Size-specific social interactions and foraging styles in a shallow water population of mutton snapper, *Lutjanus analis* (Pisces: Lutjanidae), in the central Bahamas

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Synopsis

Field observations quantified the effects of fish size and time of day on activity patterns, intraspecific encounters, and foraging styles in mutton snapper, *Lutjanus analis,* during the spring and winter of 1991. Fish ranged in size from 15 to 65 cm fork length (FL), and were associated with an artificial patch reef system located on a shallow seagrass meadow in the Exuma Cays, Bahamas. The most common, non-resting diurnal activities were intraspecific chasing and displacing, and feeding. Intraspecific displacing was significantly higher during midday compared to morning or evening. The highest proportion of intraspecific encounters (combined chasing and displacing events) occurred among medium (25–35 cm FL) and large (> 35 cm FL) fish. The few large fish observed (13% of population) initiated the same proportion of encounters as the predominant (50%) medium fish. The remaining (37%) small fish (> 25 cm FL) were the least aggressive. Dark barred and dark nape color patterns were associated with displacing and chasing, respectively. Fish exhibited considerable variability in feeding behavior. Proportionally fewer fish fed during midday compared to morning or evening, although small fish fed proportionally more often than medium or large fish despite time of day. Picking was the primary feeding mode and was observed during all times of day. Winnowing was observed during midday and evening, whereas midwater strikes were confined to morning and evening. Small fish displayed proportionally higher picking and midwater strikes during morning and evening, respectively, compared to medium or large fish. However, large fish winnowed proportionally more often than small or medium fish during evening. Dark barred color patterns were associated with feeding on the substrate, whereas no color changes occurred during midwater strikes. Our results indicate that *L. analis* forms dominance hierarchies and that high variability in foraging styles, according to fish size and time of day, may be a means to reduce intraspecific competition.
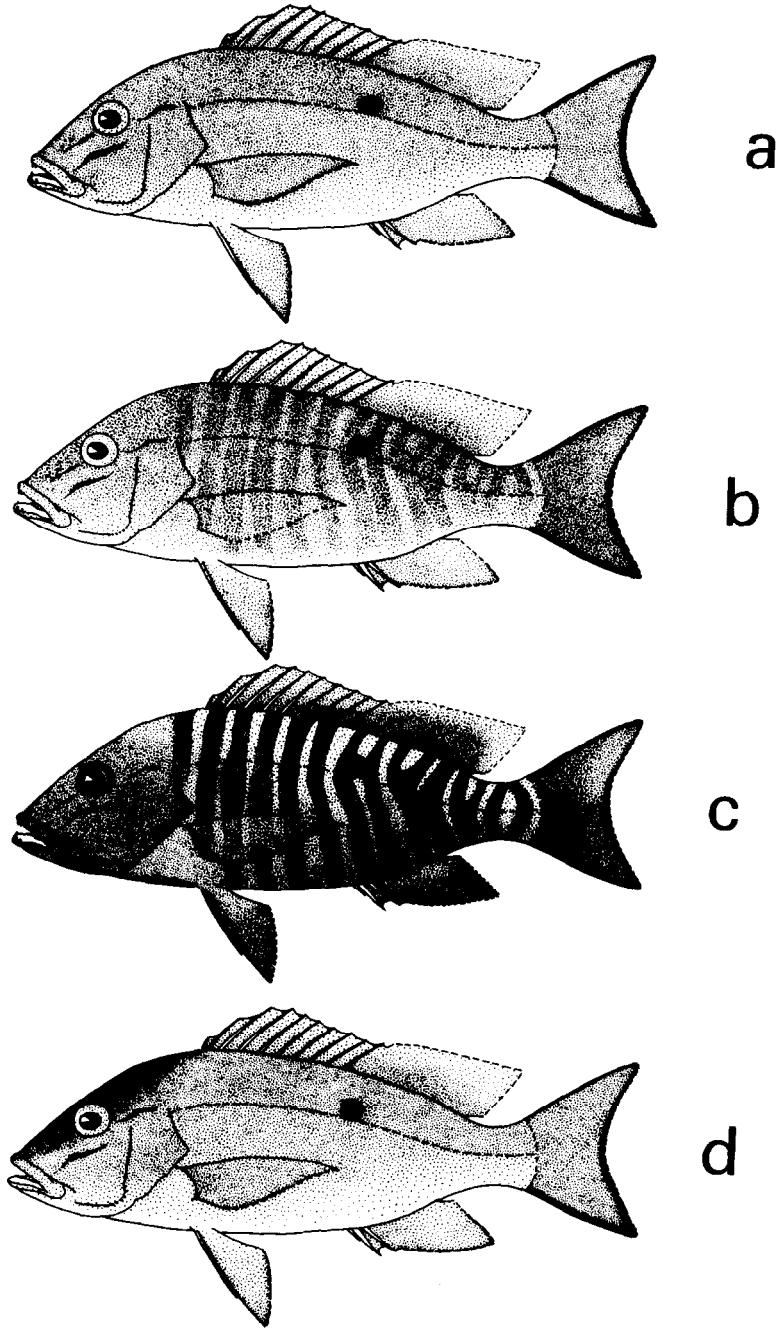
Fig. 1. Color pattern displays in *Lutjanus analis*. Fish changed from the normal pattern (a) to dark barred patterns (b, c) during intraspecific displacing events and when feeding on the substrate. The dark nape pattern (d) was observed only during intraspecific chasing events. Color patterns were ephemeral and blended into one another.

