Activity Patterns, Diet, and Shelter Site Use for Two Species of Moray Eels, *Gymnothorax moringa* and *Gymnothorax vicinus*, in Belize

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Activity patterns, diet, and shelter site use were compared between two species of moray eels, the spotted moray, *Gymnothorax moringa*, and the purplemouth moray, *Gymnothorax vicinus*, in the shallow backreef habitat of the Belize Barrier Reef. We tracked eels tagged with acoustic transmitter tags, analyzed stomach contents, and surveyed shelter sites in a 150-m by 250-m survey area of patch reefs and coral rubble. The study site supported primarily subadult to early adult eels (379–947 mm TL). We made 490 *G. moringa* and 344 *G. vicinus* sightings in 74 census days. Shelter site use was similar for both species. *Gymnothorax moringa* left shelters nearly twice as often as *G. vicinus* (62.5% of nights vs 36.4%). Both species moved primarily at night and ranged less than 10 m to approximately 100 m from shelter for periods less than 1 h to more than 9 h. Forays were mainly in the open grassbed away from patch reefs, rubble, or other shelter. *Gymnothorax moringa* fed nearly twice as often as *G. vicinus* (39.4% empty stomachs versus 70.0%), consistent with the difference in activity patterns of tagged fish. Prey included fishes (primarily wrasses), small crabs, and octopus; however, *G. moringa* specialized on small crabs, and *G. vicinus* specialized on fish. *Gymnothorax vicinus* moved and fed primarily on nights with inclement weather, whereas *G. moringa* did so on both calm and inclement nights. Fish consumption increased on inclement nights for both species, and crab consumption increased on calm nights. Piscivory by *G. vicinus* appears to have been enhanced by their feeding on inclement nights.

MORAY eels are an important component of coral reef fish communities. Of 16 families of piscivorous fishes on a Hawaiian reef, the Muraenidae had the largest impact on the community based on their relative abundance and the proportion of fish in their diets (Parrish et al., 1986). The removal of moray eels from a different Hawaiian reef resulted in an increase in size and abundance for two resident planktivorous fish species (J. Stimson, S. Blum, and R. Brock, unpubl.). In the Caribbean, moray eels were the only piscivore capable of routinely occupying and invading the refuges of smaller-sized prey fish (Hixon and Beets, 1993), and moray eels were part of a suite of piscivorous fishes that significantly reduced the survivorship of early postsettlement reef fishes (Carr and Hixon, 1995). Competition for food and subsequent resource partitioning may be more common among upper-level predators, such as moray eels, because they are less restricted by predation from higher trophic levels, and they limit their own food supply (Hairston et al., 1960; Schoener, 1974; Gerstell and Bednarz, 1999).

This study examined possible resource partitioning between two of the most common species of Caribbean moray eels, the spotted moray, *Gymnothorax moringa*, and the purple mouth moray, *Gymnothorax vicinus*. The study was conduct-ed in a shallow back-reef habitat of the Belize Barrier Reef containing primarily subadult and early adult eels. Residence patterns and potential shelter use were examined through daily censuses, spatial and temporal activity patterns were examined by tracking eels tagged with acoustic transmitter tags, and dietary patterns were examined by stomach content analysis.

MATERIALS AND METHODS

Study site.—Field research was conducted in the waters surrounding Tobacco Caye, a 2-ha island located at approximately 16°53′N and 88°04′W, 19 km from the mainland and directly on the Belize Barrier Reef. Eel censuses were conducted in an approximately 150 m by 250 m backreef area that was a mixture of shallow (< 2 m) turtle grass beds (*Thalassia testudinum*) and sand/coral rubble habitat, with numerous small patch reefs (most less than 1 m in diameter) and coral rubble interspersed throughout. Tracking and collection of eels was conducted in the census area as well as in similar shallow (< 3 m) backreef habitats extending up to 1 km north of the island.

Shelter census.—For six weeks, between 12 February and 26 March 1990, the census area was searched twice each day (between 0900 and

1100 h, and between 1400 h and 1600 h) for the presence of moray eels. During the first five days of the census and every two to three days thereafter, new eels were located by swimming strip surveys across the entire census area. Five snorkelers spaced approximately 5 m apart swam parallel transects across the width of the census area until the entire area was covered. Because this habitat was comprised of small, interspersed reef and rubble structures, rather than a large continuous reef, essentially all structures suitable for adult moray eels could be individually inspected during each survey. Each shelter occupied by an eel was permanently marked with a numbered float and thereafter was checked twice each day for the duration of the six-week period. The presence or absence and the species of eel were recorded daily for each shelter.

Each shelter was classified by size (length, width, height), water depth, and surrounding habitat (G = grass bed, S = sand/rubble, or B = within 1m of the border between G and S). Volume of each shelter was roughly estimated by multiplying the length, width, and height. Each site was assigned a qualitative index of the ease with which we could visually locate an eel within the site ("D" = difficult, "I" = intermediate, and "O" = obvious). Eels could be present but completely hidden from view in D sites and were easily seen in O sites. At least some portion of an eel could generally be seen in I sites, but the possibility that some eels could hide completely could not be eliminated.

During the census, eels were observed but never handled or captured. If the same species of eel was observed in the same site on consecutive days, it was considered the same eel unless distinguishing characteristics proved otherwise. Residence was defined as uninterrupted occupancy of a single site by a single eel, expressed as the total number of consecutive days at a site. For sites classified as D or I, if an eel was absent at a site on one day but present at that site on the day before and the day after, the eel was considered present, but not seen. This protocol is consistent with that of Abrams et al. (1983).

