
- Gotshall, D.W. 1964. Increasing tagged rockfish (Genus Sebastes) survival by deflating the swim bladder. Calif. Fish and Game. 50(4):243-260.
- Griffin, D.R. 1955. Hearing and acoustical orientation in marine animals. Deep Sea Res. 3:406-417.
- Haaker, P.L. 1978. Observations of agonistic behavior in the treefish, Sebastes serriceps (Scorpaenidae). Calif. Fish and Game. 64(3):227-228.
- Haines, G. 1974. Sound underwater. David and Charles. Newton Abbot, England. 208 pp.
- Hallacher, L.E. 1974. The comparative morphology of extrinsic gasbladder musculature in the scorpion fish genus Sebastes (Pisces: scorpaenidae). Proc. Calif. Acad. Sci. 40(3):59-86.
- Harris, G.G. and W.A. van Bergeijk. 1962. Evidence that the lateral line organ responds to near-field displacements of sound sources in water. J. Acoust. Soc. Amer. 34:1831-1841.
- Harris, G.G. 1967. Discussion. In Marine Bio-Acoustics, Vol. 2 W.N. Tavolga (ed.). Pergamon Press, Oxford. p. 156.
- Hart, J.L. 1973. Pacific Fishes of Canada. Fish. Res. Board Can. Bulletin 180. Ottawa 740 pp.
- Hayne, D.W. 1949. Calculation of size of home range. J. Mammal. 30:1-18.
- Hinde, R.A. 1970. Animal Behaviour: A synthesis of Ethology and Comparative Psychology, 2nd ed. McGraw-Hill Book Co., New York. 394 pp.
- Hinkel, T.J., and R. Maier. 1974. Isolation and aggression in Siamese fighting fish (Betta splendens). Psychol. Rep. 34:1323-1326.

- Hobson, E.S. 1965. Diurnal-nocturnal activity of some inshore fishes in the Gulf of California. *Copeia* 1965(3):291-302.
- Hobson, E.S. 1968. Predatory behavior of some shore fishes in the Gulf of California. Fish and Wildl. Serv., Bureau of Sport Fishes and Wildl. Res. Rept. No. 73. 92 pp.
- Hobson, E.S. 1971. Cleaning symbiosis among California inshore fishes. *Fish. Bull.* 69:491-523.
- Jakobsson, S., Radesater, T. and T. Jarvi. 1979. On the fighting behaviour of Nannacara anomala (Pisces, cichlidae) males. *Z. Tierpsychol.* 49:113-119.
- Keenlyside, M.H.A. and F.T. Yamamoto. 1962. Territorial behaviour of juvenile atlantic salmon (Salmo salar L.). *Behav.* 19:139-169.
- Keenlyside, M.H.A. 1965. Why fishes fight. *Animals* 6:184-187.
- Kim, J.O. 1975. Factor analysis. In *Statistical Package for the Social Sciences* (2nd. ed.). N.H. Nie, C.H. Hull, J.G. Jenkins, K. Steinbrenner, D.H. Bent (eds.). McGraw-Hill, New York. pp. 468-514.
- King, J.A. 1973. The ecology of aggressive behavior. *Ann. Rev. Ecol. Syst.* 4:117-138.
- Leaman, B.M. 1976. The association between the black rockfish (Sebastes melanops Girard) and beds of the giant kelp (Macrocystis integrifolia Bory) in Barkley Sound, British Columbia. M.Sc. Thesis, University of British Columbia. 108 pp.
- Lorenz, K. 1966. On Aggression. Cox and Wyman Limited. Fakenham, Norfolk. 273 pp.
- Matsubara, K. 1943. Studies on the scorpaenoid fishes of Japan. The Transactions of the Sigenkagaku Kenyusho. Nos. 1 and 2. 486 pp.
- McCutcheon, F.H. 1958. Swimbladder volume, buoyancy, and behaviour in the pinfish, Lagodon Rhomboides (L.). *J. Cell Comp. Physiol.* 52:453-480.
- McElderry, H.I. 1979. A comparative study of the movement habits and their relationship to buoyancy compensation in two species of shallow reef rockfish (Pices, Scorpaenidae). M.Sc. Thesis, University of Victoria. 169 pp.

