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Note

Estimating the impact of sea kraits on the anguilliform fish community (Congridae, Muraenidae, Ophichthidae) of New Caledonia

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Abstract – It has been previously shown that two guilds of predators, the sea kraits and their prey, the anguilliform fish (predator themselves), are far more abundant and diverse than previously suspected in coral reefs of the Indo-Pacific area. Based on diet, foraging range, feeding rate, and population size of two sea krait species, we estimated the annual uptake of anguilliform fish around Signal Island, New Caledonia. We found that more than 4000 snakes live on this 15 ha islet and that they can take up to 45 000 fish (>1.3 t) per year, essentially from 10 fish species previously considered as rare. One third of these fish are captured on the reef flat, the two other thirds within a 17 km radius surrounding Signal Island. We suggest that the foraging areas of the different snake populations belonging to numerous islets (and the surrounding reef flats) overlap greatly.

Key words: Predation / Anguilliform fish / Sea krait / Uptake

1 Introduction

Predation is recognized as a crucial structuring process in most communities (Carpenter et al. 1985; McCann et al. 1998) including coral reefs (Hixon 1991; Jennings and Polunin 1997). For instance, the number of trophic levels exerts a strong regulatory influence on the whole ecosystem (Finke and Denno 2004). However, given the logistical difficulties to assess simultaneously the complex trophic relationships of various levels, detailed studies on the interactions at the level of the whole food web are still scarce (Hixon 1991; Caley 1993). In addition, since many predator species are highly cryptic and consequently difficult to sample, their actual role on the functioning of coral reef ecosystems remains particularly unclear (Kulbicki 1997). Any opportunity to collect substantial amounts of information on poorly known, albeit abundant, guilds of predators is useful for a more general understanding of the trophic structures of coral reefs ecosystems.

Recent work has identified an important predator-prey system in two sites of the western Pacific Ocean: the Republic of Vanuatu and New Caledonia. It was shown that the biodiversity and the biomass of at least two trophic levels represented by sea snakes and their prey have been massively underestimated due to the use of inappropriate sampling methods (Reed et al. 2002; Ineich et al. 2007). Four species of sea kraits (Laticaudid sea snakes; *Laticauda colubrina*, *L. frontalis*, *L. saintgironsi*, *L. laticaudata*) occur in very large numbers in Vanuatu and New Caledonia and feed on more than 50 species of anguilliform fish that are themselves predators: mostly morays, congers and snake-eels (Reed et al. 2002; Ineich et al. 2007). In New Caledonia, an analysis of the diet of sea kraits (*L. laticaudata* and *L. saintgironsi*) revealed 15 new species of anguilliform fish (Ineich et al. 2007; Séret et al. 2008). More generally, large populations of sea kraits are widespread in the Indo-Pacific coral reef areas (Voris 1972; Voris and Voris 1983; Heatwole 1999).

A detailed long-term study has suggested that the population of sea kraits from a single islet in New Caledonia might exert an important predation pressure on the surrounding anguilliform fish guild (Ineich et al. 2007). The study relied on various assumptions however. Most notably, the foraging ranges of the sea kraits were unknown; all the estimates were calculated by mixing the two snake species and by pooling all the different prey species together. Further investigations provided information on the specific foraging ecology of the two snake species (Brischoux et al. 2007b). Consequently, the respective diet, feeding rate and foraging areas exploited by the snakes (soft-bottoms for *L. laticaudata* and the coral matrix for *L. saintgironsi*) have been documented

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(Brischoux et al. 2007b). Simultaneously, mark recapture data collected between 2002 and 2006 on a large number of individuals (>4000 snakes identified) enabled us to estimate accurately population sizes. In the current study, combining such recently available information and using estimates of the number and the biomass of more than 40 species of fish eaten by the sea kraits, a precise evaluation of the consumption of anguilliform fish by sea kraits in New Caledonia was performed.

