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**GROUPE AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL,  
REPUBLIC OF MALDIVES: PART 1. HABITAT, BEHAVIOR, AND  
MOVEMENT PATTERNS**

**BY**

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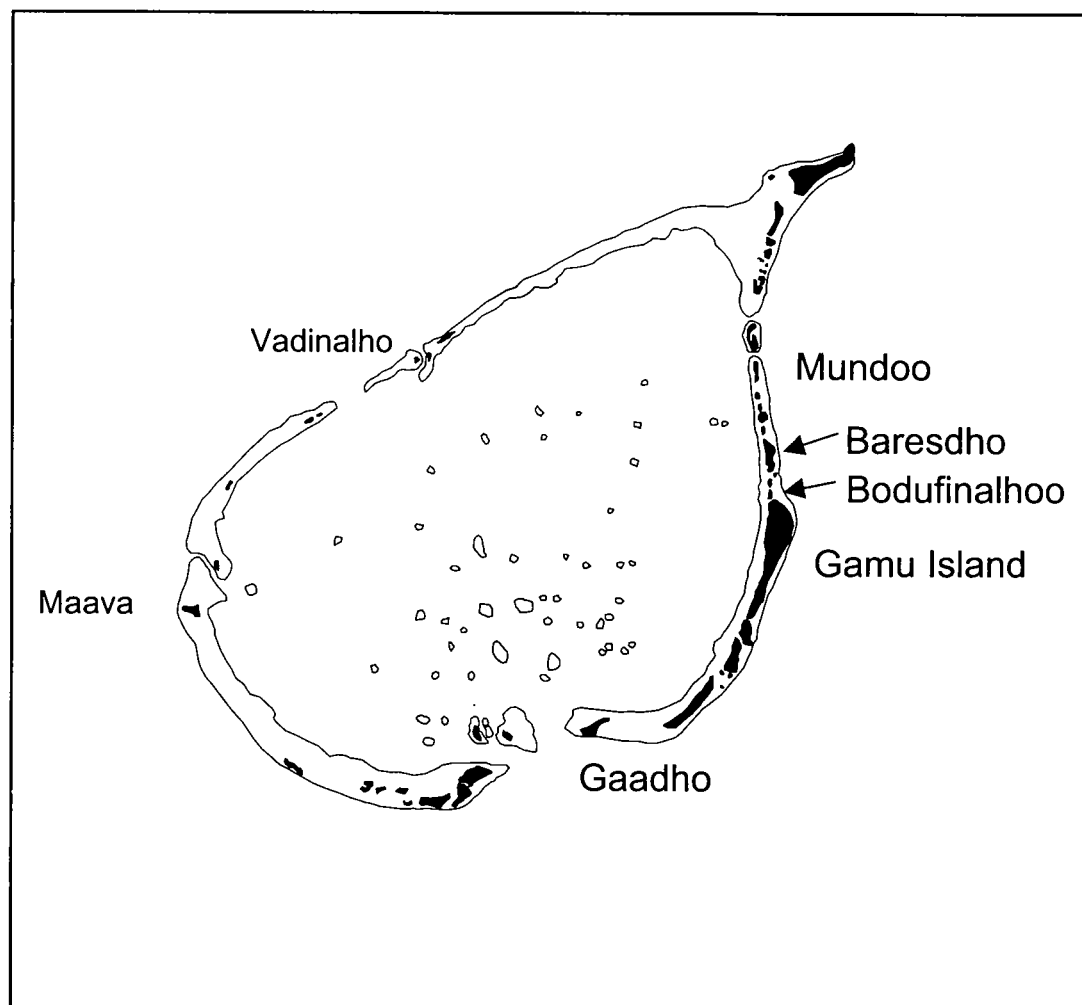


Figure 1. Map of Laamu Atoll showing study sites mentioned in the text.

# **GROUPER AND NAPOLEON WRASSE ECOLOGY IN LAAMU ATOLL, REPUBLIC OF MALDIVES: PART 1. HABITAT, BEHAVIOR, AND MOVEMENT PATTERNS**

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ROBERT D. SLUKA<sup>1</sup>

## **ABSTRACT**

Grouper and Napoleon wrasse ecology was studied in Laamu Atoll, Republic of Maldives. Studies were divided into three basic categories: 1) habitat utilization; 2) behavior; 3) movement patterns. Habitat use was studied on several spatial scales: 1) among coral reef zones; 2) among sites within a zone; 3) within one site. Behavioral studies focused on how much time grouper spend in cleaning, active, and nonactive behavior. A tagging study was initiated to examine interisland movement patterns. Major results of this study include:

1. Development of a spatial model of grouper-habitat interactions. At the largest spatial scale, grouper relative abundance was predictable among sites of the same habitat type separated by tens of kilometers; several grouper species showed consistent preferences for one type of habitat over another. However, absolute grouper density was not predictable among sites within the same habitat type. Grouper density varied by site and was not significantly correlated with structural features of the surrounding coral reef. At the microhabitat scale, grouper were found more often in areas of a site with specific habitat features.

2. There were species-specific patterns in behavior. Cleaning behavior occupied 0-20% of individuals' time. Active behavior was correlated with size in several species. The amount of time grouper spent being cleaned by cleaner fish differed by habitat type.

3. Smaller grouper species (maximum total length < 50 cm) showed no inter-island movement. In fact, several individuals were observed under the same coral head several months in a row.

4. Grouper density did not vary through time at permanently marked transects. This was due to both the stationary nature of their habits and the high variability in the data.

## **INTRODUCTION**

Groupers (Pisces: Serranidae, subfamily Epinephelinae) are top-level predatory fish found in warm waters throughout the world (Heemstra and Randall, 1993). Of the 15 genera and 159 species known to date, 8 genera and 66 species are found in the western Indian Ocean, Red Sea or Persian Gulf (Heemstra and Randall, 1993). The most abundant genera in this region is *Epinephelus*, constituting 68% of known species.

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Juvenile groupers have a greater spatial distribution than adults (Jory and Iverson, 1989) and tend to live more near-shore (Beaumarriage and Bullock, 1976). This pattern is most likely due to the dispersal of larvae out of the range of environmental conditions in which adults can survive (Jory and Iverson, 1989). Juveniles are cryptic, not straying far from crevices and staying under coral heads (Nagelkerken, 1979a). Gag *Mycteroperca microlepis* and red grouper *Epinephelus morio* juveniles show an ontological shift in habitat, migrating from seagrass beds to reefs as they grow (Ross and Moser, 1995). Eggleston (1995) showed that post-settlement Nassau grouper (25-35 cm total length (TL)) were found exclusively in algal-covered coral clumps, early juveniles (60-150 cm TL) were found outside of, and adjacent to, algal-covered coral clumps, and larger juveniles (> 150 cm TL) were associated with patch reefs.

Juvenile groupers have a greater abundance of crustaceans in their diet than any other taxonomic group. Crabs were the dominant prey item of juveniles on Bahamian patch reefs (Grover et al., 1992). Adult groupers are generalized, opportunistic carnivores exhibiting an ambush mode of feeding, staying close to the substrate, and lunging while expanding their mouth and engulfing their prey (Parrish, 1987). Groupers can also suck prey out of crevices by rapidly expanding their mouths (Burnett-Herkes, 1975). They feed at all times of the day, but feeding tends to be crepuscular, peaking at dusk and dawn (Parrish, 1987; Sluka and Sullivan, 1996a). There is no shift in diet with depth at the taxon level. However, the species composition of prey items changes with depth (Parrish, 1987), probably because of differences in distribution of prey items as opposed to changes in selection by groupers. Prey consumption differs by habitat type, season and grouper size (Harmelin-Vivien and Bouchon, 1976; Kingsford, 1992). It is generally thought that as groupers grow larger their diet shifts from mainly crustacean to mainly fish, but data suggest that prey preferences are species specific.

Grouper tend to be secretive fish, occupying caves, crevices, and ledges (Smith, 1961). Juveniles tend to occur closer to shore than adults (Stewart, 1989). Groupers require habitat for shelter, food, and cleaning stations (Parrish, 1987; Sullivan and de Garine, 1994). The relative abundance of groupers varies among coral reefs at several spatial scales. At the largest spatial scale, there are biogeographic differences in grouper relative abundance. For example, several grouper species are found on coral reefs along the continental shelf regions of the northern Indian Ocean that are not found in the coral atolls of the Maldives (Heemstra and Randall, 1993). Within a biogeographic province, grouper relative abundance differs among coral reef types or zones (Alevizon et al., 1985; Shpigel and Fishelson, 1989; Sluka and Sullivan, 1996b; Sluka and Reichenbach, 1996). These differences among zones may be consistent among biogeographic provinces. For example, *Cephalopholis argus* is most abundant on reef crests in both the Gulf of Aquaba and the Republic of Maldives (Shpigel and Fishelson, 1989; Sluka and Reichenbach, 1996). Several species of grouper are loosely attached to structural features of coral reefs, such as *Plectropomus* spp., *Variola louti*, and *Gracila albomarginata* (Sluka and Reichenbach, 1996).

