

AGGRESSIVE BEHAVIOR AND SOCIAL HIERARCHY IN THE
PINFISH, LAGODON RHOMBOIDES (LINNAEUS)

By

Wayne F. Hadley

Bachelor of Science

Oklahoma State University

Stillwater, Oklahoma

1962

Submitted to the faculty of the Graduate College
of the Oklahoma State University
in partial fulfillment of the requirements
for the degree of
MASTER OF SCIENCE

JAN 10 1968

AGGRESSIVE BEHAVIOR AND SOCIAL HIERARCHY IN THE
PINFISH, LAGODON RHOMBOIDES (LINNAEUS)

Thesis Approved:

Thesis Adviser

Roy W. Jones

L. Herbert Bunnay

Wray C. Davis

N. N. Durham

Dean of the Graduate College

658787

ACKNOWLEDGEMENTS

I wish to take this opportunity to thank Dr. R. J. Miller for his advice and criticism in the preparation of this thesis. Dr. J. C. Briggs' encouragement and advisement in the initiation of the study and the collection of the data were invaluable. Thanks are also due to Dr. T. C. Dorris, Dr. R. W. Jones and Dr. L. H. Bruneau who read and criticized the manuscript.

The research on which this thesis is based was done at the Institute of Marine Science of the University of Texas at Port Aransas, Texas. The use of these facilities and the cooperation of the staff is gratefully acknowledged.

TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION	1
II. MATERIALS AND METHODS.	3
III. OBSERVATIONS	5
Markings	5
Patterns	9
Pattern Expression	9
Aggressive Behavior.	11
Appeasement Behavior	12
Cleaning Behavior.	12
Digging.	14
Shell Turning.	15
Burying.	15
Hierarchical Organization.	15
Territoriality	20
IV. DISCUSSION	23
Appeasement.	23
Aggressive Behavior.	24
Schooling.	24
Territorial Control.	26
Hierarchy.	26
V. SUMMARY	30
LITERATURE CITED	32

LIST OF FIGURES

Figure	Page
1. Ocellated.	6
2. Banded	6
3. Predorsal Bar.	7
4. Jugular Darkening I.	7
5. Jugular Darkening II	8
6. Subdorsal Darkening.	8

LIST OF CHARTS

Chart	Page
1. Courses of Agonistic Bouts.	13
2. Numbers of Aggressive Bouts Per Hour.	17
3. Size-Rank Relationships - Group I.	18
4. Size-Rank Relationships - Group II.	19

CHAPTER I

INTRODUCTION

This investigation was conducted to describe aggressive behavior patterns and associated color displays in the pinfish, Lagodon rhomboides (Linnaeus), to determine if social order would develop in small captive groups, and, by observations in nature, to evaluate the occurrence and function of these phenomena in the ecology of the animal.

Pinfish are small Sparid fishes reaching a maximum length of a little over 200 mm. They are found in bay and inshore marine habitats from Cape Hatteras to Yucatan. Their systematics and ecology were reviewed by Caldwell (1957). He dealt only briefly with aspects of their behavior.

Aggressive behavior and social hierarchy of fishes have been studied by many workers. Social hierarchy has been recorded in captive groups of Mustelus canis (Allee and Dickinson, 1954), Colisa lalia (Forselius, 1957), Lepomis cyanellus (Greenburg, 1947), Platyopocilus maculatus (Braddock, 1945 and 1949), Gambusia affinis (Caldwell and Caldwell, 1962), Trichogaster trichopterus (Miller, 1964), Xiphophorus helleri (Noble and Borne, 1938), Ptychoceilus oregonense (Pfeiffer, 1965), Hemichromis bimaculatus (Noble and Curtis, 1939), Stephanolepis cirrhifer (Okaichi et al, 1958), Salmo gairdneri (Newman, 1956 and Stringer and Hoar, 1955), Danio malabaricus (Haas, 1959), Betta splendens (Braddock and Braddock, 1955), Mollienesia latipinna (Baird, 1965), Oryzias latipes

(Magnuson, 1962), Gambusia hurtadoi (McAlister, 1958), and Salvelinus fontinalis (Newman, 1956). Records of naturally occurring social order in fishes are almost non-existent. Newman (1956) observed S. gairdneri and S. fontinalis to hold shifting territories in the wild and found that a larger fish could drive a smaller individual out of the territory previously occupied by the smaller. Thus, a social structure of a functional nature existed though the fish may not have recognized the others as individuals.

CHAPTER II

MATERIALS AND METHODS

The fish used in these experiments were collected on hook and line in the boat basin at the Institute of Marine Science, Port Aransas, Texas. They ranged in size from 115 to 146 mm. The twelve individuals comprising Group I were collected between January 8, 1963 and January 15, 1963, and the twelve in Group II were collected on February 19, 1963.

The groups were placed in separate 75 gallon aquaria which were part of a recycling sea water system. Aeration was supplied by air stones in each tank. The water in the system was taken from the boat basin. It was regularly tested for salinity and pH. Salinities were held between 33 and 37 ppt by the addition of distilled water to replace that lost by evaporation. The pH was not adjusted, but rather, when a level was reached that seemed detrimental to the experimental animals, the entire system was emptied, cleaned, and new water added. This was done on 19 and 26 February. Artificial lighting was provided between the hours of 7 a.m. and 5 p.m. daily.

The fish were fed daily, an hour before observations were made. The food consisted of frozen commercial bait shrimp (Penaeus sp.), frozen anchovies (Anchoa mitchelli) and an occasional squid (Lalys sp.).

The test animals were marked by a series of notches cut in the caudal fins. The marks on Group I were renewed on February 19.

Observation periods were one hour in length. The result of each agonistic bout was recorded for both individuals. In a given bout, the fish that fled or postured subordinately was recorded as the loser and the other as the winner. Encounters were not recorded under the following conditions: 1) the winner was in his own territory; 2) the loser was attacked from behind; 3) the loser had been defeated just prior to the bout in question.

Preliminary laboratory observations were made on several other groups of pinfish with substantially the same results. The collections of data from these groups were sporadic and for this reason they are not presented here.

Observations of pinfish in nature were made from the surface and with the use of skindiving gear.

CHAPTER III

OBSERVATIONS

Markings

Variation in the markings of pinfish is accomplished primarily by concentration or dispersion of melanin pigments. The yellow and blue markings are relatively stable regardless of the behavior being performed.

Changes in the melanophores result in the formation of five distinct markings which singly or in combination comprise a particular color pattern. The markings are characterized as follows:

Pectoral Ocellus -- A circular area of dispersed melanophores one third of the body depth below the dorsal origin (Figure 1).

Banded -- A series of eight or nine dark bands extending ventrally from the middorsal line (Figure 2).

Predorsal Bar -- One or two short, dark bars extend ventrally from the middorsal line just anterior to the dorsal origin. These bars are the upper portions of the second and third darkened components of Bands (Figures 3 and 4).

Jugular Darkening -- The throat and lower cheek are darkened (Figures 4 and 5).

Subdorsal Darkening -- The area extending from the posterior predorsal bar to the caudal peduncle becomes uniformly dark (Figure 6).