Introduction

Marked changes in body size during ontogeny in most reef fishes is associated with the outcome of intraspecific social interactions and dynamic shifts in foraging styles. For example, absolute and relative body size has a tremendous influence on the intensity of competitive interactions, leading to varia-

ble growth rates and the size structure of populations (Doherty 1982, Jones 1987). In addition, older and larger fish often have a more diverse diet than smaller fish due to improved prey location and handling techniques, and an expansion of niche width due to decreasing vulnerability to predators (Schmitt & Holbrook 1984, Werner & Gilliam 1984, Osenberg & Mittlebach 1989). However, before we can predict population-level consequences of competitive interactions or ontogenetic niche shifts, we need quantitative behavioral observations of size-specific asymmetries in both species interactions and foraging styles. Below, we describe a series of field observations on the effects of fish size and time of day on social interactions and foraging styles in a population of mutton snapper, *Lutjanus analis* (Pisces: Lutjanidae), in the central Bahamas.

L. analis (Fig. 1) is a medium size (≤ 12 kg) snapper that is frequently associated with seagrass beds (Starck 1971, Weinstein 1985), and feeds primarily on nocturnally active crustaceans (Randall 1967, Claro 1981). This species is an important component of shallow water reef fisheries in the tropical western Atlantic (Bortone & Williams 1986). At the turn of the century, *L. analis* was commonly sold at fish markets in Puerto Rico, Cuba and Florida (Evermann & Marsh 1900, Schroeder 1924). During recent years, overfishing at shelf edge spawning aggregations has contributed to a major decline in landings, and in some locations, a total collapse of the fishery (Brownell & Rainey 1971, Gulf of Mexico Fishery Management Council 1992).

Much of the extant literature concerning *L. analis* (i.e., age and growth, reproductive and trophic biology) is based on samples from commercial catches (Rojas 1960, Erhardt & Meinel 1977, Pozo 1979, Claro 1981, 1983, Mason & Manooch 1985, Palazón & González 1986). Behavioral observations of wild fish are few, and have usually been recorded in fish catalogues (Longley & Hildebrand 1941, Böhlke & Chaplin 1968), or ancillary to the study of other species (Myrberg et al. 1969, Colin 1971, Starck 1971, Eggleston et al. 1990, 1992). Given the rapid overexploitation of *L. analis* in certain areas, and the lack of quantitative field observations on the behavioral ecology of this species, we quantified the relative importance of fish size and time of day on social interactions and foraging styles in a population associated with an artificial patch reef system during the spring and winter of 1991.

Materials and methods

Study site

In the central Bahamas, *L. analis* forms small groups of variable size fish that occupy seagrass meadows near inlets and patch reefs (G.D. Dennis unpublished data). Behavioral observations were conducted while snorkeling at an artificial patch reef site off Lee Stocking Island, Exuma Cays, Bahamas (23° 46.21' N, 76° 06.59' W) during the spring (29 March – 31 May) and winter (4–15 December) of 1991. The primary reef (Reef 1) was located in a shallow (2.7 m) *Thalassia testudinum* (seagrass) meadow, and was constructed of two overturned skiffs, rubber tires, and scrap aluminum (area = 491 m^2). A smaller reef (Reef 2) was located in deeper water (4 m), 100 m west of Reef 1, and was composed of corrugated fiberglass roofing material, halved steel drums, and empty propane tanks (area = 78 m^2). We determined the position and distance between Reef 1 and Reef 2 using a Magellan™ global positioning system unit. We determined reef areas using a waterproof measuring tape while SCUBA diving. Although natural patch reefs occur in the area, we selected these artificial reefs for their large number (n ≈ 40) of resident *L. analis*. Since it has been reported that *L. analis* is active during the day and the night (Randall 1967, Starck 1971), we examined daily changes in behavior as well. We did not perform nighttime observations since a previous study (Eggleston et al. 1990) and personal observations indicated that, although *L. analis* associated with shelter on seagrass during the day, fish dispersed widely over the seagrass bed at night.

Observations and analysis of non-resting activity patterns

Diurnal variation in non-resting activity patterns of *L. analis* was quantified during three daily time pe-
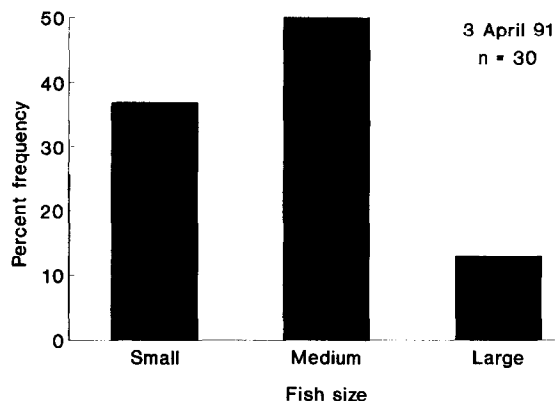
Fig. 2. Size frequency of *Lutjanus analis* sampled from a population associated with an artificial patch reef (Reef 1) located off Lee Stocking Island, Exuma Cays, Bahamas. Fish from 3 April 1991 are shown, where small = below 25 cm fork length (FL), medium = 25–35 cm FL, and large = above 35 cm FL. Fork lengths were estimated visually by comparing fish to a known scale.