Red hind *Epinephelus guttatus* home-range size was not related to body size and had a median value of 862 m<sup>2</sup> (Shapiro et al., 1994). Graysby home-range size was estimated as 23.7 m<sup>2</sup> for 5-15 cm individuals and 27.6 m<sup>2</sup> for 15-25 cm individuals (Sullivan and Sluka, 1996). *Cephalopholis argus*, *C. hemistiktos*, and *C. miniata* home range sizes were found up to 2000 m<sup>2</sup>, 62 m<sup>2</sup> and 475 m<sup>2</sup>, respectively. Larger grouper

species, such as *Plectropomus leopardus* (maximum total length > 1 m), can have home-range sizes up to 18,797 m<sup>2</sup> (Zeller, 1997). Tagged groupers have been shown to have high-site fidelity and return to their original reefs when displaced (Bardach, 1958). However, a small percentage of individuals may travel long distances to spawning aggregations or simply move over time (Samoilys, 1997).

The demand for fresh seafood by wealthy Asians has fostered a lucrative trade in live reef fish throughout the Indo-Pacific. Reef fish, especially grouper, are caught by fishermen, held in cages, then shipped by boat or air to Hong Kong, China, or Singapore. This fishery has resulted in overfishing in a number of countries and has fostered the use of fishing practices that destroy coral reefs (cyanide and dynamite use). A fishery for live grouper has recently started in Maldives and is now showing signs of overfishing (fish less abundant, smaller in size, fishermen moving farther away from previous fishing grounds to seek more fish). Little is known about the biology and ecology of grouper from Maldives. This study provides basic information on grouper ecology that can be used to develop a management plan for a sustainable live fish-food trade.

This study seeks to add to the basic knowledge of grouper ecology in the Indian Ocean in general and specifically in Maldives. Data were collected in three main areas of study: 1) distribution among habitat types; 2) behavior; 3) movement patterns. This study presents some of the first information on grouper ecology in Maldives.

## METHODS

### Study site

The Republic of Maldives is a chain of coral reef atolls stretching from about 7 degrees north latitude to 0.5 degrees south latitude. This study was carried out at the research facility of the Oceanographic Society of Maldives located on Gamu Island, Laamu Atoll (Fig. 1). The southern atolls of the Maldives are distinctly different than the northern ones, having fewer channels and consequently, larger, unbroken coral reef structures (Anderson, 1992). For the purposes of this study, reefs have been placed into three main categories: outside atoll rim, inside atoll rim, and faros. Reefs found on the side of the islands facing the open ocean are termed outside and those on the side of the islands facing into the central atoll lagoon are termed inside. Faros are circular reef structures that rise from the central atoll floor. There is a typical zonation for most reefs progressing from inshore to offshore with a shallow sandy lagoon, reef flat, reef crest, and reef slope. The outside atoll rim reef slope drops precipitously to about 30-50 m, slopes gently for about a half kilometer to 125-170 m depth, then drops again to abyssal depths (Anderson et al., 1992; Anderson, 1998). The inside atoll rim reef slope drops steeply to about 20-30 m and then grades into a sandy bottom which occupies the inner portion of the atoll. Laamu Atoll inner lagoon reaches 73 m in depth. Faros are similar in zonation with a reef flat, crest and slope.

### Length estimation training

Observers were trained to estimate grouper size accurately to the nearest 5 cm following the method of Bell et al. (1985). Thirty-five pvc lengths were cut to roughly approximate a normal distribution. Pvc pipes were strung along a 3 mm rope and laid in a sandy area of Gamu harbor at approximately 8-10 m depth. Observers slowly swam by

the pvc lengths at a distance of approximately 3 m and recorded the lengths in 5 cm categories on underwater paper (< 7.5 cm, 7.6-12.5 cm, 12.6-17.5 cm, ... 77.5-82.5 cm). Observers then compared their estimate to the true distribution of pvc lengths and determined their particular bias (i.e. under- or over-estimating length). This process was then repeated. On the third pass, the observers were asked to estimate the size of the pvc length and then examine the actual size which was discreetly written on the pipe. Observations are considered accurate to  $\pm 2.5$  cm.

### Habitat

An atoll-wide survey was conducted by examining three types of reef slopes (outside atoll rim, inside atoll rim, and faros) each at four sites: Gaadhoo, Maavah, Mundoo, and Vadinalhoo (Fig. 1). At each site, six 15-minute surveys were completed consisting of two observers swimming side by side in a zig-zag pattern between 9 m and 18 m depth. Both observers searched for *Cheilinus undulatus*, *Plectropomus areolatus*, *P. laevis*, *P. pessuliferus*, and *Variola louti*.

The four former species are highly sought after for the live fish-food trade and all five species are amenable to rapid and accurate identification and enumeration using this method (Newman et al., 1997). These species are rarer than smaller grouper species which makes them less amenable to sampling using plot-based survey methodologies (i.e. transects or point counts). The two observers helped each other and all results were recorded on one tally sheet. Groupers within site range were enumerated and their size estimated to the nearest 5 cm. Water visibility was such that the bottom was visible even if deeper than 18 m. All groupers observed were counted even if outside the depth boundaries, which were chosen mainly for diver safety. Data were analyzed using a one-way nested ANOVA with habitat as the fixed factor and sites nested in habitat. Data were tested for homoscedasticity and  $\log(x+1)$  transformed where appropriate. A presence/absence list of all grouper species observed was compiled while searching for the aforementioned species. Species counts were analyzed using one-way ANOVA with habitat as the main factor in one analysis and east/west sites in another analysis.

Transects (12 m x 20 m, width by visual estimation,  $n=14$ ) were laid in the inner atoll rim reef slope habitat between Gamu and Bodufinalhoo (Fig. 1) and the total number of *Cephalopholis argus* enumerated. Size of each fish was visually estimated following training (Bell et al., 1985). Size was converted to biomass using a weight-length relationship calculated from unpublished data collected in Maldives (Sluka, unpublished data). Relief of the site was assessed by randomly selecting 10 1-m<sup>2</sup> quadrats along the length of the transect line and measuring the vertical distance between the deepest and shallowest point in the quadrat. A Pearson correlation coefficient was calculated to determine if there was a significant relationship between *C. argus* biomass and vertical relief.

Microhabitat utilized by groupers was compared to the surrounding benthos of the site off the island of Bodufinalhoo (Fig. 1). Six grouper species were observed: *Anyperodon luecogrammicus* ( $n=4$ ), *Cephalopholis argus* ( $n=30$ ), *C. leopardus* ( $n=3$ ), *C. miniata* ( $n=4$ ), *Epinephelus merra* ( $n=5$ ), and *Plectropomus areolatus* ( $n=6$ ). The maximum size of these species ranges from 20-60 cm (Randall, 1992). The point-intercept method was used to assess the benthic composition at the point where a grouper was observed. A 1 m<sup>2</sup> quadrat, divided into 25 points, was laid on the reef and the

benthos under each point was placed into one of ten categories: plate coral, massive coral, branching coral, other coral, macroalgae, octocoral, sponge, sand, rubble or pavement. Pavement was defined as any dead coral surface that was not colonized by benthos, not including turfing algae. Depth was measured from the surface to the midpoint of the quadrat. Relief was calculated as the difference between the shallowest and deepest point in the quadrat. Depth was recorded to the nearest 0.3 m. The general benthos at the site was defined by laying five 50-m transects perpendicular to the prevailing depth gradient. Twenty points along each transect line were randomly chosen to assess the benthos using the same method as above. Due to the reef profile and diving limitations, only 60 quadrats were sampled for the general reef benthos. The mean number of points recorded in each benthos category was compared to the same category for all grouper species combined using a t-test (Zar, 1984). One-way ANOVA was used to compare each benthic category among all grouper species and the general site benthos (Zar, 1984). Post-hoc Tukey tests were used to determine which means were significantly different.

### Behavior

The diurnal activity patterns of six grouper species (*Cephalopholis argus*, *C. miniata*, *Epinephelus merra*, *Plectropomus areolatus*, *P. laevis*, *P. pessuliferus*) were studied on coral reefs between Gamu and Baresdhoo islands (Fig. 1). Observations occurred January 13-22, 1997 between 1000 and 1400 hours local time. Groupers are known to forage more actively during crepuscular periods (Parrish, 1987; Shpigel and Fishelson, 1989; Brule et al., 1994; Sluka and Sullivan, 1996a). Thus, this study focused on activity patterns and particularly the importance of cleaning behavior during less active times of the day.

