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Feeding Periodicity and Prey Habitat Preference of Red Snapper, *Lutjanus campechanus* (Poey, 1860), on Alabama Artificial Reefs

JESSICA R. MCCAWLEY, JAMES H. COWAN, JR., AND ROBERT L. SHIPP

Conclusive understanding of the role temperate artificial reefs play in the trophic dynamics of *Lutjanus campechanus* (Poey, 1860) is limited. Thus, diel feeding habits of red snapper on artificial reefs were examined using gut fullness, diet composition, and prey habitat preferences. Red snapper were collected by hook and line from artificial reefs off Alabama in July and Aug. 2000. Examination of stomach contents found red snapper feeding upon fish, demersal crustaceans, and pelagic zooplankton. Although other studies suggest that lutjanids primarily feed nocturnally, red snapper in this study fed throughout the day and night. Significant differences in gut fullness were found between 2-hr time intervals; however, no obvious pattern in feeding periodicity was evident. Although fish was the largest diet component by weight for both day and night during diel sampling, examination of prey habitat preferences indicate that red snapper fed on more water-column organisms during the day and more sand- or mud-associated organisms at night. Based on our interpretation of these results, we hypothesize that red snapper reside above the reefs during the day, opportunistically feeding mostly upon water-column-associated organisms and some benthic prey. At night they may move away from the reef to consume nocturnally active fishes and benthic crustaceans.

Red snapper *Lutjanus campechanus* (Poey, 1860) is a highly exploited reef fish in the Gulf of Mexico (Gulf) that occupies both natural hard-bottom and artificial habitats (Moran, 1988; Render and Wilson, 1996; Fischer et al., 2004). Catch statistics indicate that red snapper landings in the Gulf appear to be concentrated around two centers, one off southwest Louisiana and one off Alabama (Goodyear, 1995; Schirripa and Legault, 1999; Patterson et al., 2001; Patterson and Cowan, 2003). The fishery off Louisiana is dominated by commercial landings, whereas the fishery off Alabama is dominated by recreational landings (Schirripa and Legault, 1999; Patterson et al., 2001). The natural near-shore bottom off Alabama is primarily sand and mud, thus red snapper are taken primarily over artificial reefs (Szedlmayer and Shipp, 1994; Minton and Heath, 1998; Patterson and Cowan, 2003). In fact, the Alabama shelf has one of the largest artificial reef programs in the nation with over 4,000 km² of reef permit area (Shipp, 1999), where over 15,000 artificial reefs have been deployed (Szedlmayer and Shipp, 1994; Patterson et al., 2001; McCawley et al., 2003). Similarly, the commercial fishery off Louisiana is dependent upon artificial reefs in the form of oil and gas platforms. Red snapper are one of the most abundant finfish species on artificial reefs off Alabama and one of the most abundant finfish

on platforms off Louisiana (Stanley and Wilson, 1996; Strelcheck et al., 2005). However, the role these reefs play in the daily life, especially the feeding periodicity, of this heavily exploited (SEDAR, 2005) species is limited.

Daily feeding rhythms in fishes are complex processes influenced by environmental, behavioral, and physiological constraints (Cortes, 1997). A dominant overriding force affecting the behavior and activity of fishes is the diel pattern of light and dark (Helfman, 1986; Wootton, 1990). In tropical and temperate latitudes, fishes usually forage diurnally, nocturnally, or in a crepuscular pattern (Helfman, 1986; Wootton, 1990; Bosclair and Marchand, 1993; Buckel and Conover, 1997). Considerable information has been amassed on diel feeding patterns of freshwater fishes; however, such information on marine fishes, especially temperate marine reef fishes is limited (Helfman, 1978; Popova and Sierra, 1985). In a review Helfman (1986) states that most assume that these fish behave similarly to their tropical counterparts found on coral reefs. Although the role that temperate reefs and especially temperate artificial reefs play in the daily activities of top reef predators is becoming better understood (e.g., Lindquist and Clavijo, 1993; Lindquist et al., 1994; Fabi et al., 2006; Lindberg et al., 2006; McCawley and Cowan, in revision) specific knowledge of the role that Al-

abama artificial reefs play in red snapper trophic dynamics (see limited studies by Siegel, 1983 and Bailey, 1995), especially over the diel cycle, is generally lacking (but see also Ouzts and Szedlmayer, 2003). The objective of this study was to examine the diel feeding patterns and diet composition of red snapper on artificial reefs, focusing on differences in diet between day and night. This objective was accomplished by determining gut fullness, using descriptive indices to examine diet composition, and by examining prey habitat preferences.

METHODS

Collection.—Red snapper were collected by hook and line, using cut squid for bait, from artificial reefs in the Hugh Swingle General Permit Area in the northern Gulf off Alabama in July and Aug. 2000. Sampling occurred from midafternoon one day to mid- to late morning the following day, because many daytime samples had already been obtained in July and Aug. in McCawley and Cowan (in revision). Approximately 10 fish were captured every 2 hr for gut content analysis. Multiple low-relief (<3 m high, 2–10 m³ volume) artificial reefs made mostly from materials of opportunity were fished in order to prevent depletion at any single reef. Temperature, salinity, and dissolved oxygen measurements were taken throughout the sampling period with a Sea Bird Electronics Conductivity Temperature Depth probe (CTD) (model SBE-25 Sealogger).

Upon capture, the total length (TL) and fork length (FL) of each fish was measured to the nearest millimeter and sex was determined by examination of reproductive tissue before the stomach was removed. Each stomach was preserved in 10% formalin for at least 48 hr then transferred to 70% isopropyl alcohol in the laboratory. Stomachs were then dissected, prey items removed and identified to the lowest possible taxonomic level, and each taxon weighed to the nearest 0.01 g after being blotted dry. Empty stomachs were either labeled as 'genuinely empty' or 'distended' according to the description of Treasurer (1988).