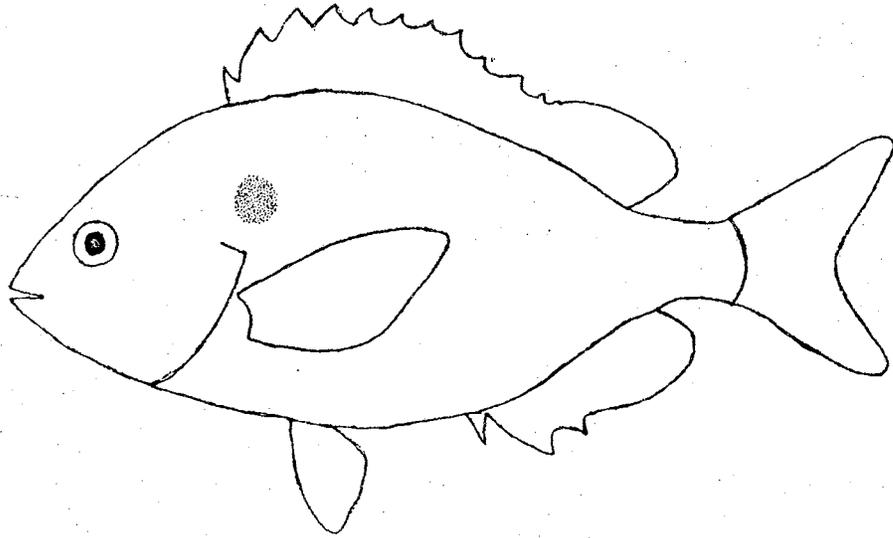


Figure 1. **OCELLATED**

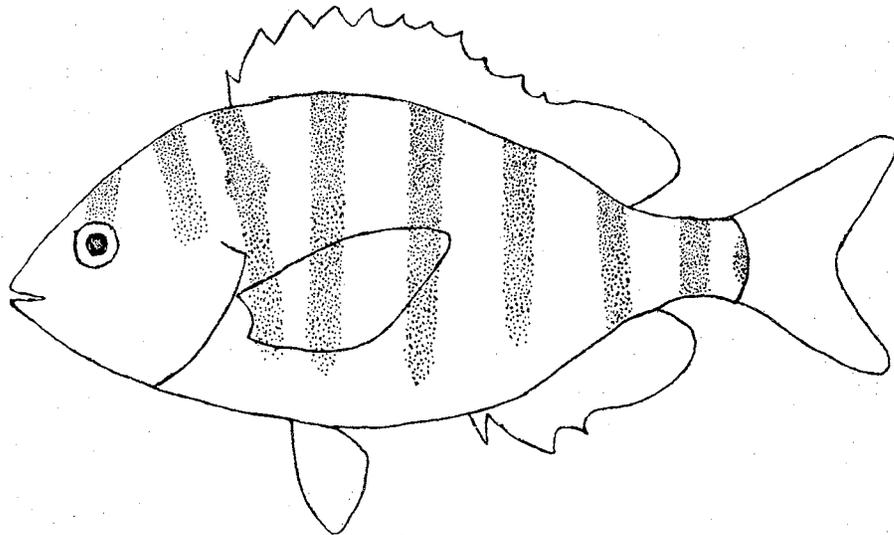


Figure 2. **BANDED**

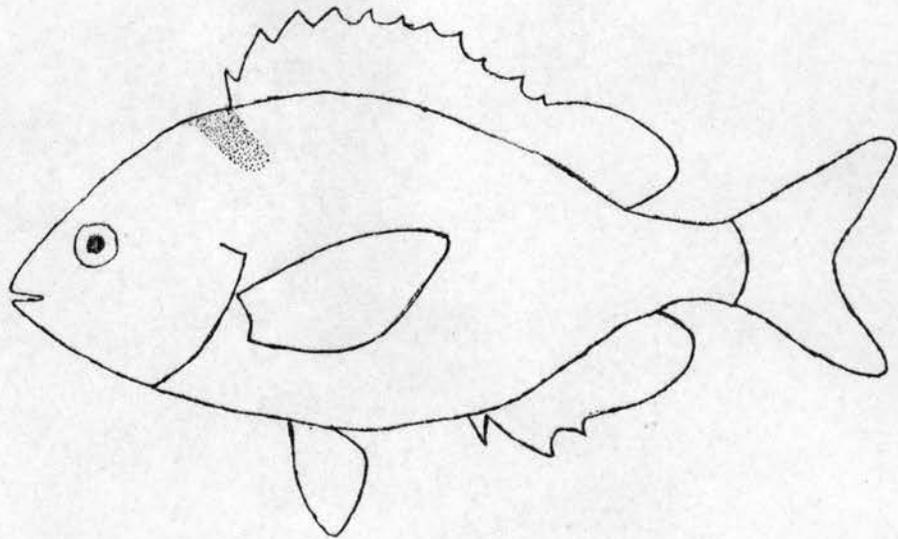


Figure 3. **PREDORSAL BAR**

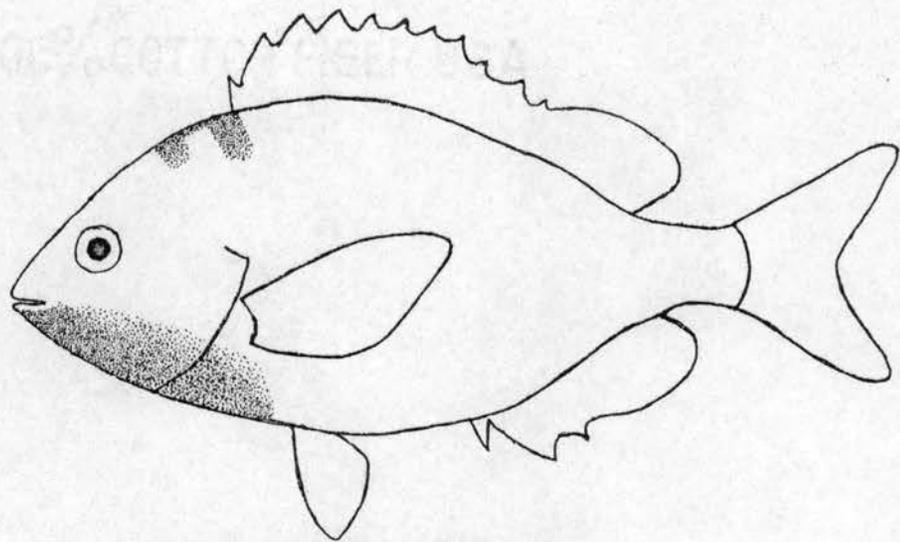


Figure 4. **JUGULAR DARKENING I**

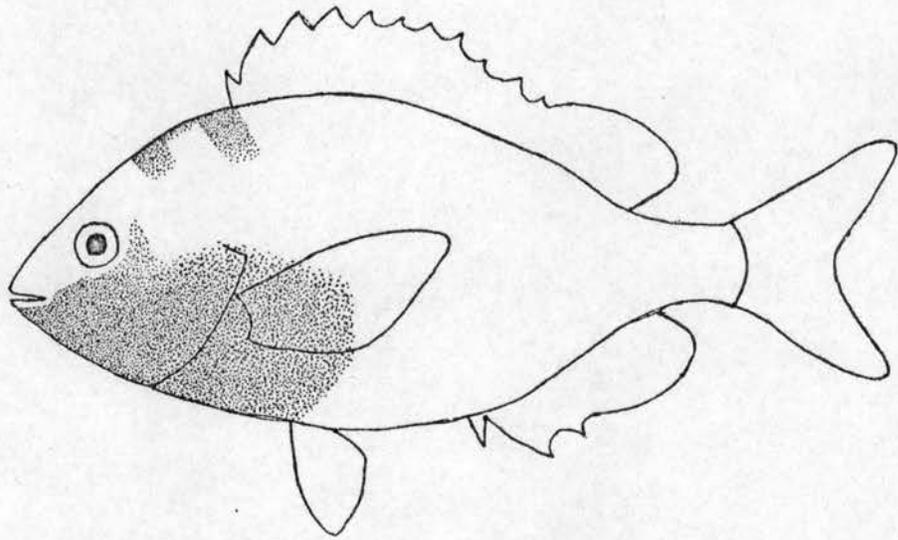


Figure 5. **JUGULAR DARKENING II**

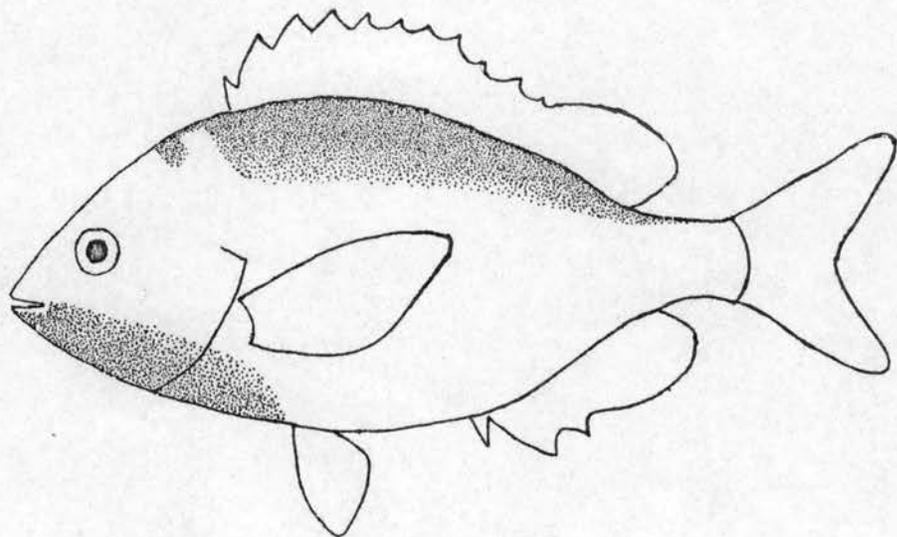


Figure 6. **SUBDORSAL DARKENING**

Patterns

The five color patterns listed below are associated with distinct behaviors or stages thereof. Ocellated and Banded are each displayed in a unique behavior while Predorsal Bars, Jugular Darkening, and Subdorsal Darkening represent successive stages in a single behavior pattern.

Ocellated -- The pectoral ocellus is the only dark area on the body (Figure 1).

Banded -- The bands described above are expressed. The pectoral ocellus is also dark but is incorporated into the third band (Figure 2).

Predorsal Bar -- The bar at the dorsal origin appears. The small bar anterior to it may or may not be displayed, but occurs only in the presence of the posterior bar (Figures 3 and 4).

Jugular Darkening -- This pattern includes the jugular darkening and the predorsal bars described earlier. Both predorsal bars are always manifest when Jugular Darkening is displayed. The inner areas of the premaxillae and mandibles are usually darkened. The area of the lower cheek and throat that is darkened varies in size (Figures 4 and 5).

Subdorsal Darkening -- This pattern includes the markings comprising the Jugular Darkening pattern plus the subdorsal darkening described in the section on markings (Figure 6).

Pattern Expression

Ocellated -- This pattern is the most common in nature. When a pinfish is not engaged in aggressive behavior or attempting to hide the

Ocellated pattern is shown. The ocellus fades slightly when the fish is frightened or is making appeasement movements in the presence of a social superior. The slight blanching of the ocellus is not sufficiently distinct to merit a separate pattern designation. Fish showing this pattern were unlikely to engage in aggressive behavior.

Banded -- This pattern is a cryptic one. It was observed only in fish attempting to hide themselves when flight was impossible. When I entered the room at night it appeared that this pattern was displayed. It may be the common night pattern.

Predorsal Bars -- Predorsal Bars was most commonly observed on fishes holding a territory. Fishes thus marked defended their territory against social inferiors but might or might not challenge an equal entering their territory. A social superior's entry would rarely be contested when this pattern was displayed by the resident. The presence of both bars seemed to indicate a slightly higher readiness to engage in aggressive behaviors than when a single bar was present.

