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Coming up for air: thermal-dependence of dive behaviours and metabolism in sea snakes

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Summary statement:

Interactions between thermal environment, body activity and bimodal respiration show that with rising water temperatures, sea snakes may become more susceptible to fishing related mortality through reduced apnoeic capacity.

Abstract

Cutaneous gas exchange allows some air-breathing diving ectotherms to supplement their pulmonary oxygen uptake, which may allow prolongation of dives and an increased capacity to withstand anthropogenic and natural threatening processes that increase submergence times. However, little is known of the interplay between metabolism, bimodal oxygen uptake and activity levels across thermal environments in diving ectotherms. Here, we show in two species of sea snake (spine-bellied sea snake; *Hydrophis curtus* and elegant sea snake; *H. elegans*) that increasing temperature elevates surfacing rates, increases total oxygen consumption, and decreases dive durations. The majority of dives observed in both species remained within estimated maximal aerobic limits. While cutaneous gas exchange accounted for a substantial proportion of total oxygen consumption (up to 23%), unexpectedly it was independent of water temperature and activity levels, suggesting a diffusion-limited mechanism. Our findings demonstrate that rising water temperature and a limited capability to up-regulate cutaneous oxygen uptake may compromise the proficiency with which sea snakes perform prolonged dives. This may hinder their capacity to withstand ongoing anthropogenic activities like trawl fishing, and increase their susceptibility to surface predation as their natural environments continue to warm.

Introduction

Air-breathing aquatic animals often use different strategies to prolong dive durations to maximise access to underwater resources and minimise predation risk at the surface (Heithaus and Frid, 2003; Lima and Dill, 1990). Diving ectotherms face an additional challenge due to an inability to physiologically thermoregulate, as water temperature is influential in governing dive duration due to a 2 – 3-fold change in physiological rate processes with a 10˚C change in temperature (Clarke and Fraser, 2004; Schmidt-Nielsen, 1997). The increase in metabolic requirements caused by increasing temperature can significantly influence the diving behaviours of air-breathing aquatic ectotherms in the context of predation risk, interactions with threatening processes, and accessing important underwater resources (Campbell et al., 2010a; Campbell et al., 2010b; Heatwole et al., 2012; Pratt et al., 2010). As many air-breathing aquatic ectotherms occupy a top-order or meso-predator function within their ecosystems (e.g. crocodilians, sea snakes), behavioural modifications (e.g. change in prey preference, range shifts) caused by changing environmental factors will have broad impacts on the ecosystem as a whole. Moreover, the dynamics between water temperatures, behaviour and physiology in air-breathing aquatic ectotherms become increasingly important when considering the projected increases in inter-annual and seasonal water temperatures (e.g. El Niño cycles, heatwaves; Intergovernmental Panel on Climate Change, 2014; Meehl and Tebaldi, 2004) and the potential flow-on effects for community structure and function.

Some diving ectotherms can respire bimodally and have been reported to fulfil a large proportion of their oxygen requirements cutaneously (e.g. marine snakes: Graham, 1974; Heatwole and Seymour, 1975b), or through specialised vascular structures (e.g.

freshwater turtles: Clark et al., 2008). Cutaneous oxygen uptake can be up-regulated by a redirection of blood to subcutaneous capillaries, and the exchange of dissolved gases between the capillaries and surrounding water via a transcutaneous diffusion gradient (Andersen, 1966; Glass and Wood, 1983). The capability for gas exchange through cutaneous means depends on a range of abiotic factors (e.g. permeability of skin, oxygen tension in surrounding water) and physiological attributes (e.g. oxygen tension in blood, oxygen-carrying capacity of blood, cardiac output, body temperature) (Heatwole and Seymour, 1976; Lillywhite and Ellis, 1994). The capacity to uptake oxygen cutaneously varies considerably between different species of aquatic ectotherms (Heatwole et al., 2012; Heatwole and Seymour, 1975b; Heatwole and Seymour, 1978; Herbert and Jackson, 1985; Pratt and Franklin, 2010). For example, file snakes (e.g. *Achrochordus granulatus, A. arafurae*) display very low metabolic rates in comparison to other marine snakes (Heatwole and Seymour, 1975b), and their capacity for cutaneous gas exchange is thought to increase dive durations by up to 30% (Pratt et al., 2010). Moreover, bimodally-respiring freshwater turtles can display up-regulation of cutaneous oxygen consumption (up to 100% in *Elseya albagula*) to prolong dive durations in response to environmental conditions or stress (Herbert and Jackson, 1985; Mathie and Franklin, 2006).