riods: morning (0600–1000 h), midday (1100–1500 h) and evening (1500–1900 h). Ten two-hour observation bouts were performed within each time period during 29 March–31 May 1991, under all tidal conditions (flood, ebb, and slack). Behavioral observations were recorded from one of six locations around Reef 1 (area including reef ≈ 1500 m²). If fish were not encountered at one location, the observer moved to another location until fish were found. The non-resting behavior of all *L. analis* observed was recorded for approximately 10 minutes at each location. Fork lengths (FL) were estimated visually by comparing subjects to a known scale (30 cm length of a hand-held underwater slate). Fish were placed into one of three size classes: small (below 25 cm FL), medium (25–35 cm FL), and large (above 35 cm FL). Small, medium and large fish were aged 1+ yr, 2+ yr, and 3+ yr, respectively (sensu Pozo 1979, Claro 1981, Mason & Manooch 1985). Figure 2 shows the length frequency of *L. analis* (size range = 15–65 cm FL) at Reef 1 on 3 April 1991.

We categorized non-resting behaviors as one of three common activities: chasing, displacing, and feeding. Chasing was defined as an intraspecific encounter whereby two fish rapidly swam head to tail for an extended distance. Displacing was defined as an intraspecific encounter whereby a feeding or resting fish (respondent) yielded its position to, or

defended its position against an approaching intruder. Feeding was defined as an action to capture food. Chasing and displacing were recorded as one of nine encounters (intruder vs. respondent) based on contestant size: small vs. small (SS), small vs. medium (SM), small vs. large (SL), medium vs. small (MS), medium vs. medium (MM), medium vs. large (ML), large vs. small (LS), large vs. medium (LM), or large vs. large (LL). Although feeding events were scored during the spring, feeding mode and size-related feeding differences were not quantified. In addition, approximately 10% of the total events recorded were interspecific interactions; these were not used in the subsequent statistical analyses.

To determine how daily activity patterns varied according to time of day and behavioral mode, we used a two-way fixed factor ANOVA model with proportional activity of *L. analis* as the response variable, and time of day (morning, midday, and evening) and behavioral mode (chasing, displacing, and feeding) as factors. We calculated proportional activity as the number of chasing, displacing and feeding events observed for all size classes, divided by the total number of events recorded during an observation bout. To determine how fish size influenced the outcome of intraspecific behavioral interactions, we used a three way, fixed factor ANOVA model with proportional encounters as the response variable, and contestant size (SS, SM, SL,
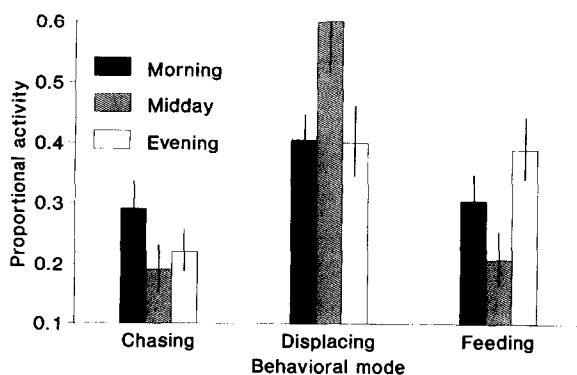

Fig. 3. Non-resting, diurnal activity patterns in *Lutjanus analis*, comparing proportional activity during three time periods (morning: 0600–1000 h, midday: 1100–1500 h, and evening: 1500–1900 h) as a function of the three most common behavioral modes (intraspecific chasing and displacing, and feeding). Values are means ± SE.

Table 1a. Results of a two-way ANOVA (model I) testing the effects of behavioral mode (chasing, displacing, and feeding) and time of day (morning, midday, and evening) on proportional activity (arc-sine square-root transformed) of *Lutjanus analis* during the spring of 1991.

Source of variation	SS	df	MS	F
Behavioral mode	0.93	2	0.47	12.73**
Time of day	0.00	2	0.00	0.03 NS
Behavioral mode × time of day	0.48	4	0.12	3.26*
Error	2.96	81	0.04	

* $p < 0.02$, ** $p < 0.001$, NS $p > 0.05$.

MS, MM, ML, LS, LM, and LL), behavioral mode (chasing and displacing), and time of day (morning, midday, and evening) as factors. We calculated proportional encounters as the number of chasing and displacing events for each of the nine encounters described above, divided by the total numbers of intraspecific encounters recorded during an observation bout.

ANOVA models were used following procedures outlined in Underwood (1981). Proportions were arc-sine square-root transformed to meet assumptions of normality and homogeneity of variance (Zar 1984). In all cases, the variances were homogeneous as determined by Cochran's C-test, or hy-

Table 1b. Tukey's tests of mean proportional activity (arc-sine square-root transformed) of *Lutjanus analis* for the interaction effect of behavioral mode × time of day. Treatment levels that are not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of proportional activity.

