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Abundance, biomass and habitat use of moray eels in Barbados, West Indies, determined by a modified visual census method

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Abstract

Visual censuses performed during the day underestimate cryptic and nocturnal fish species, including large, carnivorous moray eels. This study developed a census method for morays and used it to determine their density, biomass, distribution and microhabitat use on coral reefs in Barbados. The five species recorded varied in time of highest abundance. Therefore, densities were based on the time when each species was most visible (day or night). Observed densities were corrected for proportion of individuals not visible based on repeated surveys of the same transects. Density (5-6 morays $125m^{-2}$) and biomass estimates (1-3.7 kg 125 m^{-2}) per site were much higher than those reported in previous censuses and comparable to those of other predatory families. The relative abundance of species varied among sites, and species and size classes also differed in their shelter site use. The higher density and biomass found are believed to be due to the improved method.

Résumé

Les décomptes visuels diurnes sous-estiment l'abondance des poissons cryptiques et nocturnes, incluant les murènes. Une méthode de comptage a été developée pour les murènes et utilisée pour déterminer leur densité, biomasse, distribution et utilisation du microhabitat sur des récifs coralliens de la Barbade. Les cinq espèces trouvées avaient des périodes d'abondance maximale différentes. Par conséquent, les densités ont été basées sur la période d'abondance maximale de chaque espèce. Les densités observées ont été corrigées pour la proportion de murènes non visibles durant les comptages répétés du même transect. Les densités (5-6 murènes 125 m^{-2}) et biomasses estimées (1-3.7 kg 125 m^{-2}) par site étaient beaucoup plus élevées que celles d'autres études et comparables à celles d'autres familles de prédateurs. L'abondance relative des espèces différait entre les sites. Les espèces et les classes de grandeurs variaient aussi dans leur utilisation d'abris. Les densités et biomasses élevées obtenues semble être le résultat de la méthode améliorée.

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and

for the morays of the future!

1 Introduction

Our knowledge and understanding of coral reef ecosystems is largely based on what we see. Since most studies are performed during the day when we detect certain species better than others, our views are often biased. While the diurnal community is mostly composed of herbivores, omnivores and some carnivores, the nocturnal community is largely dominated by predatory species (Helfman 1986). These species can therefore have a substantial ecological importance in the reef community while being often neglected or under represented in studies due to their low apparent numbers during daytime. One such group, with species that grow to large sizes and whose members are largely thought of as nocturnal and cryptic, is the moray eel family (Muraenidae). Very little is known about the ecology of this family.

There are approximately 200 species of morays worldwide (Robins et al. 1991, Böhlke & Chaplin 1993, Smith 1997, Böhlke & Smith 2002) ranging in adult length from just a few centimetres to more than three metres (Böhlke & Randall 2000). In general, morays can be seen with their head protruding from an opening in the reef structure during daytime. They are sometimes seen repeatedly in the same hole for extended periods of time, but length of residency appears variable within and among species ranging from one day to perhaps several months (Abrams et al. 1983, Abrams & Schein 1986, Young 1992, Fishelson 1997). Several moray species appear to use different shelters over time (Abrams et al. 1983, Young 1992), but their habitat use has been the subject of few studies. Abrams et al. (1983) described the habitat types and species of coral heads with which two species of Caribbean morays were

associated, and Young (1992) described the shelter use of two Caribbean species in a shallow backreef habitat.

Very few studies have considered the mobility of morays. The evidence suggests that some species, like the goldentail moray (*Gymnothorax miliaris*), are site-attached and restricted to an area of 5-6 m diameter (Smith & Tyler 1972, Abrams et al. 1983). Other species such as the purplemouth moray (*G. vicinus*) and the spotted moray (*G. moringa*) have much greater mobilities, being capable of travelling approximately 100 m overnight and up to 400 m over a few months (Young 1992, Chapman & Kramer 2000).

Morays are carnivorous. They eat fish, crustaceans, and octopi (Hiatt & Strasburg 1960, Randall 1967, Parrish et al. 1986, Yukihira et al. 1994). Some are known to mainly use their sense of smell for prey detection (Bardach et al. 1959, Tannenbaum et al. 1992, Fishelson 1995, Fishelson 1997), while others use sight (Chave & Randall 1971, Fishelson 1997). Their foraging and feeding behaviours vary depending on their diet and have been described in part for several species (Kondo 1955, Winn 1955, Bardach et al. 1959, Bardach & Loewenthal 1961, Chave & Randall 1971, Miller 1989, Tannenbaum et al. 1992, Young 1992, Fishelson 1995, Fishelson 1997). Despite appearances, they are not strictly sit-and-wait predators because several species travel distances away from their resting sites in search of food (Young 1992, Fishelson 1997), and some even leave the water to catch crabs at low tide (Chave & Randall 1971). They can be seen moving between shelters and poking their heads

into holes in the reef, and their elongate shape allows them to reach into the shelters of small prey, often inaccessible to other predators.

Data on moray abundance are very scarce in the literature compared to other fish families. The main exceptions are studies by Bardach (1959), Bardach et al. (1959), Smith & Tyler (1972), Christensen & Winterbottom (1981), Brock (1982), Abrams & Schein (1986), Parrish et al. (1986), Young (1992), Fishelson (1997) and Hodgson & Liebeler (2002). This paucity of data is due to a combination of factors that make morays more difficult to study. Moray eels have been described as primarily active at night (Bardach et al. 1959, Hiatt & Strasburg 1960, Collette & Talbot 1972, Smith & Tyler 1972, Fishelson 1997) when light limitation restricts observations. However, some species appear primarily active during the day (Chave & Randall 1971, Böhlke & Randall 2000, Humman & Deloach 2002). By both day and night, their habits are cryptic and secretive, which make them hard to find. Reports of attacks and injuries from their sharp teeth, with some species reported as venomous (Randall 1969, Böhlke & Randall 2000), have given them a bad reputation and people generally see them as more difficult to handle and study than other fish families. No real effort has been made to change this yet. Species of morays in certain locations also can cause ciguatera poisoning if consumed (Randall 1969, Böhlke & Randall 2000, Hokama & Yoshikawa-Ebesu 2001), contributing to their bad reputation.

The major problems in studying morays relate to the limitations of the methods for determining the abundance of fishes. The main methods presently used are visual

census techniques, generally limited to daytime. These methods have become increasingly popular because they present several advantages over other methods. They are non-destructive, quick, cheap, adaptable and permit the collection of a wide range of biological data in situ. However, they are known to underestimate small and cryptic fishes, including morays (Brock 1982, Ackerman & Bellwood 2000, Willis 2001). On the other hand, chemical collections using ichthyocides such as rotenone are commonly used to obtain a complete sample of a resident fish community as most fishes in the area are killed. However, some swim away or do not die while others are lost through predation and currents, and some hole-dwelling species like morays can die in locations inaccessible to the researchers (Christensen & Winterbottom 1981). Ichthyocides also remove a large number of fish which is not desirable in many ecological studies and is usually not permitted in reserves. Chemical collections are also rarely quantitative because their goal is often to determine species richness of an area or to obtain specimens. Furthermore, it is often difficult to determine the extant of the area affected by the chemical and thus to calculate abundance or biomass per unit area.

Although the advantages of visual methods are numerous, several biases have been identified (Brock 1982, Sale & Sharp 1983, Harmelin-Vivien et al. 1985, Thresher & Gunn 1986, St John et al. 1990, Sale 1997, Thompson & Mapstone 1997, Kulbicki 1998, Samoilys & Carlos 2000). A number of studies have used modifications of the traditional methods to make them more appropriate to the question/organism studied, and efforts to reduce or correct certain biases have been made. For example, several

successive passages can be used to count mobile, benthic or small fish in turn (Chabanet et al. 1997, De Girolamo & Mazzoldi 2001, Miller & Gerstner 2002, Nanami & Nishihira 2002), the width of transect (Sale & Sharp 1983, Cheal & Thompson 1997) and observer speed (Lincoln Smith 1988) can be selected according to the behaviour, size and visibility of the organism studied or a combination of several methods can be used (Thresher & Gunn 1986).

One problem that persists is the underestimation or non-representation of small, cryptic and/or nocturnal species in quantitative studies of fish communities (Harmelin-Vivien et al. 1985, Ackerman & Bellwood 2000). The underestimation of fish by visual methods is generally considered acceptable for comparing relative abundances, but the ecological implications of neglecting small, cryptic and nocturnal species have not been studied or considered very often (Ackerman & Bellwood 2000). A few studies have tried to address this problem by using modified visual census methods (Stewart & Beukers 2000, De Girolamo & Mazzoldi 2001) or a combination of visual and chemical methods (Christensen & Winterbottom 1981, Ackerman & Bellwood 2000, Willis 2001), but only one included morays (Christensen & Winterbottom 1981). These studies mostly supported Brock's (1982) observations that morays and other small or cryptic species are much more abundant than are apparent in visual censuses. In a study by Parrish et al. (1986), the family Muraenidae was found to have the most important piscivorous impact of 16 Hawaiian families of resident fish collected by rotenone, suggesting that they play a disproportionately large role compared to the attention they have received.

This study aimed to determine how abundant morays are on coral reefs and indirectly how important they may be in the reef ecosystem. The main objectives of this study were 1) to develop an appropriate census method to estimate the abundance and biomass of moray eels and 2) to use this method to gather data to supplement the scarce biological, behavioural and ecological knowledge on morays. Once elaborated, the method was used more specifically to answer the following questions: a) What muraenid species are found in the study area? b) Do they differ in activity/visibility patterns? c) What are the density and biomass of the species present? d) How do density and size vary by species, habitat and site? and e) Do species and size classes differ in their microhabitat/shelter use or other behaviour? Additional biological information on the species present was also gathered opportunistically.

2 Methods

2.1 Study area

The study took place in Barbados from March to December 2001. Four reef sites where morays had been observed were selected because they presented different habitat types and fishing pressures. All were located on the sheltered west coast of Barbados, inside and outside a marine reserve (Folkstone Marine Park). The reserve includes a 2 km long stretch of the coastline and extends offshore to approximately 0.7 km to include a section of a bank reef. Fishing is not allowed in the reserve

except cast-netting for clupeids (Rakitin & Kramer 1996), but some poaching by hook and line and spear fishing occurs both on the fringing reefs and the offshore bank reef (pers. obs.). Boating and other recreational activities are permitted throughout the reserve except in a small area, demarcated by marker buoys, where boat use is limited to glass-bottom boats. This small area is located adjacent to the Bellairs Research Institute and includes two frequently studied fringing reefs. Fishing pressure outside the reserve is low, with the main methods being Antillean fish traps, hook and line, spearfishing (Rakitin 1994) and occasional seining and gill-netting (pers. obs.). The four sites are described in detail below.

2.1.1 Bank reef site

The bank reef site was a section of the offshore submerged barrier reef, running parallel to shore, approximately 0.7 km from the shore off Holetown and inside the reserve (near the mooring for Fisherman's dive site, 13°11'0" N, 59°38'47" W). Additional information on the reefs of Barbados can be found in Lewis & Oxenford (1996). This study site is a patch reef habitat with moderately high to high patch reef cover over a sandy bottom but with occasional larger sandy patches. Coral heads are generally 0.5-1.5 m in diameter. Depth ranged from 15 m on a plateau sloping abruptly down to the sea bed offshore and inshore (to ~ 40 m depth), but the study area was limited to a maximum depth of 20 m on each slope. Coral head densities were especially high on the slopes. The study area measured approximately 120 m from slope to slope by 80 m long parallel to shore.

2.1.2 Fringing reef in the reserve

The reserve fringing reef was a large reef located in the reserve, adjacent to Bellairs Research Institute (South Bellairs Reef, 13°11'27" N, 59°38'34" W). It is a fringing reef with characteristic zonation including a backreef, crest and spurs and grooves zones (Lewis 1960, Lewis & Oxenford 1996) and an additional unusual zone here referred to as reef flat. This zone extends offshore from the backreef on the southern portion of the reef, but is distinct from the crest and spurs and grooves in that it has sparse corals and sea fans on a surface that is fairly flat and low in structural complexity. There was no clear transition between the backreef and the reef flat other than a gradual increase in depth (to 2-3 m). Depth of the reef ranged up to 10 m at the seaward end of the spurs and grooves zone. The area studied extended approximately 250 m from the shore to the seaward edge of the reef and measured 120 m parallel to shore, concentrated in the middle of the reef area. This included most of the reef area which measures 3.47 ha (Lewis 2002).

2.1.3 Fringing reef outside the reserve

The non-reserve fringing reef exhibited typical zonation with a backreef, reef crest and spurs and grooves zones. It was located just north of the Folkstone Marine Park and separated from the reserve reefs by a bay of about 250 m (Heron Bay Reef, 13°11'48" N, 59°38'37" W). This reef did not extend as far offshore as the one in the reserve, and the maximum depth was 8 m at the seaward end. The area studied was approximately 130 m by 130 m. This included the entire width of the reef from shore

to the seaward edge and approximately half the length parallel to shore, concentrated on the southern portion.

2.1.4 Patch reef habitat

A patch reef habitat located farther north on the west coast of Barbados (starting ~ 30 m offshore from Tropicana fringing reef, 13°13'11" N, 59°38'42" W) was chosen as the fourth site. It is an extensive patch reef habitat with a few sandy areas and coral head density ranging from low near the fringing reef to high near the middle of the area studied and on the offshore slope. Coral heads were generally 0.5-1.5 m in diameter. Depth ranged between 7 m and 13 m, gently sloping down to an offshore drop-off starting at a depth of 12 m. The area studied was approximately 125 m by 125 m. The boundaries of this area are not well defined, and its total size is unknown.

2.2 Study design

The researcher with one of two assistants performed all censuses. Prior to sampling, the researcher trained the assistants in moray detection, identification, measurement and in determination of microhabitat characteristics. Efforts were made to reduce observer differences as much as possible before sampling started.

The sampling periods were 9-20 August and 12 October to 14 November 2001. Each of the four sites surveyed were divided into zones; three or four zones for the fringing reefs and three zones, stratified by depth, for the bank reef and the patch reef habitat. Three or four replicate transects were censused per zone. The zone with the highest

structural complexity at each site received the greatest effort (four replicates). This gave a total of 10 transects of 25 x 5 m transects per site except on the reserve fringing reef which had 13, due to the extra zone.