Behaviors were defined as one of three categories: cleaning, active, and non-active. A grouper was considered cleaning if a cleaning organism (fish or shrimp) could be observed making contact with the grouper or if a cleaning posture was exhibited (i.e. operculum flared and mouth open). Active behavior was defined as all activities where the grouper was swimming. The majority of observations in this category were from fish only swimming, but rarely included behavior interpreted to be sexual interactions or aggressive intraspecific displays among, presumably, males. Grouper behavior was defined as nonactive when the fish was not swimming, thus remaining stationary at a particular point, on or in, the water column above a coral reef.

An individual grouper was observed for 5-minute periods. The activity of an individual fish was recorded at 20-second intervals. The observation was included in analyses only if a fish was observed for the entire 5-minute period. The size and species of each grouper observed were recorded. Groupers were categorized as small, medium, or large for ANOVA based upon terciles of the maximum length for each species (Table 1).

The data were analyzed separately for cleaning, active, and nonactive behavior due to the lack of independence between observations. Histograms and normal probability plots were examined to determine if data were highly nonnormal (Zar, 1984). The cleaning data were judged to be too skewed to use parametric ANOVA (102 of 143 observations were recorded as 0). Nonparametric Kruskal-Wallis ANOVA was used to analyze cleaning behavior data. Additionally, observations on each grouper species were placed into one of two categories: cleaning or not cleaning, regardless of how much time.

Table 1. Size values used for classifying grouper into small (S), medium (M), and large (L) categories. Maximum values taken from Randall (1992).

Species	S (cm)	M (cm)	L (cm)	Max. size (cm)
<i>Cephalopholis argus</i>	<15	16-30	>30	50
<i>C. miniata</i>	<15	16-25	>25	41
<i>Epinephelus merra</i>	<10	11-20	>20	28
<i>Plectropomus areolatus</i>	<20	21-40	>40	60
<i>P. laevis</i>	<35	36-65	>65	100
<i>P. pessuliferus</i>	<25	26-50	>50	70

a species actually spent cleaning. A Chi-square contingency table was used to assess the independence of species and cleaning behavior. Cleaning observations for *C. argus* were placed in these same two categories as well as separated by size category: small, medium or large. All other species had too few observations to warrant a separate analysis by size using Chi-square (Zar, 1984).

A two-way ANOVA was used to analyze active and nonactive behavior with species and size as fixed factors for each of the three behavior categories. Residual plots were examined for homogeneity of variance and data  $\log(x+1)$  transformed were appropriate (Zar, 1984). As two species were lacking one of the size categories (*E. merra* and *P. pessuliferus*), there were only four species compared by ANOVA. Size was never significant as a factor in the ANOVA (see results). This factor was then dropped from the model so that all six species could be included in a one-way ANOVA with species as the fixed factor and the number of 20-second time intervals observed at a particular activity the replicates. A post-hoc Tukey test was used to determine which species had significantly different means. Variances remained heterogeneous after transformation for nonactive behavior, thus nonparametric Kruskal-Wallis ANOVA was used to assess differences among species for this activity category. A Pearson correlation coefficient was used to examine significant relationships between species and size for each activity separate from ANOVA.

### Tagging study

Grouper were collected using hooks and lines between November, 1996 and February, 1997. Snorkelers baited hooks with damselfish or fusiliers which were dangled in front of individual grouper. This method appears to work well with *Aethaloperca rogaa*, *Cephalopholis* spp., and *Plectropomus* spp. In order to catch *Epinephelus fuscoguttatus* and *E. polyphkadion*, tuna heads were used as bait on hooks and lines from a boat at night, especially in the channels leading outside the atoll. Each fish was brought back to the boat, measured for fork length (mm), placed in a preweighed bucket and weighed (g). A dart tag, with a alphanumeric plastic piece attached on the end was inserted into the dorsal musculature so that the tag secured itself under the pterigiophores of the dorsal fin. Air was released from the swim bladder when expansion was observed. Fish under 250 mm were deemed too small for tagging due to the size of the tag. *Epinephelus fuscoguttatus*, *E. polyphkadion*, and *Plectropomus* spp. were double tagged, with one tag placed on each side of the fish in the same position as described above.



### Permanent transect sampling

Three 240-m<sup>2</sup> transects were established at each of two sites on the inner atoll reef slope off Bodufinalhoo Island (Fig. 1). The boundaries of each transect were marked with flagging tape and small subsurface buoys which floated approximately 1-2 m off the bottom. Two transects at each site were at approximately 10 m depth while the third ranged from 10-20 m depth. Each month one observer surveyed the transect and recorded the species and size of each individual observed. This data was then plotted by month for all sites combined to examine the variability in grouper density and species composition through time. A repeated-measures ANOVA was used to test for significant differences in mean grouper density (no. 240 m<sup>-2</sup>) among grouper species, between the two buoy sites, and among repeated sampling dates.

## RESULTS

### Habitat

The abundance of *Cheilinus undulatus*, *Plectropomus pessuliferus*, and *Variola louti* was significantly different among habitat types (faros, inside and outside the atoll), but not significantly different for *P. laevis* or *P. pessuliferus* (Table 2). The site-nested-in-habitat factor was significant for all species except *P. areolata*. *Plectropomus pessuliferus* was most abundant in faros, and least abundant outside the atoll (Fig. 2). *Variola louti* was most abundant outside the atoll, while least abundant inside the atoll.

No Napoleon wrasse were observed in quantitative surveys in inner atoll rim or faro reef slopes (Fig. 2). Abundance of Napoleon wrasse was significantly higher in the outer-atoll rim than the other two habitat types. There was significant variance in the abundance of Napoleon wrasse among outer-atoll rim-reef slope sites.

Twenty grouper species were observed during the 15-minute surveys and a total of 25 during the course of the entire study (Table 3). There were no significant differences in the total number of grouper species observed among habitat types ( $F=0.128$ ,  $p>0.05$ ). However, there were significantly more species observed on the eastern side of the atoll than on the western side ( $F=7.096$ ,  $p<0.05$ ).

Table 2. Summary of ANOVA results comparing mean grouper abundance among habitat types (inside atoll rim, outside atoll rim and faro reef slopes) and sites (n=4 per habitat)—nested-within-habitat types. Probability levels for each factor are given.

Species	Habitat factor	Site (Habitat) factor
<i>Cheilinus undulatus</i>	<0.001	<0.001
<i>Plectropomus areolatus</i>	NS	NS
<i>P. laevis</i>	NS	NS
<i>P. pessuliferus</i>	<0.001	<0.05
<i>Variola louti</i>	<0.001	<0.05

There were significant differences between the general-site benthos and all grouper-combined benthos for the categories of relief ( $t=-4.506$ ,  $df=110$ ,  $p<0.001$ ), massive coral cover ( $t=-3.335$ ,  $df=110$ ,  $p<0.001$ ), algae cover ( $t=-2.148$ ,  $df=110$ ,  $p<0.05$ ) and sand cover ( $t=3.786$ ,  $df=110$ ,  $p<0.001$ ). All other benthic categories showed no

significant differences. Grouper were found more often at points on the coral reef with higher relief, more massive corals, greater algal cover and less sand (Fig. 3).

There were significant differences among the general-site benthos and grouper-species benthos for the benthic categories of relief ( $F=5.066$ ,  $p<<0.001$ ), massive coral ( $F=6.986$ ,  $p<<0.001$ ), and sand ( $F=2.723$ ,  $p<<0.05$ ). *C. argus* (Fig. 4) and *C. miniata* were found more often in areas of higher vertical relief than were the surrounding benthos. *C. argus* was also found more often in areas of greater massive coral cover than the surrounding benthos (Fig. 4). *C. leopardus* was found more often in areas of greater massive coral cover than the surrounding benthos and all other grouper species, including *C. argus*. The surrounding benthos had a greater percentage of sand cover than positions where *C. argus* were found (Fig. 4)

Table 3. Checklist of grouper species observed during this study. See text for habitat definitions.