Jugular Darkening -- Those individuals displaying some degree of Jugular Darkening were likely to attack social inferiors or equals invading their territories. When this pattern was well developed, a fish might challenge a superior entering his territory. It was also associated with threatening and driving activities. The degree of darkening displayed by a particular fish was variable and an increase of the area darkened may be correlated with a greater probability of aggressive behavior.

Subdorsal Darkening -- This pattern was manifested at the moment display

ceased and actual fighting began. It remained throughout the actual combat period and regressed to the Jugular Darkening pattern within a few seconds after the engagement ended.

Aggressive Behavior

The aggressive behavior of pinfish resembles that of many spiny rayed fishes; the movements and postures bear a general resemblance to those of the species of Lepomis (Miller, 1963).

An agonistic bout between two fish initially consists of display. In most instances this is sufficient to end the encounter. Threat postures include a frontal display and a lateral display. In the frontal position, the fish faces its opponent with dorsal and anal spread and the pelvics extended. The pectoral and caudal beat in opposition and the body as a whole undulates. The mouth may be opened and the darkened maxillae and mandibles revealed. The Jugular Darkening pattern is displayed.

The lateral display posture is maintained with the body axis parallel or at right angles to the opponent. The color, fin position, and movements are as in the frontal display position.

Frontal displays are rarely followed by actual fighting, but may progress to mutual lateral display and thence to fighting. In lateral display the fish maintain a head to tail orientation with sides nearly touching. At this point, Subdorsal Darkening appears. The fish then whirl rapidly through the water with heads still opposite tails. This may continue for several seconds. The encounter may terminate with one fish fleeing while the victor drives or, in an equally matched pair, another mutual lateral threat may occur. In the case of a definite

decision, the loser's color pattern almost immediately changes to Ocellated and the victor's to Jugular Darkening. In an undecided encounter, both normally display the Jugular Darkening. In either event, the subdorsal darkening disappears very rapidly (see Chart 1).

Appeasement Behavior

Subordinate fish when threatened would often alter the longitudinal axis of the body with the head at an angle of approximately 45° from horizontal in response to the frontal threat of a superior. If the superior approached from above, the head was lowered. If the dominant approached from below, the head was raised. When the superior approached in the same horizontal plane, the response was variable, but most often upward. The fins were normally folded during this behavior and the Ocellated pattern shown.

A threatened subordinate might also indicate submission by tilting the vertical axis of the body away from the attacker. The fin positions and color were the same as in the previous posture.