At each site, a permanent baseline that ran through the entire length of the study area (perpendicular to shore) was marked every 10 m to serve as a reference point. Before each dive, a distance along the baseline was haphazardly selected for the location of the transect(s). The researcher decided a priori in what direction the transect was to be laid (north or south of the baseline) and at what approximate distance in order to avoid biases in choosing a location while on site. Whenever possible, the sites sampled were alternated between days so as to minimise clustering in time and avoid possible confounding lunar cycle or weather effects. However, the order was also affected by factors such as boat availability and weather.

2.3 Survey method

Each transect was censused twice between 10:00-14:00, and 20:00-00:00, generally on the same day. A 25 m measuring tape was laid over the substratum parallel to shore during the day at one of the 10 m baseline markers. It was laid so as to loosely follow the bottom contour. Day censuses were immediately performed except on one occasion where the night census had to be performed first due to strong currents at the time planned for the day census. The transect lines were left on the reef for night censuses, after which they were removed.

For each transect, structural complexity was assessed and recorded qualitatively as low, medium or high (Table 1), and the maximum bottom depth of the transect was also recorded (from a diver's depth gauge) prior to the census. Two divers swam along the 25 m line, carefully and slowly searching all possible hiding places by zigzagging within 2.5 m on each side of the line at a distance of 0.5 m or less from the substrate. This was done to reduce the biases caused by lower detection of cryptic species away from the transect line (Sale & Sharp 1983). The transect size (125 m^{-2}) and shape were determined during a preliminary study taking into account the size of the organisms studied, their abundance and spatial heterogeneity of the environment.

When a moray was detected, a marker of coral rubble wrapped with flagging tape was placed beside its shelter, and the distance along the transect line was recorded to mark its location and prevent accidental recounts. Data for each individual sighted was recorded on slates including: 1) species (based on colour patterns, dentition and descriptions in Böhlke & Chaplin (1993), Smith (1997) and Humman & Deloach (2002)) 2) head length (HL: snout to gill opening, measured using a ruler placed near the fish or estimated to the nearest 0.5 cm), 3) activity level (active or inactive), 4) exposure (% of body visible; this variable was added part way through the study), 5) microhabitat use (shelter position relative to the reef structure and type), and 6) depth (from depth gauge). See Table 1 for definitions used in activity, exposure and microhabitat use.

Table 1. Definitions used for data collected on transects or moray location during censuses

Variable	Categories	Definition
Mean structural complexity of transect	Low	Simple structure with low rugosity, few shelters and easily surveyed (e.g., backreef, reef flat, sandy area with sparse coral heads).
	Medium	More rugose with structure creating more shelters but still some lower complexity areas (e.g., some reef crest areas, some patch reefs interspersed with sand).
	High	High rugosity with multiple shelters and most difficult and time consuming to census (e.g., spurs and grooves, dense patch reefs).
Moray activity	Active	Swimming (continuous or intermittent) during the period of observation; includes passing through the transect area, predation attempts (successful or not) and prey handling.
	Inactive	Remaining quiescent in shelter with little or no movement other than gill ventilation; includes being cleaned by gobies or cleaner shrimp.

Table 1. (continued)

Moray exposure	≤25%	Little of body visible when a moray is seen in a shelter, with usually the snout, head and/or a small part of the body protruding.
	26-50%	Proportion of body visible in the shelter or protruding.
	51-75%	Same as above
	>75%	Most of the moray is visible in a shelter or it is completely exposed (can be active).
Moray shelter position	Top	Top of spur, patch reef or other structure; approximately horizontal surface located above the level of the sandy substrate.
	Side	Side of structure such as reef spur or patch; vertical or sloping surface.
	Bottom or Under	At the base of or under structure such as spurs and patch reefs: usually caves, cavities, or spaces under ledges.
	Flat	Approximately horizontal area that is not part of a complex structure, mostly open with few cavities and little structure (e.g., back reef, open sand between patches or grooves between reef spurs).

Table 1. (continued)

Moray shelter type	Hole	Tunnel with one or more openings from which usually the head and occasionally the tail protrudes. The diameter usually closely matches that of the moray.
	Crevice	Space providing mainly lateral cover with exposure from above in one or more places (includes animals sheltering among coral branches).
	Cavity	Space with opening much larger than the moray's body diameter, providing mostly overhead cover and lateral cover on one side but in which most of the body is visible from the side.

At the end of the transect, the observers recorded the time taken to perform the survey, informed the other about the number of morays seen, switched sides and surveyed each other's half of the transect in the opposite direction to look for additional (unmarked) morays. Resighted and additional morays detected were recorded as previously, and the markers were collected. Time was recorded again.

All the night censuses were performed using narrow beam pocket dive lights in order to focus the field onto the small area surveyed and avoid disturbing the morays farther along the transect. Most morays did not react to a passing light, but a focused light and a close approach for measurement sometimes resulted in a moray fleeing or withdrawing slightly deeper in its shelter (especially smaller individuals). Morays that withdrew usually re-emerged when the light was shone away or less directly, permitting measurement.

The duration of each passage over the transect ranged from 4 to 38 min and averaged 18.12 ± 6.36 min (mean ± SD) depending on the habitat complexity, the number of morays seen and time of day (day = 16.72 ± 5.69 min, night = 19.53 ± 6.33 min). No more than two transects could be surveyed on a single dive/day due to air and bottom time limitations. On the bank reef, only one could be done.

2.4 Density, size and biomass estimation

Density (number 125 m^{-2}) obtained by the addition of both observers' counts on the first passage over the transect was termed 'observed density 1' ($C_1 = C_{1\ \text{researcher}} +$

$C_{1\ assistant}$). The density of additional individuals seen by both observers on the second passage was called 'added density' (C_2). Day and night observed densities for the transect were obtained by adding C_1 and C_2.

The total length (TL) and weight (W) of morays were estimated by using the HL measurements made in the field and the species-specific relationships between TL and HL and between W and HL. These relationships were based on measurements made on fresh specimens (caught by traps, lured with bait into a mesh bag or with baited hook and line) and on additional preserved specimens from the Florida Natural History Museum. The relationships were determined through linear regression of TL on HL and linear regression of $\log_{10}$W on $\log_{10}$HL. Regressions of $\log_{10}$W on $\log_{10}$TL were also performed.

Biomass (kg 125 m^{-2}) was calculated by adding the estimated weight of all individuals from C_1 and C_2. The field HL measurements from the researcher were used whenever available to estimate TL and W of the morays seen on the surveys as they were more consistent than those from the assistants. When no HL estimate was available for a moray, the average weight for that species at that site was used. This approach was needed in only 3% of cases.

Density and biomass for the transect at the time of maximum species visibility was determined since there were significant differences in the abundance of most species with time of day. The 'total observed density' and 'total observed biomass' were

calculated for the transect by adding either the day or night observed density and biomass for each species, depending on when each was most visible on average.

If transects are being used to count organisms that are visible or detectable only part of the time, it is desirable to develop a correction factor to estimate the number actually present from the number seen. To estimate actual numbers of morays present on the transects, the 'total estimated density' and 'total estimated biomass', were corrected as follows. If counts of individual morays seen on a first passage over a transect is C_1, new individuals seen on a second passage is C_2, and the total number of morays on that transect is N, C_1/N is the average probability of detection of each moray on one passage over a transect and $1 - (C_1/N)$ is the probability of each moray being missed. Thus, the number of additional morays seen on the second passage will be the number not detected on the first one times the probability of detecting each moray. So,

$$C_2 = N\,[1 - (C_1/N)]\,(C_1/N) = (C_1N - C_1^2)/N.$$

Dividing both sides of the equation by C_1 we obtain

$$C_2/C_1 = (N - C_1)/N = 1 - (C_1/N).$$

The ratio of counts seen on the two passages is therefore equal to the probability of missing each moray on a passage. The expression can be reorganised to obtain

$$N = C_1/\,[1 - (C_2/C_1)].$$

The value $[1 - (C_2/C_1)]$, the 'proportion seen', can be used to adjust individual transect counts. For example, if 3 morays were seen on the first passage over a transect and 1 more was seen on the second one, $C_2/C_1 = 0.33$. The number of morays

on the first passage (3) should be divided by the proportion seen, 0.67, to estimate the number actually present as 4.47.

This correction assumes that the number of additional morays seen on the second passage is the same proportion of the pool of unseen morays as the number of morays seen on the first passage. Moray behaviour and morphology, habitat complexity, water clarity and diver experience will likely affect C_1 and C_2 by influencing moray visibility or detection.

When the number of morays per transect is low, stochastic variation can produce nonsense results (such as a negative estimate of the number of morays, when the number of additional morays on the second passage is higher than the number seen on the first passage) if the proportion seen is calculated separately for each transect. Thus, transects were pooled to obtain a reasonable average estimate of the proportion seen. For this study, the average proportion seen for all species, sites and times combined using means per transect for C_1 and C_2 were calculated. The calculation was then repeated separately for night and day for the three most common species and for all five species combined. The average estimated densities were then obtained using

$$N = C_1/[1 - (C_2/C_1)].$$

These values permitted calculation of the average proportional increase in estimated density over observed density ((*Mean Estimated - Mean Observed*)/*Mean Observed*) overall and for each common species individually, and these increases were called

correction factors (CF). The correction factor for each species at each time of day was then used to correct the observed density ($C_1 + C_2$) on individual transects (rather than by dividing C_1 by $1 - (C_2/C_1)$) to avoid the problem of estimating density when $C_2 > C_1$. Thus, the corrected density on each transect was:

$$Estimated\ density = \Sigma\,(Observed_{ij} + (Observed_{ij} * CF_{ij}))$$

Where i is the species and j is the time of day for the *Observed* density of each species when they were most visible and *CF* is the time and species-specific average proportional increase. The estimated densities were then used to calculate the estimated biomass per transect by multiplying the estimated density of each species by their average weight per site. 'Total estimated biomass' per transect was calculated by adding together the estimated biomass of all species at the time of their maximum visibility.

2.5 Statistical analyses

Statistical analyses were performed using SPSS 11.0 and SAS 8.0 for Windows. The analyses used will be detailed in the results section where appropriate. A significance level of 0.05 was used throughout.

3 Results

3.1 Species present

Five species of morays were recorded during the censuses. These species were the goldentail (*Gymnothorax miliaris*), spotted (*G. moringa*), viper (*Enchelycore*

nigricans), chestnut (*E. carychroa*) and chain morays (*Echidna catenata*). In addition, purplemouth (*G. vicinus*) and green morays (*G. funebris*) were seen in the study area, outside the census periods.

3.2 Visibility

Mean observed densities for each species during the day and at night were compared using Wilcoxon signed ranks tests because the data failed to meet the assumptions of normality and homogeneity of variance even after transformation (Table 2). Censuses during the day detected only three species whereas censuses at night detected five. Abundances by day and night differed; goldentail morays were more abundant during the day, whereas all others were more abundant or only seen at night. The difference was statistically significant for all species but the chain moray. The counts on the first passage (C_1) differed between the researcher and the assistants (the researcher found more, Wilcoxon signed ranks test $Z = -3.236$, $p = 0.001$) but counts of C_2 did not differ ($Z = -0.988$, $p = 0.323$).

3.3 Total length and weight calculations and correction factors

The equations to convert HL to TL and W as well as the relationships between W and TL are given in Table 3. All relationships had high R^2 values (> 0.98).

The correction factors (CF; proportional increases from observed values) and the values needed to calculate them are presented in Table 4. Correction factors differed

Table 2. Mean ± SD and median of day and night densities (no. of morays seen on two passages) of five species of morays found on 43 transects at four sites in Barbados

Species	N	Day			Night			Z^1	p^2
		Mean ± SD	Median	75th percentile	Mean ± SD	Median	75th percentile		
Goldentail	43	1.19 ± 1.07	1	2	0.44 ± 0.67	0	1	-3.937	0.000
Spotted	43	0.70 ± 0.86	0	1	1.21 ± 0.99	1	2	-2.678	0.007
Viper	43	0	0	0	0.93 ± 1.26	1	1	-4.318	<0.001
Chestnut	43	0	0	0	0.28 ± 0.70	0	0	-2.640	0.008
Chain	43	0.12 ± 0.39	0	0	0.21 ± 0.56	0	0	-0.877	0.380

Note that the 25th percentile is not reported because it was always 0

[1] Comparison using Wilcoxon signed ranks tests

[2] P-values are 2-tailed

Table 3. Regression statistics for relationships between total length (TL) and head length (HL), $\log_{10}$ weight (W) and $\log_{10}$ HL, and $\log_{10}$ W and $\log_{10}$ TL for five species of Muraenidae

Species	HL-TL (TL = a + b (HL))					
	N	Intercept a	Slope b	R^2	HL range (mm)	TL range (mm)
Goldentail[1]	14	22.33	6.68	0.95	18-82	120-522
Spotted[2]	15	77.89	5.75	0.96	34-159	230-920
Viper[3]	15	33.69	6.64	0.98	15-126	121-895
Chestnut[4]	10	16.09	6.65	0.99	4-45	42-308
Chain[5]	14	3.10	7.08	0.99	19-80	128-545
	HL-W ($\log_{10}$ W = $\log_{10}$ a + b $\log_{10}$ HL)					
	N	log a	b	R^2	HL range (mm)	W range (g)
Goldentail	14	-3.46	3.22	0.95	18-82	4-347
Spotted	13	-3.51	3.12	0.98	34-159	16-2183
Viper	14	-3.35	3.04	0.99	15-126	2-870
Chestnut	8	-2.97	2.68	0.98	4-45	0-40
Chain	14	-3.46	3.18	1.00	19-80	4-340

Table 3. (continued)

	TL-W ($\log_{10} W = \log_{10} a + b \log TL$)					
	N	log a	b	R^2	TL range (mm)	W range (g)
Goldentail	14	-5.92	3.11	0.95	120-522	4-347
Spotted	14	-6.80	3.39	0.98	230-920	16-2183
Viper	14	-6.72	3.32	0.99	121-815	2-870
Chestnut	8	-6.45	3.19	0.99	42-308	0-40
Chain	14	-5.85	3.06	1.00	128-545	4-340

1. Goldentail max. TL = 700 mm (Smith & Böhlke 1990).

2. Spotted max. TL = 1200 mm (Humman & Deloach 2002).

3. Viper max TL = 1000 mm (Smith & Böhlke 1990).

4. Chestnut max. TL = 340 mm (Robins & Ray 1986).

5. Chain max. TL = 710 mm (Smith 1997). Note that there was a typo in Claro (1994), chain moray max TL was supposed to be 650 mm not 1650 mm (R. Claro, pers. comm.).

