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Effects of Oceanic Salinity on Body Condition in Sea Snakes

François Brischoux[1, 2, *], Virginie Rolland[3], Xavier Bonnet[1], Matthieu Caillaud[4] and Richard Shine[5]

[1] Centre d'Etudes Biologiques de Chizé, CEBC-CNRS UPR 1934, 79360 Villiers en Bois, France
[2] Department of Biology, University of Florida, Gainesville, FL 32611, USA
[3] Department of Biological Sciences, PO Box 599, State University, Jonesboro, AR 72467, USA
[4] IFREMER Nouvelle Calédonie, LEADNC, Campus IRD, BP 2059, 98846 Nouméa Cedex, Nouvelle Calédonie, France
[5] School of Biological Sciences A08, University of Sydney, Sydney, NSW 2006, Australia

*: Corresponding author : F. Brischoux, email address : francois.brischoux@gmail.com

Abstract:

Since the transition from terrestrial to marine environments poses strong osmoregulatory and energetic challenges, temporal and spatial fluctuations in oceanic salinity might influence salt and water balance (and hence, body condition) in marine tetrapods. We assessed the effects of salinity on three species of sea snakes studied by mark–recapture in coral-reef habitats in the Neo-Caledonian Lagoon. These three species include one fully aquatic hydrophiine (*Emydocephalus annulatus*), one primarily aquatic laticaudine (*Laticauda laticaudata*), and one frequently terrestrial laticaudine (*Laticauda saintgironsi*). We explored how oceanic salinity affected the snakes' body condition across various temporal and spatial scales relevant to each species' ecology, using linear mixed models and multimodel inference. Mean annual salinity exerted a consistent and negative effect on the body condition of all three snake species. The most terrestrial taxon (*L. saintgironsi*) was sensitive to salinity over a short temporal scale, corresponding to the duration of a typical marine foraging trip for this species. In contrast, links between oceanic salinity and body condition in the fully aquatic *E. annulatus* and the highly aquatic *L. laticaudata* were strongest at a long-term (annual) scale. The sophisticated salt-excreting systems of sea snakes allow them to exploit marine environments, but do not completely overcome the osmoregulatory challenges posed by oceanic conditions. Future studies could usefully explore such effects in other secondarily marine taxa such as seabirds, turtles, and marine mammals.

1. Introduction

Secondarily marine, air-breathing vertebrates provide robust model systems with which to explore the complex effects of bio-physical parameters of the oceanic environment across a range of temporal and spatial scales. Research over the past two decades has revealed strong links between environmental parameters (e.g., sea surface temperature, primary production, sea-ice extent, El Niño or La Niña events, fisheries offtake) on population parameters such as abundance (e.g., Baez et al. 2011), growth rates (e.g. Quillfeldt et al. 2007), survival (e.g. Rolland et al. 2010), breeding probabilities (e.g. Jenouvrier et al. 2003), breeding success (e.g., Leaper et al. 2006; Lee 2011), and aspects of individual behaviour such as spatial ecology and foraging success (e.g. Pinaud et al. 2005; Weimerskirch et al. 2010). In several taxa, environmentally-induced variation in such traits ultimately influences population dynamics (Forcada et al. 2006; Rolland et al. 2009). Understanding such links can enhance our ability to predict biotic responses to environmental perturbations (Jenouvrier et al. 2009; Wolf et al. 2010).

Although simply documenting empirical links between environmental variation and population responses is useful, an understanding of the proximate mechanisms that cause such links provides a stronger (and more general) basis for accurate prediction (Helmuth et al. 2005; Kearney and Porter 2009). In most cases, such mechanisms will include several intermediate steps between the physical properties of the marine environment and their ultimate effects on individuals, or populations, of predators. All species of secondarily marine vertebrates use the oceanic environment to forage, so that the effects of physical oceanic parameters on apex predators likely are mediated by intermediate trophic levels (Pinaud et al. 2005). Even apparently direct effects such as those of currents, fronts, or the extent of sea-ice on the at-sea distribution of seabirds or marine mammals, may in fact be mediated by the distribution of trophic resources (Bost et al. 2009).

Clearly, however, not all impacts of environmental variables on organismal function work via intermediate steps such as shifts in availability of food; some environmental effects act directly on the individual organism (Tomanek and Somero 2000; Helmuth et al. 2002). For example, water temperature directly affects body temperatures (and thus metabolic rates) of ectothermic vertebrates, and hence influences the duration of their dives (Storey et al. 2008; Priest and Franklin 2002; Pratt and Franklin 2010); and substantially modifies the energy budgets of endothermic divers (Butler and Jones 1997; de Leeuw 1996; Grémillet et al. 2001). Although typically overlooked (but see Gutiérrez et al. 2011, Brischoux et al. 2012), salinity poses a major physiological challenge to air-breathing marine vertebrates. Because seawater is hyperosmotic to body fluids, marine species gain salt and lose water across permeable surfaces (Schmidt-Nielsen 1983). Drinking of seawater (e.g., during prey capture) imposes a supplementary salt-load (Costa 2002; Houser et al. 2005). Thus, most marine vertebrates must regulate their osmotic balance (Schmidt-Nielsen 1983). Excreting excess salt through specific structures (salt glands in non-mammalian vertebrates [Peaker and Linzell 1975]; reniculate kidneys and elongated nephrons in marine mammals [Ortiz 2001]) can entail significant energetic costs (Schmidt-Nielsen 1983; Ortiz 2001; Gutiérrez et al. 2011). Dehydration due to osmotic loss of water to a saline medium is another risk faced by marine vertebrates (Lillywhite et al. 2008). Taken together, these elements suggest that oceanic salinity may impose significant energetic and hydric costs to air-breathing vertebrates.