- McInerney, J.E. and J.H. Yearsley. In press. Sound production in nine species of rockfish (genus Sebastes).
- Miller, R.J. 1978. Agonistic behavior in fishes and terrestrial vertebrates. In Contrasts in Behavior: Adaptations in the Aquatic and Terrestrial Environments. E.S. Reese and F.J. Lighter (eds.). John Wiley and Sons, New York. pp. 281-311.
- Morgan, B.J.T., Simpson, M.J.A., Hanby, J.P. and J. Hall-Craggs. 1976. Visualizing interaction and sequential data in animal behaviour: theory and application of cluster-analysis methods. Behaviour 56:1-43.
- Moulton, L.L. 1977. An ecological analysis of fishes inhabiting the rocky near shore regions of northern Puget Sound. PhD. Dissertation, University of Washington. 181 pp.
- Myrberg, A.A. Jr., E. Kramer and P. Heinecke. 1965. Sound Production by cichlid fishes. Science 149:555-558.
- Myrberg, A.A. Jr. 1972a. Ethology of the bicolor damselfish, Eupomacentrus partitus (Pisces: Pomacentridae): a comparative analysis of laboratory and field behaviour. Anim. Behav. Monogr. 5:199-283.
- Myrberg, A.A. Jr. 1972b. Using sound to influence the behaviour of free-ranging marine animals. In Behaviour of Marine Animals, Vol. 2. H.E. Winn and B. Olla (eds.). Plenum Press, New York. pp. 435-468.
- Myrberg, A.A. and R.E. Thresher. 1974. Interspecific aggression and its relevance to the concept of territoriality in reef fishes. Am. Zool. 14:81-96.
- Narins, P.M. and R.R. Capranica. 1977. An automated technique for analysis of temporal features in animal vocalizations. Anim. Behav. 25:615-621.
- Newman, M.A. 1956. Social behaviour and interspecific competition in two trout species. Phys. Zool. 29:64-81.
- Nice, M.M. 1941. The role of territory in bird life. Amer. Mid. Natur. 26:441-487.
- Ogden, J.C. and N.S. Buckman. 1973. Movements, foraging groups, and diurnal migrations of the striped parrotfish Scarus croicensis Bloch (Scaridae). Ecology 45:589-596.
- Packard, A. 1960. Electrophysiological observations on a sound-producing fish. Nature 187:63-64.

- Parvulescu, A. 1964. Problems of propagation and processing. In Marine Bio-Acoustics. W.N. Tavolga (ed.). Pergamon Press, Oxford. pp. 87-100.
- Parvulescu, A. 1967. The acoustics of small tanks. In Marine Bio-Acoustics, Vol. 2. W.N. Tavolga (ed.). Pergamon Press, Oxford. pp. 7-13.
- Popper, A.N. and R.R. Fay. 1973. Sound detection and processing by teleost fishes: a critical review. J. Acoust. Soc. Amer. 53(6):1515-1529.
- Popper, A.N. 1974. The response of the swim bladder of the goldfish (Carassius auratus) to acoustic stimuli. J. Exp. Biol. 60:295-304.
- Quast, J.C. 1968. Fish fauna of the rocky shore zone. In Utilization of the kelp bed resources in southern California. W.J. North and C.L. Hubbs (eds.). Calif. Dept. Fish and Game. Fish. Bull. 139:35-55.
- Radakov, D.V. 1973. Schooling in the Ecology of Fish. Halsted Press (John Wiley and Sons), New York. 173 pp.
- Reese, E.S. 1975. A comparative field study of the social behaviour and related ecology of reef fishes of the family Chaetodontidae. Z. Tierpsychol. 37:37-61.
- Rosenthal, R.J. 1980. Shallow water fish assemblages in the northeastern Gulf of Alaska: habitat evaluation, species composition, abundance, spatial distribution and trophic interaction. A report prepared for the National Oceanic and Atmospheric Administration Outer Continental Shelf Environmental Project. Alaska Coastal Research, Homer, Alaska. 83 pp.
- Sale, P.F. 1972. Effect of cover on agonistic behaviour of a reef fish: a possible spacing mechanism. Ecology 53:753-758.
- Sale, P.F. 1977. Maintenance of high diversity in coral reef fish communities. Amer. Nat. 111 (978):337-359.
- Sale, P.F. 1978. Reef fishes and other vertebrates: a comparison of social structures. In Contrasts in Behaviour: Adaptations in the Aquatic and Terrestrial Environments. E.S. Reese and F.J. Lighter (eds.). John Wiley and Sons, New York. pp. 313-346.
- Salmon, M. 1967. Acoustical Behaviour of the menpachi, Myripristis berndti, in Hawaii. Pac. Sci. 21:364-381.
- Sand, O. and A.D. Hawkins. 1973. Acoustic properties of the cod swim bladder. J. Expt. Biol. 58:797-820.