Table 4. Average proportion seen and correction factors (CF) for estimating average moray densities from visual census data using two passages over the same transect. Data shown for the three most abundant species and for all five species combined.

	Day				Night				Overall[1]			
	Observed density[2]	Prop seen[3]	Estimated density[4]	CF[5]	Observed density	Prop seen	Estimated density	CF	Observed density	Prop seen	Estimated density	CF
Goldentail	1.19	0.61	1.38	0.17	0.44	0.73	0.48	0.08	0.81	0.65	0.92	0.14
Spotted	0.70	0.64	0.80	0.15	1.21	0.32	2.23	0.85	0.95	0.45	1.37	0.43
Viper	0	0	0	0.00	0.93	0.46	1.31	0.41	0.47	0.46	0.66	0.41
All species	2.00	0.61	2.35	0.18	3.07	0.45	4.42	0.43	2.54	0.52	3.32	0.30

1. Based on 43 day and 43 night, 86 combined transects.

2. Average observed moray densities obtained by adding the densities from two consecutive passages over the same transect.

3. Calculated as $[1- (C_2/C_1)]$, where C_2 is the average number of morays on the 2nd passage and C_1 is that of morays on the 1st passage.

4. Average estimated moray densities obtained by dividing the number seen on the 1st passage by the average proportion seen.

5. Average proportional increases in estimated densities over observed densities used as correction factors.

between species and times of day. The correction factor at time when each species is most abundant was smallest for goldentail morays during the day with 17%, largest for spotted morays at night with 85% and intermediate for viper morays at night with 41%. It averaged 30% for all five species for night and day combined and this average was used to estimate density of the two rare species.

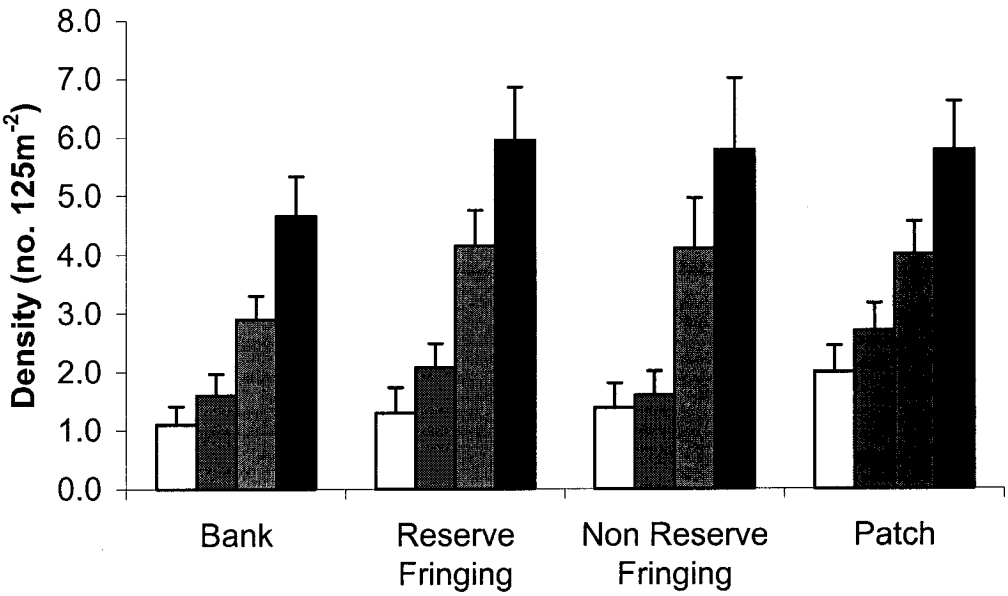
3.4 Effectiveness of the modified method

The effects of improvements at each step of the census method for all species combined are shown in Figure 1. A second passage over the transect during the day increased observed densities by a factor of 1.4. (Wilcoxon signed ranks test, $Z = -3.874$, $p < 0.001$). Using data from the time when morays were most visible increased the observed densities by a factor of almost 2 over the previous step ($Z = -4.667$, $p < 0.001$). The species-specific correction factors further increased the estimated total moray density by a factor of 1.5 ($Z = -5.712$, $p < 0.001$). Overall, the method increased estimated density by about 4 times the estimate of a single daytime census.

3.5 Factors influencing density

The maximum observed and estimated densities per transect were of 11 and 15.3 morays 125 m^{-2} respectively with an overall estimated average of 5.6 morays. To determine the statistical strength of the effects of species, site, zone and structural complexity on the density of morays, 'total observed density' was used in the analysis because the error around the 'estimated density' is more difficult to determine. The

Figure 1. The effect of improvements in the underwater visual census method on the estimated density of all species of morays combined in each of 4 sites. For each site, bars show from left to right: Step 1: using a fixed width transect searched slowly, Step 2: adding additional individuals seen on a second passage over the same transect, Step 3: basing the density calculation on the time when each species is most visible (day or night, counts from two passages), Step 4: correcting densities based on an estimate of the proportion of morays missed. Error bar = 1 SE


Density (no. 125m-2)
8.0
7.0
6.0
5.0
4.0
3.0
2.0
1.0
0.0
Bank
Reserve Fringing
Non Reserve Fringing
Patch

estimated density showed generally similar trends and is shown in Figure 2a as the best estimate of actual value. Density did not meet the assumptions of ANOVA, even after transformation, due to its Poisson distribution, and therefore a generalized linear model with Poisson error distribution and log link function was used to determine the effect of species, site, zone nested within site and structural complexity (all considered fixed, categorical variables) on density. The model selection was by backwards elimination to find the minimal model that adequately explained the data. The factors selected for the minimal model are those that, when removed, significantly increase the deviance of the model (Crawley 1993).

There was no effect of reef zone as a nested factor overall on the density, so it was not included in the model with the other factors. However, there was an increasing trend in density from low in the backreef, medium in the crest, to high in the spurs and grooves and the reef flat zones. There were also some differences among zones in the patch reef and bank reef sites but with no particular trend. The minimal model included *site*, *species*, *site*species* interaction and *complexity* and explained 34.5% of the deviance from the null model ([dev. null model – dev. minimal model]/dev. null model; Table 5).

The relative density of the species varied among sites (*site*species* interaction, type 1 analysis, likelihood ratio (L.R) $\chi^2 = 28.82$, $p = 0.004$). Figure 2a shows the differences in estimated densities per species at each site (observed densities have similar trends). All five species were found at all sites except that chain morays were

Figure 2. Estimated mean (+1 SE) a) density b) total length (sample size above bar) and c) biomass for five species of morays (G = goldentail, S = spotted, V = viper, Ct = chestnut and Cn = chain) at four reef sites in Barbados based on species correction factors for proportion of morays missed applied to observed densities obtained by two passages over the same transect at the time when each species is most visible

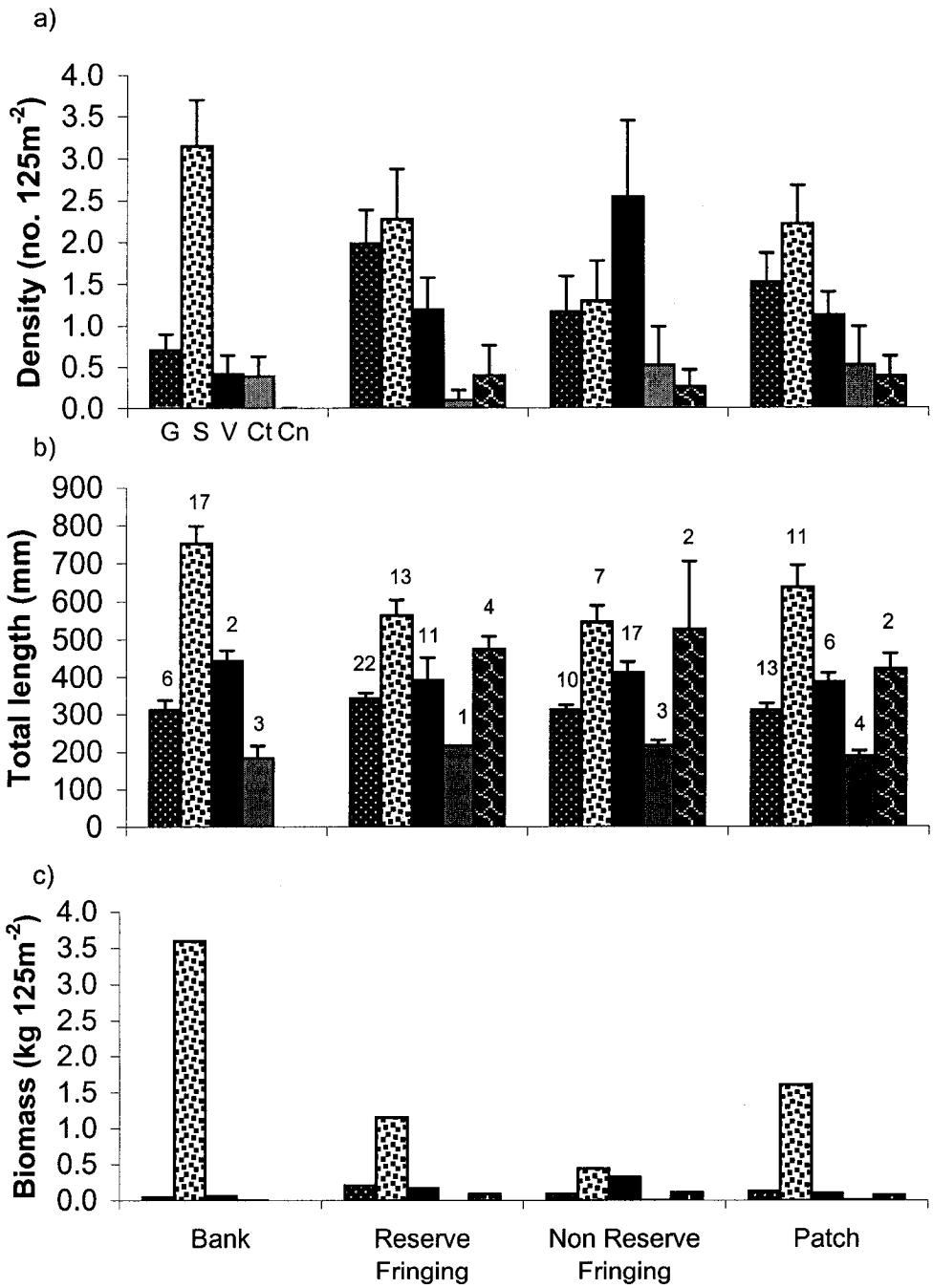

a)
Density (no. 125m-2)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
G S V Ct Cn
b)
Total length (mm)
900
800
700
600
500
400
300
200
100
0
17
6
2
3
22
13
11
1
4
10
7
17
3
2
13
11
6
4
2
c)
Biomass (kg 125m-2)
4.0
3.5
3.0
2.5
2.0
1.5
1.0
0.5
0.0
Bank
Reserve Fringing
Non Reserve Fringing
Patch

Table 5. Model selection procedure by backwards elimination for the factors affecting density of morays. The factors tested included reef *site* (4: bank, reserve fringing, non-reserve fringing and patch reef), moray s*pecies* (5: goldentail, spotted, viper, chestnut, chain) and structural c*omplexity* (low, medium, high)

Model	Factors included	Deviance	df	Likelihood Ratio	df	p
Null	Intercept	296.18	214			
Saturated	site + species + complexity + (site*species) + (site*complexity) + (species*complexity) + (site*species*complexity)	152.84	160			
1.	Saturated model - (site*species*complexity)	177.57	180	24.73	20	0.212
2.	Model 1 - (species*complexity)	186.47	188	8.90	8	0.350
3.	Model 2 - (site*complexity)	193.55	193	7.08	5	0.215
4.	Model 3 - (site*species)	222.37	205	28.82	12	0.004
Minimal	Model 3: site + species + complexity + (site*species)					

not seen on the bank reef during the censuses, although they were observed there at other times. Spotted morays were in highest density on the bank reef (3.15 morays 125 m^{-2}) and lowest on the non-reserve fringing reef (1.30 morays 125 m^{-2}). The density of viper morays followed the opposite pattern with highest density on the non-reserve fringing reef (2.54 morays 125 m^{-2}) and lowest on the bank reef (0.42 morays 125 m^{-2}). Goldentail morays had higher densities on the reserve fringing reef (1.98 morays 125 m^{-2}) and the patch reef (1.52 morays 125 m^{-2}) and the lowest density on the bank reef (0.70 morays 125 m^{-2}). Chestnut and chain morays were in similar low densities at all the sites. The reserve fringing reef and patch reef had similar general patterns of abundance for the most common species, with spotted morays being most abundant followed by goldentail and viper morays and with rare chestnut and chain morays.

Densities differed among species (*species* effect: type 1 analysis, L.R. $\chi^2 = 61.41$, $p < 0.001$) with spotted, goldentail and viper morays being the most abundant species overall. The total observed densities of all three species were similar, but spotted morays clearly became the most abundant overall after correction (mean estimated density of 2.24 morays 125 m^{-2} for spotted vs 1.39 and 1.31 morays 125 m^{-2} for goldentail and viper, respectively).

The overall densities did not differ significantly among sites (*site* effect: type 1 analysis, L.R. $\chi^2 = 3.07$, $p = 0.381$) but moray density tended to be lower on the bank reef. However, densities differed among structural complexity levels (*complexity*

effect: type 1 analysis, L.R. $\chi^2 = 9.33$, $p = 0.009$). Mean density did not differ significantly between medium and high complexity habitats (5.91 vs. 6.29 morays 125 m^{-2}; LSM $\chi^2 = 0.56$, $p = 0.45$) but it was lower in low complexity habitats (3.29 morays 125 m^{-2}; LSM for low vs. medium $\chi^2 = 5.68$, $p = 0.017$ and for low vs. high $\chi^2 = 8.06$, $p = 0.005$).

