FACTORS INFLUENCING THE ESTABLISHMENT OF DOMINANCE HIERARCHIES OF THE GREY TRIGGERFISH (*BALISTES CAPRISCUS*)

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TABLE OF CONTENTS

LIST OF FIGURES

LIST OF APPENDICES

ABSTRACT

FACTORS INFLUENCING THE ESTABLISHMENT OF DOMINANCE HIERARCHIES OF THE GREY TRIGGERFISH (*BALISTES CAPRISCUS*)

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The grey triggerfish (*Balistes capriscus*) is a common species in Atlantic sub-tropical waters. Little is known about the behavior of this species, other than feeding habits. The primary objectives of this study were to determine the factors influencing the social hierarchy of wild-caught grey triggerfish in a captive, but naturalistic, setting. From observations of four groups of triggerfish (N = 19 fish), I provide a description of triggerfish behaviors and coloration patterns, and an explanation of the social context in which suites of behaviors are used by dominant, middle-ranking, and subordinate fish. Specific objectives addressed were: (1) What is the dominance structure of a triggerfish group and what factors affect its establishment? Is the hierarchy linear or circular, and what are the direct consequences of the hierarchy on individuals? (2) Does the size and/or sex of the fish influence the dominance status? (3) Is the group dominance structure related to the dominance status of an individual within a dyad? Sixteen behaviors and nine coloration patterns were described for the grey triggerfish. These behaviors were categorized into dominant, subordinate and neutral behaviors, and their frequency was used to score the fish for dominance hierarchy matrices. Grey triggerfish groups formed linear hierarchies as measured by Landau's Index of Linearity ($h = 1.0$ for groups 1, 3, & 4 and $h = 0.95$ for group 2 in dyads; $h = 1.0$ for all groups in group settings). Dyadic hierarchies, however, are not necessarily good predictors of the hierarchies in group settings, as they only predicted 2 of the 4 group hierarchies. In the two hierarchies that were not predicted from the dyad results, both dominant and subordinate animals switched ranks. As for the factors influencing the formation of the hierarchy structure, size is the greatest influence on the highest ranking fish (alpha), (dyads $R^2 = 0.72$, $p = 0.0001$, groups $R^2 = 0.59$, $p = 0.0001$) while an individual's ranking influences body colorations and postures. Sex played no role in influencing status or behavior. Dominant fish displayed *Approach* and *Pass* behaviors more frequently than middle-ranking or subordinate fish ($p = 0.0001$, and $p = 0.006$, respectively). *Trigger up* and *Head down* behaviors were more frequently displayed by middle-ranking and subordinate fish than dominant fish (Bonferroni-Dunn, $p = 0.038$ and $p = 0.0001$, respectively). Coloration patterns were not independent of fish rank, with dominant fish using a *Light banding* pattern most often and middle-ranking and subordinate fish using it infrequently (2-factor ANOVA, $p = 0.008$, Bonferroni-Dunn, $p = 0.045$ and $p = 0.006$, respectively). Subordinate fish most often displayed *Grey* coloration (Bonferroni-Dunn, $p = 0.022$), while dominant fish never displayed *Grey*.

INTRODUCTION

Many animal social systems, where group relationships may be long-term, are based on a dominance hierarchy. These hierarchies help provide structure to the social system, such that agonistic interactions are reduced between group members. Wilson (1980) describes a dominance hierarchy as a physical domination of some members of a group by other members, in a relatively orderly and long-lasting pattern. They typically are either linear or nonlinear in form. Linear hierarchies are transitive in nature, with a top-ranking (alpha, α) individual that dominates all others, a second-ranking (beta, β) individual that dominates all but the alpha, a third-ranking (gamma, γ) individual that dominates all others besides the alpha and beta, etc. Nonlinear hierarchies are intransitive (circular) in nature, such that the alpha dominates the beta, the beta dominates the gamma, and the gamma dominates the alpha (Lehner, 1996). While an observed hierarchy may initially appear to be linear, individuals of middle-ranking may repeatedly supplant each other over time, resulting in a dynamic reshuffling of ranks (Han de Vries, 1998). Because of these possible alterations in hierarchies, Drews (1993) re-synthesized the concept of dominance as a pattern of repeated, agonistic interactions between pairs of individuals, with a predictable outcome in favor of the same dyad member and a lack of response from its opponent rather than an escalation of aggression. The consistent winner is defined as the "dominant" while the consistent loser is defined as the "subordinate."

The determinants of a dominance hierarchy may be based on many factors that differ from species to species due to differences in access to a limited resource (e.g., food, shelter, space, access to mates, etc.). Most methods for determining hierarchy structures are based on dominance relations between pairs of animals ("dyads", Drews, 1993) or triads rather than small groups (which would provide dominance ranking information). Recording the outcome of competition over resources, or contact upon initial and repeated meetings, for each pair in a group reveals that one individual often supplants all others, while middle-ranking and bottom-ranking individuals displace each other in an intransitive manner.

In a group larger than two individuals, a matrix is used to simplify the relationships between the individuals (Jameson et al., 1999), and to derive a dominance hierarchy of the group (Martin and Bateson, 2000). The dominant individual is placed at the top of the matrix while the most subordinate individual is at the bottom. Linearity may be determined using one of several available models. One such model, *Landau s index of linearity*, provides a measure of the degree to which a dominance hierarchy is linear. This test of linearity is then used to reorganize a dominance matrix to find an order that is most consistent with a linear hierarchy (Han de Vries, 1998).

Domination of others is typically a factor of individual characteristics (e.g., body size, sex), as well as contextual factors and chance (Francis, 1983, 1988; Landau, 1951, 1965). Contextual factors may include the order in which an individual is added to the group, or the outcome of the most recent fight in which the individual participated (i.e., "winner" and "loser" effects). Dugatkin (1997) developed a computer model to examine winner and loser effects on the development of dominance hierarchies, whether linear or circular. In this system, recent winners are more likely to win subsequent fights, while recent losers are less likely to win subsequent fights against all but other losers (Chase et al., 1994; Jackson, 1991). Dugatkin (1997) found that when winner effects alone were important, individual rank was clearly defined. When only loser effects were important, a clear alpha emerged, but the ranks of the subordinate members were often unclear due to a lack of aggressive interactions. If, however, individuals are capable of assessing their own fighting abilities relative to those observed from other group members, then a more complex picture arises. In this simulation, observers (bystanders) of a conflict self-assessed their own ability to win a conflict against individuals currently engaged in an agonistic interaction. Because this process of self-assessment is continual and affects the bystander s decision to engage in a conflict with another group member, the potential for repeated alterations in ranking is greater than previously expected. As bystanders change their assessment of the protagonists fighting abilities along with their own assessment of their ability to defeat the protagonist(s), the assessment of rank within small groups (e.g., 5 individuals) becomes increasingly difficult and nonlinear (Dugatkin, 2000).

Dominance Hierarchy Studies

Most dominance hierarchy studies focus on birds, primates, other mammals, and fish. In leghorn chicken hens, hierarchy formation can be viewed as a developmental process where preceding dominance interactions influence succeeding ones (similar to the winner/loser effects examined by Dugatkin (1997) and Chase (1982). Chase (1985) suggested a jigsaw puzzle approach to explain the structure of these dominance hierarchies and aggressive behavior. This jigsaw puzzle approach assumes that certain types of finer-scale structures (e.g., sequences of single, successive, aggressive actions on individuals) give rise to larger-scale patterns underlying the dominance relationships. The jigsaw puzzle model requires that for hierarchies to be linear, the dominance relationships between triads must be completely transitive. If a mixture of transitive and intransitive relationships exist, then non-linear hierarchies result. By examining the linearity of many dominance hierarchies across taxa, transitive dominance relationships appear to be predominant (Chase, 1982; 1985; Chase and Rohwer, 1987; Goessmann et al., 2000; Mendoza and Barcahs, 1983; Nelissen, 1985), which suggest that winner effects alone are acting in hierarchy formation.

Many social organization and dominance studies focus on fish. Most experiments usually involve dyads or triads, and the factors affecting dominance in these relationships. Beacham and Newman (1987) and Dugatkin and Ohlsen (1990) examined the importance of fish body size, aggressive experience, social experience, and the formation of dominance structure as determinants of dominance hierarchies for the pumpkinseed sunfish *Lepomis gibbosus*. Beacham and Newman (1987) found that asymmetries resulting from prior social experience affected the outcome of future dominance contests of *L. gibbosus* of similar size. In dyad competitions involving *L. gibbosus*, prior winners defeated prior losers thus influencing their ability to assess their own fighting abilities (named the Resource Holding Power or RHP of combatants). RHP dramatically altered the outcome of his simulations of winner and loser effects. Dugatkin and Ohlsen (1990) used fish weight as a measure of resource holding power. They found that smaller fish accustomed to receiving a greater number food items won a significant number of contests against larger fish that received fewer food items. While the food value expectation of a fish had a strong effect on which fish attacked first, it did not affect which fish emerged as the dominant.

In pumpkinseed fish, winners were very likely to win subsequent contests only if they fought opponents within a short period of time. If, however, they fought opponents after a waiting period exceeding 1 h, they tended to have a lower than expected chance of dominating their second opponent (Chase et al., 1994). These results suggest that winner effects may be of only short-term importance. Winner and loser effects have been found in blue gourami (*Macropodus opercularis*), three-spined sticklebacks (*Gasterosteus aculeatus*), and swordtails (*Xiphophorus helleri*), with the effects lasting a variable period of time depending on species (Francis, 1983; 1987; Bakker and Sevenster, 1983; Beaugrand et al., 1996).

In salmonids, body size is generally a good indicator of social status. Large individuals of *Salmo salar* often become dominant as they become larger and win more and more contests; however, a smaller fish with a greater number of prior wins may emerge dominant over a larger fish with fewer number of prior wins. Results suggest that prior wins and losses influence an individual s fighting ability to a greater extent than size, thereby affecting its position in the hierarchy (Metcalfe et al., 1992). Individual size characteristics and prior contest experience influence triadic dominance structure in the green swordtail *Xiphophorus helleri* and suggest that individual differences are more determinant than various paths of resolution (Beaugrand and Cotnoir, 1996). In a study to determine who picks on whom, Castro and Caballero (1998) found that dominant juvenile white-seabream, *Diplodus sargus cadenati*, carry out aggressive attacks selectively on fish whose subordination level is immediately inferior to their own to establish a peck-dominance hierarchy. The level of subordination is directly related to an individual s body size. Dominant fish with greater access to food grow faster.

In African cichlids, *Melanchromis auratus,* dominance behavior in a group of animals cannot be predicted accurately from the interactions of all possible pair formations (Nelissen, 1985). While groups of *M. auratus* typically established and maintained linear dominance hierarchies after three days via specific communicative displays that consisted of body postures (lateral body and fin displays), coloration, and pattern changes, these hierarchies were not necessarily predictable from prior dyadic interactions.

Other fish studies have focused on visual communication between opponents in several species of fish, particularly cichlids (Beeching 1995, Dawkins and Guilford 1993). Beeching (1995) described how Oscars, *Astronotus ocellatus*, when defeated in combat, undergo a change in color pattern in which the normal olive-green to brown body coloration darkens to near black with irregular white barring. Beeching s (1995) results showed that the dark and banded coloration pattern inhibits aggression by dominant tank mates. Dawkins and Guilford (1993) described the rapid and frequent changes of body coloration of the terminal phase of the adult male bluehead wrasse, *Thalassoma bifasciatum*. Body coloration changed from a bright green when aggressive towards other fish to opalescent when courting females and spawning. Their results suggest body coloration indicated fish intention and gave an indication of immediate future behavior. Juvenile Atlantic salmon, *S. salar*, typically adopt a uniformly pale coloration when on a light-colored substrate; darkening of the body and sclera, associated with an aggressive encounter with a dominant fish, signals submission (O Connor et al., 1999). Abbott et al. (1985) showed that darkened subordinate rainbow trout, *Oncorhynchus mykiss*, change their body postures when dominant fish are present. Subordinates generally retreated to a corner and appeared to increase the curvature of their dorsal outline, referred to as a hunched posture.