Species	Outside	Inside	Faro	Lagoon
<i>Anyperodon luecogrammicus</i>	+	+	+	
<i>Aethaloperca rogaa</i>	+	+	+	
<i>Cephalopholis argus</i>	+	+	+	+
<i>C. boenak</i>		+		
<i>C. leopardus</i>	+	+	+	
<i>C. miniata</i>	+	+	+	
<i>C. sexmaculata</i>		+	+	
<i>C. spiloparaea</i>		+	+	
<i>C. urodeta</i>	+	+	+	
<i>Epinephelus caeruleopunctatus</i>	+	+	+	+
<i>E. fasciatus</i>	+	+		
<i>E. fuscoguttatus</i>	+	+	+	
<i>E. macrospilos</i>		+		
<i>E. melanostigma</i>	+	+		
<i>E. merra</i>		+	+	+
<i>E. ongus</i>		+		
<i>E. polyphkadion</i>	+	+	+	
<i>E. spilotoceps</i>	+	+		
<i>E. tauvina</i>	+	+		
<i>Gracila albomarginata</i>	+	+	+	
<i>Plectropomus areolatus</i>	+	+	+	
<i>P. laevis</i>	+	+	+	
<i>P. pessuliferus</i>	+	+	+	
<i>Variola albimarginata</i>	+			
<i>V. louti</i>	+	+	+	

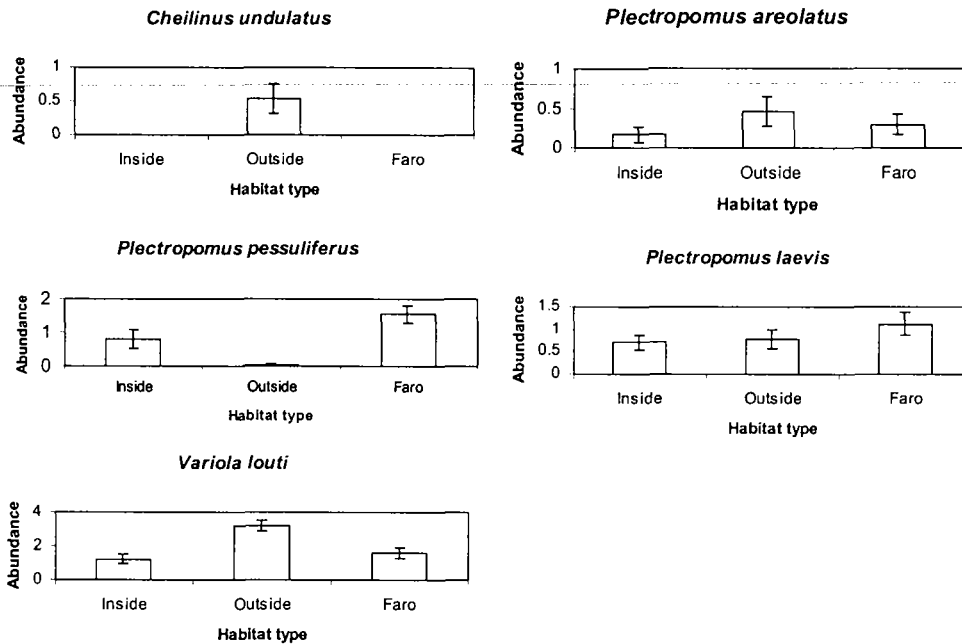


Figure 2. Mean abundance (no 15 minute<sup>-1</sup>) among three reef slope habitat types: inside the atoll rim, outside the atoll rim, and in faroes.

### Behavior

One hundred forty three grouper were observed among six species: *Cephalopholis argus* (n=75), *C. miniata* (n=19), *Epinephelus merra* (n=15), *Plectropomus areolata* (n=13), *P. laevis* (n=14), and *P. pessuliferus* (n=7). There were significant differences in the mean time spent cleaning among the six grouper species ( $p < 0.05$ , Figure 5). *E. merra* was never observed cleaning. There is high variability in the data with *P. laevis* observed to spend the most time cleaning (approximately 20%). The amount of time spent cleaning was significantly related to size in *C. argus* ( $r = 0.23$ ,  $p < 0.05$ ), but in no other species.

Cleaning behavior was independent of species ( $X^2 = 8.85$ ,  $df = 5$ ,  $p > 0.05$ ). The distribution of number of groupers observed cleaning is similar to those observed not cleaning, except for the case of *E. merra*. Cleaning behavior and size were independent for *C. argus* ( $X^2 = 0.091$ ,  $df = 2$ ,  $p > 0.05$ ).

Neither size, species, nor the interaction effect were significantly influencing the amount of time spent on active behavior by observed groupers ( $p > 0.05$ ). Size was dropped from the model and all six grouper species were examined for significant differences in active behavior (see methods). There were significant differences in the amount of time spent in active behavior among species ( $p < 0.001$ ). Figure 5 and a Tukey test showed that *E. merra* spent significantly less time in active behavior than the other species. There were no significant differences among all other species. Size was significantly correlated with active behavior in *C. miniata* and *P. pessuliferus* (Fig. 6).

There were no significant differences in nonactive behavior among species, size categories, nor in their interaction ( $p > 0.05$ ). There were significant differences among species when size was dropped from the model and all six species included ( $P < 0.001$ ).

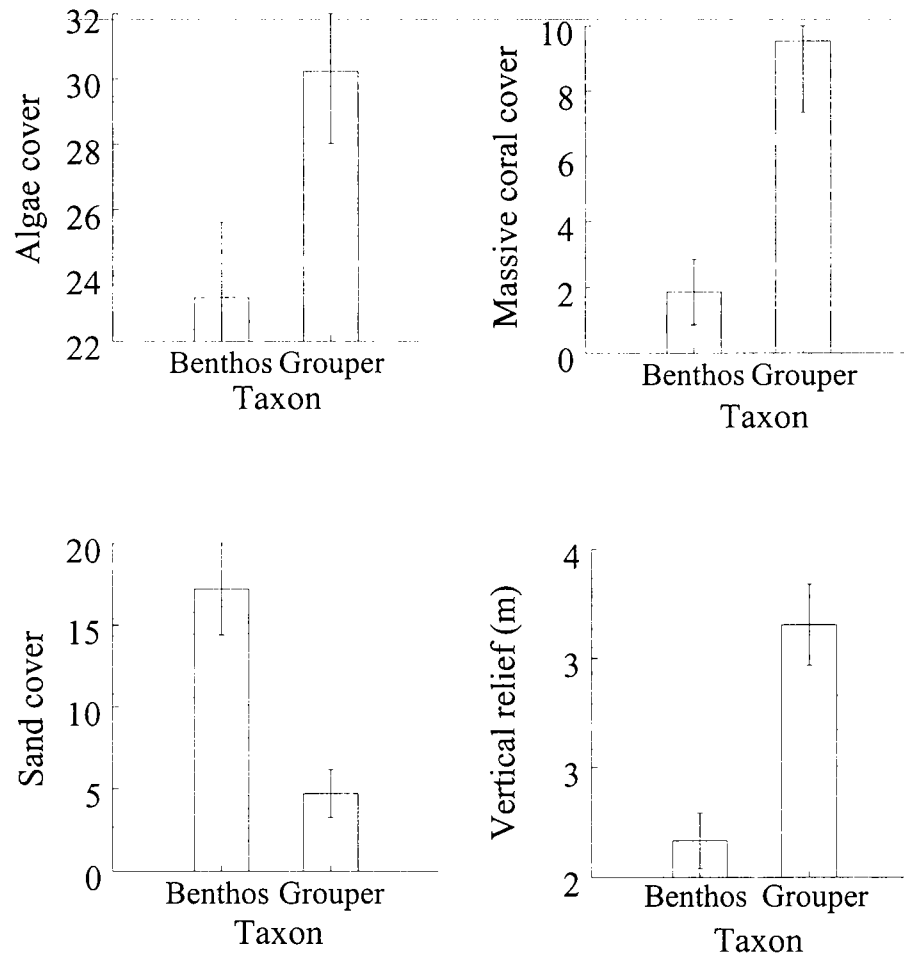


Figure 3. Plots showing differences in the habitat use by grouper versus the general surrounding benthos of the site. Histogram bars for each taxon show the value of the habitat variable (relief or percent coverage) where 52 individual groupers were observed and 60 1 m<sup>2</sup> plots of the surrounding coral reef.

Figure 5 shows that *E. merra* spent significantly more time in nonactive behavior than all other species. Figure 6 shows that there were significant relationships between *C. miniata* size and the amount of time spent on nonactive behavior. Larger individuals spent less time on nonactive behavior than smaller individuals. The relationship between time spent on nonactive behavior and size for *P. pessuliferus* was almost insignificant ( $p=0.055$ ).