3.6 Size

To determine how each of the three most abundant moray species varied in TL among habitats, nested ANOVAs were performed. TL met the assumptions of ANOVA. The factors tested were *site* and *zone* within site as fixed factors. The average TL of each species at each site are found in Figure 2b.

For spotted morays, size did not vary among zones within a site ($F = 0.554$, $p = 0.809$), but it varied between sites ($F = 3.398$, $p = 0.027$). The difference was mostly due to a significantly greater TL on the bank reef than on the reserve fringing reef (Bonferroni, $p = 0.024$) and a nearly significantly greater TL on the bank reef than on the non-reserve fringing reef ($p = 0.079$). For goldentail and viper morays, TL did not vary among zones (goldentail, $F = 0.763$, $p = 0.650$; viper, $F = 0.894$, $p = 0.535$) nor among sites (goldentail, $F = 0.894$, $p = 0.453$; viper: $F = 0.468$, $p = 0.707$). The size difference was not tested for chestnut and chain moray due to their low sample sizes, but their average TL appeared to vary little between sites (Figure 2b).

3.7 Biomass

The estimated biomass of each species is shown in Figure 2c. The difference in biomass among sites and species could not be tested statistically because it was derived from density and weight estimates. The spotted moray was the largest of the five species and made up most of the biomass. In contrast to the density results, the bank reef had the highest biomass of all sites which was related to the presence of a high density of spotted morays there, combined with their larger average size. The non-reserve fringing reef had the lowest biomass apparently as a result of a low density of spotted morays and their smaller average size.

3.8 Activity, exposure and shelter site use

To determine whether moray species differed in their activity, exposure and shelter site use (position and type), and whether these variables varied with time and size-class for each species, they were tested for associations using log-linear models. Backwards elimination was used to determine the minimal model accurately representing the data. The number of variables tested simultaneously was limited by the number of cases available for each categorical combination. Data from the five species could be used only for the activity analysis, and only the three most abundant species met the sample size requirement for log-linear analyses with sufficient power in the exposure and shelter type analyses. Size classes were established so as to have four moray size-classes spanning the whole size range of all species (~0-100 cm): <25 cm, 26-50 cm, 51-75 cm and >76 cm. It is important to note that some species are found in only two size classes due to their small maximum size or to the absence

or non-detection of large or small individuals. Differences between species and size classes (for species with at least three size classes: spotted and viper morays) were further analysed using simple 2-way contingency tables. The results for the other species are presented despite the limited analysis because they are so poorly known.

3.8.1 Activity

The minimal model for the variables species, activity and time included significant associations between species and activity (if removed, L.R. χ^2 change = 33.21, $p < 0.001$) and species and time (if removed, L.R. χ^2 change = 87.76, $p < 0.001$; Appendix I, Table 1). No 3-way or time-activity associations were present, so activity did not differ with time or with an interaction between time and species.

Overall, the percentage of morays seen active was low (0 - 45%; Table 6). Spotted morays appeared to be the most active, especially at night ($\chi^2 = 4.70$, $p = 0.03$). Goldentail morays were all seen in shelters during the censuses and rarely ever seen swimming. However, they appeared more alert during the day; some were seen halfway out of their shelter with their head swaying back and forth. One was also seen attacking a crab during the day. No chestnut morays were seen active, and chain morays were only seen active at night during the surveys. No clear pattern was detected in the activity of different size-classes (spotted moray: $\chi^2 = 1.33$, $p = 0.52$, viper moray: $\chi^2 = 1.96$, $p = 0.38$).

Table 6. Percentage of active morays for day, night, overall per species and size class

Size class	Day			Night			Total		
(cm)	N	Percent active	Percent inactive	N	Percent Active	Percent inactive	N	Percent active	Percent inactive
a. Goldentail									
≤ 25	6	0	100	2	0	100	8	0	100
26-50	44	0	100	14	0	100	58	0	100
Total	50	0	100	16	0	100	66	0	100
b. Spotted									
26-50	11	27	73	14	21	79	25	24	76
51-75	8	12	88	20	45	55	28	36	64
> 76	7	14	86	15	27	73	22	23	77
Total	26	19	81	49	33	67	75	28	72
c. Viper									
≤ 25	-	-	-	6	0	100	7	0	100
26-50	-	-	-	25	12	88	19	16	88
51-75	-	-	-	8	25	75	13	15	75
Total	-	-	-	39	13	87	39	13	87
d. Chestnut									
≤ 25 (all)	-	-	-	12	0	100	12	0	100
e. Chain									
≤ 75 (all)	5	0	100	7	29	71	12	17	83

Dashes mean that there are no data available

3.8.2 Exposure

The minimal model for the variables species, exposure and time included significant interactions between species and exposure (if removed, L.R. χ^2 change = 22.24, p = 0.001) and again species and time (if removed, L.R. χ^2 change = 44.21, $p < 0.001$; Appendix I, Table 2). No 3-way or time-exposure associations were present, so exposure did not differ with time or with an interaction between time and species.

In general, morays were rarely completely visible, and most of the time, had less than half their body exposed when they were found in a shelter (Table 7). Usually, only the snout or the head and a small part of the body were visible. However, species varied in their pattern of exposure. Spotted morays were more exposed than viper and goldentail morays during the night (spotted vs. viper: $\chi^2 = 18.90$, $p < 0.001$ and spotted vs. goldentail: $\chi^2 = 12.74$, $p = 0.005$). Spotted morays were more exposed at night ($\chi^2 = 9.10$, $p = 0.03$), with a shift from the greatest percentage of individuals in the <25% of body visible during the day to the >75% at night. There was also a size-class association with exposure in spotted morays ($\chi^2 = 17.40$, $p = 0.01$), with a tendency for larger individuals to be more exposed, but there was no such pattern for viper morays ($\chi^2 = 8.58$, $p = 0.20$). Goldentail morays rarely showed more than half of their body. A greater percentage, however, tended to be deeper into their shelter (<25% of their body exposed) at night, although this was not significantly different from the day ($\chi^2 = 1.13$, $p = 0.29$). Since chestnut and viper morays were never seen during the day censuses, their exposure is considered to have been 0%.

Table 7. Percentage of morays in each category of body exposure for day and night

Size class	Percent exposure during the day					Percent exposure during the night				
(cm)	N	≤25	26-50	51-75	>75	N	≤25	26-50	51-75	>75
a. Goldentail										
≤ 25	3	33	67	0	0	1	100	0	0	0
26-50	26	46	35	8	11	10	60	30	0	10
Total	29	45	38	7	10	11	64	27	0	9
b. Spotted										
26-50	7	72	14	0	14	10	50	10	0	40
51-75	4	25	50	0	25	12	0	25	25	50
> 76	5	40	20	40	0	12	0	25	25	50
Total	16	50	25	12.5	12.5	34	14.7	20.6	17.6	47.1
c. Viper										
≤ 25	-	-	-	-	-	4	50	25	25	0
26-50	-	-	-	-	-	19	74	10	0	16
51-75	-	-	-	-	-	2	50	50	0	0
Total	-	-	-	-	-	25	68	16	4	12
d. Chestnut										
≤ 25 (all)	-	-	-	-	-	10	40	50	10	0
e. Chain										
≤ 75 (all)	2	50	0	0	50	7	43	14	0	43

Dashes mean that there are no data available

3.8.3 Shelter position and type

The log-linear model selection for species, position and type (see Appendix I, Table 3) gave a minimal model with significant associations between species and position (if removed, L.R. χ^2 change = 55.69, $p < 0.001$) and position and type (if removed, L.R. χ^2 change = 30.86, $p < 0.001$).

All species except chestnut morays were found in all positions on the reef (Table 8), but species varied in their relative use of positions. Spotted morays differed from goldentail and viper in their position (spotted vs. viper: $\chi^2 = 33.88$, $p < 0.001$ and spotted vs. goldentail: $\chi^2 = 35.97$, $p < 0.001$). They were found mostly in shelters at the bottom of spurs or under coral heads and in shelters on flat positions whereas goldentail and viper morays were found mostly on the top or the sides of spurs and coral heads. Goldentail and viper morays were similar in their position use ($\chi^2 = 6.11$, $p = 0.11$), but goldentail morays tended to use the top more and viper morays to use the sides. There was a difference in position between size classes for both spotted and viper morays. Morays of different size classes tended to occupy different positions (spotted: $\chi^2 = 18.62$, $p = 0.005$ and viper: $\chi^2 = 19.01$, $p = 0.004$), producing a vertical zonation pattern. There was a tendency for small viper morays (≤ 25 cm) to be found in higher numbers than expected on flat areas, whereas medium sized ones (26-50 cm) tended to be found on top and large ones (51-75 cm) on the sides of structures. For spotted morays, the medium sized ones were found in all positions but in slightly higher numbers than expected on the sides, and the large and very large (> 75 cm) are respectively found more often than expected on flat and bottom/under

Table 8. Percentage of morays found in each different position on the reef and type of shelter

Size class		Position				Shelter type		
(cm)	N	Top	Side	Bottom/Under	Flat	Hole	Crevice	Cavity
a. Goldentail								
≤ 25	7	71	0	14	14	43	29	29
26-50	58	47	24	10	19	69	31	0
Total	65	49	21.5	11	18.5	66	31	3
b. Spotted								
26-50	19	5	21	37	37	74	5	21
51-75	15	20	0	33	47	47	13	40
> 76	16	0	6	88	6	31	31	38
Total	50	8	10	52	30	52	16	32
c. Viper								
≤ 25	6	17	33	0	50	83	17	0
26-50	21	52	33	10	5	71	29	0
51-75	6	0	100	0	0	67	17	17
Total	33	36	46	6	12	73	24	3
d. Chestnut								
≤25 (all)	12	33	58	8	0	17	75	8
e. Chain								
≤75 (all)	12	50	8	25	17	58	25	17

positions (note that small spotted morays were never seen). Chestnut morays seemed similar to viper morays in their position use (mostly found on sides), whereas there was no clear pattern for chain morays.

The exclusion of the association between species and shelter type did not make a significant difference in the model describing the data when position was also in the model (if removed, L.R. χ^2 change = 7.16, $p = 0.12$). All species were found in all shelter types, using primarily holes. However, there appears to be a difference in their average shelter type use (contingency table for species and shelter type: $\chi^2 = 25.69$, $p < 0.001$). Spotted morays differed from the other species (spotted vs. other species: $\chi^2 = 25.16$, $p < 0.001$) in that they used cavities more often although they also primarily used holes (52%). Goldentail and viper morays used similar shelter types ($\chi^2 = 0.47$, $p = 0.79$); primarily holes, then crevices and very rarely cavities. As size classes of spotted morays increased, the use of crevices and cavities tended to increase whereas the use of holes tended to decrease ($\chi^2 = 8.05$, $p = 0.09$). This was not the case for viper morays ($\chi^2 = 5.07$, $p = 0.28$). Chestnut morays were found mostly in crevices (often small spaces between live coral branches). Like most other species, the majority of chain morays were found in holes.

When looking at the interaction between shelter type and position in a 2-way contingency table ($\chi^2 = 35.70$, $p < 0.001$), we can see that overall, there were more morays than expected in crevices at the top of structures, more in holes on the sides of

structures, more in cavities at the bottom of or under structures and more in holes on the flat.

4 Discussion

4.1 Moray diversity on Barbados coral reefs

Seven species of morays were seen at the study sites in Barbados. These species were all known to occur in the Caribbean and are the most commonly reported.

There are currently 22 species of morays from two subfamilies (Muraenidae and Uropteryginae) reported for the Western Atlantic, found from Bermuda to Brazil, but mostly concentrated in the Caribbean area (Robins & Ray 1986, Robins et al. 1991, Böhlke & Chaplin 1993, Smith 1997, Humman & Deloach 2002). However, most of these other species were not expected to be found in Barbados because several do not occur in the Caribbean (*G. saxicola*, *G. hubbsi*, *G. nigromarginatus*, *G. kolpos*, *Muraena retifera*, *M. pavonina*), some are large but rare (*G. maderensis*, *G. polygonius*, *Muraena robusta*, Smith 1997), are found in deep water (*G. conspersus*, Böhlke & Böhlke 1980) or are very small and have rarely been seen (*Monopenchelys acuta* (Humman & Deloach 2002), *Uropterygius macularius* (Smith 1997), *Anarchias similis* (Robins & Ray 1986)). If these other species had been present in the area, I believe that most would have been seen. Exceptions may have been the smallest species because we detected few small individuals, but small chestnut morays less than 25 cm TL, and therefore within the adult size range of the very small species listed above, were detected. Two species possibly present in Barbados based on their distribution but not seen are the Caribbean ocellated moray (*G. ocellatus*) and the

broadbanded moray (*Channomuraena vittata*). They both live on coral reefs and reach fairly large sizes of 61 and >100 cm, respectively (Claro 1994, Humman & Deloach 2002). I therefore would have expected to see these species had they been present in the habitats surveyed.

4.2 Moray diel patterns of activity

The results showed that the moray species studied varied in their diel abundance, activity and exposure. These measures were used as different indicators of activity. Higher numbers seen during the day or night can serve as an indication of time of greatest activity. Differences in the proportion of individuals seen active can tell when a species spends the greatest proportion of time swimming or foraging outside its shelter, whereas exposure can indicate alertness where a greater body exposure is thought to be an indication of a greater state of arousal.

More goldentail morays were recorded during the day than at night, and there was a slightly greater proportion in the lowest exposure category at night. Although none were seen swimming during the censuses, they were occasionally observed swimming and foraging during the day but never at night. Using swimming or foraging as a measure of activity may be relatively insensitive to the changes in a species that leaves shelter only briefly to catch prey. It was noted, however, that goldentail morays appeared to be much more mobile in their shelter (swaying back and forth, going in and out) during the day than at night where they remained nearly motionless. This evidence suggests that goldentail morays are primarily diurnally

active. On the other hand, spotted morays were recorded more often and were more active and exposed at night than during the day. They are therefore believed to be primarily nocturnal. Viper morays were never seen during day censuses but they were seen at night when a proportion was active. Their exposure was lower than that of spotted morays but similar to that of goldentail morays, with the majority being in the <25% exposure category. This suggests that viper morays are also nocturnal but perhaps more secretive and hence harder to detect than spotted morays. Results for chestnut morays were similar to those for viper morays, and they are also believed to be nocturnal, because they were only seen at night in the surveys. Their smaller size, however, may have made them harder to detect. None was ever seen active outside a shelter. For chain morays, the classification into diurnal or nocturnal is harder due to the small sample size, their presence during both day and night and their similar exposure at both times. However, some were observed to be active at night whereas none were seen active during the day. They are therefore tentatively classified as nocturnal. On dives outside the census period, a few chain morays were seen swimming near sunset and were also counted in censuses at dawn. Consequently, this species may actually be crepuscular.