Grey Triggerfish Studies

The grey triggerfish, *Balistes capriscus*, is commonly found on both sides of the Atlantic, in tropical to semi-tropical waters from Argentina to Canada and from Angola to the British Isles. It is also found in the Mediterranean, and is very common in the Gulf of Mexico (Samuelson and Einarsen, 1996). Triggerfish are important members of reef fish assemblages and are found on artificial reefs in subtropical waters. Vose and Nelson (1994) and Kurz (1995) have studied their feeding habits off the Florida coast and found that preferred prey consists of bivalves, barnacles, and sand dollars. Triggerfish are also capable of feeding on gastropods, urchins, and other hard-prey items. The commercial harvest of the grey triggerfish in the northeastern Gulf of Mexico has created a need to know more about the biology of this species; hence, their age at maturity, growth, and mortality have been further studied by Johnson and Saloman (1984). Grey triggerfish reproduction has been studied by Johnson and Saloman (1984) in the northeastern Gulf of Mexico while Ofori-Danson (1990) has studied it off Ghanaian coastal waters. Few studies have focused on behavior (Salmon et al. 1968).

Social groups are rare for balistid triggerfish, as most are aggressive towards conspecifics and patrol territories; however, groups of grey triggerfish can be found in abundance on reefs in subtropical waters (Vose and Nelson, 1994). In studies on the benefits of grouping behavior or the benefits of weaponry vs. defensive posturing in spiny, clawed, and slipper lobster species, the grey triggerfish has been seen to cooperate in the subjugation of spiny, clawed, and slipper lobsters (Herrnkind et al. 2001; Lavalli and Spanier, 2001; Barshaw et al. in review). Nonetheless, only one fish appeared to consume the majority of the flesh obtained, and distinct differences in status seemed to exist, but it was not clear if this one fish was the largest (Lavalli et al. 2000). Thus, there is the opportunity to examine the determinants of the dominance hierarchies of this common Atlantic balistid fish.

Objectives

The primary objective of this study is to understand the social hierarchy of wild-caught grey triggerfish in a captive, but naturalistic, setting and provide a description and social explanation for their behaviors. Specific questions addressed are: (1) What is the dominance structure of a triggerfish group? Is the hierarchy linear or circular, and what are the direct consequences of the hierarchy on individuals? (2) Does the size and/or sex of the fish influence the dominance status? (3) Is the group dominance structure related to the dominance status of an individual within a dyad? By using the methodology developed by Nelissen (1985) for African cichlids, I observed the formation of the grey triggerfish group dominance hierarchies, and determined the factors important for individual status.

METHODS AND EXPERIMENTAL DESIGN

COLLECTION AND HANDLING OF ANIMALS

Members of intact schools of grey triggerfish were fished from St. John s Bay in the northeastern Gulf of Mexico via hook and line, using squid as bait. The depth from which the fish were reeled (~ 20 m) resulted in their swimbladders expanding, and inserting an 18 gauge needle into the lateral post-opercular surface to penetrate the swimbladder relieved the expansion. This caused no apparent injury to the fish and they resumed normal swimming activities immediately following the penetration of the swimbladder. The fish were then transported to the Florida State University Marine Laboratory (FSUML) in Sopchoppy, FL and held in outdoor pens with ambient, flowing seawater for several weeks. After this recovery period, they were transported via a Fish Box with aeration to either the Keys Marine Laboratory (KML) on Long Key, FL or to the National Marine Fisheries Service (NMFS) facility in Panama City, FL. During holding and transport times, the triggerfish were held in their original groups to maintain the group ties and hierarchies from their respective reefs. All fish were fed daily a diet of frozen squid or crustaceans.

Upon reaching their final destination, the fish were allowed 2 days of acclimation to the runways of the KML or to the cages at NMFS. They were then netted and measured to the nearest 1 mm standard length (snout to caudal peduncle), and randomly tagged through the caudal peduncle just below the lateral line with colored Floy tags (white, red, yellow, or blue). One fish in each group was not tagged, but was pierced through the caudal peduncle in the same position and manner as the tagged fish.

After tagging, fish were individually isolated, both physically and visually, from each other. Isolation pens were constructed of black plastic diamond mesh aquaculture netting (3/4 diameter) and assembled with cable ties. Oblong pens, divided into two halves and blocked on the ends and middle with black plastic to prevent physical and visual interaction of the fish, were placed in the non-experimental sections of the KML runways (Figure 1a). At the NMFS facility, isolation pens consisted of a fenced-in section 6 m long x 1 m wide x 1 - 1.5 m deep (due to tidal fluctuations), adjacent to the observation platform and north of the observation sections. This 6-m long section was divided into six 1 m long x 1 m wide x 1 - 1.5 m deep compartments. Placement of three fish from one group was alternated into these compartments with three fish from another group to prevent visual and physical interactions between individuals of the same group (Figure 1b). I used a 1-m wide passageway when moving fish from between the pens and observation sections. The remaining four fish (two from each group) were isolated by placement into opposite sections of two-quartered 2 m diameter pens placed approximately 3 - 4 m apart (Figure 1b). These two pens were placed south of the observation arenas.

Experimental Conditions

The experimental facility at the Keys Marine Laboratory consisted of a large concrete-lined waterway (~300 m) supplied with water from the adjacent Florida Bay. I partitioned a section of this runway, measuring 5 m long x 5 m wide x 1 m deep into a mesocosm for observation of the fish dyads and groups (Figure 1a). A 2-m high platform was placed at one end of the mesocosm to allow observations and videotaping of interactions with no disturbance to the fish. Trials were run on two separate groups of triggerfish in summer months from June-July, 2001. Water temperatures ranged from 29.5°C to 34°C in these mesocosms during these months. I also used large caged enclosures located at the National Marine Fisheries Service research center in St. Andrew Bay, Panama City, FL for observations of two fish groups in winter/spring months from March-April, 2002. Water temperatures ranged from 14.5°C to 22°C during these months. These cages were partitioned to match the sizes of mesocosms at the Keys Marine Laboratory (5 m wide x 5 m long x 1 - 1.5 m deep). Observations and videorecordings were conducted from a 2-m high observation platform (adjacent dock) minimizing disturbance to the fish.

ETHOGRAMS

Grey triggerfish behaviors and coloration patterns were catalogued during dyad interactions. These behaviors were described in all contexts and were scored to aid in determination of hierarchical position.

HIERARCHICAL DETERMINATION

Dyad Hierarchy After an isolation period of 48 hours, I introduced random pairs of the tagged triggerfish into the study section of the mesocosm or cages and began 30-min observations per pair. Only two pairings of fish per group per day were possible

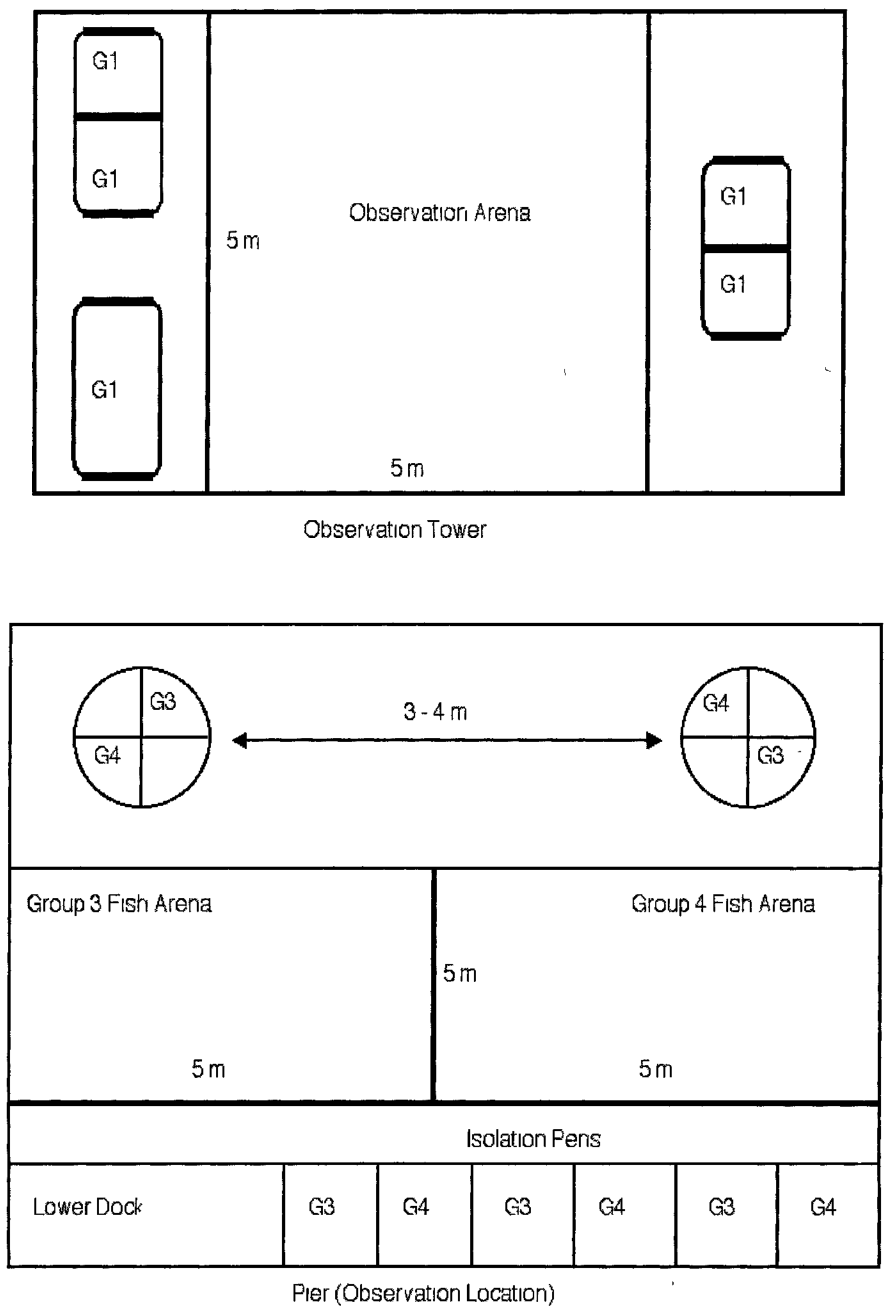

Figure 1: (A) Observation arena and pens at KML. G1 indicates the position of the fish when not placed in the areans. (B) Observation arenas and pens at NMFS. G3 and G4 indicate the positioning of the fish from Group 3 or 4 when not in the arenas. Thickened lines indicate presence of black plastic partitioning to prevent fish from physically or visually contacting other fish.

Table 1: Example of a Dyadic Pairing Regime

Day	Fish Pairings
1	Yellow x Blue
	No Tag x White
	Red not fought
2	Yellow x No Tag
	Red x Blue
	White not fought
3	No Tag x Blue
	White x Red
	Yellow not fought
4	White x Yellow
	No Tag x Red
	Blue not fought
5	White x Blue
	Yellow x Red
	No Tag not fought

to allow fish to recover from their interactions before pairing them with other fish (see Table 1). Observations consisted of cataloguing aggressive interactions, displays, and responses (e.g., approaching, veering into, chasing, biting, trigger and body position, and coloration patterns) for 15 min before feeding and 15 min after feeding. Interactions between individuals remained high if feeding occurred mid-observation; otherwise, after an initial period of interaction between two fish, the fish tended to decrease their activities and thus their interactions. During the feeding period, one or two morsels of food (squid) were introduced into the mesocosm or cage from the observation platform. Once every fish pairing possible was completed, the pairings were randomly repeated for a second run to confirm the dyad hierarchy.

Group Hierarchy Observations of the dyad hierarchy acted as a control for the group study. Group observations began after the establishment of the dyad hierarchy was confirmed via the second set of pairings. Fish comprising the study group were placed into the observation section of the runway or cage (where they stayed for the remainder of the experiment) and observed *ad libitum* for 1 h. Fish were then fed from the observation platforms and *ad libitum* observations continued for an additional hour. All interactions between fish were videorecorded and vocal descriptions of the behaviors were also recorded either directly onto the videotapes or onto a microcassette recorder. The group observations were repeated daily until the fish hierarchy remained stable for a period of 3 consecutive days. A stable hierarchy was considered to be one in which a particular pattern of behaviors was maintained over time (as per Nelissen, 1985). At the conclusion of the group trial, individual fish were sacrificed for sexing by gonadal examination (FSU Animal Care and Use Committee Protocol #0105, Lobster/Triggerfish Behavior).