Thirty-six additional strip surveys and censuses of the same area were conducted in June 1990, February, March, and July 1991, and February and March 1992. The number of censuses for each month was 11, 5, 6, 2, 6, and 6, respectively. In general, these were not on consecutive days and could not be used to assess the length of continuous residence at a site; however, they were valuable for the identification of new sites and the long-term monitoring of eel abundance in the census area. Because these surveys were not used to determine residence duration, new sites were not assigned D, I, or O classifications.

Diet analysis.—Moray eels were collected for stomach content analysis in February, March, and June 1990, February, March, July, and August 1991, and February and March 1992. The majority of eels were captured within the census area after the initial six-week census, but the entire capture area extended approximately 1 km north of Tobacco Caye in similar habitats. Eels were captured individually at their shelters by sedating them with quinaldine, luring them by hand into catch bags with bait, or by overturning small, nonliving shelters and netting the free-swimming eels. Because the eels were observed underwater at all times during capture, regurgitation was apparent, and in the five cases in which it occurred, the prey items were collected with a dip net. The majority of eels were collected between 0600 h and 0800 h, and all stomach contents were examined within 2 h of capture.

Captured eels were anesthetized with 300 ppm tricaine methanesulfonate (MS 222). In most cases, immersion in MS 222 caused the eels to spontaneously regurgitate any food in their stomach, which, if not intact, was removed by sieving through a fine nylon mesh. Particularly spiny or sharp-edged food items, such as larger fish skeletons, would sometimes not be regurgitated but could be felt in the stomach by stroking the eel's belly. In these cases, the eels were sacrificed with an overdose of MS 222 to collect the contents.

Stomach contents were identified to the smallest possible taxonomic unit, measured, and weighed after blotting. In August 1991, after the completion of all tracking, 21 *G. vicinus* and 27 *G. moringa* were sacrificed to verify the reliability of the MS 222 regurgitation method. The proportion of empty stomachs for both methods was compared using a chi-square test of homogeneity.

Individuals that were not sacrificed were branded (while anesthetized) with a hot wire for identification and released the same day at their point of capture. Usually, brands could not be seen during a visual census without recapturing the individuals, because only small portions of the body could be observed within the shelter sites. Based on recaptures, brands remained recognizable for approximately two months.

Weather conditions and the stage of the moon on the nights preceding capture were monitored. Nights were classified as having

calm or inclement weather. Calm nights were characterized by a Beaufort sea state of 2 or less (Smith, 1974) and a lack of rain showers. Inclement nights included those nights with a sea state of 3 or higher or rain showers.

To identify species-specific differences in the proportion of empty stomachs, a chi-square test of homogeneity was performed for four different treatments of the data: all captures, all captures processed before 1000 h; all captures after eliminating repeated measures, and all captures before 1000 h after eliminating repeated measures. Because contents were generally in a more digested state if collected later in the day, eels caught in the afternoon may have had empty stomachs simply because of the rapid digestion of a small meal. Ten in the morning was chosen as an arbitrary cut-off to eliminate this bias. Also, eight previously captured and marked eels of each species were recaptured for diet analysis. If feeding behavior is consistent within but not among individuals, the data would be biased by these recaptured individuals. To eliminate repeated measures, the data were analyzed for only the first capture of each individual. A chi-square test for the same four treatments was also used to compare the proportion of empty stomachs for both species after feeding on calm nights versus inclement nights.

To examine the possibility of dietary resource partitioning between the two species, a Horn Index of Niche Overlap (Horn, 1966) was computed based on the percent by weight of prey items in the stomach contents, and Morisita's Index of Niche Overlap (Morisita, 1959) was computed based on the numerical abundance of prey items in the stomach. In an analysis of seven measures of niche overlap, Smith and Zaret (1982) found Morisita's measure to be the least biased test overall and the Horn Index to be the least biased test for data that cannot be expressed as numbers of individuals. Only data from eels with food in their stomachs (all captures) were used for these calculations. A randomized nonparametric bootstrapping technique was used in which the data were shuffled based on a random number table resulting in two groups of eels as before, but now divided at random rather than by species. For both indices of niche overlap, this shuffle procedure was performed 100 times, and an index was computed for each permutation. The true index value was then compared by rank to the 100 randomly generated values. A true value significantly lower than the generated values indicates a lower degree of overlap than would be randomly predicted and thus the existence of resource par-

titioning. Because of the possible bias introduced by recaptured individuals, these tests were run for both all stomach content collections and for all collections after eliminating repeated measures. In the latter case, for eels captured more than once, the percent by weight data were averaged, and the total number of prey items was pooled, so that each individual was only counted once.

Tracking and activity patterns.—Ten eels were tracked in February and March 1990 and February, March, and July 1991. Eels were tagged with a VEMCO (Halifax, Nova Scotia) V-2 acoustic transmitter tag. This tag is 38 mm by 8 mm, has a battery life of about 12 days, a range of up to 200 m, and transmits at one of three frequencies between 65 and 76 kHz. Two eels tracked in July 1991 were tagged with a larger V-3 VEMCO tag, which measured 58 mm by 16 mm, and has a longer battery life and range. Tracking was from a small boat equipped with a VEMCO V-10 directional hydrophone and VR-60 receiver, or a hand-held underwater VEMCO unit. When eels moved, the boat was paddled or motored into position above the eel (accurate to within 3 m) approximately every 15 min, and weighted floats were dropped into the water to mark the eel's location. The next day, the position of these floats was plotted, as were depth, time of placement, and habitat (grassbed or sand/rubble) for each float.