These diel activity patterns are largely consistent with the periods of activity reported by Humman & Deloach (2002) in which goldentail were classified as 'foraging in daytime' rather than nighttime as in earlier editions of their book. The other moray species are all reported to forage in the open at night (Humman & Deloach 2002). Spotted morays were classified by Bardach (1959) as nocturnal based on monitored

swimming (activity) patterns in aquaria. Morays have been generally described as nocturnal, but Helfman (1986) classified them in the category 'without well-defined activity periods'. This is likely due to the few studies done on muraenids relative to other fish families and the difficulty in determining when they are actually active since most of the time they appear quiescent. However, at least some other morays have been identified as diurnal. For example, *G. pictus*, a Pacific moray, was reported to have been seen foraging in shallow waters and to even leave the water at low tide to catch crabs during the day (Chave & Randall 1971). Also, in a recent review of morays of the Hawaiian Islands, Böhlke & Randall (2000) stated that they believed that most morays are actually primarily diurnal based on their observation of few morays foraging at night over several years spent studying them.

Few morays in this study appeared active. We witnessed very few predation attempts over more than 200 hours spent looking for morays. In a tracking study in Belize, Young (1992) followed spotted and purplemouth morays foraging out of their resting sites at night into seagrass beds and back. Some individuals followed fairly constant routes but others did not. This could indicate that some morays may behave similarly to some haemulids and lutjanids (Helfman 1986). However, there were no seagrass beds near my study sites, and it is not clear whether morays generally stay on the reefs at night or move into adjacent sandy areas to feed.

4.3 Density and biomass of morays

Best estimates of moray density obtained on individual transects ranged between 1.2 and 15.3 morays 125 m^{-2}, averaging 5.6 morays 125 m^{-2}. Biomass ranged from less than 0.1 to 6.6 kg 125 m^{-2}, with an average of 2.0 kg 125 m^{-2}.

4.3.1 Comparison with other studies

Only four previous studies surveyed morays exclusively (Abrams et al. 1983, Abrams & Schein 1986, Young 1992, Fishelson 1997). Abrams et al. (1983) and Abrams & Schein (1986) repeatedly surveyed, during daylight hours, a patch reef habitat in the U.S. Virgin Islands that appeared to be approximately 6000 m^2. Density estimates for the two most abundant species in the area (goldentail and spotted morays) were between 0.10 and 0.17 morays 125 m^{-2}, based on the results from the two studies corrected by a miss rate. Fish in 'residence' (in the same shelter for several days) that were not seen on one day but had been seen on the previous and following day were assumed to have been present but missed. The miss rate was estimated as the proportion of the fish in residence on each day made of these fish that were not seen but were assumed to be present, and was applied to correct actual counts (Abrams & Schein 1986). The maximum number of goldentail and spotted morays they sighted on any one day was 10 which represents a density of 0.21 morays 125 m^{-2} compared to a maximum of about 9 morays 125 m^{-2} and an average of 3.62 morays 125 m^{-2} in my study for these two species. Young (1992) repeatedly surveyed a shallow backreef area of approximately 44 000 m^2 in Belize during the day while he studied

spotted and purplemouth morays (other species that I surveyed were not seen at his study site). The maximum number of these two species seen on any one day was 24 morays or the equivalent of 0.07 morays 125 m^{-2}, which is much lower than the average estimate for all the species that we recorded and appears smaller than that for spotted morays alone in similar habitats, even though spotted morays were not very abundant in the back reef zones in the study area (only two individuals were seen during the day and one at night on six backreef transects). The average moray density estimate from the present study is therefore about 25-80 times greater than those from these other Caribbean studies.

Densities appeared much higher in the Gulf of Aqaba, Red Sea, than in the Caribbean (Fishelson 1997). An example of density data obtained in evening censuses using bait over the same area (200 m^2) for four consecutive evenings led to a density estimate of a maximum of 14.4 morays 125 m^{-2}, including five species (Fishelson 1997). This value is still within the upper range of my estimated densities per transect (15.3 morays 125 m^{-2}). Density was based on an area surveyed of 200 m^2, but bait was apparently present in the water and morays were seen to be attracted from a distance. Therefore, the area actually sampled by the study was likely greater, and the density may have been overestimated. *Siderea grisea* comprised 60-80% of the morays seen, and this genus is not found in the Caribbean.

A few studies have recorded moray densities as part of multispecies surveys (Bardach 1959, Rakitin 1994, Valles 2000, Stewart & Jones 2001, Whiteman & Côté 2002 and

M. Kulbicki, pers. comm.). All these studies reported much lower densities than found in my study, ranging from 0.03 to 1.25 morays 125 m^{-2}, with a maximum of two species except for Kulbicki's study, which recorded 12. Of particular interest for comparison with my results are studies by Rakitin (1994) and Whiteman & Côté (2002) in Barbados. In Rakitin's study, spotted and goldentail morays were counted on transects at sites inside and outside the reserve (including the fringing reefs from this study) during daytime visual censuses. The mean density obtained (0.15 morays 125 m^{-2}) was similar to that obtained by Abrams et al. (1986) and Young (1992) elsewhere in the Caribbean, but was much lower than mine. Whiteman & Côté (2002) conducted censuses to determine the density of clients of cleaner gobies. These included goldentail morays at a density equivalent to 0.33 morays 125 m^{-2}. This value is slightly greater than those of other studies from the Caribbean, but lower than my estimated average density for goldentail morays (1.39 morays 125 m^{-2}).

Reef Check, an organization using volunteers led by scientists to perform censuses of indicator species worldwide to monitor the health of coral reefs, found no morays at 81% of 302 reefs surveyed, which was viewed as a sign of overfishing (Hodgson & Liebeler 2002). In comparison, only 23% of surveys from my study had zero densities after one passage during a daytime census. Even the average density from just one daytime passage (1.44 morays 125 m^{-2}) was higher than that from most of the studies previously mentioned. Also, at least one moray was seen on every transect when densities of each species when most abundant were considered. This suggests

that the search method and experience of the divers may have a very large influence on the densities of morays detected.

An exception to the pattern of low detected abundances in multispecies censuses is the study by Smith & Tyler (1972) in the U.S. Virgin Islands. Through repetitive day and night censuses of the same small patch reef area and by mapping the location of all fishes, they obtained a density of three morays in their small area or about 10 morays 125 m^{-2} (although the precise surface area sampled was not completely clear). This is almost twice as high as my mean density but within the range of observed and estimated densities in similar complexity habitats. This study provides additional evidence that repeated censusing of the same area during day and night yields higher moray density estimates. Mapping can be very accurate, but it is also a very time consuming method for determining abundance. As such, it has not been used very frequently for reef fishes (Thresher & Gunn 1986). Nonetheless, the study by Smith & Tyler (1972) also suggests that patch reef habitats can have very high densities of morays. Additional evidence for high densities on patch reefs comes from two studies of predation on small patch reefs (natural and artificial) where abundance appears high, although the surface area of those reefs is not provided (Carr & Hixon 1995, Beets 1997).

Chemical collections generally claim to find greater numbers of morays than visual methods. However, few are quantitative and provide the area sampled to determine density. Randall (1963) investigated the fish productivity potential of artificial reefs

by constructing one (150 m^2) with concrete blocks. After more than two years, he removed all the fish using an enclosed poison collection. Two moray species were collected (spotted: 3 and purplemouth morays: 4), and their density represented 5.83 morays 125 m^{-2} with a biomass of 3.42 kg 125 m^{-2} which are very similar values to the ones I obtained. Morays were the 7th most important family in terms of biomass (4.5% of the total biomass collected). Randall (1963) also compared the values from the artificial reef to those from chemical collections on two natural fringing reef sections (one of ~600 m^2, 0-5.5 m deep and the other of ~300 m^2, 0-4.5 m deep). The collections on the natural reefs found spotted, goldentail, viper, chain and green morays as well as unidentified, small *Gymnothorax* sp. (<25 cm) and *Uropterygius* sp. Total density on the first natural reef was equivalent to 4.16 morays 125 m^{-2} (with six or seven species) and a biomass of 0.61 kg (3% of total biomass collected). These values are also very similar the ones from my sites. Density was much higher on the second reef though, with 30.72 morays 125 m^{-2} (with five species), but only making up 0.61 kg 125 m^{-2}, the exact same biomass as that on the first reef (also 3% of total biomass collected). The difference in density but not in biomass was because a green moray was caught on the first reef and made up most of the biomass, whereas more than half of the individuals collected on the second reef were of the very small (<23 cm) *Uropterygius* sp. Even though the second reef had a very high density, by excluding the *Uropterygius* sp. we did not find, the density (14.73 morays 125 m^{-2}) falls within the range of values from my study. These results, however, suggest that I underestimated small individuals and possibly entirely missed small species.

Brock (1982) tried to determine the accuracy of the visual census method by comparing its results to those from enclosed rotenone sampling of a large patch reef in Hawaii of approximately 1500 m^2 planar area. The visual censuses only detected three species of morays (no densities available) whereas the rotenone sample collected 212 specimens of 14 species. This represents 17.7 morays 125 m^{-2} assuming a planar area, though the density would be lower if total surface area were used because the patch reef was at least 8.5 m high with high live coral cover, thus presumably highly structurally complex. The density based on the actual surface area is therefore likely to fall within the range of the estimates from my method.

Kulbicki (pers. comm.) obtained densities of morays and other fish species in New Caledonia and other locations in Polynesia by rotenone collections of known surface area (N = 68). His average densities obtained with rotenone (1.74 to 4.12 morays 125 m^{-2}, depending on the biotope and including 35 species) were much higher than those he obtained in daytime visual censuses (~0.03 moray 125 m^{-2}, including 12 species). They are, however, very close to my estimates. These values may be more difficult to compare here though due to the differences in locations, number of species present and even size of morays. The morays in Kulbicki's study were on average twice as large as in my study (~0.7 kg vs. ~0.3 kg). Therefore, despite a slightly lower density, biomass in his study area should be greater.

In summary, the densities I obtained suggest that morays are much more abundant than generally reported in day visual censuses. The discrepancy between my

densities and those of other studies is unlikely to be entirely explained by spatial and temporal variation because densities of morays recorded in other recent studies done in Barbados were also low. My densities and biomasses are also of the same order of magnitude as those from chemical collections which are generally presumed much more complete and accurate than visual estimates for cryptic species. However, chemical collections seem better at determining the density of small individuals. I believe that the focus on the moray eel family, the experience of the observers and the modifications to the method for this group are likely to have played a major role in explaining why I found much higher densities than in other studies.

4.3.2 Comparison with other families of predatory fish

Several studies have excluded morays and other nocturnal fish from their surveys and assumed that their numbers were negligible. However, studies such as Parrish et al. (1986) and Stimson et al. (1982) suggest that they are in fact quite important both in relative numbers and in piscivorous impact. Here, I compare muraenid density and biomass with those of other well known predatory families.

For the Serranidae in the Caribbean, average densities range from less than 1 to 8.75 fish 125 m^{-2} (Randall 1963, Roberts 1995, Hodgson & Liebeler 2002, Miller & Gerstner 2002). For the Lutjanidae, estimates are between 0.16 and 20 fish 125 m^{-2} (Randall 1963, Roberts 1995, Hodgson & Liebeler 2002, Miller & Gerstner 2002). Density estimates for reef resident predators including lutjanids, serranids and haemulids in the Caribbean and Bermuda are between 5.83 and 18 fish 125 m^{-2}

(Bardach 1959, Randall 1963, Roberts 1995, Miller & Gerstner 2002) and predator biomass estimates range from 0.6 to 2.2 kg 125 m^{-2} at Saba Island, Netherlands Antilles (Roberts 1995), to 3.36 kg 125 m^{-2} in Bermuda (Bardach 1959), and 7.16 to 7.34 kg 125 m^{-2} on natural reefs in the U.S. Virgin Islands (Randall 1963).

Overall predator densities around the world range from less than 1 to 37.5 fish 125m^{-2} (Bardach 1959, Randall 1963, Roberts 1995, Russ & Alcala 1996, Connell & Kingsford 1998, Stewart & Jones 2001, Miller & Gerstner 2002) and biomass from 0.6 to 8.25 kg 125m^{-2} (Bardach 1959, Randall 1963, Roberts 1995, Russ & Alcala 1996, Jennings & Polunin 1997). These estimates vary depending on the method used, the habitat and area surveyed, history of the fishery and number of species and families of predatory fish included. Most did not include morays. For these reasons, the ranges presented should be considered with caution and are only presented for rough comparisons. My average moray density (5.6 morays 125 m^{-2}) and biomass (~ 2 kg 125 m^{-2}) are well within the range of other commercially important predatory families usually recorded (< 1 to 20 fish 125 m^{-2}) and their biomass appears even large for a single family compared to those reported for several predator families combined (0.6 to 8.25 kg 125 m^{-2}).

4.4 Moray density and size in relation to species and habitat

4.4.1 Relative abundance and biomass of moray species

Moray species found at the study site differed in their abundance. Generally, spotted morays were the most abundant (40% of morays seen), followed by goldentail (25%),

viper (23.5%) and rarer chestnut (6.5%) and chain morays (5%). Green and purplemouth morays seen in the area appeared in very low abundance. In terms of relative importance for biomass, the spotted moray was the largest as well as the most common species and it made up most of the moray biomass (81%). It was followed in importance by viper (8%), goldentail (6%), chain (4%) and chestnut morays (<1%), corresponding to the decreasing order of their maximum length. These values suggest that the spotted moray is the most important moray species in Barbados. The proportion of these species obtained through chemical collections by Randall (1963) on two fringing reefs corresponded well with the above values, with spotted morays being the most abundant (33%) followed by goldentail (31%), viper (23%) and chain morays (11%). The order for biomass was also similar but one large green moray made up over 50% of the total biomass at the two sites combined. In contrast, Randall found a very high abundance of individuals from the genus *Uropterygius* at one of the sites, suggesting that this species is common but not usually detected by visual census. The absence of chestnut morays from the collections is surprising, but this species was not described until 1976 (Böhlke & Böhlke 1976) and some may have been misidentified as *Uropterygius* sp.