Enumeration of stomach contents.—The relative contribution of each of several prey categories was determined using four methods: (1) percent composition by weight (%W); (2) percent composition by number (%N); (3) percent frequency of occurrence (%FO); and (4) percent index of relative importance (%IRI). The %FO was calculated as follows: %FO = num-

ber of stomachs containing one particular prey category/number of stomachs with any prey (excluding bait) (Bowen, 1996). The %IRI was calculated as follows (Pinkas et al., 1971, later modified by Hacunda, 1981): $IRI = (\%N + \%W) \times \%FO$, where N = number, W = weight, and FO = frequency of occurrence. The %IRI was calculated by dividing the IRI value for each prey category by the sum of the IRI values and multiplying by 100. These descriptive indices were used to examine the diet from each sampling trip and of each 2-hr interval, in addition to aggregated day vs night comparisons. The %W, %N, and %FO were chosen to describe the diet because they are the most commonly used diet indices (Bowen, 1996). These three indices provide different information and when used separately can often provide different pictures of the diet, with %W often overemphasizing large items and %N overemphasizing small items (Liao et al., 2001). The percentage of empty stomachs and the percentage of stomachs empty because of regurgitation were compared for 2-hr intervals, in addition to aggregated day vs night comparisons.

Day was defined as the hour after sunrise to the hour before sunset and night included the hours between sunset and sunrise. For the day vs night comparisons, stomach contents from both sampling trips were combined and then redistributed into day and night time periods. The nonparametric permutation analysis of similarities procedure ANOSIM (PRIMER; Clarke and Warwick, 1994) was used to test for significant differences in diet between day and night using each fish as a replicate.

The identifiable contents of all stomachs were divided into eight major prey categories: fish, adult *Squilla empusa* (Say, 1818), crabs; *Sicyonia* spp., *Loligo* sp., pelagic zooplankton, miscellaneous benthic/demersal-associated species (hereafter miscellaneous benthic species), and *Ogyrides alphaerosiris* (Kingsley, 1880). Larval fish were not included in the pelagic zooplankton category; rather they were grouped with fish (because it was difficult to determine if they had flexed). In addition, not all demersal species were grouped in the miscellaneous benthic species category. This category contained only those benthic taxa that did not fall within one of the other major categories. For descriptive purposes, adult *S. empusa*, crabs, and *Sicyonia* spp. are sometimes grouped together for discussion purposes and referred to as "demersal species." The diet also consisted of an unidentified-material category, which was defined as that which had no recognizable

bones or hard parts, thus preventing classification into any of the categories listed above. However, unidentified material was not included in all analyses because %N, %FO, and %IRI cannot be determined for this category.

Diet studies can introduce bias depending on how prey items identified with different taxonomic resolution are grouped together (Hansson, 1998). To reduce bias and to provide more detailed diet information, five of the eight major prey categories (fish, crab, *Sicyonia* spp., pelagic zooplankton, and miscellaneous benthic species) were further subdivided and combined with the three other prey types that consisted of a single species or genus, i.e., adult *S. empusa*, *Loligo* sp., and *O. alphaerostriis*, for a total of 33 groups. The fish category comprised nine groups: unidentified fish, Ophichthidae, Triglidae, Haemulidae, Syngnathidae, *Ophidion* spp., *Anchoa hepsetus* (Linnaeus, 1758), *Stenotomus caprinus* (Jordan and Gilbert, 1882), and fish larvae. The crab category consisted of four groups: unidentified crabs, *Portunus gibbesii* (Stimpson, 1859), *Portunus sayi* (Gibbes, 1850), and Calappidae. The *Sicyonia* spp. group comprised three groups: *Sicyonia* spp., *Sicyonia dorsalis* (Kingsley, 1878), and *Sicyonia brevivostriis* (Stimpson, 1871). The pelagic zooplankton category was further subdivided into nine groups consisting of larval *S. empusa*, crab megalopae and zoea, order Amphipoda (hereafter amphipods), order Octopoda (juveniles only), Scyllaridae (larvae only), Palaemonidae, *Pneumodermopsis* spp., *Cavolinia* sp., and *Lucifer faxioni* (Borradaile, 1915). Finally, the miscellaneous benthic species group was further subdivided into five smaller groups: class Gastropoda, Pasiphaeidae, *Solenocera* spp., *Glycera* spp., and *Albunea paretii* (Guerin-Meneville, 1853). This more detailed breakdown of prey was examined for each diel sampling trip as well as by day vs night using the same descriptive indices described above.

Fullness calculation.—The weight of each red snapper collected during the sampling trips was estimated by using the length–weight regression: $\log \text{weight} = 3.014 (\log \text{FL}) - 4.7799$, determined from red snapper collected during a separate year-long sampling study (McCawley and Cowan, in revision). A fullness value was determined for each fish using the equation [Adams and Breck (1990); modified from Duarte and Garcia (1999)]: $\text{fullness} = (\text{total weight of prey} - \text{bait weight}) / \text{estimated weight of red snapper}$. A fullness index was then calculated for each fish by dividing its fullness value by the maximum fullness value from

all samples. There was a separate maximum fullness value for each sampling trip. The average fullness index and standard error were then determined for each 2-hr interval on each trip. Since these data were not normally distributed, a nonparametric Kruskal–Wallis test was used to test for a significant difference among average fullness values (Adams and Breck, 1990) per 2-hr interval for each month. If significant differences were found, Dunn's multiple comparison test (Zar, 1996) was performed to determine which 2-hr intervals were significantly different from each other. A percent empty (%Empty) value was also recorded for each 2-hr interval using the equation: $\% \text{Empty} = [(\text{number of fish per hour} - \text{number of fish with prey}) / \text{number of fish per hour}] \times 100$.

Prey habitat preference.—Habitat preferences were designated from the literature for each of the 33 prey categories. Five major habitat types were identified: sargassum-associated (SA), sand/mud-associated (SM), reef- or structure-associated (R), water-column-associated (WC), and found on a variety of habitats (V). An SA organism was defined as one that lives amongst floating sargassum. SM organisms were defined as those organisms that live on the sand or mud bottom, as well as those that spend most of their time burrowed in the mud [such as a shrimp eel (Ophichthidae) or mantis shrimp (*S. empusa*)]. An R organism was liberally defined as an organism that would not otherwise be found in a particular habitat unless a reef (artificial or natural) or some type of structure was present (e.g., sea horse family Syngnathidae). WC organisms were mostly planktonic organisms or those swimming within the water column, such as *Loligo* sp. An organism that was not characteristic of any one habitat type was classified as V. These habitat types then were paired with each prey's %W contribution to the diet and summed by habitat type in order to determine the cumulative contribution made to the diet by prey from each habitat for day and night.