#### Tagging study

Two hundred four grouper among nineteen species were caught during the tagging study. Sixty-two percent (127/204) of these individuals were of a taggable size. The most frequently caught species was *Cephalopholis argus*, followed by *Epinephelus*

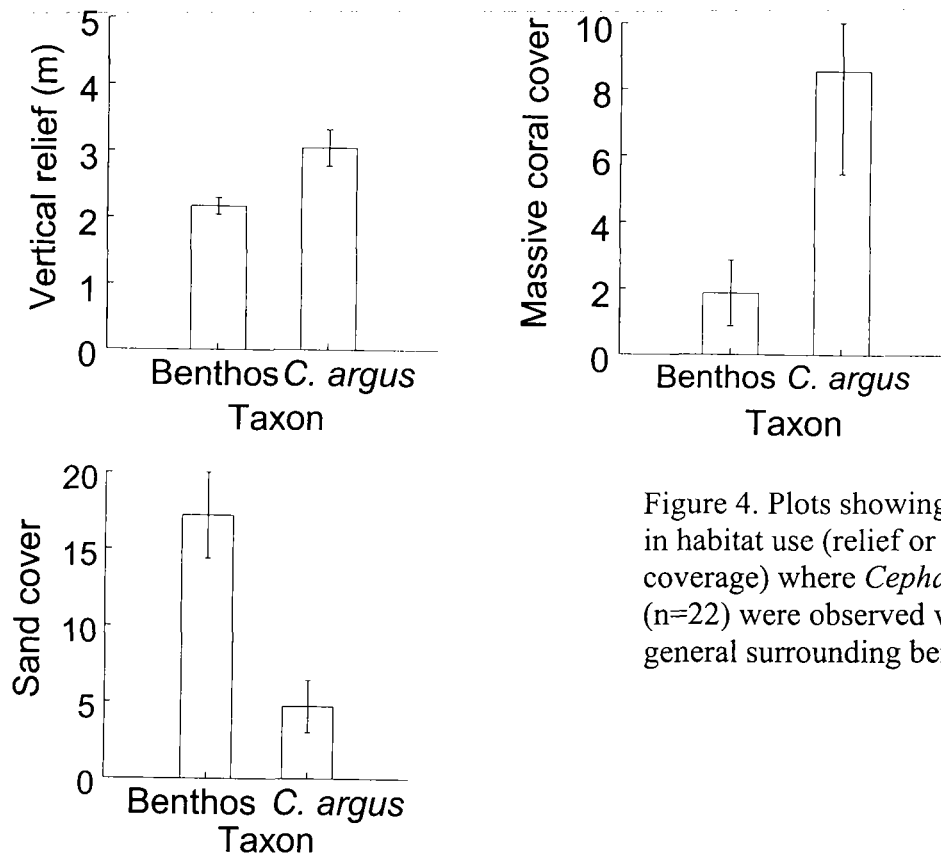


Figure 4. Plots showing the differences in habitat use (relief or percent coverage) where *Cephalopholis argus* (n=22) were observed versus the general surrounding benthos (n=60).

*spilotoceps* and *C. miniata*. None of these species are targeted in the live fish-food trade, but appear to be most easily caught. The targeted species, *E. fuscoguttatus*, *E. polyphekadion*, and *Plectropomus* spp., constituted only 13% of grouper caught during the tagging study. The tag return rate was about 9%, as 11 tags were returned or sighted underwater. Five of these 11 tags could not be used to provide information on movement patterns due to the tag being unreadable underwater, problems with fishermen reporting returns, or fish purposely being displaced to examine homing behavior. Of the six fish for which there is reliable data, three (two *C. argus* (287 and 355 mm TL) and one *Aethaloperca rogaa* (360 mm TL)) were observed at the same site 183, 145, and 145 days later, respectively. One of these two *C. argus* was observed at the permanent transect site repeatedly, almost always in the same 240 m<sup>2</sup> transect. The *A. rogaa* was resighted twice underwater, one month apart, both times under the exact same coral head. There was also no interisland movement for one *C. miniata* (320 mm TL, 18 days between captures), one *Gracila albomarginata* (314 mm TL, 57 days), and one *P. laevis* (366 mm TL, 19 days).

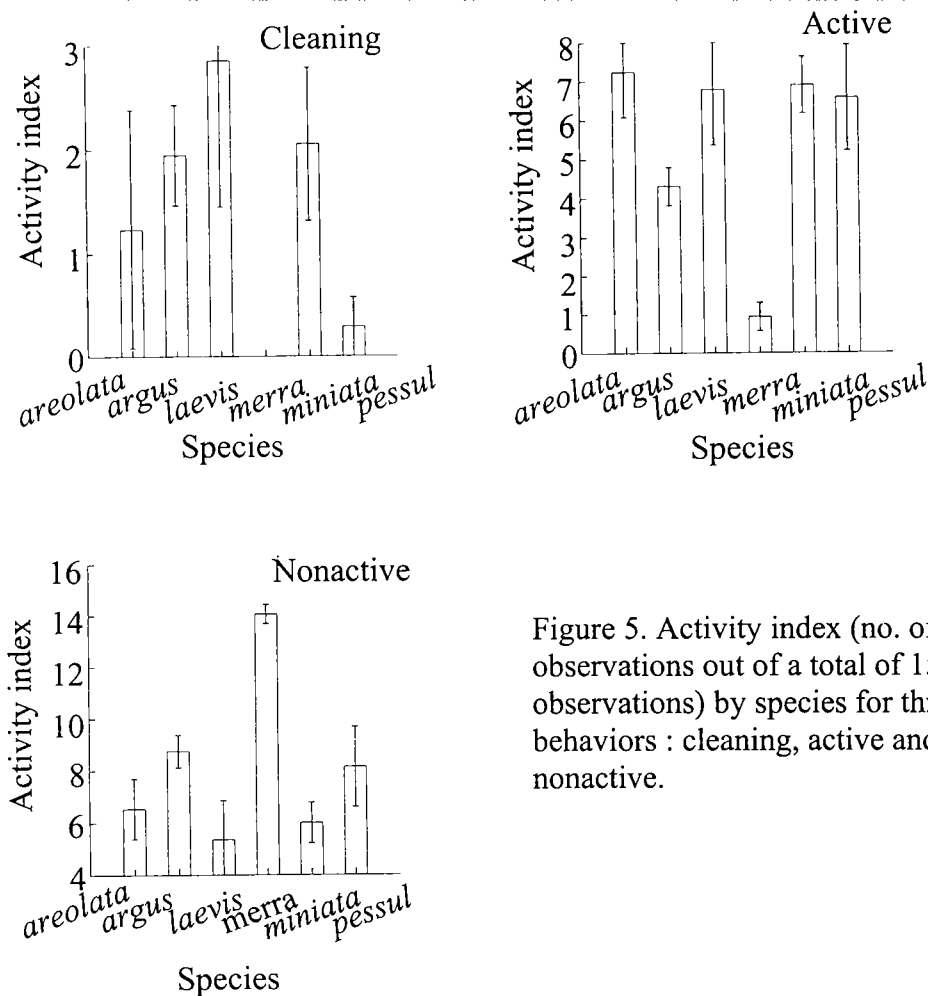


Figure 5. Activity index (no. of observations out of a total of 15 observations) by species for three behaviors : cleaning, active and nonactive.

#### Permanent transect sampling

There were significant differences in mean grouper density among species. A post-hoc Tukey test indicated that there were significant differences in species density for each of the nine time periods when considered separately. *Cephalopholis argus* density was greater than *C. miniata* density and both were greater than all other grouper densities (Figure 7). There was no significant difference in grouper density between the two buoys and no species x buoy factor interaction. This indicates that the overall grouper density was not significantly different between the two buoys and that no species was significantly more abundant at one buoy or the other. There was also no significant difference in overall grouper density through time, nor any interaction factor between time and grouper species or site. This indicates that grouper density did not change significantly through time nor did it change through time for any species. The change in *C. argus* density through time was examined separately, but was also not significantly