2 Material and methods

2.1 Sea snake populations

Two species of sea-kraits co-occur in New Caledonia: *L. saintgironsi* (Cogger and Heatwole 2006) and *L. laticaudata* (Saint Girons 1964; Ineich and Laboute 2002). Although 10 islets have been sampled, we concentrated most of the research effort on Signal Island (a 15-ha islet situated in the southwest lagoon of New Caledonia; 22°1745.93 S; 166°17′34.70 E). In this study site, more than 2600 individuals of these two snake species (*L. saintgironsi*, $N = 1246$ and *L. laticaudata*, $N = 1425$) have been individually marked (by scale-clipping) during 6 field trips, from November 2002 to December 2006. The total number of searching days was 177. More than 3800 recaptures (ranging from 1 to 23 per snake) of marked snakes (915 for *L. saintgironsi*, 2942 for *L. laticaudata*) have been obtained. The morphological characteristics of each snake have been recorded, notably Snout-Vent Length (SVL), sex, and body mass (Bonnet et al. 2005; Brischoux and Bonnet 2008; Brischoux et al. 2007b).

As snakes typically exhibit marked time and inter-individual heterogeneities in the probability of capture, accurate population size estimates require taking into account these factors (Bonnet and Naulleau 1996; Bonnet et al. 2002). On average sea kraits alternate foraging trips at sea with resting periods on land on a two-weeks basis (Brischoux et al. 2007b, Ineich et al. 2007). This means that during short time surveys (i.e., <1 week), many animals are captured repeatedly because they remain on land while roughly half of the snakes evades sampling. Therefore, short time sampling sessions tend to miss most of the characteristics of the time-heterogeneity in the probabilities of capture, generating a risk of underestimating the whole population size. During a long field session -58 consecutive days on Signal Island-, the main assumptions to perform population size estimates were satisfied (Otis et al. 1978). The influence of migration and mortality did not complicate the estimates. Indeed, the snake populations were considered as closed because sea kraits tend to be philopatric (Shetty and Shine 2002) and survival is high during a less than 2 months period (Bonnet et al. 2002). Population size estimates were performed separately for each sea krait species using CAPTURE program software (Otis et al. 1978). We also calculated the approximate biomasses represented by both species of sea kraits using the mean body mass of the snakes belonging to each size class combined to population size estimates (discarding individuals with a prey in the stomach and/or vitellogenic females; Fig. 1).

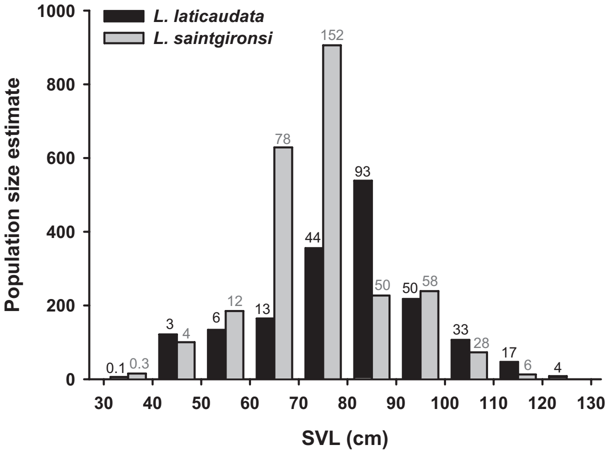

Fig. 1. Size-frequency distribution of each snake species based on population size estimates (*Laticauda laticaudata* and *L. saintgironsi* are represented with black and grey bars respectively). For each 10-m body size class of snakes, the estimated total biomass (kg) is provided (numbers above the bars). SVL: snout vent length.

2.2 Quantities and biomass of the prey consumed

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 fishes, it was easy to force them to regurgitate (Brischoux and Bonnet 2008). On Signal islet, more than 430 prey items were collected, measured and identified (Böhlke et al. 1999; Smith 1999a, 1999b; Smith and McCosker 1999; see Brischoux et al. 2007a for details).