RESULTS

Site description.—All sampled reefs occurred at similar depths and were experiencing similar water mass characteristics when sampled. CTD data revealed similar bottom conditions around the reefs on both trips: salinity 33–36 psu, temperature 23–28 C, and 4–7 mg/liter dissolved oxygen. Reefs sampled on both trips were in 20–25 m of water. Extensive side-scan

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TABLE 1. Prey contained in all red snapper stomachs from the July and Aug. diel sampling trips collected on Alabama artificial reefs based upon four descriptive indices for eight prey categories ranked in decreasing order of importance for each index. %W = percent weight, %N = percent number, %FO = percent frequency of occurrence, %IRI = percent index of relative importance, and Misc. benthic spp. = miscellaneous benthic species.

Trip	Prey Type	%W ^a (rank)	%W ^b (rank)	%N (rank)	%FO (rank)	%IRI (rank)
July	Unidentified material	40.23 (1)				
	Fish	31.46 (2)	42.67 (1)	29.33 (2)	48.91 (2)	45.80 (1)
	Adult <i>Squilla empusa</i>	2.59 (6)	3.24 (6)	2.93 (8)	4.35 (7.5)	0.35 (7.5)
	Crab	13.66 (3)	18.86 (3)	13.59 (3)	25.00 (3)	10.55 (3)
	<i>Sicyonia</i> spp.	5.13 (4)	6.41 (4)	4.89 (4)	6.52 (6)	0.96 (4)
	<i>Loligo</i> sp.	1.84 (7)	3.23 (7)	2.96 (7)	4.35 (7.5)	0.35 (7.5)
	Pelagic zooplankton	4.37 (5)	20.02 (2)	38.15 (1)	52.26 (1)	40.30 (2)
	Misc. benthic spp.	0.19 (9)	2.18 (8)	3.65 (6)	11.96 (4)	0.91 (5)
	<i>Ogyrides alphaerostris</i>	0.53 (8)	3.39 (5)	4.50 (5)	7.61 (5)	0.78 (6)
August	Unidentified material	16.84 (3)				
	Fish	34.69 (1)	42.73 (1)	41.02 (1)	52.17 (1)	65.50 (1)
	Adult <i>Squilla empusa</i>	6.73 (6)	7.77 (5)	6.56 (6)	10.87 (5)	2.33 (5)
	Crab	9.70 (4)	11.23 (3)	14.52 (3)	23.91 (3)	9.23 (3)
	<i>Sicyonia</i> spp.	20.07 (2)	23.20 (2)	19.30 (2)	26.09 (2)	16.62 (2)
	<i>Loligo</i> sp.	7.67 (5)	8.87 (4)	7.78 (5)	8.70 (6)	2.17 (6)
	Pelagic zooplankton	4.13 (7)	6.00 (6)	9.54 (4)	17.39 (4)	4.05 (4)
	Misc. benthic spp.	0.17 (8)	0.19 (7)	1.30 (7)	4.35 (7)	0.10 (7)
	<i>Ogyrides alphaerostris</i>	0.00 (9)	0.00 (8)	0.00 (8)	0.00 (8)	0.00 (8)

^a Represents the % W including the unidentified material category

^b Represents the % W excluding the unidentified material category

sonar work in the region (Schroeder et al., 1988; Dufrene et al., 2003; Strelcheck et al., 2005) indicates that these reefs were placed upon sediments indicative of the Mississippi-Alabama-Florida sand sheet, and are relatively uniform in composition with little vertical relief.

Overall description of diet by trip.—On the July sampling trip, fishing occurred between 1300 and 1000 hr. Stomachs were collected from 159 red snapper ranging in length from 267 mm to 590 mm FL, with a mean of 359 mm, a median of 344 mm, and a mode of 300 mm FL. Of these 159 stomachs, 92 contained identifiable prey (57.9%), 29 were empty (18.2%), 15 contained only bait (9.4%), and 23 contained only unidentified material (14.5%). Of the 29 stomachs classified as empty, 25 were considered ‘truly’ empty (86.2%) and four (13.8%) were considered ‘distended’ or empty because of regurgitation.

In Aug., fishing occurred between 1700 and 0800 hr. Stomachs were collected from 109 red snapper ranging in size from 295 mm to 560 mm FL, with a mean of 382 mm, a median of 375 mm, and a mode of 345 mm FL. Of these 109 stomachs, 46 contained identifiable prey (42.2%), 44 were empty (40.4%), 14 contained

only bait (12.8%), and five contained only unidentified material (4.6%). Of the 44 stomachs classified as empty, 34 were considered ‘truly’ empty (77.3%) and 10 (22.7%) were considered ‘distended’ or empty because of regurgitation. The empty and bait-only stomachs from both trips were excluded from further analyses. All red snapper with prey were reproductively staged as adults. Both of these sampling trips occurred during the third-quarter moon.

Eight prey categories.—Using descriptive indices, the largest prey category for July by %W was unidentified material (Table 1). After exclusion of this category, red snapper stomachs from July contained primarily fish and pelagic zooplankton (Table 1). Fish was the largest category by %W (42.7%) and %IRI (45.8%) followed by pelagic zooplankton (20.0% W and 40.3% IRI) and crab (18.9% W and 10.6% IRI). However, by %N and %FO, pelagic zooplankton was the largest category (38.1% N and 53.3% FO). When the demersal species were combined (i.e., adult *S. empusa*, crabs, and *Sicyonia* spp.), they made up the second largest category by %W (28.5%).

Fish was the largest prey category by weight from Aug. (34.7% W) and unidentified material only the third largest category (16.8% W)

after *Sicyonia* spp. (20.1%) (Table 1). After removing unidentified material, fish remained the largest category by all indices (42.7% W) followed by *Sicyonia* spp. and crabs. When demersal species were combined they again made up the second largest category by %W (42.2%).

Thirty-three prey categories.—When the stomach contents were resolved into the highest taxonomic resolution (33 prey categories), unidentified material was the largest contributing category for both July and Aug. After removing unidentified material, the 10 largest prey categories for July were (listed by decreasing %W) unidentified fish, unidentified crabs, *Cavolinia* sp., *Sicyonia* spp., larval fish, amphipods, *P. gibbesii*, *O. alphaerostriis*, adult *S. empusa*, and Ophichthidae. The 10 largest categories for Aug. were (listed by decreasing %W) *A. hepsetus*, unidentified fish, *S. dorsalis*, *Loligo* sp., *S. brevirostris*, adult *S. empusa*, *P. gibbesii*, unidentified crabs, larval fish, and Palaemonidae. However, by all other indices (%N, %FO, %IRI) unidentified fish was the largest contributor to the diet of red snapper in Aug.

