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RESEARCH ARTICLE

Anguilliform fishes and sea kraits: neglected predators in coral-reef ecosystems

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Abstract Despite intensive sampling efforts in coral reefs, densities and species richness of anguilliform fishes (eels) are difficult to quantify because these fishes evade classical sampling methods such as underwater visual census and rotenone poisoning. An alternative method revealed that in New Caledonia, eels are far more abundant and diverse than previously suspected. We analysed the stomach contents of two species of sea snakes that feed on eels (*Laticauda laticaudata* and *L. saintgironsi*). This technique is feasible because the snakes return to land to digest their prey, and (since they swallow their prey whole) undigested food items are identifiable. The snakes' diet consisted almost entirely (99.6%) of eels and included 14 species previously unrecorded from the area. Very large populations of snakes occur in the study area (e.g. at least 1,500 individuals on a small coral islet). The snakes capture approximately 36,000 eels (972 kg) per year, suggesting that eels and snakes play key roles in the functioning of this reef ecosystem.

Introduction

Coral reef ecosystems are renowned as biodiversity hot spots (Roberts et al. 2002), but many are in crisis due to threats such as global warming, over-fishing and marine pollution (Walker and Ormond 1982; Linden 1999; Hughes et al. 2003; Riegl 2003). Such threats are worsening over time (Rogers 1990; Hughes 1994; Guinotte et al. 2003; Pandolfi et al. 2003; Sheppard 2003; Bellwood et al. 2004). To conserve these complex ecological systems, we need to understand how they function. Predation may exert a critical influence on complex ecosystems such as these, by enhancing the stability (resilience) of the whole community (Carpenter et al. 1985; McCann et al. 1998; Finke and Denno

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2004). Unfortunately, some biotic components of these systems are highly cryptic, and hence difficult to sample in any quantitative fashion. For example, moray eels are widespread in tropical oceans but are very secretive and often nocturnal, and hence difficult to sample. Consequently, their actual abundance and diversity remain poorly known (Kulbicki 1997).

We adopted a novel approach to address this problem, using data on feeding rates and prey types of sea kraits (sea snakes from the genus *Laticauda*) that are specialist predators on anguilliform fishes (henceforth named "eels" for simplicity). Sea kraits forage at sea but return to land to digest their prey. The snakes readily regurgitate freshly ingested prey items, facilitating dietary analysis (Heatwole 1999; Reed et al. 2002). High densities of sea kraits occur in many areas of the western Pacific Ocean (Heatwole 1999). Since 2002, we have been conducting ecological studies on two species of sea kraits within the New Caledonia lagoon, providing an extensive data-set on the eels consumed by these snakes. To compare our results to those from other methods of surveying eel populations, we have taken advantage of long-term surveys conducted to assess fish communities in the same region (Kulbicki 1997). Thus, these two large data-sets provide a robust opportunity to compare results obtained from classical sampling methods versus analyses of predator (snake) stomach contents. We specifically addressed the following issues.

- The densities and species diversity of the eel fauna, as assessed by classical sampling techniques (underwater visual censuses and rotenone poisoning).
- The densities and species diversity of the eel fauna, as assessed by forced regurgitation of snake stomach contents.
- The rate of prey consumption by sea kraits, and hence the overall offtake of eels by these marine predators.

Material and methods

Underwater surveys

The relative abundance and diversity of fish communities have been assessed in various reef ecosystems across the South Pacific Ocean, primarily based on underwater visual censuses but also (to a lesser extent) using rotenone, fishing lines, trawls and gill nets (e.g. Jennings and Polunin 1995; Kulbicki 1997; Samoilys and Carlos 2000; Willis 2001; Letourneur et al. 2000; Kulbicki et al. 2000). For the current study, we used data from transects [based on underwater visual censuses (UVC)] and rotenone poisoning stations. The UVCs were performed in a radius of 40 km around the snake sampling area (Signal Island). All rotenone stations were performed in the southwest lagoon within a 20 km radius of Signal Island. Within this area, the topography of the lagoon is well known (see http://www.shom.fr/ for precise maps of the area). The lagoon is approximately 15–20 km wide between the mainland and the barrier reef. The bottom is relatively flat, ranging between 10 and 29 m in depth, and slightly deeper toward the mainland. Two narrow passes (facing two rivers) open the external barrier and stretch from the drop-off to the lagoon for a distance of roughly 10 km with a maximal depth of 70 m. Thirty reef flats (0–15 m deep; 17 of them with small islets <10 ha) are scattered in this area of the lagoon. The drop-off is very steep: 1 km into the open sea the depths is greater than 150 m, and quickly reaches 800 m. Our surveys were performed on shallow reefs, easily accessible by the divers (0–30 m); thus, the passes and the deep drop-off were not sampled. Other parts of the neo-Caledonian lagoon are similar to our own study area in terms of depths, reef flats and drop-offs (maps available from http://www.shom.fr/).