Interaction			
Behavioral mode	Time of day		
Chasing	Midday	Evening	Morning
Displacing	Evening	Morning	Midday
Feeding	Midday	Morning	Evening
Time of day	Behavioral mode		
Morning	Chasing	Feeding	Displacing
Midday	Chasing	Feeding	Displacing
Evening	Chasing	Feeding	Displacing

potheses were rejected at α-values lower than the p-value of the test for homogeneity of variance (Underwood 1981). Differences among means were revealed using Tukey's multiple comparison test, as recommended by Day & Quinn (1989).
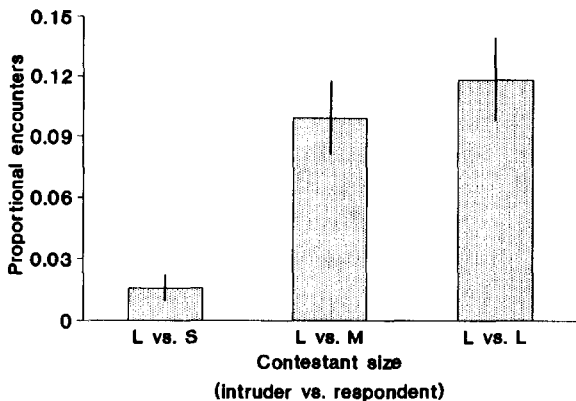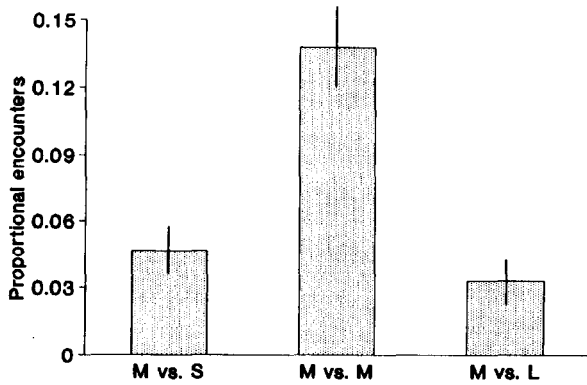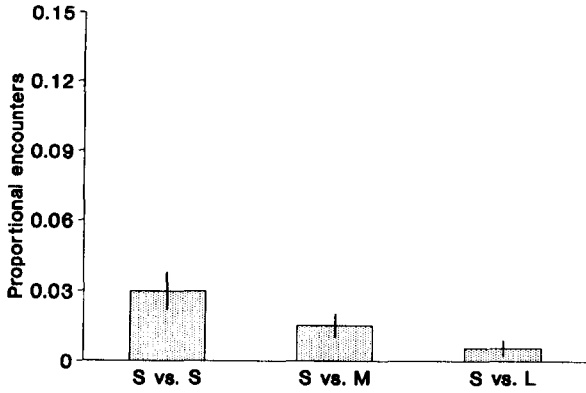
Observations and analysis of foraging styles

During the spring of 1991, *L. analis* were observed using one of three feeding modes: picking, winnowing, and midwater strike. We defined picking as activity spent capturing epifaunal prey. Winnowing was defined as the capture and subsequent separation of infaunal prey from mouthfuls of debris-laden substrate (sensu Schmitt & Holbrook 1984). Pelagic or suprabenthic prey were captured using midwater strikes. Size related differences in the number of fish feeding were apparent as well. Based on these observations of foraging activity during the spring, we modified our sampling approach in the winter (4–15 December) of 1991 to focus on how daily feeding modes varied according to fish size and time of day.

Daily behavioral observations were again divided into three time periods: morning (0600–0800 h), midday (1030–1230 h), and evening (1530–1730 h). Behavioral observations were performed only during the flood tide to maximize visibility. Six two-hour replicate observation bouts were performed during each sampling period. The feeding activities (picking, winnowing, and midwater strikes) of six individuals from each of three size classes (small, medium, and large) were recorded for five minutes per individual during each observation bout. Individual fish were identified by body size, scars, fin anomalies or shape of the black, upper body spot

Fig. 4. Social interactions (combined intraspecific chasing and displacing events) of *Lutjanus analis,* comparing proportional encounters as a function of contestant size. Paired letters represent encounters between intruders (first letter) and respondents (second letter), where S = small (below 25 cm fork length [FL], M = medium (25–35 cm FL), and L = large (above 35 cm FL). Values are means ± SE.

(Fig. 1). Fish were selected as encountered from all *L. analis* observed within 20 m to either side or end of a 100 m transect between Reef 1 and Reef 2 (area including both reefs = 5600 m²). Individual fish were followed only once during an observation bout to insure independence between measurements.

To determine how daily feeding activity varied according to fish size and time of day, we used a two-way, fixed factor ANOVA model with proportional feeding activity as the response variable, and fish size (small, medium, and large) and time of day (morning, midday, and evening) as factors. We calculated proportional feeding as the number of fish within each size class (small, medium, and large) feeding during each two-hour sampling period, divided by six (the total number of fish followed in each size class). To determine how daily feeding modes varied with fish size and time of day, we used a three-way fixed factor ANOVA model with proportional feeding modes as the response variable, and fish size (small, medium, and large), behavioral mode (picking, winnowing, and midwater strikes), and time of day (morning, midday, and evening) as factors. We calculated proportional feeding modes as the number of picking, winnowing, and midwater strike events, divided by the total number of events recorded during each five minute observation period for the individual fish in each size class.