Gut fullness and hourly diet.—A Kruskal–Wallis test found a statistically significant difference between mean gut fullness values per 2-hr interval in both July ($p = 0.0002$) and Aug. ($p = 0.0008$). August had higher overall average gut fullness values than July (Fig. 1). In July (Fig. 1A), the hours with the highest gut fullness values were the 1500–1600 hr and 1900–2000 hr intervals. Dunn's test found these hours to be significantly different from the 1700–1800 hr interval. In Aug. (Fig. 1B), the morning hours from 0300 until 0800 hr had the highest gut fullness. For Aug., the 0700–0800 hr interval was significantly different from the 1900–2000 hr and 2100–2200 hr intervals, according to Dunn's test.

Even though significant differences were found between 2-hr time intervals, there was no obvious pattern in the feeding periodicity of red snapper (Fig. 1). The Aug. data suggest a pattern of crepuscular feeding with higher gut fullness values around dusk and pre-dawn hours. Although the July data exhibit a feeding peak at dusk, it did not show intense pre-dawn feeding. Combined data indicate that red snapper fed almost continuously throughout the day and night. The red snapper with the fullest stomach in July was taken during the 1500–1600 hr and the red snapper with the fullest stomach in Aug. was taken at sunrise during the 0500–0600 hr.

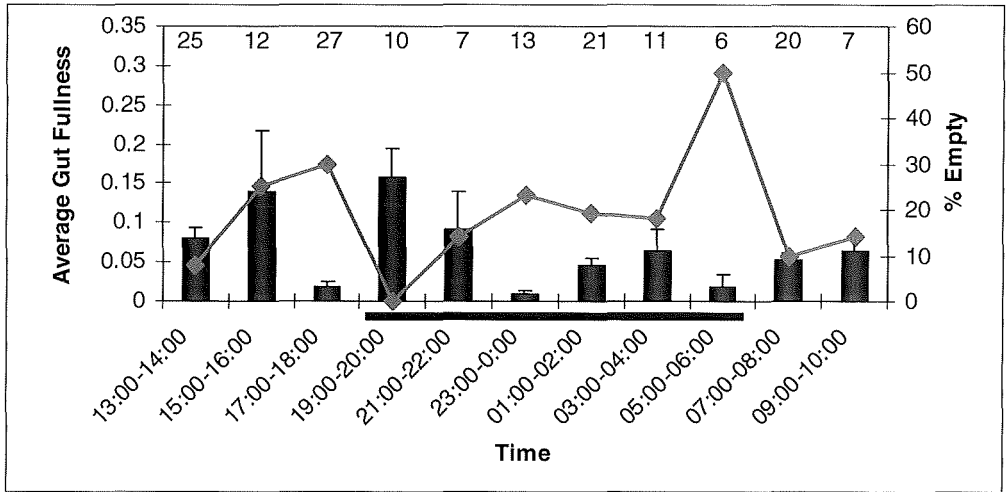
The percentage of empty stomachs varied over the 24-hr cycle but did not always correspond to the lowest gut fullness values (Fig. 1). In July, the percentage of empty stomachs was sometimes large, even when other red snapper caught during the same time period had high average fullness values. This was most evident at 1500–1600 and 2100–2200 hr when gut fullness was high, 25% and 14.3%, respectively, of red snapper had empty stomachs. During Aug., red snapper stomachs were between 40–50% empty per hour, except in the pre-dawn to dawn hours (between 0300 and 0800 hr) when the percentage of empty stomachs decreased as the average gut fullness increased, thus indicating that a smaller percentage of the stomachs collected during that time were empty. Moreover, the stomachs that did contain food were very full, or had large gut fullness values.

The percentage of 'genuinely empty' stomachs was compared to the percentage of stomachs empty due to regurgitation (distended). In July, all hours except 1300–1400 hr and 1700–1800 hr apparently had 0% regurgitation. However, the 1300–1400 hr and 1700–1800 hr hours contained red snapper with 4.0% and 11.1%, respectively, of stomachs empty due to regurgitation (thus possibly resulting in lower fullness values for these hours). In Aug., the hours from 1700 to 0000 hr had 8.3% to 18.2% of stomachs empty due to regurgitation, but 0% regurgitation was observed thereafter. With this in mind, a more pronounced feeding intensity in the afternoon hours (July and Aug.) and early evening (Aug.) may be indicated.

Descriptive indices for 2-hr intervals revealed that fish prey was present in red snapper diets in every 2-hr interval in both July and Aug. However, the proportion of fish prey substantially increased at sunset (97.6% W July and 92.9% W Aug.) in both months (Fig. 2). In July, fish prey also increased in the diet again after sunrise (59.6–60.1% W in the hours after sunrise). In Aug., fish prey also made a large contribution by weight in the 1900–2000 hr (92.9% W) as well as the 2100–2200 hr and 2300–0000 hr (75.0% W and 59.1% W, respectively).

Specifically, on the July sampling trip demersal crustaceans (*Sicyonia* spp., crabs, and adult *S. empusa*) were present throughout the day and night, and contributed a larger portion to the diet by %W at night (Fig. 2A). There was an inverse relationship between the amount of demersal crustaceans eaten and the amount of pelagic zooplankton eaten. This trend was more apparent when the diet was

A.



B.

