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The ontogeny of social behavior in a Hawaiian damselfish, *Abudefduf abdominalis*

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University of Hawaii, 1990
THE ONTOGENY OF SOCIAL BEHAVIOR IN A HAWAIIAN DAMSELFISH,
*Abudefduf abdominalis*

A DISSERTATION SUBMITTED TO THE GRADUATE DIVISION OF THE UNIVERSITY OF HAWAII IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE OF

DOCTOR OF PHILOSOPHY

IN

ZOOLOGY

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By

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"If you have build castles in the air, your work need not be lost; that is where they should be. Now put the foundations under them."

Henry David Thoreau

This work is dedicated to all those who have allowed me, and even helped me, to build castles in the air; especially to my parents, Jori and Frank and to my companion for life, Fenny. Mahalo.
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Finally, a special debt of gratitude to Evelyn (Fenny) Cox who proofread this tome, contributed to the graphics, expressed her opinion on all aspects of this work (to my benefit), provided distractions, spurred me on, and lifted my spirits always; ko'u aloha.
ABSTRACT

The ontogeny of social behavior of juvenile *Abudefduf abdominalis* was studied by comparing development at the age of settlement to shallow water habitats, and at one, two, and three months post-settlement. Food resources were manipulated to test the hypothesis that the presence of a defendable food resource would result in earlier expression of aggression and alter the way Modal Action Patterns (MAPs) were used socially.

Field studies indicated that the distribution of juveniles in shallow water did not overlap with adult fish. The diet of the juveniles from two habitats differed. Fish from the tidepool habitat fed on plankton, and potentially defendable algae, while fish from buoys fed mostly on plankton, assumed not to be defendable.

Frequency and duration of MAPs, after dominance was established, were recorded during paired encounters between similar sized fish from each habitat or reared in the laboratory with different diets. Most MAPs were expressed at the time of settlement. Food preferences were altered based on experience. The dominant fish fed more on the previously experienced food resource and displaced the subordinant fish from the preferred food type.

Modal Action Patterns were categorized into four functional groups: feeding, attack, threat, and self-defense based on preceding-following MAP transitions within individual fish. Dominant and subordinant roles were recognized by differences in MAP frequencies and placement of MAPs within functional groups. Attack MAPs became more consistently associated with food resources in the dominant fish.
Erect-fins developed into a threat display used by the dominant fish, instead of chase, to displace the subordinant fish. Information transmitted between the fish increased as they aged with more information being exchanged from the dominant fish to the subordinant fish. Rules governing the switching from one group of MAPs to another were proposed based on significant transitions between specific MAPs. One rule may account for the development of resource defense. The dominant fish followed feeding on the experienced diet with attack. Thus, feeding on a good food resource, but of unknown defendability, was linked to attack as a test of the potential for defense.
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Chapter I

GENERAL INTRODUCTION

THE STUDY OF BEHAVIORAL ONTOGENY

The ontogeny of an individual, from a zygote to adult, involves five mechanisms: the formation of units, the maintenance of units, the differentiation of units depending on functions, the organization of units into larger or more complex entities, and the selective loss of units (Cowan 1979). The mechanisms are the same whether the units are cells or behavioral acts. The genes and the environment both provide the influences that are involved in defining the final product, but it is the process of development, ontogeny, that creates the unique individual.

Historically genes and environment have been presented as opposing forces controlling ontogeny even though this dichotomy has been refuted repeatedly (e.g., Hinde 1970, Lehrman 1970). Most often the process of development has been attributed to the genetic component, describing it as biological and innate rather than psychological and acquired (Oyama 1982). Ontogeny is now considered to be the interaction of genes and the environment that results in the development of the individual (Immelmann et al. 1981).

Some attempts to resolve the issue have created even more confusion. Lorenz (1965) redefined innate to equal phylogenetically adapted characters that included learned components of imprinting (italics my emphasis). West and King (1987) used the term "ontogenetic niche" as the "set of ecological and social circumstances
inherited by organisms" (italics my emphasis). Bateson (1976) added two new categories besides innate and acquired; one that involves both previous categories, but for specific outcomes, and the other for outcomes that affect a large number of behavior patterns in some general way. Bateson's determinants of behavior all combine elements of genes or environment and some aspect of ontogeny into discreet units that then interact with each other. Again the process of development has been included within the constructs of the variables themselves and not kept separated.

There must be some constraint to produce individuals that will recognize each other for reproductive purposes, given the wide range of environmental factors encountered by individuals. This constraint has been wrongly attributed solely to the similar genetic makeup of the individuals collectively referred to as a species. The environment can also be very restrictive. The individual may reside within a relatively homogeneous location, such as within the uterus, or may be incapable of detecting, and hence responding, to environmental cues due to a lack of sensory input. Conversely, the genetic code is no longer considered a perfect template but subject to variations in the number of replicate segments coding for particular proteins and the amount of neutral genetic material that seems to remain untranscribed (Dobzhansky 1970). It is better to treat ontogeny as reacting on a species-typical genome and a species-typical environment (Oyama 1982).

The species-typical environment includes all extrinsic and intrinsic cues perceived directly or indirectly by the organism. If
this perceived information has an effect on the organism, either immediate or delayed, then it is considered an experience of the individual. This definition of experience closely follows Schneirla (1966), and, though broad and inclusive, it functions well and allows for the development of new methodologies in measuring experience, such as single neuron recordings.

HIERARCHICAL ORGANIZATION OF BEHAVIOR DURING ONTOGENY

There are changes during ontogeny in the organization of behavior. Neurons become integrated into systems under the control of "command neurons", stimulation of which results in a sequence of neuron activity that can be observed as behavior (Willows and Hoyle 1969). This integration can also occur in afferent neural pathways involving perception (Hubel and Wiesel 1962 and 1963). Such a simple system can be understood in terms of "hard wiring", but superimposing several more levels of command structure renders this approach impossible to track. This is because there are so many ways in which the command structure could be "wired" and still create the same observed output. It therefore becomes easier to think in terms of "software" that states the decision or command sequence that results in expressed behavior (Dawkins 1976).

The development of this hierarchical organization is first seen at the neuronal level. The earliest behaviors tend to be spontaneous activity in components of sensory-motor arcs (Gideiri 1966) that with time and further neurological development become more organized (Bekoff 1981). The central nervous system seems to be the origin of
coordinated motor activity (Dawkins 1983) and other higher orders of the decision hierarchy. Behavior patterns are sometimes first seen in non-social contexts (Tooker and Miller 1980). Over time these behavior patterns change little in form but can change in intensity (Bergmann 1971), frequency (Groothuis 1989a), context (Ward and Barlow 1967), or combine to form displays (Wyman and Ward 1973, Groothuis 1989b).

The context in which particular motor actions are used give some indication of how the hierarchy develops. Behavior systems are composed of sub-systems that need not be exclusive to one system (Hinde 1970, Baerends 1984). Preexisting motor patterns can be expressed in new contexts (Ward and Barlow 1967, and Tooker and Miller 1980). Isolated systems can integrate to form larger or higher order systems (Kruijt 1964, Hailman 1967), or motor patterns can become more restrictive in which contexts they are expressed (Chalmers 1980). The higher order levels can be classified on functional or causal terms depending on how well the systems are understood.

The ontogeny of aggression is particularly difficult to classify within the hierarchy. Aggression appears early in some fishes (Cole and Noakes 1980) but also is functional only when situations arise where it is advantageous, as in territorial defense (Fernald and Hirata 1979) or at sexual maturity (Davis and Kassel 1975). Bakker (1985) noted heterogeneous causation of aggression in sticklebacks describing juvenile, courtship, and dominance types of aggression. All three types of aggression in Bakker's study responded to artificial selection. Some displays used in non-aggressive contexts
share origins with aggression and fear (Baerends 1984, Groothuis 1989b) and become distinct during development with the integration of other causal systems.

SOCIAL EXPERIENCE DURING ONTOGENY

The effect of intraspecific social contact has been studied in fishes. Deprivation experiments, even though limited in their usefulness, have shown that social contact and aspects of the physical environment have an impact on social ontogeny (Shaw 1962, Pinckney and Anderson 1967). Low densities of fish show an increase in aggression, especially if aggression is used for territorial defense (Fernald and Hirata 1979). High densities of fish usually show a decrease in aggression (Coss and Burgess 1981, Newton 1982), although Fenderson, Everhart, and Muth (1968) found an increase in aggression in crowded hatchery salmon as opposed to wild salmon. Other forms of stress, such as handling, isolation, and cold temperatures, also reduce aggression in poeciliids (Newton 1982). Both crowding and isolation resulted in a decrease in dendritic development that appeared to be permanent (Burgess and Coss 1982).

Social experience is a factor determining dominance status. Fish with previous dominance success tend to win when matched with similar sized opponents (Frey and Miller 1972, Francis 1983, Bakker and Sevenster 1983, Abbott, Dunbrack, and Orr 1985, and Franck and Ribowski 1987). These studies have also shown that length differences of as little as 2-5% can override the advantage of prior success. The effect of such contests wanes after a week in most fishes.
ECOLOGICAL INFLUENCES DURING ONTOGENY

The effect of ecological factors on the ontogeny of behavior has not been as well studied. Stamps (1978) found that juvenile Anolis aeneus lizards showed all displays of adults and that the expression of displays was correlated to the ability to defend perch or shelter sites. A comparison of four centrarchid fishes revealed that agonistic behaviors appeared after a shift in habitat (Brown and Colgan 1985). The question arises whether a new environment releases the onset of the behavior or is the appearance of a new behavior a function of greater opportunity to express this behavior in the new environment? Hoelzer (1987) manipulated shelters as a contested resource and found that, while agonistic behaviors were present in the repertoire at an early age, they were not used unless a defendable resource, shelter in this case, was present. Hoelzer made no attempt to study the impact of defendable resources on the organization of the behavior.

FISH AS SUBJECTS FOR STUDYING BEHAVIOR ONTOGENY

Fish can be good subjects for ontogeny studies. They exist in a variety of sizes and longevity, and display a wide range of natural history traits that provide excellent models for behavior studies (Noakes 1986). The behavioral repertoire is not unmanageably large, and they often have distinctive displays (Huntingford 1986). Many species produce numerous offspring, allowing for some control over genetic variability. Parental care can occur and ranges from immediate abandonment to well into the juvenile stage. The study of
the earliest stages of vertebrate behavior ontogeny is difficult in groups with hard, opaque shelled eggs or prolonged internal maturation, such as in mammals. Many species of fish, however, hatch as relatively undeveloped free swimming larvae which allows direct observation of earlier stages of behavior ontogeny (Noakes and Godin 1988). Also, important ontogenetic events such as sex change can occur during adulthood (Warner 1984) facilitating the study of behavior changes during these events.

There are disadvantages as well. Most critical is the difficulty of rearing the earliest stages. Successful rearing of early larval stages has been accomplished for only a small percent of the thousands of known species. There is also only limited comparative data available for fish behavior.

*Abudefduf abdominalis*, the Hawaiian Sergeant or maomao, is a common near-shore and reef fish in Hawaii. This species attains a maximum length of 230 mm S.L. and is gonochoristic. The early life history of this species was well documented by Helfrich (1958). The eggs hatch after about 5-6 days incubation, during which time the male defends the nest. The larvae are planktonic for a period of 18-28 days (Radtke 1985), and then settle in shallow water, often close to seawalls, reef crests, under floating structures or within tidepools. Initial social contact probably occurs after settlement. Observation of larvae reared in captivity show no social interactions between fish prior to settlement (Helfrich 1958, personal observation). Similar sized juveniles aggregate together and eventually integrate into the adult populations in deeper water. The adults are considered
omnivores (Helfrich 1958, Hobson 1974), and feed during the day in large aggregations above reefs or near shore. The only obvious territorial behavior involves nest and egg defense by the males (Helfrich 1958, Walters 1967).

PRIMARY RESEARCH GOALS

My study describes the effect of altering the defendability of food resources on the ontogeny of behavior. The hypothesis is that the presence of a defendable food resource should lead to the earlier expression of aggressive acts related to that defense. The earlier expression of particular acts should then alter the sequence of acts and influence the formation of the higher levels of behavior organization.

Chapter II deals with the diet and natural history of A. abdominalis in two different habitats. Specifically: are there differences in diet between two naturally occurring populations, and are there changes in diet with increasing size of the fish? This chapter also validates, within the size range of fish in this study, the use of fish length as an estimate of fish age.

The descriptive analysis of behavior acts and the differences in frequency and duration are presented in Chapter III. Three factors are considered: age, diet, and social rank. Age of the fish indicates different stages in development. Diet treatments compare fish reared with either a defendable food resource or a non-defendable food resource. Social rank represents differences in the use of behavior acts due to the dominance relationships between fish.
Chapter IV describes differences in the organization of behavior with respect to age, diet, and social rank in terms of sequences of Modal Action patterns (MAPs) within individual fish, and between fish that are paired together. Communication between dominant and subordinant fish will also be compared between the groups of fish.

All aspects of this study combined will help to elucidate how individuals modify their behavior responding to differences in environmental experience and the level of behavioral organization at which these effects occurs.
Chapter II

DISTRIBUTION AND DIET OF Abudefduf abdominalis IN TWO HABITATS

INTRODUCTION

The post-settlement juvenile stage of many reef fishes, including Abudefduf abdominalis, inhabit environments different from those of the adults. This difference may relate to the smaller fish being unable to procure suitable shelter, the smaller size of food items necessary for smaller fish, or survival of juveniles given the physical forces (i.e., water motion) in the adult habitat. It is important to include natural history aspects of this life stage in considering the development of social behavior or understanding adult behavior. If fish are segregated by size, social interactions would occur between individuals of similar size and age and thus preclude the use of adults as "role models" for juveniles.

Post-settlement juvenile A. abdominalis occur in tidepools, on reefs, and under floating objects (Helfrich 1958). It is unknown if these habitats are further subdivided by different size classes of young fish, and to what extent the distribution of juveniles overlaps that of adults.

Limited knowledge exists on the diet of the juveniles. Helfrich (1958) examined 103 fish and found a wide range of food items. His analysis grouped some juvenile size classes with adults and made interpretation of the juvenile diet difficult. Newly settled A. abdominalis may not be able to consume the same food types as the adults due to morphological or physiological constraints.
Age determination is important in estimating the amount of experience a fish has. Fish length can be used if growth is linear over the range of fish sizes collected. This can be validated by analyzing the relationship of fish length with an accurate measure of age. Otoliths have been used to determine the age of fish (see Campana and Neilson, 1985 for review). The otolith increments in *A. abdominalis* are deposited daily (Radtke, 1987) and settlement marks can be detected (Radtke, 1985). Radtke (1985) further noted a linear relationship between the number of daily otolith increments, the length of the sagitta and the total length of *A. abdominalis* in individuals up to 37 mm TL.

This portion of my study has three goals: to determine the abundance and distribution of *A. abdominalis* in juvenile habitats in time and space; to identify any shift in diet during development; and to further document the relationship between fish length, sagitta length, and daily otolith increments.

**MATERIALS AND METHODS**

**Abundance**

The abundance of *Abudedefduf abdominalis* was determined by visual counts along a series of transects extending from the highest water mark to offshore at two sites on Oahu, Hawaii. Each transect consisted of a 10 m wide strip perpendicular to the shoreline that was subdivided into 5 x 10 m quadrats. There were four adjacent transects at each site.
The Sandy Beach transect area (Fig. 1) consisted of a broad basaltic intertidal shelf with pools and a subtidal area extending 50 m off shore to a depth of 6 m. The area was within the Sandy Beach State Park. The tidepools supported a wide range of filamentous and fleshy algae and associated invertebrates. The intertidal zone ended at a 3 m drop off into the subtidal zone. At low tide, sea level was about 1 m below the top of the drop off. The subtidal substrate was flat basalt with sand intrusions and an occasional basalt outcropping. Coral cover was less than five percent. The intertidal and subtidal areas were tabulated separately. The tidepools were visually censused at low tide, and fish counts were expressed as numbers of fish per 100 m² of water surface. Tidepools represented 767 m² of submerged surface area or about 43% of the total tidepool transect area. The subtidal area surveyed was 1800 m².

The Kaneohe Bay site (Fig. 2) was at the Southeast corner of Moku o Loe within the Marine Refuge. Transects began at the sea wall and extended across the reef flat and down the reef slope to a depth of 6 m for a total area of 1600 m². The depth of water on the reef flat was less than 1 m. Porites compressa was the most abundant coral. Pocillopora damicornis and Montipora verrucosa were also common. Filamentous algae were present on the coral rubble and on the sea wall.

The number and size of A. abdominalis in each 5 x 10 m quadrat were visually censused at low tide. Seven size classes were established based on the standard length of the fish: less than 19.9 mm, 20-39.9 mm, 40-59.9 mm, 60-79.9 mm, 80-99.9 mm, and 100 mm and...
Figure 1. Map of the Sandy Beach transect area.
Figure 2. Map of Moku o Loe (Coconut Island) transect area.
greater. Fish 100 mm and greater in length were considered adults.

The accuracy of estimating the size classes was tested by first estimating the number and sizes of A. abdominalis in a tidepool outside of the transect area and then collecting all the fish from that tidepool. The error was calculated as the percent of fish misplaced into another size class when visually censused. Less than 4% of the A. abdominalis were visibly grouped into the wrong size class. There were no significant differences in the number of fish per class between the visual estimates and the actual measurements ($X^2 = 0.03, df = 2, N = 79$). All fish from in this analysis were subsequently used for gut content analysis.

**Diet**

The diet of A. abdominalis was determined by gut content analysis. A total of 148 fish were collected from January 1986 to January 1987. Collections were made at monthly intervals from tidepools at Sandy Beach in areas away from but similar to the transect area. The fish were killed by gradual hypothermia, chilling the sea water to just above freezing. This technique worked best to retain the food items in the gut. Collections were then kept frozen until dissection. The total and standard lengths of the fish were measured with dial calipers before the guts were removed. The otoliths were retained. The entire gut was excised from the esophagus to the anus. Fish were classified by standard length (S.L.) into five groups which corresponded to those used later in the behavior study.
but which differed from the size classes used in estimating the
distribution and abundance of fish.