Cleaning Behavior

On 26 May 1963, during a period of very clear water, large schools of Mugil cephalus were moving along the beach of Mustang Island near the Institute of Marine Science in a northeasterly direction. Observations from the jetty revealed an almost continuous procession of mullet. The schools traveled along the beach side of the jetty, rounded the seaward end, proceeded through the ship channel and thence into the bay. At different points on the channel side of the jetty I observed five pinfish, all between 40 and 70 mm standard length, interacting with

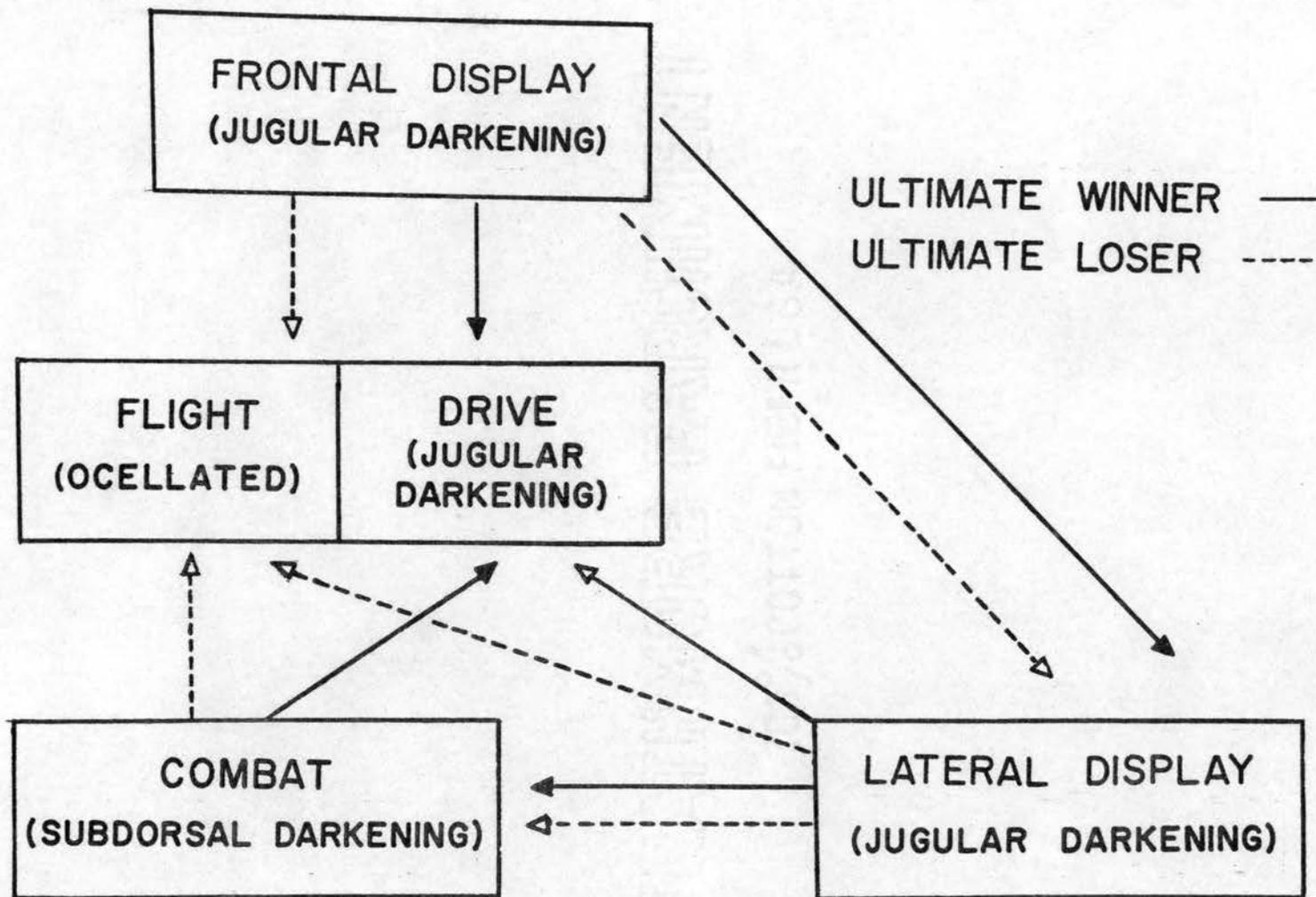


Chart 1. Courses of Agonistic Bouts

the mullet. A number of pinfish were observed but only five were engaged with the mullet. These five, though acting alone, behaved similarly. As the shoals moved past the jetty stones, the pinfish moved into a position a few inches below them. In all cases the pinfish maintained this position and displayed the Ocellated pattern. Single mullet were seen to leave the school, descend to the level of the pinfish and assume a stationary position with the foreparts shifted upward approximately 20° from the horizontal. The pinfish then approached and appeared to nibble at various parts of the mullet. The mullet often tilted the vertical axis of the body toward the pinfish. After a period of approximately fifteen seconds, the pinfish ceased its attention and the mullet rejoined the school. One of the pinfish observed behaved in this manner with seven mullet in an interval of about five minutes and then left its position beneath the school.

On 6 June 1963 in the Institute of Marine Science boat house a small school of mullet was seen lying almost stationary at the surface of the water. A pinfish approximately 50 mm in standard length approached them and nibbled at the bodies of three mullet which assumed a head up position at its approach. Breder (1962) observed similar behavior on the Florida coast.

Digging

Pinfish were observed on four occasions to approach the sand substrate at an angle and rapidly engulf a quantity of sand by the sudden opening of the mouth coordinated with the expulsion of water from the gill slits. The finer ingested material was then ejected through the gill slits and the coarse material through the mouth. In

all cases, the behavior was repeated at least twice in the same spot. Nothing could be seen that might have served as a stimulus for this behavior. It seems likely that this is a method for securing benthic food organisms inhabiting shallow burrows.

Shell Turning

Shell turning was observed twice in the laboratory. In both instances, a fish with opened mouth approached half of an oyster shell lying on the bottom. The mandible was pushed under the rim of the shell and, without closing the mouth, the fish flipped over the shell by a rapid elevation of its foreparts. The fish then quickly reoriented toward the area previously occupied by the shell and appeared to observe it closely. This appears to be another adaptation for securing food.

Burying

On two occasions pinfish were seen to engage in an activity Caldwell (1957) termed burying. In both instances the fish were struck by a net while removing them from the aquarium for remarking. Immediately they descended to the bottom and by rapid undulations of the body buried themselves in the sand substrate, assuming the Banded color pattern. They emerged in a few minutes and their previous color patterns were displayed. The instances reported by Caldwell (1957) were similar.

Hierarchical Organization

Group I

The fishes of Group I had been held in the aquarium approximately

thirty days before observations were begun. As Chart 2 shows, the number of aggressive encounters on day one was little different from the number on day thirty. A straight-line dominance hierarchy had been established at this time. This situation prevailed for the entire course of the experiment, although some changes in rank occurred.

Size has been shown to be an important factor in rank determination by Allee et al (1948), Caldwell and Caldwell (1962), Miller (1964), Newman (1956), and others. As Charts 3 and 4 show, the larger fish of any pair was likely to be dominant. However, some cases of a smaller fish dominating a larger individual were seen. This implies that another factor, or factors, was operable in determining rank. No information to support any theory regarding this occurrence was gathered.

No correlation could be made between rank and sex.

Changes in rank were not infrequent. An upward change in rank was typically of a single position and might involve encounters spread over a period of one to three days. The pair usually fought repeatedly before a definite dominant-subordinate relationship was evolved. This relationship might endure or later be reversed. Again, the cause of these fluctuation is unknown.