ANOVA models were again used following procedures outlined in Underwood (1981), and proportions arc-sine square-root transformed to meet assumptions of normality and homogeneity of variance (Zar 1984). Variances were homogeneous as determined by Cochran's C-test, or hypotheses rejected at α-values lower than the p-value of this test (Underwood 1981). Differences among means were revealed using Tukey's multiple comparison test, as recommended by Day & Quinn (1989).
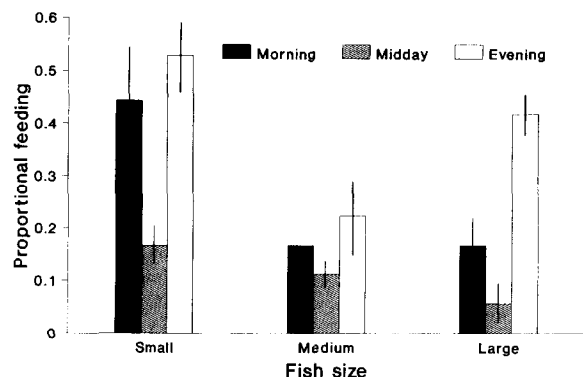
Table 2a. Results of a three-way ANOVA (model I) testing the effects of contestant size (SS, SM, SL, MS, MM, ML, LS, LM, and LL), behavioral mode (chasing and displacing), and time of day (morning, midday, and evening) on proportional encounters (arc-sine square-root transformed) between conspecific *Lutjanus analis* during the spring of 1991.

Source of variation	SS	df	MS	F
Contestant size	3.00	8	0.38	21.00*
Behavioral mode	0.40	1	0.40	22.22*
Time of day	0.04	2	0.02	1.11 NS
Contestant size × behavioral mode	0.30	8	0.04	2.09 NS
Contestant size × time of day	0.38	16	0.02	1.31 NS
Behavioral mode × time of day	0.05	2	0.03	1.45 NS
Contestant size × behavioral mode × time of day	0.25	16	0.02	0.87 NS
Error	8.69	486	0.02	

* $p < 0.001$, NS $p > 0.031$ (Cochran's C-test rejected homogeneous variances at $p < 0.031$).

Results

Non-resting activity patterns

During the spring (29 March–31 May) of 1991, diurnal activity patterns of *L. analis* varied significantly according to the type of behavioral mode displayed, but not according to time of day (Table 1a). However, the behavioral mode by time of day interaction effect was significant, precluding generalized conclusions about the behavioral mode main effect (Underwood 1981). The interaction effect was due to significantly higher displacing activity during midday compared to morning or evening, and significantly higher midday displacing activity vs. chasing or feeding during the same time period (Table 1b, Fig. 3).

The most common diurnal activity among conspecific *L. analis* were attempts by intruders to displace respondents from feeding or resting sites. The outcome of displacing events was size dependent. When an intruder was larger, the respondent be-

haved submissively and offered little resistance. For instance, medium and large intruders were often observed taking prey from smaller conspecifics. During these encounters, a respondent usually swam a short distance away (< 5 m), but frequently returned to its original position after the intruder departed. Displacing events were not overtly hostile. When contestants were of similar size, however, the encounters were more aggressive. To ward off intruders, respondents displayed dark barred color patterns (Fig. 1b, c) and extended their dorsal fins, or flicked their caudal fins downward. Intruders used nudges, jaw snapping or lateral headbutts during such disputes. Rapid intraspecific chases were another common activity among *L. analis*, and primarily involved similar size fish. The distance covered during a chase was usually greater than 25 m, and intruders frequently displayed a dark nape (Fig. 1d). Occasionally, respondents followed intruders after a chase.

Encounters between conspecific *L. analis* varied significantly as a function of contestant size and be-

Table 2b. Tukey's test of mean proportional encounters (arc-sine square-root transformed) between conspecific *Lutjanus analis* for the main effect of contestant size. Paired letters represent encounters between intruders (first letter) and respondents (second letter), where S = small, M = medium, and L = large. Treatment levels not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of proportional encounters.

Main effect

Contestant size

SL	LS	SM	SS	ML	MS	LM	LL	MM

Fig. 5. Foraging styles in *Lutjanus analis,* comparing proportional feeding activity during three time periods (morning: 0600–0800 h, midday: 1030–1230 h, and evening: 1530–1730 h) as a function of fish size (small: below 25 cm fork length [FL], medium: 25–35 cm FL, and large: above 35 cm FL). Values are means ± SE.

havioral mode, but not according to time of day (Table 2a). The significant contestant size effect was due to the significantly higher proportion of MM, LM, and LL encounters compared to all other possible encounters (Table 2b, Fig. 4). The significant behavioral mode effect was due to the higher proportion of displacing (0.072 ± 0.007; pooled mean ± SE) vs. chasing (0.039 ± 0.005) events irrespective of contestant size.