Prey size, prey species, and the probability to find a snake with a prey in the stomach vary with snake body size and snake species in a non-linear way (e.g., certain prey are eaten solely by the adults from one snake species). Therefore it was necessary to run the analysis separately for each snake species and to take into account the influence of snake body size. To achieve this, the snake's SVL data were divided into classes of 10 cm (from 30–40 cm to 110–120 cm in *L. saintgironsi* and to 120–130 cm in *L. laticaudata*). Within each size class and using the population size estimates (see results), we calculated the number of snakes belonging to each size class (Fig. 1). In other words, for each species of sea krait, we calculated the size-frequency distribution based on population size estimates combined with the frequency of each size class calculated through the mark-recapture data (Fig. 1). We then calculated the proportion of snakes with a prey in the stomach and the occurrence and the dimensions of the different prey consumed (based on allometric equations, the size [length] and the mass of the prey consumed by each size class of snakes was estimated; Brischoux et al. 2007a; Table 1). As a consequence, it was possible to calculate the number of specimens (and the biomass) of each prey species that was consumed at a given time (Total number, Table 1). The annual consumption of prey was calculated under the assumption that on average a snake required 7 days to find, catch a prey and come back on land, plus another week to fully digest it and undertake a new foraging trip (Brischoux et al. 2007b; Ineich et al. 2007). Therefore, the number (and the biomass) of more than 40 fish species calculated at any given time was multiplied

Table 1. List of the prey species consumed by *Laticauda saintgironsi* and *L. laticaudata*. Fish length corresponds to the mean total length of individuals eaten (minimum-maximum). Total number corresponds to the number of preys consumed every two weeks (*L. saintgironsi* + *L. laticaudata*). Total number per year = Total number x 26. Biomass was calculated by multiplying total number per year by mean mass of each prey species. Minimum and maximum biomasses were calculated using sea kraits population size error.