Group II

Observations of aggressive encounters of fishes of Group II were begun the day following their captures. As Chart 2 shows there was little activity during the first few days, with a gradually increasing number of bouts occurring until a peak was reached. This was followed by a decline to a level similar to that shown by Group I. Braddock

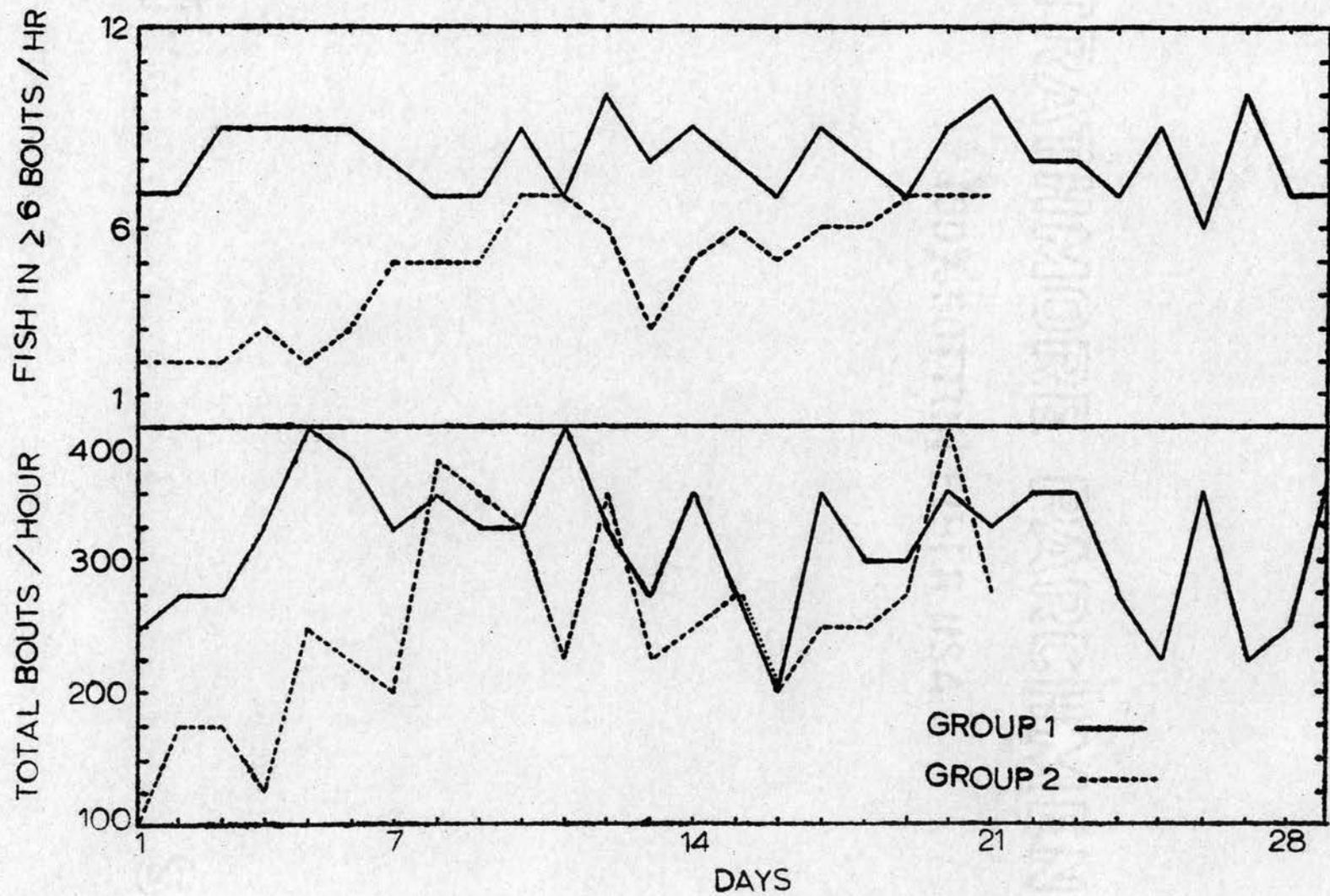


Chart 2. Numbers of Aggressive Bouts Per Hour

GROUP I

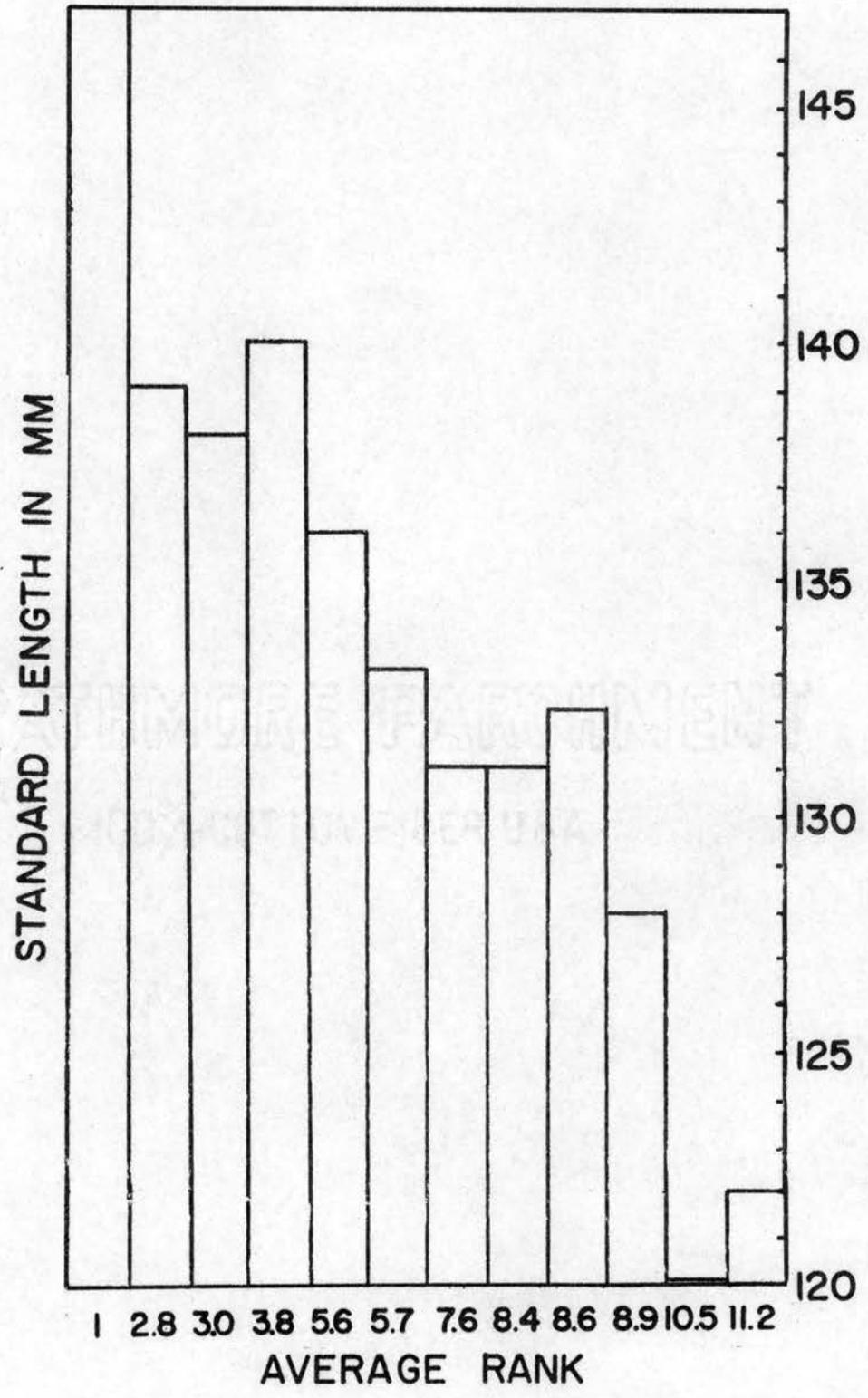


Chart 3. Size-Rank Relationships - Group I

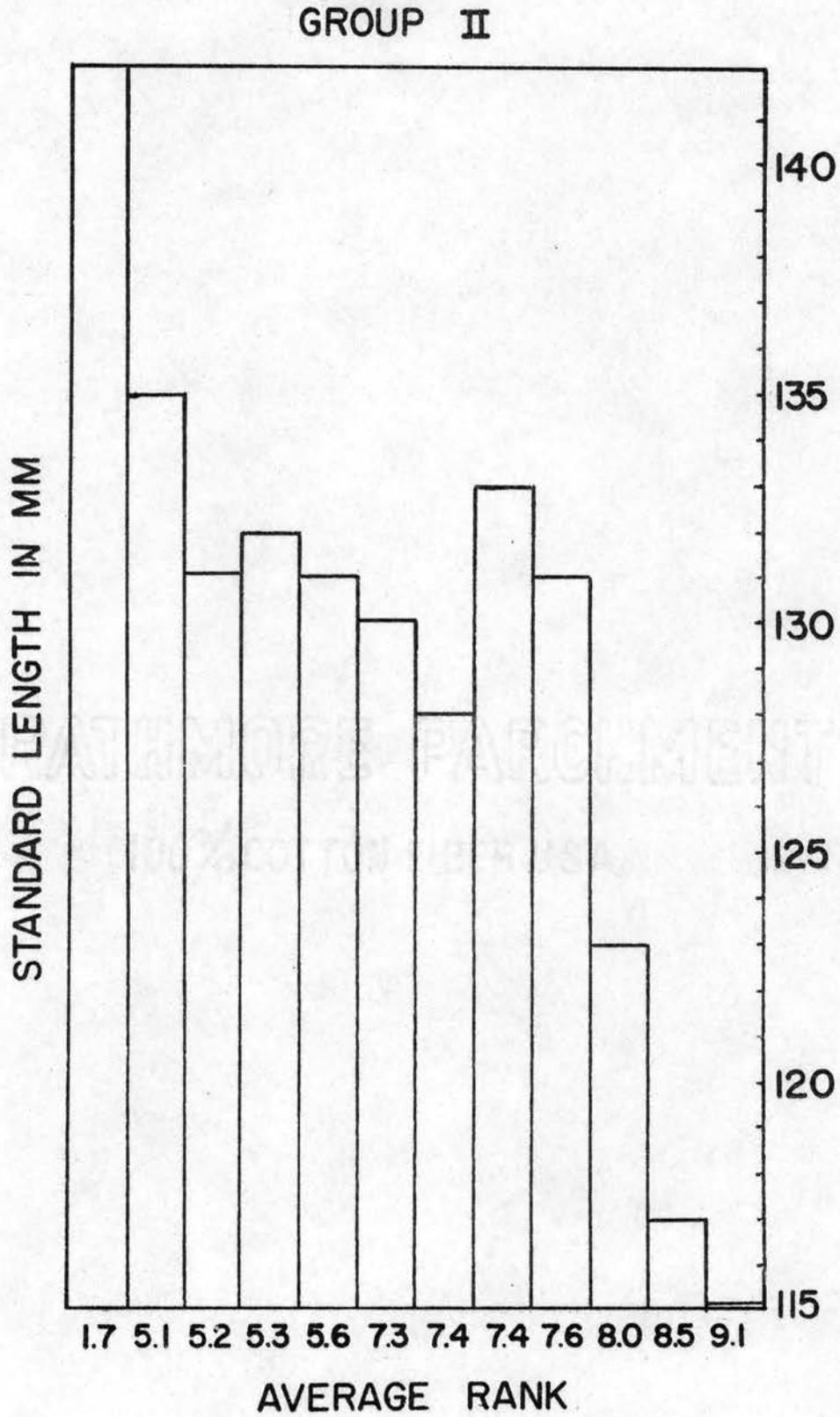


Chart 4. Size-Rank Relationships - Group II

(1945) found a similar rise and subsequent decline in aggressive behavior in newly formed hierarchies of Platyopocilus maculatus. Aggressive encounters began with only a few individuals attacking (Chart 2). Gradually more showed aggressive behaviors and at the peak level all were involved. The subsequent decline in number of bouts may have been due to the increasing territoriality of the fish. An individual holding a territory rarely left it and while resident was unlikely to engage in encounters with any fish but those whose territories overlapped his own. Prior to the definition of territories, movement was random and encounters with other individuals more frequent. Thus, in this situation, territorial behavior served to decrease the number of aggressive encounters.

After the initial period of instability, which was characterized by rapid changes in rank, a hierarchy similar to that of Group I developed. A straight-line hierarchy of drive-right type was established and changes were as described for Group I. The aggressive behaviors observed were the same for both groups.

Territoriality

The defense of an area was characteristic of fishes held in the laboratory. The aquarium was divided into a number of small individual territories owing to the large number of individuals present. There was a positive correlation between rank and size of the territory. Fish 1 held the entire tank, moving freely and driving or ramming the others at will. In general, fishes 2 and 3 each held a half. They defended these areas against each other and sporadically drove subordinate fish from them. Fish 4-8 generally held small subterritories within the