Abrams et al. (1983) determined that the spotted moray was also the most abundant moray species on Coki Reef, U.S Virgin Islands, followed by the goldentail moray, but in different relative proportion from my study (5:1 vs. 1.6:1). Also similarly, the chain moray and an unidentified brown moray (which may have been the chestnut moray) were in low relative abundances; each making up 4% of all sightings (Abrams

et al. 1983). In contrast, however, the proportion of viper morays was much lower in their study than in mine (5% vs. 23.5%), perhaps because only day censuses were performed by Abrams et al. (1983).

The two main species found by Young (1992), in the large shallow backreef habitat with seagrass beds that he surveyed in Belize, were the spotted and purplemouth morays that co-occurred in similar abundances. Other species (green, goldentail and chain morays) were rarely seen in or near the area surveyed. In Barbados, the only purplemouth moray seen at a study site was also in a shallow backreef habitat but this species was definitely not as abundant as the spotted moray. Böhlke & Chaplin (1993) reported finding purplemouth morays in shallow rocky reefs rather than in coral reefs, being frequently caught in turtle grass beds. Young (1992) also reported that divers in Belize claimed to have never seen purplemouth morays on the forereef either, and Abrams et al. (1983) did not see this species in the deeper reef habitat they surveyed. This suggests that this species may prefer shallow backreef areas, possibly where seagrasses are present, and that their abundance at the sites studied in Barbados is lower than at other locations. Green morays were also rare at those sites but they appear to be more abundant in other areas such as in Florida, where it is the species most frequently seen on surveys (http://www.reef.org/data/twa/geog.htm). This species requires large shelters to accommodate its size, and such shelters did not appear to be very abundant at the sites surveyed in Barbados.

On widespread monitoring fish surveys in the Caribbean, the species seen in the highest percentages of dives are generally in the following order: spotted, goldentail, green and chain morays, with rare sightings of purplemouth, viper, chestnut and other moray species (http://www.reef.org/data/twa/geog.htm). This order of relative frequency of encounter and differences throughout the Caribbean are thought to be related to their relative abundance but may also be affected by habitat preferences, size and the ability of the divers to detect and correctly identify them.

4.4.2 Density and size in relation to habitat

The relative abundance and biomass of each species varied differently among my study sites. Some of these differences could be explained by differences in habitat at the different sites, which could affect moray distribution. Moray density and size (TL for the three most abundant species) did not differ significantly between zones at each site, but power to detect differences was low due to the low sample size in each zone (3-4 transects) and the high variance in density. There was a trend, however, for the fringing reefs to have a higher density in the spurs and grooves zone, a lower one in the crest and the lowest in the backreef zone. The extra zone (reef flat) on the reserve fringing reef had low relief but a moray density even higher than that of the spurs and grooves zone at that site. I had expected to find larger differences between zones since they varied in their shelter availability, which is much lower in the backreef than in the crest and spurs and grooves zones. The high density of morays on the reef flat was surprising, and it may have been related to the presence of juveniles of several other species and serve as a nursery habitat or a feeding ground for morays.

The lack of significant differences or particular trends among zones on the patch reef and bank reef sites was perhaps less surprising as the habitat was more homogeneous between the zones which differed mostly in depth. However, some zones had slightly higher densities than others.

A better relation between moray density and habitat was that with structural complexity; densities were higher in medium and high complexity than in low complexity habitats. All species were recorded in all complexity levels except for chestnut morays that were not recorded in low complexity areas. In general, low complexity habitats were found in the backreef zones and also in patch reef habitats with low coral head densities, whereas the medium and high complexity habitats corresponded to crest and spurs and groove zones and to patch reef habitats with moderate to high coral head densities. These results are consistent with those of several other studies where a positive relationship between fish abundance and/or richness and structural complexity was found (e.g., Luckhurst & Luckhurst 1978, Chabanet et al. 1997, Connell & Kingsford 1998, Nagelkerken et al. 2000b, Aburto-Oropeza & Balart 2001, Nanami & Nishihira 2002). This relationship is thought to be due to the increase in abundance of shelter sites with complexity and an increase in heterogeneity, allowing for more individuals and species to co-exist. Such relationship had never previously been reported for morays but could be expected since they are strongly associated with shelters. Morays in highly structurally complex habitats may still have been underestimated due to the impossibility to verify every shelter in some areas. Morays found in low complexity areas such as the

backreef were usually seen in the few shelters available and thus where complexity was higher locally (e.g., a coral head). This suggests that spatial scale is important when determining complexity and that microhabitat variables probably play an important role in moray distribution.

Average moray density did not differ significantly among the reef sites studied. The bank reef had a slightly lower estimated density (~5 morays 125 m^{-2}) than the other sites (~6 morays 125 m^{-2}), but its biomass was the greatest (3.7 kg vs. < 2 kg 125m^{-2}). When broken down by species, differences in species contribution to the site abundance and biomass became apparent. Spotted morays were the most abundant species (being especially abundant on the bank reef), except on the non-reserve fringing reef where viper morays were the most numerous. Goldentail morays were most abundant on the reserve fringing reef and least abundant on the bank reef. These results are generally consistent with those of Abrams et al. (1983) who reported total numbers of morays in three habitat types studied as similar, but with variation in relative abundance of species among them. They found that spotted morays were more abundant in sandy areas interspersed with coral heads and denser coral head habitats (i.e., patch reef habitats like on the bank reef), whereas viper and goldentail morays were seen most frequently in coral over rock habitat (continuous reef, i.e., similar to fringing reefs). The reserve fringing reef and the patch reef habitat had similar overall densities of the three most abundant species, which is hard to explain since they constituted very different habitats.

In terms of size differences between sites, spotted morays were larger on the bank reef, and because their highest density was also at that site, their biomass on the bank reef was the greatest. The lowest spotted moray biomass was on the non-reserve fringing reef where they had the lowest density, but where their size was no statistically different than at the other sites. There were no significant size differences or trends detected for the other species among the sites.

The general habitat differences found at the study sites were not sufficient to explain the patterns of abundance and biomass of the species. The difference in the abundance, size and biomass of spotted morays might suggest an effect of fishing because it is the only species commonly caught in traps, and they were found in low density and biomass at one of the two fished sites. Viper morays were concomitantly much more abundant at that site. This may indicate a competitive or predation interaction between spotted and viper morays, but this cannot be determined with certainty with so few sites. Fishing intensity on the non-reserve reefs studied appeared low during the study period, and poaching did occur on the reefs in the reserve (mostly by hook and line at night and spearfishing). Therefore, this may have reduced possible differences in fishing intensity inside and outside the reserve and confounded potential fishing effects on the other fished reef (patch reef).

Other factors that potentially affected the apparent density of morays at the different sites include the weather and lunar cycle. Spotted and purplemouth morays were previously found to forage more frequently on dark and inclement nights (Young

1992). For this reason, I tried not to cluster sampling of a site in time or during particular weather conditions, but most of the bank reef was sampled at the end of the study due to the impossibility to access that site for a period of time. By chance, all the non-reserve fringing reef transects were censused on the two darker phases of the moon. Therefore, the higher abundance of viper morays and the lower abundance of spotted morays at that site might be correlated with different visibilities on darker moon phases. Weather was not recorded systematically but there could also be a correlation between weather and the visibility of some species as it can affect turbidity and hence light levels which in turn can affect fish behaviour (Harmelin-Vivien et al. 1985, Young 1992).

4.5 Microhabitat characteristics affecting moray shelter site use and distribution

Most of the morays observed were using shelters, but species were found to differ in the position of their shelters relative to the reef structure. Although all moray species were found in most positions, spotted morays were located mostly in positions closer to the sea bottom such as under coral heads, at the bottom of spurs or on the reef flat, whereas goldentail and viper morays were generally seen on the spurs or coral heads, with goldentail being more often on top and viper on the sides. The pattern was not as clear for the rarer species, but chestnut morays were also mostly seen on the top and sides of reefs. There was also evidence of differences in shelter position with size-class for viper and spotted morays where, in general, smaller size classes are found more often on flat areas and top of structures, medium on the top and sides and large and very large at the bottom of and under structures. This thus produced a

vertical zonation pattern by species and size-class with some overlap. An association between shelter position and type was also found with generally more morays seen in crevices at the top, in holes on the sides and in cavities at the bottom of or under reef structures.

Fishelson (1997) also reported larger individuals of *Gymnothorax* spp. to be found closer to the sea bottom and smaller ones higher on the rocky wall. Vertical zonation on a small scale in coral reefs has not been the focus of much research. On a larger scale, Gosline (1965) described a zonation pattern for some closely related species showing little overlap along the rocky slope of Hawaiian Islands, which seemed partly structured by wave action. Also, Vivien (1973) classified fish groups based on a vertical zonation according to where they live relative to the reef structure (within, on, close to) and the water column (pelagic, surface). A similar pattern of small scale vertical zonation to the one I found was reported by Molles (1978) for other fish families present on artificial reefs. Species appeared stratified in vertical bands on the reefs with some overlap, supporting the idea of vertical zonation as a mechanism for resource partitioning.

In general, morays were seen most often in holes, but spotted morays differed in that they used cavities more frequently than the other species did. There was also a trend for spotted morays to change their shelter type use with size by using progressively more crevices and cavities and fewer holes when larger. The apparent preference of morays for holes appears related to their body size and shape and to the amount of

cover provided by this type of shelter (maximum cover) compared to the other types identified.

Shelters are known to be important for reef fishes mostly as refuges from predation (Shulman 1985, Hixon & Beets 1989, Hixon 1991, Buchheim & Hixon 1992, Hixon & Beets 1993) but few studies have looked at shelter preferences and microhabitat use (e.g., Roberts & Ormond 1987, Hixon & Beets 1989, Hixon & Beets 1993, Patzner 1999, La Mesa et al. 2002). Hixon & Beets (1989) studied shelter characteristics in fish communities on artificial reefs and found that hole size was an important characteristic, with fish choosing holes of size close to their own and that those could be a limiting resource. Consistent with my observations, morays were also found by Hixon & Beets (1993) to prefer holes in which their body just fit. In my study, as in others (Abrams et al. 1983, Young 1992), shelters for morays did not seem limiting because a large proportion of apparently suitable shelters appeared to be unoccupied, but the preferred type and size could be more difficult to find for certain species or certain size classes. Abrams et al. (1983) described typical shelter spaces for morays to be about 0.5 m^3 with one or several openings and with an average entrance diameter of 10 cm for goldentail and 23 cm for spotted morays, which seem a bit large compared to the average body diameter that we observed (<5 cm for goldentail and <8 cm for spotted morays). These spaces were typically found in lobular corals for goldentail morays, where they inhabited small interstices, and in large coral heads for spotted morays (Abrams et al. 1983). The use of more cavities and fewer holes in larger spotted morays might indicate that appropriate holes for

their body diameter and length may be limiting or that as morays become larger, their need for cover decreases as they become less vulnerable to predation or abiotic factors. Alternatively, the preference for holes could be related to a function other than just cover, for e.g., the support it provides. It was noted that when goldentail morays in shelters were captured by fish hooks for diet and measurements, they were able to resist even great force in pulling them out of their hole. This 'grip' could be used in providing stability for handling a struggling prey or in escaping predation through a quick retreat or a firm hold.

The association between shelter position and type suggests that the presence of certain moray species and sizes at certain positions is related to the distribution and abundance of preferred shelter types at those positions. The availability of each shelter type on the reef was not quantified due to the difficulties involved in measuring and characterizing them, but larger shelters such as cavities appeared generally more abundant at the base of structures where erosion of coral rocks occurs, whereas small holes and crevices were typically found higher, associated with live coral such as finger coral (*Porites porites*) and lobular corals. This could possibly explain how species with different maximum sizes and different size classes could be distributed vertically, with smaller morays found higher on structures and larger ones lower or under the structure. Availability of large shelter sites is thought to be an important factor affecting the distribution of large fishes, and there is some evidence of correlation between the availability of such shelters and the number of large fish (Williams 1991). Hence, not only vertical position on the reef but also the

distribution of shelters of appropriate size among zones and sites will likely affect the distribution of morays. Differences in the relative abundance of coral species making up the shelters and their morphology which changes with depth could have affected the abundance of moray species at the study sites. For example, this could help explain why there were more large spotted morays on the bank reef where spaces underneath the numerous coral heads provided them with shelters of suitable size.

Alternative hypotheses that could explain the vertical distribution pattern observed include competition for shelter sites, distribution of preferred prey, distribution of predators or a combination of all these factors. There is little evidence at present to support any of these hypotheses. In contrast with several other reef fish species (Shulman 1985), no moray has been seen aggressively defending a shelter, and more than one individual have been seen sharing a shelter without apparent aggression (pers. obs., Young 1992). Shelter use according to prey distribution is difficult to determine because the diet of moray species is still poorly known. Similarly, predation on morays is rarely observed, but they are known to be eaten by transient and resident piscivores, including other morays (Randall 1967, Parrish et al. 1986, Young 1992).

4.6 Validity of the method

This study detected significantly higher densities of morays at each step of the modified census method from 1) using a fixed width transect searched slowly in a zigzag pattern to 2) adding additional individuals sighted on a second passage, to 3)

basing the density calculation on the time when each species is most visible (day or night, results from two passages) and finally 4) correcting these densities based on an estimate of the proportion of individuals missed.