Prey species	**Fish length (cm)**	**Total number**	**Total number per year**	**Biomass (kg)**		
				Total	**Min**	**Max**
Anarchias allardicei	15.4 (12-19)	11 (4+7)	286	1.03	0.96	1.12
Anarchias cantonensis	22.7 (19-28)	15 (15+0)	390	5.46	4.98	6.22
Anarchias seychellensis	16.0 (15-17)	5 (5+0)	130	0.50	0.47	0.58
Anarchias sp.	18.4 (17-20)	3 (3+0)	78	0.46	0.45	0.58
Cirrimaxilla formosa	26.4 (23-35)	27 (8+19)	702	17.01	16.23	18.79
Conger sp.	30.4 (15-51)	220 (39+181)	5720	381.22	356.59	407.03
Echidna sp.	32.8 (28-37)	4 (4+0)	104	4.99	4.38	5.47
Echidna unicolor	22.4 (19-27)	6 (6+0)	156	2.01	1.69	2.11
Enchelycore pardalis	20.3 (16-25)	17 (17+0)	442	3.71	3.36	4.19
Gymnothorax albimarginatus	23.9 (15-33)	171 (0+171)	4446	77.14	72.87	81.56
Gymnothorax chilospilus	24.3 (14-33)	535 (499+36)	13 910	251.02	214.72	258.83
Gymnothorax cribroris	25.6 (17-29)	3 (0+3)	78	1.41	1.47	1.64
Gymnothorax eurostus	36.2 (20-51)	75 (72+3)	1950	135.77	120.82	150.31
Gymnothorax fimbriatus	29.9 (17-44)	75 (75+0)	1 950	74.77	66.86	83.51
Gymnothorax formosus	30.7 (22-37)	10 (10+0)	260	8.44	7.65	9.56
Gymnothorax margaritophorus	27.9 (21-33)	72 (72+0)	1872	92.29	82.26	102.75
Gymnothorax moluccensis	30.6 (19-61)	61 (3+58)	1586	44.06	41.72	46.96
Gymnothorax nudivomer	24.5 (22-31)	7 (0+7)	182	2.94	2.59	2.90
Gymnothorax pindae	31.1 (18-45)	63 (60+3)	1638	67.11	59.48	73.94
Gymnothorax pseudothyrsoideus	37.9 (25-42)	4 (4+0)	104	7.59	6.65	8.31
Gymnothorax reevesi	20.3 (17-24)	21 (17+4)	546	4.94	4.32	5.29
Gymnothorax reticularis	27.6 (22-31)	8 (0+8)	208	6.00	5.72	6.40
Gymnothorax richardsonii	24.9 (19-32)	25 (8+17)	650	12.29	11.48	13.32
Gymnothorax sp.1	20.9 (16-25)	6 (6+0)	156	1.75	1.46	2.65
Gymnothorax sp.2	30.7 (24-36)	3 (0+3)	78	2.96	2.51	3.95
Gymnothorax undulatus	26.5 (23-32)	13 (13+0)	338	6.75	6.16	7.69
Gymnothorax zonipectis	20.0 (15-27)	8 (8+0)	208	1.88	1.78	2.22
Muraenichthys sp.	18.3 (15-23)	64 (0+64)	1664	13.20	12.38	13.86
Myrichtys maculosus	20.6 (19-22)	5 (0+5)	130	2.44	2.48	2.78
Myrophis microchir	16.3 (14-22)	68 (0+68)	1768	16.14	15.30	17.13
Plotosus lineatus	15.0 (11-19)	21 (0+21)	546	7.80	7.28	8.15
Ptereleotris sp.	9.5 (6-12)	18 (0+18)	468	3.07	2.90	3.25
Scuticaria okinawae	32.3 (26-41)	3 (3+0)	78	4.23	3.36	4.20
Scuticaria sp.	33.5 (32-34)	3(3+0)	78	4.09	3.25	4.06
Scuticaria tigrina	28.5 (22-39)	27 (27+0)	702	38.66	34.92	43.61
Strophidon sathete	32.0 (29-34)	3 (3+0)	78	1.35	1.40	1.75
Uropterygius alboguttatus	27.0 (22-34)	3 (3+0)	78	2.69	2.26	2.82
Uropterygius concolor	19.6 (13-26)	24 (18+6)	624	5.63	5.01	6.08
Uropterygius macrocephalus	24.5 (21-27)	9 (9+0)	234	3.98	3.38	4.23
Uropterygius sp.	21.7 (12-37)	6 (6+0)	156	2.98	2.57	3.21
Uropterygius supraforatus	30.9 (25-38)	25 (25+0)	650	27.50	24.11	30.11
Uropterygius xanthopterus	25.7 (23-28)	8 (8+0)	208	4.38	3.88	4.84
Unidentified fish	9.0 (7-11)	6 (0+6)	156	4.37	4.13	4.62
Total		1761 (1053+708)	45 786	1358.0	1228.2	1462.6

by 26 (52 weeks per year divided by two). Overall, such estimates integrated the selection operated by the snakes depending upon their species (dietary specialization; Brischoux et al. 2007b; Brischoux et al. unpublished data), their size (ontogenetic shift, Brischoux et al. unpublished data), and their respective feeding rate. Minimum and maximum biomasses of the fish were calculated using sea kraits population size standard error.

2.3 Results and discussion

The population size estimated on Signal Island was of 4087 snakes (1700 ± 96 [mean ± SD] *L. laticaudata* and 2387 ± 264 *L. saintgironsi*, representing more than 660 kg of snakes, Fig. 1), a value greater than our previous estimates (average of 1418 individuals, Ineich et al. 2007). The combination of three factors may explain such a difference. First, a long time survey (58 consecutive days on Signal island) permitted to take into account the marked time variation of the snake's catchability (e.g. repeated captures of the same individuals when digesting on land and no capture or recapture of snakes foraging at sea). Second, the increasing proportion of individually marked snakes enabled to process larger number of snakes (i.e. as a large number of snakes were already marked, less time was devoted to the long marking process of new individuals) and to sample the island more efficiently. Third, the use of a new capture technique based on the lifting of large beach-rocks enabled to sample the snakes more efficiently. Overall, based on five years of surveys, the accuracy of population size estimates was continuously perfected and the very high current value of 4000 snakes for a small island appears realistic.