Underwater visual censuses

This is the most popular method for surveying fish communities. The UVC surveys were performed by counting the fish observed along a 50 m transect by two divers, one on each side of the transect. For each sighting, the species and its estimated body length were recorded together with the distance of the fish from the transect line. This type of information allows estimates of the density and biomass of each species encountered (Buckland et al. 1993). A total of 1,592 transects were performed on an array of reef types (Tables 1, 2). Transects were performed using distance sampling with no distance constraint (Buckland et al. 2001). In other words, the observers noted all the fish they could see, recording the distance of each observation from the transect line. Most of the fish were observed within the first 5 m. The duration of a transect survey depended on fish density, ranging between 75 and 90 min. The mass of the fish was estimated using mass/length data obtained on freshly caught specimens measured in the laboratory (Kulbicki 1988; Kulbicki and Wantiez 1990; Kulbicki et al. 2005). We estimated densities and biomasses of fish using algorithms developed by Kulbicki and Sarramégna (1999). Previous studies have indicated that the precision of length estimates is usually within 15% when mixing several species, and 5% when working on single species (Harvey et al. 2000).

Table 1 Underwater visual census (UVC) surveys in various sites of the southwestern New Caledonia lagoon suggest a very low density of eels

Site	No. of transects	No. of eels sighted	Eels/m²	No. of eel species	Mean eel length (cm)	Mean eel mass (g)
Noumea-1	90	7	0.00052	6	53 ± 30	148
Noumea-2	108	1	0.00006	1	30	34
Barrier reef	330	12	0.00017	4	86 ± 30	527
South West	800	29	0.00019	5	79 ± 25	431
St Vincent Bay	72	9	0.00052	3	91 ± 22	618
Algae-beds	192	4	0.00014	3	45 ± 10	97

Size (total length, cm) and mass (g) represent the mean (±SD) estimated body size and body mass of the eels. UVC samples mostly comprised very large fishes

Table 2 A comparison of three methods for estimating population densities of eels (Congridae, Muraenidae and Ophichthidae) in the New Caledonia lagoon

Sampling technique	Sampling period	Sampling effort: no. of days	No. of eels sampled	No. of species detected
UVC	1996–2001	1,323	85	8
Rotenone	1986–2003	57	247	29
Sea snakes	2002–2004	56	354	46

UVC underwater visual census

Rotenone poisoning

The rotenone poisoning sessions were performed by enclosing 300 m² of reef with a fine mesh net (1 cm stretched mesh) reaching from the bottom to the surface, then releasing 5 kg of rotenone powder (10% active ingredient) mixed with seawater and liquid soap. On each rotenone station, four divers deployed a 60 m circular net. This net had a 1-cm stretched mesh in order to prevent the escape of small fish, and was secured to the sea floor. Once the net was set, each diver dispersed 3 l of rotenone paste. A total of 8 dm³ of powder was used on each station. The fish died within 5 min and were collected by the divers, helped by four people, on the surface. The entire catch was brought to the laboratory; each specimen was later identified, measured and weighed, allowing the estimation of density and biomass per species. The densities of eels obtained from rotenone sampling were estimated by dividing the number of fish by the surface sampled (N/300 m²). A total of 57 rotenone collections were performed in the southwest lagoon of New Caledonia between 1986 and 2003. The rotenone data were already available before we undertook fish sampling using sea kraits. Thus, for the comparative purposes of the current study, we simply used previously collected samples.

