Integrative and Comparative Biology

Integrative and Comparative Biology, volume 52, number 2, pp. 257–273
doi:10.1093/icb/ics080
Society for Integrative and Comparative Biology

SYMPOSIUM

Thermal Biology of Sea Snakes and Sea Kraits[1]

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From the symposium "New Frontiers from Marine Snakes to Marine Ecosystems" presented at the annual meeting of the Society for Integrative and Comparative Biology, January 3–7, 2012 at Charleston, South Carolina.

[1] Since the senior author is editor of ICB, the review of this article was handled by the Assistant Editor so as to maintain anonymity of the reviewers.

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Synopsis Temperature probably had no direct effect on the evolution of sea kraits within their center of origin, a geologically stable thermal zone straddling the equator, but may have indirectly affected expansions and contractions in distributions beyond that zone through global fluctuations that caused alternation of higher and lower sea levels. The northern limit of the *Laticauda colubrina* complex seems to be the 20°C isotherm; in the south, the range does not reach that isotherm because there is no land (also a habitat requirement of sea kraits) within the zone of suitable temperature. The relationship of temperature to the pattern of geographic variation in morphology supports either the hypothesis of peripheral convergence or the developmental hypothesis but does not distinguish between them. Quadratic surfaces relating cumulative scores for coloration and morphological characters to global position showed a strong latitudinal component and an even stronger longitudinal one in which the direction of the latitudinal effect was reversed between east and west. A multivariate analysis revealed that while morphological characters vary significantly by location and climate when tested separately, when the influence of location on morphology is taken into account, no residual relationship between climate and morphology remains. Most marine snakes have mean upper temperature tolerances between 39°C and 40°C and operate at temperatures much nearer their upper thermal limits than their lower limits but still avoid deleterious extremes by diving from excessively hot water to deeper, cooler strata, and by surfacing when water is cold. At the surface in still water in sunlight, *Pelamis* can maintain its body temperature slightly above that of the water, but whether this is significant in nature is questionable. As temperature falls below 18–20°C, survival time is progressively reduced, accompanied by the successive occurrence of cessation of feeding, cessation of swimming, and failure to orient. Acclimation does not seem to be in this species' repertoire. In the water column, marine snakes track water temperature; on land, sea kraits can thermoregulate by basking, selecting favorable locations, and by kleptothermy. *Laticauda colubrina* adjusts its reproductive cycle geographically in ways that avoid breeding in the coldest months. Mean voluntary diving time is not temperature-dependent within the normal range of temperatures experienced by marine snakes in the field, but is reduced in water colder than 20°C. On land, much as while diving in the sea, sea kraits maintain long periods of apnea; intervals between breaths are inversely related to temperature.

Introduction

Temperature is a pervasive feature affecting almost every facet of the ecology, biogeography, physiology, and biochemistry of organisms. Within the context of global warming, exacerbated by anthropogenic contributions, it has become critically important to assemble what is known about the role of temperature in the biology of individual taxa and to predict their responses to rising temperature for use in

Advanced Access publication June 4, 2012

planning feasible conservation strategies. Not only is knowledge of thermal responses to present conditions essential, but also much useful information can be gleaned from assessing how past conditions have influenced geographic distributions and shaped the biological attributes of present-day species. This paper is a contribution toward those ends in that it summarizes the available information on the thermal biology of marine snakes, especially the sea kraits (*Laticauda* spp.), assesses the previous and present roles of temperature in the life of these animals, and in so doing identifies areas in need of further study.

This paper is structured by beginning with the influence of temperature on the evolution and paleogeography of sea kraits, followed by an assessment of temperature as a factor limiting present-day distributions. Next is a teasing apart of the effects of temperature relative to other factors in influencing patterns of geographic variation in morphological characters. The focus then shifts from biogeography to organismal biology, including the tolerances of sea kraits and other marine snakes to temperature, their ability to thermoregulate, and how temperature affects diving behavior. Finally, a discussion relates all of this to a scenario of rising global temperatures. This article consists mainly of literature reviews, but the section ‘‘Temperature versus other variables’’ has not been published previously except in thesis form. Consequently, for that section methods are explained in more detail than elsewhere, although there is not a separate overall section on methods.

Sea kraits

Sea kraits (genus *Laticauda*) constitute a group of eight species of semi-marine snakes with flattened paddle-like tails that forage for their prey, mainly eels, in the sea, primarily on coral reefs. Unlike the true sea snakes (viviparous proteroglyphous snakes that never voluntarily leave water), sea kraits come out on land to rest, digest their food, court, mate, and oviposit. Their biology has been summarized by Shine (1991), Heatwole and Guinea (1993), Greer (1997), Heatwole (1999, 2010), Ineich and Laboute (2002), and Heatwole et al. (2005). Culotta and Pickwell (1993) provided an extensive bibliography of the literature on sea snakes and sea kraits.

Sea kraits diversified into three species-complexes (see Heatwole et al. 2005), each with one nominate widespread species, and one or more derivative species with restricted range(s). These are: (1) the *Laticauda colubrina* complex, with the nominate species, *L. colubrina*, widespread, and three species with restricted ranges: *L. guineai* (southern Papua-New Guinea), *L. saintgironsi* (New Caledonia and the Loyalty Islands), *L. frontalis* (Vanuatu); (2) the *L. laticaudata* complex, with *L. laticaudata* (widespread) and *L. crockeri* (Rennel Island in the Solomon Islands); and (3) the *L. semifasciata* complex, with *L. semifasciata* (widespread) and *L. schistorhyncha* (Niue).

Paleotemperatures and the evolution of sea kraits

The general trend during the Cenozoic from a warm Cretaceous climate to a cooler Quaternary one (Frakes et al. 1992; Kent and Muttoni 2008; Veron 2008) was not gradual, but was punctuated in the late Cenozoic by an alternation of low sea levels during glacial periods when global water was locked in the polar ice caps, and elevated ones following release of some of that water during warmer interglacials (Voris 2000; Hall 2002, 2009; Hanebuth et al. 2011). Not all regions were equally affected as an area known as the ‘‘coral triangle’’ remained thermally stable during these vicissitudes (Kent and Muttoni 2008). It is precisely within the coral triangle that sea kraits arose and underwent most of their speciation and divergence into present-day morphologically identifiable infraspecific demes during the past 30 million years (Slowinski et al. 1997; Keogh 1998; Lee and Scanlon 2002; Scanlon and Lee 2004; Heatwole et al. 2005; Cogger and Heatwole 2006; Sanders et al. 2008; Kelly et al. 2009; Heatwole 2010); the present distribution of sea kraits extends only slightly beyond the coral triangle on its western and northern borders, but somewhat more extensively southeasterly. Thus, the evolution of sea kraits occurred in a thermally stable environment and any thermal influence on early divergence probably was not direct but rather was mediated indirectly through a thermal effect on fluctuating sea levels that alternately opened and closed dispersal routes, thereby leading to peripheral migrations from the center of origin in northern New Guinea, followed by at least partial isolation of populations (Heatwole 2010). Later, as individual species expanded their ranges beyond the coral triangle into thermally less stable waters, water temperature played a more immediate role, with expansions of distributions during warmer periods and contractions during cooler ones. One of the most recent speciation events in the complex, the divergence of *L. frontalis* from *L. saintgironsi*, was estimated on the basis of gene sequencing to be ~180,000 years ago, roughly coinciding with the penultimate glacial maximum (Lane and Shine 2011).

There were many cycles of fluctuation in sea level (Voris 2000; Hannebuth et al. 2011) and of oscillations in paleotemperatures of the sea in peripheral areas (Sabaa et al. 2004; Heatwole 2010). Even in the face of such thermal variation, sea temperatures may not have been the immediate influence. The distributions of corals also underwent cycles of contraction and expansion (Veron 2000, 2008) and since sea kraits are largely dependent upon coral reefs, their changes in distribution may have been linked to corals rather than directly to temperature. The coral triangle probably served as a climatic refuge during glacial periods, not only for corals (Veron and Kelly 1988) but also for sea kraits; from this refugium both taxa could redisperse during warmer times.