For eels tagged in 1990, the tag was placed inside a piece of fish or conch and fed to an eel while in its daytime shelter. Once tagged, an eel was given 24 h to acclimate and then tracked for three nights between 1800 h and 0600 h (dusk to dawn). Of nine eels tagged this way, reliable tracks (in which the tags were known to be in place) could only be obtained for two *G. moringa* and one *G. vicinus.* The morning after the final night of tracking, eels were captured, if possible, using bait to lure them into a catch bag. Eels were then anesthetized with MS 222, total length and wet weight were recorded, stomach contents were collected via regurgitation, and eels were branded and returned to their shelter site the same morning.

In 1991, tags were surgically implanted into the peritoneal cavity of the eels. After being anesthetized with MS 222, a 15-mm incision was made approximately 3 cm anterior of the anus, and the tag was pushed into the cavity. The incision was swabbed with a 1% oxytetracycline solution and then closed with two to three dissolving sutures. This technique had been previously tested on three *G. moringa* acclimated for several months to 380-liter aquaria. All individ-
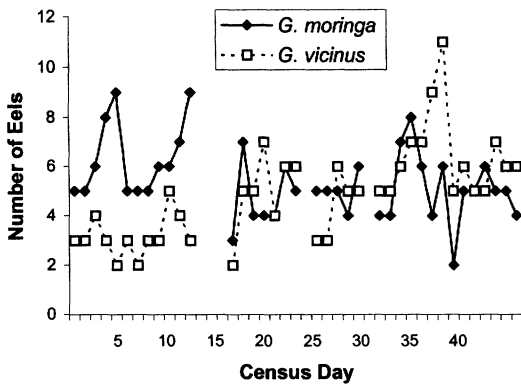
Fig. 1. Daily abundance of *Gymnothorax moringa* and *Gymnothorax vicinus* during the original six-week census, 12 February to 26 March 1990. Three interruptions occurred because of weather.

uals returned to normal activity levels within two to three days, as determined from daily video analysis spanning one week before and after surgery (Young, 1992). Based on these trials, eels in the field were returned to their capture site and given three days to recover from surgery, after which they were monitored once every hour for six consecutive days. When the eels left their shelter, and thus began a foray, they were followed continuously until returning to their shelter or until establishing daytime residence at a new site. Start and finish times were recorded for each foray to within the nearest hour, and weather conditions and moon phases were monitored as in the diet analysis studies. The morning after the sixth tracking night, eels were captured, if possible, using quinaldine and were processed as previously described. For each species, the data from all tracking nights were pooled for analysis of activity patterns.

RESULTS

Census.—Moray eels occupied 37 shelters within the survey area during the 1990 six-week census and an additional 31 sites during the 36 subsequent censuses from 1990 to 1992. The sites consisted of small, mostly dead patch reefs and coral rubble rocks with a mean calculated volume and standard deviation of 0.31 ± 0.31 m^3. Limited live coral cover consisted of mainly *Montastrea annularis*, *Agaricia tenuifolia*, or *Millipora* spp. The ratio of G:S:B sites within the census area was 19: 23:26, and the ratio of D:I:O sites from the original six-week census was 9:14:14.

During the 74 total census days from 1990 to 1992, 842 moray eel sightings were made, including 490 of *G. moringa*, 344 of *G. vicinus*, and eight of the green moray, *Gymnothorax funebris*. These totals include repeated sightings of resident eels, but no eels were counted more than once per day. Other species observed infrequently near Tobacco Caye, but not within the census area, included the goldentail moray, *Muraena miliaris*, and the chain moray, *Echidna catenata*. *Gymnothorax moringa* was observed in 64 of the 68 eel sites (94.1%), whereas *G. vicinus* used only 34 sites (50.0%). Thirty sites (44.1%) were used by both species at some point during the study. Daily abundance varied for both species (Fig. 1) and ranged from two to 13 for *G. moringa* (average 6.6) and two to 11 for *G. vicinus* (average 4.7). Daily totals for both species combined ranged from five to 17.

Changes in eel abundance and size were observed within the census area between years. As seen in Table 1, the average daily abundance was similar for both species in 1990, but *G. vicinus* was significantly less abundant than *G. moringa* in 1991 and 1992 ($P < 0.001$, Mann-Whitney *U*-test). Despite the removal of 21 *G. vicinus* and 27 *G. moringa* from the census area and from surrounding habitats during the final weeks of the 1991 field season, no significant difference in daily abundance was found for either species between 1991 and 1992 ($P = 0.56$ and 0.12, respectively, Mann-Whitney *U*-test). Mean eel length, however, increased significantly for *G. moringa* from 515 mm to 586 mm between 1991 and 1992 ($P = 0.04$, $n = 36$ and 19, respectively, Mann-Whitney *U*-test). The slight decrease for *G. vicinus* from 622 mm to 583 mm was not significant ($P = 0.23$, $n = 30$ and 19, respectively, Mann-Whitney *U*-test).

TABLE 1. MEAN DAILY ABUNDANCE (EELS/DAY) AND STANDARD DEVIATION OF *G. moringa* AND *G. vicinus* WITHIN THE CENSUS AREA FROM 1990 TO 1992. Both species were similarly abundant in 1990, but *G. vicinus* was significantly less abundant than *G. moringa* in 1991 and 1992 (Mann-Whitney *U*-test).