Fish sampling via sea kraits

Sea krait ecology

Sea kraits (Elapidae, Hydrophiinae) are large (to 1.5 m) venomous sea snakes that forage in the ocean, mostly on eels, and return to land to digest their prey (Heatwole 1999). Consequently, many of the snakes found on land contain prey in the stomach. Sea kraits also come to land to slough their skins, to reproduce (for mating and egg-laying) and possibly for other reasons (e.g. resting, recovering from injuries: Shetty and Shine 2002c). These snakes are active foragers and by virtue of their elongate bodies and small heads, are able to penetrate deep into the coral matrix to locate and extract eels hidden within these complex structures. Although many authors have mentioned that sea kraits are abundant throughout the Pacific, there are few data on their population densities, and thus, their ecological role remains poorly understood.

Studies on sea kraits in Fiji and Vanuatu have shown that these animals are highly philopatric (Shetty and Shine 2002a) that they feed on eels (Reed et al. 2002; Shetty and Shine 2002b; Shine et al. 2002), and that they require about 1 week to fully digest a large eel (Shetty and Shine 2002c). Two species of sea kraits occur in New Caledonia: *Laticauda saintgironsi* (formerly regarded as part of the wide-ranging *L. colubrina*: Cogger and Heatwole 2005; Heatwole et al. 2005) and *L. laticaudata* (Saint Girons 1964; Ineich and Laboute 2002).

Population size

On Signal Island (a 6-ha flat islet situated in the southwest lagoon of New Caledonia, 15 km west of Nouméa and 10 km from the external reef barrier; 22°17′45.93 S; 166°17′34.70 E) we individually marked (by scale-

clipping) more than 1,000 individuals of these two snake species (*L. saintgironsi*, $N = 424$ and *L. laticaudata*, $N = 579$) during three field trips, from November 2002 to March 2004. Each year, we (one to three people) performed three standardised surveys per day (30 min to 1 h in duration, one early in the morning, one at dusk and one at night). This timing encompasses the most intense terrestrial activity of the snakes. We patrolled a 450-m section of the shore comprising flat beach rocks (80%) and small sandy beaches (20%). The snakes are primarily restricted to this southwestern part of the islet (unpublished data). The total number of searching days was 41. For each snake, we recorded snout–vent length (±1 cm) and body mass (±1 g, with an electronic scale). We obtained 420 recaptures of marked snakes (90 for *L. saintgironsi*, 330 for *L. laticaudata*) and estimated population sizes of snakes from these mark–recapture data using the CAPTURE program (Otis et al. 1978; Bonnet and Naulleau 1996; Bonnet et al. 2002).

Diet

We focused on relatively intact (recently ingested) prey items, as we forced snakes to regurgitate (through gentle palpation) only when we estimated from initial palpation that the prey was firm and hence, not yet digested. We weighed each prey item and preserved it for later identification, primarily based on dentition, at the MNHN laboratory. Sea kraits swallow their prey whole, either tail or head first. In many cases of head-first digestion, the eel's head was already partly digested by the time that we captured the snake and thus, dental characters were missing from the prey item. Overall, we were able to confidently identify only 18.8% of the total number of prey items regurgitated by our snakes.

Because the consumed eels are very large relative to the snakes that eat them, and the snake's body wall is very thin compared to the diameter of the fish, it was often possible to measure the diameter of the prey in the snake's stomach in situ (see Shine and Sun 2003 for validation of this method), except when the prey was too digested and became soft during palpation. In this way we could obtain data on prey size without unnecessarily stressing the snake or depriving it of its prey.

We identified 105 regurgitated prey items, and measured diameters of 271 prey. Data on the mass and the midbody diameter of regurgitated, freshly ingested prey allowed us to characterise the relationship between prey diameter versus prey mass [log mass prey (g) = 1.88 log (diameter of prey, mm)]—2.00; $r = 0.81$, $F_{1,\ 82} = 154.2$, $P < 0.0001$). From this relationship, we estimated the mass of prey items for which we had only midbody diameter measurements (because they were measured in situ, or were regurgitated but were too fully digested to be weighed). Using this prey diameter/prey mass relationship, we could also quantify the size distribution of ingested eels, and then extrapolate that distribution to estimate the number of prey items of different body sizes that are taken by the Signal Island snakes every year.

Duration of digestion

To estimate feeding rates, we needed data not only on the proportion of snakes with freshly captured prey, but also on the duration of digestion. From recapture data within survey periods, we could assess the time required for a snake to digest a prey (i.e. the minimum time elapsed between the capture of a snake with a recently ingested prey and its recapture with an empty stomach).