Even corals may not have been the immediate factor. Coral reefs are the habitat of various species of eels on which sea kraits prey (Brischoux et al. 2009; Heatwole 2010) and the snakes may not be limited directly by the lack of corals so much as by the lack of their required food. Thus, the thermal effect in peripheral areas may have been third order, with the corals responding to temperature and the eels depending upon the corals, and the sea snakes upon the eels.

Role of temperature in the present biogeography of sea kraits

The *L. colubrina* complex is distributed within the tropics and subtropics approximately equidistantly around the equator (Fig. 1). Sea-surface temperatures (SST) generally are higher in a central band along the equator and decline toward both the northern and southern limits of the range of sea kraits (but with significant regional variation influenced by sea

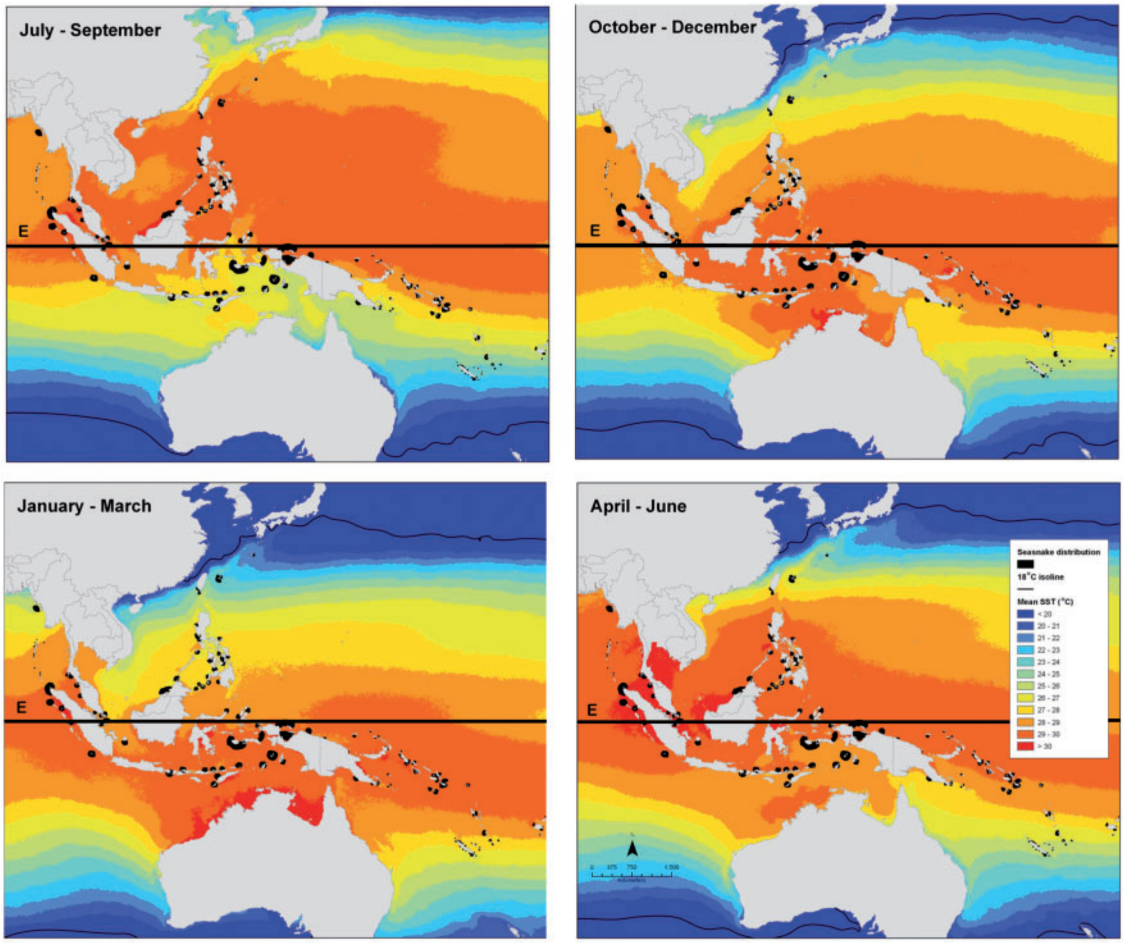

Fig. 1 Mean surface temperatures of the sea (SST) for different times of year over the geographic range of the *Laticauda colubrina* complex. Irregular black lines represent the 18°C isotherm. Straight black line marked "E" indicates the equator. Black dots indicate known localities for species in the complex taken from Heatwole et al. (2005). SST data from NOAA's National Oceanographic Data Center, Satellite Oceanography Group (http://nationalatlas.gov/atlasftp.html#sstalli).

currents; see animation in Supplementary Data). The breeding range of *L. colubrina* is contained within the 20°C isotherm. During the coolest times of the year in the north (Fig. 1, upper right and lower left) cold water extends through the Sea of Japan, along the Korean Peninsula, into the Yellow Sea and southward into the East China Sea, and finally as a narrow coastal tongue between the mainland Chinese coast and Taiwan. The presence of this seasonally colder water may be the reason why *L. colubrina* only is found on the milder seaward side of Taiwan and not on the western side facing the mainland. This cool water is in close proximity to both the Taiwanese and the Ryukyuan populations and may well limit their expansion to the northwest. At its southern limits, this cold water does not extend far seawards and in fact, both the Taiwanese and Ryukyuan populations lie in an area of milder maritime conditions to the north of the maximum southward penetration of this tongue of cold water. Except for the southern tip of Kyushu, however, the main islands of Japan are in water of <18°C for the coldest time of year and thus probably too cold to support a breeding population of sea snakes (see below). The only specimen of sea krait reported from the main islands of Japan was one with a labeled provenance of Nagasaki, near the border of the 18°C isotherm. The Kuroshio Current eddies southward from Japan to the Ryukyus, i.e., in the wrong direction for waif transport and this specimen may have been erroneously labeled. If the locality is correct, it was probably a waif as an undetected breeding population in such a well-studied site is highly unlikely.

There is no comparable body of cold water at the immediate southern edge of the range of the *L. colubrina* complex. There, mean SST during the coolest periods, are within the range experienced by the snakes at other times of year (Fig. 1). This does not mean that temperature does not limit the distribution of sea kraits in the south, however. Dry land is also a habitat requirement of snakes in the *L. colubrina* complex and there are no islands in the warm water south of the snakes' range. The nearest land to the south is New Zealand, which does lie below the 20°C isotherm at least part of the year (Fig. 1, bottom). Waif sea kraits come ashore on the New Zealand coast from time to time (McCann 1966; Gill 1997) so they are clearly capable of reaching there, yet they do not establish breeding populations. It is likely that lack of land within the southern band of suitable year-round temperature is the limiting factor to the southward range-extension of sea kraits.

Sea kraits occur in Australia only as waifs. The absence of breeding populations there has generated various hypotheses, all of which are beyond the scope of this paper and none of which involve temperature because sea temperatures around much of Australia are suitable; the matter remains an unresolved mystery (Heatwole 2010).