areas held by 2 and 3. They were able to successfully defend these areas against fish lower in rank but were defeated by or did not challenge a dominant entering their territories. When an individual was able to rise in rank, he frequently would usurp the territory of the fish that lost rank. The individual that lost his position was left without a territory and, for a time, was defeated by all who challenged him. Characteristically, within a day he would have claimed the territory previously held by the new dominant or would have established a new territory from the area of a subordinate. Fish 9-12 were seldom able to hold a territory. They were tolerated in the area of a dominant and might commonly be found in a particular spot but they rarely attempted to defend it.

In nature territorial behavior was observed on only five occasions. On three nights, 21, 22, 23 May 1963, a pinfish was seen to maintain a position near a piling beneath a light at the Institute of Marine Science boat basin, a favored feeding site. On all three nights it chased other pinfish from a circle of approximately 2 feet diameter surrounding the piling. The full sequence of threat and fighting was observed with the color patterns as observed in the laboratory. Whether the same fish was involved on all occasions could not be determined.

During a period of unusually clear water on 3 March 1963, a group of pinfish was seen feeding on the underside of a barge moored in the boat basin. A heavy growth of plants covered the hull, and the fish nosed about in this material occasionally securing a food organism. When another pinfish approached to within 8 or 10 inches, the individual approached would either turn toward the intruder and drive him away or ignore him completely. No instances of intruders attacking the fish in

residence were observed. The attacking fish showed Predorsal Darkening. No territorial defense occurred in the sense that a specific area of the bottom was defended but rather an area around the attacker was defended. The fish roamed freely over the bottom and a fish that had previously been driven from an area might enter it unmolested when the attacker had gone.

On 8 May 1963 while diving under the Institute of Marine Science research pier, I saw a pinfish of approximately 120 mm length drive others away from its position near a piling. While engaged in this activity it displayed the Jugular Darkening pattern.

CHAPTER IV

DISCUSSION

Appeasement

Appeasement movements and the associated blanching of pigment are not complex. Observations in the field revealed no instances of appeasement behavior; rather, a subordinate would simply retire from the vicinity of an aggressor when threatened. It is difficult to imagine a situation other than spawning behavior (unknown in this species) where it would be advantageous to appease rather than flee. It seems possible that the appeasement posturing seldom if ever occurs in nature.