Foraging trip duration

In the same way, we could assess the time required for a snake to undertake a successful foraging trip. We used the time elapsed between successive captures on individual snakes that were first caught when leaving the island (captured on the beach while moving toward the sea) with an empty stomach, and then recaptured when coming back on land to digest (i.e. hauling onto the beach with a full stomach).

Results

Estimating the abundance of eels using underwater surveys

Underwater visual census

Results from this technique suggested that eels are rare: we found a mean density of only 4.6 ± 2.8 eels/ha (data shown are mean ± SD, in this all subsequent results; ranging from 0.6 to 5.2 fish/ha; Table 1). Despite a massive survey effort, UVCs detected only 8 of the 95 eel species known to occur in New Caledonia (Tables 2, 3). The eels recorded during visual census surveys were generally very large (mean mass 438 ± 306 g), with few individuals less than 100 g and none under 10 g (Fig. 1).

Rotenone poisoning

This method revealed many smaller eels, higher species diversity, and higher population densities of anguilliform fishes than were observed during UVCs

Table 3 List of the fish species seen during underwater visual surveys (UVCs) in the SW lagoon of New Caledonia, caught by rotenone in the SW lagoon, or prey found and identified in the stomach of the sea kraits

Family	Species	Status	UVC	Rotenone	Snakes
Moringuidae	*Moringua ferruginea*			X	
Xenocongridae	*Kaupichthys diodontus*			X	
Muraenidae	*Anarchias allardicei*	First report			X
	Anarchias sp.	Known			X
	Echidna nebulosa		X		
	Echidna polyzona			X	
	Echidna sp.	Known			X
	Echidna unicolor	First report			X
	Enchelycore bayeri			X	
	Enchelycore pardalis	First report			X
	Gymnomuraena zebra			X	
	Gymnothorax australicola	First report			X
	G. albimarginatus	Known	X	X	X
	G. buroenis	Known		X	X
	G. chilospilus	Known		X	X
	G. cribroris	First report			X
	G. dorsalis	First report			X
	G. eurostus	Known		X	X
	G. favagineus	First report			X
	G. fimbriatus	Known		X	X
	G. flavimarginatus		X	X	
	G. fuscomaculatus	Known		X	X
	G. gracilicauda	First report			X
	G. javanicus		X	X	
	G. meleagris	Known	X	X	X
	G. melatremus			X	
	G. moluccensis	First report			X
	G. monochorous	Known		X	X
	G. margaritophorus	Known		X	X
	G. nudivomer	Known		X	X
	G. pindae	Known		X	X
	G. pseudothyrsoideus	Known		X	X
	G. reevesi	First report			X
	G. reticularis	First report			X
	G. richardsoni	Known		X	X
	Gymnothorax sp.	Known			X
	G. undulatus	Known		X	X
	G. schizomatorhynchus			X	
	G. zonipectis	Known		X	X
	Scuticaria tigrina	Known			X
	Scuticaria okinawae	Known			X
	Siderea picta		X		
	S. thyrsoidea		X	X	
	Stophidon sathete	Known			X
	Uropterygius alboguttatus	First report			X
	U. concolor	Known			X
	U. fuscoguttatus	Known			X
	U. macrocephalus	First report			X
	Uropterygius sp.	Known			X
	U. cf. *xanthospilus*	Known			X
Ophichthidae	*Leiuranus semicinctus*			X	
	Muraenichthys sp.	Known			X
	Myrophis microchir	First report			X
	Myrichthys maculosus	Known			X
	Ophichthus cephalozona			X	
	Ophichthus sp.	Known			X
	Schismorhynchus labialis	Known			X
Congridae	*Conger cinereus*	Known	X	X	X
Microdesmidae	*Ptereleotris* sp.	Known			X
Plotosidae	*Plotosus lineatus*	Known	X	X	X

Status (for prey only): already known for New Caledonia (e.g. MNHN collection...), versus first report for the area