Role of temperature in geographic variation

Three hypotheses

Heatwole et al. (2005) noted that geographically remote (northern and southern) peripheral populations of *L. colubrina* share some characteristics or suites of characters that differ from those of intervening central populations. Because temperature also shares this pattern, i.e., with the latitudinal peripheries of sea kraits' distribution experiencing lower temperatures than the central areas, the two phenomena possibly are causally related. Three hypotheses have been advanced to account for such a congruent pattern (reviewed by Heatwole et al. 2005; Heatwole 2010). Although two of these were posed in terms of a wider environmental context, here they will be discussed in thermal terms first, then examined more broadly. They are (1) Hypothesis of peripheral convergence. This view is that peripheral populations resemble each other in some attributes more than they resemble central ones, not because of close genetic relationship but merely because they adapt independently, but convergently, as species expand their ranges into new thermal environments differing from that occurring at the center of origin of the taxon. Under this scenario, the characteristics of central populations would be ancestral to the derived peripheral ones. (2) Hypothesis of central divergence. This explanation is the antithesis of the previous one in that it postulates peripheral populations to be genetically similar and to exhibit the primitive condition, with the central phenotypes being derived. This implies that present peripheral environments resemble those to which the species was subjected historically and to which they became adapted. Subsequently, as conditions changed in the center, populations there adapted to the new conditions and diverged from the peripheral ones whose stable thermal environment had not exerted selective pressure for change. (3) Developmental hypothesis. In terrestrial snakes, some meristic characters (such as those defining the infraspecific variants of *L. colubrina*) as well as size and shape of the body, shedding, locomotor performance, and behavioral responses relating to feeding, thermoregulation, hibernation, and avoidance of predators, have been shown to depend on the temperature at which the embryos develop (e.g., Fox 1948; Fox et al. 1961; Osgood 1978; Burger 1990, 1991, 1998a, 1998b; Burger et al. 1987; Lourdais et al. 2004). Thus, geographic variation in phenotype can reflect physiological responses to different thermal environments during development, rather than genetic differences among populations in response to disparate selective pressures. The validity of some of the early papers supporting this view has been challenged on statistical grounds (Arnold and Peterson 2002) and Buckley et al. (2007) pointed out that such phenotypic plasticity may be ephemeral post-hatching and thus sometimes have only temporary ecological significance.

Available information now allows decision between the first two of these hypotheses for sea kraits. The center of origin of sea kraits has been identified as what is now northern New Guinea, near the center of the present distribution of *Laticauda* (Guinea 2002; Heatwole 2010). Furthermore, that area (the coral triangle) has been more stable thermally over the history of this taxon than have the peripheral areas at higher latitudes (see "Paleotemperatures" section). Thus, of the first two explanations, the hypothesis of central divergence does not accord with observations and can be discounted. Present data are consistent with the hypothesis of peripheral convergence, but since that explanation and the developmental hypothesis are not mutually exclusive, the relative validity to which each of these may apply to particular characters remains undecided.

Temperature versus other variables

The spatial congruence of geographic patterns of morphological variation with that of temperature could be coincidental. Accordingly, analyses were carried out to ascertain the relative importance of different factors in explaining geographic variation in *L. colubrina* and to assess whether temperature, rainfall, latitude, and longitude exerted significant independent impacts on the pattern of variation.

Quadratic surface: methods

Seventeen variable characters of scutellation and color pattern employed in the hierarchical study of infraspecific variation by Heatwole et al. (2005) and Heatwole (2010) constituted the original dataset of morphology. It was pared first by eliminating the characters that were stable throughout the geographic range, i.e., those for which there were only rare departures from the norm, or for which variants occurred in only one or a few isolated localities. Then, because almost all variable characters exhibited sexual dimorphism, all juveniles and other specimens whose gender (for whatever reason) could not be determined were eliminated. The result was a dataset of 203 females and 225 males.

Temperature data were from the Coral Reef Watch Operational 50 km Satellite Nighttime Climatologies (coralreefwatch.noaa.gov/satellite/hdf/index.html) and National Oceanographic Data Centre, Satellite Oceanography Group (http://nationalatlas.gov/atlasftp.html#sstalli) of the National Oceanic and Atmospheric Administration (NOAA) of the United States. Their software (Coast Watch) was used to convert data files into binary floating-point files. This provided temperatures for each month from nine years of satellite data (1985–1993). These were smoothed by taking the average over a $5^\circ \times 5^\circ$ grid of nearest cells, thereby correcting for missing values of some locations. An orthogonal transformation matrix was constructed and a factor analysis carried out, using a varimax rotation to accentuate large effects.

Data on mean precipitation in mm per day from $2.5^\circ \times 2.5^\circ$ grids over a 30-year period (1979–2008 with no missing values) were obtained from the Global Precipitation Climatology Project (GPCP) of the National Aeronautics and Space Administration (NASA) (precip.gsfc.nasa.gov) of the United States.

A Principal Components Analysis (PCA) (SAS 9.1.3 Service Pack 4, SAS Institute Inc., Cary, NC, USA), was conducted in which latitude and longitude were related to morphological characters by summing the scores of the individual principal components for both of the two major sets of characters that contributed to PC1 and PC2 and plotting them against the geographical coordinates separately by gender (Figs. 2 and 3). More detailed description of the methods is provided by Heatwole (2010).

Quadratic surface: results

When first scores were plotted against latitude there was a decline in values from south to north without a reversal in direction across the equator. This result, however, could have been confounded by longitudinal, or other, effects and when both latitude and longitude were considered together the U-shaped trough, expected on the basis of symmetrical thermal adaptation, occurred at all levels of longitude for both of the two major sets of characters that contributed to factors 1 and 2. The unexpected results were that the trough was not symmetrical around the equator and the longitudinal effect was even stronger than the latitudinal one. For both sexes, in the east the latitudinal effect was greater with higher cumulative scores in the north, whereas in the west, the

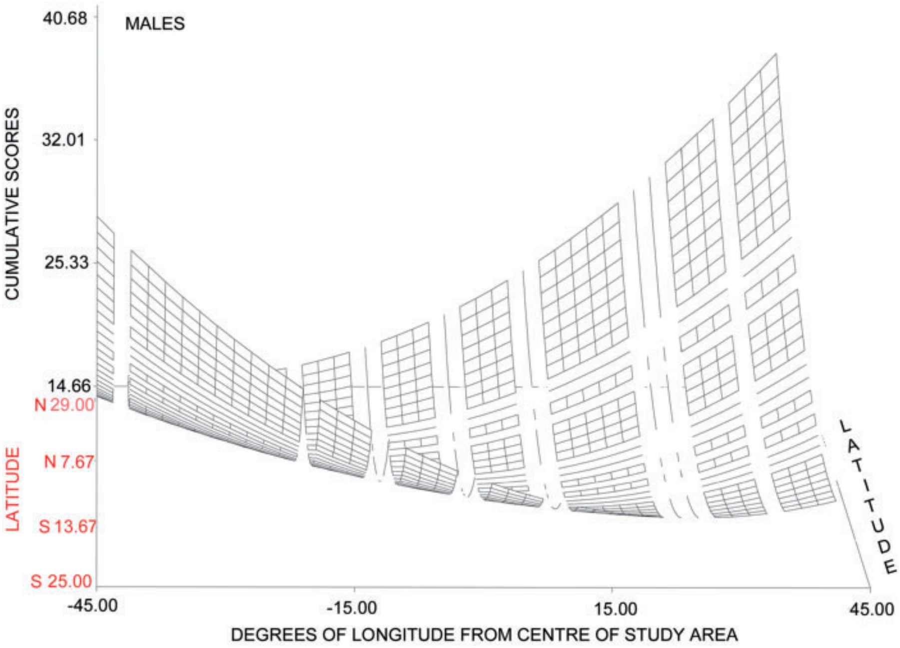

Fig. 2 Quadratic surface relating cumulative principal scores in the multivariate analysis to latitude and longitude for males. Values of latitude are actual degrees of latitude north (N) and south (S). Values of longitude are expressed, not as actual longitudes, but as degrees of longitude east of the center of the study area (positive values) and degrees west of the center of the study area (negative values). For both measures, fractions of degrees are expressed on a decimal scale rather than as minutes and seconds.