Herein, we test the hypothesis that salinity may impose costs to marine tetrapods, using three species of sea snakes from the family Elapidae as our study system. Two independent phylogenetic transitions from terrestrial to marine life have occurred within this family

(Hydrophiinii and Laticaudinae) (Heatwole 1999). Extensive research on these taxa offers a robust ecological and physiological background to understand potential effects of salinity. Importantly, the degree of reliance upon marine versus terrestrial habitats varies extensively among species within these lineages. Hydrophiines are totally aquatic, whereas laticaudines are amphibious (Heatwole 1999). Within the laticaudines (sea kraits), some taxa use terrestrial habitats more frequently than do others (Greer 1997, Bonnet et al. 2005, Lane and Shine 2011a,b), and laticaudine species vary in their ability to tolerate saline conditions (as measured by dehydration rates in seawater) (Lillywhite et al. 2008). Maintaining osmotic balance seems to pose a physiological challenge to marine snakes, and some species require access to fresh or brackish water for their survival (Bonnet and Brischoux 2008; Lillywhite et al. 2008). Finally, salinity likely influenced the evolutionary transition to marine life in snakes, and currently constrains the diversity and geographic distributions of sea snakes (Brischoux et al. 2012).

This combination of traits renders the elapid sea snakes a powerful model system with which to explore the effects of salinity on marine vertebrates. Salinity might affect sea snakes through two pathways: (1) the energetic costs of excreting excess salt (Peaker and Linzell 1975; Gutiérrez et al. 2011), and (2) dehydration due to water loss from the body to the surrounding seawater (Lillywhite et al. 2008). Both of these processes should influence a snake's body mass (through utilization of body reserves for the former, and due to water loss for the latter), and hence its body condition (mass relative to body length, *sensu* Bonnet and Naulleau [1995]). We thus explored the effect of salinity on the body condition of three species of sea snakes (a hydrophiine sea snake, *Emydocephalus annulatus*, and two laticaudine sea kraits, *Laticauda laticaudata* and *Laticauda saintgironsi*) from populations that we have regularly surveyed through mark-recapture studies since 2002 on the coral reefs of New Caledonia. Because these species differ in their degree of reliance on oceanic habitats (see above), we adopted two complementary approaches. First, we used a large time-scale analysis to compare inter-annual variation in body condition to concurrent variation in oceanic salinity. Second, we used a finer-scaled approach to explore potential effects of salinity at temporal and spatial scales relevant to each species' ecology.

2. Materials and Methods

2.1. Study species and study sites

Amphibious sea kraits (*Laticauda* spp.) at Signal Island

Two species of sea kraits occur in New Caledonia, *Laticauda laticaudata* and *L. saintgironsi* (Brischoux and Bonnet 2009; Lane and Shine 2011a,b). Both species are amphibious: they forage at sea, mainly for anguilliform fish (moray eels, conger eels, and snake eels) (Brischoux et al. 2007, 2009, 2011) but return to small islands to digest their prey, slough their skins, mate, and lay eggs (Brischoux and Bonnet 2009). *L. saintgironsi* is more terrestrial than is *L. laticaudata* as measured through locomotor ability on land (Shine et al. 2003b; Bonnet et al. 2005) and habitat selection (Bonnet et al. 2009). When on land, *L. laticaudata* is mainly found under rocks that are submerged at high tide (Bonnet et al. 2009), whereas *L. saintgironsi* ventures farther inland (Bonnet et al. 2009; Lane and Shine 2011a). As a result, the primarily aquatic *L. laticaudata* spend most of the time in intimate contact with seawater, while the more terrestrial *L. saintgironsi* can more easily obtain freshwater during rainfall events (Bonnet and Brischoux 2008; Bonnet et al. 2009).

At sea, the two species forage in different habitats and take different prey species (Brischoux et al. 2007, 2009, 2011), and thus differ in the spatial extent and duration of their foraging trips (Brischoux et al. 2007, Fig. 1). When kept in seawater, the primarily aquatic *L. laticaudata* dehydrates less rapidly than does *L. colubrina*, a sister species of *L. saintgironsi* (Lillywhite et al. 2008, Lane and Shine 2011b).

Since 2002, we have regularly surveyed sea krait populations on Signal Island, in the South-Western Lagoon of New Caledonia (22°17′S, 166°17′E, Fig. 1). This small island is situated midway between the external barrier reef and the main island of New Caledonia (Fig. 1) (see Bonnet and Brischoux 2008; Brischoux and Bonnet 2008, 2009 for details on our field procedures). For the current study, we focus on the 2002 to 2008 period, when we have detailed data both on sea kraits and on oceanic salinity (see below) (Fig. 2). Our mark-recapture dataset included 1007 individually marked *L. laticaudata* and 1127 recaptures (N= 2134), and 699 individually marked *L. saintgironsi* and 444 recaptures (N=1143, see "Analyses" below).