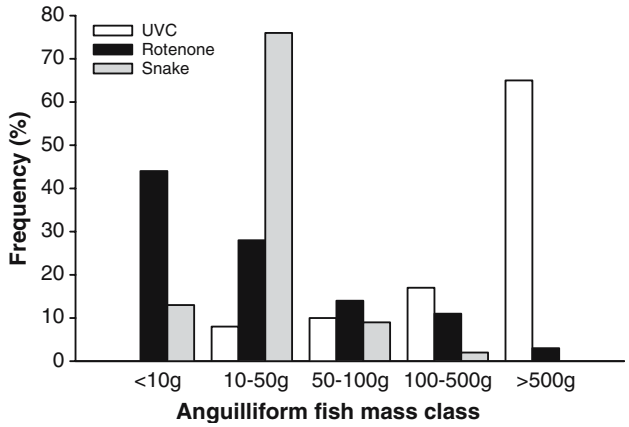

Fig. 1 Size (body mass) frequency distributions of anguilliform fishes caught by rotenone ($N = 241$), observed by underwater visual surveys (UVC, $N = 64$), or eaten by snakes ($N = 331$)

(Tables 2, 3). The mean density of eels from the rotenone stations was 180 eels/ha ($N = 57$ stations). A total of 45 eels were caught, with an average body mass (91 g) one-quarter that recorded during visual surveys (Fig. 1).

The average density of eels estimated using rotenone was 180 fish/ha, 40 times greater than the density suggested by UVCs (4.6 fish/ha). However, the mean density of large eels (heavier than 100 g) revealed by rotenone poisoning was only 4.6 times greater than that revealed by UVCs (18 fish/ha vs 3.9 fish/ha). The total eel biomass estimated using rotenone (1.27 g/m^2) was five times that based upon UVC data (0.25 g/m^2); this difference dropped to threefold, however, when restricted to data on the largest fish (>100 g) (0.70 g/m^2 for rotenone, 0.23 g/m^2 for UVCs). Thus, UVC surveys clearly generated unrealistically low estimates of eel numbers, and were highly biased toward large individuals.

Population size of sea kraits

Based on rates of recapture of marked animals, Signal Island supported an average of 1,418 individual snakes (estimates for each field trip ranged from 1,095 ± 212 to 1,921 ± 449, extreme values ranging from 771 to 3,071). This figure is likely to be an underestimate because although we marked more than 1,000 individuals, the proportion of unmarked snakes remained high throughout our study (68.2 ± 20.9%). We were able to process (mark, measure) only about 100 snakes/day, so could sample only a fraction of the total number of snakes that were visible on the beach.

Duration of digestion

Prey were detectable by palpation for 6.0 ± 3.1 days (range: 3–12 days, $N = 15$). Therefore, ingested preys are detectable for about a week in free-ranging snakes, in agreement with data from captive Fijian sea kraits (Shetty and Shine 2002c).

Foraging trip duration

Successful foraging trips lasted generally about a week (6.6 ± 4.0 days, range: 1–16 days, $N = 32$).

Number and size of eels consumed by snakes

Approximately one-third of the snakes contained prey at capture (33.7%). Because they take 1 week to digest their prey, and feed all year round (based on our fieldwork in all seasons), we estimated that the snakes on Signal Island consume a total of about 36,000 eels per year. That is, if each snake feeds once every 2 weeks (1 week to forage, 1 week to digest), it will take an average of 26 prey items per year. Thus, the 1,418 snakes on Signal Island will consume 1,418 × 26 = 36,868 anguilliform fishes.

The mean mass of intact prey items was 38.6 ± 34.3 g ($N = 84$). The mean estimated mass of partly digested prey (based on midbody diameter) was 27.3 ± 18.5 g ($N = 311$) (comparing these two values: t test, $P = 0.07$, using Ln-transformed data to meet the normality assumption). A t test for paired samples suggests that our use of the prey-diameter versus prey-mass regression to calculate prey mass was relatively accurate (comparing the actual mass with the estimated mass of each intact fish: $t < 0.001$, $N = 84$, $P = 0.99$, using Ln-transformed data to meet the normality assumption). The slightly (although not significantly) greater mean mass of regurgitated prey items than partly digested prey items probably reflects the more rapid digestion of smaller prey, thus reducing sample sizes for intact small prey items and biasing our sample of intact fishes toward larger specimens. Consequently, we used the more conservative (and likely, more realistic) estimated mean value (derived from 311 diameter measurements of partly digested prey items) to calculate the total biomass of the offtake. Calculated on this basis, we estimate that the snakes from Signal Island consume about 972 kg (36,868 prey items × 27 g) of eels every year.

