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Diurnal Time-Activity Budgets Of Schoolmaster Snapper (Lutjanus Apodus) In South Water Caye Marine Reserve (Belize)

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DIURNAL TIME-ACTIVITY BUDGETS OF SCHOOLMASTER SNAPPER (*LUTJANUS APODUS*) IN SOUTH WATER CAYE MARINE RESERVE (BELIZE)

By
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ABSTRACT

Diurnal time-activity budgets from a sample of 588 schoolmaster snapper (*Lutjanus apodus*, Family Lutjanidae) were recorded over a period of two and a half weeks in the South Water Caye Marine Reserve (Belize) during May and June of 2010. Each fish was observed for a 20-second time period, and the amount of time they spent swimming, stationary (resting), foraging, and performing "other" (less common activities) behaviors was recorded.

The specific objectives of my study were to: (1) quantitatively describe the behavior of schoolmaster with time-activity budgets, (2) assess differences in schoolmaster size distribution by location (habitat type), and (3) analyze differences in activity budgets within and among varying size classes.

Lutjanus apodus spent significantly more time resting (54%) and swimming (44%), than foraging or performing "other" activities (e.g., aggression, and being cleaned). Foraging behavior was rarely observed during daylight observations, which corroborated previous investigations and local knowledge that this species feeds nocturnally. Larger schoolmaster dominated reef habitats, whereas the smaller specimens favored shallow intertidal and mangrove habitats. There were significant differences spent in behaviors for all size classes, when size class was used as a criterion. *L. apodus* spent significantly more time swimming during mornings than later in the day, and those observed in the shallowest habitats spent more time swimming than those in deeper habitats.

Introduction

Lutjanus apodus (schoolmaster snapper, Family Lutjanidae) are the most prevalent snapper species found in the Caribbean (Randall 1996). They are a subtropical species, closely associated with coral reef habitats that fringe seagrass beds and mangrove-lined shores (Verweij *et al.* 2007). They are commonly seen throughout the day, making them ideal candidates for diurnal-behavioral observation, which was the central objective of this study.

Many fish demonstrate species-specific migration patterns, behavior and habitat usage (Hammerschlag-Peyer and Layman 2010). Closely related species of Lutjanidae (e.g., *L. apodus* and *L. griseus*) and individuals within a species can vary substantially in niche usage, movement, and behavior (Hammerschlag-Peyer and Layman 2010). Unfortunately, fishery management to-date has mostly treated fish populations as homogenous units; thus unique foraging behaviors and habitat variations are frequently overlooked in modern preservation efforts (Hammerschlag-Peyer and Layman 2010). A better understanding of the overall behavior, migration patterns, and habitat usage of common reef fish, including *Lutjanis apodus,* is crucial to contemporary conservation efforts.

Species-specific behavioral studies could shed light on important habitats and activity patterns of reef fish. A thorough understanding of relationships among biological processes, behavior, and habitat is essential for pinpointing valuable fish niches and establishing protected areas (Hitt *et al.* 2011a). Behavioral ecologists can gain a better sense of a particular species' daily behaviors by making observations and compiling time-activity budgets (Altman 1974). A time-activity budget is a quantitative means of expressing how an animal divides its time into certain behaviors (Altman 1974). How an animal spends its time among different activities, or in different habitats, can provide valuable information about its ecological significance and niche (Parker and Pianka 1974). This principle is often used, and time-activity budgets commonly employed, to study the behavior of birds and land animals (Ryan and Dinsmore 1979, Gaston and Nasci 1989). Time-activity budgets can also be extended to study the behavior of fish. How a fish divides its time during the course of a day will impact its ability to feed, survive, find a mate, and ultimately reproduce. By closely studying how members of a particular species spend their time, more detailed information can be gained concerning conservation, management, and species preservation.

The time-activity budgets for my investigation focused on diurnal behavior of *Lutjanus apodus.* Schoolmaster have a sizeable head with a pointed snout, making them easy to identify. A large pair of upper canines is sometimes visible, even when the mouth is closed (Humann and DeLoach 2002a). They are silvery-gray in color (commonly with a coppery tinge), and have eight pale vertical stripes down their midsection (Humann and DeLoach 2002a, Figure 1). All fins are yellow, and in large adults the vertical stripes might be faint or completely absent (Randall 1996). Juveniles possess a distinct, dark-gray bar through each eye and demonstrate different habitat preferences than adults (Humann and DeLoach 1999, Figure 2).

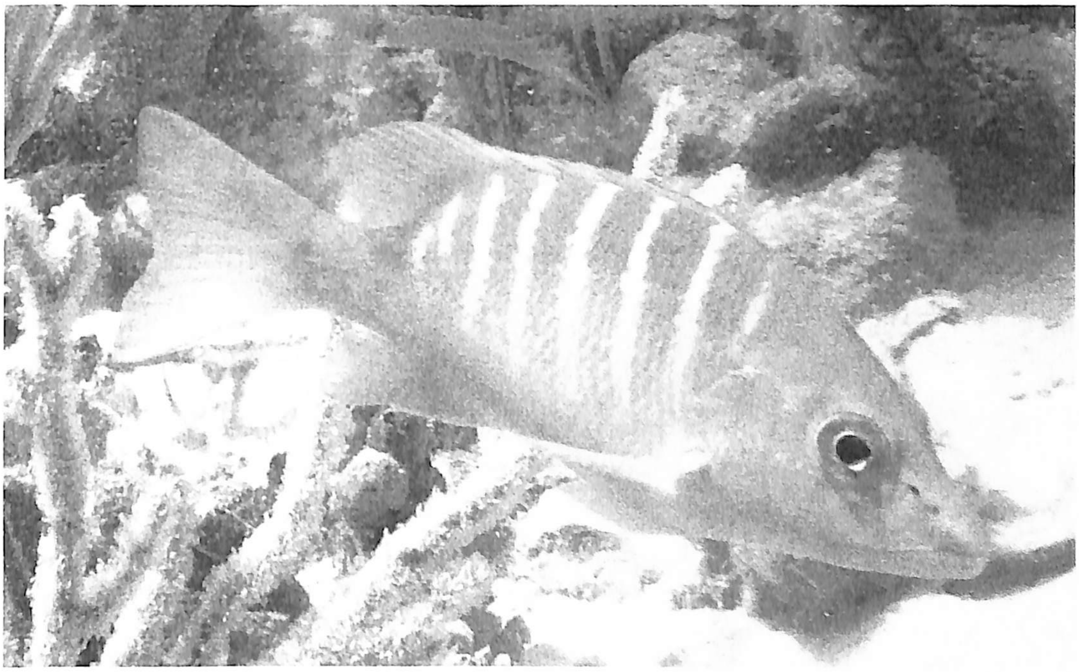

Figure 1: Photograph of adult schoolmaster (by Gary Gaston).

Figure 2: Photograph of juvenile schoolmaster (by Gary Gaston).

Lutjanus apodus are commercially valuable fish and considered suitable for both eating and sporting purposes. *L. apodus* typically range in length from 15 to 60 cm, the most common size range being 25-46 cm (Humann and DeLoach 2002a). Adults prefer a depth range of 3-24 m (Froese and Pauly 2012). Mature schoolmaster are sometimes observed resting in large gatherings during the day, and they often hover in the shade of large coralline or rocky structures (Humann and Deloach 1999). *L. apodus* are commonly found near or behind staghorn (*Acropora cervicornis*) and elkhorn (*Acropora palmata*) coral projections, or near well developed Carribean sea fans *(Gorgonia ventalina)* (C. Howe, personal observation). Adult *L. apodus* frequently engage in a behavior known as "staging," or facing into the current to rest out in the open (*sensu* Luo *et al.* 2009). This behavior commonly takes place in large, mixed-species groups of fish (C. Howe, personal observation).

Juveniles mostly live and seek refuge among mangrove prop roots (usually amid prop-roots of red mangroves, *Rhizophora mangle* (Humann and DeLoach 1999). As juveniles increase in size, they spend less time among prop roots and eventually move permanently onto the coral reef. Direct evidence of connectivity between mangrove prop-root community habitats and coral reefs was provided in a tagging study, where the tagged movements of sub-adult schoolmaster were observed (Verweij *et al.* 2007). Lower instances of predation on juveniles living among mangrove roots, and their tendency to feed mostly at midday while maintaining a short distance from roots, suggests a protective, nursery function of mangrove habitats (MacDonald *et al.* 2009). Neither of these studies provided detailed information on behavior or activity budgets.

Lutjanus apodus employs the use of multiple habitats (mangroves, grassbeds, and coral reefs) to carry out different behaviors and life stages. Research on the feeding ecology of schoolmaster suggests that they feed both in the water column and along the bottom (Randall *et al.* 1967). Experiments conducted in the West Indies established that their diets consist of small fish, benthos, and predominately small crustaceans (Randall 1967). In southwestern Puerto Rico, stomach-content analyses indicated that smaller schoolmaster (< 7 cm) fed almost exclusively on small crustaceans, whereas larger specimens (> 7 cm) favored piscine (fish) prey (Rooker 1995). *L. apodus* demonstrate a strong preference for live prey, and have been determined to be non-ideal candidates for aquiculture (Cole *et al.* 1999). No data on feeding periodicity or activity budgets during daylight have been conducted for this species.

It was assumed *a priori* that *L. apodus* feed diurnally, as many of their close relatives such as the yellowtail snapper (*Ocyurus chrysurus*) commonly feed during the day (G. Gaston, personal observation). This assumption proved false during preliminary observations for the study. Interviews with Belizean fishermen further indicated that *L. apodus* were usually caught only after dark or very early in the morning, near areas covered in seagrass, not diurnally as originally assumed. Due to low incidences of daytime feeding behavior, I decided to also focus on swimming, stationary, and "other" behavior when compiling time-activity budgets for my research.

Specifically, the objectives of my study were to: (1) quantitatively describe the behavior of schoolmaster with time-activity budgets, (2) assess differences in schoolmaster size distribution by location (habitat type), and (3) analyze differences in activity within and among size classes. With the use of time-activity budgets, I investigated the diurnal behavioral ecology of the *L. apodus* to gain a better understanding of how this common, Caribbean reef fish divided its time into various behaviors.

Materials and Methods

Study Sites

This study was conducted within the 52 km^2 South Water Caye Marine Reserve, Belize (Central America). Eleven different observation locations were used within the reserve. Seven sites consisted of reef habitat and focused on adult *L. apodus*. Four sites consisted of shallow intertidal and mangrove habitats, and focused on juveniles. Most observations were conducted off the south end of South Water Caye (SWC), about 14 km from mainland Belize (Figure 3).