ANALYSIS

Four replicate trials were conducted with fish from different social groupings caught from the northeastern Gulf of Mexico. Videotapes were analyzed to produce an ethogram of dominant, subordinate, and neutral behaviors and coloration patterns. After testing for homogeneity between pre-food and post-food dyad trials, these trials were combined. Three 5 x 5 and one 4 x 4 chi-square contingency tables (for groups 1, 2, and 4, and group 3, respectively) were used to determine if the frequency of colorations displayed was independent of the status of the fish for each of the four groups of fish

(Zar, 1999). Dyadic hierarchies were then examined by scoring the frequency of agonistic behavior and coloration by a particular fish and constructing a dominance matrix. This matrix was tested for linearity using Landau s index of linearity (h):

$$h=\left(\frac{12}{n^3-n}\right)\sum_{a=1}^{n}\left[\frac{v_a-(n-1)}{2}\right]^2$$

where:

n = number of animals in the group
v_a= number of animals that individual a dominates

This index ranges from zero to 1.0, with an h value of 1.0 indicating perfect linearity. Values of h greater than 0.9 denote a strong linear hierarchy. Each individual s Landau s linearity index value is its rank in the hierarchy. However, if two individuals were assigned an identical index value based on Landau s linearity, it would be problematic to determine individual rank within the group. Thus, I used an individual s calculated dominance index (zero to 1.0) to sort the fish according to its alpha to omega position within the group hierarchy. Behavioral data analyses were performed using public domain Java Applets for the analysis of behavioral data (available on the Internet at http://caspar.bgsu.edu/~software/java/1hierarchy.html) developed by Hemelrijk (1990).

The hierarchies resulting from the dyadic pairings were compared to those determined for the group, where frequency of agonistic behavior and coloration by a particular fish was scored and used in the dominance matrix. The same dominance structure applet was used to calculate the group Landau s index of linearity and dominance index to determine the specific ranking of an individual in a group setting. Specific rankings were then used to assign fish into the categories of dominant (index value 1 — 0.6), middle ranking (index value 0.59 — 0.4), and subordinate (index value 0.39

— 0). The frequency of behaviors displayed by dominant individuals (alpha, beta), middle-ranking individuals, and subordinate (gamma, omega) individuals was tallied for individuals in all groups, arcsin-transformed, and compared via a 2-factor ANOVA (with rank and sex as the factors) to determine if mean frequency of all behaviors (agonistic, neutral, and submissive) differed between the different ranks and sexes of fish (Zar, 1999). Where significant differences were found, Bonferroni-Dunn post-hoc tests were used to determine which ranks and/or sexes differed in the behavior. Similarly, the frequency of different coloration patterns displayed was also tallied for dominant, middle-ranking, and subordinate individuals, arcsin-transformed, and compared via a 2-factor ANOVA to determine if mean frequency of colorations differed between different ranks and sexes of fish. Bonferroni-Dunn post-hoc tests were used to determine which ranks and/or sexes differed in the coloration patterns expressed. Size of fish was examined as a potential factor in the determination of rank by regression analysis.

RESULTS

Ethogram of Grey Triggerfish

Sixteen behaviors and eight color patterns were defined from observations of 19 individual triggerfish within the four separate groups. These behaviors and color patterns can occur in tandem and thus may convey different meanings. Nevertheless, some behaviors and colors typified dominant or subordinate individuals. Therefore, the behaviors and colorations observed were divided into agonistic displays, subordinate displays, and neutral displays. The frequencies of these behaviors were later tallied and used in determination of the dominance hierarchy matrix. Where possible, photographs of the behaviors and/or colorations were obtained.

Agonistic Behaviors:

Biting

Physical contact using teeth with harmful intention. Often results in a flight response by the attacked individual. Most often displayed by the most dominant individuals.

Chase (Figure 2)

Quickly approaching an individual with continued pursuit. Most often results in a flight response and less often results in a *Circle chase* with the attacked individual. A *Chase* is most often displayed by a fish of dominant status.

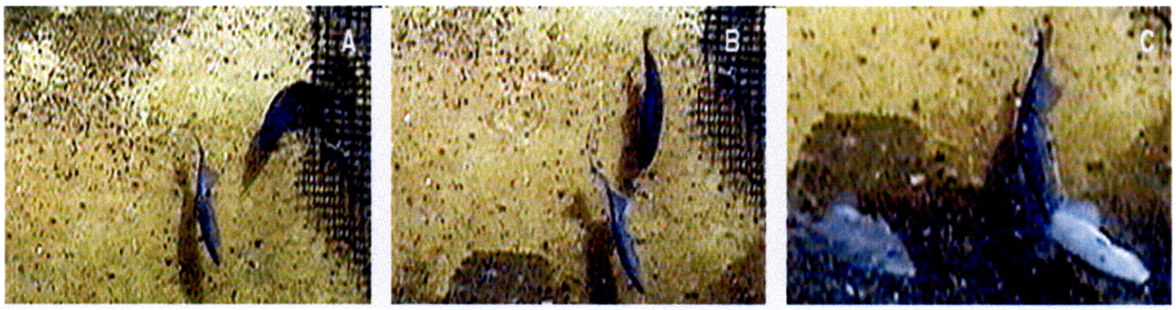

Figure 2: Sequence of behaviors involved in a typical *chase* scene. (A) *Approach* of aggressor fish. (B) Rapid swimming as the approached fish flees and the aggressor *Chases*. (C) *Veer into* by aggressor.

Circle Chase

A circle chase involves swimming in a circle in an escalated rotation of two individuals in an aggressive encounter. Most often results in a *Flee* or *Chase* response, and less often results in an *Attack Inhibition Display* (described below) by the subordinate individual.

Veer Into (Figure 3)

A sudden rush towards another fish with aggressive intent in an otherwise seemingly passive situation. May resolve towards a *Bite* or an *Attack Inhibition Display*, but most often, the attacked individual quickly flees or, more rarely, gets involved in a circle chase and then flees.

Figure 3: Top fish (dark coloration) *Veers into* another fish (white coloration).

SUBMISSIVE BEHAVIORS:

Flee

Quickly escaping an approaching fish to reduce potential harm.

Head Down (Figure 4)

The positioning of the head region of the fish at a downward angle, deviating from a horizontal plane. Aside from being a possible feeding position, a *Head-down* display is seen in conjunction with a *Trigger-up* display, subordinate coloration, and a *Hover* (this combination of displays describes an *Attack Inhibition Display* or *AID*).

Figure 4: Fish on far left (lighter coloration) displaying *Head-down* in conjunction with *AID*.

Head Up (Figure 5)

The positioning of the head region of the fish at an upward angle, deviating from a horizontal plane. Aside from being a possible feeding position, a *Head-up* display is seen in conjunction with *Trigger-up* display, subordinate coloration, and a *Hover* (this combination of displays describes another type of *Attack Inhibition Display* or *AID*).

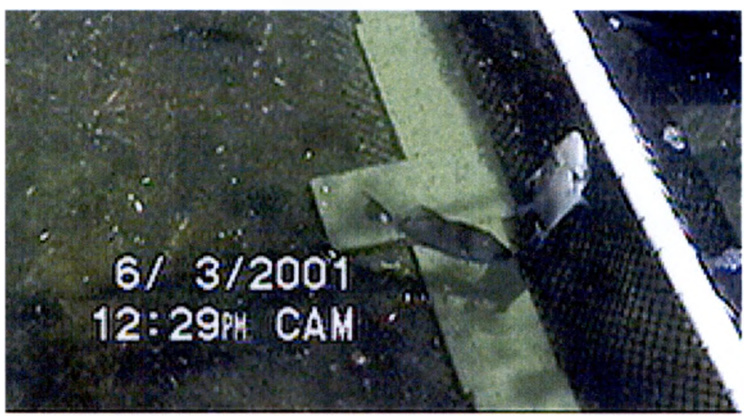

Figure 5: Right fish displaying *Head-up*.

Trigger-Up (Figure 6)

An upward and forward movement of the most anterior dorsal fin spine. This modified spine, for which triggerfish acquired their name, has many functions, e.g., selfdefense in the event of being swallowed or, when used in conjunction with a smaller ventral spine, resting or sleeping while wedged in reef structure. A solitary fish with trigger-up is often observed to be involved in an activity which requires some amount of focus on the task at hand, e.g., predatory feeding behavior or being alert to a possible threat in its vicinity. In a paired or group situation with conspecifics, the *Trigger-up* position signals subordination. In a potentially escalating situation in the presence of a dominant fish, a subordinate fish will often raise its trigger, either partially or fully. The alpha fish rarely raises its trigger in an established dominant/subordinate relationship. Lesser dominants (middle-ranking individuals) may or may not raise their trigger, depending on the situation and the stage in the establishment of the relationship. Subordinate fish are most likely to continually use the *Trigger-up* display, often as part of an *AID*. It is notable that the dorsal trigger spine has not been observed as a weapon, but mostly as a tool for communication.

Figure 6: *Trigger-up* display and *White* coloration.

Trigger-Down (Figure 7)

Opposite of above definition. Trigger is down when swimming, hovering, or inactive. Alpha fish rarely display *Trigger-up* followed by *Trigger-down* to subordinate fish unless seriously challenged.

Figure 7: Fish swimming with normal *Trigger-down* position.

OTHER OBSERVED NEUTRAL BEHAVIORS:

Approach

To come near another fish. An *Approach* is either benign or a prelude to a *Chase* or *Veer into*. An *Approach* may or may not elicit a response from either party.

Backward Swimming

Swimming in reverse, usually to get out of the way of an approaching dominant fish to avoid an altercation. Often used in conjunction with *Hover* while feeding. No quantitative data was collected on this on this behavior.

Blowing Water

Forcefully expelling water out the mouth. Observed when flipping urchins, searching for buried food items, or used to confuse larger mobile prey (e.g., spiny lobsters). No quantitative data was collected on this on this behavior.

Flatten (Figure 8)

Described as when the fish s vertical plane lies horizontally or nearly so. Observed in resting fish without a suitable crevice in which to wedge. In a resting situation, *Flatten* has been observed in conjunction with a *Mottled* color pattern. Otherwise, fish will flatten to some degree to reach a better angle for feeding or attack. No quantitative data was collected on this on this behavior.

Figure 8: *Flatten* with a *Mottled* coloration pattern.
This fish is sleeping at the bottom of the observation arena.

Hover

Suspended in place, resulting from the motion of the pectoral fins and the light fluttering of the dorsal and anal fins. Observed when feeding, prior to a rapid speed burst and bite. Also observed in conjunction with an *Attack Inhibition Display* (*AID*). No quantitative data was collected on this on this behavior.

Schooling

Fish swimming together. In triggerfish, *Schooling* is observed as unsynchronized group movement and is most often seen when fish are collectively searching for food or moving to feeding grounds. No quantitative data was collected on this behavior.

Wobble

A side-to-side rocking motion observed while swimming slowly. Infrequently seen, and mostly observed in subordinate fish after successfully keeping a dominant fish from feeding on food. No quantitative data was collected on this on this behavior.

Coloration Patterns:

Light-Banded (Figure 9)

The neutral coloration of a *B. capriscus* individual when typically found as a solitary fish. *Light-banded* is displayed by all fish in a normal state, i.e., not harassed or otherwise occupied. In a group situation, the alpha fish maintains this coloration in most situations, except feeding and resting, when it may takes on a dark-banding or mottled coloration, respectively. *Light-banded* is the most common coloration displayed by individuals of high hierarchical position.

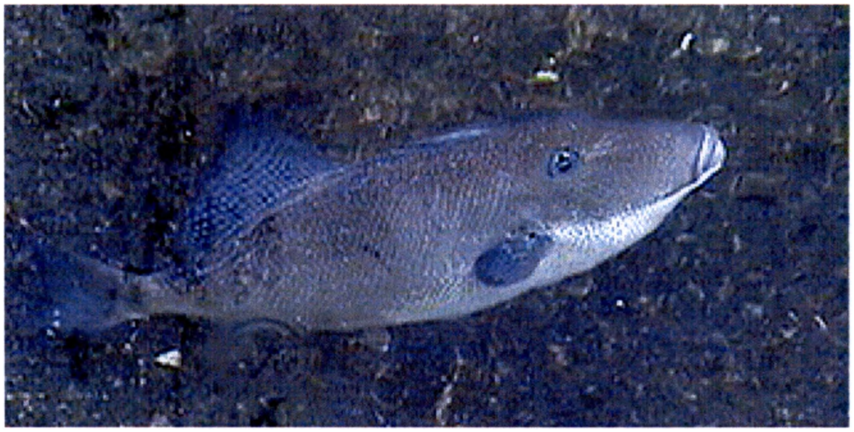

Figure 9: *Light-banded* (normal state) coloration display.

