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Are sea snakes pertinent bio-indicators for coral reefs? a comparison between species and sites

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Abstract Classical sampling methods often miss important components of coral reef biodiversity, notably organisms that remain sheltered within the coral matrix. Recent studies using sea kraits (sea snakes) as bio-indicators suggest that the guild of predators represented by anguilliform fish (Congridae, Muraenidae, Ophichthidae, henceforth "eels" for simplicity) were far more abundant and diverse than previously suspected. In the current study, eel diversity (similarity and species richness indices) estimated via sea snake sampling (SSS) was compared among six areas of one of the main oceanic biodiversity hotspot of the Pacific Ocean (southwest lagoon of New Caledonia). Based on the eel diversity in the snakes' diet, the results obtained in six areas, in two snake species, and using different estimates (ANOSIM, Shannon index…) were consistent, suggesting that SSS provided robust information. Analyses also suggested subtle, albeit significant, differences in the eel assemblages among islets. Such spatial differences are discussed in light of local management practices. As SSS is

easy to use, cost-effective, and provides the best picture of eel assemblages to date, it can be employed to monitor the eel assemblages in addition to the snakes themselves in many areas of the Indo-Pacific Ocean, thereby providing an index of the top predator biodiversity of many coral reefs.

Introduction

Given the current rate of biodiversity loss and the fact there is no geographic area spared by global changes, it is crucial to rapidly gather information on representative species, in order to evaluate the conservation status of a wide variety of ecosystems (Vitousek et al. 1997). Unfortunately, most animal species are highly cryptic, inaccessible and difficult to sample. To circumvent such difficulties, some species can be used as natural gauges or bio-indicators (McGeoch 1998). In terms of cost to efficiency ratio, useful indicators should combine a number of characteristics (Noss 1990; Pearson and Cassola 1992; Niemelä 2000). Notably, they should be widely distributed and their trophic ecology should be sufficiently known to allow inter-site comparisons. Bio-indicators should also preferably exhibit a high degree of ecological specialisation to accurately probe relevant trophic levels of the ecosystems under focus. Predators have been intensively used in this way, typically when they are relatively accessible compared to other elements of the ecosystems (Hindell et al. 2003; Cherel et al. 2004). For instance, monitoring specialised vertebrate predators enabled a precise, albeit indirect, survey of several underlying trophic levels of vast oceanic areas (Cherel et al. 2004, 2007; Ineich et al. 2007; Ménard et al. 2007; Brischoux and Bonnet 2008). In addition, specialised species are far more vulnerable to environmental perturbations

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compared to generalists, adding further importance to the necessity to scrutinise of their populations over time (Kitahara and Fujii 1994). Finally, to be useful at a large scale, bio-indicators should be relatively easy to survey.

Coral reefs are extremely rich ecosystems that are subject to considerable pressure, and that require accurate biological monitoring (Rogers 1990; Hughes 1994; Guinotte et al. 2003; Pandolfi et al. 2003; Sheppard 2003; Bellwood et al. 2004; Wilkinson 2006). However, the ecological roles and trophic interrelationships are only well understood for few organisms, notably because many species remain sheltered in the coral matrix, thereby escaping observation. For instance, important groups of coral reef predators such as anguilliform fish (henceforth named "eels" for simplicity) remain poorly known (Abrams et al. 1983; Kulbicki 1997). An examination of FishBase (Froese and Pauly 2006) reveals that most eel species are known from only a few isolated specimens and that the basic ecological information is often fragmentary and sometimes totally lacking (see Séret et al. 2008 for instance). Recently, it has been suggested that a group of sea snakes specialised on eels, the sea kraits (*Laticauda* spp.), may represent potentially useful bio-indicators for surveying the anguilliform fish assemblages in coral reefs (Reed et al. 2002; Ineich et al. 2007; Brischoux and Bonnet 2008; Séret et al. 2008). Indeed, analysis of the stomach contents of sea kraits revealed unexpectedly high densities and species richness of eels in the several coral reef areas sampled (Vanuatu: Reed et al. 2002; New Caledonia: Ineich et al. 2007; Brischoux and Bonnet 2008; Séret et al. 2008). For instance, in New Caledonia, eel sampling through sea kraits revealed 15 new species for the area and indicated that eel densities were underestimated by several orders of magnitude (Ineich et al. 2007; Brischoux and Bonnet 2008).