Increased metabolic demand in warmer waters may mean that diving ectotherms deplete oxygen stores within their lungs and tissues quicker during dives and thus may have a disproportionate reliance on other mechanisms to compensate (Dabruzzi et al., 2012; Heatwole and Seymour, 1976; Pratt and Franklin, 2010). Campbell et al. (2010a) found that freshwater crocodiles (*Crocodylus johnstoni*) displayed longer post-dive intervals in summer, in order to repay larger ‘oxygen debts’ accumulated

through anaerobic respiration as water temperatures increased. Specialised cardiorespiratory mechanisms have been linked with reducing anaerobiosis in many marine snakes (e.g. breathing tachycardia, cutaneous gas exchange; see Heatwole, 1977), however the influence of the thermal environment on these mechanisms is poorly understood. Cutaneous gas exchange in a range of 'true' sea snakes (i.e. spending their entire lives in aquatic environments) was measured by Heatwole and Seymour (1975b) with individuals acquiring up to 22% of their total oxygen via cutaneous means (at 25 – 27˚C). Graham (1974) recorded that pelagic sea snakes (*Hydrophis platura*, previously *Pelamis platura*) met up to 33% of their oxygen requirements via cutaneous gas exchange (at 26 – 28˚C). The authors of these studies acknowledged that water temperature played an important role in oxygen consumption rates, but did not quantify how changes in temperature influenced dive performance, cutaneous gas exchange and energy requirements. Increased activity patterns in divers during periods of apnoea (e.g. during feeding or mating) are likely to increase cardiac output, which in turn is expected to increase subcutaneous capillary recruitment, and ultimately elevate the capacity for cutaneous gas exchange (Hicks and Wang, 1996). Indeed, Heatwole and Seymour (1976) reported that the activity level of individual sea snakes was an important factor influencing aquatic gas exchange, with individuals classed as 'active' displaying elevated rates of cutaneous oxygen uptake, however, the influence of the thermal environment on the relationship between activity levels and bimodal gas exchange were not explicitly investigated.

From a conservation perspective, understanding the interplay between metabolic rates, bimodal gas exchange, dive behaviours and water temperature can provide insight into how susceptible diving animals might be to anthropogenic threats (Janik and

Thompson, 1996; Milton, 2001). Indeed, the interactions between these variables may be influential in the susceptibility of globally-threatened sea snakes to incidental capture by commercial and subsistence trawl fishing in tropical waters (Elfes et al., 2013). The up-regulation of cutaneous gas exchange is one mechanism by which sea snakes could reduce their risk of predation or fisheries capture at the surface, or increase their survival in trawl nets through extended dive durations. However, the capacity to up-regulate aquatic gas exchange in sea snakes across temperature and during different levels of activity remains poorly understood. This study builds on work previously conducted by Heatwole and Seymour (1975a; 1975b; 1976) by quantifying how water temperature influences dive performance of true sea snakes, as well as exploring the link between activity level and bimodal gas exchange.

Over the last two decades, sea snake populations have declined precipitously over large areas, including locations that were once renowned for their abundance and diversity (Goiran and Shine, 2013; Lukoschek et al., 2013; Lukoschek et al., 2007). The causes for these declines are currently unknown, yet fisheries related mortality and ocean warming are identified as significant threatening processes for global populations (Elfes et al., 2013; Heatwole et al., 2012). The present study provides the first empirical quantification of the links between water temperature, activity levels (via accelerometry), surfacing rates, and bimodal oxygen uptake in sea snakes, with an aim to decipher how changes in current-day and forecasted water temperatures may affect the susceptibility of sea snakes to ecological and anthropogenic threats such as predation and trawl fishing.