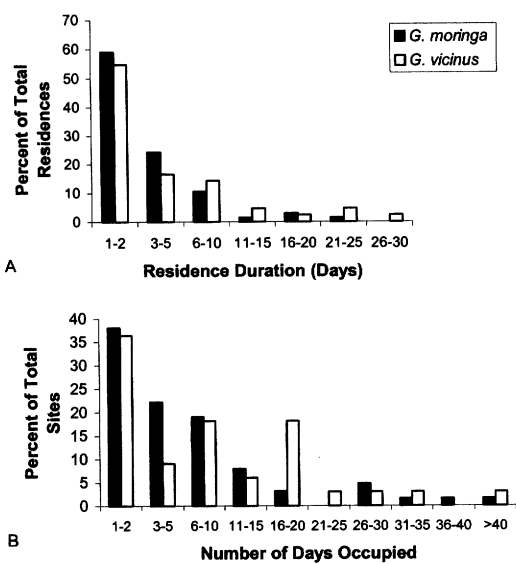| Year	No. of surveys	*G. moringa* Mean ± SD	*G. vicinus* Mean ± SD	*P*-value
1990	49	6.4 ± 2.4	5.5 ± 2.2	0.09
1991	13	6.4 ± 2.7	3.1 ± 1.9	<0.001
1992	12	7.5 ± 1.8	3.2 ± 0.9	<0.001

A

B

Fig. 2. Patterns of shelter site use by *Gymnothorax moringa* and *Gymnothorax vicinus*. (A) The distribution of residence durations during the 1990 six-week census is expressed as the percent of the total number of residences that fall within each residence duration category. The total number of discrete residences was 66 for *G. moringa* and 42 for *G. vicinus*. (B) Occupancy rates for shelter sites are expressed as the percent of the total shelter sites that fall within each category of total days occupied (based on 74 census days). Sixty-four sites were used by *G. moringa*, and 34 were used by *G. vicinus*.

Residence duration of individual eels during the initial six-week census ranged from one to 24 days for *G. moringa* and one to 27 days for *G. vicinus*. A three-day gap in the census caused by poor weather and reduced visibility interfered with the determination of residence duration for two eels. These eels, one of each species, were long-term residents at their sites, and eels of similar size and position in the shelter were present on the days immediately before and after the gap. For the sake of analysis, they were assumed to be the same eels and to have

been in continuous residence at their sites during the 3 days. For both species, greater than 50% of the observed residencies at a single site lasted only one or two days, and greater than 70% were five days or less (83% for *G. moringa* and 71% for *G. vicinus*; Fig. 2A).

The two species did not differ in their association with grassbed (G), sand (S), or border (B) habitats, based on the percent of total sightings and the percent of total shelter sites within each of the three habitat types (Table 2). Although only 38.2% of the sites in the census area were B sites, 53.9% of the *G. moringa* and 46.8% of the *G. vicinus* sightings were in B sites, suggesting a possible ecotonal preference. When considering only the 10 most frequently used sites for each species, the ratio of G:S:B was 3:1:6 for *G. moringa* and 2:2:6 for *G. vicinus*.

Shelter volume did not correlate with the total number of days of site use ($r^2 = 0.03$ for *G. moringa* and 0.12 for *G. vicinus*), nor did it correlate with the size of eels captured at each site ($r^2 = 0.13$ for *G. moringa* and < 0.01 for *G. vicinus*). The subjective grading of sites as difficult (D), intermediate (I), or obvious (O) served as a rough index of site complexity. The mean number of days occupied by *G. moringa* was 13.8 for all D sites ($n = 9$), 11.0 for I sites ($n = 8$) and 9.0 for O sites ($n = 19$), and the mean number of days occupied by *G. vicinus* was 21.1 for D sites ($n = 7$), 8.9 for I sites ($n = 7$) and 12.0 for O sites ($n = 11$). These trends suggest an effect of site complexity, but even the differences between D and O sites are not significant ($P = 0.92$ and 0.11, respectively, Mann-Whitney U-test).

Of the 64 sites used by *G. moringa*, only 25 (39.1%) were used on more than five of the 74 census days. Similarly, only 18 of 34 (52.9%) *G. vicinus* sites were occupied on more than five days (Fig. 2B). Site use was often inconsistent from year to year. The maximum number of (nonconsecutive) days in which a single site was occupied was 55 days (51 of which were *G. vi-*

TABLE 2. A COMPARISON OF THE SHELTERS USED BY *G. moringa* AND *G. vicinus* (G = GRASSBED, S = SAND, AND B = BORDER). Habitat use was considered in two ways: (1) as the percent of all sites used by each species within each habitat type; and (2) as the percent of all sightings of each species within each habitat type. Data are presented for all censuses from 1990–1992.

	% of total shelter sites used		% of total sightings	
Habitat	*G. moringa* ($n = 64$)	*G. vicinus* ($n = 34$)	*G. moringa* ($n = 490$)	*G. vicinus* ($n = 344$)
G	29.7	32.4	25.9	33.7
S	32.8	23.5	20.2	19.5
B	37.5	44.1	53.9	46.8

TABLE 3. AVERAGE PERCENT BY WEIGHT (WET) AND PERCENT BY NUMBER FOR PREY ITEMS IN THE STOMACH CONTENTS OF G. moringa ($n = 43$) AND G. vicinus ($n = 18$). Numbers in parentheses in the percent by number columns represent the numerical frequency of each prey item.