The gut contents of 24 fish used in the behavior study were
analyzed to determine the diet of these fish collected from buoys in
south Kaneohe Bay. These fish were allowed to feed on *Artemia* sp. and
the prepared benthic food as part of the experiment so these food
items were excluded from the diet analysis. The time from capture to
inspection of the guts was 2-3 hours. These fish were treated
separately because of the time delay and the supplemental feeding in
the experiment.

Food items were classified in broad taxonomic groups. Results
were expressed as counts of items and percent of wet volume,
calculated by water displacement. Algae and unidentified digested
material were not itemized. The relationship between size classes and
food items was analyzed by Spearman rank correlation coefficient
(Siegel 1956).

Aging

Ages of fish were determined from a regression equation relating
otolith daily increments, length of the sagitta, and total length.
Otoliths were removed from fresh or frozen specimens, cleaned and
dried before being measured. The sagittae were measured to the
nearest 0.01 mm on their longest axis using an ocular micrometer at
500 X magnification. Twelve selected samples were mounted
individually on scanning electron microscope stubs with epoxy and
ground on the medial surface to the level of the nucleus. The surface
was then polished with 0.3 micrometer alumina solution and coated with gold. Increments on the sagitta were viewed on a Cambridge Stereoscan 150 scanning electron microscope and a permanent record made on video tape or Polaroid type 55 film. Increments were counted radiating out from the recruitment mark (Radtke 1985) in three directions and then averaged. The regression equation was based on the 12 otoliths from this study and 21 from Radtke (1985). The statistics were calculated using the SYSTAT statistical package.

RESULTS

Abundance

_Abudefduf abdominalis_ of all size classes were present throughout most of 1986 at Sandy Beach (Fig. 3 & 4). Fish > 100 mm S.L. occurred in the tidepools only during the second half of the year, and then only in low numbers. Offshore, only the adult class was present for the entire year. The 40-79.9 mm S.L. classes occurred subtidally only during the summer. The 80-99.9 mm S.L. size class was present offshore only during the second half of the year.

*A. abdominalis* were also present at Moku o Loe throughout the year with rare exceptions (Fig. 5). The largest size class was the most consistent over the year and had the highest abundance of all size classes.

The distribution of *A. abdominalis* at Sandy Beach (Fig. 6) indicated that juveniles less than 40 mm S.L. were found only in the tidepools. The smallest fish occurred higher up the tidepools but overlapped with other size classes. Larger fish were typically found
Figure 3. Abundance of *Abudefduf abdominalis* in tidepools at Sandy Beach from December 1985 to January 1987. Histograms represent all four transects combined. Total submerged area surveyed was 767.36 m².
Figure 4. Abundance of *Abudefduf abdominalis* in the subtidal transect area of Sandy Beach from January 1986 to January 1987. Histograms represent all four transects combined. Total area surveyed was 1800 m².
Figure 5. Abundance of *Abudefduf abdominalis* at the Moku o Loe transect area from January 1986 to January 1987. Histograms represent all four transects combined. Total area surveyed was 1600 m$^2$. 
Figure 6. Distribution of *Abudefduf abdominalis* across the tidepool and offshore transects at Sandy Beach. Each histogram represents all fish in a size class from the four transects combined. Zero meters marks the sea edge at mean lower low water.
in larger and deeper tidepools nearer the sea edge. Fish in the largest size class occurred most frequently at the sea edge on either side of the 3 m drop off and in an area 20-25 m offshore.

At Moku o Loe (Fig. 7) the two smallest size classes remained very close to the sea wall and there was a subsequent shift, as the fish grew, from the sea wall to the reef slope. A large permanent adult population existed on the reef slope in the study area. Spawning occurred in demersal nests at the reef edge and slope during the warmer months of the year.

Diet

The diet of juvenile *A. abdominalis* from Sandy Beach tidepools consisted mostly of algae and copepods (Table 1). Larger size classes of fish fed more on algae and less on copepods ($r_s = 1.0$ and $-1.0$ respectively, $p = 0.01$). Frequencies of ingested large benthic invertebrates (amphipods, isopods, and gastropods) were positively correlated with fish size classes ($r_s = 0.70$, $0.98$, & $0.94$ respectively, all $p < 0.05$). Gastropod veligers and ostracods, both small, were inversely correlated to fish size class ($r_s = -0.94$, $p < 0.05$ for both). Terrestrial insects, springtails (Collembola) and winged termites (Isoptera), were also eaten frequently. Algal genera identified included: *Centroceras, Ceramium, Cladophora, Enteromorpha,* and *Polysiphonia*. Miscellaneous food items included: foraminifera, megalops, polychaetes, radiolarians, sponges, and tunicates.

The gut contents of the *A. abdominalis* collected from under buoys in Kaneohe Bay differed from the samples from Sandy Beach (Table 2).
Figure 7. Distribution of *Abudefduf abdominalis* across the reef at Moku o Loe. Each histogram represents all fish in a size class from the four transects combined. Zero meters is at the seawall. The reef crest was at about the 32 m mark.
Table 1. Gut contents of *Abudefduf abdominalis* from Sandy Beach expressed as the average percent wet volume and average number of food items per fish within each size class.

Size Class (mm S.L.)

<table>
<thead>
<tr>
<th>Food</th>
<th>Groups N=</th>
<th>41</th>
<th>36</th>
<th>36</th>
<th>27</th>
<th>8</th>
<th>N = 148</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algae</td>
<td>%</td>
<td>9</td>
<td>18</td>
<td>28</td>
<td>43</td>
<td>64</td>
<td>32.4%</td>
</tr>
<tr>
<td>Copepods</td>
<td>%</td>
<td>65</td>
<td>41</td>
<td>28</td>
<td>19</td>
<td>5</td>
<td>31.6</td>
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<td>#</td>
<td>57</td>
<td>72</td>
<td>68</td>
<td>42</td>
<td>15</td>
<td></td>
</tr>
<tr>
<td>Amphipods</td>
<td>%</td>
<td>3</td>
<td>6</td>
<td>10</td>
<td>14</td>
<td>7</td>
<td>8</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>6</td>
<td>6</td>
<td></td>
</tr>
<tr>
<td>Isopods</td>
<td>%</td>
<td>1</td>
<td>1</td>
<td>2</td>
<td>5</td>
<td>5</td>
<td>2.8</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>1</td>
<td>2</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Gastropods</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adults</td>
<td>%</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>1</td>
<td>1</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td></td>
</tr>
<tr>
<td>Veligers</td>
<td>%</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0.6</td>
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<td>#</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Ostracods</td>
<td>%</td>
<td>1</td>
<td>1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0.4</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>&lt;1</td>
<td>&lt;1</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Insects</td>
<td>%</td>
<td>2</td>
<td>12</td>
<td>17</td>
<td>15</td>
<td>8</td>
<td>10.8</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>&lt;1</td>
<td>3</td>
<td>8</td>
<td>8</td>
<td>5</td>
<td></td>
</tr>
<tr>
<td>Misc.</td>
<td>%</td>
<td>5</td>
<td>5</td>
<td>8</td>
<td>0</td>
<td>0</td>
<td>3.6</td>
</tr>
<tr>
<td>Unidentified Material</td>
<td>%</td>
<td>13</td>
<td>15</td>
<td>7</td>
<td>3</td>
<td>11</td>
<td>9.8</td>
</tr>
</tbody>
</table>
Table 2. Gut contents of *Abudefduf abdominalis* collected from under buoys in Kaneohe Bay. Diet expressed as the average percent wet volume and average number of food items per fish within each size class after exclusion of *Artemia sp.* and fish fudge.

Size Class (mm S.L.)

<table>
<thead>
<tr>
<th>Food Groups</th>
<th>N=</th>
<th>15-21.9</th>
<th>22-29.9</th>
<th>30-39.9</th>
<th>ALL CLASSES</th>
</tr>
</thead>
<tbody>
<tr>
<td>Algae</td>
<td>%</td>
<td>2</td>
<td>7.5</td>
<td>0</td>
<td>3.1%</td>
</tr>
<tr>
<td>Copepods</td>
<td>%</td>
<td>33.4</td>
<td>61</td>
<td>52</td>
<td>48.8</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>15.5</td>
<td>50.8</td>
<td>17.9</td>
<td></td>
</tr>
<tr>
<td>Amphipods</td>
<td>%</td>
<td>3.5</td>
<td>7</td>
<td>4</td>
<td>4.8</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>0.5</td>
<td>0.25</td>
<td>0.75</td>
<td></td>
</tr>
<tr>
<td>Isopods</td>
<td>%</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Gastropods</td>
<td>%</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Adults</td>
<td>#</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Veligers</td>
<td>%</td>
<td>1.5</td>
<td>0</td>
<td>0</td>
<td>0.5</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>0.1</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Ostracods</td>
<td>%</td>
<td>2.5</td>
<td>7.5</td>
<td>7</td>
<td>5.7</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>0.25</td>
<td>0.62</td>
<td>2</td>
<td></td>
</tr>
<tr>
<td>Insects</td>
<td>%</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>#</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td></td>
</tr>
<tr>
<td>Misc.</td>
<td>%</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Unidentified Material</td>
<td>%</td>
<td>57</td>
<td>17</td>
<td>37</td>
<td>37</td>
</tr>
</tbody>
</table>

32
Copepods dominated the diet of these fish. There was substantially less algae, about half the amphipods, and no isopods, gastropod adults or insects found in the guts from Kaneohe Bay. The ostracods were more abundant in the Kaneohe Bay samples but were still less than 10% of the volume.

**Aging**

The relationship between sagitta length and otolith increments was nearly linear within the size range of fish used in this study (Fig. 8, \( r^2 = .953, n = 33, p < .0001 \)). The total length of the fish and otolith increments were related, as well, in a linear fashion (Fig. 9, \( r^2 = .964, n = 33, p < .0001 \)). Total length and sagitta length were closely related to each other (\( r^2 = .970, n = 33, p < .0001 \)) (Fig. 10) and either was a good predictor of age within this size range.

**DISCUSSION**

**Abundance**

Juvenile *Abudefduf abdominalis* occurred most often in shallow water either in tidepools or in sheltered water near seawalls, piers, or floating structures. Adults were found in deeper water on the slope of the reef or off of rocky shorelines. This is consistent with the observations of Helfrich (1958). There was a tendency to find the smallest fish in very sheltered water which occurred higher in the intertidal zone or close to the sea wall. The intermediate size classes of fish ranged over much of the surveyed areas, possibly in response to varying water motion associated with wave action.
Figure 8. Plot of the relationship between sagitta length and post-settlement sagittal increments, includes data from Radtke (1985).
$Y = 54(X) - 39.4$

$r^2 = .953 \quad p < 0.0001$

$N = 33$
Figure 9. Plot of the relationship between total fish length and post-settlement sagittal increments, includes data from Radtke (1985).
$Y = 1.96(X) - 23.4$

$r^2 = 0.964 \quad p < 0.0001$

$N = 33$
Figure 10. Plot of the relationship between total fish length and sagitta length, includes data from Radtke (1985).
\[ Y = 27.39(X) - 7.8 \]
\[ r^2 = 0.970 \quad p < 0.0001 \]
\[ N = 33 \]

TOTAL LENGTH (mm)

SAGITTAL LENGTH (mm)
Helfrich (1958) notes that small sized *A. abdominalis* avoid strong surge and seek shelter in crevasses.

The surgeonfish, *Acanthurus triostegus sandvicensis*, shows a similar pattern. Randall (1961) noted that this species moved seaward from tidepools as they grew and Sale (1969a) found small juveniles (< 45 mm fork length) in shallow tidepools with larger juveniles in deeper tidepools. Sale (1969b) found that there was a relationship between fish size and distance from the shoreline in two of five transects but in these two cases distance from the shoreline also correlated with depth. Sale concluded that, for *A. triostegus sandvicensis*, the presence of cover and suitable water depth were major stimuli in the selection of habitat. Distance from the sea had slight, if any, effect on habitat selection. *Abudefduf abdominalis* may or may not respond to the same stimuli as surgeonfish, but the pattern of distribution is similar.

Fish at Moku o Loe showed a gradual transition from the settlement habitat near the seawall to the adult habitat on the reef crest and slope. The Sandy Beach site had a discontinuity in the topography that prevented easy movement from the intertidal to the subtidal zone. This discontinuity and the irregularity of tidepool depth and configuration probably obscured a pattern of gradual movement offshore with growth.

At both sites there was almost no overlap in the distributions of adults and the smallest size class. Those few adults recorded from the seawall occurred in an area where part of the seawall had collapsed and formed a shelter. Fish under 20 mm S.L. remained near
the surface adjacent to the seawall and were never seen in the vicinity of the shelters.

Diet

Helfrich (1958) analyzed the diet of *A. abdominalis* and found that they fed on a wide variety of food items. This study found that small fish fed more on copepods and less on coarse algae than large juvenile fish. The diet of juvenile *A. abdominalis*, however, indicated that even the smallest size class of fish consumed benthic algae. Helfrich (1958) noted that the morphology of the juvenile’s mouth was a miniature version of the adults except for the teeth. In fish under 70 mm S.L. the teeth were villiform in shape in contrast to the truncated shape in the adults. Villiform teeth would be less effective for feeding on algae.

A second morphological constraint explaining the diet difference may be mouth size. The ingested copepods, ostracods, and gastropod veligers were all small bodied forms that could be eaten easily by smaller fish. The amphipods, isopods, and post-settlement gastropods were larger, harder bodied, and possibly less suited to ingestion by smaller size classes of fish. The insects consumed were also relatively large and were relatively uncommon in the guts of individuals in the smallest size class of fish.

The smallest fish may have been restricted to planktonic food items due to attacks by *Bathygobius fuscus*, one of the more common fish found in tidepools. Helfrich (1958) stated that *B. fuscus* would attack small *A. abdominalis* in tidepools. Juveniles, in this study,
were seen near the bottom after they reached 25-30 mm S.L. At that size they would probably be safe from *B. fuscus* attacks.

The different diet of *A. abdominalis* from the Kaneohe Bay buoys most likely reflected differences in the availability of food groups. Randall (1967) noted that the diet of the congener, *A. saxatilis*, was variable and related to what food items were locally available. Hobson (1974) sampled 10 adult *A. abdominalis* from a midwater feeding aggregation in Kona and found mostly planktonic food items. The buoys in Kaneohe Bay were covered with a community of bryozoans and poriferans with very little algae, but these items were not found in any guts examined. Juvenile *A. abdominalis* found under buoys appear to feed heavily on planktonic copepods and a few benthic amphipods and ostracods. Some soft bodied forms may have been digested in the 2-3 hours that passed between the time of capture and when the guts were examined. The higher percentage of unidentified material in the Kaneohe Bay versus the Sandy Beach samples may reflect this difference in treatment of the samples. *Oikopleura longicauda*, a soft bodied larvacean, is common in Kaneohe Bay plankton and found in the guts of adult *A. abdominalis* (Tyler, personal communication) but was not identified from the juvenile fish guts analyzed in this study.

**Aging**

A nearly linear relationship between the total length of the fish and age was found for the fish sizes used in this study. There was no advantage in using the sagitta length as a predictor of age. Both the sagitta length and total length appeared to be equally suited to
predicting age within this period of relatively constant growth. Similar results are noted for *Stolephorus purpureus* (Struhsaker and Uchiyama, 1976). They did find a distinct inflection point at 15-17 mm S.L. but the relationship of fish length and age was linear on either side of the inflection point. Fowler (1989) noted that *Chaetodon rainfordi* and *C. plebius*, up to 300-400 days old, had a curvilinear relationship between standard length and otolith length but *C. plebius* had a linear relationship between standard length and age. Such an uncoupling of otolith growth and fish growth has been noticed by Campana and Neilson (1985), but usually after fish growth stops, or during sub-optimal conditions.

*Abudefduf abdominalis* reared in captivity show a diminishing growth rate with age (Helfrich 1958). Three broods reared showed maximum growth rates that were similar to those of this study. Similar sized fish grown for periods of 29 to 57 days showed a linear relationship. Helfrich (1958) attributed some of the decrease in growth of these broods to the lower water temperature later in the year and the possible social interaction when broods were combined into one tank.

**CONCLUSIONS**

1. Juvenile *Abudefduf abdominalis* occurred in shallow water in habitats not overlapping with the adults. There was a gradual shift to deeper water with an increase in size except in cases where shoreline topography created a discontinuity in the form of a tidal bench drop off.
2. The diet shifted from predominately small planktonic food items to larger benthic invertebrates and algae with age. Even the smallest size class consumed some algae.

3. Diet differences between habitats reflected the availability of food items. Fish from tidepools consumed plankton and algae while fish from under buoys in Kaneohe Bay fed mostly on plankton since there was little algal growth on the buoys.

4. There was a linear relationship between total length and the number of daily increments on the sagitta and a near linear relationship between the sagitta length and the otolith increments. The linear relationship is likely due to the constant growth rates during the juvenile stage and the relationship may become non-linear at maturity.
Chapter III
ONTOGENY OF BEHAVIOR IN Abudefduf abdominis

INTRODUCTION

Fishes develop species specific behaviors at an early age. In most cases, reef fishes, including damselfishes (Pomacentridae), lack any parental care after hatching (Thresher 1984). The newly hatched larvae undergo a pelagic lifestage before appearing on reefs as juveniles. The habitat into which a fish settles can be quite variable and thus the organism must be capable of responding to a wide range of environmental cues. Differences in experience, due to a variable habitat, can influence the developmental pathway of behavior leading to the synthesis of a unique individual (Kruijt 1964, Hailman 1967, Wyman and Ward 1973). If a juvenile is to survive, it must adapt to local conditions and gain the skills to best exploit resources and opportunities as they occur (Mason 1979, Oppenheim 1981). A lack of plasticity can restrict habitat use (Ferguson, Noakes, and Romani 1983).

