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Temperature Physiology of the Sea Snake *Pelamis platurus*: An Index of Its Colonization Potential in the Atlantic Ocean

(sea-level canal/surface isotherms/distribution/thermal death)

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ABSTRACT **The yellow-bellied sea snake *Pelamis platurus* occurs throughout the tropical Indian and Pacific Oceans from east Africa to Central America. Its latitudinal distribution limits coincide with the 18°C surface isotherm. *P. platurus* has upper and lower thermal tolerances of 36.0 and 11.7°C. With rapid cooling, *P. platurus* stops feeding at 16–18°C; however, it has a high resistance to cold temperature and can withstand 5°C for 1 hr. After 10 days' exposure, *P. platurus* does not acclimate to 17°C and, thus, would not be able to survive for long periods in water this cold.**

In the event of its transit through the proposed Central American Sea-Level Canal, *P. platurus* would colonize the Atlantic Ocean and, during the summer months, would be able to extend its north Atlantic distribution to as far as Cape Cod and the English Channel.

The relatively weak swimming habits of the yellow-bellied sea snake *Pelamis platurus* (Linnaeus), together with its tendency to stay in drift lines for feeding (1), facilitate the transport of this species by oceanic currents. *P. platurus* normally occurs throughout the tropical Pacific and Indian Oceans from East Africa to Central America, and occasionally penetrates into subtropical and temperate latitudes (Fig. 1) (2–8). The dispersal of *P. platurus* into the high latitudes of the western Pacific is facilitated by the warm Kuroshio Current that has occasionally carried the snake as far north as the coastal waters of southern Siberia (2). To the south, the East Australian Current has extended *P. platurus* to as far south as Tasmania (3). The Agulhas Current occasionally carries a few *P. platurus* from the coast of East Africa to Table Bay, beyond the Cape of Good Hope. The cold, upwelled coastal waters of the Benguela Current ensure that no individuals penetrate into the Atlantic Ocean (6, 7, 9).

In the eastern Pacific, *P. platurus* is able to extend its summer range north through most of the Gulf of California and to the outer coast of Baja California. This is facilitated by the northerly movement of equatorial Pacific water that displaces the California Current seaward (10). The southern range limit of *P. platurus* in the eastern Pacific is held fairly constant at about 5°C during all seasons because of the influence of the cold Peru Current (9).

The potential colonization of *P. platurus* in the Atlantic Ocean, if a sea-level canal were to be constructed across Central America, has been discussed by a number of authors (11–13). We have examined the relationship between the present distribution of *P. platurus* in the tropical Pacific and Indian Oceans and the hemispheric winter and summer surface isotherms that delimit its distribution. It is apparent (Fig. 1) that the 18°C isotherm closely agrees with the distribution limits of *P. platurus*. The capacity of this species for survival at a particular latitude depends on seasonal temperatures. Presumably, the northern- and southernmost dispersal records were for the summer months of each hemisphere, but this cannot be confirmed from the literature. If we use the 18°C isotherm as an index to the potential distribution of *P. platurus*, it appears that large areas of the Atlantic Ocean are thermally suitable for this species (Fig. 1). Our principal objectives have been to determine the potential extremes of its distribution, given its thermal tolerances, and to verify the reliability of the 18°C isotherm as a basis for explaining both its present distribution in the Indian and Pacific Oceans and predicting its potential dispersal in the Atlantic Ocean. In addition to determining tolerances, we have examined the capacity of *P. platurus* for thermoregulation and low-temperature acclimation and have observed its response to rapid changes in temperature.

MATERIALS AND METHODS

All experiments were run, within 30 days of collection, on 67 snakes collected in Panama Bay near the Pearl Islands. The snakes were held in large tanks at ambient temperatures (27–28°C) and salinities (26–30‰). Total lengths were 370–740 mm (median = 620) and weights were 19–150 g (median = 91).

Lethal temperature determination

Upper and lower tolerance temperatures of *P. platurus* were determined by the Up–Down procedure (14), which, in general, allows estimation of means and their variances in experiments that in some way alter the constitution of an organism so that it cannot be further tested (as would exposure to near lethal temperature). The Up–Down procedure concentrates testing near the mean value and, because it requires separate testing of each snake, it is accurate with smaller sample sizes; however, it does not allow the determination of the lethal temperature range. In determining the thermal tolerances of *P. platurus*, each snake was tested only once, by being placed directly into the test temperature and left for 24 hr. It was then removed to ambient sea water (26–27°C) and monitored for 12 hr. The particular test temperature to which the snake was exposed was considered lethal if the snake died within the 36-hr period.