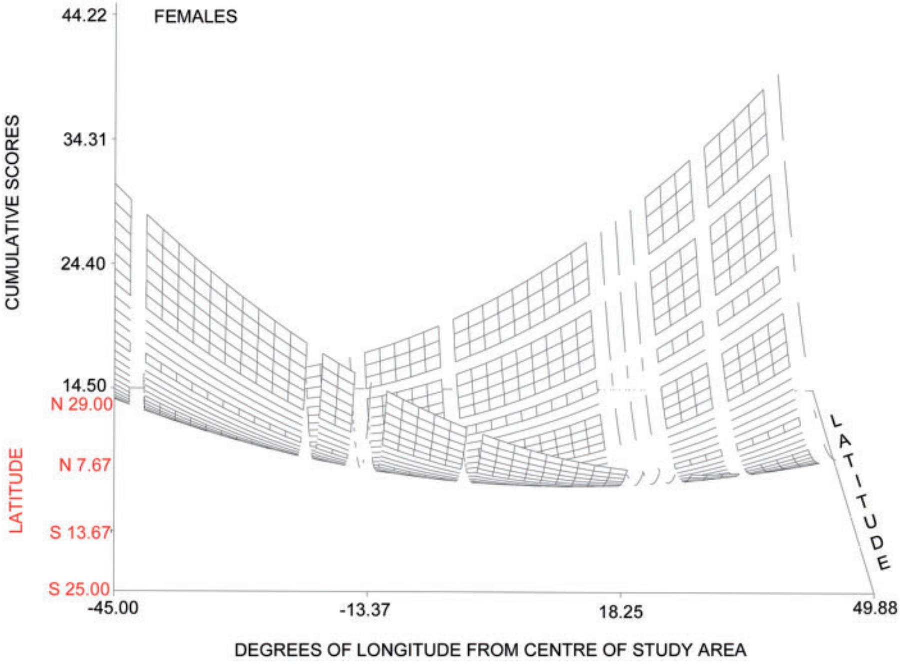

Fig. 3 Quadratic surface relating cumulative principal scores in the multivariate analysis to latitude and longitude for females. Values of latitude are actual degrees of latitude north (N) and south (S). Values of longitude are expressed, not as actual longitudes, but as degrees of longitude east of the center of the study area (positive values) and degrees west of the center of the study area (negative values). For both measures, fractions of degrees are expressed on a decimal scale rather than as minutes and seconds.

reverse was true and the highest cumulative scores were in the south. Thus, northern and southern populations may be responding to the thermal gradient but within the context of longitudinal effects. In this regard, it is important to note that the thermal environment is not entirely symmetrical around the equator and that there is marked longitudinal difference in the pattern of isotherms (Fig. 1; video in Supplementary Data). In part of the western segment of the range of *L. colubrina*, the temperatures are more variable than elsewhere, alternating seasonally between unusually warm to unusually cold in relation to the rest of the species' range; Peninsular Malaysia and western Indonesia are the hottest places anywhere in the range of the species in April–June whereas in January–March a tongue of cool water penetrates southward into the same region and conditions become cooler there than anywhere else in the range of the species except for the two most northern localities (Taiwan and the Ryukyus). The isotherms are in a more confused pattern there at all times and are less evenly stratified latitudinally than farther east where nearly parallel isotherms merely shift northward or southward with the seasons.

The quadratic geographic model achieved a reasonable fit with $R^2 = 0.76$. Although a variety of statistical variable selection methods and criteria were considered for building a more sophisticated model to include precipitation and SST, none of the models improved R^2 beyond 0.80.

Mantel tests: methods

TRMM imagery provided by NASA Goddard Earth Sciences DISC, based on data from NASA and the Japanese Space Agency (JAXA) (website: http://neo.sci.gsfc.nasa.gov/Search.html?pg=1&datasetId=TRMM_3B43M), supplied six climatic variables: Mean SST for each quarter of the year, and mean and maximum length of time between rainfall events (in months). The latter two were used rather than mean precipitation over a period of time because the length of time snakes lacked access to fresh water was believed to be more critical than how much rain actually fell (also see Lillywhite et al. 2008, 2012; Liu et al. 2012).

Three Mantel tests using Program R (2011, version 2.13.1, R Foundation for Statistical Computing) were also applied: (1) one to an Euclidean distance matrix of scutellation and color pattern to test the correlation with a geographic distance matrix (using latitude and longitude coordinates of the localities assigned to each snake; subsequently called "location"), (2) another to test the correlation with an Euclidean distance matrix of climatic data, and (3) a partial-Mantel to test the relationship between morphology and climate after controlling for the effect of location. The Mantel tests used a Pearson correlation and were based on 999 permutations. Euclidean distances require a dataset with no missing values, so at this point the datasets were further pared to remove missing values by first removing snakes for which no climatic data were available, and then by removing any characteristic that was not important in the first six PCA axes and which was missing >15% of its values in the dataset for females. Finally, any remaining snake with missing data was removed. The final dataset for females included 54 snakes and 24 morphological characteristics. The same characteristics were removed from the dataset for males, resulting in 54 snakes and the same 24 morphological characteristics used for females. Finally, the Mantel tests were re-run for each gender for climate and location, after having removed all but the most important character of any suite of characters that showed autocorrelation. The remaining characters were the numbers of (1) body bands, (2) tail bands, (3) gastrosteges, (4) subcaudals, (5) scale rows at the level of the 20th gastrostege, (6) scales in the dorsal width of the 10th black band, and (7) scales in the dorsal width of the 10th white band. There were 55 females and 70 males in these analyses.

Mantel tests: results

For females, there was a correlation between morphology and location ($M_r = 0.36$; $P = 0.001$) and between morphology and climate ($M_r = 0.17$; $P = 0.003$). However, the partial-Mantel test indicated there was no significant relationship between morphology and climate after removing the effects of location on morphology ($M_r = 0.006$; $P = 0.44$). Similarly, using the subset of characters without autocorrelations, there was a correlation between morphology and location ($M_r = 0.34$; $P = 0.001$) and between morphology and climate ($M_r = 0.21$; $P = 0.001$), but no significant relationship between morphology and climate after removing the effects of location ($M_r = 0.05$; $P = 0.191$).

For the males, there was also a correlation between morphology and location ($M_r = 0.27$; $P = 0.001$) and between morphology and climate ($M_r = 0.16$; $P = 0.041$). The partial-Mantel test showed no relationship between morphology and climate after controlling for the effects of location ($M_r = 0.041$: $P = 0.29$). Again, there was a correlation between the subset of non-autocorrelated morphological characteristics and location ($M_r = 0.267$; $P = 0.001$) and between the subset of morphology and climate ($M_r = 0.110$; $P = 0.049$), but the partial-Mantel test showed no relationship between morphology and climate after controlling for location ($M_r = -0.015$; $P = 0.581$).

While there is a pattern of morphological characteristics that vary by location and climate when tested separately, when the influence of location on morphology is taken into account, no residual relationship between climate and morphology remains. Climate is spatially correlated with location, so the apparent correlation between morphology and climate is likely an artifact of that relationship. This does not rule out the possibility, however, that an unmeasured climatic variable, such as temperature during embryonic development, might have an influence on morphology.

Temperature tolerances of marine snakes

The upper temperature tolerances of different species of sea kraits are remarkably similar. All means fall within the narrow range of 39.3–39.7°C (Table 1) and the total range in individual values only from 39.2 to 40.2°C over all species studied. Most other taxa of marine snakes also fall in that range with only one sea snake (*Lapemis curtus*) being lower and the file snake *Acrochordus granulatus* is being higher. The best comparison is with *Pelamis platurus*, the marine snake that has received the most attention (Table 2). Its mean upper lethal temperature is also ~39°C in two studies, but lower (~33–35°C) (Tables 1 and 2) in another. Snakes show debility before the immediate upper lethal is reached, however, and snakes may have short survival times at 33–35°C. Differences in methods of determining endpoints may be responsible for Dunson's and Ehlert's (1971) somewhat lower values. Their snakes all weighed <70 g whereas at least some of the other studies also used larger snakes; perhaps smaller (younger) snakes have lower thermal limits than do larger (older) ones. Also, Graham et al. (1971) measured thermal limits of 36°C when snakes were put into water of that temperature directly from ambient values; snakes in other studies that were heated gradually survived to 39°C. Thus, tolerance may depend partly on the rate at which temperature rises.