Dark-Banded (Figure 10)

An amplification of the dark portions of the *Light-banded* display. *Dark-banding* is observed in all fish simultaneously engaged in frenzied feeding or predatory attack mode. Otherwise, in a group situation, a subordinate fish may display dark banding to a more dominant fish or may display it in conjunction with an *AID*. *Dark-banded* is the second-most common coloration in terms of hierarchical positioning.

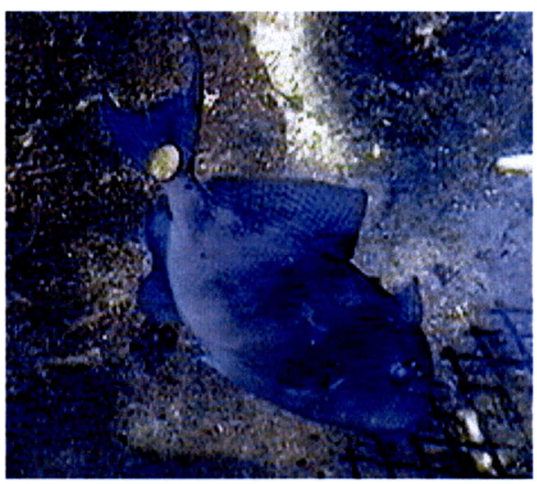

Figure 10: *Dark-banded* coloration display during feeding (also displaying *Head-down* and *Trigger-up*)

Grey (Figure 11)

A solid grey coloration often displayed in conjunction with an *AID* by a subordinate fish. Frequently displayed for a moment as a dominant fish approaches and passes a stationary subordinate fish. In terms of hierarchical positioning, *Grey* coloration is displayed by individuals of middle-rank.

Figure 11: *Grey* coloration display by uppermost fish.
Both fish have a partial *Trigger-up* display.

White (Figure 12)

A solid white coloration is always displayed in conjunction with an *AID* by a subordinate fish. *White* is the most subordinate coloration observed in terms of hierarchical positioning.

Figure 12: *White* coloration display in combination
with *Trigger-up* and *Head-up* displays (*AID*).

MISCELLANEOUS COLORATION PATTERNS:

Black (Figure 13)

A rarely observed dull black or charcoal coloration. Seen only on the fish housed at the Keys Marine Lab fish and not on those housed at the National Marine Fisheries Service fish. This coloration appears to be dominant to *Dark-banded*, but due to its rarity, very little data was collected on it.

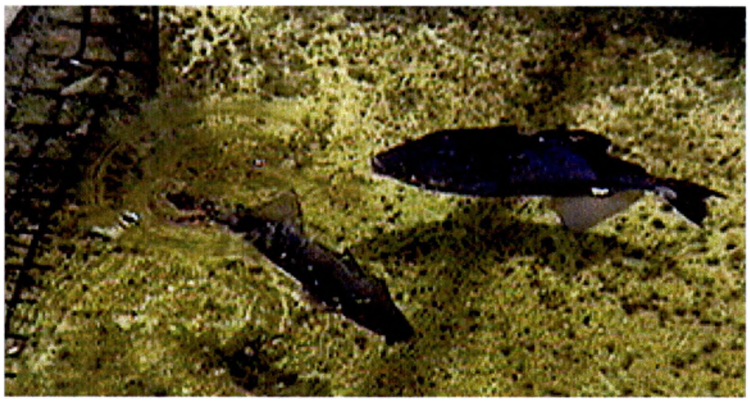

Figure 13: Uppermost fish displaying *Black* coloration.

Mottled (Figure 14)

Greatly resembles *Dark-banded* with a greater breakup of the dark coloration. Observed when a fish is resting in a *Flatten* position or when handled by human captors.

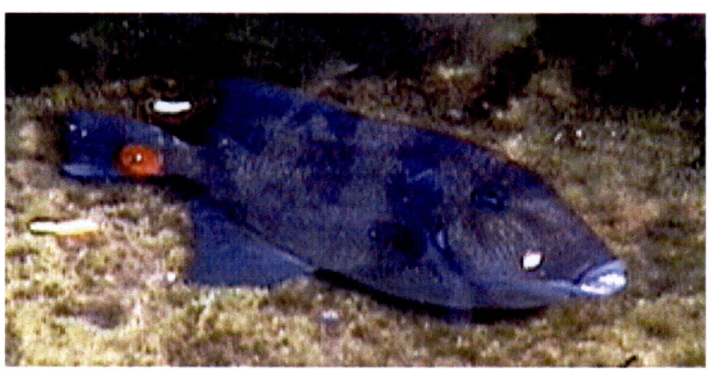

Figure 14: Fish displaying *Mottled* coloration.

Olive (Figure 15)

A near solid, olive-brown coloration seen not as a display towards another fish, but rather when in an established group milling about. Rarely seen.

Figure 15: Upper fish displaying *Olive* coloration.

Speckled (Figure 16)

A variation on the theme of *Grey* and *White* coloration. Observed as numerous spotting of a lighter coloration than the background, usually iridescent blue or green. Often seen as an intermediate between *Grey* and *White* while in an *AID* or on subordinate fish milling about in an established group. Most often displayed by the KML fish.

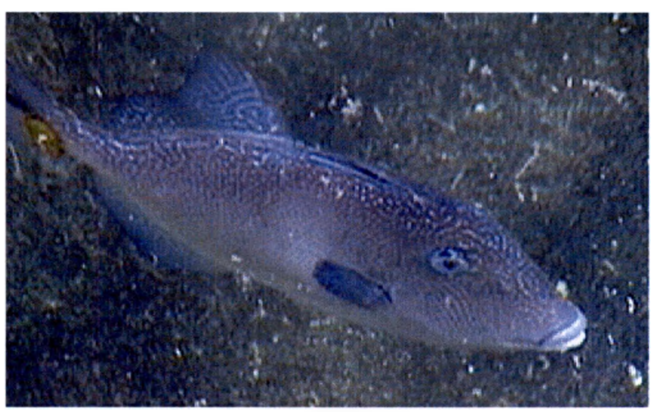

Figure 16: *Speckled* coloration pattern.

COMBINATION BEHAVIORS AND COLORATION:

Attack Inhibition Displays (Figure 17)

An *Attack Inhibition Display*, or *AID*, describes a submissive behavior or sequence of submissive behaviors designed to avoid confrontation and unnecessary energy expenditure in defending one s place in a dominance hierarchy. An alpha fish never displays an *AID*. The frequency of *AIDs* increases with greater levels of subordination, as evidenced by the increasing frequency of pale coloration, *Trigger-up*, *Head-up* or *Head-down* behaviors. Most often displayed while in a *Hover* position (usually) perpendicular to the dominant fish for which the display is meant.

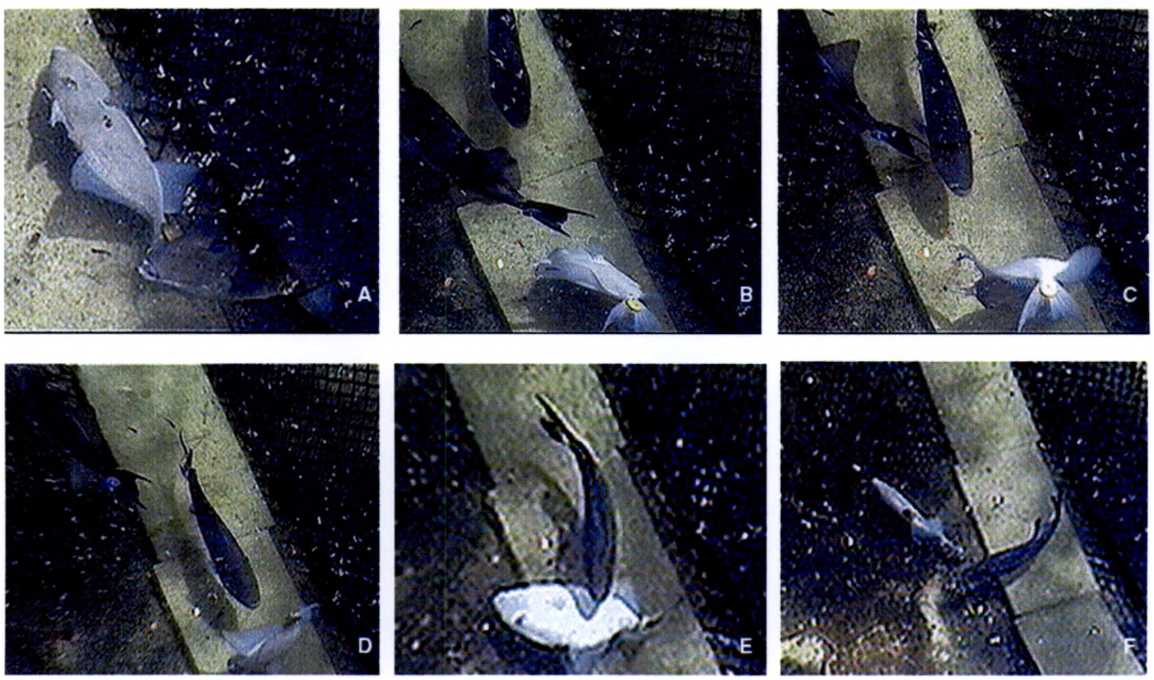

Figure 17: Sequence of behaviors involved in a typical *Attack Inhibition Display*. (A) *Approach* of dominant fish from above (out of view). (B) Color change by subordinate fish in response to approaching dominant fish. (C) *Head-down* Display. (D) *Veer into* by aggressor. (E) and (F) Rapid swimming as the approached fish *Flees* and the aggressor *Chases*. (also see Figure 12 under *White* coloration).

HIERARCHIES ESTABLISHED IN DYADIC PAIRINGS AND COLORATION PATTERNS OBSERVED

Four groups of triggerfish, composed of 4-5 individuals (for groups 1, 2, and 4, N= 5, for group 3, N = 4), were used to determine if hierarchies were linear or non-linear, and if they followed typical dyadic relationships. The behaviors and color patterns observed during the dyad observations (described above) were categorized into *agonistic* (e.g., *Bite*, *Chase*, *Circle chase*, *Veer into*, *Light-banded*, *Dark-banded*, *Black*), *submissive* (e.g., *Flee*, *Head-down*, *Head-up*, *Trigger-up*, *Grey*, *White*, *Speckled*), and *neutral* (e.g., *Approach*, *Pass*, *Flatten*, *Wobble*, *Hover*, *Schooling*, *Blowing water*, *Backwards swimming*) displays and their frequencies were tallied for each fish in the pair to determine dominant or subordinate status. These tallied frequencies were used to construct a dominance matrix for each group of fish (Tables 2-5) by scoring the frequency of agonistic behaviors/color patterns of the fish during the four 15-min observation periods. The dominance matrix was tested for linearity via Landau s Index of Linearity (*h*) and all ties in rank were sorted via a dominance index calculation for each individual (as per the Java Grinder program provided by Dr. Robert Huber, at http:///www.caspar.bgsu.edu/~software/Java/1Hierarchy.html).

In Group 1, Fish NT displayed a high frequency of agonistic behaviors, particularly *Chasing* other fish, a low frequency of *Trigger-up* behavior, and a coloration pattern consisting only of *Light-banding* and *Dark-banding* (Table 2, Figure 18). Fish W and B were ranked as the next most dominant individuals, displaying a high frequency of

Chase behavior, a low frequency of *Trigger-up* behavior, and a coloration pattern consisting of *Light-* and *Dark-banding*, as well as *White* and/or *Black*. For both Fish W and B, the frequency of *Dark-banding* was increased, while that of *Light-banding* was decreased, relative to Fish NT. Fish R and Y were the most subordinate individuals and consequently displayed a higher proportion of *White* coloration than either *Speckled*, *Light-* or *Dark-banding*, and *Black* (Figure 19). Fish R and Y showed a higher frequency of *Trigger-up* behavior (Figure 18) than Fish NT, W, or B. Coloration pattern displayed by these fish was not independent of fish rank ($X^2 = 160.3$, df = 12, $p < 0.001$). The hierarchy for Group 1 fish, based on the dyadic pairings, was perfectly linear ($h = 1$), with NT > W > B > R > Y.