Carefully searching all shelters on a transect of fixed width at close range is an important improvement for counting cryptic but relatively immobile species. Swimming a zigzag path over a relatively wide transect was necessary to search the entire area with the same effort because the habitat was too heterogeneous to survey long narrow transects of equivalent area. Methods involving the count of fish away from a central line, the use of fixed and/or fast swimming speeds or of point counts with stationary observers are not suitable for species that hide in the reef structure because distance, speed and position have a strong effect on detection (Thresher & Gunn 1986, Cheal & Thompson 1997, Thompson & Mapstone 1997, Kulbicki 1998, Kulbicki & Sarramégna 1999, De Girolamo & Mazzoldi 2001). Fortunately, such species usually show a limited avoidance response to divers and allow for a small distance of approach for close inspection (Harmelin-Vivien et al. 1985). The experience of the observers is also an important factor affecting the detection of morays as indicated by the assistants having significantly lower counts on the first passage than the more experienced researcher, even after training. Similar observer differences in counts of fish have been noted in other studies and appear to be difficult to eliminate (Christensen & Winterbottom 1981, Harmelin-Vivien et al. 1985, Thompson & Mapstone 1997, Kulbicki & Sarramégna 1999). The surface area of the survey and its duration are other factors that seem to affect observed moray

densities because censuses of smaller areas tended to detect more individuals, especially small ones, possibly by increasing the time spent per unit area (pers. obs.). Coincidentally, the studies finding the highest densities of morays were also the ones focussing their search effort on relatively small areas (Smith & Tyler 1972, Fishelson 1997, Whiteman & Côté 2002). It is suspected that the higher densities of morays found on single daytime passages in this study were not simply the result of spatial and temporal differences in study sites, but rather were due to the search method.

Using more than one passage over the same transect may improve the accuracy of the counts of species that are cryptic and thus overlooked on a single passage or of those that are intermittently visible and thus could not be seen at all (e.g., Sale & Douglas 1981). However, adding counts from two passages would not be appropriate for mobile fish where new individuals moving into the survey area could not be distinguished from individuals previously counted. Switching sides by the two observers for the second passage was expected to increase the chances that morays in a location overlooked by one observer could be detected by the other. For morays, adding new individuals detected on the second passage significantly increased the estimated density. This was likely due in part to the emergence of individuals that were hidden from view. Only 46% (night) to 60% (day) of the individuals seen on the first passage were resighted on the second passage, even though their location was marked. This suggests that there are relatively frequent changes in visibility. There are few data on the frequency of such changes in visibility, but our observations of morays tagged with acoustic transmitters showed that a moray in a shelter could

change from visible to non visible over an hour or less. Knowing the frequency of these variations would influence the optimal time interval chosen between repeated passages. It is unlikely that our counts were significantly affected by the immigration of new individuals in the area because only 14% of all individuals sighted were seen actively swimming and the censuses were done over a relatively short period. In addition, other studies indicated that residency of morays in a shelter were usually longer than one day (Abrams et al. 1983, Abrams & Schein 1986, Young 1992).

Counts of four out of the five species of morays recorded were significantly different between day and night. The fifth species showed a similar trend but it may not have been significant due to the small sample size. Also, four of the five species had higher counts at night, which appeared to be the time of greatest activity for these species. Alternatively, for other species, a greater visibility at night might result from a reduced ability to avoid the divers (e.g., for sleeping fish). These differences in abundance suggest that neither daytime nor night time surveys alone would accurately reflect the density and diversity of moray species on these reefs. The use of counts of each species at the period when it was most abundant had the largest effect of any step on the average estimated density by increasing it nearly two-fold compared to the previous step and making the new estimate 2.6 times greater than that from single daytime censuses. Unfortunately, very few fish censuses are done at night (Smith & Tyler 1972, Stone & Pratt 1979, Fishelson 1997, Nagelkerken et al. 2000a), even when studying species known to be nocturnal. This method of combining counts of species at different times is unlikely to overestimate the density

of morays except if they were not counted in all habitats in which they occur or if they were counted during periods of aggregations. This could be the case for other species such as grunts that migrate to feed on seagrass beds at night and aggregate on the reefs during the day (Helfman 1986). Although some morays (spotted and purplemouth) have shown similar movement patterns in areas where seagrass beds are present (Young 1992), the ones we counted on the reefs at night were generally more active than during the day. Some were seen feeding, and a greater proportion was seen swimming suggesting that they use reef habitats at night at least to some extent. Goldentail morays are not known to leave the reef or to have a great mobility and they appeared more active during the day than at night. Therefore, it is unlikely that their lower numbers at night are the result of migration into other areas. Moreover, few morays have ever been seen in close proximity and they are not known to aggregate. If a portion of the moray population did migrate into other non-surveyed habitats at night, then densities of individuals using the reefs would likely be underestimated.

Although repeat censuses and comparisons between counts from visual census and collections using ichthyocides indicate that censuses often underestimate fish abundance (Stone & Pratt 1979, Christensen & Winterbottom 1981, Sale & Douglas 1981, Brock 1982, Harmelin-Vivien et al. 1985, Lincoln Smith 1989, Sale 1997, Ackerman & Bellwood 2000, Willis 2001), correction factors have been rarely used to adjust observed densities and biomass. Sale & Sharp (1983) used a correction factor for the effect of reduced detection with increasing transect width to estimate

true densities. Christensen & Winterbottom (1981) calculated correction factors for densities of fish seen in tide pools on visual censuses compared to the actual numbers sampled using rotenone. The predictive power of their correction factors was then determined and was found to be effective in determining the abundance of most species except the secretive ones. These corrections depended both on the site and observers. The correction factor I used is related to mark-recapture methods which are widely used in the estimation of fish populations (Greenwood 1996). Statistics and calculations of confidence intervals of the estimates are however difficult in this case and statistics were limited to data prior to correction. Like mark-recapture methods, the correction is subject to a variety of biases. For example, the timing of the second passage could affect the proportion of fish that are visible on the second passage by not leaving enough time for previously hidden or disturbed individuals to appear and would underestimate true density. On the other hand, if the time interval is too long, individuals can move between shelters or immigrate in the area, resulting in an overestimate of the population. In addition, if size classes or species differ in their visibility, an average correction factor will increase the estimate of individuals for more visible groups (e.g., large or more conspicuous individuals/species) and decrease that of less visible ones (e.g., small fish). Although having the observers change sides and perform a second passage probably increased the accuracy of the counts on the transect, it could have resulted in a bias in the correction factor if the proportions seen varied consistently between observers. This might be the case if the proportion seen is dependent on observer experience in addition to the exposure of the morays. For example, during the second passage, the observer who finds a

greater proportion of the morays visible surveys an area with a higher proportion of morays left undetected on the first passage, whereas the observer who finds a smaller proportion now surveys an area where a smaller proportion of morays is left to detect. This increases the total counts but also inflates the correction factors. Given that both passages over the transects were performed in an average of 37 minutes and a maximum of 66 minutes, and that the inflation due to differences in observers should be small, I suspect that the density value is still an underestimate of the actual moray density.

If differences between night and day were simply a matter of missing a proportion of the fish, then the correction factors could be used to outweigh the inconvenience of using night censuses. However, the correction factors varied with time of day, and were higher at the time when species were most abundant (which was at night for four of the five species). Consequently, correction factors are time-specific and counts made during the day corrected by day correction factors still underestimate density of most species. Moreover, some species were never seen during the day, therefore making their density impossible to estimate from day censuses. Furthermore, the lower numbers during the day may reduce the precision of the counts.

4.7 Components of the method permitting weight and biomass estimation

Since some morays can reach large sizes, they have the potential for a high predatory impact on communities. Biomass is therefore a variable of interest in determining

their potential impact in a more accurate way than simply by abundance. Often, authors neglect to give moray total length because they are not completely visible in censuses or are more difficult to handle when captured (e.g., Robichaud 1996, Chapman & Kramer 2000). Methods to measure them in situ have included luring them out of their shelter (Tupper pers. comm.) and/or capturing and anaesthetising them (Young 1992), both of which were time consuming and had relatively low success.

Head measurements are a feasible, practical alternative because they show a good relationship to total length and weight and because the morays usually allow a close approach by slow moving divers (often close enough to almost touch them with a ruler). The use of a ruler should have reduced biases in size estimation found in other studies (e.g., St John et al. 1990) by providing a consistent reference against which to measure a portion of the moray.

4.8 Implications of moray abundance

Some large morays are the target of spearfishers and can be caught by hook and line and fish traps which they usually enter to feed on other fish (pers. obs.). When captured, they are generally killed for consumption or used as bait (pers. obs.). Thus, large morays may become more abundant in reserves than in adjacent fished areas and exert a significant predatory impact. In general, however, morays are not targeted by commercial and artisanal fisheries. Their slender shape also makes them harder to retain in traps, and therefore, even fairly large individuals are not caught as

by-catch. As a result, morays could be an important part of the predatory fish component of communities in heavily fished areas. As such, more attention should be given to this group of fish. However, their limited capture by fisheries in several areas and the difficulties of counting them suggests that morays are not good candidates as indicators of overfishing in monitoring programs. Reef Check added them to their list of indicator species in 2001, but, as it was mentioned earlier, 81% of their dives failed to detect morays (Hodgson & Liebeler 2002), potentially due to poor detection rather than absence.

This study indicates that morays are not as difficult to study as it is generally assumed. Preliminary trials during the course of this study showed that it is possible to safely anaesthetise, handle, tag and measure morays underwater (see Appendix II for method), and that individuals can also be tagged with acoustic transmitters and tracked to study their movements and habitat selection. Behavioural observations can also be made in situ (see additional notes on natural history in Appendix III).

4.9 Limitations and future improvements

Overall, this method appears to be the best option found so far to count morays and possibly other cryptic fish in a non-destructive way. It also permitted the gathering of additional information from the individuals sighted such as microhabitat characteristics and measurements for biomass estimation. It has however its limitations and could benefit from future improvements.

Some possible improvements should include a more rigorous training and attempt to identify and correct particular observer biases before and after the study. Then, rather than have the observers switch sides for the second passage, each should resurvey the same side and pay similar attention to keep the probability of detection constant. The use of the same species correction factors in all habitats possibly acted to reduce differences among zones. Sample sizes should ideally be larger for each zone and correction factors could be made habitat-specific. There is also some evidence suggesting that lunar cycle and weather (both affecting light levels) can have an effect on moray abundance and they should therefore be recorded and included in the analyses. There are indications that smaller individuals and species were underestimated by this method, and therefore, morays are probably still more abundant than I reported. A study of the smaller species should use narrower transects and additional repeated passages over the same area.

The problem of determining the proportion of the actual moray community the observed and estimated densities represent still remains. The use of other approaches such as quantitative chemical collections may be needed to verify those estimates, their actual biases and the accuracy of the method. I made no attempt at quantifying short term visibility patterns in this study. Since visibility patterns of morays can vary over a short period of time, knowing how they vary could help determine what proportion of the population is not visible at any given time, help determine the accuracy of the method and obtain a better estimate.

In conclusion, this study showed that morays can be censused visually and that they are abundant numerically and in terms of biomass compared to other predatory families, much more than generally reported. The high abundance and biomass were shown to be likely the result of the improved method and not simply due to differences in time and location. Several species co-occur and they are widely distributed among reef habitats of Barbados. Consequently, these predatory fish, especially the larger species, should be considered as important and potentially having a large impact on the reef community. As such, more attention should be paid to this family in coral reef ecological studies.

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APPENDIX I. Tables for the results of model selections for association between variables related to activity, exposure and shelter site use of different moray species

Statistical analyses

Log-linear models were used to test for significant associations between variables by comparing counts of individuals in each combination of categories. The minimal model accurately describing the data was selected using backwards elimination. Each interaction is successively dropped from the model starting with the highest order to test for a resulting significant change in likelihood ratio (L.R.) χ^2. The degrees of freedom and L.R. χ^2 changes are calculated by subtracting the L.R. χ^2 from the model with the interaction from that of the model without that interaction. When such change is not significant, the interaction term is dropped from the model until no more interactions can be dropped without resulting in a significant change in L.R χ^2. The resulting model is the minimal model that is valid including the most important associations between variables.

Table 1. Model selection procedure to determine the significant variable interactions between moray species, activity level and time of day (for all 5 species, 2 activity levels and 2 time periods = 20 cells, 209 cases, (>5 per cell))

Model & factors included	df	L.R. χ^2	p	df	L.R. χ^2 change	p
Saturated Species + Activity + Time + (Species*Activity) (Species*Time) + (Activity*Time) + (Species*Activity*Time)	0	0	-			
1. Saturated model - (Species*Activity*Time)	4	1.907	0.753	4	1.907	0.753
2. Model 1 - (Activity*Time)	5	5.230	0.389	1	3.322	0.068
3. Model 2 - (Species*Activity)				4	33.208	<0.001
4. Model 2 - (Species*Time)				4	87.757	<0.001
Minimal = Model 2 Species + Activity + Time + (Species*Activity) + (Species*Time)						

Table 2. Model selection procedure to determine the significant variable interactions between moray species, body exposure and time of day (for the 3 most abundant species, 4 exposure levels, 2 time periods = 24 cells, 115 cases, ~5 per cell)

Model & factors included	df	L.R. χ^2	p	Df	L.R. χ^2 change	p
Saturated Species + Exposure + Time + (Species*Exposure) + (Species*Time) + (Exposure*Time) + (Species*Exposure*Time)	0	0	-			
1. Full model - (Species*Exposure*Time)	6	6.923	0.328	6	6.923	0.328
2. Model 1 - (Exposure*Time)	9	11.497	0.243	3	4.574	0.206
3. Model 2 - (Species*Exposure)				6	22.239	0.001
4. Model 2 - (Species*Time)				2	44.205	<0.001
Minimal = Model 2 Species + Exposure + Time + (Species*Exposure) + (Species*Time)						

Table 3. Model selection for determining the significant variable interactions between moray species, shelter position and shelter type (for 3 most abundant species, 4 positions and 3 types = 36 cells, 150 cases (4.2 or ~5 per cell))

Model & factors included	df	L.R. χ^2	p	df	L.R. χ^2 change	p
Saturated Species + Position + Type (Species*Position) + (Species*Type) + (Position*Type) + (Species*Position*Type)	0	0	-			
1. Full model - (Species*Position*Type)	12	9.656	0.646	12	9.656	0.646
2. Model 1- (Species*Type)	16	16.811	0.398	4	7.155	0.128
3. Model 2 - (Species*Position)				6	30.859	<0.001
4. Model 2 - (Position*Type)				6	55.689	<0.001
Minimal = Model 2 Species + Position + Type + (Species*Position) + (Position*Type)						

APPENDIX II. A technique for anaesthetising and tagging moray eels underwater

In order to study the habitat use and mobility of morays, a method to handle, measure and tag them underwater was developed. This method was elaborated to safely handle a potentially dangerous fish while SCUBA diving without a boat or other surface platform and to minimise disturbance to the fish. No other similar underwater technique was found in the literature. The technique could be used or adapted for a variety of fish species that pose a threat to the handler or where it is preferred to perform work underwater to minimise ascents and descents by the divers, e.g., in deep water, or to prevent damage to the fish from expansion of the swim bladder during ascent. In order to obtain additional information on the mobility of morays, we also inserted internal acoustic transmitters in eels, but implantation was done in the laboratory. Sonic tracking was discontinued due to tag failures, and therefore does not appear in the thesis.