Agonistic behaviors are often influenced by environmental factors. The form of agonism depends on the defendable nature of the resource (Magnuson 1962). Aggression develops when needed (Hoelzer 1987) or is delayed to aid in social cohesion (Brown 1985), and aggression is expressed earlier in territorial species than in non-territorial species (Gorton and Gerhardt 1979). In most cases, the winner of agonistic encounters acquires the contested resource, and this leads to a better chance of survival (Stamps 1978, Fox, Rose, and Myers 1981). This assumes there is an advantage to fighting over a resource. Ecological theory states that if a limited resource is predictable in time and space then it may be energetically advantageous to defend the resource (Brown 1964, Davies 1978, Davies and Houston 1984). Individuals with access to defendable resources would have the opportunity to use agonistic behavior while others that lacked defendable resources would not. This may lead to differences in the development of social behavior.

This study was undertaken to test the hypothesis that the availability of a defendable food resource would accelerate the development of agonistic behaviors in *Abudefduf abdominalis*, the Hawaiian sergeant damselfish.

*Abudefduf abdominalis* was chosen because it is an omnivorous reef fish that, as a juvenile, settles in a wide variety of habitats after a pelagic stage that lasts about 20 to 28 days (Helfrich 1958, Radtke 1985, and Chapter II of this study). Fish were found in two discrete
habitats that differed in food resources: under buoys and in tidepools. Plankton was the predominant food source consumed at the buoys, while the tidepools provided abundant benthic algae as well as plankton (see chapter II). Plankton was assumed to be non-stationary in time and place, while benthic algae were considered a potentially defendable resource.

**MATERIALS AND METHODS**

Juvenile fish at four post-settlement ages were studied in two treatments: groups of fish that were fed only live plankton and groups of fish that were fed live plankton and fixed benthic material. Two series were run: one (field series) in which the fish were collected from buoys and tidepools at four different sizes, and the other (laboratory series) in which fish were captured as they settled on a substrate and reared for three months in the laboratory under the two treatments.

**Subjects**

*Abudefduf abdominalis* were collected with hand nets from tidepools at Sandy Beach State Park on the southeast shore of Oahu, and buoys in south Kaneohe Bay on the northeast shore of Oahu. The tidepool habitat included abundant attached algae and plankton carried into the pools by waves and high tides. The buoys were 0.6-1.0 m diameter floating at the surface in water 6-10 m deep. The submerged portion of the buoys supported an encrusting community of sponges and bryozoans.
Juvenile fish were collected at four sizes that represented four distinct age classes based on daily increments deposited in the otoliths (see chapter II): initial settlement, one, two and three months post-settlement. The initial settlers were fish that had just abandoned the pelagic stage and were first associating with some hard substrate. These individuals were identified by their incomplete pigmentation. The adult-like banded pigmentation normally develops during the first 24 hours after settling (personal observation). To avoid the influence of prior social contact, only fish found alone were used. All fish collected from each tidepool or buoy were kept separately. All fish were tested on the day they were collected. Analysis of the gut contents of the 1, 2, and 3 month old fish, after the experiment, revealed that the fish collected from the buoys fed much less on benthic food items than the tidepool fish (see chapter II).

The initial post-settlement fish were maintained in the laboratory after their first trials and tested again at monthly intervals for three months. Fish were maintained with the same diet regime found at their capture site. Two groups of six fish collected from the buoys were maintained on a plankton diet and two groups of six fish collected from tidepools were fed a diet of plankton and benthic food. Each of the four, 350 l aquaria was provided with six shelters made out of nine, 6 cm-diameter PVC (polyvinyl chloride) pipe sections 8 cm long stacked three high and three wide. Flow-through sea water was provided, and each aquarium had two air stones. Artificial lighting was provided by overhead fluorescent lights on a
12 hr. day cycle in addition to ambient lighting from windows. Sea water temperature fluctuated between 23 and 25°C during the three months. Raw plankton, collected daily from Moku o Loe lagoon, was provided ad lib. and supplemented with Artemia sp. nauplii when necessary. The benthic treatment fish were also given rocks coated with fish food mixed with agar (fudge rocks).

Testing apparatus

All observations were made at the Hawaii Institute of Marine Biology at Moku o Loe in Kaneohe Bay, Oahu. Trial aquarium size was changed from 27 l to 38 l, 57 l, and 110 l as the fish grew. Each trial aquarium was divided in half by a removable partition with a fudge rock and Artemia in both halves. The aquaria were drained, rinsed, and refilled with fresh sea water between each trial.

Testing procedures

Pairs of similar sized fish (< 5% difference in S.L.) were used for each trial. One individual was placed in each chamber of the test aquarium and left undisturbed for one hour before videotaping. Four pairs of fish were tested at each age for the two treatments. The fish were taken from different tidepools or buoys in the field series, or from different rearing aquaria in the lab series. In all cases, the largest and smallest fish collected or present in the rearing aquaria were not used. Therefore, all fish had social experience with more dominant and more subordinant fish.

A video camera was fixed in position to view the entire aquarium. The partition between chambers was removed, and the encounter
videotaped until dominance was established and for one hour thereafter. A total of 27 hours of fish interactions were video taped for the field series and 26 hours video taped for the laboratory series. Dominance was considered established when one fish gave four consecutive chases. After observations, the fish were either returned to their rearing aquaria (lab series) or frozen (field series) for otolith and gut content analysis.

**Analysis**

Videotapes were reviewed and information encoded using an electronic 16-channel event recorder (BEAST, WindWard Technology) coupled to a micro-computer. A synchronizing time signal was dubbed on one of the two videotape audio channels. This allowed repeated viewing of the tapes while encoding different behavior events. Records containing different behaviors were then merged into one complete file for each pair of fish. The minimum time resolution of the event recorder was 0.33 seconds. Each videotape session was subdivided into three segments; a pre-dominance period of variable duration and two consecutive 30 min post-dominance periods. Table 3 lists the Modal Action Patterns (MAPs) (Barlow 1968) and orientations recorded during the sessions.

**Validation of data sets**

One of the basic assumptions underlying the study of behavior is that the relationship between two different acts does not change during an observation period. This is referred to as stationarity. To validly combine data sets, stationarity must be maintained, in
Table 3. List of Modal Action Patterns (MAPs) and orientations recorded with their descriptions as used in this study.

<table>
<thead>
<tr>
<th>MAPs</th>
<th>Description</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding related:</td>
<td></td>
</tr>
<tr>
<td>Back-toward</td>
<td>Approaching an opponent tail first.</td>
</tr>
<tr>
<td>Head-up</td>
<td>A 45 degree head up body attitude.</td>
</tr>
<tr>
<td>Head-down</td>
<td>A 45 degree head down body attitude.</td>
</tr>
<tr>
<td>Near-surface</td>
<td>A fish located within two body heights of the surface of the water.</td>
</tr>
<tr>
<td>Near-substrate</td>
<td>A fish located within two body heights of the substrate.</td>
</tr>
<tr>
<td>Plankton-feed</td>
<td>Biting at objects in the water column.</td>
</tr>
<tr>
<td>Substrate-feed</td>
<td>Biting at the substrate.</td>
</tr>
<tr>
<td>Attack:</td>
<td></td>
</tr>
<tr>
<td>Approach</td>
<td>A slow movement towards the opponent.</td>
</tr>
<tr>
<td>Chase</td>
<td>A fast approach.</td>
</tr>
<tr>
<td>Threat:</td>
<td></td>
</tr>
<tr>
<td>Erect-fins</td>
<td>Erection of the medial fins.</td>
</tr>
<tr>
<td>Self-defense:</td>
<td></td>
</tr>
<tr>
<td>Withdraw</td>
<td>A slow movement away from the opponent.</td>
</tr>
<tr>
<td>Flee</td>
<td>A fast withdraw.</td>
</tr>
<tr>
<td>Present-dorsal</td>
<td>Tilting the body forward or lateral to orient the erected dorsal spines towards the opponent.</td>
</tr>
<tr>
<td>Not included in detailed analysis:</td>
<td></td>
</tr>
<tr>
<td>Close-frontal</td>
<td>Two fish facing each other separated by less than half a body length.</td>
</tr>
<tr>
<td>Parallel-swim</td>
<td>Two fish swimming side by side on a parallel course less than two body lengths from each other.</td>
</tr>
<tr>
<td>Shelter</td>
<td>A fish positioning itself in the corner between the provided rock and the glass sides of the aquarium.</td>
</tr>
<tr>
<td>Stationary</td>
<td>Remaining in a fixed location.</td>
</tr>
<tr>
<td>Swim-up</td>
<td>An abrupt change from horizontal swimming to swimming head up towards the surface.</td>
</tr>
<tr>
<td>Tail-beat</td>
<td>An exaggerated tail flexure towards the opponent.</td>
</tr>
<tr>
<td>Body orientation:</td>
<td></td>
</tr>
<tr>
<td>Frontal</td>
<td>Oriented less than 45 degrees right or left of facing the opponent.</td>
</tr>
<tr>
<td>Lateral</td>
<td>Oriented less than 45 degrees from parallel to the opponent.</td>
</tr>
<tr>
<td>Caudal</td>
<td>Oriented less than 45 degree right or left of facing away from the opponent.</td>
</tr>
</tbody>
</table>
either multiple observation sessions on the same individual at different times or when combining sessions from different individuals.

Two approaches were used to test for stationarity in this study. First, a graphic profile of the frequency of occurrence of an act over the observation session was visually inspected for patterns that might indicate a change in the distribution of that act during an observation session. Haccou (1987) has found this to be an effective guide to discovering alterations that would be cause to exclude the session from further consideration. Second, three dimensional contingency tables of preceding act, following act, and observation session were tested with log linear models (Colgan and Smith 1978) and information theory (Losey 1978). Sessions were combined if the null hypothesis that acts, or the relationship between acts, did not interact with the session could be accepted (p > 0.01) for the log linear model, \([\text{preceding-act, following-act}] \ [\text{session}]\) and the information estimate \(T_{\text{following-act}}(\text{preceding-act}; \text{session})\).

**Statistical analysis of data**

The age at which any act first occurred was noted for each of the diet treatments. The pre-dominance session was included in this part of the analysis.

The frequency of acts for each fish was calculated from the total number of occurrences in both post-dominance sessions divided by the total number of minutes. Group means and the analysis of variance were calculated using the statistical package SYSTAT. Three variables in the ANOVA were age (settlement, 1, 2, & 3 months), diet (plankton &
benthic treatments), and rank (dominant & subordinant) (Table 4).

When the main effect "age" was significant (p < 0.05) the sum of the squares was partialized to detect where differences occurred.

An activity index was created by summing the total number of times a fish shifted orientation (frontal, lateral, and caudal) during the observation period. The assumption was that the more active a fish was, the more often it would change directions.

The mean bout length of each act was derived using the BEAST program "STATISTIC". Bout lengths that were truncated by the beginning or end of a session were excluded from the analysis. Both post-dominance sessions were combined giving one value per fish. Group means and analysis of variance of the three variables were calculated using the SYSTAT statistical package.

A post hoc comparison was made of the diet treatment differences at the time of settlement. The Bonferroni procedure of multiple comparisons (Day and Quinn 1989) was used. This method of dividing alpha by the number of comparisons works well for small numbers of comparisons and guards against type I errors.

A second post hoc comparison was made with an a posteriori t-test (Sokal and Rohlf 1969) to determine if an act had an adequate opportunity to be sampled in the observation sessions prior to when it was first observed.

RESULTS

Four pairs of fish were used for each treatment in both the field and laboratory series. The data from two pairs of the settlement age

53
Table 4. Factorial design of study with number of fish within each group.

<table>
<thead>
<tr>
<th>SERIES</th>
<th>DIET</th>
<th>RANK</th>
<th>AGE (months post-settlement)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Field:</td>
<td></td>
<td></td>
<td>number of fish</td>
</tr>
<tr>
<td></td>
<td>Fed live plankton only</td>
<td>Dominant</td>
<td>0  1  2  3 4  4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subordinant</td>
<td>0  1  2  3 4  4</td>
</tr>
<tr>
<td></td>
<td>Fed live plankton &amp; benthic food</td>
<td>Dominant</td>
<td>0  1  2  3 4  3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subordinant</td>
<td>0  1  2  3 4  3</td>
</tr>
<tr>
<td>Laboratory:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fed live plankton only</td>
<td>Dominant</td>
<td>0  1  2  3 4  4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subordinant</td>
<td>0  1  2  3 4  4</td>
</tr>
<tr>
<td></td>
<td>Fed live plankton &amp; benthic food</td>
<td>Dominant</td>
<td>0  1  2  3 4  3</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subordinant</td>
<td>0  1  2  3 4  3</td>
</tr>
</tbody>
</table>
group were omitted when they died the day after the trials. They may have been injured during capture and had spent most of the time sheltered. Only three pairs of fish were available for the last month from the laboratory benthic treatment due to mortality in one aquarium.

One 30-min session was excluded for lack of stationarity. Detailed analysis revealed that the dominance order was reversed for about five minutes and this altered the patterns of behavior of each fish during the first 30-min session. Dominance reverted back to the original individual prior to the start of the second 30-min session, and only the second session was used in the analysis.

The larger of the two paired fish became the dominant fish in 72% of the trials (binomial test $z = 3.02, p < 0.002, N = 53$).

**Field Series**

All but three Modal Action Patterns (MAPs) were expressed by the fish of settlement age in both diet treatments. Present-dorsal was used in the plankton diet group at one month and not seen until the third month in the benthic diet group. Swim-up occurred in the benthic diet group at settlement and two months later in the plankton diet group. Parallel-swim was first observed one month post-settlement in both diet treatments. A post hoc t-test compared the months prior to the first occurrence with the months after first use to determine if these acts had an adequate opportunity to be sampled prior to when they were first observed. The results indicated that, given the sample size and the low frequencies of expression, these
three MAPs could have been available but lacked the opportunity for expression at an earlier time. Tail-beat, stationary, swim-up, parallel-swim, close-frontal and shelter were not considered further due to low frequencies in the post-dominance sessions.

Four MAPs and two locations were considered related to feeding. They were plankton-feed, substrate-feed, head-up, head-down, and the locations near-surface, and near-bottom. Figure 11 shows the mean count and time budget for feeding related events. The sum total of the number of plankton feeds plus substrate feeds did not differ between the dominant and subordinant fish in the two treatments.

Plankton-feed occurred more frequently in the benthic diet group than the plankton diet group. There was a gradual shift in diet over time reflecting social rank differences. The dominant and subordinant fish of the plankton diet group fed about equally from the water column initially. At one month and, to a diminishing extent, in subsequent months the dominant fish of each pair fed more on plankton. The reverse trend was evident for the benthic diet group. Initially, the dominant fish fed more on plankton than the subordinant. A month later that pattern had shifted to equal efforts by the paired fish and by the second month, the subordinant fish fed disproportionally more on plankton.

Substrate-feed was more frequent in the benthic diet group than the plankton diet group. The plankton diet group showed a decreasing amount of substrate-feed over time. The benthic diet group initially showed more substrate-feed by the subordinant fish and a shift over
Figure 11. Mean frequency of feeding related acts and percent
duration of the time spent in areas of the aquarium for the field
series. Dominant fish values are above the abscissa, subordinant fish
values are below the abscissa. ANOVA variable and significance levels
are listed within each plot. Probability levels: * = 0.05, ** =
0.01, *** = 0.001. Vertical lines = standard error of the mean.
Horizontal lines below the bars indicate non significant differences
between age groups.
\[ \square = \text{PLANKTON DIET} \]
\[ \bigcirc = \text{BENTHIC DIET} \]

**PLANKTON FEED**

- **DIET**
- **DIET X RANK**

**SUBSTRATE FEED**

- **DIET**

**HEAD UP**

- **AGE X DIET**

**HEAD DOWN**

- **DIET**

**NEAR SURFACE**

- **AGE X DIET**

**NEAR BOTTOM**

- **DIET**

MONTHS
time to the dominant fish feeding more on the substrate than the subordinant.

Head-up was used most often near the surface and may be a posture assumed while searching the surface for plankton that accumulated there. Diet differences existed with the plankton diet group having a lower occurrence of head-up than the benthic diet group. Initially, the plankton diet subordinant fish expressed head-up more frequently than the dominant, but that trend reversed at the third month. The benthic diet group showed the opposite pattern.

The mean bout length for head-up (Fig. 12) showed that at settlement the dominant fish of both diet treatments had longer bouts, but that at one month and after, they were not different or had slightly shorter bouts than the subordinants.

Head-down was seen most often while the fish inspected the bottom of the aquarium and the rocks coated with fish food. There was a diet difference with the benthic diet group expressing head-down more often. The plankton diet group showed a slight decrease in head-down over time, most noticeable in the subordinant fish. The benthic diet group had a shift from the subordinant showing more head-down initially, to the dominant fish having a higher frequency of head-down by the third month. There was no difference in the mean bout length for head-down.

Near-surface was measured as the percent of time spent in that area of the aquarium. There was an age difference that the partialized ANOVA indicated occurred between months one and two. The benthic diet group spent more time near the surface than did the
Figure 12. Mean bout length of all acts with significant bout length differences in the field series. Dominant fish values are above the abscissa, subordinant fish values are below the abscissa. ANOVA variable and significance levels are listed within each plot. Probability levels: * = 0.05, ** = 0.01, *** = 0.001. Vertical lines = standard error of the mean. Horizontal lines below the bars indicate non significant differences between age groups.
\[ \square = \text{PLANKTON DIET} \]

\[ \text{HEAD UP} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

\[ \square = \text{BENTHIC DIET} \]

\[ \text{APPROACH} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

\[ \square = \text{WITHDRAW} \]

\[ \text{DIET} \quad \text{RANK} \quad \text{AGE} \times \text{DIET} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

\[ \square = \text{ERECT FINS} \]

\[ \text{AGE} \quad \text{RANK} \quad \text{AGE} \times \text{DIET} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

\[ \square = \text{CHASE} \]

\[ \text{AGE} \quad \text{RANK} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

\[ \square = \text{FLEE} \]

\[ \text{AGE} \quad \text{RANK} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

\[ \square = \text{BACK TOWARD} \]

\[ \text{DIET} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

\[ \square = \text{PRESENT DORSAL} \]

\[ \text{DIET} \quad \text{RANK} \quad \text{DIET} \times \text{RANK} \]

\[ \text{SECONDS} \]

\[ 0 \quad 1 \quad 2 \quad 3 \]

MONTHS

MONTHS

61
plankton diet group. The plankton diet group showed no trend in rank. The benthic diet group did show a trend: The dominant fish spent more time initially near the surface and, by the third month, the subordinant fish spent more time near the surface.