Turtle-headed sea snakes (*Emydocephalus annulatus*) at Nouméa

Emydocephalus annulatus is a shallow-water sea snake that spends its entire life underwater (Cogger 1975; Ineich and Laboute 2002), and feeds on the eggs of damselfish, blennies, and gobies (Voris 1966; Guinea 1996; Ineich and Laboute 2002). Since 2002, we have regularly surveyed two adjacent sites at Nouméa, New Caledonia (22°16′S, 166°26′E; Baie des Citrons and Anse Vata, separated by a few hundred meters) (Fig. 1). Details on our field procedures can be found elsewhere (Shine 2005; Shine et al. 2003a, 2004, 2005, 2010). For the current study, we focus on the 2002 to 2008 period, as above. Our mark-recapture dataset included 443 individually marked snakes and 276 recaptures (N=719, see "Analyses" below).

Index of body condition

For each species, we quantified the body condition index (BCI) using residual scores from the linear regression between body size (snout-to-vent length [SVL]) and body mass (both variables were log-transformed for linearity) (Bonnet and Naulleau 1995). In both *Laticauda* spp., we excluded individuals with prey in the stomach as well as reproductive females (i.e., with vitellogenic follicles or oviductal eggs) from our calculations. For *E. annulatus*, our calculations excluded reproductive females, but not recently-fed individuals. Because *E. annulatus* feed only on tiny fish eggs (mean individual prey mass ~0.00008 g) (Shine et al. 2004), relative prey mass is trivial (e.g., 1000 eggs represents less than <0.1% of the snake's mean body mass).

2.2. Salinity

Because long-term, fine-scale monitoring of salinity over contrasted spatial scales were lacking, salinity in the lagoon was computed from the MARS3D (Model for Application at Regional Scales) model (further details can be found in Lazure and Dumas [2008]). The configuration is implemented on a 540m resolution horizontal grid (i.e., fitting our smallest radii, see below) and thirty layers on a vertical grid. These layers are terrain-following and distributed to enhance resolution close to the sea's surface. This grid is oriented along the longitudinal axis of the main island of New Caledonia to optimize the number of wet cells, and the total domain encompasses both our study sites.

We used a high-resolution atmospheric model (WRF) to estimate wind and heat fluxes at the sea's surface (see Lefèvre et al. 2010). The numerical solution of the BRAN model

(http://www.marine.csiro.au/ofam1/) was used to predict temperature, salinity, sea-surface height, and velocity of current along the lateral open boundary (e.g., open Pacific ocean outside the lagoon) (Fig. 1). High-frequency movements (tides and surges) of the sea-surface elevation were added to the BRAN solution by harmonic composition from ADCIRC tidal components and an inverse barometer component. Finally, river flows were included, to estimate salinity near river mouths. Comparisons of predictions against datasets from coastal stations and hydrographic surveys show a good accuracy of the model (daily mean absolute error between predicted and observed values was ~0.5% around Signal Island and ~1% around Anse Vata). We used this model to predict oceanic salinity every three days between 2002 and 2008, but we used salinity integrated over longer durations (e.g., fortnights, months *versus* calculation of daily errors), thereby decreasing the overall error over the temporal scale of our analyses.

We used our information on snakes' spatial ecology to choose appropriate spatial and temporal scales for analysis of the putative links between salinity and the snakes' body condition. At our study sites, the foraging trips of *Laticauda* spp. are bimodal (Brischoux et al. 2007): either very short (< 1 day, for one third of the foraging trips) when snakes capture a prey item on the reef flats surrounding Signal Island (mean radius of ~500 m) (Fig. 1); or much longer (1-3 weeks, for the remaining two thirds of the trips) in which case snakes capture their prey much further away (mean radius of ~14 km for *L. laticaudata* and ~21 km for *L. saintgironsi*) (Brischoux et al. 2007) (Fig. 1). As a consequence, we computed salinity values integrated over the vertical column within a radius of 500 m of Signal Island for both *Laticauda* spp., and within a radius of 14 km for *L. laticaudata* and 21 km for *L. saintgironsi* (Figs 1 and 2). By contrast, *E. annulatus* is a shallow water species, restricted to a small area around our study sites (e.g., virtually no exchange of individuals among our two study populations, despite the small distance between them [R. Shine, unpubl. Data]). We thus computed mean salinity values within a radius of 500m, centred on Anse Vata (Figs 1 and 2).

2.3. Analyses

To explore temporal and spatial extents of the effects of salinity on the snakes' body condition, we incorporated scales relevant to each species' ecology. For each study site and/or radius, we calculated average salinity over the year, month, fortnight, and week during which a snake was captured. Because the effect of salinity will be integrated over time (i.e., a snake's body condition may reflect its prior history of exposure, as well as current salinity levels), we also incorporated time-lags by calculating mean values of salinity for the month previous to the month of capture, the fortnight previous to the fortnight of capture and the week previous to the week of capture. Finally, we also computed mean salinity values over the month/fortnight/week two months/fortnights/weeks previous to the month/fortnight/week of capture. In total, we computed one time-constant model, and ten models with different temporal scales of salinity variation for the three species, over two spatial scales for the *Laticauda* spp. This resulted in a total of 53 models: 11 for *E. annulatus* and 21 each for *L. laticaudata* and *L. saintgironsi*.