Table 2: Dominance matrix constructed for Group 1 fish during dyad interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and to assess rank. DF = 12; N = 20.

Fish Code	NT	W	B	R	Y	Totals	Dominance Index	Rank	Size (in cm)
NT		96	98.2	97.3	94.2	**385.7**	**0.651**	α	30.7
W	48.68		98.73	78.95	90.79	**317.15**	**0.577**	β	27.3
B	72.45	86.36		95.04	90.9	**344.75**	**0.561**	γ	26.0
R	37.74	39.31	17.48		59.49	**154.02**	**0.331**	δ	25.2
Y	47.11	10.34	55.36	38.65		**151.46**	**0.311**	ω	22.5
Totals	**205.98**	**232.01**	**269.77**	**309.94**	**335.38**	**1353.08**			

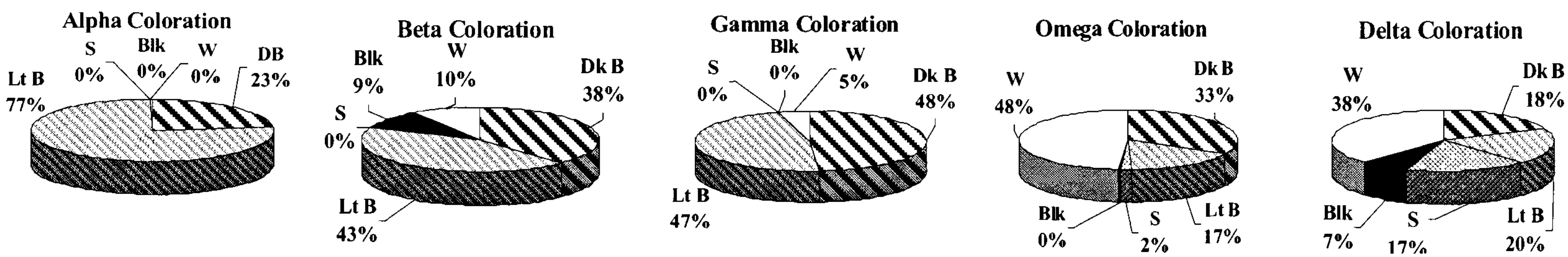

Figure 18: Color patterns of Group 1 Fish, illustrating differences in color pattern usage between high ranking fish (NT = α), middle-ranking fish (W = β, B = γ), and low ranking fish (R = δ, Y = ω). Color patterns are not independent of rank. Blk = *Black*, Dk B = *Dark-banded*, G = *Grey*, Lt B = *Light-banded*, S = *Speckled*, and W = *White*.

In Group 2, many paired fish did not initially interact and therefore agonistic, neutral, and submissive behaviors were rare. Fish R displayed both agonistic and submissive behaviors, but fewer submissive behaviors than the other fish (Table 3). Furthermore, Fish R display a coloration pattern consisting only of *Light-banding* and *Dark-banding* (Figure 19), similar to that seen in Group 1 s most dominant ranking fish. Fish B and W were ranked as the next most dominant individuals, and displayed behavioral patterns very similar to those of Fish R. However, their coloration pattern consisted of *Light-* and *Dark-banding*, as well as *White* and *Black*. For both Fish B and W, the frequency of *Dark-banding* was increased, while that of *Light-banding* was decreased, relative to Fish R. Fish NT and Y were the most subordinate individuals and consequently displayed a higher proportion of *Grey* or *White* coloration than either *Dark-banding* or *Speckled* (Figure 19). Fish Y showed a higher frequency of *Trigger-up* behavior (Table 3) than Fish NT, W, B, or R. Fish Y also showed other submissive behaviors, especially *Head-down*, and for this reason was considered the lowest ranking individual compared to the middle ranking Fish B, W, and NT. Coloration pattern displayed by these fish was not independent of fish rank ($X^2 = 156.6$, df = 12, $p < 0.001$). The hierarchy for Group 2 fish, based on the dyadic pairings, was not perfectly linear (h=0.95), but was strongly linear, with R > B >/= W > NT > Y.

In Group 3, one of the original 5 fish became sick shortly after transportation from the FSU Marine Laboratory in Sopchoppy to the NMFS research center in Panama City. Thus, this fish was not used in pair-wise interactions, nor in later group interactions. Fish NT displayed the same frequency of *Approach*, *Veer Into*, and *Chase*

Table 3: Dominance matrix constructed for Group 2 fish during dyad interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and to assess rank. DF = 12; N = 20.

Fish Code	R	B	W	NT	Y	Totals	Dominance Index	Rank	Size (in cm)
R		83.33	86.95	100	100	**370.28**	**0.66**	α	25.1
B	77.77		100	100	67.64	**345.41**	**0.576**	β	21.9
W	57.89	100		100	76.6	**334.55**	**0.498**	γ	23.6
NT	54.54	37.5	75		100	**267.04**	**0.428**	δ	21.1
Y	0	33.33	74.07	55.55		**162.95**	**0.321**	ω	22.8
Totals	**190.2**	**245.16**	**336.02**	**355.55**	**344.3**	**1480.23**			

behavior as Fish Y, but a lower frequency of *Trigger-up* and *Head-down* behavior (Table 4). Fish NT also displayed the typical dominant coloration pattern of *Light-banding* and *Dark-banding* (Figure 20). Fish Y and W displayed a more middle-ranking coloration pattern of *Light-* and *Dark-banding* in addition to *Gray*, *Speckled*, and *White*. While Fish Y and W were similar in their behavior, Fish W displayed a higher frequency of *Trigger-up* and *Head-down* behavior (Table 3). Fish B showed a higher proportion of *Grey* coloration than previously seen in any other group, as well as *White*, *Black*, and a small proportion of *Light* and *Dark-banding* relative to all other fish. It also displayed a high frequency of *Trigger-up* and *Head-down* behavior relative to all other fish in the group. Coloration pattern displayed by these fish was not independent of fish rank ($X^2 = 443.98$, df = 6, $p < 0.001$). The hierarchy was perfectly linear ($h = 1$), with NT > Y > W > B.

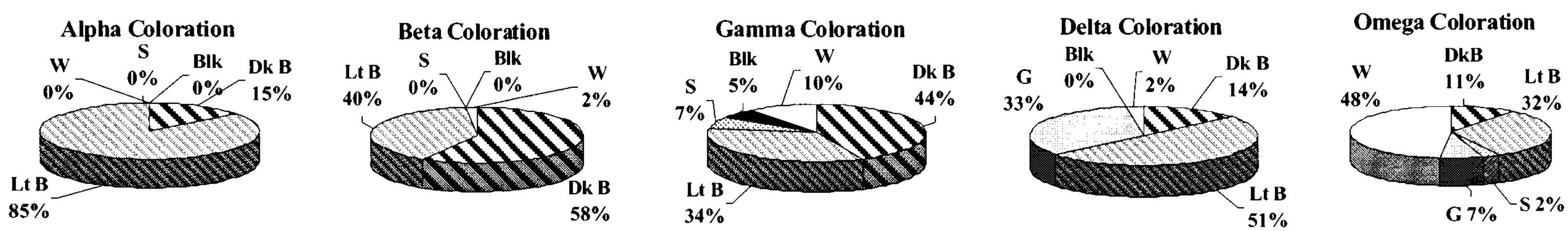

Figure 19: Color patterns of Group 2 Fish, illustrating differences in color pattern usage between high ranking fish (R = α), middle-ranking fish (B = β, W = γ, NT = δ), and low ranking fish (Y = ω). Color patterns are not independent of rank. Blk = *Black*, Dk B = *Dark-banded*, G = *Grey*, Lt B = *Light-banded*, S = *Speckled*, and W = *White*.

Table 4: Dominance matrix constructed for Group 3 fish during dyad interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and to assess rank. DF = 6; N = 12.

Fish Code	NT	Y	W	B	Totals	Dominance Index	Rank	Size (in cm)
NT		100	93.75	100	**293.75**	**0.706**	α	28.6
Y	66.66		100	77.84	**244.5**	**0.594**	β	27.3
W	48	40		100	**188**	**0.492**	γ	25.2
B	7.14	26.66	0		**33.8**	**0.108**	ω	21.3
Totals	**121.8**	**166.66**	**193.75**	**277.84**	**760.05**			

In Group 4, Fish Y displayed a higher frequency of *Approach*, *Pass*, and *Chase* behavior than the other 4 fish and almost no *Trigger-up* or *Head-down/up* behavior (Table 5). Fish Y also displayed the typical dominant coloration pattern of *Light-banding* and *Dark-banding* (Figure 21), but had the highest frequency of *Light-banding* of all alpha fish in all groups. Fish R displayed a more middle-ranking coloration pattern of half *Light-banding* and a mix of *Dark-banding* and *Gray* and varied in behavior, depending on which fish it was paired with. White coloration was present, but infrequent. While Fish W, B and NT were similar in their behavior, showing high frequencies of *Trigger-up* and *Head-down/up* (Table 5). Fish W and B showed a mix of *Grey*, *Light-* and *Dark-banding*, and *White* coloration, while Fish NT showed mostly *Dark-banding* and *Grey* coloration. This latter coloration pattern was the most unusual for an omega fish, as there was a low frequency of White coloration. Coloration pattern displayed by these fish was not independent of fish rank ($X^2 = 252.9$, df = 12, $p < 0.001$). The hierarchy was perfectly linear ($h = 1$), with Y > R > W > B > NT.

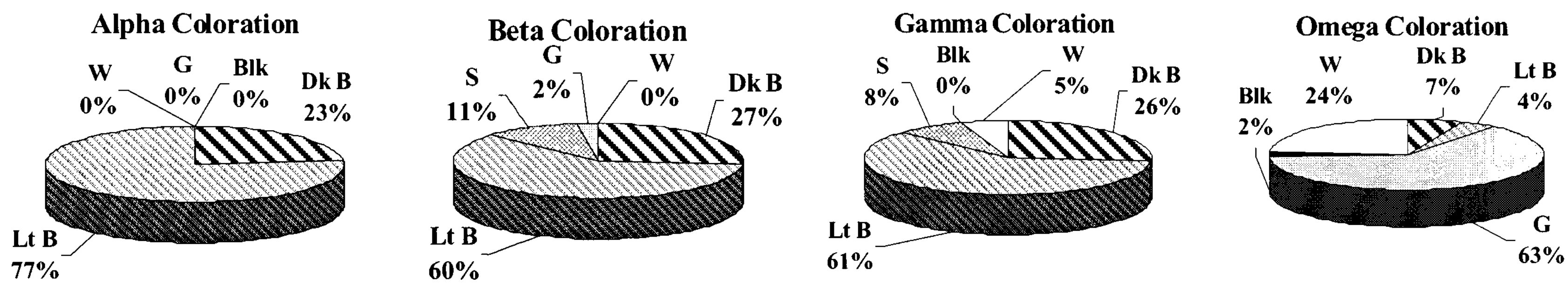

Figure 20: Color patterns of Group 3 Fish, illustrating differences in color pattern usage between high ranking fish (NT = α), middle-ranking fish (Y = β, W = γ), and low ranking fish (B = ω). Color patterns are not independent of rank. Blk = *Black*, Dk B = *Dark-banded*, G = *Grey*, Lt B = *Light-banded*, S = *Speckled*, and W = *White*.

Table 5: Dominance matrix constructed for Group 4 fish during dyad interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and assess rank. DF = 12; N = 20.

Fish Code	Y	R	B	W	NT	Totals	Dominance Index	Rank	Size (in cm)
Y		93.33	100	100	100	**393.33**	**0.875**	α	33.7
R	18.18		61.76	50	100	**229.94**	**0.57**	β	27.0
B	0	15.25		38.37	32.14	**85.759**	**0.29**	γ	24.4
W	0	37.5	34.32		68.18	**140**	**0.384**	δ	25.4
NT	38	26.92	13.04	35.48		**113.44**	**0.274**	ω	23.8
Totals	**56.18**	**173**	**209.12**	**223.8**	**300.3**	**1353.08**			

Size influenced ranking of fish in that the largest fish in each group was always the highest ranking (α). However, middle-ranking and small fish did not always follow a size-related pattern (Figure 22), such that the most subordinate fish (ω) were not always the smallest fish. Despite this, regression analysis demonstrated a strong relationship between rank and size ($F_{(1,17)} = 42.78$, $R^2 = 0.72$, $p < 0.0001$).