As possible bio-indicators for monitoring important, albeit neglected components of coral reef animal assemblages, sea kraits fulfil the requirements listed above. First, they exhibit a vast distributional range (broadly from the Bay of Bengal to the Tonga archipelago and from Japan to New-Caledonia, Heatwole 1999; Heatwole et al. 2005). Second, the foraging ecology of different species is relatively well documented (*L. colubrina* in Fidji and Vanuatu: Reed et al. 2002; Shetty and Shine 2002a; Shine et al. 2002; *L. saintgironsi* and *L. laticaudata* in New Caledonia: Ineich et al. 2007; Brischoux et al. 2007a, b, 2009a; Brischoux and Bonnet 2008, 2009; *L. semifasciata* in the Ryukyu archipelago: Su et al. 2005). Although sea kraits are highly specialised on anguilliform fish, they nonetheless feed on more than 45 species of eels (Ineich et al. 2007; Brischoux et al. 2007a, b, 2009a; Brischoux and Bonnet 2008) combining the advantage of a specialized trophic niche (e.g. bio-sampling accuracy) and the

possibility to monitor many species. As sea kraits swallow their prey whole, and because it is easy to force them to regurgitate, a large proportion of the collected prey are intact or poorly digested, which greatly facilitates identification and counting procedures (Brischoux et al. 2007a, b, 2009a; Brischoux and Bonnet 2008). Third, sea kraits occur in very high densities, are easy to capture and are docile during handling, rendering surveys particularly cost-effective (no costly or complex equipment being required; Brischoux and Bonnet 2009). Finally, their marked philopatry toward their home islet offers a powerful and simple way for comparisons between different sites, both within and among broad geographic areas (Shetty and Shine 2002b; Bonnet et al. 2009; Brischoux et al. 2009b).

Overall, sea kraits present numerous advantages to assess both the diversity and the abundance of many eel species, and therefore to accurately probe otherwise hidden and inaccessible components of coral reef fish assemblages. However, to appreciate the utility of sea kraits as bio-indicators, rigorous analyses on this issue are still required. Two species of sea kraits (Elapidae, Hydrophiinae) occur in New Caledonia: *Laticauda saintgironsi* (Cogger and Heatwole 2006) and *L. laticaudata* (Saint Girons 1964; Ineich and Laboute 2002). Using these species of sea kraits and six different sites, the aim of this study was to investigate whether the diet of sea kraits varies among sites, and to determine whether both species of sea kraits offer complementary and concordant estimates of prey diversity.

Materials and methods

Study sites

Sea krait populations were surveyed on 10 different islets in the southwest lagoon of New Caledonia from 2002 to 2008 (Brischoux and Bonnet 2009). Six islets yielded sufficient data on the snake's diet (from North to South): Ténia (T), Mba (M), Signal (S), Larégnère (L), Amédée (Am) and Améré (Ar) (Fig. 1). One species, *L. saintgironsi*, was abundant at all of the surveyed sites, while *L. laticaudata*, occurred in large numbers only at Mba, Signal and Amédée (Bonnet et al. 2009).