All models were linear mixed models with salinity as a fixed effect and individual identity as a random effect to account for individual heterogeneity (several individuals were captured more than once which could generate pseudoreplication). We used the *lmer* procedure in the lme4 package of R software (Crawley 2007). Because of temporal correlation between the various salinity variables, each variable was included in a separate model to explain variation in the body-condition index. To avoid multiple testing problems, we used an information theoretic approach to compare competing models, and for statistical inference based on the Akaike Information Criterion (AIC) (Burnham and Anderson 2002). We began model selection with the time-constant model and models with annual salinity. Then, if the best model included annual

salinity, we proceeded to examine models with salinity averaged over finer temporal scales. The best model was taken to be the one with lowest AIC and $\Delta AIC \leq 2$ (where $\Delta AIC_i = AIC_i - min$ AIC). The AIC weights ($AICw_i$), a measure of relative likelihood of each model, were calculated as $AICw_i = exp(-0.5*\Delta AIC_i)/ \sum (exp[-0.5*\Delta AIC])$.

3. Results

3.1. Annual effects

In all three species of marine snakes, models incorporating mean annual salinity were better than time-constant models (lower AICs), indicating that temporal variation in snakes' body condition was partly explained by variation in mean annual salinity (Table 1). For *Laticauda* spp., models that included mean annual salinity at the largest spatial scale relevant to snake' foraging trips (within radii of 14 or 21 km around Signal Island depending on the species) (Fig. 1) were more powerful (>90% support) in explaining variation in the snakes' body condition than were models that incorporated salinity variation at smaller spatial scales (Table 1).

3.2. Temporal and spatial effects of salinity

In the fully aquatic *E. annulatus*, variations in salinity over short (e.g., weekly) time scales were less successful at explaining temporal variation in snakes' body condition than was the model incorporating mean annual salinity (Table 2). A similar result was seen in the more aquatic of the two laticaudine species, *L. laticaudata*, whereby variation in snakes' body condition was most strongly linked to mean annual salinity over a large spatial scale (Table 3). For this species, most of the top ten models incorporated salinity values over the largest spatial scale (i.e., 14 km) (Table 3).

The more terrestrial *L. saintgironsi* showed a different pattern, with fluctuations in the body condition of this species best explained by variations in salinity over a shorter time scale (i.e., the month previous to the month of capture) (Table 4; Fig 3). Most other models with substantial support (i.e., $\Delta AIC<4$ and AICw>0.08, Table 4) involved shorter time scales as well, bracketing a time lag spanning the week before the week of capture and the month before the month of capture (Table 4). Unlike the case with *E. annulatus* or *L. laticaudata*, the model incorporating mean annual salinity was poorly supported for the more terrestrial laticaudine species (Table 4). However, similarly to *L. laticaudata* and regardless of time scale, most of the top ten models incorporated salinity values over the largest spatial scale (i.e., 21 km *versus* 500 m) (Table 4). Using model averaging (i.e., summing AIC weights of all models with salinity measured at 21km), models that included salinity calculated at the largest spatial scale received 90.6% support among all tested models.

In all three snake species, the best models (*E. annulatus*: model 1, Table 2; *L. laticaudata*: model 1, Table 3; *L. saintgironsi*: model 4, Table 4) indicated a negative effect of salinity on body condition (*E. annulatus*: slope=-0.221±0.026, $P_{Wald}<0.0001$; *L. laticaudata*: slope=-0.131±0.022, $P_{Wald} =0.0001$; *L. saintgironsi*: slope=-0.162±0.038, $P_{Wald}=0.002$, see Fig. 3). That is, higher values of oceanic salinity consistently were associated with reduced body condition in sea snakes (all slopes were negative; values not shown).

4. Discussion

To our knowledge, our analysis is the first to assess the effects of variation in oceanic salinity on the body condition of free-ranging marine snakes. As expected from the physiological challenges of living in a hyperosmotic environment, sea snakes were in lower body condition during (and following) periods of high oceanic salinity, across a range of temporal and spatial scales (Tables 1-4; Fig. 3).