Near-bottom, expressed as percent of time, revealed a diet difference: The benthic diet group spent more time near the bottom. Settlement-age subordinant fish of the benthic diet group spent the most time near the bottom, but that pattern reversed by the third month. No clear pattern emerged for the plankton diet group.

The seven MAPs related to social behavior were approach, withdraw, chase, flee, erect-fins, back-toward, and present-dorsal (Fig. 12 and 13). Differences between ranks existed for approach: The dominant fish approached the subordinant more frequently (Fig. 13). The differences in the plankton treatment were due to a decrease in the frequency of approaches made by the subordinants at month 1 and later. Conversely, the dominant fish of the benthic treatment showed a greater increase in approach frequency while the subordinant remained more stable. Diet differences varied depending on age with the plankton treatment approaching more than the benthic treatment at settlement and at month 3, and the opposite occurring at months 1 and 2.

Approach bout length (Fig. 12) showed an inverse pattern to the frequency histogram. Groups of fish that had fewer bouts had longer bouts, and groups with more bouts had shorter bouts. Age differences existed with settlement age and month 3 differing from months 1 and 2. Differences between dominant and subordinant fish were found with the
Figure 13. Mean frequency of social acts and the activity index for the field series. Dominant fish values are above the abscissa, subordinant fish values are below the abscissa. ANOVA variable and significance levels are listed within each plot. Probability levels: * = 0.05, ** = 0.01, *** = 0.001. Vertical lines = standard error of the mean. Horizontal lines below the bars indicate non significant differences between age groups.
\( \square = \text{PLANKTON DIET} \)

\( \square = \text{BENTHIC DIET} \)

- Approach: RANK ***
- Age x Diet ***

- Withdraw: Age x Diet ***

- Chase: RANK ***

- Flee: RANK ***

- Erect Fins: Age **
- Rank ***

- Back Toward: Age ***

- Activity Index:

- Present Dorsal

- Turns / Min

- Months

64
dominant fish having longer bouts in most cases. The exceptions that accounted for the significant interaction with age were plankton and benthic treatments at month 1 and the benthic treatment at month 2.

The frequency of withdraw (Fig. 13) had a trend in rank \( (p = 0.08) \), with the subordinant fish withdrawing more often than the dominant fish. Greater rank differences occurred at settling and month 3. Rank differences at months 1 and 2 were smaller.

Diet differences existed for withdraw bout length (Fig. 12), but depended on age. Initially the benthic treatment had longer withdraw bouts, but this reversed at months 1 and 2. Both diet treatments had similar bout lengths at month 3. Withdraw bout length also showed an inverse pattern to the frequency data as did the approach bout length. Subordinant fish had longer bouts than dominant fish.

Dominant fish did virtually all the chases, while subordinant fish were the ones to flee the most (Fig. 13). The bout lengths for both chases and flees (Fig. 12) show the same rank differences. Settlement age fish had longer bouts of chasing and fleeing than the older groups.

Erect-fins was expressed more often by the dominant fish (Fig. 13). Frequency of events generally decreased with age with settlement age fish differing from months 1 and 2 and those from month 3.

Bout length of erect-fins differed between ages, rank, and diet. Dominant fish had longer bouts. Settling fish had the longest bouts, longer than other ages. Months 1 and 2 showed no differences, and months 2 and 3, with the shortest bouts of all ages, had no differences. Diet differences depended on age. Initially, the
benthic treatment had longer bouts, but that pattern reversed at month 1 and again at month 2. Diet differences did not exist by month 3.

Back-toward occurred most often at settlement (Fig. 13), greatly decreasing in frequency at month 1 and then increasing again the last two months. With the exception of the settlement age group, the plankton treatment had a higher frequency of back-toward, but this pattern was obscured by the magnitude of the frequency of back-toward in the benthic treatment at settlement.

The plankton treatment had longer bouts of back-toward than the benthic treatment, except at month 2 (Fig. 12). The clearest differences were at month 1.

Present-dorsal was absent at settlement age, and became progressively more common with age in the plankton treatment (Fig. 13). The act was only expressed by the subordinant fish. The benthic treatment fish did not express present-dorsal until month 3.

The bout length of present-dorsal reflects the same patterns as the frequency of bouts. Subordinant plankton treatment fish used present-dorsal from month 1 while the subordinants of the benthic treatment did not express it until month 3.

An activity index, based on the number of times a fish changed direction per minute (Fig. 13), indicated that the newly settled fish were less active than older fish. This difference was due largely to the lower values for the benthic treatment fish at settlement. The activity index pattern was very similar to the frequency of bouts for approach and withdraw.
Laboratory series

In the laboratory series, present-dorsal was first expressed at month 1 in both treatments. Swim-up was first seen at settlement in the benthic treatment but at month 1 in the plankton treatment. Parallel-swim first occurred at month 1 in both treatments. As with the field series, a post hoc test indicated these MAPs might have occurred earlier but remained undetected due to their rarity. All other MAPs were observed at settlement.

Plankton-feed, substrate-feed, head-up, head-down, near-surface and near-bottom were associated with feeding as they were in the field series. The total amount of feeding did not differ between the dominant and subordinant fish in either diet treatment.

The frequency of plankton-feed (Fig. 14) for the first two months was higher than for the last two months of both diet treatment groups. No differences due to diet or social rank were significant, but the pattern suggested that dominant fish fed more on the plankton initially, and later fed less on plankton than subordinant fish.

Substrate-feed (Fig. 14) showed age differences separating the settlement age fish from the rest, and ages separated by two months were different from each other. Plankton treatment fish showed equal or greater incidence of substrate-feed at month 1 and later.

Differences in social rank occurred with the dominant fish of both treatments feeding more on the substrate after settlement than did the subordinant fish.

Head-up showed diet differences with the benthic treatment having a higher incidence. The subordinant fish expressed head-up more often
Figure 14. Mean frequency of feeding related acts and percent duration of the time spent in areas of the aquarium for the laboratory series. Dominant fish values are above the abscissa, subordinant fish values are below the abscissa. ANOVA variable and significance levels are listed within each plot. Probability levels: * = 0.05, ** = 0.01, *** = 0.001. Vertical lines = standard error of the mean. Horizontal lines below the bars indicate non significant differences between age groups.
than did the dominant fish, except for the settlement age benthic treatment.

Mean bout length of head-up (Fig. 15) indicated that the subordinant fish had shorter bouts at settlement, but longer bouts at month 1 and later.

Head-down (Fig. 14) was expressed least often at settlement and most often at month 1. There were no age differences between months 2 and 3, which were intermediate in frequency of occurrence to the other ages. Dominant fish used head-down more often than subordinant fish except the initial age benthic treatment.

Mean bout length for head-down (Fig. 15) also showed dominant fish having longer bouts than subordinant fish with the exception of the initial age benthic treatment.

The benthic treatment fish spent a higher percentage of their time near the surface than the plankton treatment fish (Fig. 14). Subordinant fish spent a greater percent of time at the surface with the exception of the initial benthic group. The time subordinant fish spent near the surface increased gradually over the course of the experiment. The settlement age dominant fish spent a greater percent of time near the surface than older dominant fish within each treatment.

Both treatments showed an age difference in the percent of time spent near the bottom. The settlement age fish spent less time near-bottom than the older fish (Fig. 14). There was a shift in the benthic treatment from the subordinant fish spending a greater percent of time near the bottom at settlement to the dominant fish spending a
Figure 15. Mean bout length of all acts with significant bout length differences in the laboratory series. Dominant fish values are above the abscissa, subordinant fish values are below the abscissa. ANOVA variable and significance levels are listed within each plot. Probability levels: * = 0.05, ** = 0.01, *** = 0.001. Vertical lines = standard error of the mean. Horizontal lines below the bars indicate non significant differences between age groups.
greater percent of time near the bottom when older. Plankton treatment showed no shift in rank.

The benthic treatment had a higher frequency of approach than the plankton treatment (Fig. 16). Dominant fish of both treatments approached more frequently, with the exception of the settlement age in the plankton treatment for which ranks were equal.

There was a inverse relationship between the frequency of approach and its bout length (Fig. 15). Groups with more bouts had shorter bouts. Bout lengths were longer at settlement age than later and benthic treatment fish had longer bouts than plankton treatment fish. Age did interact with rank with greater differences in rank at settlement than later.

The frequency of withdrawals was greater for the plankton treatment and subordinant fish (Fig. 16). Withdrawal bout length also had an inverse relationship with bout frequency, with groups having a higher frequency of bouts having shorter bouts (Fig. 15). The only exception was the benthic treatment at month 3. At settlement, the bout lengths were longer than at later ages. The plankton treatments had shorter bouts, except for the dominant fish at month 3.

Chase was almost exclusively performed by the dominant fish, and flee by the subordinant fish (Fig. 16). There was an age difference for both MAPs with the settlement age having a lower frequency of bouts than all the older groups. Bout lengths of chase were longer only at settlement age (Fig. 15), and both chase and flee bout lengths had the same rank differences as bout frequency.
Figure 16. Mean frequency of social acts and the activity index for the laboratory series. Dominant fish values are above the abscissa, subordinant fish values are below the abscissa. ANOVA variable and significance levels are listed within each plot. Probability levels: \* = 0.05, \** = 0.01, \*** = 0.001. Vertical lines = standard error of the mean. Horizontal lines below the bars indicate non significant differences between age groups.
Dominant fish erected their fins more often than subordinant fish (Fig. 16). Bout length of erect-fins also revealed that dominant fish had longer bouts than subordinant fish (Fig. 15). Age differences occurred with the settlement age fish having longer bouts than older fish. Diet differences existed but changed with age. Benthic treatment fish had longer bouts than plankton treatment fish at settlement and month 3, shorter bouts at month 1, and about equal bout lengths at month 2.

Settlement age fish expressed back-toward more often than older fish (Fig. 16). The benthic treatment fish and subordinant fish had a higher frequency of back-toward than their counterparts.

Subordinant fish were the only ones to use present-dorsal (Fig. 16). The act was predominantly expressed by plankton treatment fish. The bout length data (Fig. 15) indicated the same pattern. There was an interaction between diet and rank due to the absence of expression of present-dorsal by dominant fish.

Activity index (Fig. 16) revealed that dominant fish were more active than subordinants, and those of the plankton treatment were more active than the benthic treatment fish. The only age difference recorded was that settlement age fish were less active than older fish.

Treatment differences at settlement

The post hoc analysis of treatment differences at settlement time indicated that only the activity index was different ($p < 0.01$), with the plankton treatment being 20-30% more active than the benthic...
treatment. The six pairs of fish showed no other treatment differences when first observed.

DISCUSSION

This study assumed that there was no social experience between fish prior to settlement. The behavior of larval _Abudefduf abdominalis_ described by Helfrich (1958) indicated no social interaction. My own qualitative observations of a brood of _A. abdominalis_ raised from hatching in captivity confirmed a lack of social interaction until the fish gained the yellow and black banded pigmentation and settled to the bottom of the tank. After settlement, fish were aggregated and interactive. Completely pigmented juvenile damselfish have been found aggregated under oceanic floating material (personal observation) and may subsequently find their way to a reef. For this reason only fish showing no or incomplete banding were used as "settlement age" fish.

All but three of the Modal Action Patterns (MAPs) were expressed at settlement. The early expression of a nearly complete repertoire also was noted for two poeciliid fishes, _Poecilia (=Mollienesia) velifera_ and _P. latipinna_, (Parzefall 1969) and two scorpaenid fishes, _Sebastes chrysomelas_ and _S. carnatus_. (Hoelzer 1987). Brown and Colgan (1985) considered two criteria important in the onset of MAPs: size and environmental setting. In their study on four centrarchid fishes, _Micropterus salmoides, Ambloplites rupestris, Lepomis gibbosum, and L. macrochirus_, there were critical sizes for the onset of aggressive MAPs, and the expression of agonistic behavior was also
associated with environmental changes. Settlement on a reef may well provide the cues for the initial expression of certain MAPs in A. abdominalis, but since settlement occurs within a narrow size range (Radtke 1985, Helfrich 1958), the two criteria cannot be easily separated. The emergence of MAPs may be sudden and complete in form (Stamps 1978) or more gradual (Tooker and Miller 1980). The presence or extent of parental care can also be a factor in the rate of emergence of MAPs (Stamps 1978, Brown 1984), but this is not a factor in my study due to the lack of parental care after hatching. Only further detailed analyses, especially during periods of transition in the life history of organisms, can resolve the issue of how MAPs emerge in form.

The three MAPs not observed at settlement were so rare during the early months that the MAPs may not have had sufficient opportunity for expression due to insufficient sampling. Any discussion of first occurrence must take sample size into account and be cognizant that the individual may be physically able to perform the act long before the opportunity for expression arises (Bekoff 1978).

The newly settled fish collected from two different habitats showed only a difference in the activity index. The fish collected from buoys (plankton treatment) were more active than fish from tidepools (benthic treatment). This difference persisted in these fish throughout the laboratory series but did not occur in older fish collected later at the same locations for the field series. Otherwise, the fish were similar in behavior regardless of where they had settled.
Fish that experienced one of two food types during rearing were
exposed to both food types during the trials in a neutral test
aquarium. Experience with a particular diet altered food preferences.
Initially, dominants from both diet treatments preferred plankton.
With age, the subordinant fish of each diet treatment were
increasingly displaced from the food type preferred by the dominant
fish. This was most obvious in the benthic treatment. At settlement
the subordinant fish substrate-fed more, used head-down more and spent
more time near the bottom, while the dominant fish fed more on
plankton, used head-up more and spent more time near the surface.
Prior to settlement, plankton was the only food experienced. After
settlement, the dominant fish of the benthic treatment, given
experience with both foods, showed a gradual shift to the benthic
diet. The subordinant fish was gradually relegated to the other parts
of the aquarium away from the benthic food.

In spite of displacement by the dominant fish, overall feeding
rates did not decrease in the subordinant fish during the trials.
Bildsoe (1988) found that dominant Poecilia velifera did feed more and
inhibited the subordinant fish as did Koebele (1985) for the cichlid,
Tilapia zillii. Dominant hatchery and wild salmon, Salmo salar, also
feed more than subordinates (Fenderson et al. 1968). The lack of
effect in my study may be due to the availability of an alternate food
resource that the subordinant fish could utilize with reduced
interference from the dominant fish. A second explanation is that the
previous studies have dealt with long term social hierarchies while my
study presented two unacquainted fish in a neutral environment.
Insufficient time may have elapsed for the dominant fish to influence the overall feeding rate of the other fish. Reduced growth rates in subordinant A. abdominalis have been observed over longer duration studies (Helfrich 1958).

Rearing the fish in the laboratory resulted in differences from the field caught fish. Most notable were the access to the bottom of the aquarium by the subordinant fish, and the increase in substrate feeding by dominant fish especially those of the plankton treatment. Being reared in the confines of an aquarium regardless of diet resulted in familiarity with a finite "bottom" similar to that experienced by fish living in a tidepool. Prior familiarity with confined space may also explain why fish from tidepools (field series, benthic treatment) fed at a higher rate on both food types during the trials when compared to the fish collected from buoys. Feeding related activities were more similar between diet treatments in the laboratory series than in the field series. Differences in social rank were more evident in the laboratory series because both treatments reacted similarly. The field series rank differences were obscured by the different treatment effects in each group.

Activity level increased shortly after settlement and remained constant for the rest of the experiment in all three groups that had experience in a confined space. The field plankton groups showed no increase in activity with age. Again the space restrictions in the aquaria failed to duplicate the field conditions for the plankton treatment.
A decrease in bout length occurred during the first month in all cases, with only approach in the field series increasing later to the original levels. This decrease in bout length could indicate a refinement of the MAP form with early experience or that the MAPs were becoming recognized as signals, reducing the need for extended expression. This pattern is the opposite of a fiddler crab, *Uca pugilator*, (Hyatt 1977), where an increase in bout length is a factor in increasing the effectiveness of the signal. Little other work has been done in the area of changes in bout duration during development.

The criteria used to identify dominance, four consecutive chases by one fish, appeared adequate to identify the rank of a fish for the duration of a trial. Only one reversal of rank occurred (detected during validation for stationarity of MAPs) and that case was excluded from the analysis. The larger of the paired contestants won more often (72% of the time) even with length differences of less than 5%. Abbott et al. (1985) found that weight differences in Steel-head Trout, *Salmo gairdneri*, of less than 2% resulted in the larger fish winning 62% of the time, while a 5% difference in weight guaranteed that the larger fish won. A 2% difference in weight also gave similar results for the Midas Cichlid, *Cichlasoma citrinellum*, (Barlow, Rogers, and Fraley 1986). A length difference of 5 mm gave Blue Gouramis, *Trichogaster trichopterus*, a size related advantage (Frey and Miller 1972) and a 20% size difference in the goby *Padogobius martensi* the same benefit (Torricelli et al. 1989). Wilson (1975, Table 13-2) provides a selection of examples of size-related dominance ranks from both invertebrates and vertebrates.
Prior experience at winning is also important (McDonald, Heimstra, and Damkot 1968, Francis 1983, Franck and Ribowski 1987). All the fish used, except the settlement age fish, came from social groups with larger and smaller individuals than those tested. This did not control the number of winning or losing encounters prior to the trials. It did provide a stable social assemblage more similar to natural conditions than might result from any attempt to standardize their experiences. The short pre-trial isolation in the observation aquarium provided an opportunity to explore the new surroundings, to discover the food resources, and to settle down after being handled during the transfer between aquaria.