Hierarchies Established in Group Interactions

Group data was compiled from Day 1 Pre-food observations, which occurred immediately after the fish from a particular group were first placed together in the observation arena. Again, the behavioral and coloration data provided values for dominance matrices so that group dominance hierarchies could be compared to dyadic dominance hierarchies to determine if dyadic pairings were a good predictor of dominance patterns within a group of triggerfish. In the case of Groups 1 and 3, the dyadic interactions did provide a good predictor of the structure of the hierarchy. While the dominance index values for an individual changed, the actual rankings did not (Tables 2, 6 and 5, 8). In contrast, for Groups 2 and 4, the dyadic interactions were not a good predictor of the hierarchy. In Group 2, Fish NT was scored as a subordinate individual (delta) from the dyad data, but moved to the gamma position (higher rank), while Fish B, scored as the beta position in the dyad interactions moved to omega position (Tables 3 and 7). In Group 4, Fish NT moved from the omega position in the dyad interactions to the beta position in the group interactions. Fish B moved from the gamma position to the omega position. Fish R moved from the beta position to the gamma position (Tables 5 and 9). All hierarchies were found to be perfectly linear ($h = 1$).

Table 6: Dominance matrix constructed for Group 1 fish during Day 1 group interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and to assess rank. DF = 12; N = 20. Group ranks are identical to dyad ranks.

Fish Code	NT	W	B	R	Y	Totals	Dominance Index	Rank
NT		100	100	95	100	**395**	**0.897**	α
W	11.36		90.91	60	100	**262.27**	**0.659**	β
B	27.27	27.5		85.71	88.89	**229.37**	**0.531**	γ
R	6.452	7.692	11.54		16.67	**42.354**	**0.149**	δ
Y	0	0	0	0		**0**	**0**	ω
Totals	**45.08**	**135.19**	**202.45**	**240.79**	**305.56**	**928.99**		

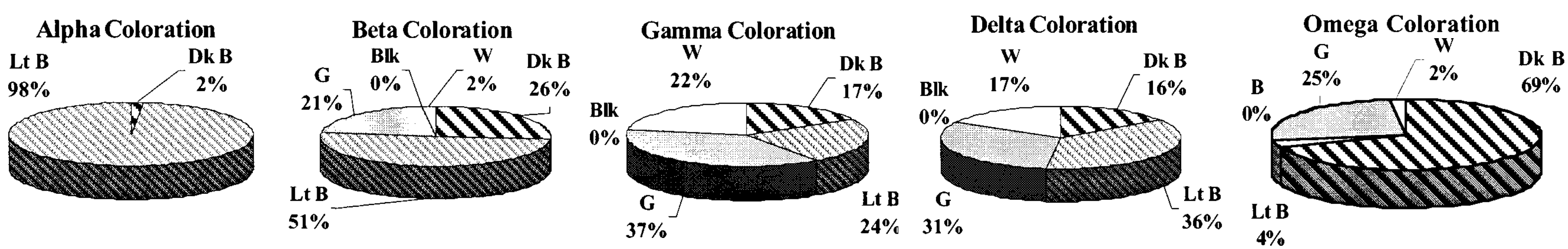

Figure 21: Color patterns of Group 4 Fish, illustrating differences in color pattern usage between high ranking fish (Y = α), middle-ranking fish (R = β), and low ranking fish (W = γ, B = δ, NT = ω). Color patterns are not independent of rank. Blk = *Black*, Dk B = *Dark-banded*, G = *Grey*, Lt B = *Light-banded*, S = *Speckled*, and W = *White*.

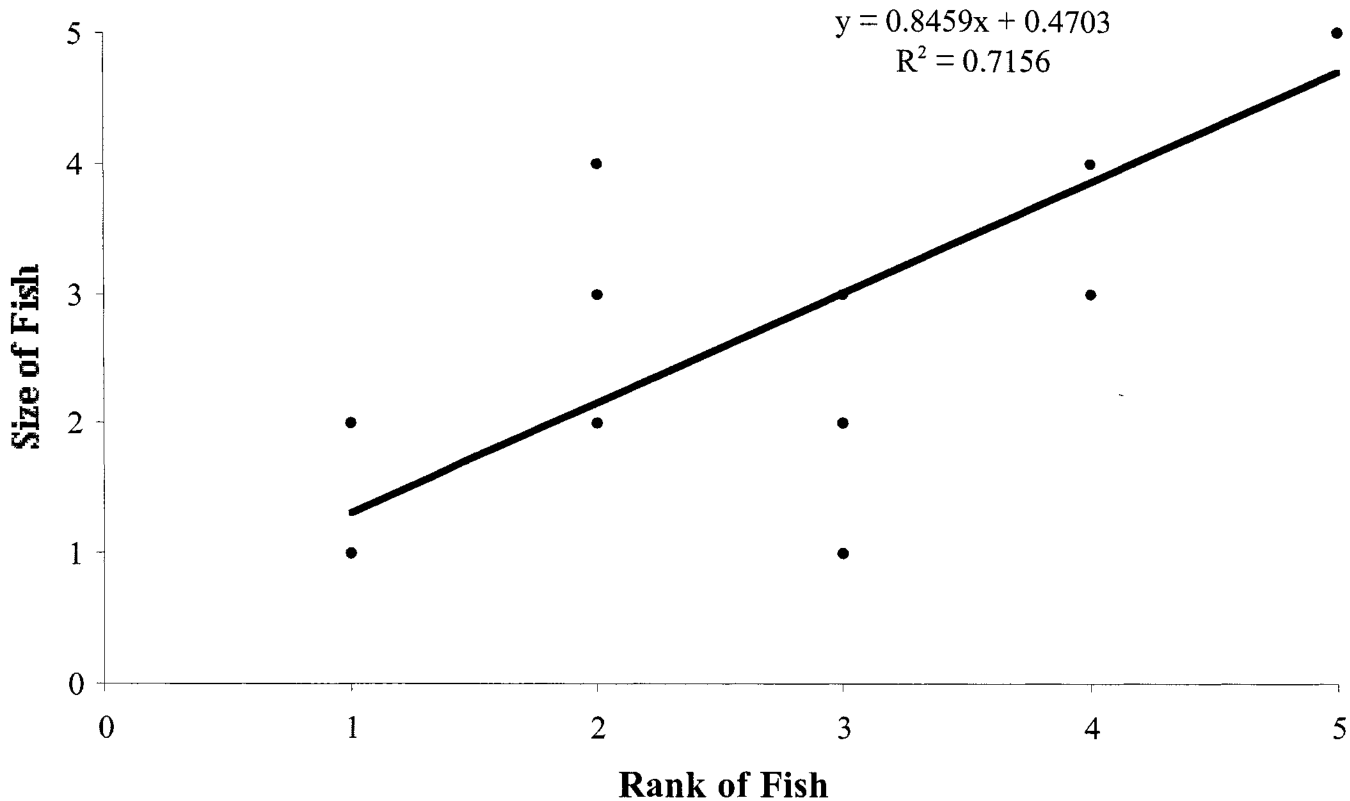

Figure 22: Fish size (5 = largest, 4 = next largest, 3 = middle sized, 2 = second smallest, 1 = smallest) versus fish rank (1 = ω, 2 = δ, 3 = γ, 4 = β, 5 = α) in dyad interactions. Slope is significantly greater than zero ($p < 0.0001$).

Table 7: Dominance matrix constructed for Group 2 fish during Day 1 group interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and to assess rank. DF = 12; N = 20. Dyad ranks are in parentheses next to group ranks.

Fish Code	**R**	**W**	**NT**	**Y**	**B**	**Totals**	**Dominance Index**	**Rank**
R		89.47	83.33	100	100	**372.8**	**0.782**	α (α)
W	27.78		76.92	100	82.35	**287.05**	**0.573**	β (γ)
NT	40	61.54		75	100	**276.54**	**0.566**	γ (δ)
Y	2.381	38.46	16.67		100	**157.51**	**0.355**	δ (ω)
B	33.33	24	35	11.11		**103.44**	**0.212**	ω (β)
Totals	**103.49**	**213.47**	**211.92**	**286.11**	**382.35**	**1197.34**		

Table 8: Dominance matrix constructed for Group 3 fish during Day 1 group interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and to assess rank. DF = 6; N = 12. Group ranks are identical to dyad ranks.

Fish Code	**NT**	**Y**	**W**	**B**	**Totals**	**Dominance Index**	**Rank**
NT		95.24	96.88	100	**292.12**	**0.74**	α
Y	54.29		100	50	**204.29**	**0.568**	β
W	47.37	60		82.35	**189.72**	**0.49**	γ
B	0.602	0	0		**0.602**	**0.002**	ω
Totals	**102.26**	**155.24**	**196.88**	**232.35**	**686.73**		

Table 9: Dominance matrix constructed for Group 4 fish during Day 1 group interactions. Frequency of dominant behaviors/colorations scored to determine dominance index for each individual fish and to assess rank. DF = 12; N = 20. Dyad ranks are in parentheses next to group ranks.

Fish Code	Y	NT	R	W	B	Totals	Dominance Index	Rank
Y		100	100	100	100	**400**	**0.756**	α (α)
NT	100		100	85.71	100	**385.71**	**0.61**	β (ω)
R	28.57	75		83.33	77.78	**262.68**	**0.54**	γ (β)
W	0	71.43	25		50	**146.43**	**0.352**	δ (δ)
B	0	0	0	0		**0**	**0**	ω (γ)
Totals	**128.57**	**246.43**	**225**	**269.04**	**327.78**	**1196.82**		

Again, size was related to rank, but not as strongly in the group setting as in the dyad setting (Table 10; $F_{(1,17)} = 24.59$, $R^2 = 0.59$, $p = 0.0001$). The largest fish was always the dominant (α); however, the most subordinate fish (ω) was not always the smallest fish (Figure 23).

Behavior and Coloration Patterns Displayed in Group Interactions

Following the behavioral observations, the fish were sacrificed and sexed. Both behaviors and coloration patterns were examined via a 2-factor analysis of variance (ANOVA) to determine if either rank or sex (or both) influenced the frequency of displays by a particular fish. Frequency data were arcsin-transformed prior to ANOVA analysis to adjust the data to an approximate normal distribution. All fish from all groups were divided into dominants (index of 1-0.60), middle-ranking individuals (index of 0.59-0.40), and subordinates (index of 0.39-0).

Fish rank, but not sex, had a significant effect on the expression of *Approach* behavior (2-factor ANOVA, $F_{05(2)} = 19.7, p = 0.0001$). While there was a trend for an interaction between rank and sex (2-factor ANOVA, $F_{05(2)} = 2.8, p = 0.094$), this trend was not significant. Post-hoc tests showed that dominant fish approached more frequently than middle-ranking and subordinate fish (Bonferroni-Dunn, $p = 0.004$ and $p = 0.0001$, respectively), and middle-ranking fish approached more frequently than subordinate fish (Bonferroni-Dunn, $p = 0.01$). Fish rank also had an effect on the expression of *Pass* behavior (2-factor ANOVA, $F_{05(2)} = 7.6, p = 0.006$), with dominant fish passing more frequently than subordinate fish (Bonferroni-Dunn, $p = 0.003$). These two behaviors often occur in conjunction, as part of an overall sequence of behavior (Lavalli and Spanier, 2001).