Management practices and conservation status greatly differed among the selected sites: Mba is a free-access classical coralline islet without particular protection status; Ténia, Signal, Larégnère and Amédée are free-access preserved areas where fishing and environmental damage are theoretically prohibited; and Améré is an islet with very limited access (tourism is prohibited) and it is situated within the only totally and efficiently protected marine area in New Caledonia. Habitat complexity was also variable
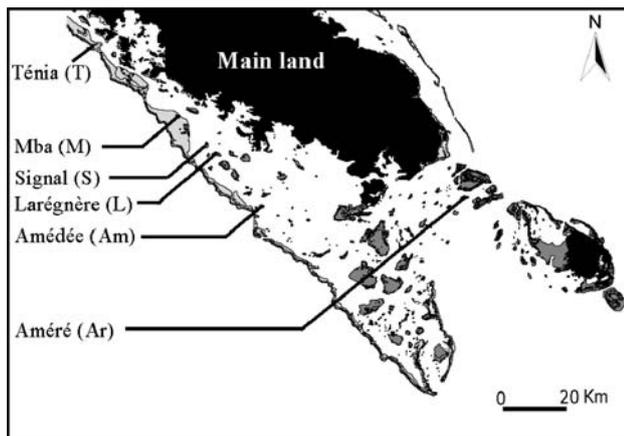
Fig. 1 Map of the south-western lagoon of New Caledonia. *Black areas* indicate emergent land (mainland and islands); *grey areas* represent coral reef flats. The barrier reef and other fringing reefs are represented by *light grey areas*

among study sites: Mba belongs to a shallow lagoon plateau connected to the barrier reef; Signal and Larégnère are typical flat coralline islets situated broadly in the middle of the lagoon; Ténia and Amédée are situated on (or very close to) the barrier reef; and Améré is situated near an extended reef flat (Andréfouët and Torres-Pulliza 2004; Fig. 1).

Snakes were collected by hand, measured (snout-vent length [SVL], ±1 cm), weighed (±1 g) and individually marked by scale clipping (Brischoux and Bonnet 2009). The abdomen of each snake was carefully palpated to check for the presence of prey in the stomach. As sea kraits feed essentially on non-spiny fish, it was easy to force them to regurgitate their prey (Brischoux and Bonnet 2009). This sea snake sampling method is subsequently referred to as SSS. Each sea krait species exhibits a peculiar diet with little overlap (Morisita-Horn similarity index of 0.15, Brischoux et al. 2007b). Such divergence in diet between the species is associated with the exploitation of different foraging sites: essentially hard-bottoms for *L. saintgironsi* versus soft and hard-bottoms for *L. laticaudata* (Brischoux et al. 2007b). Therefore, the two species provide an additional opportunity to investigate the ability of sea kraits to gauge eel assemblages and thus to perform comparisons among sites, considering each species of sea kraits separately (N = 12 zones sampled: 6 islets × 2 specific foraging habitats).

We collected, identified, and measured 1,122 regurgitated prey items (see Brischoux et al. 2007a). Data on prey habitat were gathered from FishBase (Froese and Pauly 2006, see Brischoux et al. 2007b). Habitat requirements were obtained for 29 out of the 46 eel species consumed by the sea kraits (basic ecological information was lacking for 40% of the prey). For simplicity, habitats were categorised

into three broad types: hard-bottom, soft bottom and combined hard plus soft bottom (see Brischoux et al. 2007b). Sea kraits forage both very close to their home islets and from further sites (see Brischoux et al. 2007b for estimates of foraging ranges). Using both "types" of prey will mix different geographic areas and thus provide irrelevant estimates of local diversity. As a consequence, we used only the preys that were taken during short foraging trips (∼33% of the prey, Brischoux et al. 2007b) for analyses (see below).

Like any sampling method, reliance on snake stomach contents to quantify eel abundances is subject to bias. However, data on the anguilliform fish assemblage are lacking (Kulbicki 1997; Ineich et al. 2007). Sampling these fishes via sea krait stomach contents provides a more comprehensive and accurate assessment of anguilliform fish abundance and species diversity than does any other sampling method (Reed et al. 2002; Ineich et al. 2007; Séret et al. 2008). As a consequence, sampling eels through sea kraits provides the best picture of this assemblage to date (Brischoux et al. 2009a).