- Schleidt, W.M. 1971. How "fixed" is a fixed action pattern? *Am. Zool.* 11:13.
- Schneider, H. 1964. Physiologische und morphologische Untersuchungen zur Bioakustik der Tigerfische (Pisces, Theraponidae). *Z. Vergl. Physiol.* 47:493-558.
- Schwarz, A. 1974a. Sound production and associated behaviour in a cichlid fish, Cichlasoma centrarchus. I. Male-male interactions. *A. Tierpsychol.* 35:147-156.
- Schwarz, A. 1974b. The inhibition of aggressive behaviour by sound in the cichlid fish, Cichlasoma centrarchus. *Z. Tierpsychol.* 35:508-517.
- Shaw, E. 1978. Schooling in fishes. *Amer. Sci.* 66:166-175.
- Simpson, M.J.A. 1968. The display of Siamese fighting fish Betta splendens. *Anim. Behav. Monog.* 1 (1):1-73.
- Simpson, R.E. 1974. Introductory Electronics for Scientists and Engineers. Allyn and Bacon, Inc., Boston. 577 pp.
- Skoglund, C.R. 1961. Functional analysis of swim-bladder muscles engaged in sound production of the toadfish. *J. Biophys. Biochem. Cytol.* 10:187-200.
- Spanier, E. 1979. Aspects of species recognition by sound in four species of damselfishes Genus Eupomacentrus (Pisces: Pomacentridae) *Z. Tierpsychol.* 51:301-316.
- Stringer, G.E. and W.S. Hoar. 1955. Aggressive behaviour of underyearling kamloops trout. *Can. J. Zool.* 33:148-160.
- Sustare, B.D. 1978. System Diagrams. In *Quantitative Ethology*. P. Colgan (ed.). John Wiley and Sons, New York. pp. 275-311.
- Tavolga, W.N. 1962. Mechanisms of sound production in the ariid catfishes, Galeichthys and Bagre. *Bull. Amer. Mus. Nat. Hist.* 124:1-30.
- Tavolga, W.N. 1965. Review of marine bioacoustics: state of the art: 1964. Tech. Rep. Navtradevcen 1212-1. 100 pp.
- Tavolga, W.N. 1968. Animal Communications: Techniques of Study and Results of Research. T.A. Sebeok (ed.). Indiana Univ. Press, Bloomington. pp. 271-288.

- Thresher, R.E. 1978. Territoriality and aggression in the three spot damselfish (Pisces; Pomacentridae): an experimental study of causation. *Z. Tierpsychol* 46 (4):401-434.
- Tinbergen, N. 1957. The functions of territory. *Bird Study*. 4:14-27.
- Tinbergen, N. 1959. Comparative studies of the behaviour of gulls (Laridae): a progress report. *Behaviour* 15:1-70.
- van Bergeijk, W.A. 1964. Directional and nondirectional hearing in fish. *In* *Marine Bio-Acoustics*. W.N. Tavolga (ed.). Pergamon Press, Oxford. pp. 281-299.
- Weston, D.E. 1967. Sound propagation in the presence of bladder fish. *In* *Underwater Acoustics*, vol. II. V.M. Albers (ed.). Plenum Press, New York. pp. 55-86.
- Wiepkema, P.R. 1961. An ethological analysis of the reproductive behaviour of the bitterling (Rhodeus amarus Bloch). *Arch. Neerl. Zool.* 14:103-199.
- Wilson, E.O. 1975. *Sociobiology: The New Synthesis*. Belknap Press, Harvard University Press, Cambridge, Mass. 679 pp.
- Winn, H.E. 1964. The biological significance of fish sounds. *In* *Marine Bio-Acoustics*. W.N. Tavolga (ed.). Pergamon Press, Oxford. pp. 213-231.
- Winn, H.E. 1972. Acoustic discrimination by the toadfish with comments on signal systems. *In* *Behaviour of Marine Animals: Current Perspectives in Research*, vol. 2: Vertebrates. H.E. Winn and B.L. Olla (eds.). Plenum Press, New York. pp. 361-385.
- Zar, J.H. 1974. *Biostatistical Analysis*. Prentice-Hall, Inc., Englewood, Cliffs, N.J. 620 pp.

Appendix I. Listing of sex, weight, and standard length for individual fish used in agonistic encounters.