The expression of two behaviors originally classified as subordinate *Trigger-up* and *Head-down* was also influenced by rank of the fish. *Trigger-up* was displayed more frequently by subordinate fish than middle-ranking fish (2-factor ANOVA, $F_{05(2)} = 13.11, p = 0.0008$, Bonferroni-Dunn, $p = 0.014$), and more frequently by middle-ranking and subordinate fish than dominant fish (Bonferroni-Dunn, $p = 0.038$ and $p = 0.0001$, respectively). There was a tendency for there to be an interactive effect between rank and sex for the expression of *Trigger-up* (2-factor ANOVA, $F_{05(2)} = 3.19, p = 0.075$), but this trend was not significant. *Head-down*, often used in conjunction with *Trigger-up*, was displayed more frequently by subordinate fish than middle-ranking fish (2-factor ANOVA, $F_{05(2)} = 11.86, p = 0.0012$, Bonferroni-Dunn, $p = 0.017$), and by subordinate

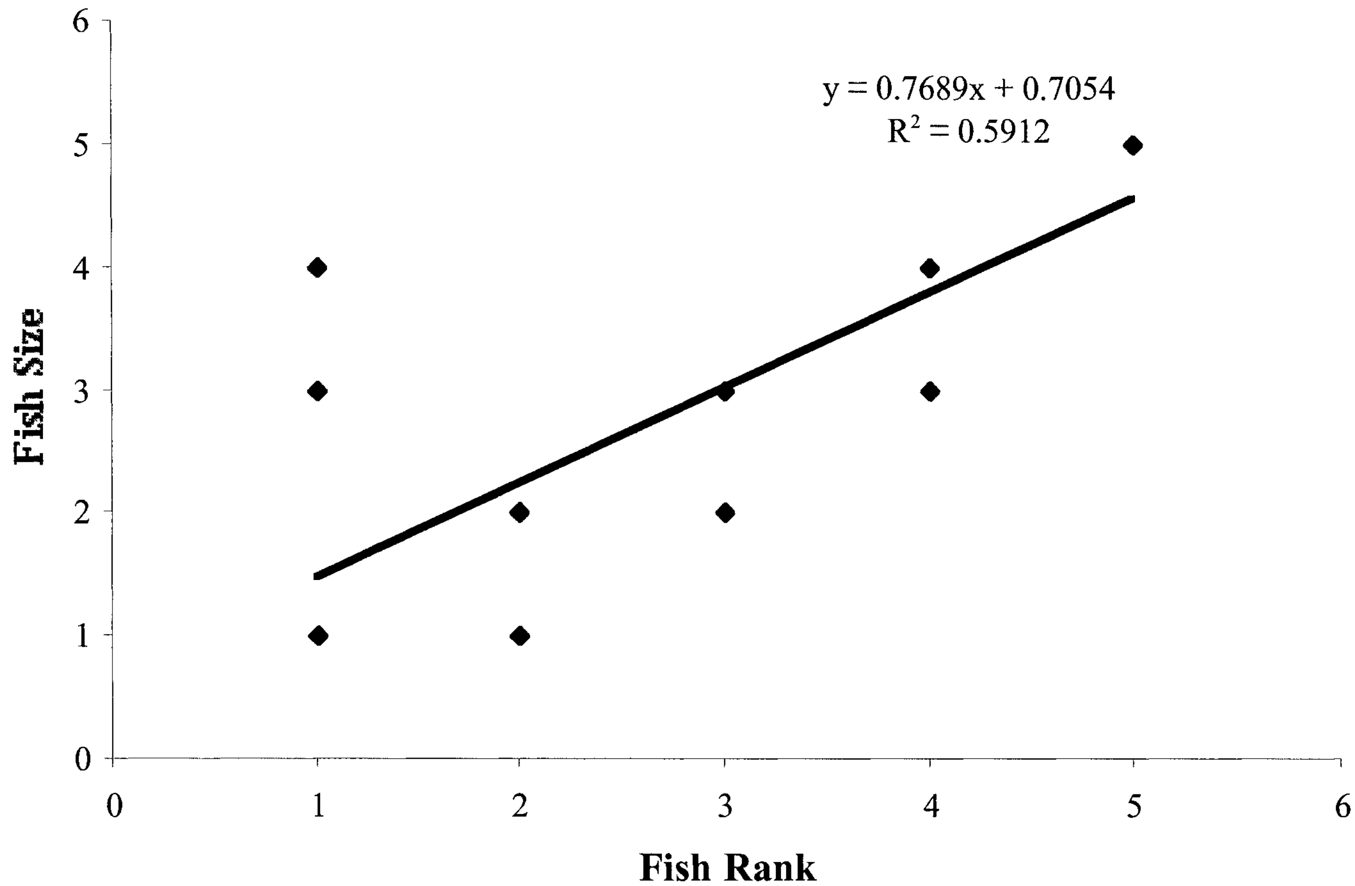

Figure 23: Fish size (5 = largest, 4 = next largest, 3 = middle sized, 2 = second smallest, 1 = smallest) versus fish rank (1 = ω, 2 = δ, 3 = γ, 4 = β, 5 = α) in group interactions. Slope is significantly greater than zero ($p < 0.0001$).

Table 10: All 19 fish coded, ranked, sexed, and sized in standard length given in cm.

Group	Fish Code	Dyad Rank	Group Rank	Sex	Size SL(cm)
1	NT	α	α	M	30.7
	W	β	β	M	27.3
	B	γ	γ	M	26.0
	R	δ	δ	F	25.2
	Y	ω	ω	F	22.5
2	R	α	α	M	25.1
	B	β	ω	F	21.9
	W	γ	β	F	23.6
	NT	δ	γ	F	21.1
	Y	ω	δ	F	22.8
3	NT	α	α	F	28.6
	Y	β	β	F	27.3
	W	γ	γ	M	25.2
	B	ω	ω	F	21.3
4	Y	α	α	M	33.7
	R	β	γ	F	27.0
	B	γ	ω	M	24.4
	W	δ	δ	M	25.4
	NT	ω	β	M	23.8

more than dominant fish (Bonferroni-Dunn, $p = 0.0007$). There was no difference in the expression of *Head Down* by middle-ranking and dominant fish.

There was no effect of rank or sex on the expression of *Veer-Into*, *Chase*, *Flee*, *Bite*, or *Head-up* behavior. These behaviors were infrequent compared to the other behaviors (Figure 24). See Appendix 1 for ANOVA tables.

As with some behaviors, there was a significant effect of rank, but not sex, on the expression of various coloration patterns (Figure 25). *Light banding* was expressed significantly more often by dominant fish than either middle-ranking or subordinate fish (2-factor ANOVA, $F_{05(2)} = 7.22$, $p = 0.008$, Bonferroni-Dunn, $p = 0.045$ and $p = 0.006$, respectively). Middle-ranking and subordinate fish displayed the same frequency of *Light-banding*. While there was no significant effect of rank or sex on the expression of *Dark-banding*, there was a trend for rank to have an effect (2-factor ANOVA, $F_{05(2)} = 2.99$, $p = 0.085$). *Grey* coloration was expressed significantly more frequently by subordinate fish than dominant fish (2-factor ANOVA, $F_{05(2)} = 3.88$, $p = 0.048$, Bonferroni-Dunn, $p = 0.02$), but dominants and middle-ranking fish, as well as middle-ranking and subordinate fish, expressed this coloration with the same frequency. Despite *White* coloration being seen frequently paired with submissive behaviors (*Head-down*, *Trigger-up*), there was no significant effect of rank or sex on its expression, although there was a trend for rank to exert some effect (2-factor ANOVA, $F_{05(2)} = 3.51$ $p = 0.06$). *Speckled* and *Black* coloration were so infrequently displayed by any rank of fish that they could not be examined for rank and sex effects. [See Appendix 2 for ANOVA tables.]

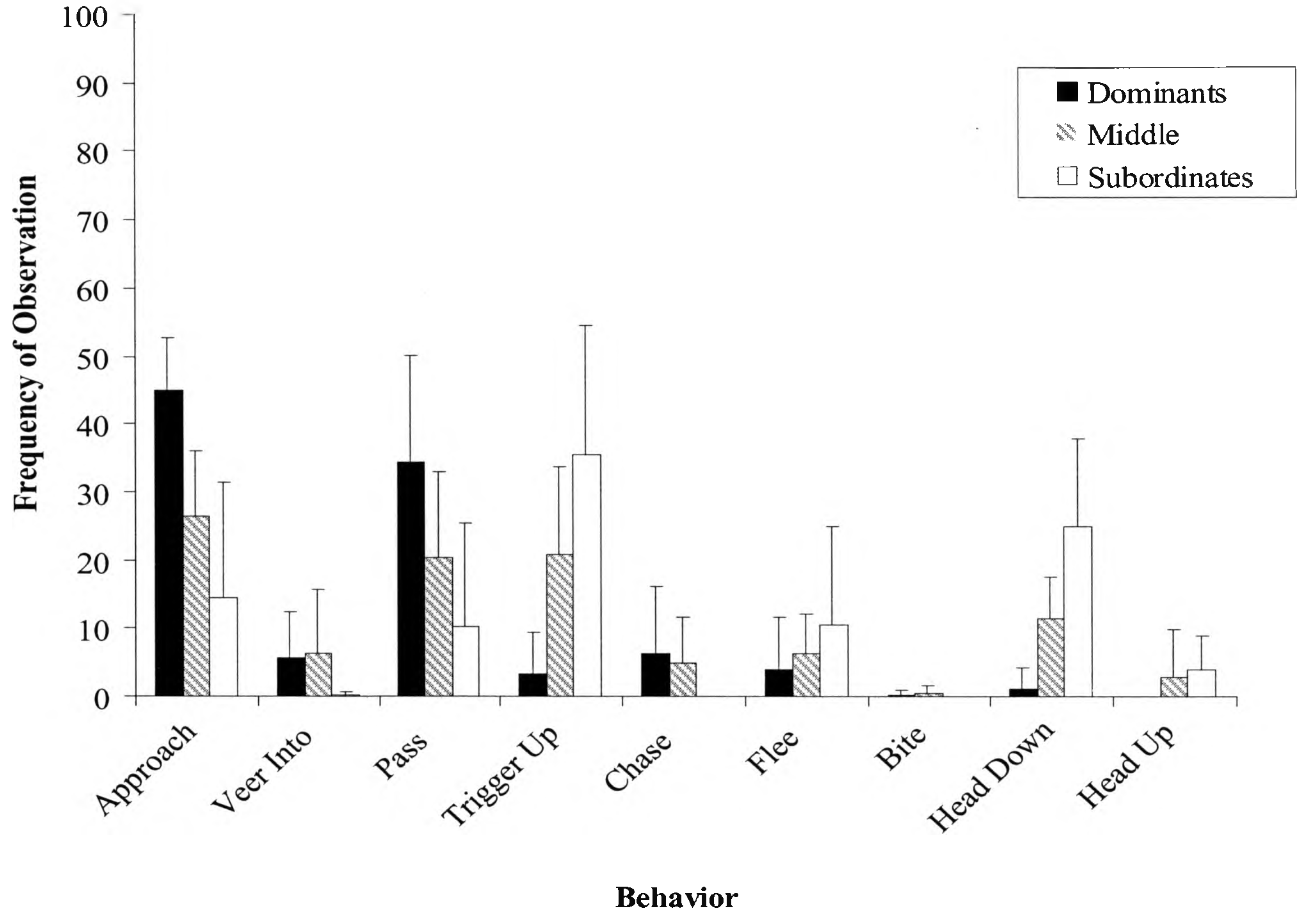

Figure 24: Frequency of observed behaviors for dominant, middle-ranking, and subordinate fish in a group (4 to 5 fish together) interaction setting. N = 6 for dominant fish and middle-ranking fish; N = 7 for subordinate fish. N = 9 for females; N = 10 for males.