Analyses

Usually, saturation curves are used to estimate the minimal sample size required to compare species diversity among sites (Chao estimator, Colwell 2005). Previous analyses suggested that the lower limit to characterise species richness from SSS was ∼50 prey items per sea krait species and per site (Brischoux et al. 2007b; Brischoux et al. 2009a). However, in some cases (4 among 12), the sample size of regurgitated eels was much smaller (Mba [N = 24 prey items] for *L. laticaudata*; Améré [N = 45 prey items], Mba [N = 38 prey items] and Ténia [N = 39 prey items] for *L. saintgironsi*). In order to retain these sites in the analyses, we used alternative (complementary) techniques that allow taking into account such disparity in sample size among sites. Notably, we used two complementary approaches: (i) analyses of similarity, ANOSIM (Clarke 1993), to compare the differences in species compositions, and (ii) the Shannon diversity index (Magurran 1988) and standard rarefaction technique (Koellner et al. 2004) to estimate species richness.

Analyses of similarity (ANOSIM)

ANOSIM is a non-parametric test designed to evaluate spatial differences and temporal changes in the assemblages of species (Clarke 1993; Chapman and Underwood 1999). ANOSIM procedures are based on the comparisons of intra- and inter-group distances calculated as average ranked values (often the Bray-Curtis measures of dissimilarity) of the abundances and the types of organisms among

samples. The ANOSIM statistic R is based on the difference of mean ranks between groups (r_B) and within groups (r_W) (N stands for the sample size):

$$R = (r\_B - r\_W)/(N(N - 1)/4)$$

The output statistic provides R-values ranking between -1 and 1, and a P-value to assist decision making: two sampled units are considered similar when R is equal to 0 and are considered totally different when R is equal to 1 (or -1, although negative values pose difficulties in interpretation, see Chapman and Underwood 1999).

Species richness

As the sampling effort was unevenly distributed, two different approaches were employed to estimate the species richness. First, Shannon diversity indices were calculated to compare the species richness of sea krait diets among islets. However, because the Shannon index is very sensitive to sample size bias (Magurran 1988), 1,000 random sub-samplings were performed for each site to compare the distributions of Shannon diversity indices among sites. This procedure involved a random sub-sampling, set up at 90% of the minimal common sample size among all sites (38 prey for *L. saintgironsi* and 24 prey for *L. laticaudata*), to generate a distribution of Shannon indices (see Fig. 2). Second, standard rarefaction techniques (widely used to compare the number of species in a collection of samples with uneven sample sizes, Koellner et al. 2004) were used. Rarefaction is a procedure for analysing the number of species (species richness) among collections, when all collections are scaled down to the same number of individuals. The number of expected species can be estimated from a random sample of individuals, drawn without replacement from individuals distributed among species. The estimated number of species was calculated for each study site based on the smallest sample size (depending on the snake species).

All analyses were performed using the Vegan library in R 2.5.1.