There are some limits to our study however, as our analysis did not include other environmental factors (such as water temperature or availability of food) that should also influence the body condition of free-ranging sea snakes. Incorporating such factors is difficult, for several reasons. First, the divergent life histories of the two families included in this study preclude a straightforward inclusion of these parameters. For example, including measurements of water temperature (if available) in our models would be straightforward for the totally aquatic *E. annulatus*, but not for amphibious sea kraits that come back on land to digest their prey. Thus, for both *L. saintgironsi* and *L. laticaudata*, thermal data would have to somehow combine at-sea and on-land thermal regimes (e.g., under beach rocks, in bird burrows) (Bonnet et al. 2009). That complexity prevents simple comparisons of similar models among species. Second, it was logistically impossible to obtain (or to model) detailed data for those parameters over the duration of our study, and for the range of temporal and spatial scales we used. In addition, variation in salinity may directly affect the prey of the snakes. However, this hypothesis is not robustly supported by available data. First, the two lineages of sea snakes we examined in this study are highly divergent in their diets. Sea kraits feed on relatively large (mostly sub-adult and adult) anguilliform fish (Brischoux et al. 2007, 2009, 2011), while *E. annulatus* feeds exclusively on the eggs of damselfish, blennies, and gobies (Voris 1966; Guinea 1996; Ineich and Laboute 2002). It is unlikely that high salinity could similarly affect two contrasting life-stages of two different fish lineages over similar temporal scales. Second, such putative direct effects of salinity on prey species cannot explain the different effects of salinity we found between the most terrestrial taxon (*L. saintgironsi* - sensitive to salinity over a short temporal scale, see results) and the more aquatic species (*E. annulatus*, fully aquatic and *L. laticaudata*, highly aquatic; both being sensitive to salinity over an annual scale). Thus, we cannot totally evaluate the impact of variation in salinity relative to other sources of variation (such as in temperature or food supply); all we can say is that our analyses suggest that oceanic salinity (a parameter largely overlooked to date) affects a sea snake's body condition. Future studies could usefully attempt to quantify the relative contributions of various environmental parameters.

Models incorporating mean annual salinity were better predictors of snakes' body condition than were time-constant models, as expected if (1) all three snake species were negatively affected by salinity, and (2) they integrate the negative effects of salinity over a long period of time (Table 1, Fig. 3). Incorporating variation in salinity over shorter timescales did not improve our ability to predict variation in body condition in two of our study species, the totally aquatic *E. annulatus* and the highly aquatic *L. laticaudata*; in both of these taxa, annual salinity was the best predictor of body condition among all variables tested (Tables 2, 3). In contrast, the more terrestrial species (*L. saintgironsi*) appeared to be sensitive to fluctuations in salinity over shorter timescales (weeks to months) (Table 4). This time lag is consistent with the probable duration of a snake's most recent foraging trip at sea prior to capture (= 1 to 3 weeks) (Ineich et al. 2007; Brischoux et al. 2007). Digestion of a large meal requires one to two weeks (Ineich et al. 2007; Brischoux et al. 2007), so the foraging cycle (prey capture at sea and its subsequent digestion on land) is likely to last two to five weeks. As our analysis omitted snakes with prey items in their digestive tracts, the duration of the foraging cycle dovetails well with our conclusion that

body condition in *L. saintgironsi* is affected by oceanic salinity over the preceding few weeks (Table 4).

In combination, our results suggest that *L. saintgironsi* is more sensitive to salinity over a short time than are the other taxa. There are three plausible (and complementary) reasons for this difference. First, *L. saintgironsi* is exposed to oceanic salinity only intermittently (during foraging bouts) so may be affected by conditions only at that time rather than averaged over a broader timescale. Second, the more terrestrial habits of this species (Bonnet et al. 2005, 2009; Lane and Shine 2011a) increase its access to freshwater during rare and unpredictable rainfall events (Bonnet and Brischoux 2008). Such events may allow *L. saintgironsi* to restore osmotic balance, regardless of oceanic levels of salinity (Bonnet and Brischoux 2008, see also Lilywhite et al. 2008). Third, higher dehydration rates in seawater (assessed in *L. colubrina*, a sister species of *L. saintgironsi*) (Lane and Shine 2011b) suggest that local salinity should affect body condition more rapidly in *L. saintgironsi* than in *L. laticaudata* (Lillywhite et al. 2008). All three of these processes might render body condition in *L. saintgironsi* sensitive to short-term rather than long-term levels of oceanic salinity.

Both *L. laticaudata* and *L. saintgironsi* sometimes forage close to their home-island (on the reef flat within 500 m, Fig. 1) and sometimes much farther away (mean radius of 14 km and 21 km for *L. laticaudata* and *L. saintgironsi* respectively) (Brischoux et al. 2007) (Fig. 1). The strongest effects of salinity on the body condition of these snakes are over the larger spatial scales (Tables 1-4), perhaps because the longer trips expose snakes to those salinity conditions for a prolonged period (Brischoux et al. 2007). In contrast, the highly sedentary *E. annulatus* is affected by salinity levels over a small spatial scale (i.e., 500 m) (Fig. 1).

In summary, the invasion of marine habitats by terrestrial snakes has been accompanied by a wide range of morphological, behavioural, and physiological modifications that have enabled these animals to thrive in tropical oceans (Heatwole 1999; Aubret and Shine 2008, Brischoux and Shine 2011). Nonetheless, adaptations to marine life may not have completely emancipated snakes from the constraints associated with salt balance and water balance in a hyperosmotic environment (Lillywhite et al. 2008, Brischoux et al. 2012). Reflecting their ancestral dependence on fresh water, even these highly specialized marine snakes exhibited reduced body condition after periods of higher-than-average oceanic salinity. Although variation in salinity through time in the Neo-Caledonian lagoon is relatively minor (e.g., ~1 PSS [Practical Salinity Scale]), sea snakes are exposed to salt overloading because for prolonged periods they remain in intimate contact with an hyperosmotic medium with very limited access to fresh water (Bonnet and Brischoux 2008; Lillywhite et al. 2008). Our analysis clearly detected negative effects despite the low range of variation in oceanic salinity. In support of these results, salinity constrains the current diversity and geographic distributions of sea snakes (Brischoux et al. 2012). Other populations of marine snakes are found in areas that fluctuate from very dilute to full-strength saltwater, and may show much more dramatic effects. Also, our correlative analysis does not allow teasing apart the effects of the energetic costs of excreting excess salt (Peaker and Linzell 1975; Gutiérrez et al. 2011) and/or the dehydration due to loss of water to the surrounding sea (Lillywhite et al. 2008). Experimental approaches will be crucial for unravelling the respective contributions of these two different, but complementary, physiological processes. Such experimental approaches also would improve our understanding of the mechanisms and intensity of the effect of salinity on marine snakes' body condition. In addition, future studies could usefully examine the effect of salinity on traits such as growth rates, survival, reproductive frequency, and reproductive output, as well as exploring the impacts of other environmental parameters such as temperature, rainfall, and availability of food. Fluctuations in oceanic salinity might well influence the population dynamics of this overlooked