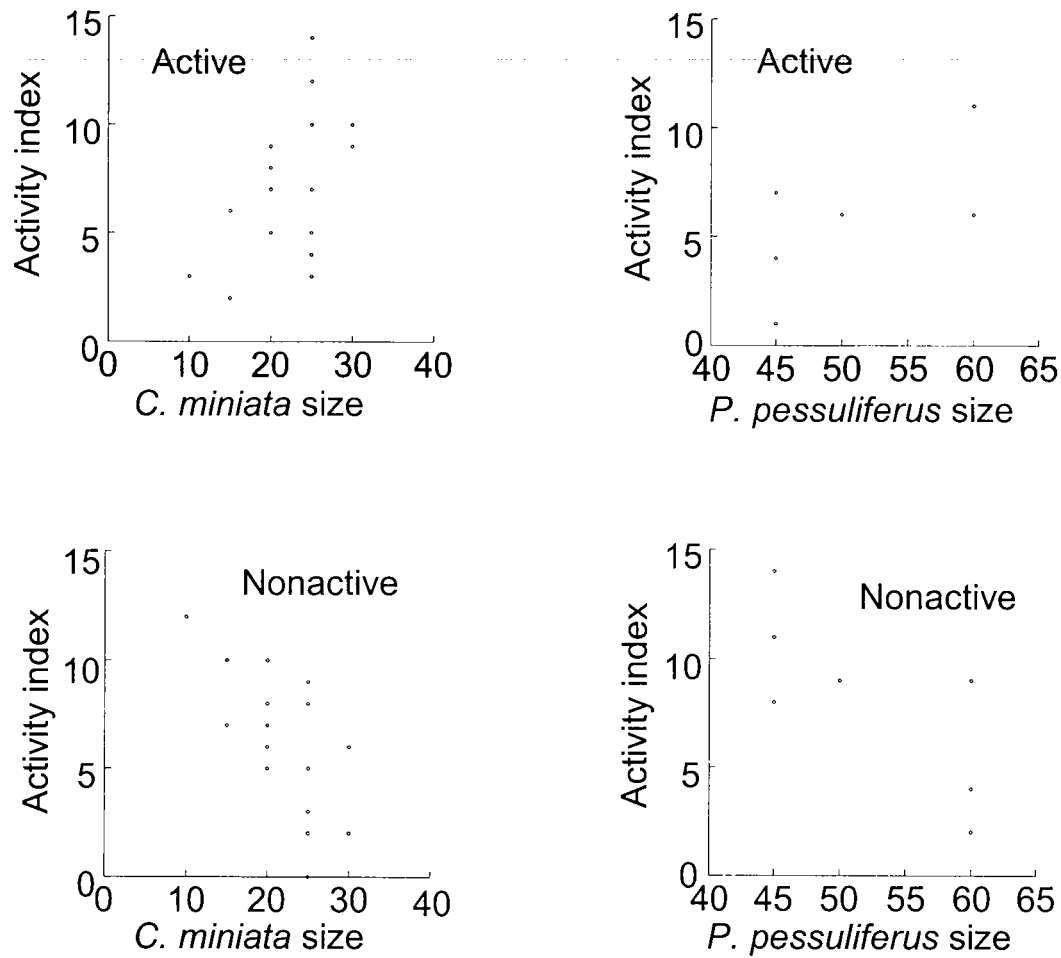


Figure 6. Relationship between active and nonactive behavior indices and grouper size. As the activity index increases, the amount of time an individual spent at a particular behavior increases.

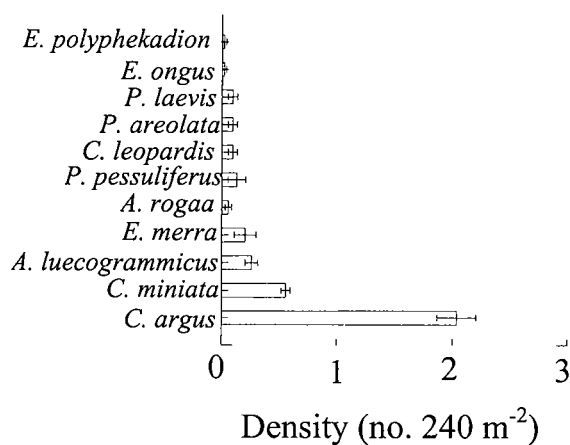
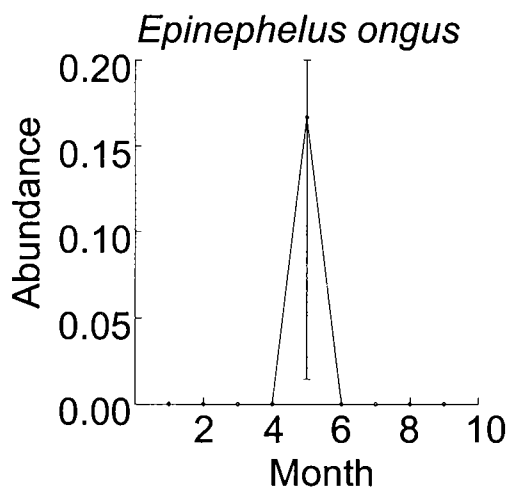
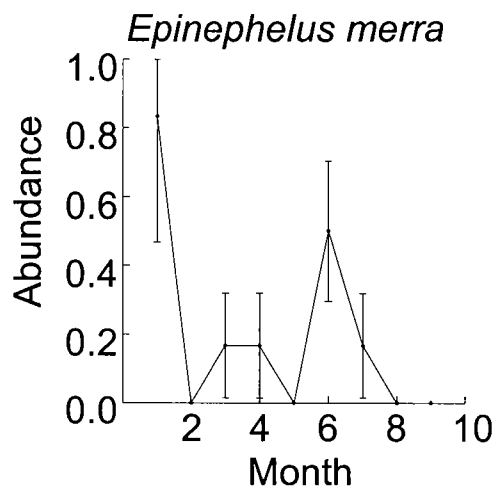
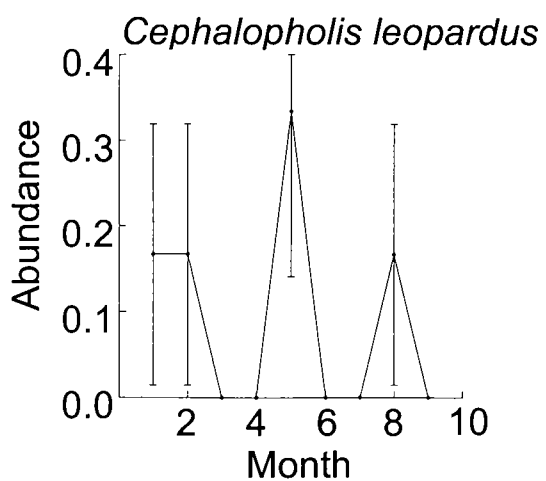
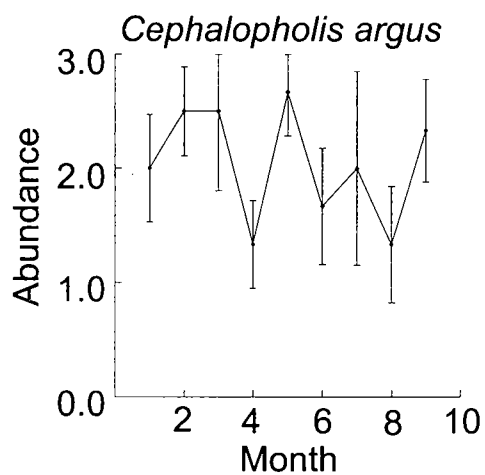
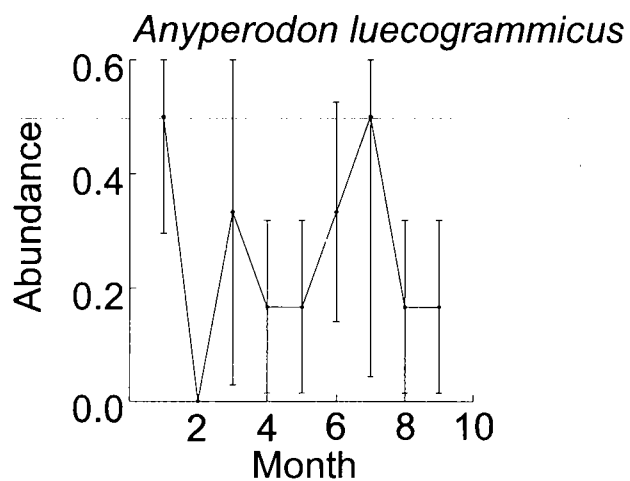
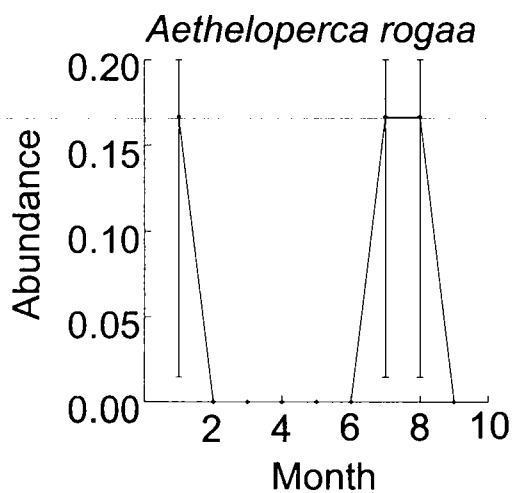


Figure 7. Grouper density in permanent transects.