The precise characterisation of the sea kraits diet (Brischoux et al. 2007b) combined with population size estimates (Fig. 1) revealed that the sea kraits take a huge quantity of fish per annum, both in terms of number and biomass (Table 1). The uptake of the snakes was particularly oriented toward 10 fish species (estimates >1000 individuals consumed per year per species, 80% of total uptake, Table 1), among which one species was under strong pressure (*Gymnothorax chilopsilus*, >10 000 fish killed by the snakes from Signal island, 30% of total uptake, Table 1). Because these fish species are also the main prey consumed by sea krait populations from other islets, they must occur in large numbers to sustain the high consumption rates of the snakes. However, classical sampling methods (under water visual census or rotenone poisoning; Kulbicki 1997) provided a very different picture. Few anguilliform fish were identified despite a massive sampling effort: 364 anguilliform fish during >1350 surveys (Ineich et al. 2007), and less than 150 specimens among the 10 species frequently caught by the snakes (e.g., only 22 *G. chilopsilus*, M. Kulbicki pers. comm.). Several species were found in the stomach of the snake solely (e.g., *Cirrimaxilla formosa*; Séret et al. 2008).

Each sea krait species selects a particular habitat to forage (hard *versus* soft bottoms) and hunt both in the vicinity of and at distance from their home-islet (Brischoux et al. 2007b). One third of the prey is taken on the 130 ha reef flat around Signal islet, representing approximately 15 000 preys (44 865/3) per year. The remaining 30 000 fish (roughly 1 t) are caught during longer trips within a mean radius of 17 km from the islet (Brischoux et al. 2007b). Therefore, the consumption of anguilliform fish by the sea kraits is important both in the reef flats and in the soft bottoms of the lagoon.

Although the research effort on the other sampled islets was less intensive, Signal Island is probably not exceptional in terms of the number of inhabiting snakes. Indeed, in all the islets visited except one ($N = 10$, Brischoux and Bonnet 2008), large populations were observed and many islets which are well renowned for their very high snake densities have not been surveyed yet. It is therefore likely that the whole sea krait population of the lagoon of New Caledonia is represented by several thousands of individuals. Inevitably, the foraging areas of the different populations overlap greatly. Overall, these results on the consumption of anguilliform fish by sea kraits suggest that these two guilds of predators are more important than previously estimated and thus might play key roles in the functioning of the coral reefs of New Caledonia.

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References

Böhlke E.B., McCosker J.E., Smith D.G., 1999, Muraenidae. In: Carpenter K.E., Niem V.H. (Eds.) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific 3, FAO, Rome, pp. 1643–1657.

Bonnet X., Naulleau G., 1996, Catchability in snakes: consequences on breeding frequency estimates. Can. J. Zool. 74, 233–239.

Bonnet X., Ineich I., Shine R., 2005, Terrestrial locomotion in sea snakes: the effects of sex and species on cliff-climbing ability in sea kraits (*Serpentes*, Elapidae, *Laticauda*). Biol. J. Linn. Soc. 85, 433–441.

Bonnet X., Pearson D., Ladyman M., Lourdais L., Bradshaw D., 2002, "Heaven" for serpents? A mark-recapture study of tiger snakes (*Notechis scutatus*) on Carnac Island, Western Australia. Austral Ecol. 27, 442–450.

Brischoux F., Bonnet X., 2008, Life history of sea kraits in New Caledonia. Mem. Mus. Nat. Hist. Nat., in press

Brischoux F., Bonnet X., De Crignis M., 2007a, A method to reconstruct anguilliform fishes from partially digested items. Mar. Biol. 151, 1893–1897.

Brischoux F., Bonnet X., Shine R., 2007b, Foraging ecology of sea kraits (*Laticauda* spp.) in the Neo-Caledonian lagoon. Mar. Ecol. Prog. Ser. 350, 145–151.