The capacity of *Pelamis* to acclimate is slight, with practically identical values for various endpoints of heat stress between animals acclimated at 17 and 27°C. Testing of animals in air gave more variable results than did tests in water.

There have been no studies of the tolerances of sea kraits to low temperatures, although body temperature of *L. saintgironsi* (then called *L. colubrina*) has been recorded as low as 12°C (Saint Girons 1964,

Table 1 Heat tolerances of some marine snakes

	Temperature (°C)		
Taxon	T_B	T_E	Upper lethal
Sea Kraits			
Laticauda colubrina	29.0; 26.7–30.1	29.0 (T_W); 25.9–30.3 (T_S)	39.7
Laticauda laticaudata	–	27.0–30.4 (T_A)	39.3; <40.0[a]
Laticauda semifasciata	–	–	39.7
Laticauda saintgironsi[b]	27–33	28.3 ± 3.5 (T_S) (maximum = 37.4[a])	<40.0[c]
Sea Snakes	22.8–27.7[d]	22.8–27.7 (T_w)[d]	
Astrotia stokesii	–	–	39.0
Hydrophis ornatus	–	–	39.5
Hydrophis elegans	–	–	39.3
Lapemis curtus	–	–	37.8
Homalopsinae			
Cerberus rhynchops	–	–	39.9
File Snake			
Acrochordus granulatus	–	–	41.2

Data from Saint Girons (1964, 1990), Heatwole (1981a), and Bonnet et al. (2009). See Table 2 for data on *P. platurus*.

[a] For *Laticauda laticaudata* and *Laticauda saintgironsi* combined.

[b] Lower lethal <12°C; basks or seeks warm water at temperatures <20°C; thermal optimum 29–30°C; dies after ~1 h exposure at ~35.5°C.

[c] Temperatures above 35.5°C are debilitating and result in reduced survival.

[d] Various species combined that are not listed in table: *Aipysurus laevis, Aipysurus duboisii, Emydocephalus annulatus*.

T_A = air temperature; T_B = body temperature; T_E = environmental temperature; T_S = substrate (terrestrial) temperature; T_W = water temperature.

Table 2 Important thermal points for the yellow-bellied sea snake, *Pelamis platurus*

Thermal point	Conditions	Temperature (°C)	Authority
Heat death			
Mean T_W	Acclimated at 27°C	39.4	Graham et al. (1971)
Mean T_W	Acclimated at 17°C	39.0	Graham et al. (1971)
In water; range in T_W	Acclimated at 22.5–26.5°C	33.2–33.6	Dunson and Ehlert (1971)
In air: range in T_A	Acclimated at 22.5–26.5°C	35.4–43.4	Dunson and Ehlert (1971)
Single value of T_W	Acclimated at 25–28°C	39.8	Heatwole (1981a)
Hyperactivity; mean T_W	Acclimated at 22.5–26.5°C	36	Graham et al. (1971)
Dive response: T_W	Acclimated at 22.5–26.5°C	About 32	Graham et al. (1971)
SSTs where snakes caught (range)	Field	26.9–31.0	Dunson and Ehlert (1971)
SSTs where snakes' T_Bs measured (range)	Field	28.2–28.6	Dunson and Ehlert (1971)
T_W: range	Shallow artificial pool	18.8–32.5	Graham et al. (1971)
T_B: range	Shallow artificial pool	19.2–32.5	Graham et al. (1971)
T_B: mean (range)	Field	28.2 (26.5–30.8)	Dunson and Ehlert (1971)
T_B: one animal	Field	24.9	Brattstrom (1965)
Isotherm bounding the breeding range	Map Map	20 18	Dunson and Ehlert (1971) Graham et al. (1971)
Ceased feeding: range in T_W	Acclimated at 27–28°C	16.0–18.0	Graham et al. (1971)
Cold Death within ~12 days: T_W	Acclimated at 22.5–26.5°C	Between 14.5 and 17.0	Dunson and Ehlert (1971)
Cold Death within 2–5 days: T_W	Acclimated at 22.5–26.5°C	Between 10 and 14	Dunson and Ehlert (1971)
Cold Death within a day: T_W	Acclimated at 22.5–26.5°C	Between 5 and 7	Dunson and Ehlert (1971)
Ceased swimming: mean T_W	Acclimated to 27°C Acclimated to 17°C	8.5 7.0	Graham et al. (1971) Graham et al. (1971)
Unable to hold head up: mean T_W	Acclimated to 27°C Acclimated to 17°C	7.5 7.0	Graham et al. (1971) Graham et al. (1971)

T_A = air temperature; T_B = body temperature of the snake; T_W = water temperature.

1990). Toleration of such low temperature is significant in the light of the drifting of live waifs of sea kraits into cooler water (e.g., New Zealand) than that in which they can maintain breeding populations.

Tolerance to low temperature has been investigated in another species whose breeding range is limited by the 18–20°C isotherm, *P. platurus* (Table 2). This limitation is not because those temperatures are immediately lethal because adults appear as live waifs in cool areas, distant from their breeding range (Dunson and Ehlert 1971). *Pelamis* ceases feeding below ~16°C and survival time decreases progressively as temperatures fall below that level until it is only a day at 7°C. At lower temperatures, swimming ceases (8°C) followed by failure to orient (~7°C) (Table 2).

Thermoregulation

Relationship of body temperature and water temperature

The size and shape of an animal determines its thermal exchanges with its environment. Smaller animals have a lower content of heat than do larger ones, but a relatively greater surface area through which heat can be gained or lost. Furthermore, the elongate form of snakes maximizes the surface-area to volume ratio. A long cylinder has a much higher s-a:v ratio than does a sphere of equal volume; thus, snakes have a high surface area through which heat can pass (in either direction) compared to a low volume of corpus to heat or cool (Heatwole and Taylor 1987). Given this relationship of surface area to volume, and the high conductivity of heat by water, a snake would be expected to rapidly equilibrate to the temperature of its aquatic environment. Submerged snakes fulfill this expectation. Three species of sea snakes, whose temperatures were measured underwater in their natural environment at depths from 5 cm to 7 m conformed to the temperature of their ambient, or differed only within 0.2°C of it (either above or below) (Heatwole 1981a) (Fig. 4). Since most sea snakes and all sea kraits are bottom foragers, they would have little opportunity to select environmental temperatures during their underwater activities and while they are at sea they seem to be