Results

Analyses of similarity and diversity indices

Although not identical, ANOSIM and the two diversity indices produced similar trends, thereby simplifying the interpretation of the results (Table 1, Fig. 2). All the indices of similarity were small ($R < 0.20$), the curves between sample size and the expected number of species followed similar trends, and the Shannon indices remained within relatively narrow ranges. One of the more
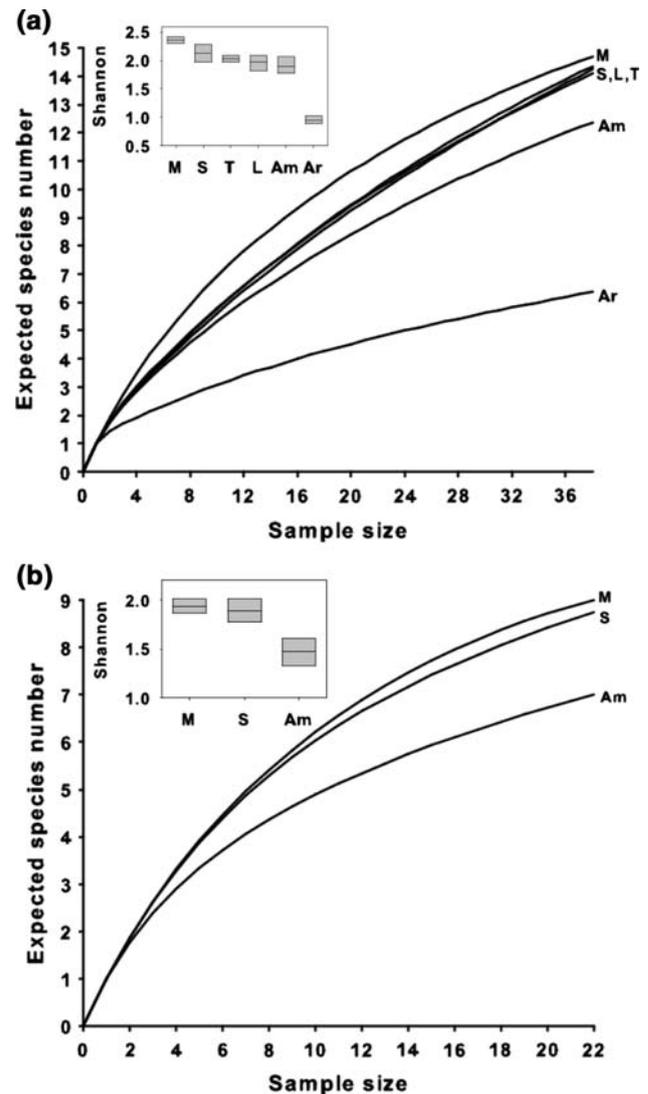

Fig. 2 Expected species number of eels (*major* figures) for the different study sites for *Laticauda saintgironsi* (**a**) and *L laticaudata*. (**b**). *Minor* figures indicate the Shannon diversity index (Shannon) distribution calculated through bootstrap resampling. *M*, *S*, *L*, *T*, *Am* and *Ar* stand, respectively, for *Mba*, *Signal*, *Larégnère*, *Ténia*, *Amédée* and *Améré*

remarkable results is that, despite strong heterogeneity in the data set (different sites, sea krait species and sample sizes), the rarefaction curves follow similar homogeneous trends (Fig. 2).

Beyond these broad trends, significant differences were detected among study sites (Appendix 1). For *L. saintgironsi*, one islet, Mba, provided the highest diversity of eel prey and differed significantly from the five other sites. Améré Island displayed the lowest diversity of the eels (Table 1, Fig. 2a). All the other sites were relatively similar, although the expected species number suggested that the diversity of the prey found in the stomachs of the snakes was lower at Amédée Island (Table 1, Fig. 2a). For

Table 1 ANOSIM tests for each of the pair-wise comparisons of the diet of sea kraits between islets

Species	Site	Amédée	Améré	Larégnère	Mba	Signal
LS	Améré	−0.105 (0.997)				
	Larégnère	0.025 (0.097)	−0.054 (0.995)			
	Mba	**0.138 (0.001)**	**0.193 (0.001)**	**0.050 (0.025)**		
	Signal	0.003 (0.207)	−0.114 (0.999)	0.011 (0.293)	**0.099 (0.009)**	
	Ténia	−0.017 (0.643)	**0.036 (0.04)**	−0.033 (0.894)	**0.055 (0.004)**	−0.029 (0.759)
LL	Mba	**0.108 (0.005)**				
	Signal	**0.046 (0.001)**			0.019 (0.221)	

Fifteen pair-wise comparisons were performed for of *Laticauda saintgironsi* (LS, six islets) and three pair-wise comparisons for *L. laticaudata* (LL, three islets). For each comparison, the values given are the *R*-statistic, and its *p*-value in parentheses. Values given in bold are statistically significant