Species	Individual	Sex	Weight (gm)	Standard Length (cm)
Black Rockfish	MEL-1	Imm.	157.8	19.8
	-2	Imm.	448.1	26.3
	-3	Imm.	564.1	28.3
	-4	Imm.	365.5	24.2
	-5	Imm.	186.2	20.5
	-6	Imm.	171.6	20.6
	-7	Imm.	216.4	22.5
	-10	Imm.	194.5	20.7
	-11	Imm.	259.6	21.7
	-12	Imm.	373.3	25.4
	-13	Imm.	519.5	29.5
	-14	Imm.	382.7	26.7
	-15	Imm.	336.2	26.7
	-16A	Imm.	325.8	23.4
	-17A	Imm.	602.9	28.0
	-18A	Imm.	264.8	23.5
	-19A	Imm.	387.9	25.0
	-20A	Imm.	354.3	25.3
	-21	Imm.	422.3	24.7
	-22	Imm.	257.1	21.5
	-23	Imm.	360.5	24.7
	-24	Imm.	366.5	24.6
	-25	Imm.	278.0	22.0
	-26	Male	902.1	33.6
China Rockfish	NEB-1	Female	316.4	23.3
	-2	Imm.	331.8	23.4
	-3A	Imm.	176.5	19.0
	-3B	Female	393.8	23.8
	-4	Imm.	366.0	22.7
	-5	Male	520.0	24.3
	-6	Imm.	181.6	18.7
	-7	Male	495.9	29.0
	-8	Imm.	402.3	23.7
	-9	Imm.	442.1	25.2
	-10A	Female	283.0	19.3
	-11	Female	444.2	24.4
	-12	Imm.	198.3	19.7
	-13	Female	447.6	24.5
	-14A	Female	414.8	24.0
	-15B	Female	536.1	26.4
	-16	Male	627.1	27.7
	-17	Male	768.1	28.7
	-19	Male	473.7	24.7
	-20	Female	570.6	27.0

Appendix II. Preceding/following matrix for black rockfish aggressive behaviour. Each entry represents the number of times the behaviour listed at the top (column) followed the behaviour listed at the side (row). The main diagonal of the matrix is empty since transitions of behaviours to themselves were not recognized (ill-defined).

Following

	BST	BTT	BFN	ORT	APP	CHG	FLD	OPD	HOV	CAR	MLK	MFT	ENC	PRN	CSW	FOL	CHS	MTH	TBO	LAP	VTP	ABT	BUT	ANP	NIP	BIT	TRN	FSW	RSW	DFT	TBA	Total
BST	6		73	13				4	92																		4	6	1		2	201
BTT	2		19	9				3	51																		2	4			1	91
BFN	1		1																								1					3
ORT	6	4		425	1			23	100								2							3			6	14	1		1	586
APP	11			10	2	5	237	175	5					2	1	6	30	47					3	7	15		28		1	1		649
CHG																							1	2								3
FLD	1							2	2																							5
OPD	10	4		15	14			200	7					14	3	11	9	7		3				6	3		22	2		2		332
HOV	109	68	3	401	178			37	2				2	1	2		3	1						1			78	69	22	10	7	994
CAR					2			4	6									1	1					1			2					17
MLK																																0
MFT																																0
ENC				1				1																								2
PRN								4	8							3	1			1				1	1							19
CSW								2	5					1						1												9
FOL								6	9						2	1											2					20
CHS	1			1	1			2	20				1	1			5							27	3		5	1				68
MTH	1			2				1	42								3			1				2			8			2		62
TBO																				1												1
LAP								2	2	1														1			1					7
VTP									1																							1
ABT																																0
BUT								3															1									4
ANP	4			8				3	54	1						14			1								31	1				117
NIP	1			2					7	1						5								1			5					22
BIT																																0
TRN	15	1		24	1				11								1							1				41	1		1	197
FSW	21	7		17	3				86																		1		1	3	1	140
RSW	1			6	3				13																		1	2				26
DFT	12							1	5																							18
TBA				2					11																							13
																																3607

Appendix III. Preceding/following matrix for china rockfish aggressive behaviour. Each entry represents the number of times the behaviour listed at the top (column) followed the behaviour listed at the side (row). The main diagonal of the matrix is empty since transitions of behaviours to themselves were not recognized (ill-defined).