assemblage of tropical, marine, apex predators (Ineich et al. 2007; Brischoux and Bonnet 2008). Osmoregulatory constraints may be important in other secondarily marine vertebrates also, such as seabirds, turtles, cetaceans, and pinnipeds (e.g. see Gutiérrez et al. 2011). For a comprehensive understanding of the impacts of climatic change on such animals, we cannot afford to ignore the potential role of oceanic salinity.

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Tables

Table 1. Selection of a model for body condition of snakes as a function of mean annual oceanic salinity. AIC is the Akaike Information Criterion. ΔAIC is the difference between the best model (lowest AIC) and the AIC of the model considered. AICw is the AIC weight representing the relative likelihood of the model considered. The best model is shown in boldface and the italicized time-constant model is used as a reference model. See text for details, and Tables 2 - 4 for the relative weights of these annual models when taking into account other temporal scales.

Model	Definition	AIC	ΔAIC	AICw
Laticauda saintgironsi				
1	**21 km**	**-1126**	**0**	**0.94**
2	500 m	-1120	5	0.06
3	*constant*	*-1115*	*11*	*0.00*
Laticauda laticaudata				
1	**14 km**	**-2145**	**0**	**0.98**
2	500 m	-2137	8	0.02
3	*constant*	*-2119*	*26*	*0.00*
Emydocephalus annulatus				
1	**500 m**	**-1183**	**0**	**1.00**
2	*constant*	*-1121*	*63*	*0.00*

Table 2. Selection of a model for temporal fluctuations in body condition of the seasnake *Emydocephalus annulatus* as a function of variation in oceanic salinity at various temporal scales. See text for details and Table 1 for legend. Model 1 is identical to that in Table 1 but is now used as a reference model. "Previous 2 months/fortnights/weeks" stand for the salinity calculated during the month/fortnight/week two months/fortnights/weeks previous to the month/fortnight/week of the snake's capture.

Model	Definition	AIC	ΔAIC	AICw
1	*Year*	*-1183.26*	*0.0*	*1.000*
3	Previous 2 fortnights	-1138.76	44.5	0.000
4	Previous fortnight	-1130.17	53.1	0.000
5	Month	-1129.46	53.8	0.000
6	Previous 2 weeks	-1128.88	54.4	0.000
7	Previous month	-1124.71	59.1	0.000
8	Fortnight	-1123.71	59.6	0.000
9	Week	-1123.07	60.2	0.000
10	Previous week	-1122.33	60.9	0.000
11	Previous 2 months	-1122.19	61.1	0.000

Table 3. Selection of a model for body condition of the sea snake *Laticauda laticaudata* as a function of salinity at various temporal and spatial scales (500 m and 14 km from the snake's home island). Only the top ten models and the time-constant model (italicized) are presented. See text for details and Table 1 for legend. Model 1 is identical to that in Table 1 but is now used as a reference model. "Previous 2 months/fortnights/weeks" represents the mean salinity calculated during the month/fortnight/week two months/fortnights/weeks previous to the month/fortnight/week of capture.

Model	Definition	AIC	ΔAIC	AICw
1	*Year - 14 km*	*-2144.92*	*0.0*	*0.998*
4	Previous 2 fortnights – 14 km	-2131.25	13.7	0.001
5	Previous month – 14km	-2128.98	15.9	0.000
6	Previous 2 weeks – 14 km	-2128.60	16.3	0.000
7	Previous 2 months – 14 km	-2128.32	16.6	0.000
8	Previous 2 weeks – 500 m	-2124.87	20.1	0.000
9	Previous fortnight – 14 km	-2122.73	22.2	0.000
10	Previous 2 months – 500 m	-2121.94	23.0	0.000
11	Previous month – 500 m	-2121.90	23.0	0.000
12	Previous 2 fortnights – 500 m	-2120.90	24.0	0.000

Table 4. Selection of a model for body condition of the sea snake *Laticauda saintgironsi* as a function of salinity at various temporal and spatial scales (500 m and 21 km from the snake's home island). Only the top ten models and the time-constant model (italicized) are presented. See text for details and Table 1 for legend. Model 1 is identical to that in Table 1 but is now used as a reference model. "Previous 2 months/fortnights/weeks" represent the salinity calculated during the month/fortnight/week two months/fortnights/weeks previous to the month/fortnight/week of the snake's capture.