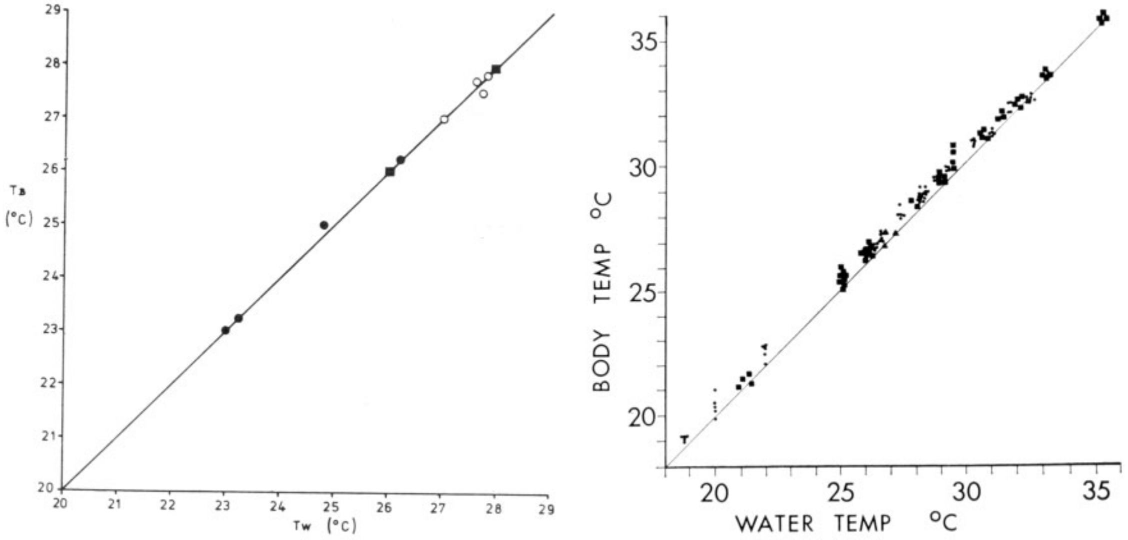

Fig. 4 Relation of body temperature (TB) to water temperature (TW). *Left*: At the site of capture of *Aipysurus laevis* (dots), *Aipysurus duboisii* (circles), and *Emydocephalus annulatus* (squares). From Heatwole (1981a). *Right*: *Pelamis platurus* in a sunlit tank in which water temperature could be artificially controlled. From Graham (1974) with permission from the American Society of Ichthyologists and Herpetologists to use their copyrighted material.

poikilotherms (non-thermoregulators that assume whatever environmental temperature they encounter). Species that forage at mid-water, although not able to maintain body temperature different from ambient on a sustained basis, could control their temperature by selecting strata of water of different temperature at different depths and thus function as thigmotherms (classification of Cowles 1962). A snake merely moving up or down within the water column, while foraging or surfacing to breathe, would track the changes in ambient temperature, but with body temperature lagging. Heatwole et al. (1978) found that snakes surfacing to breathe and returning to the bottom usually ascend and descend at a rate of 0.3–0.4 m/s (although exceptional values up to 0.9 m/s were recorded) and thus it would take ~8–10 min for a trip from sea snakes' deepest diving level (~100 m) to the surface and return. The lag in body temperature as the snake passes through strata of different temperatures may account for the slight departure from ambient values for some snakes while submerged in the sea (Fig. 4).

A snake on the surface may have avenues of thermoregulation not available in the water column. *Pelamis platurus* is the only marine snake that spends most of its time at the surface; it habitually occupies the surface of slicks and feeds on small fish that seek shelter in its shade. It has a black dorsal surface and Brattstrom (1965) suggested that this may enable it to absorb radiant energy while basking at the surface and thereby maintain its body temperature above that of the water, i.e., to function as a heliotherm. Other authors (Dunson and Ehlert 1971; Graham et al. 1971) expanded the theory to suggest that this species might alternately dive and bask and thus behaviorally regulate body temperature, i.e., a form of "shuttling." Tests of this theory found that although snakes were not warmer than the water at night, when exposed to sunlight in still water over a range of water temperatures of 18–35°C, they maintained body temperature slightly above that of the water (Fig. 4) (Graham et al. 1971). Agitation of water would enhance conductive loss of heat by snakes and conduct away that absorbed from radiant energy and Graham (1974) considered that the conditions of still water in their experiment might have over-emphasized the thermoregulatory ability of *Pelamis* in nature. Dunson and Ehlert (1971) found that in the field, *Pelamis* at the surface by day had body temperatures ranging from 2.4°C above to 1.9°C below that of the surrounding seawater. Shine et al. (2003), using physical models of sea snakes, found that the color of the model affected its temperature only when it was out of water.

Not only does *Pelamis* respond to excessively high temperatures by diving, but also when it is artificially maintained in water cooler than ~22°C it stays at the surface continuously, a response that in nature would expose it to the warmest available conditions. Diving and surfacing do not seem to be a response to thermal gradients, however, as even in water maintained at a constant uniform temperature *P. platurus* dives in warm water and tends to remain at the surface in cold water (Graham et al. 1971).

Thermoregulation on land

On land, sea kraits have a greater capacity for thermoregulation than they do in water as effective basking (heliothermism) is available to them and the land offers a greater range of thermal microhabitats for the exercise of thigmothermism (rock crevices, under debris, burrows and shade). They avoid the high extremes of diurnal temperatures on the beach by making the transition between water and land during the cooler conditions of nocturnal high tides (Guinea 1986; Shetty and Prasad 1996; Shetty and Shine 2002b). The thermal characteristics of cover are important. *Laticauda laticaudata* and *L. colubrina* are sympatric on small cays in New Caledonia; the former is more aquatic and subject to desiccation than the latter and is tied to the immediate vicinity of the sea where it is dependent on beach rocks of such sizes that the snakes are buffered against high temperatures, yet remain in warm, humid conditions (Bonnet et al. 2009). *Laticauda colubrina* is more terrestrial and resistant to desiccation and moves farther from the high tide line and uses a wider range of shelters.

Brischoux et al. (2009) discovered a most unusual mode of thermoregulation that they called kleptothermy (stealing of heat). When on land, *L. laticaudata* shares burrows with sea birds and raises its body temperature to that of the bird, either through direct contact with the bird, or by occupying a part of the burrow warmed by the bird (Fig. 5). Terrestrial lizards often select cooler sites when inactive (reviewed by Heatwole and Taylor 1987), thereby conserving energy by avoiding metabolic excesses and one wonders why this snake maintains a high body temperature when secreted in burrows. The answer may lie in its thermal requirements for digestion. In various terrestrial reptiles, the preferred temperature for digestion is ~3°C higher than that for activity such as foraging and social interactions (reviewed by Heatwole and Taylor 1987). Sea kraits come out on land after they have eaten an eel, often a very large one in relation to the snake's body size (Shetty and Shine 2002a) and kleptothermy may be a means of maintaining body temperature at the optimum level for digestion while at the same time sheltering in a safe environment.

Du et al. (2011) found that turtle embryos move within the egg and exploit small-scale thermal heterogeneity and thus engage in behavioral thermoregulation. Eggs of *Laticauda* have seldom been found and it remains to be seen whether these snakes can also thermoregulate intraovally.

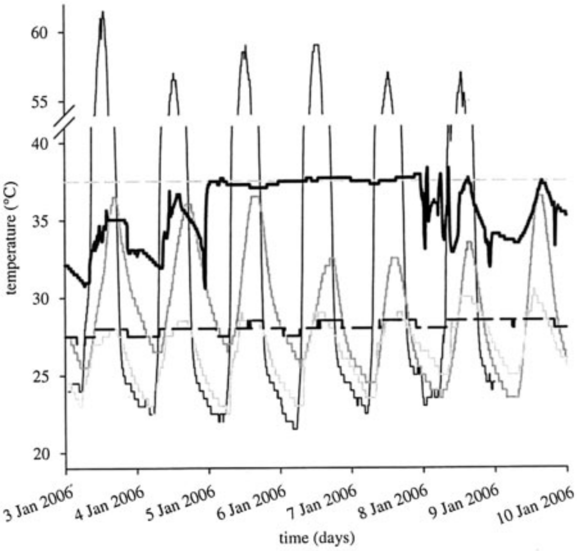

Fig. 5 Ambient temperatures and body temperatures of a *Laticauda laticaudata* on a small cay in New Caledonia. Thin black line (greatest fluctuation) = temperature in the open; gray lines = temperatures under two different pieces of beach rock; black line in step-like sequence = temperature in a vacant seabird burrow; thin-dashed gray line = constant temperature of 37.5°C (approximately the body temperature of a sea bird); thick black line = body temperature of the snake while in the burrow. Note that part of the time the snake's temperature fluctuates but not so much as environmental temperatures (two ends of the graph, but that for a period it tracks the body temperature of the bird), while apparently "stealing" heat from it. Figure 1 from Brischoux et al. (2009) (see 'References' section) reproduced with permission of the Royal Society and Highwire Press.