		Following																															Total	
		BST	BTT	BFN	ORT	APP	CHG	FLD	OPD	HOV	CAR	MLK	MFT	ENC	PRN	CSW	FOL	CHS	MTH	TBO	LAP	VTP	ABT	BUT	ANP	NIP	BIT	TRN	FSW	RSW	DFT	TBA		
Preceding	BST	1	20	20	6	6	14	1	27	94	4			2						4	1							32	71	71	1		615	
	BTT	2																															2	
	BFN	11		9	4					1																		2	2				29	
	ORT	16			29	2	28	2	10	14			3	3				1		2	2				3	2		3	8	1	5	1	396	
	APP	47		7			6	52	94	3	1	5	4				1	45	42	3	19	1	1	6	38	31	2	10	7	2	25	1	453	
	CHG	5		1				2	11									4	4		1		4	3	2	7		2	1		2		49	
	FLD	3		1	2	1			4	1							1											1	1				15	
	OPD	43		2	9	12	1	4		13	2	4						3	2		2				8	1		22	6		4		138	
	HOV	135		2	87	44	4		7		2		2	4				1		2	1							11	38	16	41	6	403	
	CAR								3	7		4	2																			1		18
	MLK								5	1	3		6						1									1					17	
	MFT								4	3	2	8										1						1					19	
	ENC	1		1						6																		3	1		1		13	
	PRN																																0	
	CSW																			1													1	
	FOL	1			1														1								1						4	
	CHS	11			2	5				2	20								6						1	20	9		1			6		83
	MTH	12			1	1				1	12							2	6							3			7	3		7		55
	TBO	5			1	1					1								1											1			11	
	LAP	5		3	1	1		1	5	3		1	1						1							1		4					27	
	VTP	1																															1	
	ABT	2								3																								5
	BUT	4		1						2	1															2								10
	ANP	15			4	5				5	27							14									1	1	5			2		79
	NIP	13			3	2				2	11							1	5							2			3			10		52
	BIT					1				1	1																							3
	TRN	30	1	25						4	23																		24	2	1			110
	FSW	96		16	5					1	37																	2		8	16			181
	RSW	55		13	6			1			5																		13		8	1		102
	DFT	96		7	6	2				1	9	2																	4	3				130
	TBA	2		1							7																							10
																																	3031	

Appendix IV. Factor loadings for each of 20 black rockfish behavioural elements on 3 factors. The first two factors account for 84% of the total common variance.

	FACTOR 1	FACTOR 2	FACTOR 3
BST	0.98209	0.03604	0.04913
BTT	0.99710	-0.04469	0.03406
ORT	0.98722	-0.02588	0.00679
APP	0.37447	-0.03022	-0.05069
OPD	0.11863	0.98159	0.00894
HOV	-0.07682	0.47124	0.58187
CAR	0.15352	0.50611	0.82386
PRN	0.00754	0.05902	0.99082
CSW	0.39382	0.16239	0.68630
FOL	-0.07760	0.39850	0.86715
CHS	0.01255	0.85153	0.29559
MTI	-0.02807	0.98521	0.16135
LAP	-0.10299	-0.11860	0.89228
ANP	-0.05158	0.95166	0.07492
NIP	-0.06000	0.97049	0.20289
IRN	0.85587	0.26478	0.25110
FSW	0.86712	-0.06225	-0.04171
RSW	0.99941	0.01001	-0.01803
DFI	0.92564	0.02237	0.17048
TBA	0.96663	-0.06822	-0.06765

Appendix V. Factor loadings for each of 24 china rockfish behavioural elements on 5 factors. The first two factors account for 75% of the total common variance.

	FACTOR 1	FACTOR 2	FACTOR 3	FACTOR 4	FACTOR 5
BST	0.02794	0.05423	0.79694	-0.06787	-0.03468
BFN	-0.06344	0.97063	-0.14934	0.08923	-0.00709
ORT	-0.08536	0.97116	0.18416	0.06984	-0.10074
APP	-0.02439	0.08673	0.06645	0.97942	-0.06553
CHG	-0.03187	0.32352	0.00468	0.93189	-0.06713
FLD	0.77386	0.13685	0.06323	0.20198	0.35757
OPD	0.84161	0.44283	0.07884	0.16261	0.04300
HUV	0.65475	0.65682	-0.08033	0.03856	-0.12025
CAR	0.32592	0.61830	0.18754	0.03207	0.45157
MLK	0.01780	-0.04468	-0.11041	-0.07772	0.50393
MFT	0.49950	-0.05533	0.21629	0.31785	0.25159
ENC	0.51392	0.34586	0.57621	0.47920	-0.01409
CHS	0.93628	-0.00668	0.09263	-0.05804	0.01818
MTH	0.99093	0.00749	0.09892	-0.05693	0.02828
TBU	0.45822	0.71787	0.24440	0.41592	-0.03970
LAP	0.96532	0.06778	0.14743	0.06229	0.14278
BUT	0.93240	-0.02654	0.04728	-0.08160	-0.10445
ANP	0.92009	-0.03055	0.04977	-0.02612	0.02725
NIP	0.98472	-0.02631	0.06414	-0.01811	-0.06405
TRN	0.15857	0.82901	0.06497	0.08301	0.24537
FSW	-0.05757	0.90962	0.26818	0.14744	-0.10007
RSW	-0.05300	0.98344	0.01828	0.09626	-0.10384
DFT	0.34841	0.09929	0.86231	0.01799	-0.08431
TBA	-0.00094	0.10599	0.90232	0.16717	-0.03409

Appendix VI. Summary of sound data used for analysis.