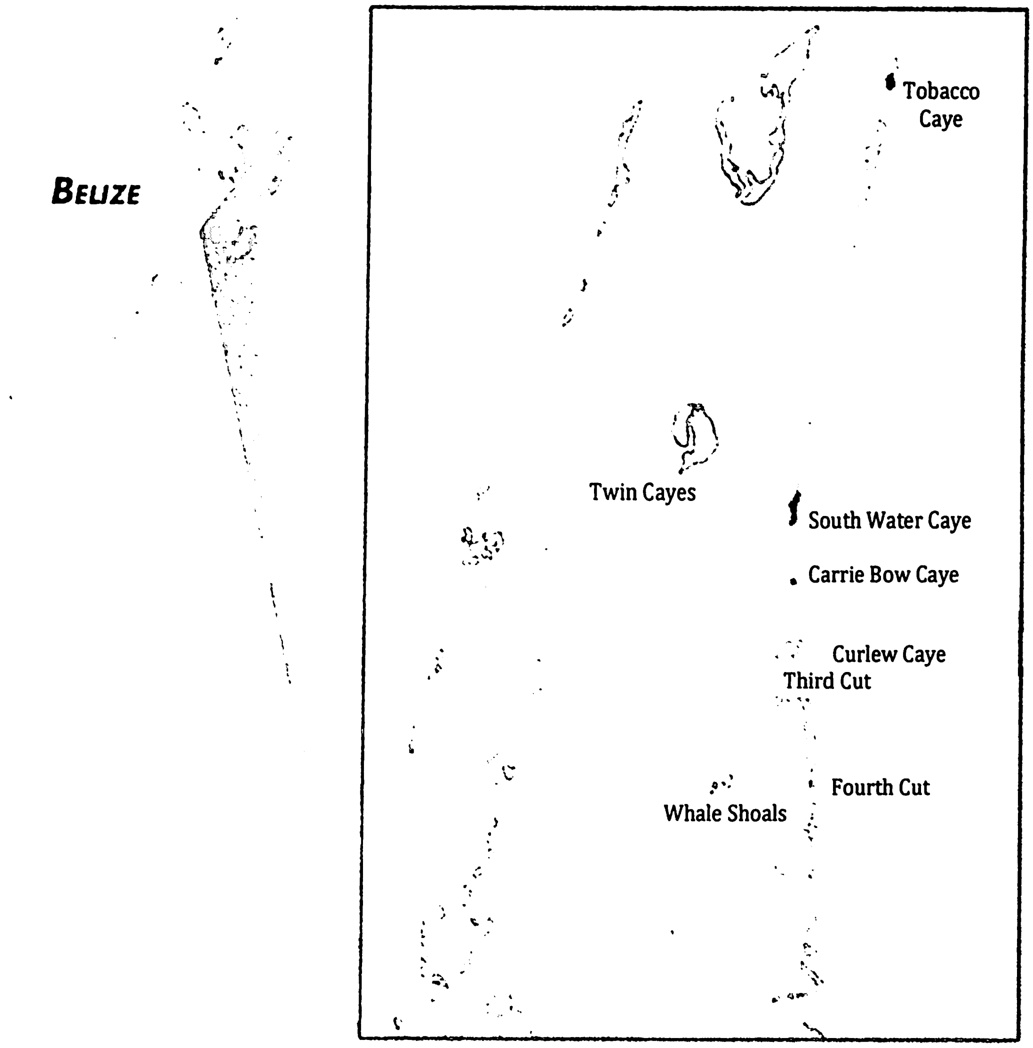

Figure 3: Map detailing entire study area in relation to mainland Belize (total research range 52 km^2, map from Gaston *et al.* 2009).

Adult Observation Site Details

Observations of adult *L. apodus* were conducted in the seven different coral reef habitats. Within these sites, most observations at each site took place on small patch reefs (< 3 acres; 0.012 km^2). Patch reefs are usually oval reef outcroppings, surrounded by sand or seagrass. They are often found within close proximity to other reefs. Many of the study sites (e.g., Fourth Cut) were in close proximity to the Belize Barrier Reef, the second largest barrier reef in the world. Barrier reefs consist of long reef segments parallel to the shoreline. They are usually separated from the mainland by a lagoon, and may include channels along their length, such as the one at the south end of South Water Caye.

Though adult observation sites varied in topography, coral makeup, and proximity to other habitats, they all contained similar species of fish. Adult schoolmaster were typically found near large elkhorn coral (*Acropora palmata)* structures or seeking shelter behind gorgonians, such as the common sea fan (*Gorgonia ventalina).* In addition to taking refuge behind common species of coral, schoolmaster often associated with yellowtail snapper *(Ocyurus chrysurus*), French grunts (*Haemulon flavolineatum)*, Caesar grunts (*Haemulon carbonarium)*, and blue-striped grunts (*Haemulon sciurus)*.

Carrie Bow Reef (16° 48.0'N, 88° 04.8'W) consists of multiple patch reefs found within a back-reef lagoon, located 100-400 m north of Carrie Bow Caye. Depth ranged from 1-3 m.

Curlew Caye (16° 47.4'N, 88° 05.0'W), a former island over washed during Hurricane Hattie (1962), is located 2 km south of SWC. Depth ranged from 1-3 m.

Fourth Cut Reef (16° 45.9'N, 88° 04.9'W) is located along a channel cut through the barrier reef, and it includes a substantial back-reef habitat. Distinguishing characteristics include a drop-off (depth change) with extensive sponge communities. The shallow-reef region ranges from 1-3 m and runs along a deep channel with an approximate depth of 7 m.

South Tobacco Channel (16° 53.5'N, 88° 03.8'W) consists of a back-reef area adjacent to Tobacco Caye Channel. It is characterized by typical back-reef corals and extensive coral development along the channel's edge. Seagrass beds can be found in the nearby channel at depths of 6-8 m.

SWC Beach (16° 48.8'N to 88° 04.9'W), the most frequently visited site, is located at the south end of South Water Caye (Suppl. 1). At the island's southern border, the Belize Barrier Reef wraps around to the west and forms a series of well-developed patch reefs. A large channel (5-6 m deep) separates SWC from Carrie Bow Caye. Observations off South Water Caye were most commonly in depths of 1-5 m.

Third Cut Reef (16° 46.7' N, 88° 5.1'W) is positioned 1.5 km south of Curlew Cay, and consists of a patch reef 300 m west of the barrier reef. The site is dominated by elkhorn coral (*Acropora palmata*), staghorn coral (*Acropora cervicornis*), and extensive reefs of lettuce coral *(Agaricia tenuifolia).* Third Cut Reef's depth ranged from 1-3 m.

Whale Shoals (16° 45.8'N, 88° 05.8'W) consists of two, extensive patch reefs 3 km west of the barrier reef and surrounded by deeper water (> 6 m). It is located due west of Fourth Cut Reef.

<u>Juvenile Observation Site Details</u>

Most observations of juveniles took place in shallow back-reef areas or among mangrove prop-root communities. Juvenile schoolmaster behavior was observed primarily in four different locations.

IZE Back-Reef (16° 48.8'N, 88° 04.9'W) consisted mainly of seagrass (primarily turtle grass; *Thalassia testudinum*) and soft-sand bottom. Mangroves were located on either side of this site and depth did not exceed 0.5 m.

IZE Dock (16° 50.4'N, 88° 04.9'W) consisted mainly of soft-sand bottom, littered with coral rubble. Juvenile schoolmaster were often observed resting in the shade of the dock, close to shore. Depth near the dock ranged from 0.2-0.5 m.

IZE Back-Reef and IZE Dock were both located in-shore from extensive seagrass beds. The main species of seagrass that formed adjacent grassbeds included, turtlegrass (*Thalassia testudinum)* and Manatee Grass *(Syringodium filiforme).*

SWC Mangroves (16° 48.8'N, 88° 04.9'W) consisted of back reef habitat that graded into sandy bottom beneath red mangroves *(Rhizophora mangle)*. Thus, this was a shaded habitat for the observation of juvenile *L. apodus* among mangrove roots. Water depth among the prop-roots did not exceed 0.4 m.

Twin Cayes Mangroves (16° 50.0'N, 88 ° 05.7'W) consisted of two large cayes formed from large communities of red mangroves *(Rhizophora mangle)*. A deep channel (> 4 m in some areas) ran through the cayes. Observations were conducted in shallower water on the perimeter of the cayes. Much of the area observed was shaded by mangroves, and included seagrass and coral-rubble bottom that graded to sand among the mangrove roots. The depth of observation at Twin Cayes Mangroves ranged from 0.5-1 m.

<u>Behavioral Observations</u>

Diurnal observations were made at the 11 study sites on 21 separate days, from late May through mid June of 2010. Weather conditions were mostly sunny and humid, with sparse rain (detailed weather information was available from Carrie Bow Caye Research Station, Belize). The average air temperature ranged from 24-29 °C and surface water temperature remained consistently around 27 °C. All observations were made during daylight hours. Observation periods lasted one to two hours, and were conducted during the morning (0700-1000 hr), mid-day (1000-1300 hr), and afternoon (1300-1800 hr). The earliest morning observation started at 0700 hr, and the latest afternoon observation started at 1700 hr.

Preliminary observations indicated that *L. apodus* spent most of their time either swimming or stationary (either alone or among other groups of resting fish). Less frequently, they would perform other miscellaneous behaviors, including acts of aggression, getting cleaned, and rubbing along the bottom to remove parasites. Feeding was rarely observed. As a result, behavior was classified into four, distinct categories; swimming, stationary (individually or in a group, and/or staging), foraging (including feeding and searching followed by picking or probing at prey), and "other" (including less-common behaviors, such as being cleaned, rubbing along the bottom to remove parasites, courtship activities, and acts of aggression).

Actual observations consisted of focal animal sampling, where each fish was observed individually, for a 20 sec time interval. Increments of 20 sec allowed fish to be watched without disturbance, and the opportunity to witness more than one type of behavior. Time intervals longer than 20 sec often resulted in active fish moving outside the study area. Fish needed to be observed the entirety of each period to be included in the data set. Fish that were actively swimming or startled were not followed or approached. Observations on 588 *L. apodus* were conducted for a total of 11,760 sec.

Observations were conducted while snorkeling, except in sites consisting of very shallow water (< 0.5 m). At shallow sites, observations were conducted from platforms (docks or shore). *L. apodus* were wary of people and had to be approached very carefully. If a fish seemed to be reactive to the presence of observers, its activities were discounted. Observed fish were chosen haphazardly, upon chance encounters while snorkeling or scanning from platforms.

Multiple study sites were visited at differing times of day based on the assumption that fish used different habitats for various behaviors, and behaviors likely varied with time of day. By increasing the number of study sites and times of day for observation, a more representative sampling of behavior could be prepared.

Size Estimation

The size of each *L. apodus* observed during the study was estimated. Fish were then put in one of four size classes based on their estimated total length (TL), to allow determination of behavior by size.

Size-class 1 (SC1) included fish ≤ 10 cm TL, roughly the length of an index finger. Size-class 2 (SC2) were fish 10-18 cm TL, about the length of a hand. Size-class 3 (SC3) included fish 18-30 cm TL, about the length of two hands (end to end). Size-class 4 (SC4) were fish ≥ 30 cm TL, longer than the length of two hands (end to end).