Appeasement behavior would seem likely to evolve in two circumstances; where flight from an aggressor was physically impossible, or where some stimulus in the environment was so attractive that the attacked fish gained an advantage by remaining. Under these circumstances the ability to lessen the intensity or frequency of attacks would be of significant benefit, and appeasement could then evolve as a derivative of normal preflight movements. In pinfish the appeasement behaviors are simple motor patterns and the response to them by the aggressor is variable. In the majority of cases fish showing appeasement behavior were not attacked by threatening superiors. This was not universally true and may have been due to the poor development of this set of behaviors or to the unnatural conditions in the tanks. Since no instance of appeasement behavior was observed in nature and no circumstances

under which it might have evolved could be postulated, it is possible that the appeasement behaviors seen in the laboratory did not represent innate behavior patterns. Rather, the behavior seen in the laboratory may have been a result of inability to flee due to spatial restriction. Under these conditions the normal flight reaction with folded fins and blanched colors is manifested but the locomotor activity is eliminated.

Aggressive Behavior

Patterns of aggressive behavior are considerably more complex than those of appeasement. As previously described, 3 color components, roughly corresponding to 3 levels of aggressive tendency, were observed. These constitute the basic threat patterns and were associated with clinal stages of aggressive behavior. In the laboratory fishes of a similar size were found to perform complete fight sequences with physical contact being made before a dominant-subordinate relationship was established. Fish of dissimilar size normally formed a stable relationship with only threat behaviors displayed. In the field, observations of aggressive encounters where threat postures were sufficient to decide the contest were the rule. In only four bouts was physical contact made. It seems probable that threat postures have become sufficiently established to serve successfully in lieu of fighting in most instances. Burkenroad (1931) noted pinfish making sounds by grinding the incisor teeth, and it is possible that some auditory stimuli may play a role in aggressive behavior.

Schooling

Schooling behavior and its ecological significance have been

reviewed by Shaw (1962). During observations of pinfish in the laboratory, it seemed that a function unmentioned by Shaw (1962) might exist. When a piece of shrimp or squid too large for ingestion was placed in a tank containing a single fish, considerable difficulty was encountered in reducing it to an edible size. The fish grasped the food and pulled vigorously, but was successful in tearing off a portion of suitable size only after a number of attempts. In nature such behavior would expend considerable energy and quite possibly increase the fish's vulnerability to predators. When a bit of food of similar size was placed in a tank containing several individuals, no difficulty of this type occurred. The simultaneous pulling by two or more fish provided the resistance necessary to tear off small pieces. A large piece of squid was reduced to ingestible pieces in a very short period. Since a pinfish in nature seems to be seldom beyond sight of another of his species, it is probable that group utilization of larger organisms normally occurs. Thus, while each individual may receive a smaller total of a given food source, more fish would benefit from it and each would be exposed to attack for a shorter period.

Schools of pinfish were seen to pursue shoals of Mugil cephalus fry in a manner similar to that of the species commonly recognized as pelagic predators. The function of the group in securing food in this situation appears to be the same; that is, the orientation of the flight of prey from a single attacker is dependent on a single stimulus source, while flight from a group is governed by a multiplicity of similar stimuli. It seems likely that errors occur more frequently where the stimuli to be screened are more complex and a feeding advantage is thereby conferred on the predators.

Territorial Control

The defense of an area against other members of their species was characteristic of pinfish in the laboratory. In the field territorial behavior was observed on four occasions as described in the section on aggressive behavior. The role of territory in the life history of this species seems to be dictated by circumstance. Field observations showed perhaps one fish in a hundred in possession of a territory. The remainder seemed to have no ties to particular terrain features but moved freely as circumstances dictated. It is possible that individuals had a home range which was not defended, and a relationship of this sort would have been undetected in this study. Predictably, all instances of a territory were correlated with some advantageous environmental condition, usually a rich food supply. Pinfish possess behavioral abilities suitable for both free ranging and territorial modes of survival, and these are expressed as environmental circumstances warrant.

Hierarchy

Formation of a relatively stable, straight-line, drive-right dominance hierarchy occurred in the laboratory. There was indication that a "monarchistic" (Collias, 1944) type hierarchy was present. In this type one dominant individual suppresses aggressive behavior between other individuals. This did occur in these experiments and it was obvious that aggressive color patterns and behaviors by fishes 2-12 caused them to be attacked by 1. In this instance the application of the term "monarchistic" dominance seems superfluous. The phenomenon observed was not due to any unique characteristic which made possible a separation of "monarchistic" and any other type of dominance hierarchy.

Rather the available space was too limited for the establishment of separate individual territories that could be defended against intruders. In these circumstances fish 1 controls the entire tank as his territory. Fishes 2 and 3 typically each defended one half of the aquarium and the remainder occupied subterritories within these. The display of aggressive coloration and behavior at the territorial boundary normally elicits display or attack from the resident. In these experiments display by fish occupying subterritories, effectively fish 2-12, elicited aggressive behaviors by the fish holding the territory (fish 1). It seems, then, that in pinfish this is no different from any other type of dominance hierarchy, but is the result of overcrowding. It is possible that if more space were available, the fish might arrange themselves in individual territories without overlap; thereby eliminating the "monarchistic" hierarchy.

The phenomenon of social hierarchy may be considered at two levels of complexity. In the first, any functional relationship between two fish whereby one is able to defeat the other may be thought of as an hierarchial organization. The other level involves more than a simple difference in aggressive ability. In it the pair of fish is divided into a dominant and a subordinate on the basis of agonistic encounters, but there is implied some knowledge of their roles. That is not to imply that the dominant is aware of his ability to defeat the subordinate, or vice verse, but that some mechanism is operable such that they display the appropriate response to each other. This concept of individual recognition has apparently been derived from studies on mammal hierarchies and extended to fish hierarchies with little or no experimental confirmation.

The two phenomena seen in this study that would seem to be most indicative of individual recognition were the long term stability of dominance patterns and the existence of appeasement behavior. The dominance relationship between some pairs of fish remained unchanged throughout the period of investigation. It is possible that the fish involved in such a relationship is influenced by the other as an individual and responds to him as such. It seems equally likely that the response may be to greater or lesser aggressive ability and that the difference in the abilities of the fish is of such a magnitude that changes in dominance are impossible. Appeasement behavior by a subordinate often takes place with no overt display by the dominant. This may be due to the recognition of the dominant as an individual by the subordinate. It may also be due to the perception of subtle color and behavioral cues displayed by the dominant and received and acted upon by the subordinate. Since the existence of individual recognition among pinfish is unproven and alternative mechanisms can be hypothesized to explain the observed phenomena no conclusion regarding its reality can be made. It is apparent, however, that this problem is central to the basis of hierarchical organization and intensive investigation is needed.

In the laboratory a stable dominance relationship between two individuals was the result of repeated aggressive encounters over a period of several days. No evidence of social order was observed in nature, and all aggressive encounters seen ended with the loser fleeing the area. For the numerous encounters seemingly necessary for hierarchical organization to occur in nature, some powerful attractive stimulus would have to exist in the environment to cause the defeated fish to remain in contact with the victor. It is difficult to hypothesize a stimulus in

the environment of pinfish which would act as a basis for maintaining repeated contacts between two individuals. Thus, the existence of naturally occurring social hierarchies in pinfish seems questionable and one is led to conclude that the organization observed in the laboratory was an artifact of confinement.