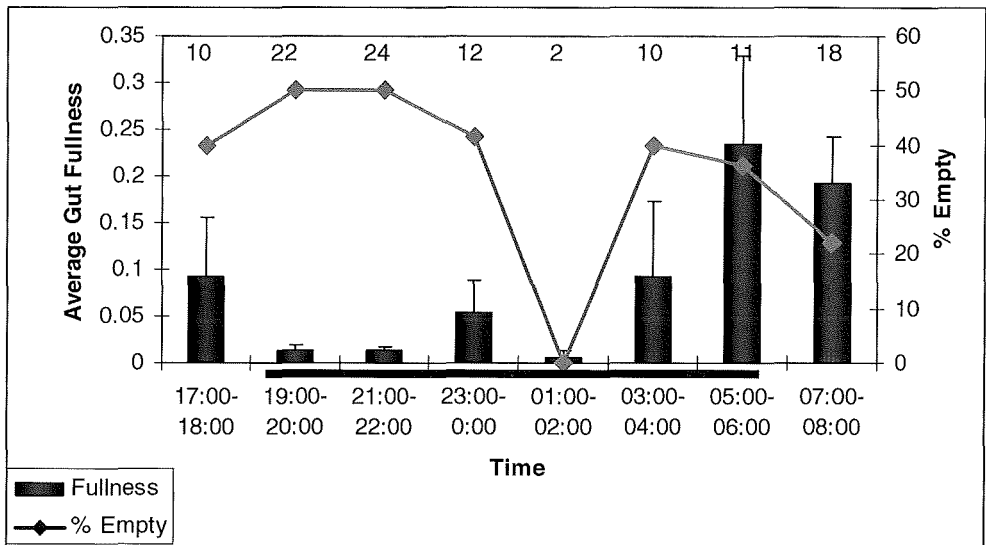


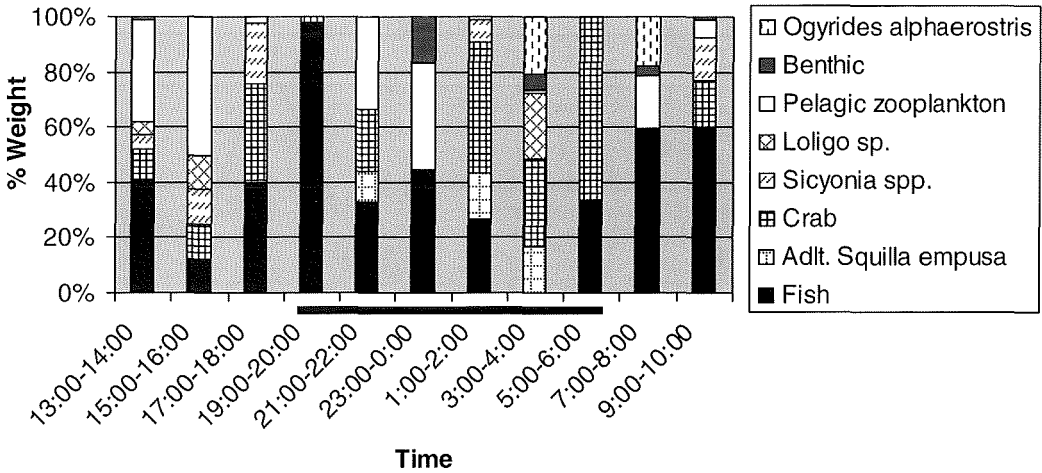
Fig. 1. Red snapper feeding periodicity for (A) July sampling trip and (B) Aug. sampling trip, with % empty line graph also included. Numbers above bars indicate number of fish collected per hour. Dark bar above times indicates night.

examined by %N, as pelagic zooplankton made up a larger percentage of the diet by number than by weight. Pelagic zooplankton were present in every hour except sunrise, but had higher %W values during the daylight hours. *Loligo* sp., miscellaneous benthic species, and *O. alphaerostriis* did not make a large

contribution to the diet, and showed no diel patterns in their presence.

In Aug., the presence of demersal crustaceans only increased in the diet from 1700–1800 hr and after 0300 hr when *Loligo* sp. were absent (Fig. 2B). Pelagic zooplankton also appeared in the diet after 0300 hr and remained

A.



B.

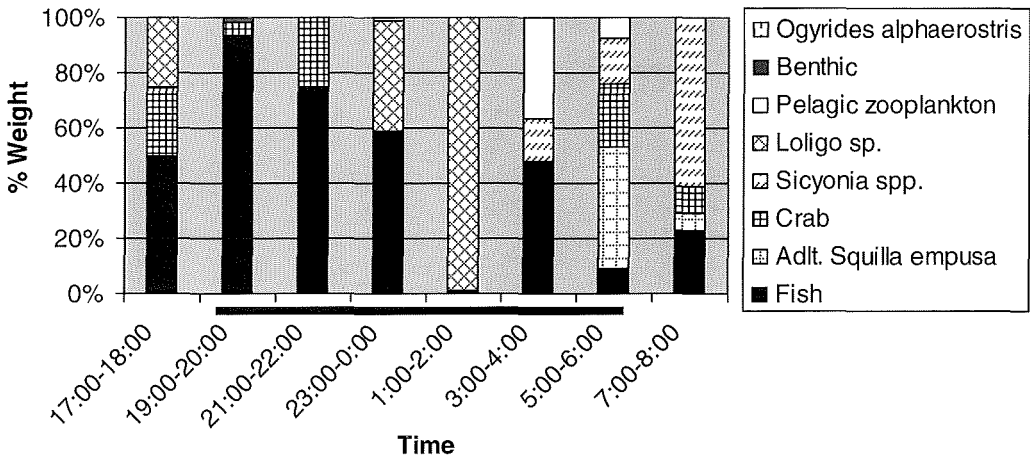


Fig. 2. All red snapper stomachs from the (A) July sampling trip and (B) Aug. sampling trip on Alabama artificial reefs broken down by hour and by % weight for eight prey categories. Dark bar above time indicates night. Benthic = miscellaneous benthic species.

through sunrise, but contributed less by %W and %N than they did during July. *Ogyrides alphaerostris* was not present in the diets of red snapper from Aug., and miscellaneous benthic species contributed only a small percentage (<1.4% W) in any given hour.

Day and night differences.—Even though red snapper fed throughout the 24-hr cycle, their diet differed qualitatively between day and nighttime hours. Gut content data from July

and Aug. were combined and then reclassified into day and nighttime hours. There were 109 stomachs collected during the day from red snapper ranging in length from 280 to 532 mm FL, of which 68 contained identifiable prey (62.4%), 21 were empty (19.3%), 12 contained only bait (11.0%), and 8 contained only unidentified material (7.3%). Of the 21 stomachs classified as empty, 16 were considered 'truly' empty (76.2%) and 5 (23.8%) were considered empty due to regurgitation. There were 159

TABLE 2. Prey contained in all red snapper stomachs collected the diel sampling trips from Alabama artificial reefs divided into day and night based upon four descriptive indices for eight prey categories ranked in decreasing order of importance for each index. %W = percent weight, %N = percent number, %FO = percent frequency of occurrence, %IRI = percent index of relative importance, and Misc. benthic spp. = miscellaneous benthic species.