Depth Estimation

In order to allow determination of behavior by depth, visual estimation of the depth at each site was made. The four depth categories were; very shallow (1 m: 0.3-1.5 m), shallow (3 m: > 1.5-3.0 m), moderate (5 m: > 3.0-4.5 m), and deep (7 m: > 4.5-6 m).

All data were recorded by graphite pencil onto a "dive slate" made of a 12 cm piece of white PVC pipe, which fit around the forearm. Data collected included the date, time of day, location, depth over which the fish was located, size class of the observed fish, and the durations of any behaviors observed. Refer to Suppl. 2 for more detailed information about recording methods.

Though the primary focus of my study was the diurnal behavior of *L. apodus*, a stomach-content analysis was performed by Dr. Gary Gaston (University of Mississippi) to see if feeding data corroborated with previous literature (Suppl. 3).

Statistical Analyses

The entire data set for my study was tested for normality, and time-activity budgets were then generated. ANOVAs were used to determine differences in behavior within size classes, among size classes, among depth ranges, and among different times of day. Fisher PLSD (post-hoc) multiple comparison tests were used to determine where significant differences (if any) could be found.

Results

A total of 588 *L. apodus* were observed during the course of my study. The majority of fish were in SC3 (Figure 4). SC1 (≤ 10 cm) made up the smallest portion of the overall sample. Of the 588 *L. apodus* observed there were 10 fish from SC1, 101 from SC2, 340 from SC3, and 137 from SC4 (Figure 4).

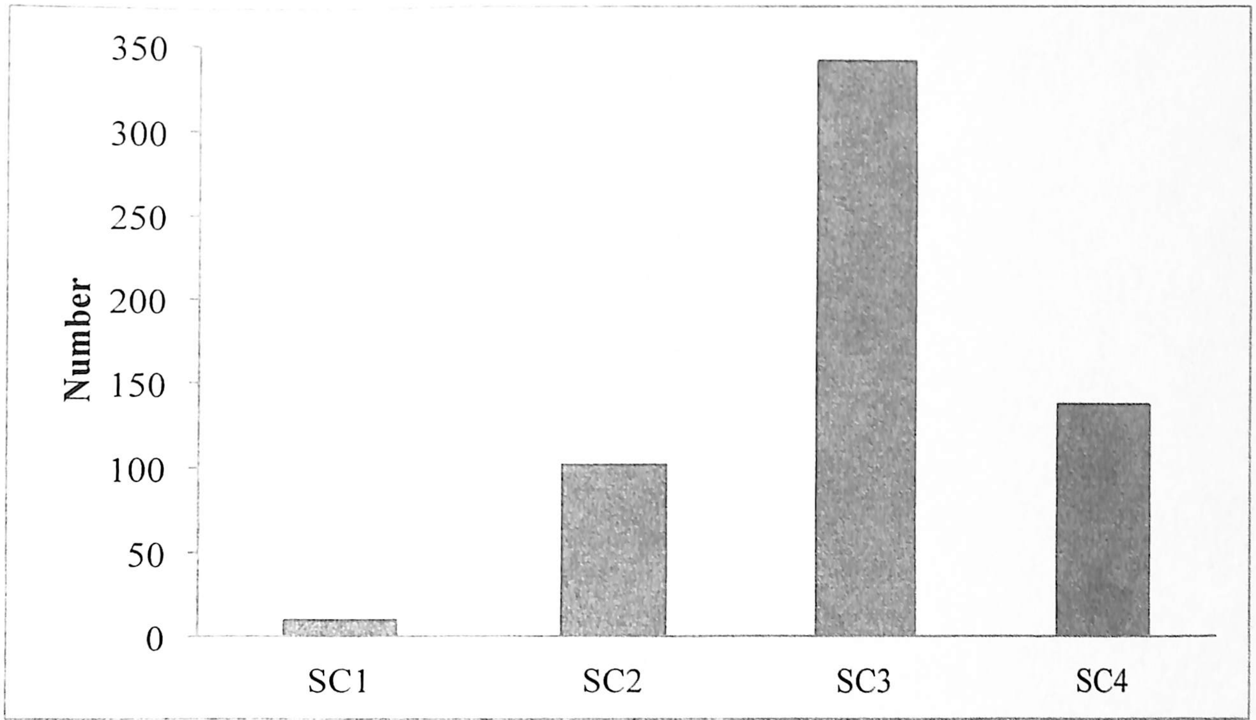

Figure 4: Number of *L. apodus* observed for each size class. SC1 (≤ 10 cm, roughly the length of an index finger), SC2 (10-18 cm, about the length of a hand), SC3 (18-30 cm, about the length of two hands, end to end), and SC4 (≥ 30 cm, longer than the length of two hands, end to end).

Observation sites that consisted primarily of patch reef habitat included Carrie Bow Reef, Curlew Caye, Fourth Cut Reef, South Tobacco Channel, South Water Caye Beach, Third Cut Reef, and Whale Shoals. The most common size category of *L. apodus* found at these locations was SC3 (Figure 5). There were no *L. apodus* from SC1 observed on reef habitats. Of the 490 fish observed near patch reefs, 26 came from SC2, 329 came from SC3, and 135 came from SC4 (Figure 5).

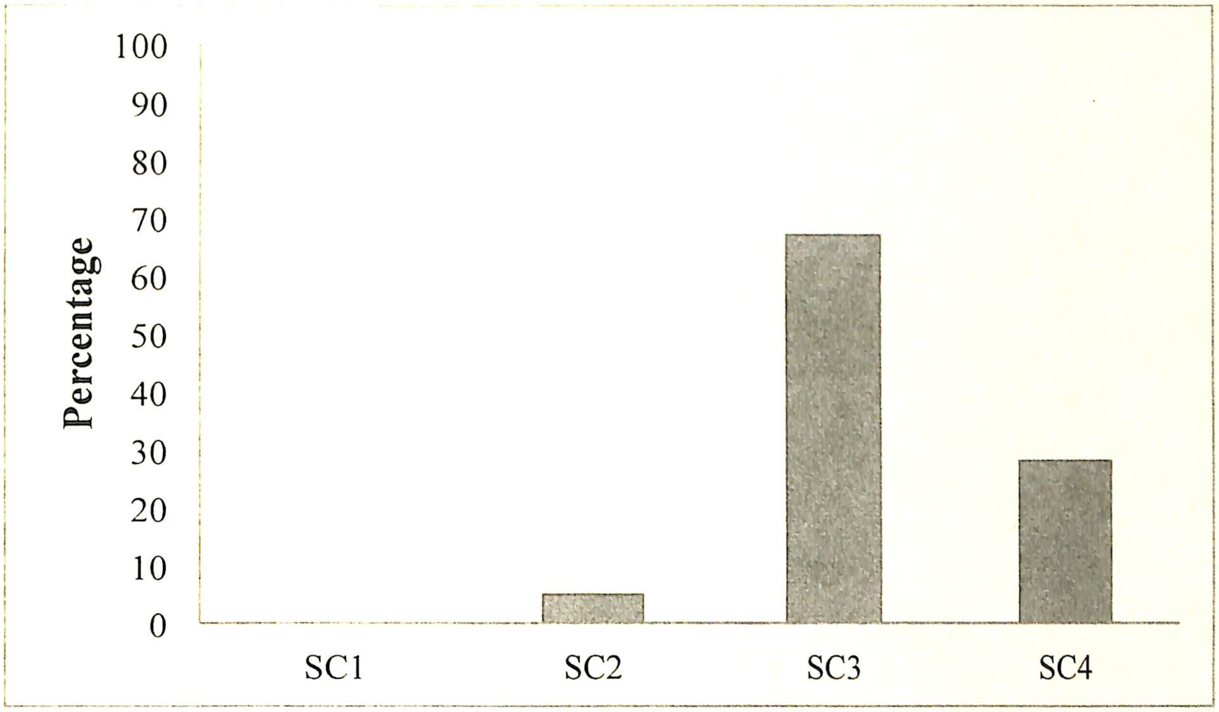

Figure 5: Proportion of *L. apodus* observed in the seven patch reef habitats by size class.

Study sites consisting of shallow intertidal and mangrove habitats included IZE Back-reef, IZE Dock, South Water Caye Mangroves and Twin Cayes Mangroves. SC2 was most commonly observed at these locations (Figure 6). These habitats were the only locations where SC1 *L. apodus* were observed. Of the 98 fish observed near mangrove and shallow intertidal habitats, 10 were from SC1, 75 were from SC2, 11 were from SC3, and 2 were from SC4 (Figure 6).

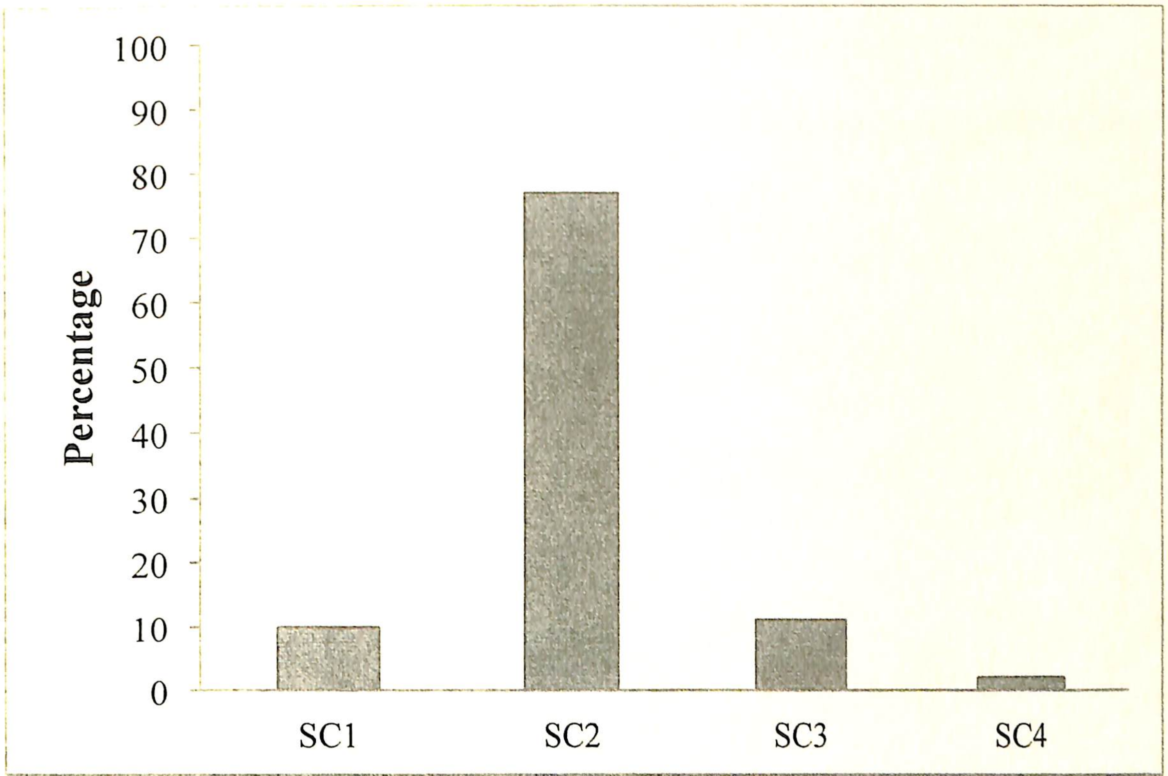

Figure 6: Proportion of *L. apodus* observed in all shallow intertidal and mangrove habitats.