Caley M.J., 1993, Predation, recruitment and the dynamics of communities of coral-reef fishes. Mar. Biol. 117, 33–43.

Carpenter S.R., Kitchell J.F., Hodgson J.R., 1985, Cascading trophic interactions and lake productivity: fish predation and herbivory can regulate lake ecosystems. Bioscience 35, 634–639.

Cogger H., Heatwole H., 2006, *Laticauda frontalis* (de Vis, 1905) and *Laticauda saintgironsi* n. sp. from Vanuatu and New Caledonia

(*Serpentes*: Elapidae: Laticaudinae) – a new lineage of sea kraits? Rec. Aust. Mus. 58, 245–256.

Finke D.L., Denno R.F., 2004, Predator diversity dampens trophic cascades. Nature 429, 407–410.

Heatwole H., 1999, Sea snakes. Australian Natural History Series. University of New South Wales, Sydney.

Hixon M.A., 1991, Predation as a process structuring coral reef fish communities. In: Sale P.F. (Ed.) The ecology of fishes on coral reefs, Academic Press, San Diego, pp. 475–508.

Ineich I., Laboute P., 2002, Sea snakes of New Caledonia. IRD et Muséum national d'Histoire naturelle Editions, Coll. Faune et flore trop., Paris

Ineich I., Bonnet X., Brischoux F., Kulbicki M., Séret B., Shine R., 2007, Anguilliform fishes and sea kraits: neglected predators in coral reef ecosystems. Mar. Biol. 151, 793–802.

Jennings S., Polunin N.V.C., 1997, Impacts of predator depletion by fishing on the biomass and diversity of non-target reef fish communities. Coral Reefs 16, 71–82.

Kulbicki M., 1997, Bilan de 10 ans de recherche (1985–1995) par l'ORSTOM sur la structure des communautés des poissons lagonaires et récifaux en Nouvelle-Calédonie. Cybium 21, 47–79.

McCann K.S., Hasting A., Huxel G.R., 1998, Weak trophic interactions and the balance of nature. Nature 395, 794–798.

Otis D.L., Burnham K.P., Anderson D.R., 1978, Statistical inference for capture data on closed animal populations. Wildl. Monogr. 62, 1–135.

Reed R.N., Shine R., Shetty S., Cogger H., 2002, Sea kraits (Squamata: *Laticauda* spp.) as a useful bioassay for assessing local diversity of eels (Muraenidae, Congridae) in the western Pacific Ocean. Copeia, 1098–1101.

Saint Girons H., 1964, Notes sur l'écologie et la structure des populations des Laticaudinae (Serpentes : Hydrophiidae) en Nouvelle-Calédonie. Rev. Ecol. 111, 185–214.

Séret B., Brischoux F., Bonnet X., Shine R., 2008, First record of *Cirrimaxilla formosa* (Teleostei: Muraenidae) from New Caledonia, found in sea snake stomach contents. Cybium 32, 191–192.

Smith D.G., 1999a, Myrocongridae: thin morays. In: Carpenter K.E., Niem V.H. (Eds.) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific 3, FAO, Rome, pp. 1641–1642.

Smith D.G., 1999b, Congridae: Conger eels. In: Carpenter K.E., Niem V.H. (Eds.) FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific 3 FAO, Rome, pp. 1680-1688.

Smith D.G., McCosker J.E., 1999, Ophichthidae: snake eels, worm eels. In: Carpenter K.E., Niem V.H. (Eds.). FAO species identification guide for fishery purposes. The living marine resources of the Western Central Pacific 3 FAO, Rome, 1662–1669.

Voris H.K., 1972, The role of sea snakes (Hydrophiidae) in the trophic structure of coastal ocean communities. J. Mar. Biol. Assoc. India 14, 429–442.

Voris H.K., Voris H.H, 1983, Feeding strategies in marine snakes: an analysis of evolutionary, morphological, behavioural, and ecological relationships. Am. Zool. 23, 411–425.