Trip	Prey Type	%W ^a (rank)	%W ^b (rank)	%N (rank)	%FO (rank)	%IRI (rank)
Day	Unidentified material	35.11 (1)				
	Fish	34.69 (2)	43.46 (1)	32.82 (2)	51.47 (1)	52.73 (1)
	Adult <i>Squilla empusa</i>	0.00 (9)	0.00 (8)	0.00 (8)	0.00 (8)	0.00 (8)
	Crab	12.72 (3)	14.23 (3)	11.92 (3)	20.59 (3)	7.24 (3)
	<i>Sicyonia</i> spp.	10.35 (4)	11.57 (4)	8.82 (4)	11.76 (4)	3.23 (4)
	<i>Loligo</i> sp.	3.04 (6)	4.45 (5)	5.15 (5)	5.88 (6.5)	0.76 (5)
	Pelagic zooplankton	3.27 (5)	21.89 (2)	35.32 (1)	45.59 (2)	35.07 (2)
	Misc. benthic spp.	0.22 (6)	1.12 (7)	2.62 (7)	8.82 (5)	0.44 (7)
	<i>Ogyrides alphaerostris</i>	0.59 (7)	3.37 (6)	3.35 (6)	5.88 (6.5)	0.53 (6)
Night	Unidentified material	31.13 (1)				
	Fish	30.60 (2)	42.03 (1)	33.51 (1)	48.57 (1)	56.58 (1)
	Adult <i>Squilla empusa</i>	7.12 (5)	9.39 (4)	8.19 (5)	12.86 (5)	3.49 (5)
	Crab	12.18 (3)	18.45 (2)	15.85 (3)	28.57 (3)	15.11 (3)
	<i>Sicyonia</i> spp.	9.31 (4)	12.27 (3)	10.41 (4)	14.29 (4)	5.00 (4)
	<i>Loligo</i> sp.	4.18 (7)	5.71 (6)	3.95 (6)	5.71 (7)	0.85 (6)
	Pelagic zooplankton	5.15 (6)	9.03 (5)	22.27 (2)	37.14 (2)	17.93 (2)
	Misc. benthic spp.	0.16 (9)	1.92 (7)	3.13 (7)	10.00 (6)	0.78 (7)
	<i>Ogyrides alphaerostris</i>	0.17 (8)	1.20 (8)	2.69 (8)	4.29 (8)	0.26 (8)

^a Represents the % W including the unidentified material category

^b Represents the % W excluding the unidentified material category

stomachs collected during the night from red snapper ranging in size from 267 to 590 mm FL in size, of which 70 contained identifiable prey (44.0%), 52 were empty (32.7%), 16 contained only bait (10.1%), and 21 contained only unidentified material (13.2%). Of the 52

stomachs classified as empty, 43 were considered 'truly' empty (82.7%) and 9 (17.3%) were considered empty due to regurgitation. Night-time had a higher percentage of empty stomachs than daytime, but both had approximately the same percentage of regurgitation (4.6–5.6%).

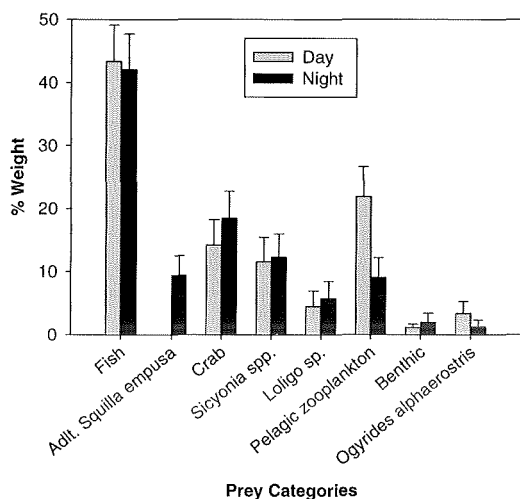


Fig. 3. Prey contained in all red snapper stomachs from the diel sampling trips on Alabama artificial reefs broken down by day and night by % weight for eight prey categories. Benthic = miscellaneous benthic species.

Eight prey categories.—When daytime and nighttime stomachs were examined by 8 prey categories, unidentified material was the largest contributor to the diet during both day and night (contributing 35.1% W by day and 31.1% W by night), with fish being the second largest contributor (contributing 34.7% W by day and 30.6% W by night) (Table 2). When unidentified material was removed, fish was the largest contributor to the diet by day by %W (43.4% W) (Table 2 and Fig. 3); however, by %N pelagic zooplankton was the largest contributor (35.3% N). By day, the top contributors to the diet (listed by descending %W) were fish, pelagic zooplankton, crabs, and *Sicyonia* spp.

Fish was also the largest contributor to red snapper diet at night (42.0% W) (Table 2), with the remaining items (listed by descending %W) consisting primarily of crab, *Sicyonia* spp., and adult *S. empusa*. Nighttime red snapper diets had more demersal crustaceans (i.e., crabs, adult *S. empusa*, and *Sicyonia* spp.) present than

daytime diets, and daytime red snapper diets had more pelagic zooplankton. Even though there were qualitative differences in diet composition between day and night, ANOSIM found no significant differences in diet composition by %W between day and night ($p = 0.251$).

Thirty-three prey categories.—When the diet was examined with a finer taxonomic resolution (33 prey categories), unidentified material remained the largest contributor by %W to red snapper diets during both day and night. After removing unidentified material, unidentified fish was the largest contributor to both daytime and nighttime diets by %W. However, by %N, *Cavolina* sp. was the largest contributor to the daytime diet. During the day red snapper diets contained a greater variety of fish than diets at night, which contained a more diverse diet of demersal crustaceans, specifically a greater variety of crabs, *Sicyonia* spp., and more miscellaneous benthic species. Daytime red snapper diets did not contain adult *S. empusa*, *S. brevis*, or calappid crabs. By day, the diet consisted primarily of (listed by descending %W) unidentified fish, unidentified crabs, *Cavolina* sp., larval fish, *S. brevis*, *Sicyonia* spp., amphipods, *Loligo* sp., *O. alphaerstris*, and ophichthid fishes. By night, the diet consisted primarily of unidentified fish, *A. hepsetus*, adult *S. empusa*, *S. dorsalis*, unidentified crabs, *P. gibbesii*, *Loligo* sp., Palaemonidae, Ophichthidae, and crab megalopa and zoea. By %N, %FO, and %IRI smaller organisms, such as amphipods and larval *S. empusa*, played a larger role in red snapper diets by both day and night. As with 8 prey categories, nighttime red snapper diets contained more demersal crustaceans than daytime diets and daytime red snapper diets contained more pelagic zooplankton.