Of the 11,760 sec of total observation time, schoolmaster spent 5,122 sec swimming, 6,530 sec stationary, 167 sec foraging, and 101 sec in "other" activities. *Lutjanus apodus* spent more time resting (stationary) during the day than any other activity (mean = 10.9 sec, n = 588; Figure 7). The second most common behavior was swimming (mean = 8.89 sec, n = 588). Foraging (mean = 0.044 sec, n = 588) and "other" behaviors (mean = 0.173 sec, n = 588) occurred very rarely during the day (Figure 7). There was a significant difference in the amount of time they spent among behavior categories (ANOVA: $F_{(3, 2351)} = 492.7$, $P < 0.0001$). *L. apodus* spent significantly more time stationary than any other behavior (Fisher's PLSD: $P < 0.0001$; Figure 7).

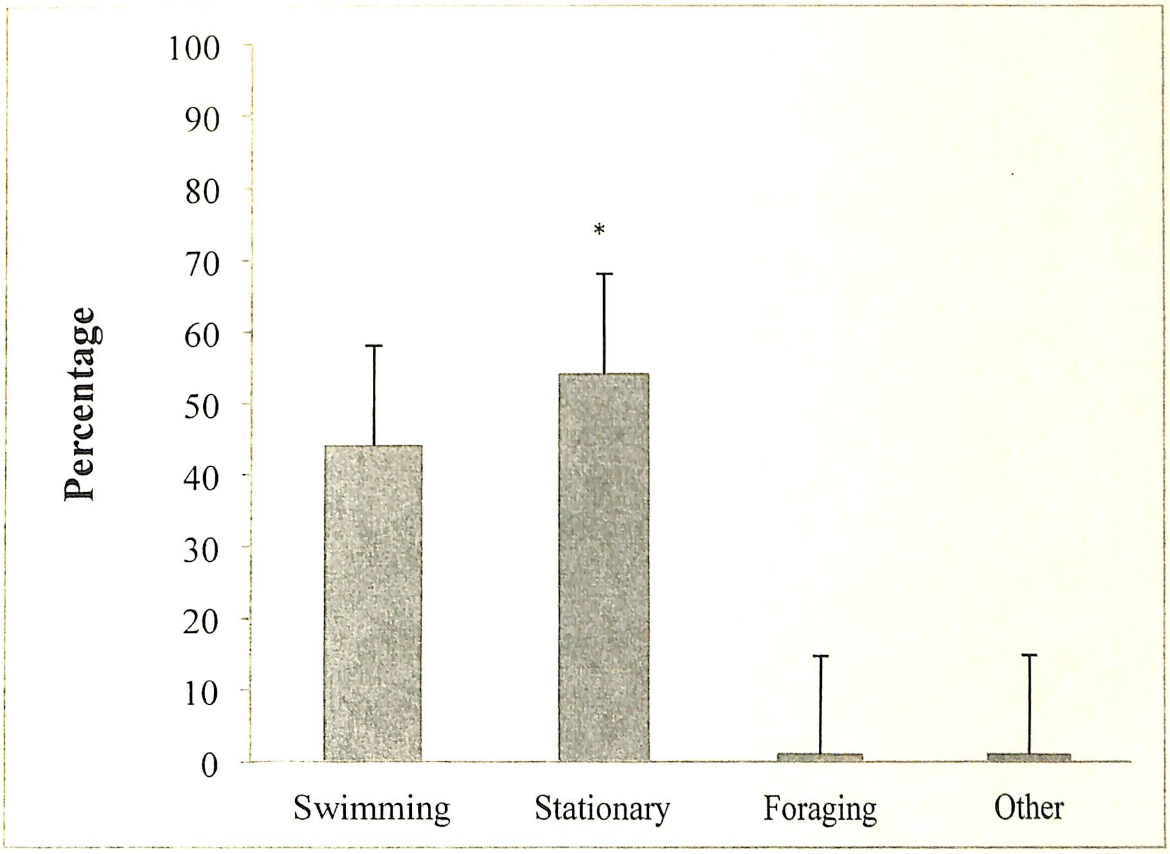

Figure 7: Time-activity budget for entire sample of *L. apodus* (n=588). Percentage time spent in each behavior. Error bars represent standard error; * = $P < 0.0001$.

SC1 fish spent more time during the day swimming than any other activity (Figure 8). Of the 200 sec of total observation time for SC1, SC1 fish spent 138 sec swimming, 57 sec stationary, and 5 sec foraging. The mean time spent swimming for SC1 was 13.8 sec (n = 10). Resting was the second most common behavior (mean = 5.7, n = 10). No "other" behaviors were observed in this size class, and a mean of only 0.50 sec (n = 10) was spent foraging. There was a significant difference in the amount of time spent among behaviors (ANOVA: $F_{(3,36)} = 17.5$, $P < 0.0001$). No time was spent in "other" activities. SC1 *L. apodus* spent significantly more time swimming than performing any other behavior (Fisher's PLSD: $P < 0.0006$; Figure 8).

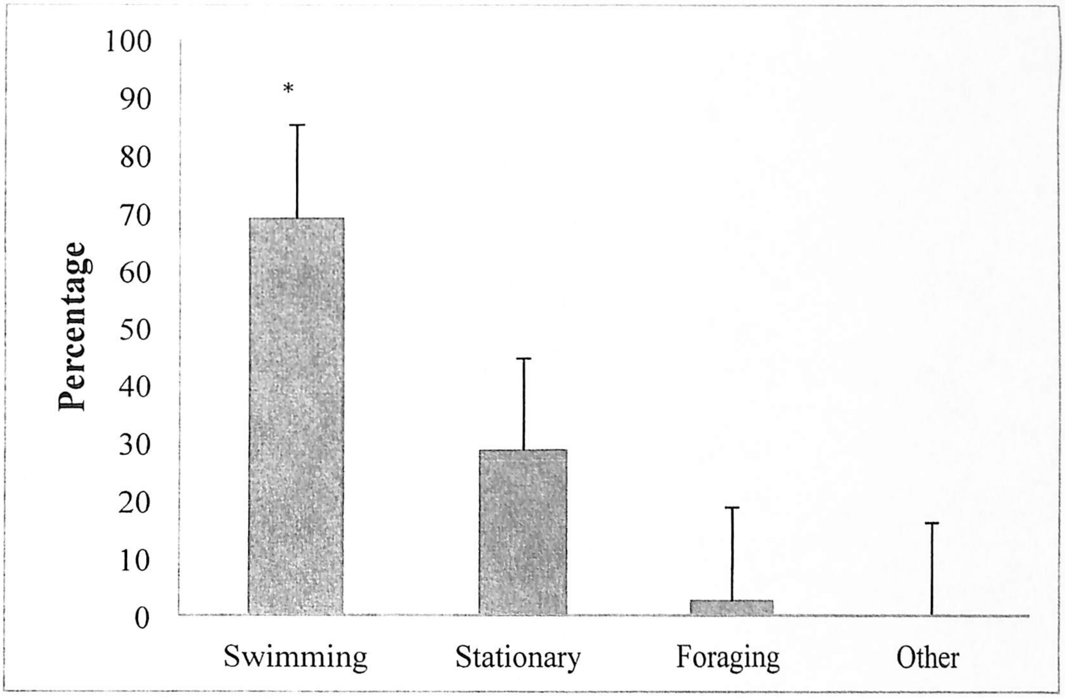

Figure 8: Time-activity budget for SC1 (n = 10). Percentage of time spent in each behavior. Error bars represent standard error. * = P < 0.0006.

A total of 2,020 sec was spent observing SC2 fish. During this time period SC2 *L. apodus* spent 1,148 sec swimming, 844 sec stationary, 14 sec foraging, and 14 sec in "other" behaviors. SC2 fish also spent more time swimming than in any other activity (Figure 9). Mean times spent swimming, stationary, foraging, and in other behaviors, were 11.4 sec (n = 101), 8.4 sec (n = 101), 0.14 sec (n = 101), and 0.14 sec (n = 101) respectively. There was a significant difference in the amount of time spent among behavior categories (ANOVA: $F_{(3,400)} = 93.2$, $P < 0.0001$). SC2 fish spent significantly more time swimming than in any other daytime activity (Fisher's PLSD: $P < 0.0004$: Figure 9).

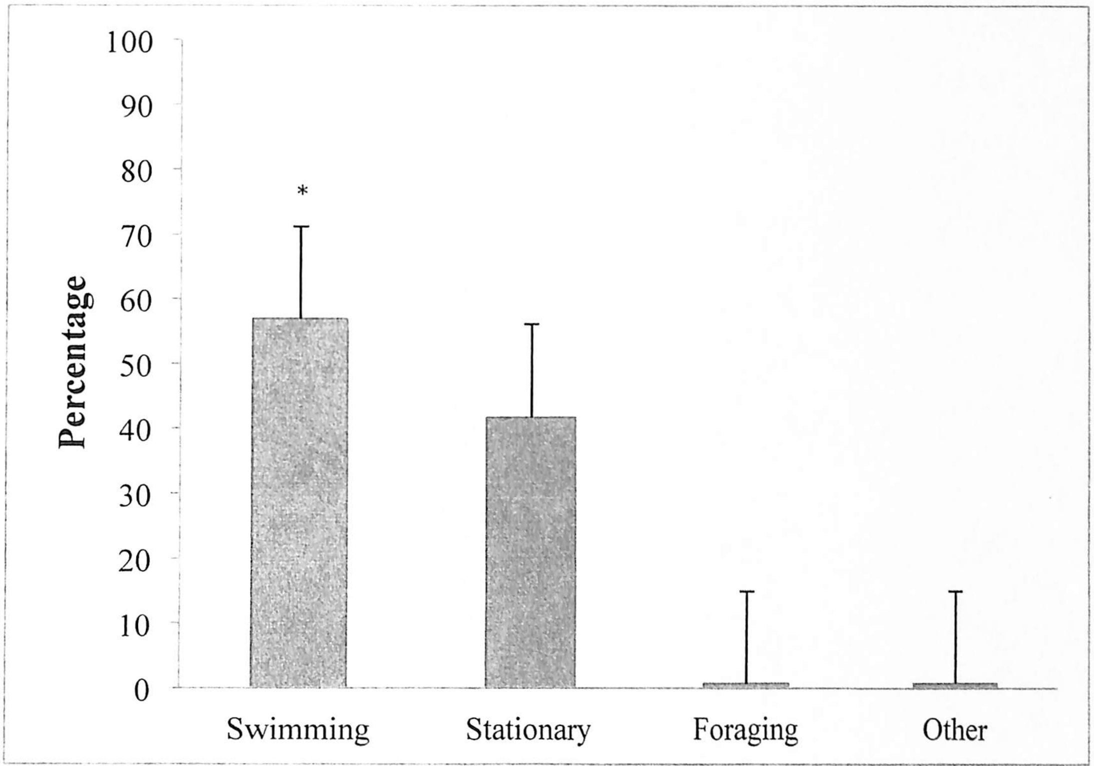

Figure 9: Time-activity budget for SC2 (n = 101). Percentage time spent in each behavior. Error bars represent standard error; * = P < 0.0004.