Prey category	G. moringa		G. vicinus	
	Percent by weight	Percent by number	Percent by weight	Percent by number
Halichoeres bivittatus	13.4	12.6 (10)	22.2	17.1 (6)
Unidentified wrasses (Labridae)	3.3	3.8 (3)	14.4	20.0 (7)
Muraenidae: moray eels	2.5	1.3 (1)	3.9	2.9 (1)
Holocentridae: squirrelfish	2.5	1.3 (1)	5.6	2.9 (1)
Unidentified fishes	5.0	7.6 (6)	13.9	8.5 (3)
Total fishes	26.7	26.6 (21)	60.0	51.4 (18)
Pitho anisodon	31.9	39.2 (31)	10.2	28.5 (10)
Mithrax sculptus	4.4	3.8 (3)	2.1	5.7 (2)
Portunus sp.	2.0	1.3 (1)	0	0
Stenorhynchus seticornis	2.5	1.3 (1)	0	0
Unidentified crabs	17.5	19.0 (15)	5.6	2.9 (1)
Total crabs	58.3	64.6 (51)	17.9	37.1 (13)
Panulirus argus (spiny lobster)	0	0	5.6	2.9 (1)
Octopus	7.5	3.8 (3)	11.1	5.7 (2)
Unidentified	7.5	5.0 (4)	5.6	2.9 (1)

cinus), followed by another site with 50 days (all of which included G. moringa, although seven days also included G. vicinus). The former site was classified as G and I with a calculated volume of 0.19 m³, and the latter site was classified as B and D with a volume of 0.54 m³.

Double occupancy of a single site was observed on 25 occasions among seven different sites. Eight of these observations consisted of two G. vicinus (two different pairs), and 17 observations were of a G. vicinus and a G. moringa together in the same hole (five different pairs).

Individual patterns of shelter site use were indicated by repeated observations of marked eels. In 1991, 26 G. moringa and 25 G. vicinus captured for stomach content analysis were marked and released at their shelter sites in and around the census area. Of these, 15 G. moringa and 11 G. vicinus were either recaptured or seen again at least once within the same month. The majority were seen at the same site, but two G. moringa were observed repeatedly at two different sites each, two others were observed at three sites each, and four G. vicinus were observed at two sites each. Alternate sites were all within 20 m of one another, except for one G. moringa, which used sites up to 75 m apart. Two additional G. vicinus, first observed in March 1990, were identified later based on distinguishing characteristics. One eel (TL = 670 mm) was captured exactly three months later in June at a site 400 m away, and the second (unmeasured) was observed in the same site in June

1990 and in four different sites within 50 m of the original site in February and March 1991.

Diet analysis.—Seventy-one G. moringa and 60 G. vicinus were captured for stomach content analysis, representing 56 and 49 known eels of each species, respectively (some eels were captured more than once). Total lengths for all captured eels ranged from 379–808 mm for G. moringa and 403–947 mm for G. vicinus, and the length-weight relationship did not differ for the two species ($P > 0.15$, test for slope of log-log plot regression line; $r^2 = 0.98$ for G. moringa, y = 3.12x−2.99, and for G. vicinus was 0.97, y = 3.16x−3.03). The size of reproductive maturity has not been reported for either eel; however, six gravid but unripe eels (five G. vicinus, TL 551–947 mm, and one G. moringa, TL 632 mm) were captured in this study. With 89% of the G. vicinus and 90% of the G. moringa in this study less than 700 mm in length, and with a maximum size for both species of approximately 1200 mm (Humann, 1989), the study site supports a primarily subadult to early adult population.

Only three of 13 prey categories were not shared by both species, and these three prey items (two crab species and spiny lobster) were rare in the stomach contents, each being found only once (Table 3). Major prey items included fishes (primarily *Halichoeres bivittatus*, Labridae), small crabs (primarily *Pitho anisodon* and *Mithrax sculptus*), and *Octopus* sp. Cannibalism was ex-

hibited by both species (a 666-mm *G. vicinus* consumed a 270-mm conspecific, and a 570-mm *G. moringa* consumed a 320-mm conspecific). The number of prey items in the stomach varied, as did meal size. The number of crabs found in a single stomach ranged from one to five for both species, and the number of wrasses per individual ranged from one to four for *G. moringa* and one to three for *G. vicinus*. Three *G. vicinus* and two *G. moringa* had eaten meals with a mixture of both fish and crabs. As a proportion of body weight, the largest single prey item for *G. vicinus* was a 77.9-g squirrelfish, *Holocentrus ascensionis*, which comprised 14.1% of the weight of a 721-mm eel, and the largest item for *G. moringa* was another *Holocentrus* sp., which, at 31.7 g, comprised 5.9% of the weight of a 669-mm eel but was estimated to have been of a comparable size to the other squirrelfish when originally eaten. For those eels with food in their stomachs, the contents of *G. moringa* averaged 1.4% of the total eel body weight, compared to 2.1% for *G. vicinus* (no significant difference, $P = 0.82$, Mann-Whitney U-test).

The average length for *G. moringa* (540 mm) was significantly smaller than the average length for *G. vicinus* (607 mm; Mann-Whitney U-test, $P = 0.003$). This size difference should not affect dietary comparisons between the two species, because no correlation was found between eel length and the percent by weight of crabs or fishes in the diet ($r^2 = 0.01$ for both crabs and fishes for *G. moringa* and 0.05 for both crabs and fishes for *G. vicinus*, $n = 35$ and 14, respectively).

Prey size was similar for both species. The crabs reached a maximum carapace width of 28 mm and were eaten by the entire size range of both eel species. Eel length was not correlated with crab carapace width, although the sample size was small for *G. vicinus* ($r^2 = 0.02$ for *G. vicinus* and < 0.01 for *G. moringa*, with $n = 5$ and 25, respectively). There was a slight tendency for larger eels to eat larger wrasses ($r^2 = 0.27$ for *G. vicinus* and 0.32 for *G. moringa*, $n = 13$ and 12, respectively, $0.025 < P < 0.05$ for both with test for significance of the correlation coefficient), but some small eels also fed on larger wrasses.