CHAPTER V

SUMMARY

Pinfish were found to behave aggressively in the laboratory, and form straight-line, drive-right dominance hierarchies. The formation of a hierarchical group was initiated with only a few fish showing aggression. The number increased daily until all were involved. In the first few days a fish's rank in the hierarchy often changed rapidly and might vary up to three positions in a single day. As the hierarchy stabilized the total number of aggressive behaviors decreased. Territorial behavior was shown, although crowding limited the number of fish possessing a territory. In a stabilized hierarchy changes in rank were usually of a single position. Size was the principal factor in determining hierarchical rank.

Aggressive behavior in both the laboratory and nature consisted of color and behavioral displays. Four color patterns were seen in agonistic encounters: Ocellated in subordinate fish; Predorsal Bar in mildly aggressive fish; Jugular Darkening in moderately aggressive ones; and Subdorsal Darkening in those engaged in physical combat. These patterns were associated with behavioral displays. A Lateral Display and a Frontal Display constitute the primary aggressive behaviors and are associated with the Jugular Darkening pattern. Subdorsal Darkening was displayed only in combat.

Pinfish threatened by a dominant displayed in a manner suggestive of appeasement but whether this was an innate pattern or simply an environmentally induced behavior was not determined.

In the laboratory pinfish engaged in two behaviors, Digging and Shell Turning, that appear to be adaptations for feeding on benthic organisms. They were seen to bury themselves when frightened.

Two observations of these fish apparently removing ectoparasites from Mugil cephalus were made in nature.

Aggressive behavior and territoriality were observed in nature but both were relatively uncommon. The color displays and behaviors were the same as those seen in the laboratory. No instances of appeasement were seen outside the aquaria nor was any evidence of naturally occurring social hierarchy obtained.

It is possible that social hierarchy in pinfish does not occur in wild populations. A functional relationship based on differences in aggressive abilities may occur but this is not, sensu stricto, social hierarchy. The formation of hierarchical arrangements based on aggression implies the existence of some attractive force to maintain the necessary association. Experiments using small groups and then increasing the available space should yield considerable knowledge concerning the relationship between aggression and attraction.

LITERATURE CITED

- Allee, W. C., B. Greenburg, G. M. Rosenthal, and P. Frank. 1948. Some effects of social organization on growth in the green sunfish, Lepomis cyanellus. Jour. Exper. Zool. 108: 1-19.
- Allee, W. C., and J. C. Dickinson, Jr. 1954. Dominance and subordination in the smooth dogfish, Mustelus canis (Mitchell). Physiol. Zool. 27: 356-364.
- Baird, R. C. 1965. Aggressive behavior and social organization in Mollienesia latipinna Le Sueur. (Unpub. M. A. Thesis, Univ. of Texas).
- Braddock, J. C. 1945. Some aspects of the dominance-subordination relationship in the fish Platypoecilus maculatus. Physiol. Zool. 18: 176-195.
- _____. 1949. The effect of prior residence upon dominance in the fish Platypoecilus maculatus. Physiol. Zool. 22: 161-169.
- _____, and Z. I. Braddock. 1955. Aggressive behavior among females of the Siamese fighting fish, Betta splendens. Physiol. Zool. 28: 152-172.
- Breder, C. M., Jr. 1962. Interaction between the fishes Mugil and Lagodon. Copeia 3: 662-663.
- Burkenroad, M. D. 1931. Notes on the sound-producing fishes of Louisiana. Copeia 1: 20-28.
- Caldwell, D. K. 1957. The biology and systematics of the pinfish Lagodon rhomboides (Linnaeus). Bull. Florida State Mus. Biol. Sci. 2: 77-173.
- Caldwell, M. C. and D. K. Caldwell. 1962. Monarchistic dominance in small groups of captive male mosquitofish, Gambusia affinis patruelis. Bull. South. Calif. Acad. Sci. 61(1): 37-44.
- Forselius, S. 1957. Studies of anabantid fishes. Zool. Bidrag Fran Uppsala. 32: 53-597.
- Greenburg, B. 1947. Some relations between territory, social hierarchy, and leadership in the green sunfish, (Lepomis cyanellus). Physiol. Zool. 20: 267-299.

- Haas, A. 1956. Uber die soziale rangordnung kleinzahliger gruppen des malabarbarblings (Danio malabaricus Jerdon). Zeit. fur Tierpsychol. 13: 31-45.
- Magnuson, J. 1962. An analysis of growth, aggressive behavior, and food and space in Medaka. Canad. Jour. Zool. 40: 313-363.
- McAlister, W. H. 1958. The correlation of coloration with social rank in Gambusia hurtadoi. Ecology 39(3): 477-482.
- Miller, H. C. 1963. The behavior of the pumpkinseed sunfish, Lepomis gibbosus (Linnaeus), with notes on the behavior of other species of Lepomis and the pygmy sunfish, Elassoma evergladei. Behaviour 22(1): 88-151.
- Miller, R. J. 1964. Studies on the social behavior of the blue gourami, Trichogaster trichopterus (Pisces, Belontiidae). Copeia 3: 469-496.
- Newman, M. A. 1956. Social behavior and interspecific competition in two trout species. Physiol. Zool. 29: 64-81.
- Noble, G. K. and B. Curtis. 1939. The social behavior of the jewel fish, Hemichromis bimaculatus Gill. Bull. Amer. Mus. Natur. Hist. 76: 1-46.
- _____, and R. Borne. 1938. The social hierarchy in Xiphophorus and other fishes. Bull. Ecol. Soc. Amer. 19(2): 14.
- Okaichi, T., H. Kai, and Y. Hashimoto. 1958. A rapid color change in the filefish. Bull. Japanese Soc. Sci. Fish. 24(6.7): 389-393. From abstr. in Biol. Abstr. 33(4): 45434.
- Pfeiffer, W. 1965. Rank order of young northern squawfish. Copeia 3: 284-285.
- Shaw, E. 1962. The schooling of fishes. Sci. Amer. 206(6): 128-138.
- Stringer, G. E. and W. S. Hoar. 1955. Aggressive behavior of under-yearling Kamloops trout. Can. Jour. Zool. 33: 148-160.

VITA

Wayne Franklin Hadley

Candidate for the Degree of

Master of Science

Thesis: AGGRESSIVE BEHAVIOR AND SOCIAL HIERARCHY IN THE PINFISH, LAGODON RHOMBOIDES (LINNAEUS).

Major Field: Zoology

Biographical:

Personal Data: Born in Arkansas City, Kansas, August 5, 1940, son of Golden C. and Louise A. Hadley

Education: Graduated from Ponca City High School, Ponca City, Oklahoma, in 1958; received Bachelor of Science degree in Zoology from Oklahoma State University in 1962; completed requirements for Master of Science degree in May, 1967, at Oklahoma State University.

Professional Experience: National Science Foundation Summer Institute, Institute of Marine Science, University of Texas, 1962; Research Assistant, Institute of Marine Science, University of Texas, 1963; graduate teaching assistant, Oklahoma State University, 1965 to 1967; Public Health Service research trainee in aquatic biology, Oklahoma State University, 1965-1967.

Professional Organizations: Member of the American Society of Mammalogists, Wildlife Society, Southwestern Association of Naturalists, American Society of Ichthyologists and Herpetologists, Oklahoma Academy of Science, Phi Sigma Society. Associate member of the Society of Sigma Xi.