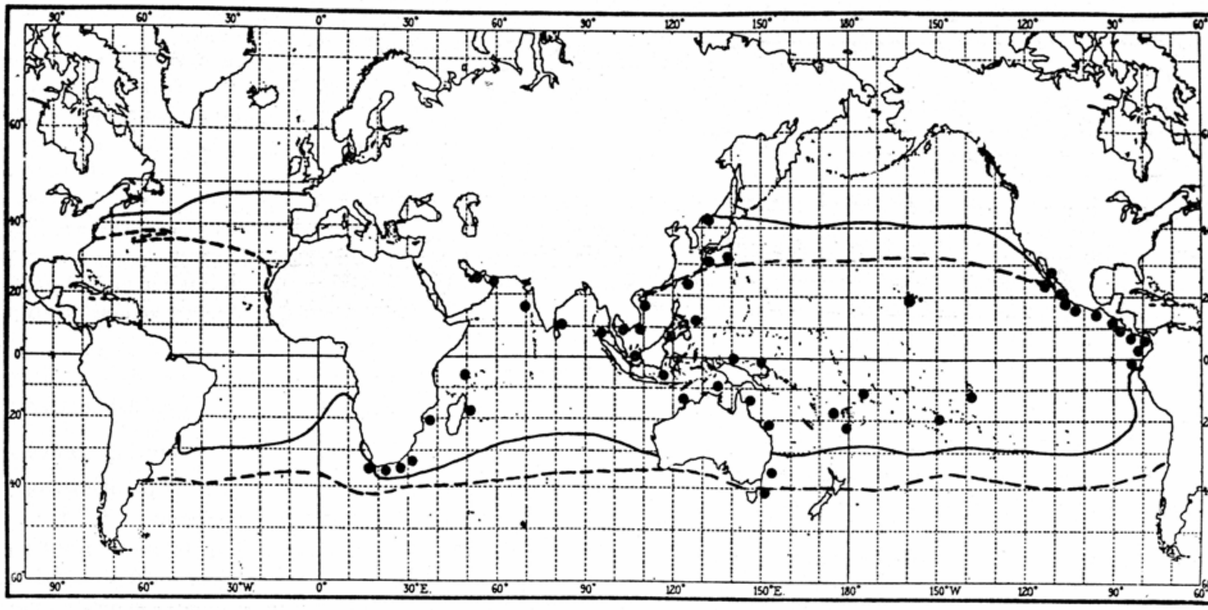

FIG. 1. Relationship between the 18°C February (*dashed lines*) and August (*solid lines*) surface isotherms and the distribution of *P. platurus* (*dots*) in the Indian and Pacific Oceans. The 18°C isotherms in the Atlantic Ocean constitute the approximate potential distribution limits of *P. platurus* in that ocean. Isotherm data are from Neumann and Pierson (8). Distribution records are from various published sources (2–7), and from collections in the Museum of Comparative Zoology and the National Museum of Natural History.

Response to temperature change

To determine the response of *P. platurus* to gradually changing temperatures, specimens were heated or cooled at constant rates from ambient sea water. For cooling, temperatures at which eight snakes (*a*) stopped swimming, (*b*) could not hold their heads up, and (*c*) became torpid were recorded. Another group of six snakes was heated, and the temperature at which they entered heat shock and died was recorded.

Thermal acclimation

To test the capacity of *P. platurus* for low-temperature acclimation, five snakes were acclimated to 17°C for 10 days and were then tested for their response to changing temperatures as above.

Feeding response with changing temperature

Six *P. platurus* were fed daily on small (20–50 mm) fish. Preliminary tests showed that the snakes could eat between 10 and 15 fish at each feeding. Snakes were cooled and the persistence of the feeding response with changing temperature was observed. One or two fish were offered at each test temperature to prevent satiation of the snake.

Thermal regulation

P. platurus may be able to regulate its body temperature by basking under the sun at the surface to absorb heat and by diving into deeper, cooler water to lose heat. To test this idea, we measure the body temperatures of five snakes exposed to sunlight in a shallow (40-cm) pool at different water temperatures. Cloacal temperatures were measured with a Schultheis thermometer within 30 sec after the snake had been caught and held in a net. Care was taken to keep the snakes in water and the experimenters wore gloves to insure minimal conduction of body heat to the snakes. Prior to body-temperature measurements, the position of the snakes in the holding-tank water column was observed. Snake positions were scored arbitrarily as either at the surface (upper 3 cm of water) or not.

RESULTS AND DISCUSSION

Thermal tolerance limits

The upper and lower lethal temperatures of *P. platurus* are 36.0 ± 0.3°C and 11.7 ± 0.2°C (mean ± SE). After preliminary testing, eight snakes were used to determine the upper-lethal limit. The test-temperature sequence was 34–35–36–37–36–35–36–35°C. Ten snakes were used to determine the lower-lethal limit, the test sequence was: 12–11–12–11–12–11–12–13-12–11°C. Lethal temperatures are underlined.