Thirty-one *G. moringa* and 26 *G. vicinus* were sacrificed to verify the efficiency of the regurgitation technique. Prey items were never found unexpectedly in a sacrificed eel after it had failed to regurgitate. The proportion of empty stomachs did not differ between sacrificed and nonsacrificed eels (Chi-square test of homogeneity, $P = 0.73$). Two *G. vicinus* and three *G.*

moringa regurgitated during capture after being netted, but their meals were recovered.

To calculate indices of niche overlap between the two species, prey were categorized as "Total Fishes," "Total Crabs," and "Other," yielding a Horn Index value of 0.866 and a Morisita's Index of 0.128 ($n = 43$ and 18 eels with food in their stomachs for *G. moringa* and *G. vicinus*, respectively). Despite the overlap in diet (Table 3), *G. vicinus* tended to specialize on fishes (60.0% of the diet by weight) and *G. moringa* specialized on crabs (58.3%). After bootstrapping and recalculating each index 100 times, none of the Horn Index values were lower than the observed value, indicating significant dietary resource partitioning between the two species ($P < 0.01$). For Morisita's Index, four of the values were lower than the observed value, again indicating a significant difference ($0.04 < P < 0.05$). Six *G. moringa* were captured more than once with food in their stomachs. Elimination of repeated measures reduced the sample size for *G. moringa* to 33. Dietary partitioning remained significant after adjusting for repeated measures ($0.01 < P < 0.02$ for the Horn Index, and $0.02 < P < 0.03$ for Morisita's Index).

The proportion of empty stomachs was significantly higher in *G. vicinus* (70.0%) than in *G. moringa* (39.4%; chi-square test of homogeneity, $P < 0.001$). Statistical significance (<0.05) was consistent for all treatments of the data (before and after 1000 h, and with and without repeated measures); therefore, only the data for all captures are reported here. The proportion of empty stomachs was not correlated with lunar quarter ($P = 0.87$ and 0.13 for *G. vicinus* and *G. moringa*, respectively, chi-square test of association). Of the total eels with fish prey, both species had a similar proportion by frequency of unidentifiable fish in the stomach contents: 42.9% for *G. moringa* and 55.6% for *G. vicinus* (no significant difference, $P = 0.55$, chi-square test of homogeneity, $n = 14$ and 12, respectively). Given the similar size and gut morphology of the two species, this suggests a comparable degree of digestion. The number of crabs found in *G. vicinus* stomachs was not sufficient for a similar comparison with this prey item.

Weather-related differences in feeding frequency and prey were found for the two species. *Gymnothorax vicinus* had empty stomachs on 82.2% of the calm nights ($n = 45$), but only on 33.3% of the inclement nights ($n = 15$), indicating a significant tendency to feed more often on inclement nights ($P < 0.001$, Chi-square test of homogeneity). *Gymnothorax moringa* demonstrated a similar tendency with 42.6% empty

TABLE 4. A COMPARISON OF THE AVERAGE PERCENT BY WEIGHT (WET) FOR PREY ITEMS IN THE STOMACH CONTENTS OF *G. moringa* AND *G. vicinus* FEEDING ON CALM NIGHTS VERSUS INCLEMENT NIGHTS.

| | G. moringa | | G. vicinus | |
Prey category	Calm ($n = 28$)	Inclement ($n = 12$)	Calm ($n = 8$)	Inclement ($n = 10$)
Halichoeres bivittatus	15.6	8.3	25.0	20.0
Unidentified wrasses (Labridae)	1.1	8.3	3.6	23.0
Muraenidae: moray eels	0	8.3	0	7.0
Holocentridae: squirrelfish	0	8.3	0	10.0
Unidentified fishes	0	16.7	12.5	15.0
Total fishes	16.7	50.0	41.1	74.9
Pitho anisodon	38.5	16.7	7.8	12.2
Mithrax sculptus	6.3	0	1.2	2.8
Portunus sp.	2.8	0	0	0
Stenorhynchus seticornis	3.6	0	0	0
Unidentified crabs	17.9	16.7	12.5	0
Total crabs	69.0	33.3	21.5	15.1
Panulirus argus (spiny lobster)	0	0	12.5	0
Octopus	7.1	8.3	25.0	0
Unidentified	7.1	8.3	0	10.0

stomachs on calm nights ($n = 54$) and 29.4% for inclement nights ($n = 17$), but the difference was not significant ($P = 0.33$). Both species ate more fishes on inclement nights (Table 4), but this trend was especially strong in *G. vicinus* (74.9% by weight). *Gymnothorax moringa* ate more crabs on calm nights (69.0% by weight). We assumed that intact and small prey items found in the stomachs in the morning were eaten the previous night. Exceptions were two *G. vicinus* and five *G. moringa*, which were assumed to have eaten prior to the night before capture based on the advanced digestion of large meals (estimated greater than 5% of the eel's body weight when eaten).

Tracking and activity patterns.—Ten moray eels (five of each species) were successfully tagged and monitored for at least one night. The pooled data comprise 576 h of monitoring for *G. moringa* and 528 h for *G. vicinus*, of which 59.5 and 36 h, respectively, were spent following actively moving eels. Eels remained in their shelters for the remainder of the time. Because of inclement weather, tagged eels were unaccounted for during 16 h for *G. moringa* and 12 h for *G. vicinus*.