	Individual	Sex	Total No. Sounds Recorded	Total No. Pulses Sampled	Behav- ioural Context
Black Rockfish	MEL-2	I	14	566	AGI
	MEL-13	I	2	61	AGI
	MEL-21	I	1	18	AGI
	MEL-25	I	1	21	AGI
China Rockfish	NEB-4	I	40	579	MII
	NEB-4		13	80	AVD
	NEB-4		53	659	COM
	NEB-6	I	3	69	AGI
	NEB-7	M	12	184	MII
	NEB-7		6	76	AGI
	NEB-7		18	260	COM
	NEB-10A	F	12	209	AGI
	NEB-11	F	4	82	AGI
	NEB-14A	F	2	46	AGI
	NEB-16	M	5	44	AGI
	NEB-19	M	2	17	MII
	NEB-20	F	6	82	AGI

Key: M - Male
F - Female
I - Immature

AGI - Aggressive interaction with
another individual
AVD - Avoidance movements
MII - Mirror image interaction
COM - Combined

Appendix VII. Computer printout of a power spectral density derived from a china rockfish aggressive sound. The three-dimensional graph shows time on 0.0400 s intervals along the abscissa (maximum of 1.76 s), frequency in 128 "bins" each approximately 19.5 Hz wide (to a maximum of 2500 Hz) along the ordinate and intensity measured in volts² as the third dimension in the body of the graph. The display is interpreted as follows: Various theoretical and practical parameters determine the length of signal that can be analysed. Here a 1.76 s portion of sound has been divided into 44 consecutive intervals, each 40 ms in duration. Reading down a column or time interval, intensity maxima are indicated with an arrowhead. Moving to the left the frequency bin in which the maxima occurs is read from the ordinate. For example, during the time period of 0.5200 to 0.5600 s from the beginning of the analysis intensity maxima are indicated in the 39 - 59 Hz, 98 - 117 Hz, 156 - 176, ..., 605 - 625 Hz, 664 - 684 Hz, and finally 2188 - 2207 Hz bins. This corresponds to about a 60 Hz fundamental together with its various harmonics to a maximum of about 2200 Hz as indicated by oscillographic analysis of the same sound. Variation in the pulse repetition rate can be seen in the occasional "drifting" of the fundamental frequency (and corresponding shift in harmonics) to a higher value.

		TIME																CONTINUED ON PAGE 190			
N	FREQ	0.0000	0.0400	0.0800	0.1200	0.1600	0.2000	0.2400	0.2800	0.3200	0.3600	0.4000	0.4400	0.4800	0.5200	0.5600	0.6000	0.6400			
1	0										1			2	4		36	29			
2	20													1		9	18	5			
3	39													13	26	100	456	133			
4	59		3	15	5	8	6	2	8	26	9	29	18	85	82	213	2228	114			
5	78			10	13	8	5	36	46	25	21	41	42	23	98	1955	45				
6	98		1	4		2	7	12	29	3	2	7	12	3	260	2110	890				
7	117				3	4	7	44	3	2	6	15	18	1153	1652	1282					
8	137			1	2	3	30	119	85	34	5	1	11	170	455	47					
9	156				2	3	31	39	136	21	2	3	1	170	1115	227					
10	176			4	1	13	15	110	22	3	2	7	1	405	758	135					
11	195			2	1	5		86	2	1		2	6	405	14	130					
12	215			6	2	2	23	130	15	1		3	2	77	672	230					
13	234						54	150	9	1				4	1409	1055	142				
14	254			4	2	1	11	52	7					2	2102	534	18				
15	273					2		29							315	127	38				
16	293						2	24	3						445	437	19				
17	313		1				6	15	5					1	961	184	2				
18	332							12							205	22	3				
19	352						1	5	1						92	90	2				
20	371							3							409	17					
21	391							2							193	92	1				
22	410														10	34					
23	430														77						
24	449														28	4					
25	469														15	7					
26	488														82	12					
27	508														72	18					
28	527														7	9					
29	547														11						
30	566														9						
31	586														1	2					
32	605														5	1					
33	625														8						
34	645														4						
35	664														6	6					
36	684														13	6					
37	703														2						
38	723																				
39	742																				
40	762															1					
41	781																				
42	801																				
43	820																				
44	840																				
45	859																				
46	879																				
47	898																				
48	918																				
49	938																				
50	957																				
51	977																				
52	996																				
53	1016																				
54	1035																				
55	1055																				
56	1074																				
57	1094																				
58	1113																				
59	1133																				