Of the 6,800 sec spent observing SC3 fish, SC3 fish spent 2,440 sec swimming, 4,157 sec stationary, 147 sec foraging, and 56 sec in "other" activities. SC3 fish spent more time resting than any other activity during my observations (Figure 10). For *L. apodus* in SC3, the mean time spent stationary was 12.4 sec (n = 340). The second most common behavior was swimming, with a mean time of 7.42 sec (n = 340). Foraging and "other" behaviors comprised a very small portion of SC3 activity, with mean times of 0.018 sec (n = 340), and 0.17 sec (n = 340) respectively. There were significant differences for time spent among the four activities in SC3 fish (ANOVA: $F_{(3,1355)} = 335$, $P < 0.0001$). Significantly more time was spent stationary than in any other behavior (Fisher's PLSD: $P < 0.0001$; Figure 10).

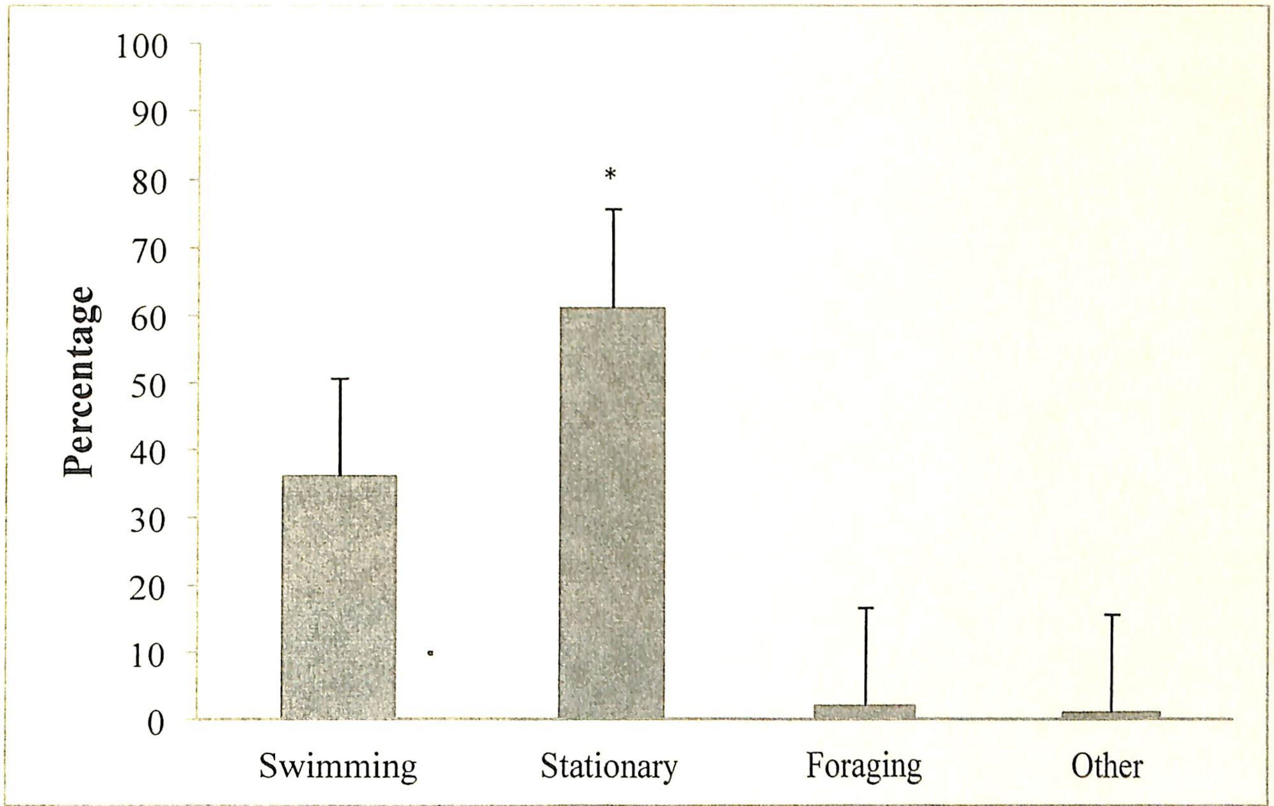

Figure 10: Time-activity budget for SC3 (n = 340). Percentage of time spent in each behavior. Error bars represent standard error; * = P < 0.0001.

SC4 schoolmaster were observed for a total of 2,740 sec, in which they spent 1,416 sec swimming, 1,292 sec stationary, 1 sec foraging, and 31 sec in "other" behaviors. The most common diurnal behavior for SC4 fish was swimming, followed very closely by resting (Figure 11). Mean times spent swimming, stationary, foraging, and in "other" behaviors, were 10.3 sec (n = 137), 9.29 sec (n = 137), 0.23 sec (n = 137), and 0.007 (n = 137) sec respectively. There was a significant difference in the amount of time SC4 fish spent among different behaviors (ANOVA: $F_{(3,548)} = 107$, $P < 0.0001$). There was not a significant difference between the amount of time SC4 spent swimming and stationary (Fisher's PLSD P = 0.1743). Stationary and swimming behaviors were significantly more prevalent than foraging and "other" behaviors (Fisher's PLSD: $P < 0.0001$; Figure 11). There was no significant difference between the amount of time SC4 fish spent foraging and in "other" activities (Fisher's PLSD: P = 0.7770; Figure 11).

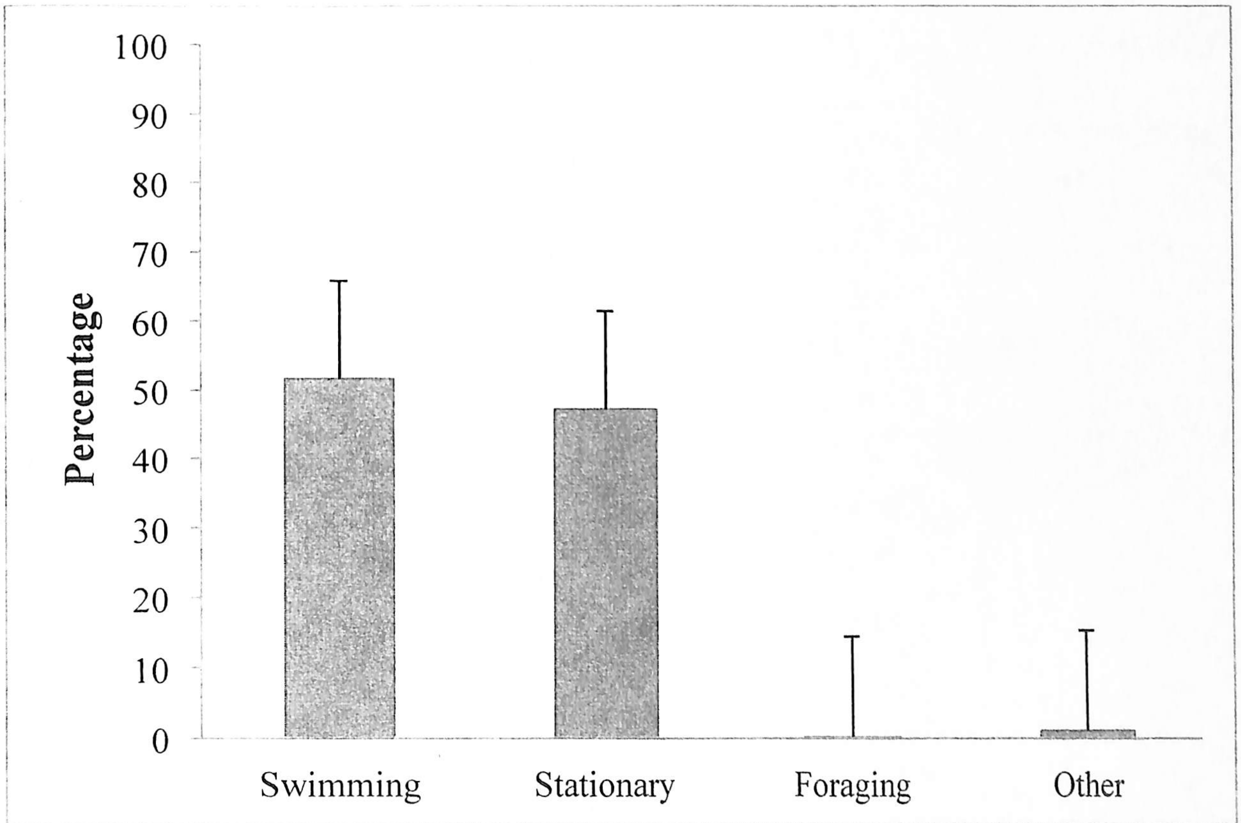

Figure 11: Time-activity budget for SC4 (n = 137). Percentage of time spent in each behavior. Error bars represent standard error.

The amount of time spent swimming tends to decrease as fish get larger. The two largest classes (SC3 and SC4) spent the least amount of time actively swimming (ANOVA: $F_{(3,585)} = 8.57$, $P < 0.0001$; Figure 12). The mean times spent swimming for SC1, SC2, SC3 and SC4 fish were 13.8 sec (n = 10), 11.4 sec (n = 101), 7.42 sec (n = 340), and 10.3 sec (n = 138) respectively.

Resting behavior tends to increase as fish grow in size (ANOVA: $F_{(3,585)} = 9.23$, $P < 0.0001$; Figure 12), with the smallest classes of fish (SC1 and SC2) spending the least amount of time stationary. The mean times spent resting were 5.7 sec (n = 10) for SC1, 8.4 sec (n = 101) for SC2, 12.4 sec (n = 340) for SC3, and 9.3 sec (n = 138) for SC4.

In addition to the amount of swimming and stationary behavior differing among size classes, they also differed within size classes (Figure 12). SC1 and SC2 spent significantly more time actively swimming than stationary (Fisher's PLSD: SC1 $P < 0.0006$; SC2, $P < 0.0004$). SC3 spent much more time resting than swimming (Fisher's PLSD: $P < 0.0001$). There was not a significant difference between the amount of time SC4 spent swimming and stationary (Fisher's PLSD: $P = 0.174$).