Opponents were drawn from separate aquaria reared under identical conditions to avoid prior experience with a particular individual fish. Fish may have been re-paired with the same fish a month later, but since the influence of a previous encounter wanes over a period of 1-14 days (McDonald et al. 1968, Francis 1983, Abbott et al. 1985, Franck and Ribowski 1987), this was not considered to be a problem.

Nearly all rank differences were consistent across the two series. The dominant fish expressed erect-fins, approach, and chase more than the subordinant fish. The subordinant fish had higher frequencies for back-toward, present-dorsal, withdraw and flee. This is consistent with rank differences in the cichlid, *Astatotilapia burtoni*, (Fero 1987). In my study, the dominant fish was more active, based on the activity index, although in the field series, this trend was not significant. In all cases where there were rank
differences in bout length, the group having the higher frequency also had the longer bouts.

Erect-fins often preceded a chase and appeared to be a threat display used by the dominant fish. Cole and Noakes (1980) considered it a threat display in Rainbow Trout, *Salmo gairdneri*, that increased in frequency after the more active components of aggression were formed. Although active components of aggression (e.g., chase) may have preceded erect-fins prior to settlement, erect-fins showed no increase in expression over the duration of this study.

Back-toward, where one fish swam backwards towards the other fish, had a pattern that did not correlate with any other MAP. Initially, it was seen during feeding episodes when the other fish was near by. Its use decreased after settlement age (month 0) especially in the field-caught fish. Feeding in the close quarters of the rearing aquaria may have contributed to its persistence, especially among the benthic diet fish. Back-toward was used more often by the subordinant fish and may have been a way for the subordinant fish to feed closer to the dominant fish without incurring a chase. Tinbergen and Baeumer (cited in Hinde 1970) noted that submissive displays developed from ritualized intention movements to flee, with the postures also associated with removing sign stimuli for aggression. For species living in social groups, as does *A. abdominalis*, such an appeasement display would allow a subordinant individual to remain within the social group (Brown 1975). This appears to be the most likely explanation at present but further investigation is required.
Present-dorsal was expressed by subordinates of the plankton treatment in response to aggression by the dominant fish and the inability to escape. Subordinate fish generally sought refuge in the upper corners of the aquarium and, on approach of the dominant fish, presented the erected dorsal fin to the front of the aggressor. I have seen a similar posture assumed by the butterflyfishes *Chaetodon trifasciatus* and *C. multicinctus* when attacked by territorial damselfishes. It is possible that the posture protects a bite zone as described for rats, *Rattus norvegicus*, (Blanchard and Blanchard 1980), but bite attempts were so rapid that video images were blurred and could not be quantified.

The laboratory series fish had a higher level of overt aggression measured by the number of chases and flees when compared with field series fish. Fenderson et al. (1968) found similar results when comparing hatchery-reared and wild salmon, attributing the differences to the effects of frequent disturbances and suppression of mutual repulsion mechanisms of spacing. While densities in the rearing aquaria were not higher than the densities found in tidepools and buoys, fish in the aquaria lacked the ability to leave the social group for extended periods as they might have in the field. This difference in space availability during rearing may have accounted for the increased aggression and the increased use of present-dorsal in the laboratory reared fish. Confined space has been found to be a factor leading to increased aggression independent of density (Myers et al. 1971). Crowding, per se, can lead to delayed development of behavior (Fernald and Hirata 1979, Coss and Burgess 1981) which did
not occur in my study; for example, present-dorsal was used earlier in the laboratory series than in the field series.

Hoelzer (1987) manipulated shelter availability as a defendable resource and found an increase in aggression with the presence of the shelters for one of two species of scorpaenid fish. While I found no increase in the frequency of aggression due to defendable food resources, I did find an increase in the frequency of defensive behaviors as did Hoelzer (1987).

The ability to express certain behavioral options at settlement is important to the survival of juvenile fish. In the presence of potentially defendable resources the individual can begin controlling those resources with possible survival benefits. Less obvious is the accommodation by subordinant individuals that may improve their survival as well. How much latitude in behavioral flexibility exists, and what affect these differences have in adulthood will necessitate longer term longitudinal studies of individuals existing in different habitats throughout their lives.

CONCLUSIONS

1. Most behaviors were expressed at the time of settlement. The form of each MAP was recognizable and complete when first seen. It is unlikely that social contact existed prior to settlement.

2. Newly settled fish collected under buoys were more active than similar fish from tidepools. This difference persisted throughout the laboratory series but was not evident in fish collected from the same locations at older ages.
3. Experience with a particular diet altered food preferences. The dominant fish fed more on the food type previously experienced and displaced the subordinant from its proximity. There were no rank differences in overall feeding rates.

4. Specific MAPs were associated with social rank. Dominant fish exhibited more approaches, chases, and erect-fins while the subordinant fish had higher frequencies of withdraw, flee, back-toward and present-dorsal.

5. The larger of the paired contestants became the dominant fish in 72% of the trials, even though differences in length were less than five percent.

6. There was no effect of diet on the agonistic MAP, erect-fins, but there were diet differences for the MAPs, present-dorsal and back-toward. Present-dorsal was used almost exclusively by the plankton diet subordinant fish when cornered by the dominant fish. Back-toward did not correlate well with any other MAP and may have been associated with feeding in close proximity of the dominant fish. It occurred mostly in the benthic diet fish.

7. The general decrease in bout length during the first month post-settlement may have indicated a refinement in form or improved recognition as signals.

8. Differences in feeding behavior existed between the field and laboratory series. The feeding behavior differences were likely masked, in the laboratory series, by both treatments experiencing a habitat similar to a tidepool. The laboratory series had higher rates of overt aggression and quicker development of submissive MAPs.
Chapter IV
ORGANIZATION OF BEHAVIOR DURING ONTOGENY

INTRODUCTION

One of the "candidate principles" of the study of behavior is that behavior is organized in a hierarchical fashion (Tinbergen 1951, Dawkins, 1976). Fundamental units such as neurons are integrated with other neurons to form motor units at one level, synchronized locomotion at another, and courtship displays at yet another level (Baerends 1984). A reductionist view may not be the most productive approach to understand the function of higher order behavior systems (Dawkins, 1976). Much of ethology is based on elucidating common processes of behavior while acknowledging differences in the structures underlying these behaviors. For example, many different species respond in the same way to the appearance of a predator.

The organization of behavior changes during ontogeny. Spontaneous activity of neurons becomes more organized and functional (Gideiri 1969). Correlating the development of the nervous system to behavioral development is difficult as it is possible that the neural circuits are completed some time before the expression of a behavior is noted (Bekoff 1978). Evidence for the gradual formation of the hierarchy of behavior comes from studies that show behavior elements first being expressed out of context (Tooker and Miller 1980, Chalmers 1980) or without signal value (Moynihan 1959) and only later become integrated into functional systems or acquiring signal value.

Two general processes have emerged to explain the formation of higher order behavior systems. The first process assumes that
behavior elements may first be multi-functional and later become more restrictive (Chalmers 1980). By becoming more restrictive, the behavior element can improve its signal value by reducing ambiguity in expression. The other approach involves isolated systems becoming integrated into larger systems; possibly, but not necessarily, at a higher level in the hierarchy (Kruijt 1964, Hailman 1967). These two processes may occur at the same time as the ontogeny of behavior is both progressive, i.e., increasing in complexity, and regressive, i.e., increasing in selectivity (Oppenheim 1980).

The results of Chapter III indicated that, while most of the Modal Action Patterns (MAPs) were expressed at settlement age, differences later developed in the frequency of use and duration for some of these MAPs. These differences varied with the age of the fish (0 to 3 months post-settlement), the diet of the fish (plankton only or plankton plus benthic food), and the social rank (dominant or subordinant). Little information about the organization of behavior can be determined from frequency counts alone. Indeed, to understand the changes in frequency, one must investigate the interaction between MAPs both within the individual fish and between fish.

The degree of relationship between MAPs within an individual can be investigated by analyzing the temporal relationship between MAPs. Those MAPs that occur close together more often than predicted by random chance indicate possible components of behavior systems or groups of acts that share common causal factors. Over time, it is possible that MAPs may form into temporally associated systems, shift from one to another preexisting cluster of MAPs, or disassociate,
thereby dissolving a behavior system. While internal factors may cause some of the changes, external environmental factors may also be important.

Interactions between individuals are also important. The social environment is an important component of the external environment (Shaw 1962, Stamps 1978). Social encounters also provide the context in which certain behavior systems are expressed, thus aiding in the understanding of the temporal sequencing of MAPs within an individual. The amount of communication between individuals can help to determine the signal value of particular MAPs and how that might change over time.

The purpose of this part of the study was to explore the way MAPs were related within individuals and what differences the presence of different food resources had on these associations. Chapter III indicated that there were no diet differences in the frequency of several agonistic MAPs, but it is possible that differences in the temporal associations formed by these MAPs could occur even if the frequencies remained unchanged.

MATERIALS AND METHODS

The data set described in Chapter III was used for this analysis. The three factors, age, diet, and social rank, remained the same. The two half-hour data segments for all but one fish were combined since stationarity was consistent for the entire hour (see Chapter III). Only the second half-hour was used for the one fish that failed to show stationarity during the first half-hour.
Temporal patterns were analyzed for each fish individually. Group mean or median values were then determined for the three factors to avoid a form of "data pooling fallacy" (Matchlis and Dodd, with Fentress 1985) where the pooled data can reveal patterns that do not exist in any of the individuals.

Event clustering

Bout structure was tested using a log-survivorship method (Fagen and Young 1978, Haccou 1987). If bouts occur randomly, i.e., the probability of a new bout beginning is constant, the frequency distribution of the intervals between bouts should fit a negative exponential curve. A logarithmic transformation of such a plot will result in a straight line. If bouts are clustered in time, forming superbouts, this log-survivorship curve will deviate from a straight line forming a concave curve. A refractory period between bouts will indicate a convex curve. The BEAST program (Windward Technology 1984, 1988) was used to plots and determine deviations from a straight line using an iterative curve fitting process and a Kolmogorov-Smirnov, one sample test.

Transitional diad matrices

Based on the analysis in Chapter III, eight Modal Action Patterns (MAPs) were selected for more detailed study. The eight MAPs were chase (dominant fish only), flee (subordinant fish only), approach, withdraw, substrate-feed, plankton-feed, erect-fins, back-toward, and present-dorsal. Preceding events-following events in MAP pairs (diads) were compiled into an 8 x 8 matrix for each fish. The focal
point for sampling was defined as the beginning of each new MAP, hereafter defined as the following act. The preceding act was defined as the beginning of the nearest preceding MAP within a maximum allowable window or lag of 10 seconds. These two acts then formed a preceding-following diad. An inter-bout gap of five seconds was invoked for substrate-feed and plankton-feed. The result was that any feeding that occurred within five seconds of a prior feeding act of the same type was combined into one long feeding bout. This was done because log-survivorship curves for the feeding MAPs indicated that some feeding was clustered and the resulting inflation of the number of feeding events tended to bias the loglinear model analysis explained below.

A series of matrices was also created of signal-response diads for each pair of fish matched together. The same MAPs were involved and the same protocol for diad formation was used with the beginning of a response by one fish as the focal act and the preceding MAP of the other fish as the signal.

The loglinear modeling utilized the BEAST programs (Windward Technology 1984, 1988) that were based on the methods described in Fienberg (1977) and Colgan and Smith (1978). A three-dimensional model was used with the first dimension being the preceding (or signal) MAP, the second dimension being the following (or response) MAP, and the third dimension being the fish subjects.

Preliminary modeling indicated that no dimensions could be eliminated as unimportant. The best fit occurred with the saturated model that included all three dimensions. Analysis of the
standardized residuals (observed - expected estimate / square root of expected) of the preceding-following diad matrices revealed that four cells had very high values and were strongly influencing the rest of the matrix. These cells were: approach preceding approach, withdraw preceding withdraw, approach preceding withdraw, and withdraw preceding approach. These four cells were removed from the analysis (declared logical zeros) because they were not of major biological interest in my study and were masking the significance of other cells in the matrix. Removal of these four cells from the analysis, however, did not improve the fit of the models. Removal of the remainder of the diagonal cells in the matrices (where MAPs follow themselves) also provided no benefit in fitting the models. None appeared to mask the possible significance of other cells; so they were included in the analysis.

**Ethograms**

Ethograms described here refer to descriptions of the relationship that MAPs have with each other. Values for the ethograms were derived from the preceding-following and the signal-response diad matrices using the standardized residual of the model showing random interaction between the preceding (or signal) MAP and the following (or response) MAP, [preceding MAP, fish subject] [following MAP, fish subject]. The magnitude of the standardized residual in a cell indicated the extent of deviation from the probability that the two MAPs were randomly associated. Only the positive values were considered in the ethogram. Median values for each group of fish were
used due to the non-normal distribution of the standardized residuals. Estimates for critical cell values, to determine significantly non-random cells, were based on Fagen and Young (1978) criteria. Because of the "informality" of these criteria (Colgan 1978), cells with values 25% below the critical cell value were included if that cell was also above the critical cell value in the other fish, the other diet treatment, or at adjacent ages. This was done since developmental trends may first be revealed at levels below the critical cell values. Transitions between preceding (or signal) and following (or response) MAPs that exceeded these criteria will be referred to as "preferred transitions". The greater the cell value departed from the predicted random model of no association, the stronger the "preference" for that transition.

The total number of preferred transitions formed for each group of fish was tallied and tested for differences across the three factors. Age differences were determined with a regression analysis. Diet differences and differences between the field and laboratory series were determined with a Chi-square Test for two independent samples (Siegel 1956). Differences between the dominant and subordinant fish were tested with a Wilcoxon matched pair sign rank test (Siegel 1956).

Information theory analysis

Communication between the pairs of fish was also measured using 3 dimensional information theory analysis (Losey 1978). The BEAST
programs (WindWard Technology 1984, 1988) were used with the signal-
response diad matrices described earlier. The information shared (T)
between the signal (s) and response (r) with the individual fish
variation (z) removed (the value given as Tz(s;r)) was determined for
all groups of fish with all values corrected for sample size. The
"arcsine" method for estimating the confidence limits was used (Losey
1978). Values for Tz(s;r) were considered significantly different if
the 95% confidence limits did not overlap. The transmission
efficiency (TE) was estimated by dividing the information shared
between the signal and response (Tz(s;r)) by the information diversity
of the signal (Hs).

Information theory measures are sample size dependent (Losey
1978). It was possible that increased Tz(s;r) values were due solely
to increased numbers of diads in the samples. This was tested,
separately for the field and laboratory series, by correlating the
total number of diads (counts) in each matrix with the Tz(s;r) values
calculated for that matrix using a Pearson product-moment correlation
test (Sokal and Rohlf 1969). Additionally, the distribution of the
number of diads was tested, using two methods described in Dixon and
Massey (1957), to see if the extreme values might be considered
outliers or not drawn from the same population as the others. The
first method was to divide the range by the sample value (q = w/s,
where w = range and s = sample value). The second method involved
ranking the samples and then comparing a subset of the range with a
subset of the sample value. *(r22 = X3-X1 / Xk-2-X1, where X1...Xk =
the ranked sample values). The size of the subset is determined by the sample size.

RESULTS

There were no consistent patterns of bout-superbout structure evident in any group of fish used in this study except for feeding Modal Action Patterns (MAPs). Clustering of non-feeding MAPs did occur for individual fish but grouping fish by series, age, diet, or social rank did not reveal interpretable results. Most fish had some superbout structure for substrate-feed and plankton-feed ranging from 1-7 seconds with most having durations shorter than five seconds, i.e., most fish would bite at several food items in succession when feeding. There was, however, no discernible pattern related to age, diet, or social rank.

The analysis of preceding-following transitions revealed no differences between ages, diet regime, social rank, or experimental series in the total number of preferred transitions formed within each group of fish. The total number of signal-response preferred transitions also did not differ between ages, diet regime, social rank, or experimental series.

Preceding-following transitions

Modal action patterns were combined into functional series or "groups" that had highly preferred transitions between adjacent MAPs that were consistent across the four months within each group of fish. This was done by visually inspecting the preferred transitions and rearranging the position of the MAPs in the figures to minimize the
distance between those highly preferred transitions that prevailed across the most months.

Two functional groups of MAPs were evident among the dominant fish (Figs. 17-20): the feeding group (substrate-feed, plankton-feed, withdraw, and back-toward), and the attack group (approach, and chase). Transitions from the feeding group to the attack group involved substrate-feed and back-toward in the benthic diet groups, and plankton-feed and back-toward in the plankton diet groups. The only exception occurred in the field series/plankton diet/month 3 fish that showed a weak transition between substrate-feed and chase. These transition patterns between groups of MAPs were not consistent across months.

Erect-fins was the most consistent transition element between the attack group and the feeding group in dominant fish. In most cases erect-fins preceded both chase and withdraw, or approach and withdraw indicating either a possible conflict situation or a threat function. Erect-fins could be considered a conflict indicator preceding the resolution by either chase or withdraw. The threat function could only be determined by interpreting the responses of the subordinant fish and is discussed later in the results.