CONTINUED

NEXT
PAGE



60	1152	
61	1172	
62	1191	
63	1211	
64	1230	
65	1250	
66	1270	
67	1289	
68	1309	
69	1328	
70	1348	
71	1367	
72	1387	
73	1406	
74	1426	
75	1445	
76	1465	
77	1484	
78	1504	
79	1523	
80	1543	
81	1563	
82	1582	
83	1602	
84	1621	
85	1641	
86	1660	
87	1680	
88	1699	
89	1719	
90	1738	
91	1758	
92	1777	
93	1797	
94	1816	
95	1836	
96	1855	
97	1875	
98	1895	
99	1914	
100	1934	
101	1953	
102	1973	
103	1992	
104	2012	
105	2031	
106	2051	
107	2070	
108	2090	
109	2109	
110	2129	
111	2148	
112	2168	
113	2188	
114	2207	
115	2227	
116	2246	
117	2266	
118	2285	
119	2305	
120	2324	
121	2344	
122	2363	
123	2383	

CONTINUED

NEXT
PAGE

►1

↓

[illegible]

N FREQ		TIME																CONTINUED ON PAGE 193			
		0.6800	0.7200	0.7600	0.8000	0.8400	0.8800	0.9200	0.9600	1.0000	1.0400	1.0800	1.1200	1.1600	1.2000	1.2400	1.2800	1.3200			
1	0			5					2	2				2	8	36	43		3	4	
2	20			2					1					4	31	5	9	2			
3	39		14	7	19	18	19	31	27	19	14	6		8	187	875	400	249	47	44	
4	59	22	13	2	16	49	79	35	122	33	38	34	88	970	3375	1122	730	258	119		
5	76	96			10	42	19	53	52	18	5	5	93	661	1843	539	224	282	73		
6	98	284	13	11	8	14	5	12	8	5	9	117	870	4631	2398	309	482	522			
7	117	279	29	15	9	20	7	14	6	6	6	35	3419	3284	4571	185	617	709			
8	137	43	1	4	24	34	30	22	5	1	20	122	6267	373	1534	119	57	15			
9	156	63	46	13	18	18	16	17	6	1	38	198	1827	2165	1022	607	843	73			
10	176	38	52	5	5	5	5	10			20	126	2370	3202	107	336	346	36			
11	195	77	7	2	5	8	7	5		3	5	127	1000	1641	140	131	53				
12	215	18	63	2	6	19	12	10	9	3	1	105	1502	4300	537	295	532	95			
13	234	29	34			11	6	10	8		6	58	3360	3771	354	136	254	80			
14	254	4		1			1	1		1	2	108	2408	168	8	42	80	6			
15	273	6	9									74	204	1850	98	62	71	4			
16	293	6	2									8	1054	760	159	12	26	13			
17	313						1		1		2	72	2149	289	28	22	45	2			
18	332	1	2								1	101	467	960	25	35	75				
19	352	2										20	112	285	25	7	23	1			
20	371	4										11	1083	335			11				
21	391											43	306	527	17		10				
22	410										1	9	41	109	21						
23	430											2	73	20	4						
24	449											8	77	37	10						
25	469											1	16	52	7		1				
26	488											2	139	61	1		1				
27	508											4	157	124	2						
28	527											2	23	45							
29	547												26	1							
30	566												19	1							
31	586												10								
32	605												3	2							
33	625												13	1							
34	645									1			3	8							
35	664												5	31							
36	684												15	13							
37	703												2			1					
38	723												1	3							
39	742												3	3		1					
40	762													7							
41	781													2							
42	801													1		1					
43	820													3							
44	840														1						
45	859													2							
46	879														1						
47	898																				
48	918																				
49	938																				
50	957																				
51	977																				
52	996																				
53	1016																				
54	1035																				
55	1055																				
56	1074														1						
57	1094																				
58	1113																				
59	1133																				