Model	Definition	AIC	ΔAIC	AICw
4	**Previous month - 21 km**	**-1149.41**	**0.0**	**0.524**
5	Fortnight – 21 km	-1146.05	3.4	0.098
6	Previous 2 fortnights – 21km	-1145.94	3.5	0.093
7	Previous week – 21 km	-1145.79	3.6	0.086
8	Previous 2 weeks – 21 km	-1145.65	3.8	0.080
9	Previous month – 500 m	-1145.59	3.8	0.078
10	Previous fortnight – 21 km	-1142.32	7.1	0.015
11	Previous week – 500 m	-1141.77	7.6	0.012
12	Week – 21 km	-1141.62	7.8	0.011
13	Fortnight – 500 m	-1139.15	10.3	0.003
1	*Year – 21 km*	*-1126.05*	*23.4*	*0.000*

Figures

Figure 1. Map of the Southwestern Lagoon in New Caledonia. Thick black circles (labelled 1, 2, 3 and 4) are centered on each study site and illustrate the spatial scales on which we focused our analyses. "1", "2" and "3" are centered on Signal Island (black dot within 1) and illustrate the 500 m, 14 km, and 21 km radii. "4" is centered on Anse Vata and illustrates the 500 m radius (Baie des Citrons is adjacent, northwest of Anse Vata and included within that circle). See text for details. Black areas indicate emergent land (main island, and small coralline islands within the lagoon), grey areas represent coral reef flats, and light grey areas represent the barrier reef and other fringing reefs. Modified from Brischoux et al. 2007.

Figure 2. Salinity around Signal Island at various spatial scales (500m, 14 km, and 21 km; upper panel) and salinity around Anse Vata (Nouméa; lower panel). Curves represent monthly means between January 2002 and April 2008. PSS: Practical Salinity Scale. See text for details.