Foraging styles (modes)

During the winter (4–15 December) of 1991, feeding activity varied significantly by fish size and time of day; the interaction effect was not significant (Table 3a). The significant fish size effect was due to the significantly higher proportion of small fish feeding vs. medium or large fish (Table 3b, Fig. 5), while the significant time of day effect was due to the significantly higher proportion of feeding activity during morning and evening compared to midday.

Picking, winnowing and midwater strikes were used by *L. analis* to capture epifaunal, infaunal, and pelagic or suprabenthic prey, respectively. Fish changed from the normal color pattern (Fig. 1a) to barred color patterns (Fig. 1b, c) when feeding on the substrate. Barred fish were cryptic, and blended well with the surrounding seagrass blades. During midwater strikes, all fins were extended, with no accompanying color change (Fig. 1a).

Prior to picking, fish approached the bottom at approximately 30° from horizontal and 'nosed around' the seagrass. While stalking, faint vertical bars developed over the entire length of the body (Fig. 1b). The bars darkened and became more distinct as fish paused prior to attack (Fig. 1c). Simultaneously, the normally pale gold or bronze iris be-

Table 3a. Results of a two-way ANOVA (model I) testing the effects of fish size (small, medium, and large) and time of day (morning, midday, and evening) on proportional feeding (arc-sine square-root transformed) by *Lutjanus analis* during the winter of 1991.

Source of variation	SS	df	MS	F
Fish size	0.48	2	0.24	9.73*
Time of day	0.82	2	0.41	16.62*
Fish size × time of day	0.19	4	0.05	1.93 NS
Error	1.11	45	0.02	

* $p < 0.001$, NS $p > 0.05$.

Table 3b. Tukey's tests of mean proportional feeding activity (arc-sine square root transformed) by *Lutjanus analis* for the main effects of fish size and time of day. Treatment levels that are not significantly different at the 0.05 level share an underline. Treatment levels are arranged in increasing order of proportional feeding.

Main effect			
Fish size	Medium	Large	Small
Time of day	Midday	Morning	Evening

came brilliant red. During picking, *L. analis* darted forward and perpendicular to the substrate. After an attack, the bars and iris faded as the fish resumed its normal color pattern (Fig. 1a) and horizontal position above the seagrass.

Winnowing was associated with shallow, sandy depressions (depth ≈ 25 cm) in the seagrass bed. Prior to winnowing, some fish removed loose seagrass blades from the depression and spat them to the side. *L. analis* then plunged its snout into the depression, up to the anterior edge of the operculum. While in this position, the head and vertical bars darkened (Fig. 1c), the iris turned dark red, and the ventral portion of the body, including fins, became a dusky red color. The barred pattern appeared more pronounced as burrowing time increased up to five seconds. During winnowing, fish ejected unwanted material through the mouth or opercular openings and swallowed the remaining material. Some fish repeated this behavior for several minutes in one location, until prey were apparently captured.

Proportional feeding activity varied significantly according to behavioral mode and time of day, but not according to fish size (Table 4a). The interaction effects of fish size × behavioral mode and behavioral mode × time of day were significant, however, the significant three-way interaction (fish size × behavioral mode × time of day) precluded generalized conclusions about the two-way interactions or the main effects (Underwood 1981). The three way interaction was due to variation in feeding modes according to fish size and time of day (Table 4b, Fig. 6).

For example, during the morning, small fish only used picking, whereas medium and large fish used both picking and midwater strikes to feed. Winnowing was never observed during the morning. The proportion of picking events by small fish was significantly higher than that of medium or large fish, and there were no significant differences between the proportion of picking and midwater strikes by medium vs. large fish. Midwater strikes were not observed during midday. Large fish were observed winnowing only, whereas small and medium fish were both observed picking and winnowing (Fig. 6). During midday, the proportion of winnowing events did not vary significantly according to fish size (Table 4b). There were also no significant differences in the proportion of picking and winnowing events by small vs. medium fish. In the evening, all three size classes of *L. analis* displayed all three feeding modes. However, small fish exhibited a significantly lower proportion of winnowing events compared to picking or midwater strikes, yet the proportion of midwater strikes by small fish was significantly higher compared to those of medium or large fish. Large fish displayed a significantly higher proportion of winnowing events compared to small or medium fish, however, medium fish used a significantly higher proportion of picking events compared to winnowing or midwater strikes (Table 4b, Fig. 6).

Table 4a. Results of a three-way ANOVA (model I) testing the effects of fish size (small, medium, and large), behavioral mode (picking, winnowing, and midwater strike), and time of day (morning, midday, and evening) on proportional feeding modes (arc-sine square-root transformed) of *Lutjanus analis* during the winter of 1991.

Source of variation	SS	df	MS	F
Fish size	0.18	2	0.09	2.49 NS
Behavioral mode	3.20	2	1.60	45.19**
Time of day	0.27	2	0.14	3.84*
Fish size × behavioral mode	0.93	4	0.23	6.61**
Fish size × time of day	0.06	4	0.02	0.46 NS
Behavioral mode × time of day	1.58	4	0.40	11.19**
Fish size × behavioral mode × time of day	1.22	8	0.15	4.32**
Error	33.41	945	0.04	

* p < 0.03, ** p < 0.001, NS p > 0.05.