Prey habitat preference.—The %W contribution of the 33 prey items was paired with each prey's habitat affiliation, then summed by habitat type over day and night (Table 3). By day, prey associated with the water-column made the largest contribution (36.8% W), followed by sand/mud-associated prey (20.2% W). At night, prey associated with sand/mud habitats made the largest contribution (35.3% W) followed by water-column-associated prey (27.2% W). The other three habitat types (reef-associated, sargassum-associated, and prey associated with a variety of habitats) made less than 3.5% W contribution to the diet by either day or night.

DISCUSSION

Results presented here should be considered in the context of the limited number of sampling trips; however, our results indicate that red snapper on artificial reefs off Alabama likely foraged on water-column organisms during the day and foraged on more sand-associated organisms at night. While these qualitative diet differences were apparent, they were not statistically significant because many of the same organisms were present in both day and nighttime diets. Similarly, studies of gut contents of other lutjanids that fed at night found them to feed primarily on sand- or mud-associated organisms, rather than reef associated prey (Starck and Davis, 1966; Grimes, 1979; Gallaway, 1980; Parrish, 1987; Sedberry and Cuellar, 1993; Mueller et al., 1994). Ouzts and Szedlmayer (2003) suggested that red snapper on artificial reefs off Alabama feed on reef and "mixed" prey during the day and reef and sand prey at night. Reef associated prey was not a major contributor to diets of red snapper in our study. Ouzts and Szedlmayer (2003) do not report prey habitat affinities for species in their prey categories, but we note that organisms they classified as "reef" we may have classified otherwise based on our interpretation of the literature. This is an important distinction, however, because, several conceptual models that relate the degree of reef-dependency to the continuum between attraction vs production (Bohnsack, 1989) or the need to consider nearest-neighbor dynamics in the spacing of reefs (Lindberg et al., 1990; Stelcheck et al., 2005; Lindberg et al., 2006), are dependent, in part, upon the degree to which the species in question derive their nutrition directly from reef-dependent prey.

Based upon data from diet composition, feeding periodicity, and prey habitat preferences, we hypothesize that red snapper on Alabama artificial reefs reside above the reef during the day opportunistically feeding mostly upon water-column-associated organisms, and some benthic prey. At night, however, they may move away from the reef in order to exploit nocturnally emerging benthic crustaceans. In a recent study off Louisiana, Westmeyer-Peabody et al. (in revision) used acoustically tagged fish to show that red snapper moved away from oil and gas platforms at night, but could not directly identify the purpose of these movements.

Our study is a first step towards understanding the role that artificial reefs play in the trophic dynamics of red snapper, especially as

TABLE 3. Percent weight (%W) of stomach contents by day and night from diel sampling trips and habitat association of prey consumed by red snapper on Alabama artificial reefs. SM = sand- and/or mud-associated; R = reef-associated; WC = water-column-associated; SA = sargassum-associated; V = a variety of habitats; and Habitat assoc. = habitat association.

Prey type	%W day	%W night	Habitat assoc.	Source
Fish				
Unidentified fish	25.47	25.58		
Family Ophichthidae	2.65	2.90	SM	Hoese and Moore, 1998
Family Triglidae	1.47	0	SM	Hoese and Moore, 1998
Family Haemulidae	1.47	0	R	Hoese and Moore, 1998
Family Syngnathidae	0.42	0	R	Starck, 1968
<i>Ophidion</i> spp.	1.47	0	SM	Hoese and Moore, 1998
<i>Anchoa hepsetus</i>	2.14	11.81	WC	Hoese and Moore, 1998
<i>Stenotomus caprinus</i>	0	1.13	R	Randall, 1968
Fish larvae	8.28	0.61	WC	Matsuura and Olivar, 1999
Crabs				
Unidentified crabs	10.78	8.19		
<i>Portunus gibbesii</i>	1.91	7.57	SM	Britton and Morton, 1989
<i>Portunus sayi</i>	1.55	1.44	SA	Williams, 1984
Family Calappidae	0	1.25	SM	Williams, 1984
<i>Sicyonia</i> spp.				
<i>Sicyonia</i> spp.	5.73	1.45	SM	Britton and Morton, 1989
<i>Sicyonia dorsalis</i>	0	9.38	SM	Britton and Morton, 1989
<i>Sicyonia brevirostris</i>	5.84	1.45	SM	Britton and Morton, 1989
Adult <i>Squilla empusa</i>	0	9.39	SM	Britton and Morton, 1989
<i>Loligo</i> sp.	4.45	5.71	WC	Britton and Morton, 1989
<i>Ogyrides alphaeostris</i>	3.37	1.20	V	Williams, 1984
Pelagic zooplankton				
Larval <i>Squilla empusa</i>	2.07	1.75	WC	Morgan and Provenzano, 1979
Crab megalopa and zoea	0.55	1.88	WC	Pohle et al., 1999
Order Amphipoda	4.92	0.03	WC	Stuck, 1978
Order Octopoda (juvenile)	0.15	0	WC	Pechenik, 1996
Family Scyllaridae (larvae)	0	0.02	WC	Pohle et al., 1999
Family Palaemonidae	1.15	3.69	WC	Pechenik, 1996
<i>Pneumodermopsis</i> spp.	2.04	1.56	WC	Van der Spoel and Dadon, 1999
<i>Cavolinia</i> sp.	10.26	0.01	WC	Van der Spoel and Dadon, 1999
<i>Lucifer faxioni</i>	0.75	0.11	WC	Williams, 1984
Misc. Benthic species				
Class Gastropoda	0.01	0.13	SM	Pechenik, 1996
Family Pasiphaeidae	0.55	0.34	SM	Williams, 1984
<i>Solenocera</i> spp.	0	1.45	SM	Williams, 1984
<i>Gylcera</i> spp.	0.48	0.01	SM	Fauchald, 1977
<i>Albunea paretii</i>	0.09	0	SM	Williams, 1984