L. laticaudata, the assemblage of prey revealed by SSS around Amédée Island was significantly poorer compared to Signal or Mba Islands (Table 1, Fig. 2b). Interestingly, although the two species of snakes exhibit disparate dietary and foraging habits (Brischoux et al. 2007b, 2009a), the analyses of their stomach contents provided biodiversity indices that ranked the sites exactly in the same order (i.e. from more to less diverse: Mba > Signal ≥ Ténia ≥ Larégnère ≥ Amédée > Améré for *L. saintgironsi* and Mba ≥ Signal > Amédée for *L. laticaudata*; Fig. 2).

Prey habitat

The analyses of the prey habitat collected on FishBase (Froese and Pauly 2006) revealed that *L. saintgironsi* took similar proportions of prey from hard-bottoms and hard-soft-bottoms in all the six sites ($X^2 = 2.71$, df = 5, $P = 0.6$; Fig. 3a). By contrast, proportions differed markedly among the three sites for *L. laticaudata*; for instance, most of the prey typically came from soft bottoms around Signal Island and from hard-bottoms around Amédée Island ($X^2 = 176.08$, df = 5, $P < 0.001$; Fig. 3b).

Discussion

Using two species of sea krait as separate bio-indicators, the results of this study provided consistent estimates of species richness among all study sites. The relationship between sample size and the richness of eels followed similar curves. The similarity indices also broadly ranked the sites in the same order as the expected species number. Because sea kraits fed on 46 species of eels that are tightly associated with different environments of the coral reef ecosystems (all species are benthic and supposedly sedentary when adult), SSS provides the most accurate technique available to monitor important predator guilds from relatively well-defined areas. The fact that the saturation curves follow similar homogeneous trends suggests that a
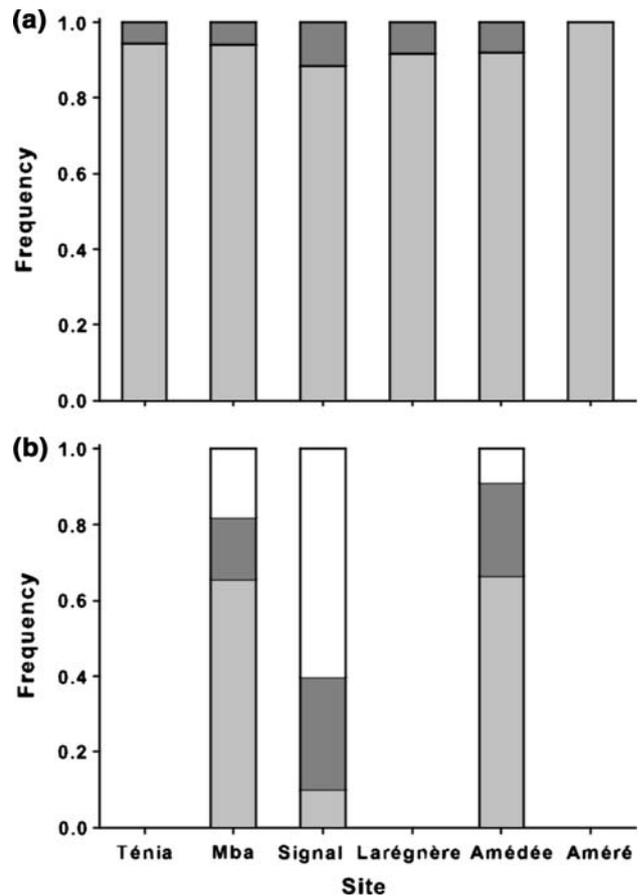