Table 4b. Tukey's tests of mean proportional feeding modes (arc-sine square-root transformed) of *Lutjanus analis* for the interaction effect of fish size × behavioral mode × time of day. Treatment levels that are not significantly different at the 0.05 level share an underline. Treatment levels that are not underlined indicate that feeding was not observed. Treatment levels are arranged in increasing order of proportional feeding modes.

Interaction

Morning

Fish size	Behavioral mode		
Small	Winnowing	Midwater strikes	Picking
Medium	Winnowing	Midwater strikes	Picking
Large	Winnowing	Midwater strikes	Picking

Behavioral mode	Fish size		
Picking	Medium	Large	Small
Winnowing	Small	Medium	Large
Midwater strikes	Small	Large	Medium

Midday

Fish size	Behavioral mode		
Small	Midwater strikes	Picking	Winnowing
Medium	Midwater strikes	Picking	Winnowing
Large	Midwater strikes	Picking	Winnowing

Behavioral mode	Fish size		
Picking	Large	Small	Medium
Winnowing	Small	Medium	Large
Midwater strikes	Small	Medium	Large

Evening

Fish size	Behavioral mode		
Small	Winnowing	Midwater strikes	Picking
Medium	Midwater strikes	Winnowing	Picking
Large	Midwater strikes	Winnowing	Picking

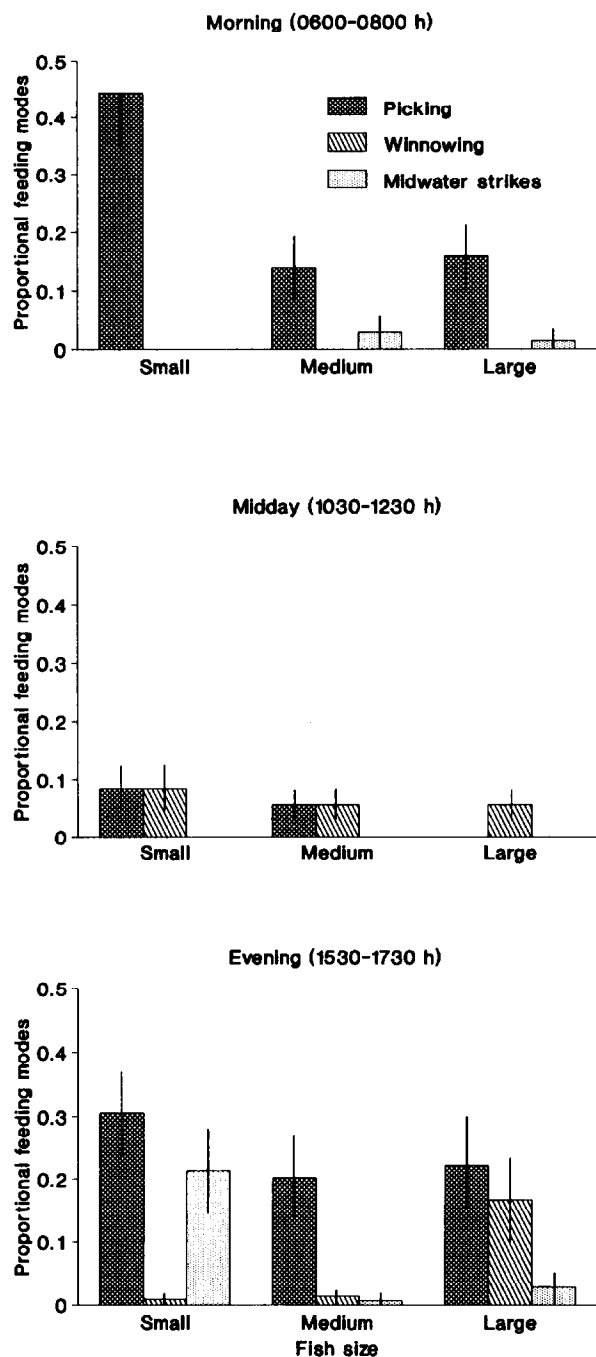| Behavioral mode	Fish size		
Picking	Large	Small	Medium
Winnowing	Small	Medium	Large
Midwater strikes	Large	Medium	Small

Fig. 6. Foraging styles in *Lutjanus analis,* comparing proportional feeding modes (picking, winnowing, and midwater strikes) as a function of fish size (small: below 25 cm fork length [FL], medium: 25–35 cm FL, and large: above 35 cm FL) and time of day. Values are means ± SE.

Discussion

Snappers are generally recognized as nocturnal predators that form inactive polarized schools during daylight hours. These schools typically associate with some form of structural relief (Starck & Davis 1966, Hobson 1968, Potts 1970, Collette & Talbot 1972). Polarized schooling fish do not form dominance relationships and rarely display aggression toward conspecifics (Keenleyside 1979). The behavior of *L. analis* observed in our study was atypical of most snappers, and was markedly different from Keenleyside's (1979) conclusions. Our results indicate that *L. analis* forms dominance hierarchies and feeds diurnally. The high variability in feeding behavior of *L. analis,* according to fish size and time of day, may be a means to reduce intraspecific competition.