Temperature and reproductive cycles

A widespread species might be able to extend its geographic range into cooler areas where the thermal limits for reproduction were not met for part of the year if it altered the timing of its breeding to coincide only with the warmer periods. Some regional, seasonal adjustment has occurred in the *L. colubrina* complex. For example, *L. colubrina* breeds aseasonally (Philippines) (Gorman et al. 1981; Bacolod 1983) or yearly twice (Sabah) (Stuebing 1988) near the central part of its range where mean SST remains at ~28–30°C year round (Fig. 1), whereas in Fiji where mean SST seasonally drops several degrees lower (26–28°C), it breeds once yearly and then only in the warmer months (Guinea 1981, 1986). An even more peripherally distributed *L. saintgironsi* on New Caledonia oviposits in the austral summer (December–February) (Saint Girons 1964, 1990); it is less active during the cold season and then its feeding cycle (hunting at sea, followed by digestion on land) is more than 2 months' duration.

Temperature and development

As in all ectotherms, reptilian eggs develop more rapidly under warm conditions than they do under cool conditions (Georges et al. 2005) and temperatures that are either too high or too low lower hatching success (Wei and Ji 2008). In viviparous, completely marine sea snakes, the embryos must develop at the body temperature of the mother and, as indicated above, she cannot thermoregulate and thus the eggs develop at the temperature of the water. Consequently, the only way of regulating the temperature at which the young develop is my adjusting the reproductive season to the thermally most favorable season of the year (see previous section). The oviparous sea kraits have an additional option, and that is the selection of terrestrial oviposition sites that have optimal temperatures for development. The eggs of sea kraits have seldom been found so little is known about the conditions under which they develop.

Reptiles have two modes of sex determination: Temperature-dependent sex determination (TSD) (crocodiles, tuatara, most turtles, and many lizards) and genetic sex determination (GSD) (snakes, some turtles, and lizards) (Modi and Crews 2005). In TSD, the temperature at which an embryo develops determines whether it becomes male or female, whereas in GSD, the sex of the animal is predetermined by its sex chromosomes and usually is not altered by thermal conditions. Organ et al. (2009) concluded that all lineages of live-bearing marine reptiles, extinct (mosasaurs, ichythyosaurs, and sauropterygians) and living (sea snakes), evolved GSD before acquiring viviparity and that this enabled their radiation into a pelagic environment in which relatively stable environmental temperatures would preclude TSD. Like sea turtles that do have TSD, sea kraits leave the sea and oviposit on land and thus theoretically have the option for TSD. However, this is unlikely as all snakes, terrestrial and aquatic, that have been tested have GSD (Modi and Crews 2005).

Even though snakes have GSD, differential mortality during development in some terrestrial snakes skews sex ratios to either a male-biased ratio or a female-biased one, depending on temperature of development (Burger and Zappalorti 1988). No data are available on whether this also occurs in marine snakes.

Thermophysiology

Temperature affects the rates of practically all physiological processes in all organisms and the same is doubtless true for marine snakes. There have been few studies on thermophysiology in this taxon, however.

The fact that marine snakes are ectothermic has implications for their ability to spend prolonged periods underwater. Because they do not rely on metabolically produced heat but rather depend on environmental temperatures for their body heat they require less energy and hence less food and can sustain much lower metabolic rates than an endotherm of equivalent size. This lower expenditure of energy means that they require less oxygen and this alone, without any special adaptations for diving, should allow them to remain underwater for longer than an endotherm of equivalent size. The metabolic rates of marine snakes, however, alone do not account for their diving ability, as they do not differ greatly in that regard from terrestrial snakes (the file snake *A. granulatus* is the only marine snake with an exceptionally lower metabolic rate than other snakes) (Heatwole and Seymour 1975a, 1975b). Rather, the combination of ectothermy, cutaneous respiration, anticipatory breathing tachycardia, and cardiac shunts permit sea kraits and sea snakes an alternative adaptation to the typical vertebrate diving syndrome of bradycardia, peripheral vasoconstriction, and contraction of an oxygen debt (Heatwole 1999). The two strategies are mutually exclusive as cutaneous respiration depends upon continuous peripheral blood flow whereas the usual vertebrate diving syndrome depends on temporarily cutting off circulation to the periphery and reducing blood flow primarily to a heart–lung–brain circuit. Sea snakes take up oxygen from the water at rates 10 to 30 times that of land snakes and remain aerobic throughout their dives (Heatwole 1999).

Figure 6 indicates the relationship of temperature to voluntary submergence time. Note that within the range of temperatures at which marine snakes are usually found in the sea, 22–29°C (Tables 1 and 2), regardless of time of day mean voluntary submergence times average 50 or fewer minutes; values were quite variable, however, and there were low submergence times at all temperatures, with no clear thermal dependence (Fig. 6) except that there were no prolonged dives in water colder than 20°C, i.e., consistent with the findings of Graham et al. (1971) discussed above. A variety of factors can influence submergence times and may mask a possible thermal effect. Heatwole and Seymour (1975a, 1975b) noted greater use of oxygen by active snakes than by inactive animals and thus active snakes would be expected to surface more often to replenish air. Snakes sometimes lie motionless on the bottom for long periods of time, seemingly asleep, whereas others continuously forage by actively swimming from one coral to another investigating crevices (Heatwole et al. 1978). Disturbance also results in lower submergence times (Heatwole 1981b).

It is clear that mean voluntary submergence time does not reflect the maximum capacity for submergence, as a few individual values depart widely from the mean. On some occasions, snakes remained submerged for well over an hour (Fig. 6). The maximum voluntary diving capacity of marine snakes seems to be to depths of 100 m for up to at least 2 h (reviewed by Heatwole and Seymour 1975a).

Tolerance limits to prolonged enforced submergence is temperature-dependent (Dunson and Ehlert 1971); *Pelamis* survived up to 24 h in water of 13°C but only up to 5.5 h at 26–29°C (Dunson and Ehlert 1971). The former temperature, however, kills snakes with free access to the surface within 4–5 days.

Campbell et al. (2010) found that in summer freshwater crocodiles (*Crocodylus johnstoni*) had a greater demand for oxygen than they did in winter and that when diving for longer than 40 min in summer they had to exponentially increase the time they spent on the surface repaying the incurred oxygen debt. They suggested that long-term warming of the aquatic environment might be detrimental to survivorship in other diving ectotherms, including snakes. Marine snakes have cutaneous respiration, remain aerobic during dives, and do not incur an oxygen debt (Heatwole 1999) and might therefore be exempt from this effect.

Although the effect of temperature on compartmentalization of respiration between pulmonary and cutaneous modes has not been elucidated for any marine snake, data are available for a freshwater species, *Acrochordus arafurae* (Pratt and Franklin 2010). In this species, total oxygen uptake increased with temperature (Q_{10} 2.52) between 20°C and 32°C. Cutaneous uptake remained temperature-independent and, consequently, all oxygen for meeting the demands of thermally elevated metabolism was supplied by an increased pulmonary exchange that, in turn, lowered the voluntary submergence time from 77 to 28 min.