Fig. 3 Proportion of prey living in the three habitat types (*light grey* hard-bottoms, *dark grey* soft bottoms, *white* hard and soft bottoms) for each study site. *Upper* figure for *Laticauda saintgironsi* (**a**) and *lower* figure for *L. laticaudata* (**b**)

relatively small sample size (50–100 eels per snake species and site [<4 days of field work]) would be enough to accurately sample the anguilliform fish assemblage. SSS, therefore, offers a technique that focuses on a little studied component of coral reef fish communities and complements other methods such as underwater visual census

(Kulbicki 1997) or remote sensing (Hochberg et al. 2003). Despite the complexity of coral reef systems, SSS specifically targets various trophic levels and/or habitats that can be used to monitor and understand major ecosystem changes. If the sampling method had been imprecise, the possibility of finding steady and systematically convergent trends among sites and species would have been very unlikely. Therefore, the similarity among the different estimators employed (ANOSIM and similarity indices) indicates that the specific assemblage of the fish captured by sea kraits was sampled with satisfactory accuracy. Such findings offer evidence that sampling bias was a minor factor in our analysis.

A combination of factors could explain the regularity of the results obtained from different sites. First, sea kraits are highly specialised predators of anguilliform fish. Second, as gape-limited predators, sea kraits select precise prey sizes. Third, sea kraits forage around their home islet during short foraging trips (Brischoux et al. 2007b). Fourth, the hunting technique of sea kraits involves the systematic exploration of cavities in the substrate (Brischoux et al. 2007b; Ineich et al. 2007). Overall, the trophic relationships between the sea kraits and their prey appeared to be very tight (Brischoux et al. 2009a) and such tightness likely generated the consistency of the associated estimates. A closer examination of our results nonetheless suggests subtle, albeit significant, differences among islets (see also Appendix 1). Although less essential when framed within a broad bio-indicators perspective, such slight differences deserve further comments.

For *L. saintgironsi*, both ANOSIM and the two diversity indices indicated that the sea krait population of Mba fed on partially divergent and more diverse prey species compared to the other sites. For instance, the proportion of the main prey, *Gymnothorax chilospilus*, was lower at Mba compared to other sites (25% in Mba vs. 50% for all the other sites, with up to 75% for Améré). Reciprocally, other eel species were more represented in the stomach contents of the snakes from Mba (e.g. *G. fimbriatus* [18 vs. 7%], *G. margaritophorus* [13 vs. 5%] and *G. undulatus* [5 vs. 1.5%]). Interestingly, the surroundings of Mba belong to a specific structure of the lagoon: a shallow lagoon plateau directly connected to the barrier reef (Andréfouët and Torres-Pulliza 2004; Fig. 1).

For *L. laticaudata*, the foraging habitat was more variable among islets (Fig. 3b). The higher proportion of eel species that live in hard-bottoms of Mba and Amédée islets was presumably due to the predominance of this type of substrate in the vicinity of these islets: i.e. the shallow lagoon plateau of Mba and the vicinity of the barrier reef for Amédée compared to the extended soft bottoms around Signal Island (Fig. 1). ANOSIM and diversity indices indicated that Amédée was less diverse and dissimilar from Signal and Mba. It can thus be hypothesised that the structure of the lagoon sea floor affects both the diversity and the abundance of the eel species available to sea kraits.