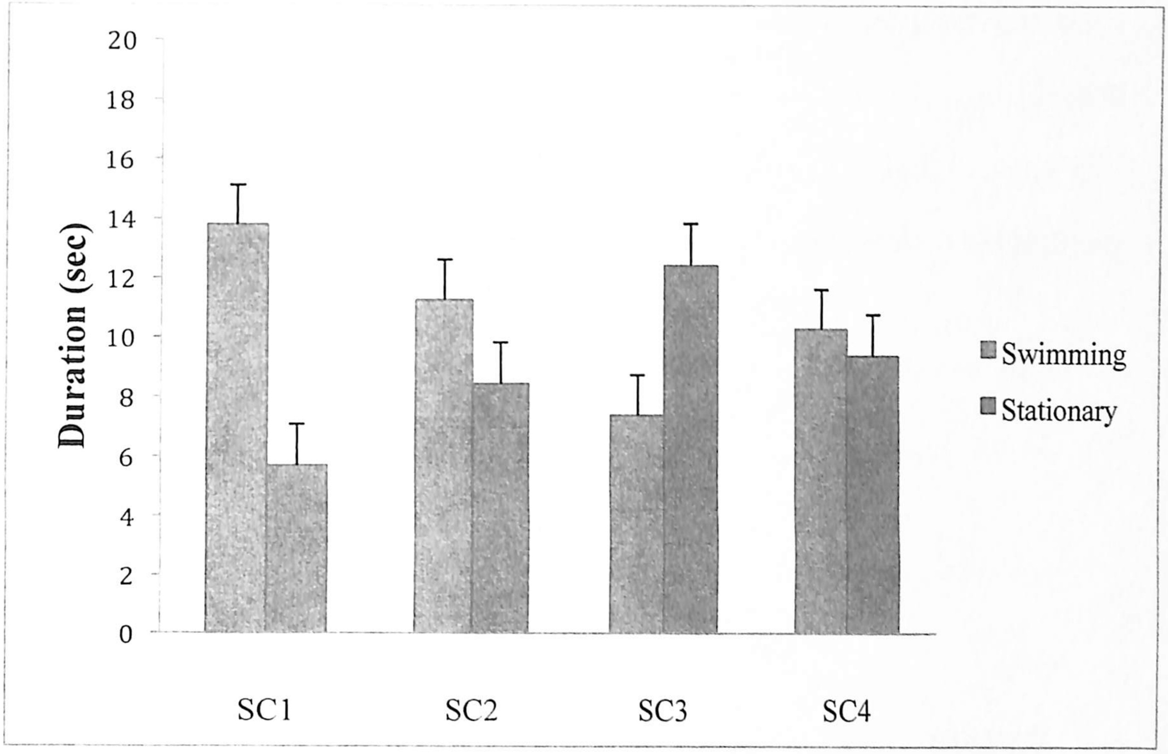

Figure 12: Mean duration (in seconds) of swimming and stationary behaviors for each of the four size classes. Error bars represent standard error.

The mean times spent swimming by time of day were 10.8 sec (n = 588) in the morning, 7.07 sec (n = 588) at mid-day, and 8.01 (n = 588) sec in the afternoon (Figure 13). Swimming behavior varied with the time of day (ANOVA: $F_{(2,586)} = 10.8$, $P < 0.0001$). Swimming activity was significantly higher in the morning between 0700-1000 hr (Fisher PLSD: $P < 0.0001$; Figure 13).

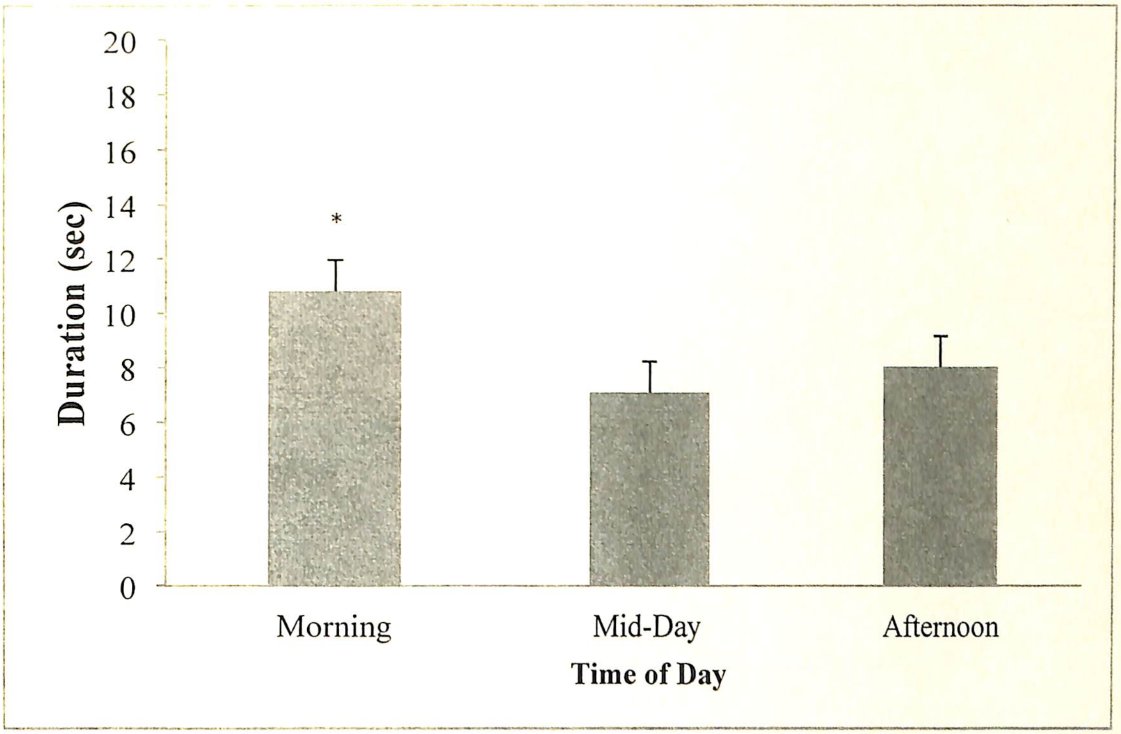

Figure 13: Mean duration (seconds) of swimming behavior of all fish (n = 588) by time of day. Morning = 0700-1000 hr, mid-day = 1000-1300 hr, and afternoon =1300-1800 hr. Error bars represent standard error; * = P < 0.0001.

Mean times spent stationary were 9.02 sec (n = 588) in the morning, 12.7 sec (n = 588) during mid-day, and 11.5 sec (n = 588) in the afternoon (Figure 14). Stationary (resting) behavior also varied with time of day (ANOVA: $F_{(2,587)} = 9.98$, $P < 0.0001$). Resting behavior was significantly less common in the morning, from 0700-1000 hr (Fisher PLSD: $P < 0.0001$; Figure 14).

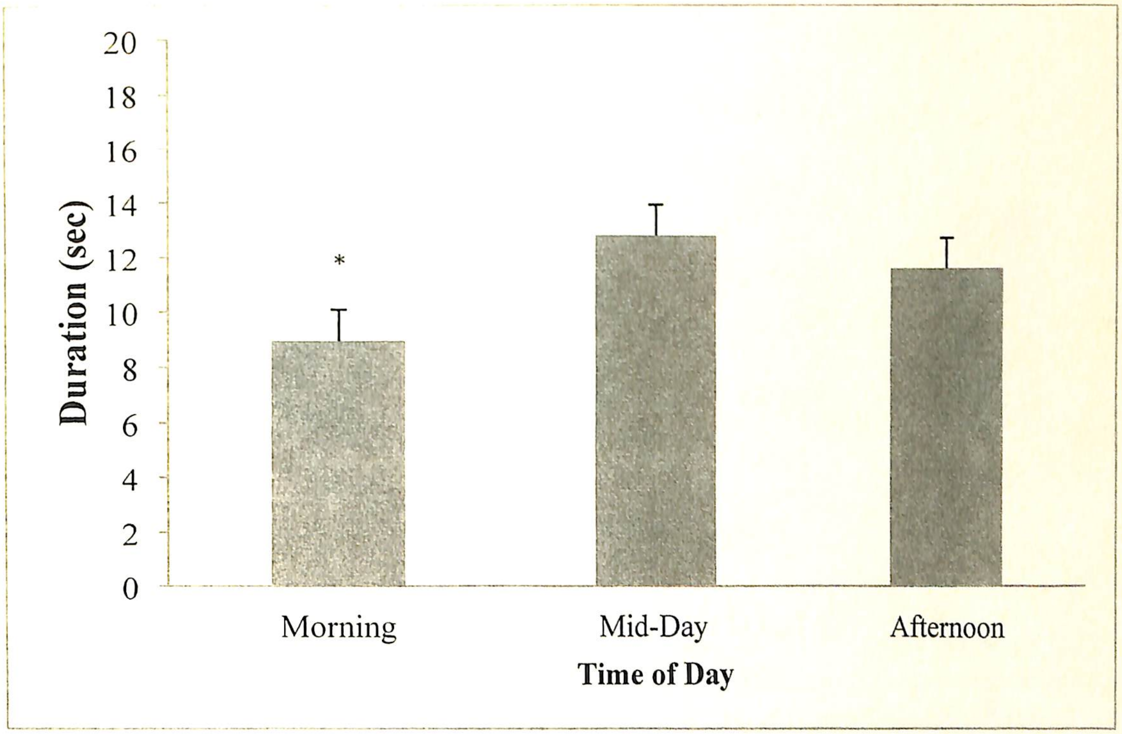

Figure 14: Mean duration (seconds) of stationary behavior of all fish (n = 588) by time of day. Morning = 0700-1000 hr, mid-day = 1000-1300 hr, and afternoon =1300-1800 hr. Error bars represent standard error; * = P < 0.0001.

The mean times spent swimming were 13.3 sec (n = 588) at 1 m, 10.4 sec (n = 588) at 3 m, 6.5 sec (n = 588) at 5 m, and 8.26 (n = 588) sec at 7 m (Figure 15). Swimming behavior varied with depth (ANOVA: $F_{(3,585)} = 17.52$, $P < 0.0001$). Significantly more time was spent swimming in very shallow water than at any other depth (Fisher's PLSD: $P < 0.0001$).