Gymnothorax moringa forays occurred on 62.5% of the tracking nights, as compared to only 36.4% for *G. vicinus* (Table 5). All movements were initiated nocturnally.

As with the dietary patterns, activity patterns were influenced by weather. The percentage of total tracking nights with inclement weather was similar for both species (33.3% for *G. moringa*

and 22.7% for *G. vicinus*). *Gymnothorax vicinus* movements were significantly correlated with weather ($P = 0.005$, Yates corrected chi-square test), with eels moving on 100% of the inclement nights ($n = 5$) but only 18% of calm nights ($n = 17$). *Gymnothorax moringa* also demonstrated a tendency to move on inclement nights (87.5%, $n = 8$) but moved on 50% of the calm nights as well ($n = 16$). The correlation between movements and weather was not significant for *G. moringa* ($P = 0.18$, Yates corrected chi-square test).

Spatial and temporal movement patterns varied among eels and for the same individual, with no obvious interspecific differences (complete descriptions and tracks for all forays can be found in Young, 1992). Distance traveled ranged from less than 10 m from the shelter hole to 90 m for *G. vicinus* and 115 m for *G. moringa*. Foray duration ranged from less than 20 min to 9 h for *G. vicinus* and 14 h for *G. moringa* (Fig. 3A). All forays began before midnight, although the exact timing varied (Fig. 3B). Three eels (two *G. vicinus* and one *G. moringa*) engaged in two separate forays during a single night, returning to their shelter site for several hours in between. All other eels moved only once per night. Movements were entirely nocturnal, with the exception of one *G. moringa* (Eel 2), which left at dusk and did not return to its shelter until 1000 the following morning. Three eels (two *G. moringa* and one *G. vicinus*) alternated between two different shelter sites over the course of the six-day tracking period, but all others used only one shelter site.

TABLE 5. NUMBER OF NOCTURNAL FORAYS BY MORAY EELS TAGGED WITH ACOUSTIC TRANSMITTERS. Under "Tracking Night," a number refers to the number of forays for that night, a zero means no movement was observed, a "*" indicates inclement weather. Exceptions to the tracking protocol include Eel 5 whose tag failed after the third night of tracking and Eel 3 who was believed to have regurgitated its tag after the first night.

Eel no.	Species	Length (mm)	Weight (g)	Tagging date	Tracking night					
					1	2	3	4	5	6
1	G. moringa	675	575	2/15/90	1	0	0			
2	G. moringa	NA	NA	3/1/90	1	1*	0			
3	G. vicinus	NA	NA	3/17/90	0					
4	G. moringa	794	908.4	2/12/91	0	0	0	1*	1*	1
5	G. vicinus	718	NA	2/12/91	0	0	1			
6	G. moringa	632	391.7	2/12/91	1	0	0	1*	1*	1
7	G. vicinus	947	1554.9	2/24/91	0	0	0	2*	0	0
8	G. vicinus	884	1620.0	2/24/91	0	0	0	2*	0	0
9	G. moringa	753	675.7	7/2/91	1	1*	0*	2*	2	1
10	G. vicinus	658	482.7	7/2/91	1	1*	1*	1*	1	0

A **Foraging Duration (Hours)**

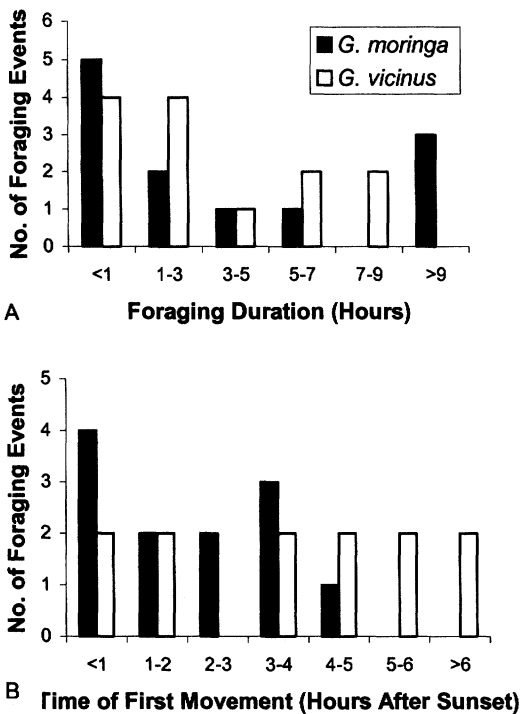B **Time of First Movement (Hours After Sunset)**

Fig. 3. The number of observed foraging events by *Gymnothorax moringa* and *Gymnothorax vicinus* for (A) various categories of foraging event duration and (B) various categories of the time of first movement from the shelter site (hours after sunset).

In 12 of 16 *G. moringa* tracks and nine of 10 *G. vicinus* tracks, eel movements were entirely in grassbed habitat, except for brief and direct transit to and from the grassbed for two sites located in sand/rubble habitats. The remaining five tracks were simply brief movements between adjacent (< 10 m) sites in sand/rubble habitat. Thus, no extended forays were in sand/rubble habitats. For the majority of the grassbed forays (67% for *G. moringa* and 56% for *G. vicinus*), eels were in open grassbeds away from any available shelters for the entire time, even when patch reefs and coral rubble were near their starting sites. No obvious visual landmarks were present along or near the pathways through the grassbeds. The remaining grassbed forays did pass through areas that included patch reefs and rubble. On long forays, eels of both species would often remain in a single spot in the grassbed for hours with no available shelter.