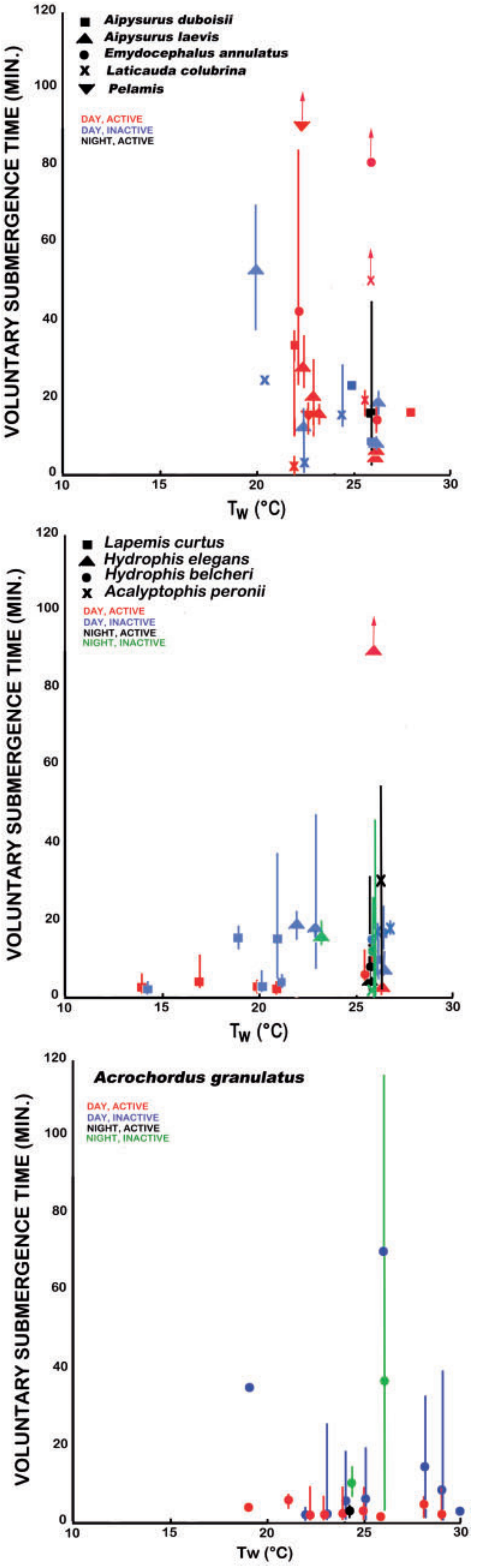

Fig. 6 Relationship of voluntary diving time to water temperature in sea kraits and sea snakes that forage on the bottom in shallow water or live near the surface (*Upper*), sea snakes feeding in the water column or on the bottom in deeper water (*Center*), and in a species of file snake foraging and feeding in shallow water (*Lower*). Vertical lines indicate the range of values; symbols indicate means or, where no range is given, single values. Symbols with *arrows* indicate incomplete submergence times that extended longer than indicated by the symbol (snake had not surfaced but was lost to view at the time indicated). Data from Pickwell (1972) and Heatwole (1975, 1981a). Day versus night and active versus inactive are coded by black and different shades of gray in the printed journal and by colors online.

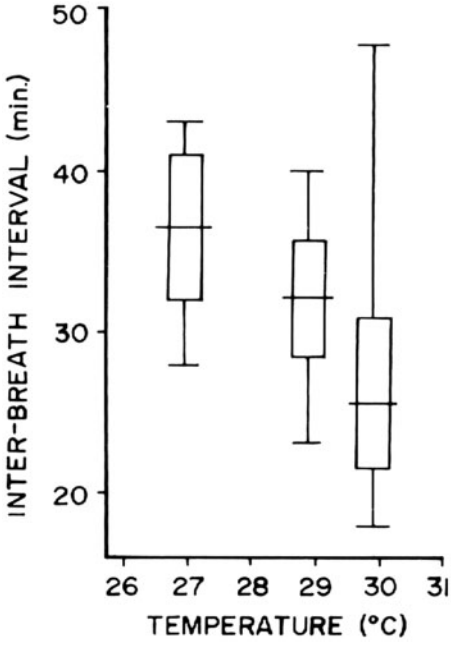

Fig. 7 The relationship between temperature and the interval between breaths of *Laticauda colubrina* when breathing on land. Vertical lines indicate ranges, central horizontal line the mean, and the rectangles two standard errors either side of the mean. From Heatwole (1981b).

Despite the duration of dives being reduced as water temperature increased, aquatic uptake was still responsible for prolonging voluntary submergence times. If the same is true for marine snakes, and their cutaneous contribution to total respiration remains constant with a greater dependence upon pulmonary respiration at high temperatures, they might squander time in making more frequent trips to the surface to breathe. This would reduce the time available for foraging, and increase the frequency of exposure to predators, such as sea eagles, that feed on the surface.

When on land sea kraits do not abandon their aquatic breathing rhythm and continue to intersperse intermittent breaths with long periods of apnea. The mean inter-breath interval in *Laticauda colubrina* ranges from ~24 to 36 min and decreases (more frequent breaths) with increasing temperature over the range experienced by these snakes in nature (Fig. 7).

Discussion

Populations of some species of sea snakes are declining (Guinea 2007) and at least two species probably have become extinct recently (M. L. Guinea, personal communication); it is urgent that the cause be ascertained as soon as possible and that the possible role of thermal biology be investigated. Several predictions/conclusions can be drawn about the probable responses of sea snakes and sea kraits to global warming. (1) Due to limited capacity for thermal acclimation, and their inability to thermoregulate while at sea, sea snakes are unlikely to be able to use these avenues for coping with global warming. The ability of sea kraits to acclimate has not been assessed; they are able to behaviorally thermoregulate on land, however, but not in the sea. (2) In nature, sea snakes' body temperatures are nearer their upper thermal limits than their lower thermal limits, giving them only a small safety margin against rising temperatures. (3) Cold water limits the latitudinal distributions of sea kraits and sea snakes and hence mild global warming could lead to an expansion of geographic range, were temperature the only consideration. (4) Because sea kraits and some sea snakes are linked to the coral reef habitat and can disperse considerable distances via sea currents and perhaps during storms and tsunamis, they can expand and contract their ranges in concert with thermally induced changes in the distribution of corals. They did so in the past and it is likely they could do so again. However, severe global warming could lead to loss of reefs rather than to an expansion of range. High temperature causes corals to lose their symbiotic zooxanthellae resulting in "bleaching" and death (Hoegh-Guldberg 1999). Also, the rising levels of CO_2 causing global warming also acidify the ocean. Low pH affects corals' microbial associates and can lead to disease of the corals (Mouchka et al. 2010). Low pH also impairs corals' ability to deposit their skeletons and reefs may be severely impacted at all latitudes, independently of local temperatures (Kleypas and Yates 2009). (5) Because oceanic acidification negatively affects plankton and other links in the marine food web (Fabry et al. 2008), even sea snakes living in non-reef habitats may suffer decline.

Future directions for research

This paper reviewed the literature on the role of temperature in the biology of sea kraits. In so doing, lacunae in the knowledge of the thermal biology of this taxon have been exposed that require additional investigation. Suggested directions for fruitful future research are to: (1) conduct detailed comparative studies of the thermal ecology in the other complexes of the genus *Laticauda*, and in marine snakes generally; (2) ascertain the effect of temperature on the rates of physiological processes, such as metabolism, respiration, digestion, heart rate, kinetics of various enzymes, and osmoregulation; (3) assess the effect of temperature on aquatic versus aerial respiration; (4) test the relative validity of the developmental hypothesis and the peripheral convergence hypotheses, by studying the effect of temperature during embryonic development on morphological characters and on post-natal/post-hatching behavioral responses; and (5) describe the effect of temperature on the reproductive cycle and development.

Acknowledgments

We are grateful to Harvey Lillywhite for the invitation to participate in this symposium. Part of the material in this paper is based on part of the senior author's Ph.D. dissertation in Geography (2010) at James Cook University. We are grateful to Carden Wallace and John Luly (members of the Ph.D. committee), Colin McCarthy and Harold Voris (official assessors of the dissertation) and to Ken Pollock, John Veron, Harvey Lillywhite, Vimoksalehi Lukoschek, and two anonymous reviewers for advice and constructive criticism. We thank Tyler Smith for assistance with Program R.

Funding

Part of this research was funded by James Cook University and part by National Science Foundation grant IOS-0926802 to H. B. Lillywhite. We thank the National Science Foundation [IOS-1132369 to H.B.L.] for financial support of publishing this manuscript. Participation in the symposium by H.H. and S.K. was partially funded by SICB.

Supplementary Data

Supplementary Data are available at *ICB* online.

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