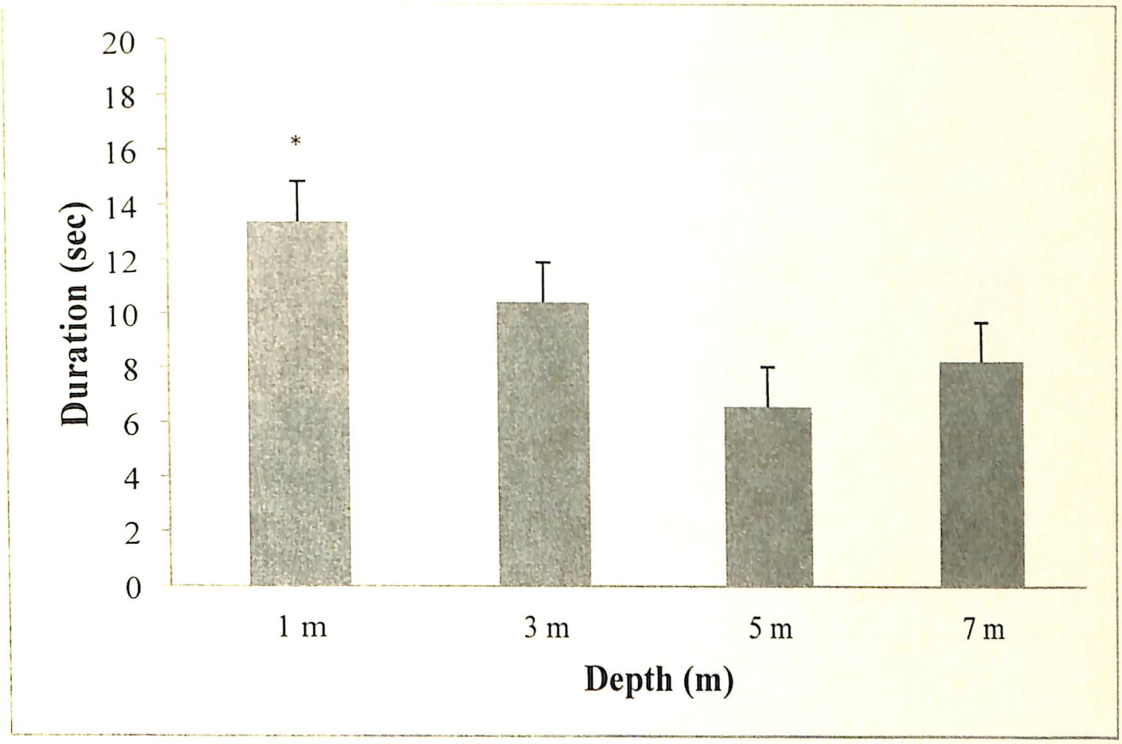

Figure 15: Mean time (sec) spent swimming at various depths, across all size classes (n = 588). 1 m = 0.3-1.5 m (very shallow), 3 m = > 1.5 m-3.0 m (shallow), 5 m = > 3.0 m-4.5 m (moderate), and 7 m = > 4.5 m-6 m (deep). Error bars represent standard error; * = P < 0.0001.

The mean times spent resting were 6.36 sec (n = 588) at 1 m, 9.53 sec (n = 588) at 3 m, 13.0 sec (n = 588) at 5 m, and 11.7 sec (n = 588) at 7 m (Figure 16). Stationary behavior also varied with depth. (ANOVA: $F_{(3,585)} = 16.5$, $P < 0.0001$). Significantly less time was spent stationary in very shallow water than at any other depth (Fisher's PLSD: $P < 0.0001$).

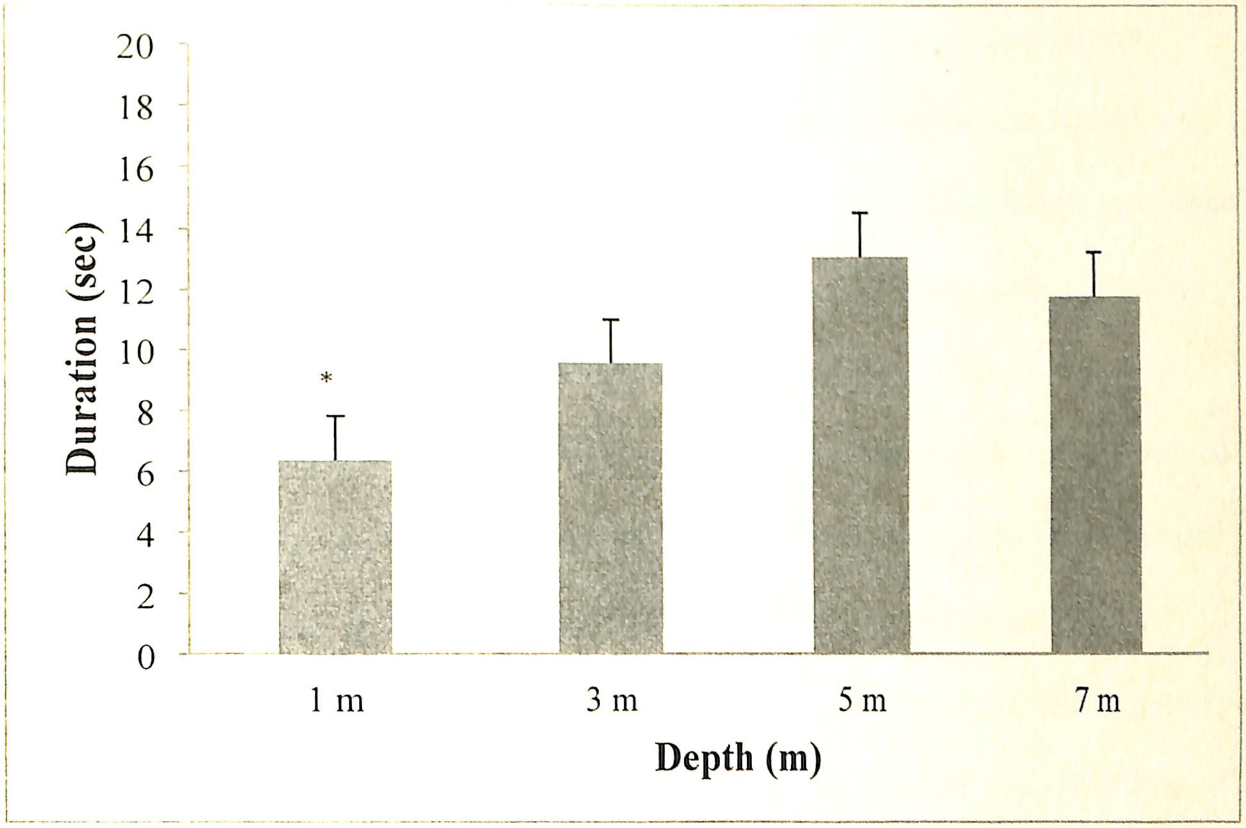

Figure 16: Mean time (seconds) spent resting at various depths, across all size classes (n = 588). 1 m = 0.3-1.5 m (very shallow), 3 m = > 1.5 m-3.0 m (shallow), 5 m = > 3.0 m-4.5 m (moderate), and 7 m = > 4.5 m-6 m (deep). Error bars represent standard error; * = P < 0.0001.

Discussion

The most salient findings of this study on *Lutjanus apodus* came from analyses and comparisons of time-activity budgets. The activity budgets provided more detailed insight into behavioral changes with age and size of this common, Caribbean fish. In addition to providing a species-specific analysis of diurnal behavior, my study corroborated prior research concerning the differing habitats of juvenile and adult schoolmaster. Changes in swimming and stationary behavior with depth and time of day were also objectively assessed.

The smallest fish in my study (SC1 and SC2) spent more time actively swimming during daylight hours, whereas larger fish (SC3 and SC4) spent more time resting. This finding is in agreement with former studies that highlighted differences in distances traveled between juvenile and adult fish (Verweij *et al.* 2007, Hitt *et al.* 2011b). Adult reef fish are not as bound to mangroves for protection as juveniles, thus their territory can be larger (Humann 1999, Verweij *et al.* 2007). Hitt *et al.* (2011b) found that tagged, adult *L. apodus* rested and maintained close distances to reefs during the day, while the majority of their traveling occurred at night. More diurnal resting behavior in larger (SC3 and SC4) *L. apodus* probably helps them to conserve energy, which would enable them to travel greater distances at night.

SC3 *Lutjanus apodus* spent significantly more time resting (61%) than all other size classes. They were the most common class of fish seen staging in large, mixed-species groups of fish. SC3 fish were the most common size of schoolmaster on the reef, and since they are not the largest of adult specimens, they may face a greater threat of predation. Reef environments do not offer the same amount of protection as mangrove nurseries (Verweij *et al.* 2007), thus reef-associated SC3 fish could possess a greater need to school and rest during the day for protection than their larger counterparts (SC4). SC4 fish also spent a large amount of time stationary, but they were often solitary or in smaller groups (C. Howe, personal observation). More commonly, SC4 fish were observed farther from reef structures and in deeper water. SC1 and SC2 *L. apodus* were found in much shallower water (usually close to shore) and were more highly active than larger schoolmaster. Increased swimming and decreased resting for small *L. apodus* could have been necessary in these dynamic, shallow habitats, where fish must maneuver around more obstacles, such as mangrove roots and coral rubble. Small fish may also have to remain more active in shallow environments because they face a greater risk of being beached with tidal surge.

The low incidence of foraging across all size classes suggests that *L. apodus* fed outside of the time constraints of my study, most likely nocturnally. This finding aligned with the commentary of Belizean fisherman, who claim that *L. apodus* are rarely caught during the day. Low occurrences of diurnal feeding also corroborated some of the existing literature on *L. apodus*. Hitt *et al.* (2011b) found that grassbeds were commonly visited by *L. apodus* after dark, which is suggestive of nocturnal foraging activity.

Foraging made up less than 3% of the overall behavior for SC2 fish and only contributed 1% of SC1 behavior. MacDonald *et al.* (2009) also found that feeding made up less than 3% of the activity budgets for small *L. apodus* living among mangrove roots.

"Other" behaviors were observed even less frequently than foraging. Some of the less common behaviors that I observed included being cleaned by other fish, acting aggressively, and rubbing along the sandy bottom to remove parasites. These behaviors are not as necessary to daily survival of *L. apodus*, thus it follows that they would be seen less regularly than more crucial behaviors (resting, swimming, and foraging).

Previous research (Verweij *et al.* 2007, MacDonald *et al.* 2009) demonstrating the fidelity of juveniles to mangrove habitats agreed with my data set concerning the habitat preferences of SC1 and SC2 fish. SC1 and SC2 schoolmaster made up 87% of the overall sample found near mangrove-dominated sites (either directly among roots or in shallow intertidal in close proximity to a mangrove lined shore).

Large *Lutjanus apodus* dominated reef habitats, with 95% of *L. apodus* found on reefs coming from SC3 and SC4. This finding agrees with existing literature on snapper species (Humann and DeLoach 2002b,c, Randall 1996). The low incidence of small and juvenile *L. apodus* on the reef suggests that migration to the reef occurs in larger fish. Only 5% of *L. apodus* found on reefs came from SC2, and none from SC1. This suggests that *L. apodus* likely makes the shift from mangrove nursery to coral reef somewhere between SC2 (10-18 cm, about the length of a hand) and SC3 (18-30 cm, about the length of two hands, end to end). SC1 fish would become too vulnerable to predation, if they were to leave mangrove prop-root communities (Verweij *et al.* 2007).