There were diet differences in the way the dominant fish related to the selected food type of each diet treatment. In the field series/benthic diet fish the preferred transitions occurred between feeding on the benthic food and conflict/threat MAP, erect-fins or chase. In those cases where substrate-feed preceded erect-fins, chase followed the erect-fins. The laboratory series/benthic diet fish did
Figure 17. Preceding-following preferred transitions for the field series/benthic diet/dominant fish at months 0-3. Direction of the arrows indicates the sequence from the preceding to the following MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the preceding and following MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Double circles indicate MAPs that followed themselves as preferred transitions. Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 18. Preceding-following preferred transitions for the field
series/plankton diet/dominant fish at months 0-3. Direction of the
arrows indicates the sequence from the preceding to the following MAP.
Widths of the arrows indicate the extent of departure from a predicted
random association between the preceding and following MAPs; i.e.,
they occurred more often than would be predicted by chance. The wider
the arrow the larger the departure. Dashed lines are preferred
transitions with values slightly below the critical cell values (see
text). Double circles indicate MAPs that followed themselves as
preferred transitions. Abbreviation for the MAPs: AP = approach, BT
= back-toward, CH = chase, EF = erect-fins, PF = plankton-feed, SF =
substrate-feed, WD = withdraw.
Figure 19. Preceding-following preferred transitions for the laboratory series/benthic diet/dominant fish at months 0-3. Direction of the arrows indicates the sequence from the preceding to the following MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the preceding and following MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Double circles indicate MAPs that followed themselves as preferred transitions. Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 20. Preceding-following preferred transitions for the laboratory series/plankton diet/dominant fish at months 0-3. Direction of the arrows indicates the sequence from the preceding to the following MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the preceding and following MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Double circles indicate MAPs that followed themselves as preferred transitions. Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
not show as direct a relationship between feeding and attack except at month 1 when substrate-feed exhibited a preferred transition to chase. At month 1 and 2 however, another feeding group MAP, back-toward did form a preferred transition with erect-fins which in turn formed a preferred transition with chase.

The field series/plankton diet/dominant fish showed a similar pattern involving plankton-feed. At months 0 and 1 plankton-feed had a preferred transition to approach which in turn formed a preferred transition with chase. Back-toward, another feeding group MAP, also formed a preferred transition with chase at month 0 and later at month 3 back-toward had a transition to erect-fins which in turn had a transition to approach. Month 3 did show the one exception with the preferred transition of substrate-feed to chase. The laboratory series/plankton diet dominant fish showed only a weak preferred transition form back-toward to approach at month 1.

The subordinant fish (Figs. 21-24) also exhibited two functional groups of MAPs: the feeding group (substrate-feed, plankton-feed, approach, and back-toward), and the self-defense group (withdraw, flee, and present-dorsal). Erect-fins was associated with feeding in benthic diet fish possibly due to the conflict involved with feeding on the preferred diet of the dominant fish which was plankton at month 0 and benthic food at month 1. The same pattern was observed for the plankton diet fish with erect-fins following substrate-feed at month 0. During month 1 and later, erect-fins was better classified as expressing conflict or threat during transitions between the feeding group and the self-defense group. Back-toward also provided a link
Figure 21. Preceding-following preferred transitions for the field series/benthic diet/subordinate fish at months 0-3. Direction of the arrows indicates the sequence from the preceding to the following MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the preceding and following MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Double circles indicate MAPs that followed themselves as preferred transitions. Abbreviation for the MAPs: AP = approach, BT = back-toward, EF = erect-fins, FL = flee, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 22. Preceding-following preferred transitions for the field series/plankton diet/subordinate fish at months 0-3. Direction of the arrows indicates the sequence from the preceding to the following MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the preceding and following MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Double circles indicate MAPs that followed themselves as preferred transitions. Abbreviation for the MAPs: AP = approach, BT = back-toward, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 23. Preceding-following preferred transitions for the laboratory series/benthic diet/subordinant fish at months 0-3. Direction of the arrows indicates the sequence from the preceding to the following MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the preceding and following MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Double circles indicate MAPs that followed themselves as preferred transitions. Abbreviation for the MAPs: AP = approach, BT = back-toward, EF = erect-fins, FL = flee, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 24. Preceding-following preferred transitions for the laboratory series/plankton diet/subordinant fish at months 0-3. Direction of the arrows indicates the sequence from the preceding to the following MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the preceding and following MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Double circles indicate MAPs that followed themselves as preferred transitions. Abbreviation for the MAPs: AP = approach, BT = back-toward, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
between the two groups: by sometimes preceding flee, preceding erect-fins at month 3 in the laboratory series/benthic fish, and preceding present-dorsal at month 3 in the laboratory series/plankton fish.

There was a shift in the benthic diet fish from back-toward preceding substrate-feed at an early age to back-toward preceding plankton-feed later. This appeared to be a result of the diet treatment manipulation. Approach instead of withdraw was included in the subordinant fish feeding group and back-toward frequently preceded as well as followed approach.

Present-dorsal was a maneuver included in the self-defense group because it clearly represented the subordinant fish's attempts to protect its lateral and posterior body regions from attack by the dominant fish. It was most used by the plankton diet fish at month 3 when the subordinant fish was unable to distance itself sufficiently from the dominant fish. This was evident by flee preceding and following present-dorsal. Present-dorsal originated at month 1 in the laboratory series/plankton diet fish (Fig. 24) preceding plankton-feed. At month 2, in the same group of fish, it preceded the feeding group MAP approach and the self-defense MAP flee. This same pattern of association occurred at month 3 in the field series (Fig. 22).

Subordinant fish feeding MAPs formed transitions to the self-defense group more often in the field series than the laboratory series (Figs. 21-24). No preferred transitions occurred between the feeding and the self-defense groups at settlement age. The field series/benthic diet/subordinant fish showed a preferred transition between substrate-feed and flee at months 1-2, and changed to between
substrate-feed and erect-fins at month 3. In the field series/plankton diet/subordinant fish, substrate-feed preceded flee at month 1 only, and changed to plankton-feed preceding flee at months 2-3. This indicated that the subordinant fish were being chased from the treatment diet more often than randomly predicted. The laboratory series showed only 2 preferred transitions between feeding MAPs and the self-defense group. The benthic diet/subordinant fish at month 2 preceded flee with plankton-feed, and in the plankton diet fish at month 1 present-dorsal preceded plankton-feed.

Several MAPs followed themselves. These repeating MAPs included substrate-feed and plankton-feed in most groups of fish, indicating feeding bouts longer than five seconds in which multiple bites were taken in succession. Back-toward also followed itself in all groups except the laboratory series/plankton diet fish. Approach and withdraw also followed themselves but were removed from the analysis because of the effect of these highly preferred transitions had on the rest of the matrix.

A summary of the placement of MAPs within the functional groups of behavior is listed in Table 5. The feeding group consisted of plankton-feed, substrate-feed and back-toward for both the dominant and subordinant fish. Withdraw was included in the feeding group for the dominant fish and approach was included in the feeding group for the subordinant fish. Erect-fins was treated separately as a conflict/threat MAP that formed a transitional link between the other MAP groups. The attack group was only expressed by the dominant fish and consisted of the MAPs; approach, and chase. The self-defense
Table 5. Summary of Modal Action Patterns (MAPs) included in each functional group of MAPs.

<table>
<thead>
<tr>
<th>Functional group</th>
<th>Dominant fish</th>
<th>Subordinant fish</th>
</tr>
</thead>
<tbody>
<tr>
<td>Feeding</td>
<td>Plankton-feed</td>
<td>Plankton-feed</td>
</tr>
<tr>
<td></td>
<td>Substrate-feed</td>
<td>Substrate-feed</td>
</tr>
<tr>
<td></td>
<td>Back-toward</td>
<td>Back-toward</td>
</tr>
<tr>
<td></td>
<td>Withdraw</td>
<td>Approach</td>
</tr>
<tr>
<td>Attack</td>
<td>Approach</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Chase</td>
<td></td>
</tr>
<tr>
<td>Self-defense</td>
<td></td>
<td>Withdraw</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Flee</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Present-dorsal</td>
</tr>
<tr>
<td>Conflict/Threat</td>
<td>Erect-fins</td>
<td>Erect-fins</td>
</tr>
</tbody>
</table>
group was evident only in the subordinant fish and comprised the MAPs; withdraw, flee, and present-dorsal.

**Signal-response transitions**

Signal-response preferred transitions for the field series are shown in Figs. 25-28 and for the laboratory series in Figs. 29-32. Dominant fish attack group MAPs (chase and approach) preceded and followed the subordinant fish self-defense MAPs (withdraw, flee, and present dorsal). Chase preceded flee in all groups except field series/benthic diet/month 0, and the reciprocal of flee preceding chase occurred in all fish groups. The preferred transition of chase to flee departed more from that predicted by a random association than did the preferred transition of flee to chase. Chase preceded subordinant fish withdraw in all fish groups at month 2 and 3, and in the field series/benthic diet and laboratory series/plankton diet at month 1. The opposite preferred transition (subordinant fish withdraw to chase) occurred only at month 0 in all fish groups. Dominant fish approach preceded subordinant fish flee at all months except for both series' benthic diet/month 3. The reciprocal preferred transition occurred during months 2 and 3 of the benthic diet in both series, and during month 1 and 2 of the laboratory series/plankton diet fish. Dominant fish approach preceded subordinant fish withdraw in all groups of fish during the first two months except the field series/benthic diet/month 1. The reciprocal preferred transition never occurred. Subordinant fish present-dorsal followed dominant
Figure 25. Signal-response preferred transitions for the field series/benthic diet at months 0-3 with the dominant fish as the signaler and the subordinant fish as the respondent. Dominant fish on the lower row and the subordinant fish on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 26. Signal-response preferred transitions for the field series/plankton diet at months 0-3 with the dominant fish as the signaler and the subordinant fish as the respondent. Dominant fish on the lower row and the subordinant fish on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 27. Signal-response preferred transitions for the field series/benthic diet at months 0-3 with the subordinant fish as the signaler and the dominant fish as the respondent. Dominant fish MAPs on the lower row and the subordinant fish MAPs on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 28. Signal-response preferred transitions for the field series/plankton diet at months 0-3 with the subordinant fish as the signaler and the dominant fish as the respondent. Dominant fish MAPs on the lower row and the subordinant fish MAPs on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 29. Signal-response preferred transitions for the laboratory series/benthic diet at months 0-3 with the dominant fish as the signaler and the subordinant fish as the respondent. Dominant fish MAPs on the lower row and the subordinant fish MAPs on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 30. Signal-response preferred transitions for the laboratory series/plankton diet at months 0-3 with the dominant fish as the signaler and the subordinant fish as the respondent. Dominant fish MAPs on the lower row and the subordinant fish MAPs on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 31. Signal-response preferred transitions for the laboratory series/benthic diet at months 0-3 with the subordinant fish as the signaler and the dominant fish as the respondent. Dominant fish MAPs on the lower row and the subordinant fish MAPs on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
Figure 32. Signal-response preferred transitions for the laboratory series/plankton diet at months 0-3 with the subordinant fish as the signaler and the dominant fish as the respondent. Dominant fish MAPs on the lower row and the subordinant fish MAPs on the upper row. Direction of the arrows indicates the sequence from the signal to the response MAP. Widths of the arrows indicate the extent of departure from a predicted random association between the signal and response MAPs; i.e., they occurred more often than would be predicted by chance. The wider the arrow, the larger the departure. Dashed lines are preferred transitions with values slightly below the critical cell values (see text). Abbreviation for the MAPs: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
MONTH 0

MONTH 1

MONTH 2

MONTH 3

133
fish approach once, at month 1 of the laboratory series/benthic diet fish. Present-dorsal never preceded any dominant fish MAPs.

Feeding by one fish very often resulted in the other fish feeding on the same food type (benthic or plankton). Only in the laboratory series/plankton diet (Figs. 30 and 32) did the two fish tested together consistently feed on different food types. In this group, initially when the dominant fish exhibited substrate-feed, the subordinant fish also showed substrate-feed. At month 1 substrate-feed by the dominant fish was followed by substrate-feed and plankton-feed in the subordinant fish. At this time, both types of feeding by the dominant fish also followed plankton-feed by the subordinant. At month 2 and 3 the dominant fish exhibited substrate-feed and the subordinant fish followed with plankton-feed. The reciprocal pattern also occurred at month 2. The signal-response preferred transitions supported the classification of MAPs into functional groups relating to feeding, self-defense, and attack behavior derived from the preceding-following diads.

Erect-fins by the dominant fish developed a threat component over the course of the study. During the first 2 months the preceding-following preferred transitions indicated that erect-fins was followed by chase in all groups of fish and this pattern persisted to month 3 in the benthic diet fish of both series. Starting at month 2 the preceding MAP erect-fins also was followed by approach and in the plankton diet groups of both series this preferred transition replaced the erect-fins to chase preferred transition. The subordinant fish
continued to flee in response to the dominant fish erect-fins even though erect-fins was no longer paired with or a reliable indicator of chasing. This indicated that dominant fish erect-fins had acquired some threat status. At month 3 in the field series and from month 1 on in the laboratory series the subordinant fish withdrew after erect-fins by the dominant fish. The dominant fish erect-fins MAP often resulted in the subordinant fish also erecting its fins. The reverse sequence occurred half as often.

**Information theory analysis**

There was no correlation between the total number of diads in each matrix and the amount of information shared between the signal and response (Tz(s;r)) values for that matrix (Pearson correlation coefficient = 0.004 and 0.085 for field and laboratory series, p > 0.05, N = 16). Testing the number of diads in each group for extreme values that might be considered outliers produced conflicting results. The first test from Dixon and Massey (1957) revealed no outliers (q = 3.8 and 3.2 for the field and laboratory series, p > 0.05, N = 16). A second test from Dixon and Massey (1957) indicated that the number of subordinant to dominant fish diads of the field series/benthic diet/month 2 was higher than expected if drawn from the same population (r² = .536, p < 0.05, N = 16). This may have indicated a sample size bias if the (Tz(s;r)) value for the field series/benthic diet subordinant to dominant fish transitions was also high, but it was among the lowest (Fig 33), so sample size bias was probably not a factor.
Figure 33. The amount of information shared between the signal and response ($T_z(s;r)$) for the field series. Horizontal and vertical bars indicate non-significant differences based on non-overlapping 95% confidence limits.
plankton diet

Age Differences

benthic diet

plankton diet
A comparison between the field and laboratory series indicated that months 1 and 2 of the laboratory series (Fig. 34) had higher Tz(s;r) values (Table 6). In only one group, plankton diet/month 3 subordinant to dominant fish, did the field series have higher value than the laboratory series. Three groups, plankton diet/month 2 subordinant to dominant fish and both dominant to subordinant and subordinant to dominant benthic diet fish/month 3, had no differences between the field and laboratory series. The laboratory series fish at months 1 and 2 seemed to be exchanging more information.

Age differences in the field series indicated a general trend for increasing Tz(s;r) values (Fig. 33). There were no differences between ages for the benthic diet/subordinant to dominant fish Tz(s;r) values. Differences in the other groups of fish most consistently separated months 0 and 1 from months 2 and 3. There was some overlap of age groups among the dominant to subordinant fish Tz(s;r) values. In the laboratory series (Fig. 34), age differences occurred with the largest differences during months 1 and 2, the smallest values at month 0, and month 3 being intermediate. The high Tz(s;r) values for the laboratory series month 1 and 2 discussed previously account for the age pattern differences between the field and laboratory series.

Differences in Tz(s;r) values between diets in the field series existed only for the subordinant to dominant fish at month 3 (Fig. 33), where the benthic diet group had a lower value. This relationship appeared to be an extension of a trend evident at month 2. The opposite was true for the laboratory series (Fig. 34): There the plankton diet fish had lower Tz(s;r) values and also indicated a
Figure 34. The amount of information shared between the signal and response ($T_z(s;r)$) for the laboratory series. Horizontal and vertical bars indicate non-significant differences based on non-overlapping 95% confidence limits.
Table 6. Ratio of field series $T_z(x;y)$ values to laboratory $T_z(x;y)$ values. Ratio of 1 at month 0 indicates same fish used in both series at that age. * = significant differences between series based on non-overlapping 95% confidence limits.

<table>
<thead>
<tr>
<th>AGE Months</th>
<th>Benthic diet</th>
<th></th>
<th>Plankton diet</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>dominant to subordinant</td>
<td>dominant to subordinant</td>
<td></td>
<td></td>
</tr>
<tr>
<td>0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>1</td>
<td>.252 *</td>
<td>.444 *</td>
<td>.264 *</td>
<td>.237 *</td>
</tr>
<tr>
<td>2</td>
<td>.405 *</td>
<td>.254 *</td>
<td>.545 *</td>
<td>.655</td>
</tr>
<tr>
<td>3</td>
<td>.930</td>
<td>.671</td>
<td>.531 *</td>
<td>2.444 *</td>
</tr>
</tbody>
</table>
continued divergence between the two diet treatments apparent earlier. The lab series also had diet differences for the dominant to subordinant/month 1 fish that diminished with time.

In all cases where there were differences in Tz(s;r) between the dominant to subordinant fish and subordinant to dominant fish the dominant to subordinant fish had the higher value (Figs. 33 and 34). The field series showed differences in the direction of information flow due to social rank at month 0 for both diet treatments and at months 2 and 3 for the benthic diet groups. In the laboratory series the dominant fish had higher Tz(s;r) values in all groups at all ages.

The transmission efficiency (TE) showed virtually the same pattern as the Tz(s;r) values. The values for TE indicated that only 0.5 to 6.0% of the total amount of information available was shared between the signaler and the responder. There was a general increase in transmission efficiency in the field series over time except for benthic diet/subordinant to dominant fish TE. The laboratory series showed a peak in transmission efficiency at months 1 and 2. The dominant fish had higher TE estimates where differences occurred between social rank, reflecting the pattern shown for the Tz(s;r) values. Overall, there were no clear differences between the two diets with regards to the TE estimates.

DISCUSSION

Preceding-following preferred transitions showed differences between the diet treatments at settlement. This suggested that, even though care was taken to collect naive, newly metamorphosed juvenile
fish, some environmental effects had already been manifested. There are several possibilities to account for early differences. First, there may have been genetic differences in the fish that settled in each habitat. Selection of a settlement site is an active process on the part of some fishes (Sale 1969a, 1969b). However, to date, there is no evidence that reef fish selecting different habitats are genetically different or, even if such differences existed, that these would affect the behavior of the fish.