Figure 3. Relationships between oceanic salinity (Practical Salinity Scale [PSS]) and body condition index (BCI) for three species of sea snakes. The panels show the relationship between mean annual salinity and mean body condition for *E. annulatus* (upper left panel), *L. laticaudata* (upper right panel), *L. saintgironsi* (lower left panel), and between mean salinity during the month previous to the month of capture and body condition for *L. saintgironsi* (lower right panel). Regression lines are drawn from the best models and error bars represent standard errors. See text for details of the analyses.
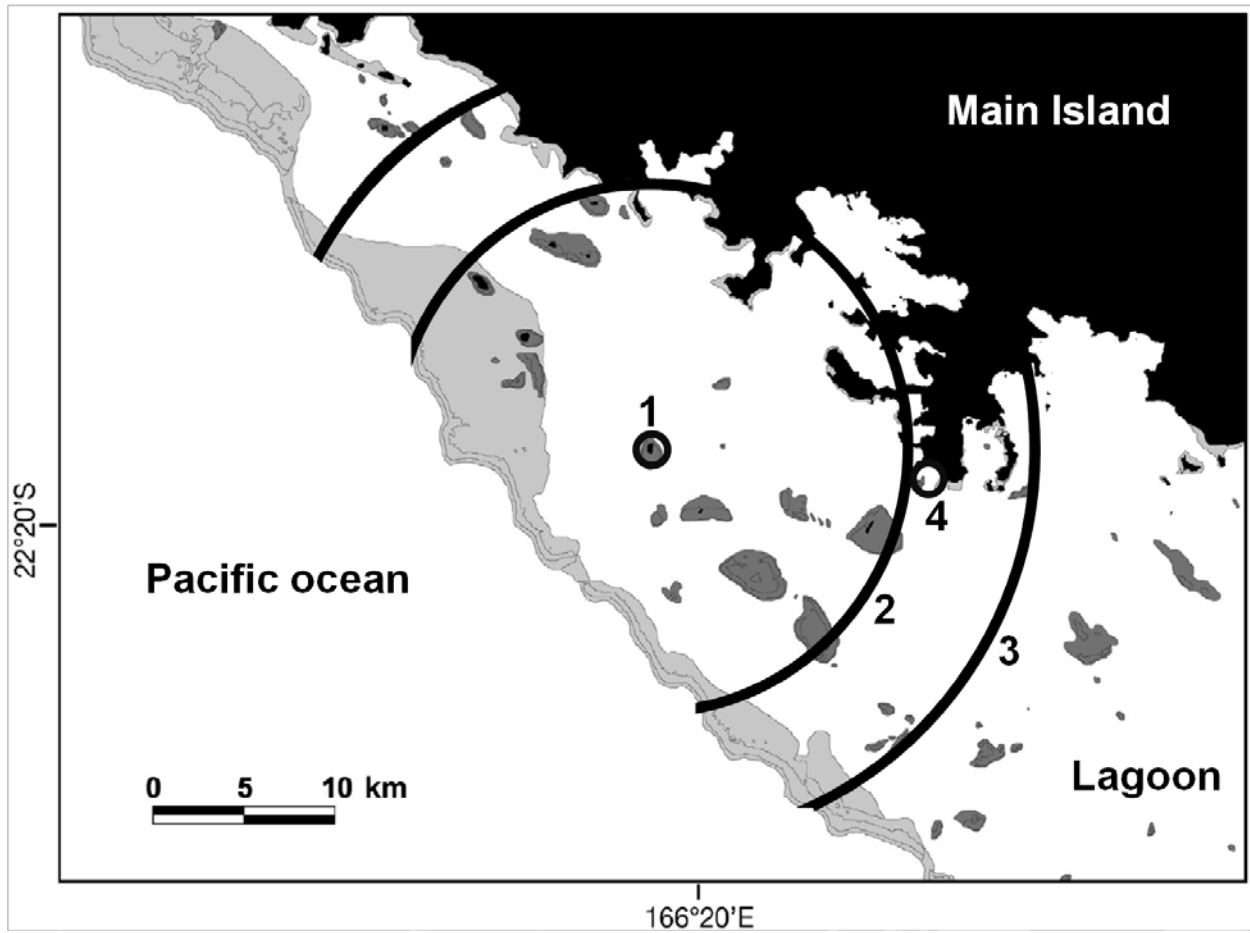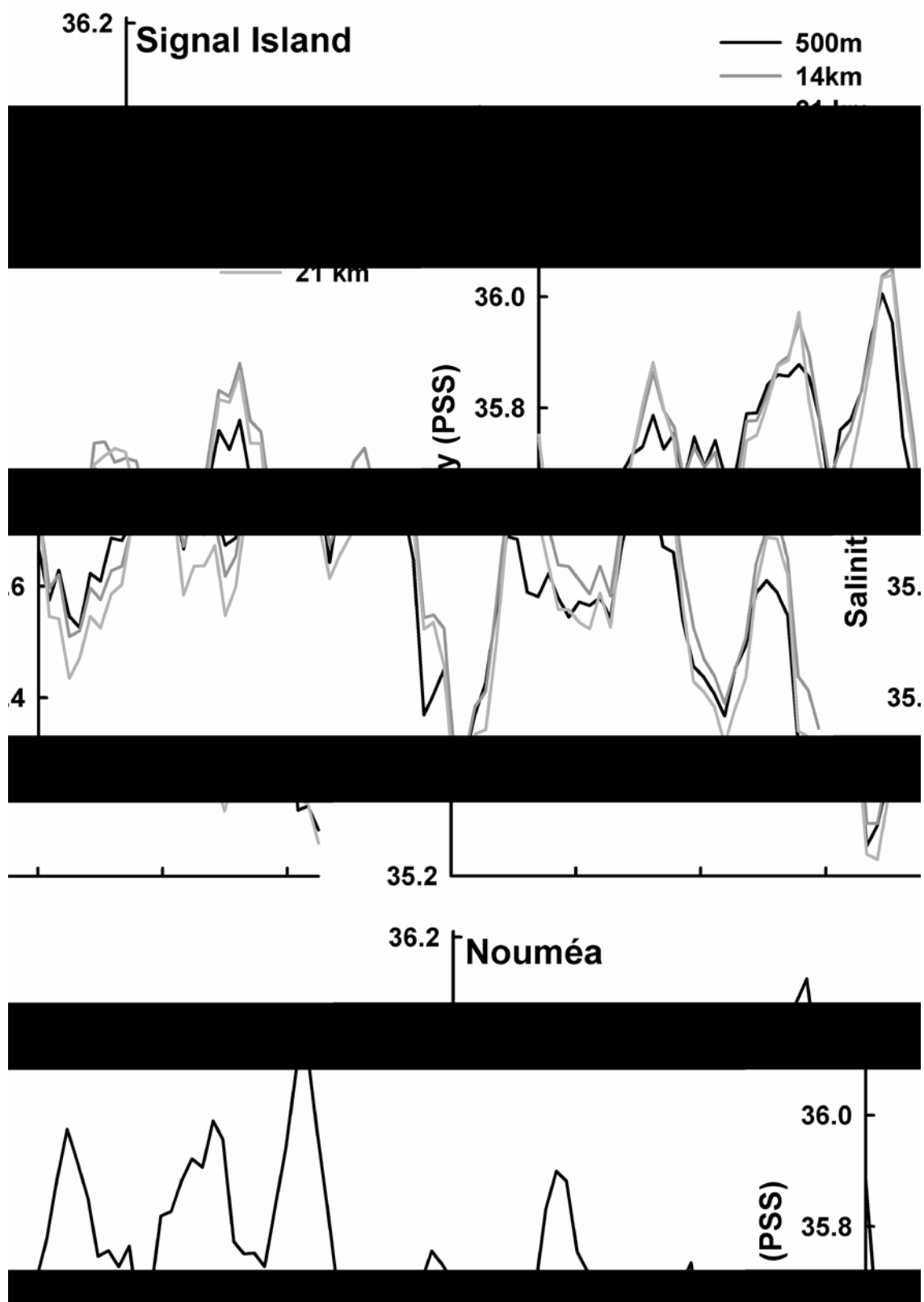
Figure 1.

Figure 2.

Signal Island

— 500m
— 14km
— 21 km

Salinity (PSS)

36.2
36.0
35.8
35.6
35.4
35.2

Nouméa

(PSS)

36.2
36.0
35.8

Figure 3.

Emydocephalus annulatus (Year, 500 m)

Laticauda laticaudata (Year, 14 km)

Laticauda saintgironsi (Year, 21 km)

Laticauda saintgironsi (Previous month, 21 km)

20