Performing the above estimates separately for each year of the study and using either maximal or minimal values for each parameter used (e.g. population size, mean eel mass) provides a way to evaluate the likely level of error in this analysis. The minimal estimated number of eels captured by the snakes was 20,046, the maximal number was 79,846; in terms of biomass the values ranged between 541 and 3,082 kg of eels consumed per year.

Comparisons with fish surveys

Species diversity

Fourteen of the eel species that we found in snake stomachs were previously unrecorded in New Caledonia (Table 3). Although our sampling survey was limited in time and space (there are hundreds of small islets in the lagoon of New Caledonia, see http://www.shom.fr/ for precise maps of the area) and identification effort (we focused only on relatively intact prey items), we found a total of 46 fish species in the stomachs of the snakes. Thus, our single sample markedly increases the list of eel species known from this region. Interestingly, we found six species of the genus *Uropterygius* in snake stomachs, but these fish were never detected during UVC or rotenone sessions. A broad survey of the ecological information available on FishBase (http://www.fishbase.org) suggested that the eel species that live hidden in coral crevices or in sand burrows (e.g. *Gymnothorax criboris*, *Strophidon sathete*, *Uropterygius alboguttatus*, *Myrichthys maculosus*) remained inaccessible to classical sampling methods, but were nonetheless captured by sea kraits. In contrast, the fish species detected by all three techniques (e.g. *Plotosus lineatus*, *Gymnothorax albimarginatus*) are known to live in a variety of habitats (e.g. coral reefs, coastal reefs). In FishBase, we found data on the depths where the fish have been observed for 29 species also consumed by the snakes. On average, the eels sampled by the snakes live at 32.7 ± 28.9 m, (range: 0–180 m, $N = 29$), and are usually observed between 5 and 60 m depth.

Body-size distributions

The fishes captured by snakes had a different body-mass distribution than those caught by rotenone or observed by UVCs (Fig. 1). Clearly, the three sampling methods target different parts of the eel community. Rotenone caught the smallest fish and the number of fish per size class decreased regularly at larger body sizes. Snakes tended to avoid both the smallest and the largest eels, focusing mostly on an intermediate size range: 73% of the eels eaten by the snakes were within the 10–50 g size class. Last, the UVCs sampled only the largest eels (66% were over 500 g), most of them far too large to be ingested by sea kraits. Thus, the component of the fish community assessed by UVC mostly comprised animals that were not available to the snakes as prey.

Fifty-eight percent of the fishes taken by the snakes (6–166 g) were within the size range of those captured during rotenone surveys (Fig. 1), but two-thirds of the fish species consumed by the snakes were not sampled by rotenone (Table 3). Overall, only about 14% of the samples from rotenone poisoning overlapped both in body size and species with the prey items taken by the snakes.

Population densities and biomass

Sea snake sampling enabled us to estimate rates of eel consumption, a type of information not directly comparable with the static density estimates generated by the two other methods. However, several points of comparison can be highlighted. Although we do not know the exact area of reef from which the Signal Island snakes took their prey, this was probably relatively small because many foraging trips are brief (see above), and many snakes hauled on the beach with essentially undigested food items in the stomach (indicating a short travel time). In addition, many of the small prey are probably shallow-water species (lagoon depth around Signal Island rarely exceeds 20 m), and sea kraits are highly philopatric (Shetty and Shine 2002a). Finally, we observed snakes capturing moray eels close to the shore (<30 m) of Signal Island. Nonetheless, long distance foraging trips are possible also. Satellite imagery reveals 130 ha of reef within a 1.6 km radius around Signal Island, and no reef beyond this distance up to 4 km. This spatial arrangement suggests that snakes may remove approximately 36,868 fishes/year in this area.

Discussion

Even with the use of correction factors, UVCs may not provide an accurate method of sampling secretive fish species such as moray eels (Jennings and Polunin 1995). The present study takes advantage of a novel method of estimating eel species richness and abundance to clarify the nature and magnitude of errors from UVC counts. Our data suggest that UVCs may underestimate the total density of eels by a factor of 40 comparing to rotenone poisoning, and at least by a similar order of magnitude if sea krait sampling serves as the reference. Rotenone poisoning is generally considered as the most efficient way to catch secretive fish species (Ackerman and Bellwood 2000). However, observations during such trials suggest that eels are often the last species to be affected by rotenone; perhaps because they live in habitats where oxygen levels are low (the reef matrix or in the sand), they might tolerate low oxygen levels and hence be able to resist the

anti-oxygen effects of the poison. Thus, some eels may survive a rotenone poisoning session, or die within the reef matrix or in the sand where they cannot be recovered.