Second, individual differences, given a small sample size, may explain the results. Huntingford (1976) found that the stickleback, Gasterosteus aculeatus, showed individual differences in aggression and that these differences were consistent over time. For my study, combining the two diet treatments at month 0 into one matrix, i.e., assuming no genetic differences, resulted in the persistence of the major preferred transitions of each fish group and produced no change in the interpretation of the data. Even if the differences could be attributed to sampling bias, there appeared to be no major effect on the results.

Third, the brief exposure of juvenile fish to tidepools or buoys prior to capture may have begun to influence their behavior. Since the confinement in the trial aquarium may be considered as more similar to confinement in a tidepool, the benthic diet fish captured from tidepools should have been more acclimated to the trial aquarium. In chapter III, the only measure showing a difference at settlement (month 0) between diet groups was the activity index, a measure of the number of turns made by a fish. The plankton diet fish were more
active than the benthic diet fish. The dominant plankton diet fish had more preceding-following preferred transitions between the functional groups of MAPs than did the dominant benthic diet fish. This supports the "brief experience" explanation for the diet group differences in that the greater numbers of transitions between groups of MAPs would likely have entailed greater activity on the part of the fish. Subordinate fish did not show as many diet differences in the preceding-following preferred transitions between the various MAP groups, possibly due to inhibition by the dominant fish.

The number of MAP categories found is a function of the scope of the study: studies investigating breeding may find territorial defense, courtship, copulation, and parental care (Baerends 1984); while studies looking at resident-intruder encounters may find only offensive and defensive aggression (Blanchard and Blanchard 1977). Caution is dictated since the Modal Action Patterns (MAPs) observed in a single, focused study may be associated with other functional groups of behavior under other circumstances or during other life history stages.

The nature of my study resulted in the categorization of behavior into four functional groups: feeding, attack, threat, and self-defense. Other aspects of the social behavior of *Abudefduf abdominalis* were intentionally excluded. Furthermore, by design, my study only considered the interaction of fish after dominance had been initially established. Most studies of aggression have concentrated on the period of time during dominance hierarchy formation. Activities such as feeding seldom occur during these initial phases of
an encounter. The period after the establishment of dominance was considered in my study since the relationship between food resources and aggression was of interest. One consequence was the elimination of several MAPs (close-frontal, parallel-swim, and swim-up) that rarely occurred after dominance was established but did exist in the initial phase of aggressive encounters. Other studies reporting mixed or weak results with reference to food resources (e.g., Blanchard et al. 1984) may reflect the inadequate expression of feeding during the trials. Other studies (Heiligenberg 1965, Rasa 1969) have found reason to separate aggression into offensive and defensive forms in fishes.

There was a possibility that some of the functional groups of preceding-following MAPs were a product of the way the MAPs were defined. Chase was defined as a rapid approach. The sequence of approach--chase--approach might be explained as being one MAP, with an initial acceleration phase and a terminal deceleration phase. Two factors argued against this. First, was the frequent asymmetry that existed in the strength of the preferred transitions approach--chase and chase--approach. In fact, there were occasions when the chase--approach preferred transition was not present. Secondly, if approach and chase were so closely linked, one would also expect the signal-response preferred transitions to be very similar. The preferred transition of dominant fish chase to subordinant fish flee was usually much stronger than the preferred transition of dominant fish approach to subordinant fish flee, and in couple of cases the dominant fish approach to subordinant fish flee preferred transition
was not significantly different than that predicted by the random model. Preferred transitions involving both approach and chase by the dominant fish preceding withdraw by the subordinant fish occurred in only one group of fish; usually it was one or the other, but not both. Approach and chase were therefore considered separate MAPs within the attack group.

The same argument can be made for the preceding-following MAPs of withdraw and flee. There was asymmetry between the strength of the preferred transition, with flee--withdraw almost always being greater than withdraw--flee. Withdraw never formed preceding-following preferred transitions with any other MAPs, while flee formed several. Subordinant fish flee and withdraw were also very independent, as signals, in forming preferred transition with other dominant fish MAPs. Withdraw and flee were, therefore, treated as separate MAPs of the self-defense group.

The terms used to describe the MAP groups follow Blanchard and Blanchard (1988) who considered attack and self-defense behavior in terms of conspecific and predator encounters. Both approach and chase were MAPs associated with decreasing the distance between the two fish and often resulted in the other fish moving away. All three MAPs in the self-defense group removed the subordinant fish from harm by displacement (withdraw and flee) or by protection of the body by maneuvering (present-dorsal).

Attack and defense are considered by Blanchard and Blanchard (1988, and 1990) to be diametrically opposed systems with no overlap. This was true for my study at a system level but not necessarily at
the individual MAP level. After month 0, flee was the only signal that formed a preferred transition with the other fish. The subordinant fish preferred transition of withdraw to dominant fish chase, at settlement, suggested a less selective response by the dominant fish or a lowered threshold was needed to release a chase. The dominant fish chase, however, was not the only signal that formed preferred transitions with flee by the subordinant fish. Dominant fish approach and erect-fins also had preferred transition with flee. There was no exclusive preferred transitions between chase and flee. The inclusion of erect-fins, in either fish, within the discussion of attack and self-defense indicated a close association with these MAPs and a threat display function. Approach and withdraw were even less exclusive in the MAPs they formed preferred transition with, yet they were clearly closely related to attack and self-defense.

Several explanations for the presence of overlap between the MAP groups in this study can be suggested. First, the MAP groups had not yet become discreet in developmental terms. During maturation there is a trend for behavioral systems to either diverge from each other, becoming more discreet and recognizable as separate behavioral groups (Chalmers 1980), or to integrate components from several origins into new systems (Kruijt 1964, Hailman 1967, Baerends 1984). Either process, if incomplete, could explain the overlap between groups.

Second, because of a limited number of MAPs available, individuals may have had to use a MAP for more than one function (Wiepkema 1961, Baerends 1984, and Fernandez-Espejo and Mir 1990). Approach and withdraw occurred in feeding context as well as the
attack and self-defense groups. *Abudefduf abdominalis* are often attracted to conspecifics that are feeding (Helfrich 1958, and personal observations). However, this does not explain the non-exclusive associations between the two MAP groups such as approach and chase both preceding flee and chase preceding both flee and withdraw.

Third, approach and withdraw may not belong in the attack and self-defense groups: rather they may function as transitions between groups. This seems unlikely since approach and withdraw never led to any MAP outside of the behavior group in which they occurred. The links were always MAPs in other groups preceding approach and withdraw. The magnitude of the preferred transition between flee and withdraw also indicated a strong association.

Last, attack and self-defense may not be two diametrically opposed systems (Adam 1979, Torricelli et al. 1989), but part of a continuum listed: chase, approach, erect-fins (possibly), withdraw, flee, and present-dorsal. Two fish interacting, after dominance was established, could be represented in this sequence as two fish progressing in opposite directions; the dominant fish towards the chase end and the subordinant fish towards the flee end. Evidence for this pattern was inconclusive in my study as neither fish used the entire continuum. Withdraw in the subordinant fish also posed a problem for this interpretation since it only preceded and followed flee, and though in an intermediate position in the continuum it never formed preferred transitions with adjacent erect-fins or approach (i.e., assuming the exclusion of erect-fins). While a continuum may be indicated at an ethological level, neurological and pharmacological
evidence (Blanchard and Blanchard 1988 and 1990) indicate separate systems for offensive and defensive aggression.

Attack MAPs in my study did not always occur in response to self-defense MAPs as suggested by Blanchard and Blanchard (1990). Rather, there was a greater probability of chase preceding flee than the reverse sequence although both transitions occurred more often than predicted by random chance. Withdraw by the subordinant fish was not followed by dominant fish approach but by dominant fish withdraw, a feeding group MAP for the dominant fish.

The function of erect-fins changed over the course of the study. Its origins appeared to be locomotion involved with tight or rapid turns and holding stationary position (Tooker and Miller 1980). Myrberg (1965) proposed that holding stationary allowed the fish to further evaluate conditions. In this study, erected medial fins were also part of the description for present-dorsal, a maneuver involving rapid, tight turns to keep the forehead and dorsal spines oriented towards the opponent. While the erected dorsal spiny fin presented formidable armament, the MAP included the anal fin and the soft dorsal fin being erected, both of which provided little protection in a frontal assault. Their function appeared to be enhancement of maneuverability.

The use of erect-fins in a conflict situation may have originated from intention movements associated with locomotion (Hinde 1970, Brown 1975). In fish, a conflict is likely to be resolved with a change in direction, which in turn would involve erection of the medial fins. Erect-fins, in my study, most often preceded chase or approach and
withdraw and also resulted in shifts from the attack group to the feeding group. The decision to approach or withdraw and the decision to switch from one behavior group to another could involve conflict within the fish. The cichlid *Pelmatochromis kribensis* is reported to erect its fins to indicate uncertainty as well (Heiligenberg 1965).

In my study, the coupling of erect-fins with feeding MAPs at month 0 and 1 was related to the fact that the subordinant fish was feeding on the food that the dominant fish was also using heavily. This would have created some uncertainty or conflict on the part of the subordinant fish as to the response of the dominant fish under this circumstance.

Erect-fins as a threat display did not involve any change in form but a change in the context in which it was used. This occurred earlier in the plankton diet fish than in the benthic diet fish. Early on, the dominant fish had preceding-following preferred transitions of erect-fins to chase and the signal-response preferred transition of erect-fins to flee by the subordinant fish. This pattern continued to month 3 in the benthic diet groups. From month 2 on for the plankton diet dominant fish, the preceding-following preferred transition was erect-fins to approach, and not chase, while the response of the subordinant fish remained flee. This shift in emphasis from attack to threat with age is reported for the poeciliids *Poecilia (=Molliesenia) velifera* and *P. latipinna* (Parzefall 1969), blue gouramis, *Trichogaster trichopterus*, (Tooker and Miller 1980), and rainbow trout, *Salmo gairdneri*, (Cole and Noakes 1980). The differences between the two diet groups indicated the value of the
food resource or its defendability. The benthic diet dominant fish with a defendable food source continued to pair erect-fins with chase more often than did the dominant fish with only plankton diet experience.

The pairing of erect-fins with attack MAPs indicated a modification of behavior based on experience and may have represented learning. The subordinant fish may have learned to anticipate a chase from the preceding erect-fins and responded to avoid attack and the dominant fish may have learned to "use" erect-fins as an effective signal to cause the withdrawal of the subordinant fish without the cost of a chase. Such contingency experiences have been described as a process during ontogeny (Watson 1981, West and King 1985, King and West 1988). The occurrence of erect-fins earlier in the plankton diet fish argues against a morphological development process but the absence of expression does not necessarily mean the absence of capability (Bekoff 1978).

The dominant fish in both diet treatments responded by following feeding bouts on the treatment diet, substrate-feed in the benthic diet fish and plankton-feed in the plankton diet fish, with attack or threat group MAPs. This indicated that, based on the preferred transitions, the dominant fish were attempting to defend the food resource with which they were associated during rearing. Defense of food occurred in both diet treatments which seemed contrary to the hypothesis that only the benthic food, being fixed in time and place, would be defended. The constantly available plankton throughout the rearing aquaria should have prevented its defense as a food resource.
Although in the absence of a more defendable food resource, the next best tactic may be to defend a portion of whatever food source was present. This would in effect have created a priority access dominance hierarchy within the vicinity of each fish. Barlow (1962) reports that young cichlid *Badis badis* first sporadically defend areas mid-water that are associated with food. *Blennius pholis* seem to defend a personal space early in development with food being one factor that influences aggression during this time (Gibson 1968). In the benthic diet treatment both plankton and benthic foods were available yet the dominant fish only paired feeding on the benthic food with aggression. If only a priority dominance hierarchy was in effect, then both food types should have been equally associated with attack and threat group MAPs.

The month 3 field series/plankton diet/dominant fish did form a weak preferred transition from substrate-feed to chase. This indicated older juveniles from under buoys had experienced a defendable benthic diet resource before capture or that they more quickly recognized the nature of the provided benthic food as a potentially defendable resource.

Present-dorsal is a maneuver to block an offensive attack by the opponent. It is comparable to rats rolling over on their backs to protect the back from bites during an offensive attack (Blanchard and Blanchard 1980). Posterior areas of a fish, its anal fin, caudal fin and peduncle, appear to be frequent bite targets as indicated by numerous references to fin damage and carouseling in the literature (e.g., Barlow 1962, Simpson 1968, Tooker and Miller 1980, Brown and
The appearance of present-dorsal did not seem related to ontogenetic processes, but rather to situations requiring a defensive posture. The inability of the subordinant fish to escape from the dominant fish often resulted in the subordinant fish being trapped in a corner where it exhibited present-dorsal until it could flee or the dominant fish ended the encounter. Why present-dorsal was used almost exclusively by the plankton diet fish cannot be explained. Both diet treatments in the laboratory series expressed present-dorsal at month 1, so the MAP was present in the fishes repertoire at month 1. The earlier appearance of present-dorsal in the laboratory series may have been related to the higher levels of aggression compared to the field series fish (see chapter III).

The values for the transmission of information between fish \( T_z(s;r) \) and the transmission efficiency (TE) paralleled each other in all groups of fish. The similarity in the information content of the signal \( H_s \) across all groups seemed to account for the correlation between the \( T_z(s;r) \) and TE since TE was defined as \( T_z(s;r)/H_s \). This made it easier to interpret the results as the TE showed the same relationship between groups of fish as did the \( T_z(s;r) \) values and differences between groups of fish could be compared using the 95% confidence limits calculated for the \( T_z(s;r) \) values.

There was an increase in the amount of information exchanged between fish with an increase in age. This was most obvious in the field series although the pattern was not the same in each group of fish. The transmission of information from subordinant to dominant fish remained unchanged only in the field series/benthic diet.
treatment. The laboratory series showed the same pattern except that the intermediate months had higher values than did the last month. This was probably due to the confinement within the rearing aquaria forcing an earlier increase in communication. Overall, the amount of information transmitted increased with age.

Diet differences existed only in three groups of fish. The amount of information transmitted from the subordinant to dominant fish in the field series/benthic diet/month 3 was lower than the plankton diet group and represented a diverging trend due to the consistently low $T_z(s;r)$ in the benthic diet fish. Baer (1980) suggested that fewer very effective signals could result in better communication by minimizing the possibility of confusion in the responder. There were no highly preferred transitions formed among the seven signal MAPs and seven response MAPs in the benthic diet fish, while the plankton diet fish had a highly preferred transition from flee to erect-fins among only four signal and four response MAPs. This difference may have contributed to the low transmission of information from subordinant to dominant fish in the benthic diet fish.

The diet differences in the laboratory series may also relate to more persistent signals. The differences in the dominant to subordinant fish at month 1 indicated that the benthic diet fish had highly preferred transitions from dominant fish withdraw to subordinant fish approach, and dominant fish approach to subordinant fish plankton-feed than did the plankton diet fish. The differences between diet treatments at month 3 in the information transmitted
reflected the fact that there was less uncertainty of the response in the plankton diet fish and so less information was transmitted.

The amount of information exchanged from the dominant fish to the subordinate fish was greater than from the subordinate fish to the dominant fish in all but the field series/plankton diet fish. In this group, even though the 95% confidence limits of the Tz(s;r) did overlap, the trend was the same as in the rest of the groups.

There are few other studies that compare the direction of information flow between dominant and subordinate individuals. Of those, most indicate that the exchange of information is higher from the loser to the winner than the opposite (Hazlett and Bossert 1965, Baer 1980, Hazlett 1980). Only Moehring (1972) shows the same pattern as my study. The difference seems to be related to the methodology and time scale involved in the trials. Baer (1980), studying surgeonfishes (Acanthuridae), Hazlett and Bossert (1965), and Hazlett (1980), studying hermit crabs (Paguridae and Diogenidae), all recorded brief encounters that ended with the first withdrawal and appropriately called the contestants winners and losers since no stable dominance order was established. During such initial contact both individuals probably reacted similarly, escalating together until one changed and began to act different from the other. This eventual loser, by fact of changing its behavior, provided the other with more information and resulted in the higher transmission values for subordinate to dominant preferred transitions.

My study omitted these initial encounters and used interactions only from the hour after dominance was established. The two 30 min
segments allowed for repeated encounters to occur between the same two subjects. Moehring (1972), similarly, used a one hour period for each pair of fish but did not separate the initial dominance forming segment from the record. She did note that for male-male encounters of the goby *Psilogobius mainlandi* the first five minute period had a higher frequency of aggressive acts and that subsequent periods were more stable. This stability was probably due to the establishment of dominance during the first five minutes. The pattern of interaction during the remaining 55 minutes could have obscured any different pattern present only in the first five minutes.

After dominance was established, Moehring (1972) indicated that subordinant fish could avoid injury by being responsive to the dominant’s activities while the dominant fish could ignore the subordinant’s signal and not be responsive. This could also be the case in my study. The greater differences in $T_z(s;r)$ and $TE$ between the dominant and subordinant fish in the laboratory series, especially months 1 and 2, were likely due to the increased responsiveness of the subordinant fish confined in the rearing aquaria. This was particularly obvious for the dominant fish signal to subordinant fish response preferred transition of chase to flee and withdraw to approach that were higher in the laboratory than field series.

CONCLUSIONS

1. Modal Action Patterns (MAPs) could be categorized into four functional groups: feeding, attack, threat, and self-defense. The number of functional groups was determined by the nature of the study,
in my case, only MAPs associated with feeding and agonistic behavior were considered resulting in only four groups.

2. The MAPs approach and withdraw were associated with two different groups depending on social rank. Approach occurred with chase in the attack group of dominant fish, but in subordinant fish approach was grouped with feeding related MAPs. Withdraw was associated with self-defense MAPs in subordinant fish, but with the feeding group in dominant fish.