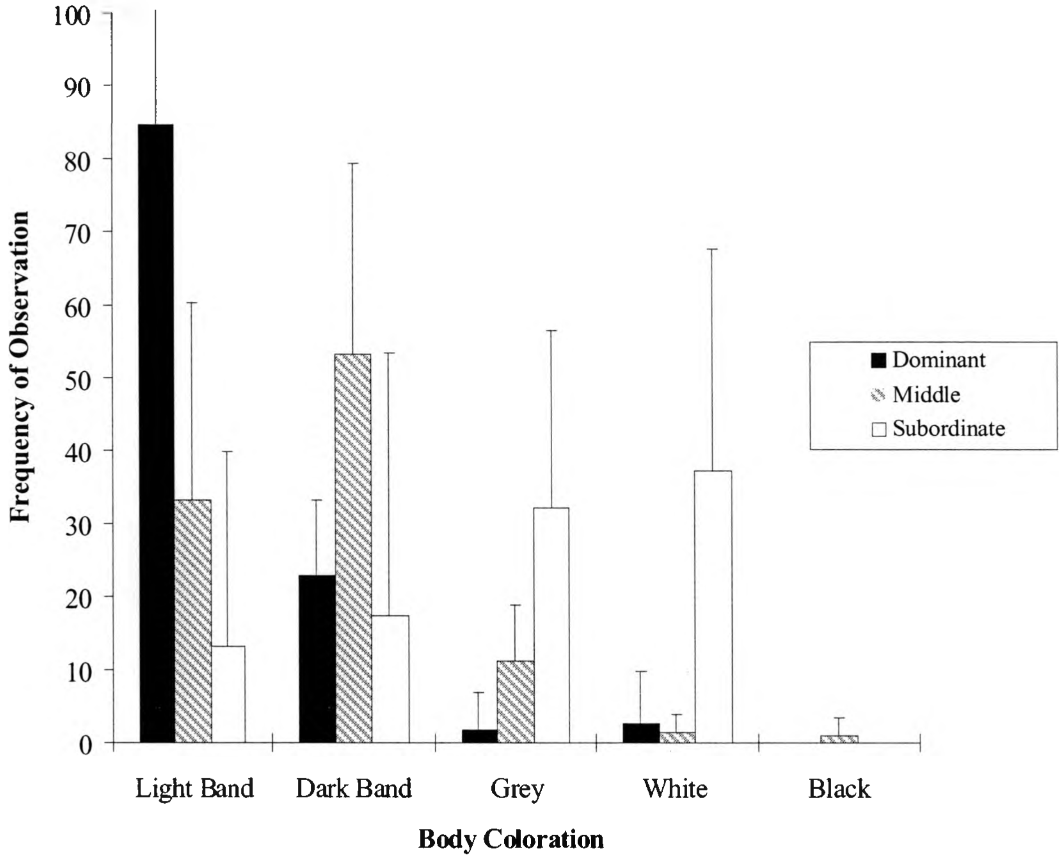

Figure 25: Frequency of observed coloration patterns for dominant, middle-ranking, and subordinate fish in a group (4 to 5 fish together) interaction setting. N = 6 for dominant fish and middle-ranking fish; N = 7 for subordinate fish. N = 9 for females; N = 10 for males.

DISCUSSION

Sixteen interactive behaviors and eight coloration patterns were described for the grey triggerfish (*Balistes capriscus*). Many of these behaviors are part of their normal daily behavioral repertoire and are used for feeding activities as well as fish-fish interactions (see Lavalli and Spanier, 2001 for a description of the typical feeding behaviors of grey triggerfish). For the most part, these behaviors could be classified as agonistic, neutral, and submissive behaviors, although some neutral behaviors could be either agonistic or submissive when paired with certain coloration patterns which provided a contextual background to the behavior. For example, approach and passing behaviors are neutral, being common for both fish-fish interactions and feeding interactions. However, when paired with *Light-* or *Dark-banding* coloration or *White* coloration, they could present a more complex picture of agonism or submission. Thus it is important, in these fish, to examine not only the posturing, but the concomitant coloration pattern, to determine the context of the behavior displayed.

In small groups (N = 4 and 5), these fish form linear hierarchies (Landau s h= 0.95 - 1.0) when observed in semi-naturalistic settings. This study reveals that different ranks of individual grey triggerfish are communicated to conspecifics by the use of body postures coupled with changes in body coloration in both dyadic and group observations. However, this analysis was based entirely on visual observations. It is known that triggerfish communicate through the use of species-specific sounds produced by teeth scraping, and through a pectoral fin spine modification which rubs a post opercular drumming membrane that is connected to the swimbladder (Salmon, et al. 1968). Since no hydrophone recordings were made simultaneously with the behavioral recordings, it is unknown if these fish also used sound to indicate status.

Few fish studies discuss changes in coloration (O Connor, et al. 1999; Salmon et al. 1968) and body posturing (Abbott et al. 1985) when fish are part of a dominance hierarchy. O Connor et al. (1999) found that juvenile Atlantic salmon, *Salmo salar*, darken body coloration and eye sclera in response to an encounter with an attacker, suggesting that the subordinate fish s coloration is used to thwart future aggression. Salmon et al. (1968) described escape and aggressive behavior of several species of triggerfish (e.g. *Balistes capriscus, B. vetula*). In queen triggerfish, *B. vetula*, the aggressive or dominant fish employed color changes as well as sound production. In *B. vetula*, the dominant fish displays bright yellow opercula, while subordinates were dark or light brown. Middle-ranking and subordinate ranking grey triggerfish in this study routinely display colorations different from the most dominant fish. This suggests, as found in O Connor et al. (1999), that subordinate fish use darker or lighter coloration to thwart aggression, unnecessary energy expenditure, and possible injury. Rainbow trout, *Oncorhynchus mykiss*, employ a hunching body posturing and darkening in coloration when communicating defeat to an attacker (Abbott et al. 1985). The same color changes employed by middle- and subordinate-ranking triggerfish, mentioned above, are routinely added to the body postures of changing head position (up or down) and erecting the dorsal trigger to further communicate their subordinate status and lack of challenge to the dominant fish.

There is an apparent relationship between body coloration and posture displays within the dominance hierarchy. The frequency of displays during an encounter is determined by the ranking of both the actor and the reactor. This relationship was demonstrated in both the dyad and group observations. The frequency of *Light-banded* coloration was greatest for dominant and middle-ranking individuals, while the frequency of *Grey* coloration was greatest for subordinate and middle-ranking individuals. Middle- and subordinate-ranking fish displayed behaviors making up *Aggression Inhibition Display* (*Head-down* and *Trigger-up*) more frequently, and there was a tendency for them to display pale (*Grey* or *White*) coloration more frequently as part of this appeasement display. Dominant fish approached and passed other fish much more frequently, probably due to their higher activity levels. More active fish were also more likely to engage in *Approach* behavior, which then led to subsequent behaviors (*Pass*, *Chase*, *Circle Chase*, *Bite*, *Flee*, *Trigger-up*, *Head-down/up*, etc.). In the group setting, more active fish also tended to elicit a greater frequency of AID from less active fish. Less dominant fish were typically more inactive, suggesting that they attempted to avoid interactions by reducing overall activity. Thus, an alpha individual is likely to have the highest frequency of aggressive interactions with the beta individual, the beta with the gamma, and so on, in a linear fashion, while subordinates are likely to avoid confrontations with higher ranking individuals. If true, it would demonstrate a very structured communication system in the dominance hierarchy with a resultant minimal energy cost to maintain the hierarchy. Furthermore, if all fishes take care to maintain their dominance relationship with their neighbor, the hierarchy of the group should not change (Nelissen, 1984).

The largest fish were the highest ranking fish both in dyadic settings and group settings. Nevertheless, lowest ranking individuals were not necessarily the smallest fish, suggesting that it is only the largest size that is important for determining the highest rank. Smaller individuals rarely challenged the largest fish; instead, a smaller individual that approached a dominant fish would use an appeasement display (AID) until the dominant fish left the vicinity of the subordinate or engage in some other activity unrelated to the subordinate. Most appeasement interactions took place when fish were getting reacquainted after dyad pairings and were finding their place in the group hierarchy. When fights occurred between fish, results seem to suggest that they occurred between fish of closely related sizes. Castro and Caballero (1998) observed this same phenomenon in their study of the dominance hierarchy of juvenile white seabream, *Diplodus sargus cadenati*. In contrast to size, sex exerted no effect on the ranks of the fish.

In studies examining winner and loser effects, winners were more likely to win subsequent contests if they fought opponents within a short time frame (usually immediately to < 1 h). Triggerfish used during the dyad portion of this study had a full day to recover in isolation before being subjected to future contests. The magnitude of this extra time may have reduced the influence of winner and loser effects. The same triggerfish used during the group hierarchy observations were subjected to instantaneous action and reaction; thus, winner and loser effects were more apparent. Fish from groups 1 and 3, where the dyad contests predicted the group hierarchy, show indications of winner effects, as evidence by the clear rankings of the individuals within the group hierarchies. Fish from groups 2 and 4, where dyad contests did not accurately predict the group hierarchy, show signs indicative of loser effects. Loser effects are characterized by the emergence of a clear alpha and a shuffling of subordinate ranking individuals. This shuffling of the subordinates is often due to a lack of aggression on their part (Dugatkin, 1997). This was the case with fish from groups 2 and 4 where subordinates did not interact greatly with higher ranking fish. Since I was not specifically looking for winner/loser effects, many of the factors responsible for *B. capriscus* hierarchy assemblage remain unclear.

Many dominance studies have been based on pairwise fights (Beacham and Newman, 1987; Dugatkin and Ohlsen, 1990) between individuals. As with African cichlids (Nelissen, 1985), grey triggerfish dyad observations and rankings were not a good predictor of the subsequent group hierarchies. Shuffling of middle and subordinate ranks occurs and can affect which fish are ultimately ranked as the most subordinate. In lieu of these findings, the use of dyad fights should be reserved for situations in which individuals are rarely found in social groupings. By understanding both the body posturing/movement patterns and the coloration patterns, one can easily identify ranks of grey triggerfish in wild settings on their home reefs.

APPENDIX 1

ANOVA Tables for Behavior Versus Fish Rank and Sex

ANOVA Table for Approach

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	294	147	19 714	.0001	39 428	1 000
Fish Sex	1	001	001	125	7298	125	062
Fish Rank * Fish Sex	2	.043	021	2 851	.0941	5.702	.454
Residual	13	097	007				

ANOVA Table for Veer Into

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	011	005	1 469	2659	2 939	.251
Fish Sex	1	.001	.001	161	6944	161	066
Fish Rank * Fish Sex	2	014	007	1 914	.1868	3 828	317
Residual	13	048	004				

ANOVA Table for Pass

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	244	122	7 645	0064	15.290	891
Fish Sex	1	.001	001	.078	7847	078	058
Fish Rank * Fish Sex	2	.047	023	1.458	2683	2 917	249
Residual	13	.208	016				

ANOVA Table for Trigger Up

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	311	156	13 110	0008	26 220	991
Fish Sex	1	006	006	.547	4726	547	103
Fish Rank * Fish Sex	2	076	038	3 190	0746	6 381	501
Residual	13	154	012				

ANOVA Table for Flee

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	009	.005	.432	6584	863	104
Fish Sex	1	.010	.010	.908	.3579	.908	.138
Fish Rank * Fish Sex	2	027	.014	1.288	3088	2 576	.224
Residual	13	.139	011				

ANOVA Table for Chase

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	007	.004	932	4186	1.864	.173
Fish Sex	1	9 071E-5	9 071E-5	.023	8823	.023	052
Fish Rank * Fish Sex	2	.012	.006	1.464	2671	2.928	250
Residual	13	052	004				

ANOVA Table for Head Down

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	.189	095	11 857	.0012	23.715	983
Fish Sex	1	010	010	1.296	.2755	1 296	176
Fish Rank * Fish Sex	2	001	4 992E-4	063	.9397	.125	058
Residual	13	.104	.008				

ANOVA Table for Head Up

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	003	.001	.574	5767	1 149	.123
Fish Sex	1	4 415E-5	4.415E-5	018	8947	018	052
Fish Rank * Fish Sex	2	008	.004	1 655	2290	3.309	278
Residual	13	032	002				

APPENDIX 2

ANOVA Tables for Coloration Patterns Versus Fish Rank and Sex

ANOVA Table for Light Band

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	1.870	935	7.224	.0078	14 447	.872
Fish Sex	1	.148	148	1.143	3045	1.143	161
Fish Rank * Fish Sex	2	764	382	2.952	0877	5 904	468
Residual	13	1 683	129				

ANOVA Table for Dark Band

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	699	.349	2.992	0853	5 984	474
Fish Sex	1	092	092	.790	.3902	.790	126
Fish Rank * Fish Sex	2	348	174	1.491	.2613	2 981	254
Residual	13	1 518	117				

ANOVA Table for Grey

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	247	.123	3 881	.0477	7 763	.590
Fish Sex	1	.001	.001	017	.8989	017	052
Fish Rank * Fish Sex	2	.008	004	.132	8776	264	.066
Residual	13	414	032				

ANOVA Table for White

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	486	.243	3 515	0602	7.031	.544
Fish Sex	1	005	.005	.079	.7825	.079	.058
Fish Rank * Fish Sex	2	028	.014	.203	8185	407	075
Residual	13	899	069				

ANOVA Table for Black

	DF	Sum of Squares	Mean Square	F-Value	P-Value	Lambda	Power
Fish Rank	2	3.472E-4	1.736E-4	.977	.4024	1.954	.179
Fish Sex	1	1.500E-4	1.500E-4	.844	.3749	.844	.131
Fish Rank * Fish Sex	2	3 472E-4	1 736E-4	977	.4024	1 954	.179
Residual	13	.002	1 777E-4				

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