Summary of habitat association of prey
by day and night

Habitat type	% W contribution	
	Day	Night
SM	20.20	35.32
R	1.89	1.13
WC	36.76	27.18
SA	1.55	1.44
V	3.37	1.20

they relate to the energetic consequences associated with the need to obtain prey that is not directly associated with reef habitats. Advances in technology such as hydroacoustics and ultrasonic telemetry are being combined with diet studies (Cowan, pers. comm.) to gain further knowledge about the behavior of predator and prey during foraging. Future studies should compare diet and behavior differences for adult red snapper on artificial vs natural reefs, and do this on a seasonal basis.

Red snapper from our sampling trips opportunistically consumed fish, demersal crustaceans, and pelagic zooplankton. More specifically they consumed unidentified fish, larval fish, and Ophichthid fishes; demersal crustaceans including, *Sicyonia* spp., *S. brevirostris*, *S. empusa*, *S. dorsalis*, and portunid crabs; and pelagic zooplankton including, *Cavolinia* sp., amphipods, and organisms from the family Palaeomonidae. These prey items are not uncommon items in red snapper diets. Parrish (1987), in a literature review of the trophic biology of lutjanids, reported that the principal food groups in most studies were fish and decapod crustaceans, which is consistent with this study. He also found that crabs, specifically portunid and calappid crabs, and shrimps and other crustaceans (especially stomatopods) were frequently consumed. Parrish (1987) and Stearns (1884, cited in Camber (1955)) have reported that snappers often ate zooplankton, specifically pteropods (i.e., *Cavolinia* sp.), which were consumed in high numbers during the day in this study. Also similar to our study, Siegel (1983) reported that red snapper on artificial reefs off Orange Beach, Alabama consumed primarily fish and crabs, specifically portunids and albanids, both of which were found in the red snapper stomachs we examined. Two other studies of red snapper diet off Alabama also found red snapper to be consuming *Sicyonia* spp. in high numbers, especially in the summer months (Siegel, 1983; Bailey, 1995), which we found.

Even though a complete sampling during daylight hours did not occur, results from a seasonal study in the Hugh Swingle Permit Area (McCawley and Cowan in revision) that sampled primarily during daylight hours found very similar prey items to those described herein. Briefly, McCawley and Cowan (in revision) found red snapper during summer ($n = 95$) to be consuming primarily fish (24.5% W), demersal crustaceans (47.4% W) and pelagic zooplankton (20.1% W) in similar proportions to this study. Thus, our diel samples are representative of red snapper diets obtained during

daylight hours during summer months in the same general location (McCawley and Cowan, in revision).

Red snapper collected on Alabama artificial reefs during July and Aug. had significant differences in gut fullness values; however, feeding occurred continuously. The variability in gut fullness may be attributable to the opportunistic feeding pattern exhibited by red snapper. Likewise, the reef-to-reef prey availability may also have contributed to the lack of a distinct pattern in fullness. Small numbers of fish collected in certain hours likely may have limited our ability to detect differences between some hours. In one other study, Ouzts and Szedlmayer (2003) examined feeding periodicity of red snapper off Alabama and also found red snapper to be feeding continuously throughout the 24-hr cycle. However, that study found the highest gut fullness values during the day with moderate fullness values at night and dawn, and the smallest fullness values at dusk. In contrast, we found increased gut fullness at dusk in July and Aug., and higher gut fullness at dawn on the Aug. trip. It is possible that the differences between our results and those of Ouzts and Szedlmayer (2003) are attributable to the latter study's collection of nighttime samples around lighted oil and gas platforms, with differences attributable both to disparity in vertical relief between platforms and the lower relief structures typical of artificial reefs used in the Alabama program, and to the artificial lighting around the platform.

Previous diet studies of red snapper have speculated that they are nocturnal foragers (Beaumariage and Bullock, 1976; Grimes, 1979). Gallaway (1980) examined gut fullness of red snapper collected from an oil platform in the northern Gulf off Texas and found the highest gut fullness values in the morning, intermediate values in the afternoon, and lowest values in the early evening. However, no red snapper were captured at night in that study. He suggested that red snapper fed throughout the night and morning, and at least some during the day.

Studies of other lutjanid feeding habits also have reported nocturnal feeding (Longley and Hildebrand, 1941; Randall and Brock, 1960; Hobson, 1965; Starck and Davis, 1966; Randall, 1967; Hobson, 1968; Starck and Schroeder, 1971; Parrish, 1987; Sedberry and Cuellar, 1993; Muellar et al., 1994), and/or limited diurnal feeding (Randall and Brock, 1960; Hobson, 1965; Starck and Davis, 1966; Hobson, 1968; Parrish, 1987). Helfman (1986) suggested that for fishes in temperate environments,

the patterns of diel foraging behavior are not as distinct as they are for fishes on tropical coral reefs. This blurring of specific feeding times because of differing lengths of twilight (Helfman, 1986) could have caused the discrepancy between our results and the results of other lutjanid studies, most of which were conducted in tropical waters. Thus, temperate red snapper, such as the ones examined here, may have a less-defined feeding period than their tropical counterparts.

The increase in fish prey found in the stomachs of red snapper at dusk could be because of the increased activity of these prey fishes at this time (Helfman, 1986). At dusk, diurnal prey fishes are seeking cover and nocturnal prey fishes are emerging, thus predators are maximally active and successful, often because of a visual advantage (Helfman, 1986). Mueller et al. (1994) specifically states that twilight is often a time of major activity for lutjanids. Hobson (1968, 1974) suggests that large reef predators, such as snappers, lurk above the bottom, striking small prey fishes that remain in the water column during twilight. We also believe that demersal crustaceans were more prevalent in the diet at night in our study because most of these organisms (e.g., *Sicyonia* spp., *S. empusa*, and crabs) are more active at night, often emerging to feed or reproduce (Hobson, 1965; Sedberry and Cuellar, 1993; Williams, 1984; Cronin et al., 1994).

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