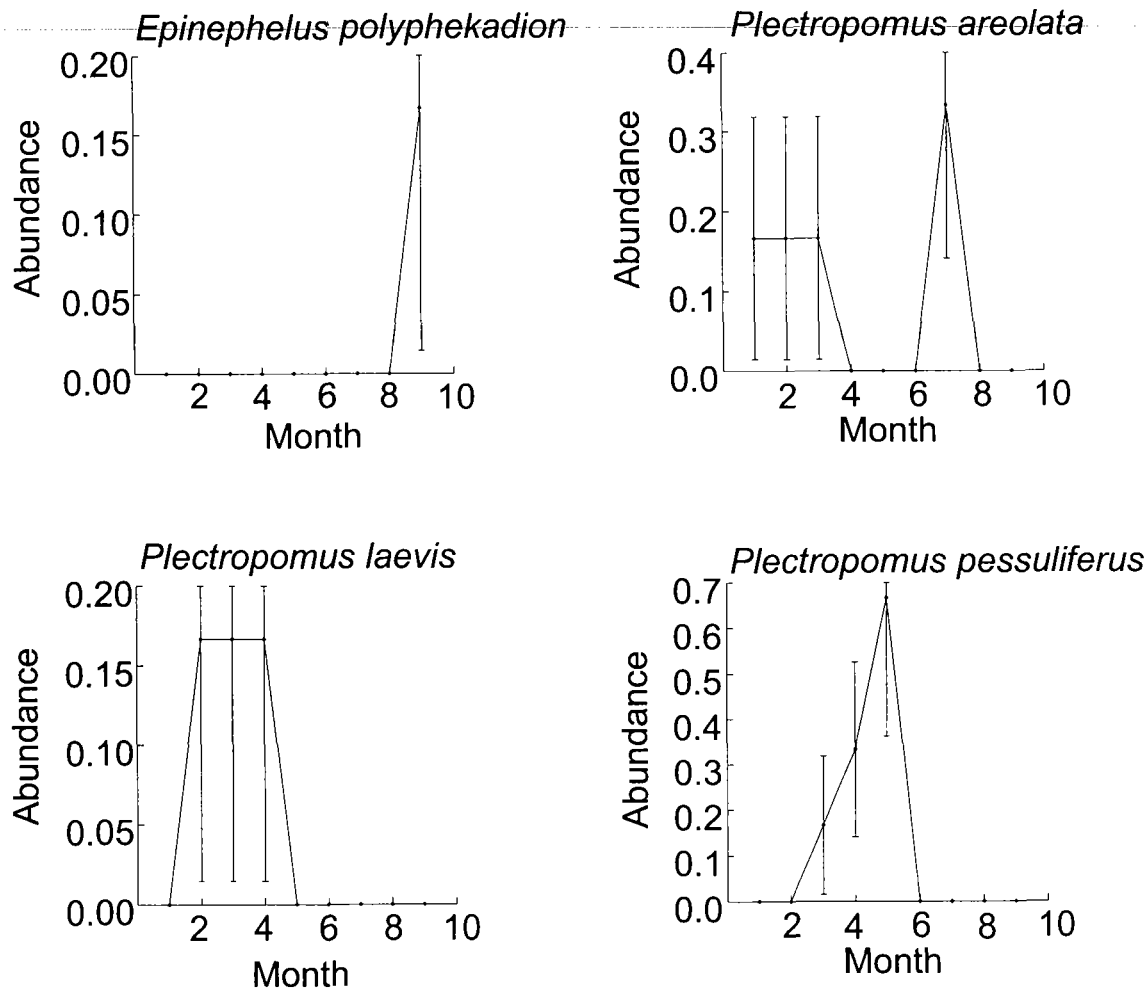


Figure 8. Mean abundance (no. 240 m<sup>-2</sup>) in six permanent transects. Months start in November 1996 (1) and end in July 1997 (9).

different ( $p > 0.05$ ). Figure 8 shows that there was significant variance among monthly means

## DISCUSSION

### Habitat

Many coral-reef fish species and assemblages are known to be qualitatively and/or quantitatively related to particular features of the reef structure. Families such as the Labridae, Chaetodontidae, and Scaridae are only found in coral-reef habitats (Choat and Bellwood, 1991). Quantitative features of the reefs themselves, such as coral cover or habitat complexity, influence the relative abundance of species and absolute abundance of particular species (reviewed in Jones, 1991). The relationship between habitat and coral-reef fish abundance varies depending upon the scale one examines.

Relationships between quantitative features found at a microscale do not necessarily hold between reefs separated by many meters or kilometers (Syms, 1995).

The relative abundance of grouper varies among coral reefs at several spatial scales. At the largest spatial scale are biogeographic differences. For example, several species of grouper are found on coral reefs along the continental shelf of the northern Indian Ocean that are not found in Maldivian atolls (Heemstra and Randall, 1993). Within a biogeographic province, the relative abundance of grouper differs among coral-reef types or zones (Alevizon et al., 1985; Shpigel and Fishelson, 1989; Sluka and Sullivan, 1996b; Sluka and Reichenbach, 1996; Newman et al., 1997). These differences may be consistent among biogeographic provinces. For example, *Cephalopholis argus* is most abundant on reef crests in both the Gulf of Aquaba and the Republic of Maldives (Shpigel and Fishelson, 1989; Sluka and Reichenbach, 1996). Quantitative relationships between absolute abundance and habitat parameters have been few. Nagelkerken (1979b) showed a significant relationship between coral cover and graysby (*C. cruentata*) abundance. Sluka et al. (1996a) showed a similar relationship for this species in the central Bahamas, but not in the Florida Keys (Sluka, 1995). It appears that fishing has a much greater influence on the abundance of grouper species that are targeted by fisheries than on quantifiable habitat features (Sluka et al., 1996b, 1997). On the smallest spatial scale, the behavior of groupers has been shown to be significantly influenced by the surrounding habitat (Sluka, 1995; Sluka et al., in press). Groupers were found to spend more time in microhabitats of coral reefs with specific habitat features (e.g. cleaning stations, high vertical relief). Sluka (1995) found that *C. cruentata* preferentially occupied high-relief habitats over surrounding low-relief habitats and that larger fish were found more often in microhabitats of higher relief than smaller fish. Similarly, Sluka et al. (1998) found that the average size of *C. cruentata* was greater in higher-relief coral-reef types than lower-relief types.

#### Grouper habitat relationships in Maldives

Two grouper species were more abundant in a particular habitat than others. This likely indicates a preference for these habitats rather than the result of fishing as fishing pressure has been low. *Variola louti* was most abundant on reef slopes outside the atoll rim while *Plectropomus pessuliferus* was most abundant in faro reef slopes. Randall and Brock (1960) stated that *V. louti* was most abundant in passes between islands and on the outside of the barrier reef in French Polynesia. *Epinephelus merra* was the dominant grouper in lagoonal Acroporid patch reefs. This is consistent with other studies showing this species to be abundant in shallow water lagoons (Randall and Brock, 1960; Chave and Eckert, 1974; Heemstra and Randall, 1993; Sluka and Reichenbach, 1996). There were significant differences in density among sites for most species indicating that, while there may be general preferences for one habitat type over another, a species' absolute abundance cannot be predicted by knowledge of habitat type. This is consistent with grouper habitat studies in the Caribbean (Sluka, 1995; Sluka et al., 1996b) and Australia (Newman et al., 1997).

Sluka and Reichenbach (1996) studied the density of groupers among several types of habitats in Gaagandu, North Male Atoll and Olhugiri, Thaa Atoll. The median number of groupers  $240 \text{ m}^{-2}$  on an inner-reef slope was much greater than on reef crests or a large Acroporid reef. Twenty-two species of grouper were observed, with *C. miniata*

and *C. urodeta* being the most abundant on the reef slope, *C. argus* on reef crests and the Acroporid reef. *Epinephelus merra* was the most abundant grouper in shallow lagoons. At Thaa Atoll, Sluka and Reichenbach (1996) surveyed both the outer- and inner-reef crest grouper assemblages. The outer- and inner-reef crests were both dominated by *C. argus*. However, *C. urodeta* was more abundant on the outer-reef crest. In Laamu Atoll, *C. urodeta* are more abundant on outer-reef slopes than inner-reef slopes.

Diversity did not differ significantly among the three reef-slope habitats in this study. However, diversity was greatly reduced in lagoonal habitats. There were 25 species observed throughout the course of this study, but only 3 in lagoons. Shakeel and Ahmed (1996), Adam et al. (1998), and Anderson et al. (1998) list 41 species as occurring in Maldives. Several species were observed on reefs inside the atoll rim and on faros, but not outside the atoll rim: *Cephalopholis sexmaculata*, *C. spiloparaea*, and *Epinephelus merra*. Only one species, *Variola albimarginata*, was observed outside the atoll rim, but not in other habitats. However, only one individual of this species was observed during the course of this study.