Spotted morays (size range: 740-1050 mm) were caught using Antillean traps or by luring them into a mesh bag using bait. The Antillean traps were modified to have two large doors (~50 x 50 cm), one on each side, to allow a diver to release fish underwater. Once a moray was caught, two divers swam to the trap with their equipment. This included a net (soft, fine mesh bag on a hoop with a handle) with a drawstring that allowed it to be closed once the moray was inside and a 1 m PVC pipe (10 cm diameter) with a cap at one end and a slot at the other into which a PVC door

could be inserted to prevent the escape of the fish. A small hole in the pipe allowed the anaesthetic to be introduced with a syringe. One diver captured the moray in the trap using the net which was then closed to prevent escape. Then, the pipe was placed at the opening of the net and the string was released slightly and retightened to form a seal around the pipe. The divers then gently guided the moray into the pipe from the net. Once the moray was in the pipe, the PVC door was slid into place. A diver then introduced the anaesthetic using a 10 cc syringe. In the future, the design of the door of the pipe could be improved by being made more watertight, to prevent loss of anaesthetic. Syringes needed to be weighted or firmly attached to a mesh bag to prevent them from floating away.

Clove oil was used as an anaesthetic. Based on Eristhee et al. (2001), a 10% clove oil solution was prepared by dissolving 10 ml of clove oil extract in 90 ml of ethanol. The pipe could contain about 7 l of water in addition to an adult moray. For that volume, at least 5 ml of clove oil solution were needed to anaesthetise morays larger than 750 mm within 3 to 5 min. After about 4 minutes (depending on the size of the moray and movement within the pipe), anaesthesia was checked by opening the door and sliding the moray out while keeping the net around the pipe to prevent escape. If the fish was still moving or showing respiratory movements, it was reinserted in the pipe and more anaesthetic was injected. Once the fish had stopped breathing, it was returned to the net which was again closed. It was then measured and tagged in two locations through the mesh of the net using Floy anchor tags and tagging gun. Recovery was rapid (< 2 min) because the anaesthetic dispersed quickly. Fish were

kept in the net during recovery (usually < 5 min) and were then released. When possible, morays were followed and observed to ensure full recovery.

Eleven of 12 morays captured were successfully anaesthetised, measured and/or tagged underwater. Three additional morays were tagged from a boat or from shore. Half of these 14 morays were recaptured or resighted at least once. Tag retention did not appear to be high because one of the two tags inserted was often missing on recaptured or resighted individuals. This seem to be the case more frequently for tags inserted through the dorsal fin near the tail compared to the ones behind the head, inserted through the fin or in the musculature. Perhaps this was because tags were removed when morays squeezed through narrow openings, knotted themselves or because they were able to bite them off.

The method reduced the use of a boat and the time taken to go back to shore for tagging. Previous tagging studies using fish captured in traps usually lifted the trap out of the water and emptied the fish into a tank on the boat before the fish were tagged. Tagging under water subjected morays to fewer manipulations and required much less time. Such in situ tagging enabled the morays to stay immersed throughout, which seemed to reduce their stress and the risk of bite injuries to the handler. The moray could also resume breathing fresh seawater immediately and could be released exactly at the point of capture. Recovery occurred rapidly (full recovery in < 10 min).

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APPENDIX III. Notes on the natural history of moray eels in Barbados

Spotted moray (*Gymnothorax moringa*)

Spotted morays were the most abundant and potentially the most ecologically important moray species on Barbados coral reefs. They were found in all areas surveyed and over a broad range of depths from < 1 to 18 m (8.2 ± 4.8 m, N = 77, (mean ± SD)).

Reaction to bait

Spotted morays seemed to be the most olfactory species. When presented with bait (fish scraps), they would readily emerge from cover to eat the bait and could be lured into a mesh bag even during the day, as reported by Young (1992). Moving a piece of fish in front of them did not seem to elicit a visual response as they did not orient their head towards the fish but it rather lagged behind, as if following a chemical plume. Morays caught in traps may have been attracted to the smell of injured fish. When we released or tagged spotted morays caught in traps, several regurgitated fish (up to three) that were presumably eaten while in the trap. Bardach et al. (1959) also concluded that spotted morays were primarily olfactory. However, Fishelson (1997) found that *Gymnothorax* spp. in the Red Sea were primarily visual and even followed the more olfactory *Siderea griseus* to bait.

Diet

Determining the diet of morays is difficult due to the difficulty of finding and capturing them and to the large proportion of empty stomachs (Hiatt & Strasburg 1960, Randall 1967, Parrish et al. 1986, Young 1992, Yukihira et al. 1994). All stomachs of spotted morays caught by means other than traps were empty (N = 4). In traps, they ate mostly parrotfish (*Scarus taeniopterus*, *S. iserti*, *Sparisoma aurofrenatum*), which seemed to be the most fragile species, often losing scales and becoming injured. Other species regurgitated included grunt (*Haemulon* sp.) and an octopus. An octopus beak was also regurgitated by a spotted moray captured in a trap. Because the moray had probably not been in the trap long enough to completely digest an octopus and octopi are not generally caught in traps, the moray presumably ate the octopus before it entered the trap. In the Virgin Islands, six spotted morays which contained food items had only fish in their stomachs (Randall 1967). Young (1992) found that crabs made up about 60% of the spotted morays' diet in Belize with the rest including fish and octopi. The morays there appeared to forage mostly in the seagrass beds. In general, larger morays appear to be more piscivorous (Yukihira et al. 1994).

Capture and recapture

Spotted morays caught in traps during the study were tagged (see Appendix II). Of the 14 morays tagged, half were recaptured in the same trap or observed one to three times in the same general area. Recaptures generally occurred within one month of tagging, 36 days being the longest period between tagging and recapture, but occurred

most frequently close to the tagging period (search and trapping ceased approximately two months after tagging). This agrees with other studies in which short-term resightings occurred within a small area, but some morays were recaptured much farther away a few months later (Abrams et al. 1983, Young 1992, Chapman & Kramer 2000).

Variations in colouration

A colour difference in two collected spotted morays of approximately the same size (760 mm and 802 mm) was observed. The smaller moray was a female (potentially close to spawning, with a red and swollen urogenital opening). The edges of its fins were white, and its background colour was yellowish. Two other adult females that had been previously dissected were of similar size (745 and 785 mm), but their fin margin colouration was not noted. The 802 mm moray was a male. The edges of its fins were black, and its background colour was white. Dissection of preserved specimens at the Natural History Museum of London did not confirm nor refute the possibility that fin and background colour are sexually dimorphic because all of 9 individuals large enough to be mature had a black fin margin, and none had ovaries. The only specimen with a white fin margin was small (606 mm), and gonads were not identifiable. A similar colour pattern difference was mentioned in Smith (1997), where individuals are described as having yellow or white background colouration with more or less dense black spots, and pale and small individuals as having pale fin margins, whereas darker and large individuals have dark fin margins. There has been no previous suggestion that this could be linked to sexual dimorphism however.

Other moray species are sexually dimorphic. For example, the ribbon moray (*Rhinomuraena quaesita*) changes sex and colour as it grows (Boruchowitz 2001), and some species have sexually dimorphic dentition (Böhlke & Randall 2000).

Interactions with conspecifics

Interactions between morays were rare and brief. In one instance at night, a large spotted moray was observed over sandy substrate with the anterior half of its body raised, about 1 to 2 m in front of another spotted moray in a shelter. Similar behaviour observed in *Gymnothorax kidado* was described as courtship and was followed by spawning (Moyer & Zaiser 1982). Unfortunately, one of the morays fled at the diver's approach. In another instance during the day, two large spotted morays briefly interacted. One swam towards the other, and they entwined their bodies before swimming quickly away in different directions. Entwining of the bodies has been associated with spawning behaviour for other moray species (Moyer & Zaiser 1982, Ferraris 1985). Vertical incisions were noted on the flank of the larger moray, similar to those left by a moray that bit the observer.

Interactions with cleaners

During the day, spotted morays were often seen in cavities at the bottom of spurs with cleaner gobies (*Elacatinus* spp.) on them. An injured spotted moray had two to three gobies on its head picking at the injury and the moray was twitching as if it were being bitten and trying to shake the gobies off. In at least one instance, cleaner shrimp (*Periclemenes pedersoni*) were observed on a spotted moray. Whether

morays actively visit the cleaning stations or whether gobies clean them when in their vicinity is not clear. It is not clear either what gobies eat on morays, because they do not have scales where parasites usually attach, but it is presumed to be mucus (pers. obs. and E.A. Whiteman pers. comm.). However, at least one species of parasitic monogenean platyhelminth has been described from *G. kidado* in Japan (Kearn 1993).

Goldentail morays (*Gymnothorax miliaris*)

Goldentail morays were common at the study site. They were also found in all areas surveyed but were in areas slightly shallower than spotted morays on average (< 1 – 19.5 m, 6.0 ± 4.3 m, N = 68 (mean ± SD)). They could be best observed during the day, but little activity was observed because they mostly stayed within their shelter.

Reaction to bait and capture

Contrary to congeneric spotted morays, goldentail morays appeared primarily visual. Head motion tended to follow the position of bait more closely than that of spotted morays. They also appeared to react to smell (based on observations made when squirting fish extracts in their vicinity). Their body diameter was typically smaller than the mesh of commercial traps (4.1 x 3.2 cm). Therefore, they were never captured in these traps. Small minnow traps (< 1 cm mesh size) baited with rotten fish, live crabs, crab or fish extracts also failed to capture them, even when placed next to their shelter. They would eat fish presented to them but were never successfully lured entirely out of their shelter.

The only way found to catch goldentail morays was by using a hook and line underwater. They readily swallowed a baited hook, and, once the hook was stuck in their jaw, they could be pulled out of their hole. This required considerable effort though. Once out of their hole, they would start knotting their body to free themselves and it was critical to place them quickly in a net or mesh bag. Goldentail morays appear to be more visual and diurnal than other species of Caribbean morays. In that respect, they appear more similar to other species of *Gymnothorax* in the Red Sea (Fishelson 1997).

Diet

Very little information was gathered on the diet of goldentail morays (6 of 7 guts of captured individuals were empty). An unidentified shrimp was found in the stomach of one individual. A goldentail moray was also observed attacking a small crab in daytime. This limited evidence supports previous reports that crustaceans are part of their diet (Pattengill et al. 1997, da Silva & Vanda 1998).

Interactions with cleaners

Only two individuals were seen with gobies cleaning them. Both species of cleaner gobies present in Barbados (*E. evelynae* and *E. prochilus*) have been reported to clean goldentail morays (Whiteman & Côté 2002).

Variations in colouration

A few goldentail morays were much lighter than the others (reverse colouration) with a yellow background and dark spots or a dark net-like pattern (Humman & Deloach 2002).

Viper moray (*Enchelycore nigricans*)

Viper morays were much more abundant than expected based on the literature but were observed only at night. They were found in most of the habitats surveyed from < 1 m to 18 m (5.1 ± 3.9 m, N = 39 (mean ± SD). They were quite shy, so we did not see much behaviour and we were not able to experiment with their response to bait as easily as with spotted and goldentail morays.

Diet

Only one viper moray was caught in an Antillean trap (dark red colouration, 813 mm TL). This species is generally more slender than the other species and most smaller individuals may have been able to pass through the mesh of the traps. A viper moray (475 mm TL) caught at night using quinaldine and nets regurgitated a small, undigested octopus. Another small specimen was caught using a hook baited with fish, but its stomach was empty. Small individuals at night snapped at zooplankton attracted to the dive lights. It is possible that with their very long pointed teeth, small viper morays could catch and eat these small organisms. No information on the diet of this species was found in the literature.

Variations in colouration

Differences in colouration in this species were marked. Humman & Deloach (2002) mentioned that, contrary to adults that are almost uniformly dark red-brown, juveniles have a light brown background with dark, bold reticulate patterns. However, the ones we observed tended to have a dark, purplish-red background with lighter mottled patterns and may have been at a more advanced stage of colour transition than the individuals described by Humann & Deloach (2002). Also, some large individuals with the elongated nostrils characteristic of adults still showed this mottled pattern.

Other species

Chain morays (*Echidna catenata*) and chestnut morays (*Enchelycore carychroa*) were rarely observed on the censuses. No chestnut and only two chain morays were captured, so little can be said about their diet and behaviour. We found evidence of crustaceans (small crabs) in the gut of the two individual chain morays captured, which matches previous reports (Randall 1967).

A green moray (*G. funebris*) was caught in a trap. It had eaten several parrotfish and a large spotted moray which were regurgitated as the observers approached the trap underwater. Spotted morays normally only regurgitated when netted and handled for anaesthesia and tagging. If this regurgitation suggests that green morays are more nervous in response to divers, this may have affected the ability of the observers to detect this species during surveys.

Additional notes on natural history

Morays much smaller than 20 cm were never seen. This could be because such small individuals were undetectable or that juveniles of most species do not use the habitats surveyed. Fishelson (1997) mentions seeing fairly high densities of juvenile morays (10 - 12 cm TL) in very shallow subtidal areas in the Gulf of Aqaba, Red Sea. I limited the search to reef areas deeper than 50 cm at low tide for practical reasons but it is not impossible that small morays could have been found in shallower water and/or other habitats where there is sand, loose rocks and coral rubble. H. Valles (pers. comm.) found that small morays in Barbados colonized small experimental patch reefs composed of pieces of coral rubble. An area of coral rubble (mostly dead finger coral) which was not surveyed in this study is found on the south side of the reserve fringing reef. It might serve as a nursery for juvenile fish such as morays as it provides small shelters and is an important habitat for recruits from other species (H. Valles, pers. comm., Öhman et al. 1998). Some morays are also known to bury themselves in the sand (Young 1992, Humman & Deloach 2002), and this might be the case for small juveniles and it would make them virtually impossible to detect by visual census.

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APPENDIX IV. Approval from Animal Care