The lethal temperatures found by this method agree with the data of Ehlert (15), who found upper- and lower-lethal ranges of 33–37°C and 10–12°C for a Mexican population of *P. platurus*. This species never experiences temperatures as extreme as 36 and 11°C and, as with most organisms, the range of thermal tolerances exceeds the range of environmental temperatures (16). This points out the ecological importance of sublethal temperatures that influence distributions by affecting such processes as reproduction and feeding.

Response to changes in temperature

Specimens of *P. platurus* that were heated from ambient temperature at a constant rate (5°C/hr) became hyperactive at 36°C. At 39°C, the snakes became comatose and soon died. Attempts to reverse the comatose condition by returning the animals to water at 26°C were unsuccessful (Table 1). This snake can be cooled rapidly to temperatures below its lethal tolerance limit. At a cooling rate of 17°C/hr the snakes lost their capacity to swim at 8.5°C. Below 7.5°C, they were unable to raise their heads to the surface and respire. At temperatures below 6°C, they were in deep torpor and did not respond to mechanical stimuli such as prodding or pinching with forceps (Table 1); all individuals that were kept at tem-

TABLE 1. *Effects of temperature change on Pelamis platurus*

Event	27°C group	17°C group
Heat coma (death)	39.4 (6)	39.0 (5)
Cold-temperature swimming cessation	8.5 (8)	7.0 (5)
Head drop	7.5 (8)	7.0 (5)
Torpor	6.0 (8)	6.5 (5)

Comparisons between a group kept at ambient temperature (26–27°C) and one acclimated to 17°C for 10 days. Median values are given; sample sizes are in parentheses.

peratures below 5°C for 1 hr revived when returned to 26°C and survived indefinitely.

Thermal acclimation

Snakes acclimated to 17°C when cooled lost their capacity to swim at 7.0°C, but the temperatures at which they could not hold their heads up (7.0°C) and became torpid (6.5°C) were not different from those found for the 27°C group (Table 1). When warmed, the acclimated snakes began to swim immediately (7.5–8.0°C) and all survived. The temperature at which snakes acclimated to 17°C go into irreversible heat coma (39.0°C) is not significantly different from that of the group acclimated to 27°C (39.4°C) (Mann Whitney U test, $P > 0.20$, Table 1). *P. platurus* does not make any compensatory adjustment of its thermal range after a 10-day exposure to 17°C. This species may have only a limited range of temperatures to which it can acclimate, and 17°C may be beyond the range. Temperatures from 17°C to the lower-lethal limit (11°C) may be regarded as incipiently lethal. At these temperatures, the debilitating effects of low temperature may result in drowning or starvation.

Feeding response with changing temperature

When the feeding group was cooled at a slightly lower rate (12°C/hr), one snake stopped taking food at 20°C (Table 2). At 18°C, three snakes did not feed; at 16°C, all snakes had stopped feeding. When the water was warmed from 16°C to ambient temperature, two snakes fed at 18°C; three at 20°C; and five at 23°C. On the next day (27°C), all snakes took food. These experiments suggest that one of the factors limiting the distribution of *P. platurus* to within the 18°C isotherm is reduced feeding at and below this temperature.

TABLE 2. *Feeding response of Pelamis platurus as a function of temperature*

	Time (min)	Temperature (°C)	Number of snakes that fed
Cooling phase	0	26.0	6
	16	23.5	6
	33	20.0	5
	50	18.0	3
	65	16.0	0
Warming phase	80	16.0	0
	91	18.0	2
	101	20.0	3
	116	23.0	5
	140	27.0	4

TABLE 3. *Body temperatures and vertical distribution of P. platurus in a tank as a function of water temperature*

Water temperature	Mean body temperature	Difference $\bar{x} \pm SE$	Vertical position: Surface	Vertical position: Not surface
18.8	19.2	0.36 ± 0.02	5	0
20.0	20.4	0.44 ± 0.07	5	0
22.0	22.5	0.50 ± 0.06	5	0
26.8	27.2	0.38 ± 0.04	2	3
28.2	28.7	0.50 ± 0.04	3	2
30.4	30.8	0.36 ± 0.02	—	—
30.6	30.7	0.18 ± 0.03	2	3
32.4	32.4	0.12 ± 0.02	0	5
32.5	32.5	0.08 ± 0.01	0	5
27.4	27.4	0.08 ± 0.02	—	—

Measurements at 27.4°C were made at night (2100); all other measurements were made from 0900–1500 on bright sunny days. The mean difference between body temperature and water temperature and its standard error are given. Size range 525- to 720-mm total length (mean = 588); weight 43.2–115.5 g (mean = 78.5) (n = 5).