Of the 10 eels tracked, four *G. moringa* and two *G. vicinus* were successfully captured for diet analysis the morning after their final tracking night. Only two eels (both *G. moringa*) had food in their stomachs. One (Eel 1) had not left its

shelter for two nights but had an intact octopus in its stomach. Unidentified crab fragments were found in the stomach of the other (Eel 9), which had moved between 2230 and 0230 the night before. Three of the four eels with empty stomachs (Eels 4, 6, and 7) had moved the night before capture.

DISCUSSION

Despite overlap in shelter use, diet, and activity patterns, *G. moringa* and *G. vicinus* partitioned food resources and followed divergent weather-related activity patterns. Resource partitioning has been suggested for four genera of Red Sea moray eels with distinct morphological differences (Fishelson, 1995, 1997), but our study is the first to document resource partitioning caused by behavioral differences between otherwise morphologically similar congeners. Our study does not address the question of whether this resource partitioning is the result of interspecific competition.

Overall, *G. moringa* specialized on crabs as prey, and *G. vicinus* specialized on fish. Both dietary analyses and activity patterns independently demonstrated that *G. vicinus* had a strong preference to move and feed on inclement nights, whereas *G. moringa* did so on both calm and inclement nights. Fish consumption was greater on inclement nights for both species. On calm nights, crab consumption was greater for *G. moringa* and increased for *G. vicinus*. Therefore, the piscivorous pattern exhibited by *G. vicinus* appears to have been enhanced by their feeding on primarily inclement nights. Randall (1967) found *G. moringa* to be 100% piscivorous, which conflicts with our findings. This may reflect ontogenetic or habitat-related niche differences, because his collections included larger adults and sampled larger reefs.

Based on the percent of empty stomachs, *G. moringa* fed on average twice as often as *G. vicinus* (60.6% vs 30.0% with prey in stomachs, respectively). Foray frequency for *G. moringa* was also nearly twice that for *G. vicinus* (62.5% of nights vs 36.4%). Movement does not automatically imply feeding, as evidenced by stomach content collections from three of the tagged eels, but within a species, the feeding and foray frequencies were remarkably similar. The only comparable study of eel activity patterns was on the conger eel, *Conger cinereus*, in Hawaii, in which movements were also found to be nocturnal, with alternating nights of activity and inactivity (Domokos, 1992).

The high incidence of empty stomachs is not uncommon in studies of moray eels. Many col-

lections of *Gymnothorax* spp. for diet analysis
have encountered a majority of empty stomachs
(62% empty for Hiatt and Strasburg, 1960; 76%
for Randall, 1967; and 100% and 54%, respec-
tively, for E. S. Hobson, unpubl. and 1974).
Moray eels may be infrequent foragers, return-
ing to their shelter sites where they can remain
for days with little movement or energy expen-
diture (Hobson, 1974; Abrams et al., 1983).

Gymnothorax vicinus may compensate for its
less frequent feeding rate by obtaining more
per meal than *G. moringa* and expending less
energy per day. *Gymnothorax moringa* specialized
on crabs, which have less caloric value than fish-
es. We estimated the caloric value of the average
meal for each species using wet weight caloric
equivalents from Cummins and Wuycheck
(1971) for the major prey categories from Table
3: 1058 Cal/g for Labridae (the primary fish
prey), 1493 Cal/g for all other Osteichthyes,
348 Cal/g for Majidae (spider crabs such as *P.
anisodon* and *M. sculptus*, the primary inverte-
brate prey), 817 Cal/g for all other crustaceans,
and an arbitrarily assigned intermediate value
of 800 Cal/g for "Other." Based on these val-
ues, the average meal for *G. moringa* contains
752 Cal/g, versus 1003 Cal/g for *G. vicinus*. Be-
cause meal size did not significantly differ be-
tween the two species, *G. moringa* would need
to feed 1.33 times as often as *G. vicinus* to obtain
the same number of calories. In fact, both the
stomach content and the tracking data indicate
that *G. moringa* feeds and leaves its shelter near-
ly twice as often as *G. vicinus*.

For both species, daily abundance fluctuated
during the 1990 six-week census. It is unlikely
this variability was an artifact of missed sight-
ings. Eels were difficult to see in less than one-
quarter of the shelters, and eels did not signif-
icantly differ in their use of difficult shelters ver-
sus those in which they were obvious. Thus, the
observed fluctuations likely reflect daily move-
ments into and out of the census area. Consis-
tent with observations by Abrams et al. (1983),
the majority of residences at a single site were
only one or two days in duration, and several
eels of both species used multiple sites.

Partitioning of shelters was not observed, al-
though *G. moringa* used a much larger percent-
age of the total eel sites (94% vs 50%). This
difference may reflect the decreased abundance
of *G. vicinus* in 1991 and 1992 or a more gen-
eralized behavioral pattern by *G. moringa*, as in-
dicated by both tracking and stomach content
data. The apparent surplus of suitable shelters
in our study does not eliminate the possibility
that competition may occur for preferred shel-
ters along a gradient of site quality, as implied

by the frequent occupation of specific shelters.
Hixon and Beets (1989) found the number of
individual moray eels to be positively correlated
with shelter availability in the U.S. Virgin Is-
lands. In our study, abundance returned to
preremoval levels within six months after the re-
moval and sacrifice of 48 eels (21 from within
the census area and 27 from the surrounding
areas, representing well above the maximum
daily count of 17 eels in the census area). Mean
lengths did not decline (they actually increased
for *G. moringa*), indicating replacement by im-
migrants rather than a slow recolonization by
new recruits.

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