Surprisingly, the site which contained the most diverse anguilliform fish assemblage was the only islet (Mba) not included within a protected perimeter. Moreover, the diet of the snakes of the more protected site (Améré) displayed the least diverse eel assemblages. Since protection measures generally enhance animal diversity and density (Wantiez et al. 1997), these results were somewhat paradoxical. Two non-mutually exclusive hypotheses can be proposed. First, the eels of New Caledonia are extremely cryptic organisms which are not targeted by fishermen, and that shelter within burrows and crevices, thereby limiting the impact of protection status. Perhaps anguilliform fish assemblages rather co-vary with refuge availability more than with conservation status. Mba and its surrounding reef flat apparently exhibit the most peculiar habitats that possibly offer a range of shelters to the various anguilliform fish consumed by the sea snakes from this area (Andréfouët and Torres-Pulliza 2004; Fig. 1). By contrast, Améré is very distant from the barrier reef and perhaps offers less diversified habitats. Alternatively, the strong protected status of Améré may promote higher population densities of fish (Wantiez et al. 1997; pers. obs.) including anguilliform fish. Sea kraits might feed heavily on their main prey species when available (i.e. *G. chilospilus* for *L. saintgironsi*, Brischoux et al. 2007b, 2009a), leading to an apparent lower prey diversity. In support of this view, the sea kraits from Amérée are extremely abundant but also larger and heavier compared to the other sites (unpublished data). Precise information on these issues is still lacking and further investigations would be useful to tease apart the impacts of protection status from habitat complexity on the eels' diversity, density and on their predators: the sea kraits.

In terms of bio-indication, *L. saintgironsi* seems to be the best candidate to gauge anguilliform fish associated with neo-caledonian coral reef ecosystems. Compared to *L. laticaudata*, this species is more ubiquitous and easier to sample (diurnal), thus simplifying sampling effort. Nonetheless, the use of *L. laticaudata* can give valuable insights on the eel assemblages of soft bottom substrates (Brischoux et al. 2007b). Overall, the high diversity of sea krait species, their large geographic range (notably for close species from the *L. colubrina* complex, Heatwole et al. 2005) and the variation in diet between sites and species make sea kraits a powerful bio-indicator to perform geographic comparisons of the eel assemblages at small (e.g. south west neo-caledonian lagoon) and large (e.g. Indo-Pacific coral reefs) spatial scales, and can also give access to an important, albeit unknown, part of the anguilliform fish ecology in coral reef areas.

Appendix 1

See Table 2.

Table 2 List of the eel species sampled through SSS at the different sampling sites

Prey species	T	M	S	L	Am	Ar
Anarchias allardicei	X		X		X	
A. cantonensis	X		X		X	
A. seychellensis	X		X		X	
A. sp.				X		
Cirrimaxilla formosa		X	X	X	X	
Conger sp.	X	X	X	X	X	
Echidna sp.			X			
E. unicolor			X		X	X
Enchelycore pardalis			X	X	X	
Gymnothorax albimarginatus	X	X	X	X	X	
G. chilospilus	X	X	X	X	X	X
G. cribroris			X			
G. dorsalis			X		X	
G. eurostus	X	X	X	X	X	X
G. fimbriatus	X	X	X	X		
G. formosus		X	X	X	X	
G. fuscomaculatus	X	X	X	X		
G. margaritoforus	X	X	X	X	X	
G. moluccensis		X	X		X	
G. nudivomer			X		X	
G. pindae	X		X	X	X	
G. pseudothyrsoideus	X					
G. reevesi		X	X		X	
G. reticularis			X			
G. richardsonii	X		X	X	X	
G. sp.1			X			
G. sp.2			X			
G. sp.3						X
G. sp.4						X
G. undulatus		X	X	X	X	
G. zonipectis			X		X	
Muraenichthys sp.	X	X	X	X	X	

Table 2 continued

Prey species	T	M	S	L	Am	Ar
Myrichtys maculosus	X	X	X			
Myrophis microchir			X		X	
Scuticaria okinawae			X		X	
S. sp.			X		X	
S. tigrina	X		X	X	X	
Strophidon sathete			X			
Uropterygius alboguttatus		X	X			
U. concolor		X	X	X	X	
U. fuscoguttatus			X			
U. macrocephalus		X	X			
U. polyspilus				X		
U. sp. 14b	X		X		X	X
U. supraforatus	X	X	X	X	X	
U. xanthopterus	X		X			

M, S, L, T, Am and Ar stand, respectively, for Mba, Signal, Larégnère, Ténia, Amédée and Améré. Note that both species of sea kraits have been pooled

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