Observations confirmed that in addition to behavior differing among size classes of *L. apodus,* it also varied with depth and time of day. Swimming activity was significantly higher in the morning (between 0700-1000 hr) than at any other time. A higher prevalence of swimming in the morning might suggest that schoolmaster have recently returned to the reef from a night of foraging, and that they are now searching for places to gather and rest. During late afternoon (before dusk), I frequently observed large groups of adult schoolmaster staging at the edges of reefs. These adults could potentially be gathering to forage in the nearby grassbeds, after dark.

Swimming behavior was also most common at shallower depths (1 m and 3 m). This could be attributed to the observation that SC1 and SC2 fish were the most common sizes in shallower habitats, and their activity was dominated by swimming. Smaller fish are often targeted as prey by larger piscivores, thus increased swimming behavior in smaller fish may also aid in predator avoidance.

My study was the first to focus on the diurnal time-activity budgets of multiple sizes of *L. apodus*, even though limited time-activity data have been provided for juvenile schoolmaster (MacDonald *et al.* 2009). Differences in time spent in behavior categories among size classes suggest ontogenetic shifts in behavior, including relationships between life-stages and behavior, depths and behavior, or habitats and behavior. Future studies that include nocturnal behavior could clarify the results I observed, and help explain the complex roles among fish activities. Most existing literature on *L. apodus* (my study included) focused solely on their diurnal behavior out of necessity; nocturnal observations without disturbance of the subject are nearly impossible. Upcoming advancements in technology could allow nocturnal observations and better data on time-activity budgets. Future and more comprehensive behavioral studies on *L. apodus* and other reef fish, that incorporate time-activity budgets for all times of day and night, will improve our understanding of fish behavior and be of great help to fisheries management.

Acknowledgments

First and foremost I would like to extend great thanks to my thesis advisor, Dr. Gary Gaston (University of Mississippi), who has supported me throughout the entire process. Dr. Gaston not only helped me with my initial research and data collection, but also gave countless hours of his time to editing my paper and patiently answering my every question. Without Dr. Gaston's dedication and assistance, completing my thesis would not have been possible. I could not have asked for a better advisor, mentor, and professor to supervise my project.

Many people deserve recognition for helping make my field research possible. I would especially like to acknowledge John and Jennifer McDougall (IZE managers) for helping arrange my travel reservations, accommodations, and daily boat trips to observation sites. Their hospitality and superior organizational skills were crucial to my research. IZE staff members, Norman and Wilfred were superb navigators and boat captains. I extend my sincere gratitude to them for taking me to daily study locations.

After collecting my data, I was in great need of assistance with statistical analyses. I would like to recognize Dr. Carl J. Schwartz (Simon Frasier University) for organizing my data set and testing it for normality. I would also like to extend considerable gratitude to Dr. Denis Goulet (University of Mississippi), who spent numerous hours reorganizing and analyzing my entire data set. His patience and dedication to helping students is impressive, and I was very lucky to receive his aid.

I would like to thank Dr. Glenn Parsons (University of Mississippi) and Dr. Denis Goulet for agreeing to be members of my thesis committee and for their excellent revisions. Finally, I would like to thank to the Sally McDonnell Barksdale Honor College for giving me

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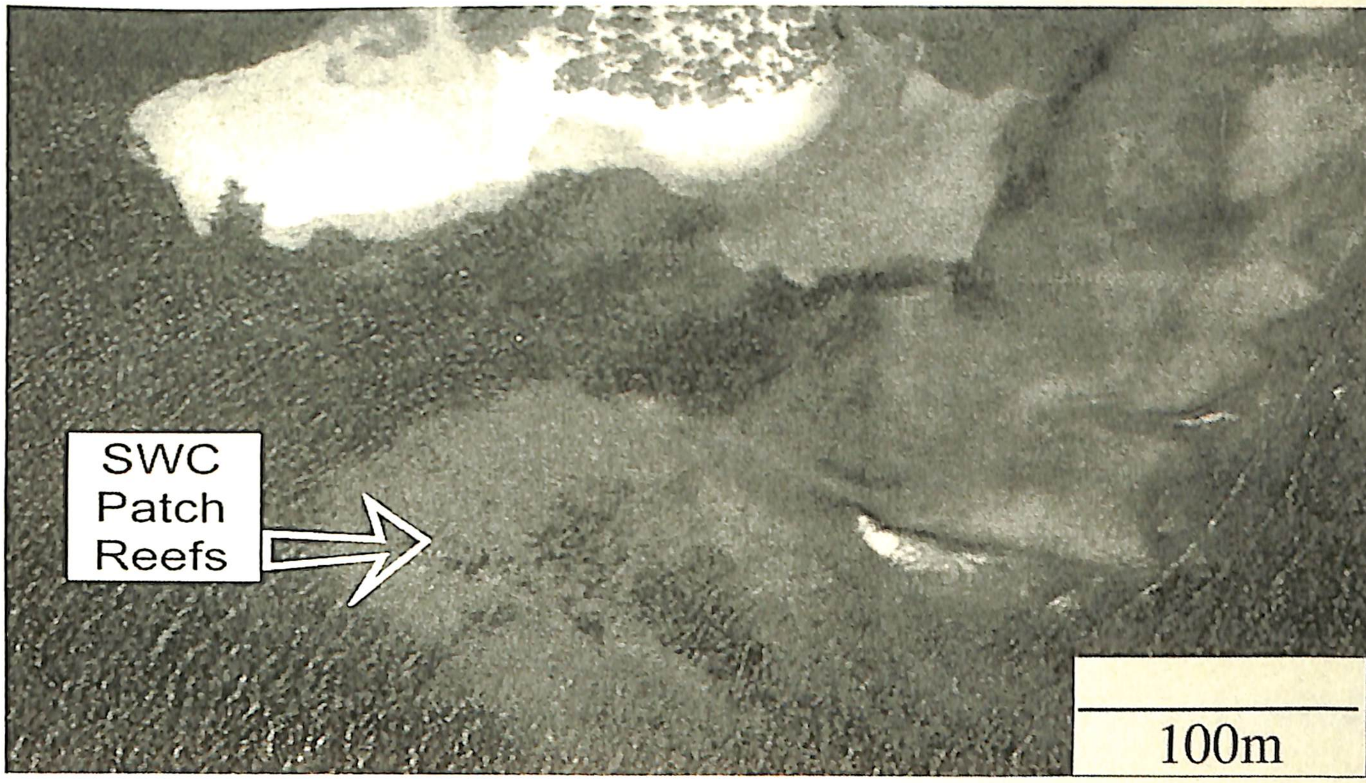
Supplemental Information

Suppl. 1: Satellite image of the primary study site off South Water Caye (Belize, Central America). Beach at the south end of the island is shown at the top of the photo. The barrier reef is to the right. An arrow points to the main area of observation (region characterized by well developed patch reefs). Image taken from Google Maps.



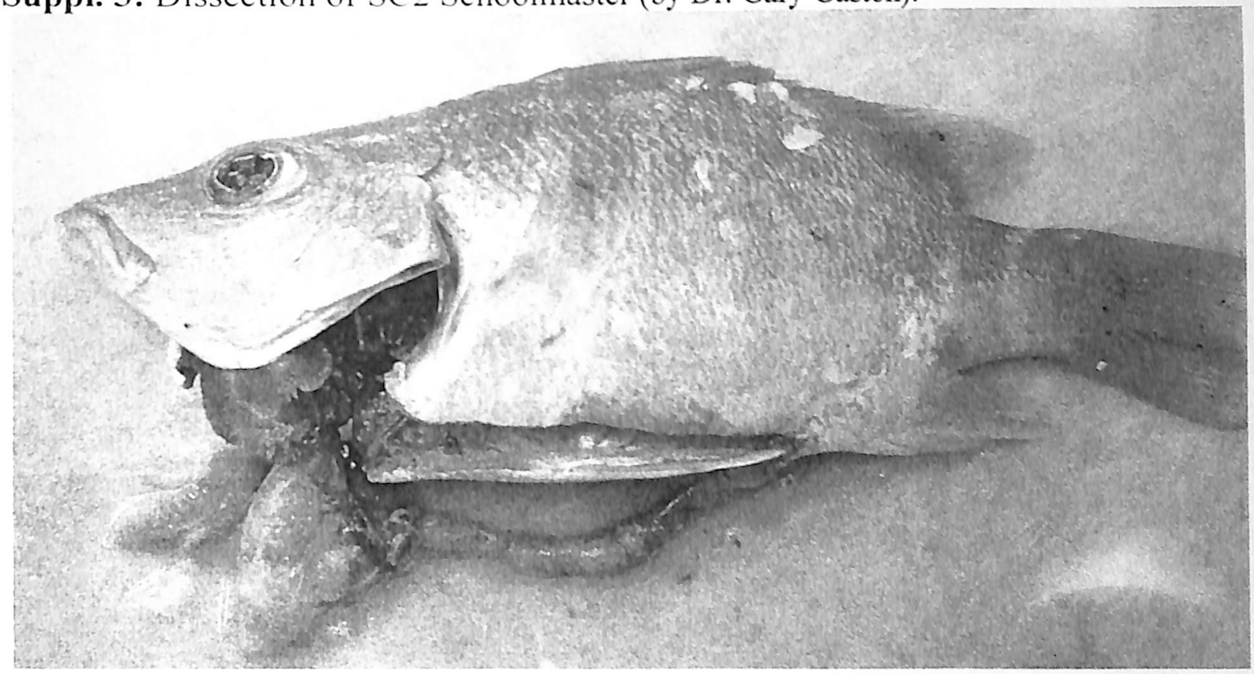
Suppl. 2: Sample grid to represent how recordings were made on dive-slate (units are seconds per behavior).

	Size Class 1	Size Class 2	Size Class 3	Size Class 4
Swimming	0	0 0	0 0	0 0
Stationary	0	0	0	0 0
Foraging	0	0	0	0
Other	0	0	0	0

Data were organized for further analyses into size categories, listed across the top of the grid, and behavior categories down the side. Time spent (in seconds) performing certain behaviors was recorded in the appropriate boxes. The above grid was sketched onto the PVC dive-slate before each observation block.

After activity data were collected on dive slates, data were copied into a spiral-bound notebook along with corresponding dates and times. Miscellaneous behaviors, air temperatures, and observation locations were also noted. All data from the notebook was eventually entered into a Microsoft Excel spreadsheet to be saved and further analyzed.

Suppl. 3: Dissection of SC2 Schoolmaster (by Dr. Gary Gaston).



In addition to collecting data to formulate time-activity budgets, a stomach content analysis was performed by Dr. Gaston. The 17 cm *Lutjanus apodus* was caught on artificial bait on the back reef off South Water Caye. Dr. Gaston dissected it before it died (which may affect gut-contents data), and preserved the stomach contents.

The stomach of the dissected fish contained only partially intact remains of two, small crabs (Family Majidae). This singular stomach-content analysis supported existing data, which held that smaller *L. apodus* fed primarily on small crustaceans (Rooker 1995).