CONTINUED

NEXT
PAGE

60	1152			
61	1172			
62	1191			
63	1211			
64	1230			
65	1250		1	
66	1270			
67	1289			
68	1309			
69	1328			
70	1348			
71	1367			
72	1387			
73	1406			
74	1426			
75	1445			
76	1465			
77	1484			
78	1504			
79	1523			
80	1543			
81	1563			
82	1582			
83	1602			
84	1621			
85	1641		2	
86	1660		2	
87	1680			1
88	1699			
89	1719			
90	1738			
91	1758			
92	1777			
93	1797		1	
94	1816		1	
95	1836			
96	1855			
97	1875			
98	1895			
99	1914			
100	1934			
101	1953			
102	1973			
103	1992			
104	2012			
105	2031			
106	2051			
107	2070			
108	2090			
109	2109			
110	2129			
111	2148			
112	2168			
113	2188			
114	2207			
115	2227			
116	2246			
117	2266			
118	2285			
119	2305			
120	2324			
121	2344			
122	2363			
123	2383			

CONTINUED

NEXT
PAGE



7
▶16
3

1
▶4
1

[illegible]

N FREQ		TIME										
		1.3600	1.4000	1.4400	1.4800	1.5200	1.5600	1.6000	1.6400	1.6800	1.7200	1.7600
1	0	2								3	3	1
2	20	3								2	2	
3	39	29								15	3	23
4	59	▶135	▶44	▶242				▶39	▶67	▶78	▶22	▶79
5	76	66	27	132	▶7	6	27	▶34	11	40	17	39
6	98	61	2	32	▶4	3	12	22	22	15	2	28
7	117	▶63	27	69	▶6	7	56	55	▶63	12	36	4
8	137	63	▶114	▶141	6	▶40	▶76	▶59	37	▶13	▶105	19
9	156	47	69	48		19	30	21		6	45	▶83
10	176	2		5	1	5	6	6	5	4		23
11	195	23	31	9	▶6	3	4	6	9	2	20	6
12	215	▶99	▶66	▶11	5	20	▶19	▶7		2	▶37	▶82
13	234	25	19	3	▶7	▶22	2	2		1	7	34
14	254					2		1		1	2	7
15	273	6	1	1			2	1			4	▶12
16	293	▶7				2	1			1		
17	313			1		2	1	2		▶2	1	10
18	332	1	1			1	▶5	2		1	▶5	2
19	352		1		1		1				4	
20	371	1										▶4
21	391											
22	410											1
23	430											
24	449											
25	469											
26	488											
27	508											
28	527											
29	547											
30	566											
31	586											
32	605											
33	625											
34	645							1				
35	664							1				
36	684											
37	703											
38	723											
39	742											
40	762											
41	781											
42	801											
43	820											
44	840											
45	859											
46	879											
47	898											
48	918											
49	938											
50	957											
51	977	CONTINUED										
52	996	NEXT										
53	1016	PAGE										
54	1035											
55	1055											
56	1074											
57	1094											
58	1113											
59	1133											

60	1152
61	1172
62	1191
63	1211
64	1230
65	1250
66	1270
67	1289
68	1309
69	1328
70	1348
71	1367
72	1387
73	1406
74	1426
75	1445
76	1465
77	1484
78	1504
79	1523
80	1543
81	1563
82	1582
83	1602
84	1621
85	1641
86	1660
87	1680
88	1699
89	1719
90	1738
91	1758
92	1777
93	1797
94	1816
95	1836
96	1855
97	1875
98	1895
99	1914
100	1934
101	1953
102	1973
103	1992
104	2012
105	2031
106	2051
107	2070
108	2090
109	2109
110	2129
111	2148
112	2168
113	2188
114	2207
115	2227
116	2246
117	2266
118	2285
119	2305
120	2324
121	2344
122	2363
123	2383

CONTINUED

NEXT
PAGE



VITA

Surname: Fletcher Given Names: Val Edward

Place of Birth: New Westminster, B. C.

Date of Birth: February 14, 1946

Educational Institutions Attended with Dates of Entering
and Leaving:

University of Victoria, Victoria, B. C. 1964 to 1969

University of Victoria, Victoria, B. C. 1974 to 1981

_____ to _____

Degrees, Diplomas, Etc., Awarded, with Dates and Names of
Institutions:

B.Sc. 1969 University of Victoria

Honors and Awards:

Publications:

PARTIAL COPYRIGHT LICENSE

I hereby grant the right to lend my thesis or dissertation (the title of which is shown below) to users of the University of Victoria Library, and to make single copies only for such users or in response to a request from the library of any other university, or similar institution, on its behalf or for one of its users. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by me or a member of the University designated by me. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Title of Thesis

A COMPARATIVE ANALYSIS OF THE BEHAVIOURAL ECOLOGY,

AGONISTIC BEHAVIOUR AND SOUND PRODUCTION IN

TWO SPECIES OF INSHORE EASTERN PACIFIC ROCKFISH

(GENUS SEBASTES)

Author 

Val E. Fletcher ,

June 29, 1981