Thermal regulation

Body temperatures of *P. platurus* average slightly above ambient temperature over the range 18.8–32.5°C (Table 3). Body temperatures measured at night are in close agreement with water temperature. As the water cooled, the snakes spent more time on the surface. At 32°C, all the snakes were on the bottom of the tank and, in addition, some occasionally exhibited a "dive" response by putting their heads on the bottom and swimming vigorously.

A single observation in 1933 records a body temperature of 24.9°C *for P. platurus* in 25°C water, but no other data are available (17). Cowles (18) suggested that *P. platurus* may have a basking behavior and Brattstrom (17) classified *P. platurus* as one of a group of aquatic reptiles that bask at the surface. The data presented here indicate that in sunlit waters, and over the range of normal surface temperatures (20–30°C), *P. platurus* can maintain a body temperature slightly warmer than ambient. In unusually warm water (32°C), *P. platurus* tends to avoid the surface water and may try to dive. At unusually cool temperature, it is less active and lies on the surface. It is conceivable, but not yet demonstrated, that *P. platurus* regulates its body temperature behaviorally by alternately basking and diving.

When a snake is basking at the water surface, the blackened upper portion of its body is emergent. This coloration would facilitate the absorption of solar energy; it may also function for ultraviolet filtration and countershading. The high heat capacity of water and the probable inability of *P. platurus* to generate metabolic heat would make thermoregulation difficult on overcast days and at night. This would also be true at high latitudes because the water is cooler and the angle of incident solar radiation is less.

Atlantic colonization

The failure of *P. platurus* to pass through the existing Panama Canal is not surprising. Although it can tolerate fresh water for at least 6 weeks (C. Kropach, unpublished data), *P. platurus* probably avoids the low-salinity waters of the canal entrance. The seaward flow of water and turbulence of the Pedro

Miguel and Miraflores locks do not favor the transit of a weakly swimming surface animal. If the snakes did transit the two sets of Pacific locks and got into the fresh waters of Gatun Lake, it is unlikely that they would find their way through the myriad drainages and backwaters of the lake to the Atlantic Gatun locks.

The sea-level canal across Central America will readily permit the transit of *P. platurus* to the Western Atlantic Ocean. The occurrence of large numbers of snakes in the coastal water of Panama Bay insures that a certain number will get into, and pass through, the canal which, as presently proposed, will be an open body of water 600 feet wide, with no barriers and a net daily flow from the Pacific to the Atlantic.

P. platurus may be able to successfully colonize the Atlantic Ocean. No sea snakes live at present in the Atlantic, and *P. platurus* would not face competition from related organisms. It may be very successful in feeding on small fishes, particularly those associated with *Sargassum* drift lines. *P. platurus* is ovoviviparous; one female snake can bear as many as six juveniles. Juvenile snakes are ecologically and behaviorally similar to adult snakes and are not likely to become separated from the colonizing propagule.

P. platurus remains viable in water as cool as 18°C, but it is not known whether adults living at this temperature would be capable of reproduction. Rubinoff and Kropach (12) suggest that initial predation pressure may be quite high, but further studies are necessary. Allowing for not too severe predation pressure and sufficient food, *P. platurus* would occur regularly within the 18°C isotherms of the Atlantic Ocean (Fig. 1). Atlantic distribution will depend on surface current patterns. Most snakes will be carried north by an extension of the South Equatorial Current through the Caribbean Sea, into the Gulf of Mexico, and around Florida into the Gulf Stream by the Florida Current. In the Gulf Stream, *P. platurus* could extend along the east coast of North America as far as Chesapeake Bay in winter and Cape Cod in summer. The lesser width of the North Atlantic Ocean in comparison to the Pacific Ocean makes it conceivable that *P. platurus* could be transported across the Atlantic in the Gulf Stream and North Atlantic Drift. During summer months individuals might conceivably reach the English Channel.

Although a small counter-clockwise surface current gyre in the region of Panama would propel snakes towards Colombia and Venezuela, strong surface currents would oppose their migration towards the northeastern coast of South America. It is possible that snakes carried across the North Atlantic by the Gulf Stream and then south by the Canary Current could get into the Atlantic equatorial system and be carried back across the Atlantic and distributed along the coasts of South America by the South Equatorial and Brazil Currents. The high resistance of *P. platurus* to cooling will facilitate the occasional transport of this species outside the 18°C isotherm. Occurrences would be rare, but it is possible that some snakes that were carried into warm bays or tide pools could become active.

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