If dominance systems are to operate efficiently, individuals must either respond to cues highly correlated with dominance, or they must use individual recognition (Morse 1980). Ostensibly, this is the function of displacing behavior in *L. analis.* These events were not overtly hostile, and respondents behaved submissively at the approach of larger, intruding conspecifics. Since hierarchies provide effective methods of resource exploitation under stringent conditions of little cover and high population density (Morse 1980), it follows that our study site would be an ideal 'staging ground' for the establishment of a hierarchy.

The highest proportion of intraspecific encounters (combined chasing and displacing events) occurred among medium (25–35 cm FL) and large (> 35 cm FL) fish. The few large fish observed (13% of population) initiated the same proportion of encounters as the predominant (50%) medium fish. The remaining (37%) small fish (< 25 cm FL) were the least aggressive. A comparable social structure was reported by McFarland & Hillis (1982), who observed that large juvenile *Haemulon flavolineatum* (French grunts) exerted dominance over smaller conspecifics at resting sites. Likewise, in laboratory studies, Ryer & Olla (1991) showed that the intensity of intraspecific aggression among juvenile *Oncorhynchus keta* (chum salmon) increased with age. During these experiments, individuals that aggres-

sively monopolized food sources established dominance relationships.

Subordinate individuals may find it advantageous to behave in different ways from dominant fish, rather than compete directly for scarce resources (Magurran 1986). This was evident in the size-specific foraging styles displayed by *L. analis*. During daylight hours, small fish fed proportionally more often than medium or large fish. Ontogenetic differences in feeding patterns have been reported for other snappers such as *Lutjanus griseus, Rhomboplites aurorubens,* and *Lutjanus apodus* (Starck 1971, Grimes 1979, and Rooker 1991, respectively). Through gut content analysis, these authors determined that juvenile snapper feed diurnally, and adults nocturnally. We interpret our findings as a mechanism to reduce intraspecific competition (sensu Magurran), since small *L. analis* frequently incurred losses to larger conspecifics. However, the differences may be related to size-specific metabolic rates reported for many fish (Smith 1989). For example, cultured juvenile salmonids such as *Salvelinus fontinalis, Salmo trutta,* and *Oncorhynchus mykiss* (brook charr, brown and rainbow trout, respectively) require feed at a greater percentage of their body weight per day than larger conspecifics (Buterbaugh & Willoughby 1967).

Intraspecific competition may decrease when individuals vary their choice and handling of prey (Ringler 1983). Fish may specialize in a few methods to capture prey, or may alternatively be generalists, which employ most if not all methods available to the species (Curio 1976, cited in Magurran 1986). *L. analis* varied its feeding behavior by alternating between picking, winnowing, and midwater strikes according to fish size and time of day. For instance, small fish specialized in picking behavior during the morning, whereas large fish specialized in winnowing during midday. Picking was observed during all times of day, whereas midwater strikes were observed during the morning and evening only. In the evening, *L. analis* employed all three feeding modes, however, individual differences were detected according to fish size (Table 4b, Fig. 6).

Picking and midwater strikes appear to be the normal feeding modes for most lutjanids (Hobson 1968, 1974, Starck 1971). Still, the winnowing behavior of *L. analis* seems unusual among snappers. Feeding mechanisms such as winnowing have evolved to capture prey that are hidden during the day and not available to other fish (Starck & Davis 1966). For example, off the southern California coast, adult *Embiotoca jacksoni* (black surfperch) winnowed more often than juveniles, which enabled adults to take advantage of, and to be more selective of a broader taxonomic range of prey (Schmitt & Holbrook 1984). We observed a similar pattern in *L. analis*. During midday and evening, all fish employed winnowing, yet large fish exhibited a higher proportion of winnowing compared to smaller conspecifics.

Predation risk may influence winnowing behavior as well. During winnowing bouts, fish are vulnerable to predation since they spend several seconds burrowed into the substrate. Because large fish are less vulnerable to predation than smaller conspecifics (Milinski 1986), a size refuge may enable large *L. analis* to winnow more often during times of increased predation risk such as the evening.

Twilight periods are a time of major activity for lutjanids (Hobson 1968, Starck 1971). Previous food habit studies show that nocturnally active crustaceans are the major prey of *L. analis* (Randall 1967, Claro 1981). Presumably, the high proportion of *L. analis* feeding during the morning and evening can be attributed to the twilight activity of these prey items. Moreover, midwater strikes were observed only during the morning and evening. This suggests that piscivory in *L. analis* is important during twilight hours, which is typical of lutjanids (Helfman 1986).

In summary, we have presented evidence of size-specific asymmetries in social interactions and foraging styles of *L. analis*. Our results indicate that *L. analis* forms dominance hierarchies, which in turn influence the impact of behavioral mode, fish size and contestant size upon proportional activity and intraspecific encounters. Our results also show that *L. analis* exhibits considerable variability in feeding behavior. For example, small fish displayed proportionally higher picking and midwater strikes during morning and evening, respectively, compared to medium or large fish. High variability in foraging

styles, according to fish size and time of day, may therefore be a means to reduce intraspecific competition within the hierarchy.

Acknowledgements

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