The offtake rates of sea kraits suggest that eels, especially small moray eels, are more abundant and diverse in the New Caledonian lagoon than would be suspected from current methods used to survey marine ecosystems. Many eels, especially small specimens, remain hidden within the matrix of the coral edifices and escape observation. Sea kraits can penetrate deep into the interstices of coral substrates, and thus extract eels from situations in which they would otherwise remain invisible. Although we cannot directly extrapolate our results to all coral reefs of the western Pacific, the striking contrast in estimates of eel densities and diversity from different survey methods reinforce Reed et al.'s (2002) suggestion that sea kraits may offer a powerful and simple sampling method to assess the importance of this little known part of reef fish assemblages. Unless we know the size of the area covered by foraging snakes, however, we can interpret these data only in relatively broad spatial terms. Secondly, the remarkably high numbers of sea kraits plus their specialised diet of eels and high feeding rates suggest that these amphibious snakes may play a significant role in the trophic structure of the lagoon ecosystem. Sea kraits (and thus, presumably, the eels on which they feed) are common throughout New Caledonia (Saint Girons 1964; Ineich and Laboute 2002; Bonnet et al. 2005) and much of the Pacific (Pernetta 1977; Heatwole 1999; Shetty and Shine 2002c).

Sea kraits themselves are potentially an abundant food resource (standing-crop biomass of approx. 324 kg of snakes for Signal Island alone) for predators such as sharks, cod and large moray eels (Ineich and Laboute 2002). Complex food-webs incorporating multiple predatory species on different trophic levels may enhance the resilience of the ecosystems in and around coral reefs (Bellwood et al. 2003; Hughes et al. 2003). However, to date, eels and sea snakes have not been incorporated into such models (note the recent review by Bellwood et al. 2004), probably reflecting the difficulty of sampling these components of the system.

Some of our results about population densities of eels rely upon a series of calculations that embody various estimates (of feeding rates, etc.); errors in any of these estimates will necessarily affect the accuracy of our predictions. Our estimates on snake population size are likely to be accurate as the assumptions for capture–mark–recapture calculations were met: the sedentary behaviour of sea kraits together with the short time period for each capture–recapture episode means that we can legitimately treat the Signal Island snakes as a closed population where rates of migration, recruitment and mortality are negligible (Otis et al. 1978; Bonnet and Naulleau 1996; Bonnet et al. 2002). In fact, our inability to process all the snakes we encountered suggests that we are more likely to have underestimated rather than overestimated population size, rendering our calculations conservative. We have also assumed that snakes forage mainly on the bottom of the lagoon around the small islands, searching for prey in depths of 0–60 m, and about 30 m on average. This inference fits well with available data on the ecology of the eels (FishBase) consumed by the sea kraits (depth records range from 5–60 m, 33 m on average). As we observed several snakes catching their prey in the Signal Island reef flat, and recorded some very short successful foraging trips undertaken by the snakes (<1 day), we can be confident that eels are indeed taken from the reef immediately adjacent to the islet. Consequently, the assumption that most preys are taken in the shallow matrix coral and in the soft bottom of the lagoon is realistic. Other estimates are more subject to error. For example, although the sea kraits feed all year, there may well be seasonal fluctuations in the intensity of predation, or in the sizes and types of prey that are taken. Such effects will be opposed by other simplifications in our analysis: for example, we neglected the fact that snakes often regurgitate several preys rather than a single eel. Such complexities will have little overall effect on our main conclusions, because of the great disparity between estimates of eel biomass and diversity from the sea krait diets versus those from other methods. However, one assumption in our calculations is critical in this respect: the total area over which the snakes forage. It remains possible that some snakes travel much further and deeper than we have inferred, and if this behaviour were common, our density estimates would need to be revised downwards (unless sea kraits from other island populations travel to forage around Signal Island, thus cancelling out any such effect). Importantly, this uncertainty does not alter the fact that eels and sea snakes are far more abundant than previously thought, and hence may contribute significantly to the ecological functioning of the coral-reef ecosystem.

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