3. The dominant fish associated feeding on the treatment diet with attack and threat group MAPs. Dominant fish exposed to the addition of benthic food during rearing followed substrate-feed and back-toward with preferred transitions to the attack and threat groups. Plankton-feed did not lead to attack or threat MAPs. Dominant fish exposed to plankton only during rearing had preceding-following preferred transitions from plankton-feed to MAPs of the attack and threat group.

4. Benthic food was treated as a defendable food resource by the benthic diet fish, but plankton was treated the same way by the plankton diet fish. When plankton was the only food available the dominant fish perhaps attempted to defend that area of the water column in which it was feeding at the time.

5. Erect-fins probably originated from a locomotion function used frequently in conflict situations. It developed into a threat display after pairing with approach and chase in the dominant fish eventually causing the subordinant fish to flee without approach or chase. Erect-fins developed into a threat display earlier in the laboratory series/dominant fish than in the field series/dominant fish. The
possibility that learning plays a role in this process is noted but not proven.

6. Present-dorsal was a maneuver used by the subordinant fish to thwart an offensive attack by the dominant fish. It appeared early but was only used extensively at month 3 in the plankton diet groups when the subordinant fish was unable to escape the dominant fish.

7. There was an increase with age in the amount of information transmitted between fish. The efficiency of transmission also increase with age in most cases. The increases occurred earlier in the laboratory series probably due to the confinement within the rearing aquaria.

8. There were few differences between diet groups in the amount of information transmitted between fish. Those cases where differences existed indicated that a few highly preferred transitions increased the effectiveness of the signals and reduced the confusion in the respondent.

9. Overall, the amount of information exchanged from the dominant to the subordinant fish was higher than in the opposite direction. Subordinant fish were more attentive to the actions of the dominant fish than vice versa.
Chapter V

GENERAL DISCUSSION

Most of the Modal Action Patterns (MAPs) exhibited by juvenile *Abudefduf abdominalis* were present at the time of settlement to near shore, shallow water locations. The expression of a relatively complete repertoire so early in development appears to be a characteristic of species that lack parental care of the young (Burghardt 1978, Stamps 1978, Brown 1984). The availability of MAPs at an early age may be adaptive and serve the immediate needs of the individual (Oppenheim 1981). Three MAPs were not expressed at settlement age: parallel-swim, present-dorsal, and swim-up. Their absence may be attributed to a lack of neuro-anatomical development, the proper releaser, or an opportunity for expression. The onset of MAPs can be marked by development of the neuro-anatomy associated with the motor patterns (Gideiri, 1966, 1969, Bergmann 1971, Berg 1972), and this possibility cannot be excluded in my study. Lack of expression of a MAP, however, may not indicate the lack of capability to express the MAP. Bekoff (1978) found that the neurological circuits used to produce coordinated behavior in rats and chickens were present some time before the behavior was observed. What may be lacking is the appropriate releaser to allow the expression of the MAP. This appears to be the case for two species of scorpaenid fishes: the expression of agonistic behavior was dependent on the presence of a defendable resource (Hoelzer 1987). In my study, a lack of releasers was a possible cause for some MAPs being rarely expressed. The MAPs, tail-beat and close-frontal, occurred more
frequently during escalated agonistic encounters when dominance was being established. After dominance was established, these MAPs lacked opportunities for expression as agonistic encounters seldom escalated to the level where these MAPs were observed. Sheltering did not occur often, possibly due to the lack of a sufficiently strong releaser in the form of an adequate shelter. These three MAPs were among those dropped from further analysis due to their low occurrence.

There is another reason why a MAP may go undetected. If the act is rare in occurrence and the sample size small, then there is a strong likelihood of omission. In my study, this may account for the absence of present-dorsal, swim-up, and parallel-swim at settlement age. If the ontogeny of a MAP occurs by the gradual increase in frequency of expression (Groothuis 1969a), then the onset of a MAP may be attributed to a later time, unless sampling is adequate to detect the MAP's presence.

The hierarchical organization of behavior was evident in the association of different MAPs with the roles of dominant and subordinant. The dominant fish showed more approach, chase, and erect-fins, while the subordinant fish expressed more withdraw, flee, back-toward, and present-dorsal. This has also been shown in other studies, including the cichlid, Astatotilapia burtoni, (Ferno 1987) and the rat, Rattus norvegicus, (Fernandez-Espejo and Mir 1990).

Further evidence for hierarchical organization came from the functional groups of MAPs that were derived from the preferred transitions formed between preceding-following MAPs within each fish and signal-response MAPs between the paired fish. These transitions
occurred more frequently than predicted by a model assuming only random associations between MAPs. The four groups of MAPs apparent in my study were: feeding, attack, threat, and self-defense. After dominance was established, the dominant fish expressed MAPs of the attack group and the subordinant fish expressed MAPs of the self-defense group. Both fish exhibited feeding and threat MAPs.

Figure 35 shows a schematic of the hierarchy of MAPs as used in my study. It follows the terminology of McFarland and Sibly (1975) with "Activities" representing major categories of behavior such as nest building, feeding, or courtship. These are composed of "Actions" that do not overlap each other temporally, e.g., mate search and copulation. A group of "Characteristics" then describes each action, although a characteristic can be used by more than one action. In my study, the MAPs were the characteristics and the functional groups were the actions.

Modal action patterns were not exclusively confined to one functional group. As indicated by Hinde (1970), McFarland and Sibly (1975), and Baerends (1984), MAPs can belong to more than one action category (functional group). For A. abdominalis, approach and withdraw occurred in both feeding and agonistic groups, although used differently depending on social rank. Approach was classified in the attack group of the dominant fish and the feeding group of the subordinant fish. The reverse was true for withdraw; it was associated with self-defense in the subordinant fish and feeding in the dominant fish.
Figure 35. Hierarchical classification scheme based on the functional groups of Modal Action Patterns (MAPs) derived from the median preceding-following preferred transitions described in Chapter IV. Terminology of categories based on McFarland and Sibly (1975) (see text). Solid lines indicate linkages between different levels of the hierarchy. Dashed lines indicate uncertain linkages based on indirect evidence. Abbreviations: AP = approach, BT = back-toward, CH = chase, EF = erect-fins, FL = flee, PD = present-dorsal, PF = plankton-feed, SF = substrate-feed, WD = withdraw.
HIERARCHICAL CLASSIFICATION

ACTIVITIES

HUNGER

SEARCH

ATTACK

AGONISM

CHARACTERISTICS

(ACTIONS)

SF

PF

BT

AP

WD

CH

FL

PD

EF

SELF-DEFENSE

AGONISM

DOMINANT ROLE

SUBORDINANT ROLE
In Figure 35, the functional group of feeding in Chapter IV has been separated into two action categories, Eat, and Search, within the activity of Hunger. Substrate-feed and plankton-feed were directly related to the ingestion, or attempted ingestion of food items. Back-toward and both approach and withdraw, in the feeding context, indicated searching for food. Approach and withdraw had highly significant preceding-following preferred transitions with themselves and with each other. These preferred transitions were excluded from the matrices because they were considered less interesting in a social context and masked other interesting transitions between social MAPs (see Methods, Chapter IV). The way approach and withdraw were defined, in this study, remains a problem because there was a high probability, even a logical necessity, that one followed the other when the two fish were acting independently of each other’s actions. This is further supported by the fact that the pattern for the activity index, a measure of the turning frequency, was very similar to the pattern for the frequency of approach and withdraw. Much of this time was probably involved with searching for food.

The preferred transitions that linked dominant-fish-withdraw to the feeding group MAPs appeared related to what the subordinant fish was doing. The signal-response preferred transitions indicated that after a dominant-fish-withdraw, the subordinant fish often did an approach or began feeding, both MAPs categorized as hunger related, based on the preceding-following preferred transitions of the subordinant fish. Feeding by one fish often resulted in feeding in the other fish, so withdraw by the dominant led indirectly to feeding
by the dominant fish. The same type of signal-response linkage occurred in the case of subordinant fish approach. The dominant fish responded to an approach with feeding or an approach. If feeding was the response, then both fish were likely to begin feeding simultaneously although not necessarily on the same food type.

The number of groups of MAPs found depends on the nature of the study. Those studies concentrating on agonism may find a similar suite of actions as my study, but the inclusion of MAP groups like feeding may depend on an experimental design that would allow the expression of feeding behavior. Other studies concentrating on, for example, grooming (Lefebvre and Joly 1982, Berridge 1990) or pre-spawning behavior (Baerends 1984) would find different groupings of behaviors.

The hierarchy of organization described in my study is based on functional groups, but there may be an overlapping hierarchy of decisions (Dawkins 1976). A "software" program of such a decision hierarchy would take the form of a series of rules that would indicate under what conditions behavior would change from one act to another. Although I express the rules in the form of "action rules" as discussed by Dawkins (1976), I do not mean to imply that the fish are necessarily "programmed" in this fashion. There is a decision sequence that appears to function in dominant juvenile A. abdominalis: if feeding on a potentially defendable food resource, then attack subordinant. This rule would be adaptive if the subordinant fish was displaced from a good food resource. Feeding by the dominant fish on a good resource, but of unknown defendability would be linked with a
test of the feasibility of defense. If the subordinant could be
excluded repeatedly, then the resource would be considered defendable.
If the resource was not defendable then the fish would cease
attempting to defend it. This did not necessarily occur in the trial
aquaria and is discussed later.

Another decision sequence by the dominant fish could be expressed
within the individual: If a threat display is used, then switch to
feeding. This decision sequence could also be stated in terms of
interspecific action: if the subordinant fish withdraws, then the
dominant fish switches to feeding. These two rules are associated
since threats by the dominant fish were often followed by subordinant
fish withdraw. Which decision is actually being made in this case can
not be determined, and in fact, both might occur. The decision can be
made based on either motivational state within the individual, or the
actions of the other fish that are compared with prior experience.

The subordinant fish followed a decision sequence: if attacked,
then exhibit self-defense. This decision is clearly adaptive in that
the subordinant attempts to avoid injury. At a later stage of
development another decision became evident: if threatened, then
exhibit self-defense. This appears to be an example of a preexisting
MAP being expressed in a new context (Ward and Barlow 1967, Tooker and
Miller 1980). It is possible, although not demonstrated in my study,
that the contingency between attack MAPs and erect-fins led to
learning by the subordinant fish that erect-fins was a good predictor
of an imminent chase. If so, then learning may play an important role
in formulating new decisions within the hierarchy. But Losey and
Sevenster (in press) failed to find this effect with agonistic behavior in a stickleback.

These examples of decision sequences have been stated in terms of changes between functional groups of MAPs. The exact structure of the decision hierarchy is unknown. The first decision may be to switch from one functional group to another, followed by another series of decisions as to which specific MAP to use. For example, the subordinant fish's decision: if attacked then exhibit self-defense, could be followed by a second decision as to whether to respond by withdraw, flee, or present-dorsal. An alternative structure of the hierarchy is a series of decisions between each pair of signal-response MAPs. Both processes may exist simultaneously. Decisions that lack alternative responses or must occur quickly for survival are more likely to be single choices directing one response. Other cases, where options are available, may proceed as a nested series of decisions.

Decision rules may also occur within a functional group of MAPs. In my study, both substrate-feed and plankton-feed followed themselves forming a series of feeding events that were considered a superbout. A simple rule that could explain this pattern would be: if feeding undisturbed, then continue feeding. This rule would work as long as food was available and the stomach was not full, as was the case in my study.

This study manipulated the availability of a defendable food resource to note differences during the ontogeny of social behavior. All life stages of A. abdominalis, from hatching to adults, feed on
plankton (Helfrich 1958). My study indicated that they also consumed benthic foods if these were available. This species is omnivorous and feeds on whatever food resources are present, as does its congener A. saxatilis (Randall 1967). The field series fish collected from the tidepool habitat fed more on benthic food items than did the fish collected from under the buoys, reflecting the availability of those food types in each habitat.

_Abudefduf abdominalis_ is normally territorial only during the breeding season when adult males defend nest sites containing eggs deposited by females (Helfrich 1958, Walters 1967). Adults of unknown sex have been observed defending small feeding territories during a period when large quantities of commercial fish food was used to supplement their natural diet (personal observation). This would be consistent with the theory that a limited resource, that is predictable in time and space, may be energetically advantageous to defend (Brown 1964, Davies 1978, Davies and Houston 1984). Food resource defense, however, has not been described for this species under natural conditions. Manipulation of food resources in such an omnivore may only produce subtle behavior differences unless drastic alterations in food resources are imposed. Extreme differences in any condition can indicate the limits of a process but reveal little about the normal development of the process. It is important to keep manipulations within the range of natural variation of environmental conditions so that "normal" ontogenetic outcomes can be observed (Simmel and Baker 1980).
Some differences were noted between the field caught fish and the laboratory reared fish. The initial group of settlement age fish collected individually from different buoys were more active than those captured individually from different tidepools. This higher level of activity persisted in these same fish when assigned to the laboratory series/plankton diet group. It appeared to be a characteristic of this group of fish and not related to the buoy habitat because fish collected later from the same buoys, as the field series/plankton diet fish, did not show this higher level of activity.

The densities of *A. abdominalis* reared in the laboratory were comparable to densities found in tidepools and under buoys, but there were differences in the degree of confinement between the field and laboratory environments. The laboratory aquaria provided no means to escape from other fish. In the field, there was the option to leave the tidepool and enter another during the high tide submergence of the rocky shoreline. Similarly, fish could abandon the buoys if subjected to intense intraspecific competition and seek shelter elsewhere, although probably at a higher cost than in tidepools due to the lack of nearby alternate habitats. The laboratory series fish had higher frequencies of attack and threat MAPs as a likely result of the confinement. Present-dorsal occurred more frequently in the laboratory, probably due to the inability of the subordinant fish to escape from the dominant fish. It did occur in the field series, but at an older age.

The amount of information exchanged between fish was also higher in the laboratory series for months 1 and 2 than in the field series.
Although shelters were provided in the rearing aquaria, they were seldom used by the fish. The fish reared in aquaria were, therefore, in constant visual contact with each other, and this, along with the increased agonism, may have enhanced efficiency of communication. Fish from tidepools were not always in visual contact due to irregularities in tidepool topography, and fish on buoys, likewise, could also be out of view of conspecifics.

During this study, the benthic food was treated as a defendable resource by the fish. The dominant fish of both diet treatments fed more on the food type previously experienced. Initially, the dominant fish of the benthic diet group fed more on plankton and spent more time near the surface possibly because plankton represented the food type most likely encountered during the pelagic larval stage prior to settlement. After exposure to the benthic food resource the dominant fish spent more time near the bottom and fed more on the benthic food. Magnuson (1962) found that medaka, *Oryzias latipes*, would shift from scramble to contest feeding patterns when the food distribution was fixed at a location and the amount of food was limited. The benthic diet dominant fish also associated substrate-feed with attack and threat group MAPs by way of preceding-following preferred transitions. Other studies have found an increase in aggression associated with better resources. Spurr (1974) found that Adelie penguins, *Pygoscelis adeliae* with better nest sites were more aggressive and Fox et al. (1981) found that lizards, *Uta stansburiana*, occupying better habitat were more aggressive and had higher survivorship.
The plankton diet dominant fish also showed preceding-following preferred transitions between plankton-feed and attack MAPs, but this seemed to be associated with a personal space type defense. Defense of a portion of the water column by juvenile fish has been reported by Barlow (1962) for the cichlid *Badis badis* and Gibson (1968) for *Blennius pholis*. These ephemeral spatial defense zones, displacing the opponent from near proximity, may indicate attempts to defend the resources within a sphere surrounding the defender. Such efforts could form the origins of resource defense. A mechanism for cost-benefit analysis feedback would then restrict attempts to those resources that proved economically defendable. The one hour duration of the trials probably provided insufficient time to detect the dominant fish abandoning the defense of the plankton.

The availability of a defendable resource did not lead to an earlier expression or higher frequency of attack MAPs in juvenile *A. abdominalis*. This was contrary to the results of Stamps (1978) for lizards and Hoelzer (1987) for scorpaenid fish, where shelter or perch sites were considered. An increase in frequency need not always occur to indicate territorial defense. The same number of attack events can be redistributed and become associated with a particular function such as resource defense. This would constitute a shift in context for the MAPs (Ward and Barlow 1967, Tooker and Miller 1980). As described above, this appears to be the case for *A. abdominalis*. Attack MAPs became more consistently associated with the food resource in the dominant fish.
Erect-fins most likely originated from a locomotive function often used in conflict situations that later developed into a threat display. Wiepkema (1961) considered several threat displays in the bitterling, *Rhodeus amarus*, to have close temporal association with attack behavior and to occur in between attack and escape responses. There was no increase in the frequency of expression over the three months, but erect-fins did become paired with attack MAPs and still maintained a link to the feeding group MAPs, especially withdraw. Keenleyside and Yamamoto (1962) stated that such displays acquire signal value that other individuals come to understand and use to avoid fights. A general shift during development from direct attack to threat has been described for other fishes (Parzefall 1969, Tooker and Miller 1980, Cole and Noakes 1980).

The ontogeny of erect-fins as a threat display could be explained in terms of learning. Contingency experiences are considered part of ontogeny (Watson 1981, West and King 1985, King and West 1988), and both fish could benefit by associating erect-fins with an impending chase. The subordinant fish which learned the threat would avoid injury by fleeing sooner (Keenleyside and Yamamoto 1962). The dominant fish would avoid the cost of a chase while still displacing the subordinant fish. Erect-fins acquired threat status earlier in the laboratory series concurrent with the increased opportunity for pairing with chase due to the higher frequency of both MAPs at months 1 and 2. While the development of erect-fins as a threat display can be explained in terms of learning, this conclusion must remain
speculative as other possible processes were not investigated in my study.

A. abdominalis, is able to settle into a variety of habitats because of its omnivorous diet and the ability to modify its behavior in response to environmental factors such as food resources. This would be of benefit to most fishes with a pelagic life stage and possibly little control over what habitat it might encounter at settlement age.
LITERATURE CITED


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