Groupers were shown to have specific microhabitats that were utilized preferentially to the surrounding habitat. Fish were found more often in areas of higher structural complexity. This was evidenced by individuals being located in areas of higher vertical relief, greater massive coral (likely also reflecting relief) and algal cover, and lower sand cover. This corroborates the general observation that groupers prefer caves, crevices and holes (Smith, 1961).

While groupers behaviorally prefer areas of a coral reef with high relief, knowledge of this habitat feature cannot be used to make predictions about grouper abundance. Thus, while grouper relative abundance on a large scale (biogeographically and among types/zones of coral reefs) has predictability, the abundance at a particular site appears to be influenced more by factors such as recruitment variability and fishing pressure than habitat. This is especially true for species targeted for harvesting. Some smaller species in the Caribbean have shown quantitative relationships between habitat features and abundance (Nagelkerken, 1979a; Sluka et al., 1996a). This was not the case for the abundant grouper *Cephalopholis argus* in Maldives.

Sluka and Reichenbach (1996) also made observations on the degree of association between grouper and their habitat. Several grouper species such as *Plectropomus* spp., *Variola louti*, and *Gracila albomarginata* were loosely attached to structural features of coral reefs. *Aethaloperca rogaa* appeared to be intermediate between these free-roaming species and the more site-attached species such as *Cephalopholis* spp. and *Epinephelus* spp. Several *Cephalopholis* species had significantly clumped distributions likely indicating the patchy nature of their habitat and the close association with habitat features. In this study, *C. argus* was found more often in sites with a higher vertical relief, greater massive coral cover, and lower sand cover. This is similar to many grouper species that prefer areas with high vertical relief (Nagelkerken, 1979a; Sluka et al., 1996a). This result indicates that *C. argus* will be found more often within a particular site where there are specific habitat features of the coral reef. Can *C. argus* abundance then be predicted among sites based on these same features? Based on these observations and those of other grouper species in the Caribbean (Sluka, 1995; Sluka et al., 1996a,b, 1998, in press) and Australia (Zeller, 1997), it appears that the movement patterns and behavior of grouper within a coral reef are affected

significantly by specific, quantifiable features of the coral-reef habitat. The most likely position of a grouper on a particular coral reef can be predicted based upon a knowledge of habitat preferences of the grouper and quantified habitat features of the coral reef. However, this knowledge will not allow one to predict the abundance of grouper across a wide spatial scale (i.e., among coral reefs). Knowledge of the habitat features of a coral reef does not generally correlate with the abundance of individuals.

## Behavior

Grouper behavior studies have mainly focused on spawning activities (e.g. Smith, 1972; Shapiro, 1987; Carter, 1988; Donaldson, 1989, 1995a; Samoilys and Squire, 1994; Zabala et al., 1997), with the exception of a few studies examining time-activity budgets (Sullivan, 1993; Sullivan and de Garine-Wichatitsky, 1994; Donaldson, 1995b; Sluka and Sullivan, 1996a), diel behavioral changes (Collette and Talbot, 1972; Nemtzov et al., 1993) and inter- and intra-specific interactions (Shpigel and Fishelson, 1991; Donaldson, 1995b). Diel, seasonal and habitat-related differences in predation were studied by Kingsford (1992) and Brule et al. (1994).

Groupers are active throughout the day with crepuscular peaks of foraging activity (Parrish, 1987; Sluka and Sullivan, 1996a; but see Brule et al., 1994). There appears to be little activity at night (Zeller, 1997); however, some species will feed during the night (Randall, 1965, Brule et al., 1994; Sluka, pers. obs.). Grouper spend a significant portion of their day resting, usually perched on a coral head or perhaps hiding in and amongst the numerous holes on a coral reef (Donaldson, 1995b; Sluka and Sullivan, 1996a). Behavior patterns are influenced by the disruption of social structures (e.g. fishing) (Sullivan, 1993). There also appear to be some weak differences in behavior between males and females (Donaldson, 1995b). Grouper activities and behavior are significantly influenced by cleaning activities (Sluka and Sullivan, 1996a; Sluka et al., 1999).

The cleaning of ectoparasites by conspecifics has been attributed either to a mutually beneficial relationship in which both host and cleaner receive benefits (Poulin and Vickery, 1995) or a parasitic relationship in which hosts are stimulated into behavioral changes which allow cleaners to feed easily (Losey, 1993). There is little evidence that the lack of ectoparasite cleaning affects fish health (Youngbluth, 1968; Losey, 1972; Gorlick et al., 1987; Grutter, 1996a; Poulin and Grutter, 1996). However, fish spend significant amounts of time cleaning (Poulin and Grutter, 1996; Sluka and Sullivan, 1996a) and cleaners can remove great amounts of parasites (Grutter, 1996b). Grouper may spend significant amounts of time being cleaned (Sluka and Sullivan, 1996a; Samoilys, 1997) and space utilization is directly influenced by the presence or absence of a cleaning station (Sluka et al., 1999). It appears that the proximate cause of cleaning behavior, from the fishes' point of view, is tactile stimulation (Losey, 1993). From the cleaner's perspective, feeding appears to be the motivation for cleaning behavior (Poulin and Grutter, 1996).

In this study, cleaning behavior differed among species from the small grouper species *Epinephelus merra*, which was never observed cleaning, to the large grouper species *Plectropomus laevis* observed cleaning approximately 20% of observation time. There was, though, no general relationship between size and the amount of time spent cleaning as might be expected due to higher parasite loads on larger individuals. Sluka et

al. (1999) hypothesized that cleaning stations may also be used in dominance hierarchies to show the dominant individual. They came to this conclusion after observing the largest grouper in the experiment displace smaller grouper and other species (including a much larger barracuda) from the cleaning station and then move on and not be cleaned. This behavior was also observed one time in this study where a larger *Cephalopholis argus* individual displaced a smaller individual of this species from a cleaning station. The coral grouper *C. miniata* was observed cleaning about 13% of the observation time. However, Figure 9 shows that when the actual time spent cleaning is not considered, more individuals were observed to clean during an observation time than not clean. This species tends to move a lot, having one of the highest indices of active behavior. Thus it appears that this species cleans often, but not for long durations.

Active behavior, defined as a behavior involving swimming, was significantly less in *Epinephelus merra* than in other species. Two species, *Cephalopholis miniata* and *Plectropomus pessuliferus*, showed increasing active behavior with increasing size. Thus, larger individuals spend more time swimming, presumably foraging and potentially engaging in reproductive behavior. Shpigel and Fishelson (1989) showed that the home-range size of males and the larger individuals is greater than females.

#### Tagging study

The general conclusion of the tagging study is that smaller grouper species generally do not move significant distances during a six-month time scale. In fact, one individual was observed underneath the same coral head several months in a row. Another individual was almost always observed in the same permanent transect. As will be described more fully in the next section, several non-tagged *C. miniata* were also observed hiding in the same group of coral heads over a nine-month period.

The movement patterns of grouper have been relatively little studied (Zeller 1997). Bardach (1958) showed that grouper stayed at the point of tagging for about one month and then shifted habitat. However, Zeller (1997) showed that grouper did not move significantly over a one-year period. Davies (1995) showed that 74% of recaptured *Plectropomus leopardus* (n=143) were caught in the same 2-2.5 km section of a reef in which they were originally released. Most of the movements of this species were only 200-400 m in distance. However, Zeller (1997) using ultrasonic tagging, showed that daily movements of *P. leopardus* may be up to 835 m (mean of 192 m). The home-range size was up to 18,800 m<sup>2</sup>. There was a significant difference in the home-range size between fringing reefs (10,500 m<sup>2</sup>) and patch reefs (18,800 m<sup>2</sup>). Generally, it appears that most individuals move a very short distance over several months or years, but a few individuals move many kilometers (PDT, 1990; Davies, 1995; Collins et al., 1996). These long-distance movements may be associated with movement to spawning aggregations (Burnett-Herkes, 1975; Van Sant et al., 1994).

#### Permanent transect sampling

*Cephalopholis argus* was the most abundant grouper in the six permanent transects. This species did not exhibit significant differences in mean density over time. However, there was significant variability in the data. It is possible that the sample size was too low to detect changes. However, Figure 16 shows that the density range for this species was about one individual per transect. The other species were generally rare and

the density did not change through time as it was generally very low. One transect showed an interesting pattern. In this transect there were large coral heads with several *C. miriata* using them for shelter. This species was only observed in this transect and always underneath these coral heads. The number of fish in the transect ranged from three to five, likely due to the cryptic nature of the habitat rather than new individuals arriving. The fish were noticeably bigger at the end of the study than in the beginning. Data from the permanent transects indicate that the grouper assemblage at this site is variable but relatively stable over the short term.

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