Materials and methods

Animals, tagging and experimental protocols

Two species of sea snake (spine-bellied sea snake, *Hydrophis curtus* and elegant sea snake, *H. elegans*) were collected from wild populations within Cleveland Bay, Queensland, Australia (19.20°S, 146.92°E). Twenty-two individuals (*Hydrophis curtus*, n = 12 and *H. elegans*, n = 10) in visibly healthy condition and large enough to be implanted with an acoustic transmitter were secured within breathable catch bags and transported to the National Sea Simulator facility (SeaSim) at the Australian Institute of Marine Science (AIMS) in Townsville. After 3 – 4 days of acclimation to individual holding tanks supplied with flow-through seawater (27 ± 0.5˚C [actual range]; 12:12 h day:night cycle), snakes were surgically implanted with tri-axial accelerometer acoustic transmitters (Vemco. Ltd., Model V9AP-2H, 69 kHz, 3.3 g in water) and allowed to recover in their individual holding tanks for another 4 – 5 days. Surgeries involved administering a local anaesthetic (Xylocaine®; lignocaine) at the site of implantation, followed by a small ventro-lateral incision (c. 2 cm) approximately 4 – 5 cm anterior to the cloaca. The transmitter was inserted into the peritoneal cavity and the incision was closed using monofilament surgical sutures. Each transmitter was uniquely coded, transmitted measurements of acceleration (m s^{-2}), and had a battery life of approximately 38 days. Acceleration data were transmitted on a pseudorandom repeat every 19 – 21 s and were sampled at 5 Hz for a period of 16 s every second transmission cycle. Acceleration data were calculated as an average root mean square (RMS) value representing the body acceleration from all three axes ($\mathrm{RMS} = \sqrt{A_x^2 + A_y^2 + A_z^2}$) over each sampling period and ranged between 0 – 3.465 m s^{-2} (resolution 0.014 m s^{-2}). A high pass filter was used to remove the static contribution to overall acceleration measurements prior to calculations of RMS. Water

temperature in the holding tanks was changed to either 21 or 30˚C (at a rate of ~2˚C h^{-1}) prior to moving the snakes to custom-designed respirometers at the same temperature (Fig. S1).

Following at least a 12 h settling period, animal body acceleration (m s^{-2}) was measured using acoustic receivers simultaneously while measuring cutaneous and pulmonary oxygen consumption rates ($\dot{V}o_{2cut}$ and $\dot{V}o_{2pul}$, respectively) at four temperature treatments (21, 24, 27 and 30˚C; randomised between stepping up from 21˚C or down from 30˚C to avoid extreme changes in temperatures between treatments). Measures of $\dot{V}o_2$ were recorded over a period of 24 hours for each temperature treatment, after which the water temperature was adjusted at a rate of ~1°C h^{-1} to reach the next treatment temperature. Individuals were allowed an hour to acclimate to the new temperature before recordings commenced to ensure that body temperatures reached equilibrium with water temperature. All individuals from both species were tested over all four water temperature treatments. Respirometers were run empty once before and once after each batch of snakes to record any background microbial respiration in the water and any potential drift in the oxygen sensor system. Respirometers were removed from the water bath after each batch of experiments, cleaned and flushed with freshwater to minimise microbial growth. The oxygen consumption rates of four of the 22 individuals (3 *Hydrophis curtus* and 1 *H. elegans*) were measured both before and after the surgical procedure at all four temperatures to test if tag insertion had an effect on $\dot{V}o_2$ and surfacing frequency.

Calculation of metabolic parameters

Several metrics related to the consumption of oxygen and diving performance of sea snakes were calculated using the recorded oxygen traces (using contactless oxygen sensor spots; Firesting, PyroScience, Germany) within aquatic and aerial chambers of respirometers (Figs. S2 and S3 respectively). The cutaneous oxygen consumption rate ($\dot{V}o_{2cut}$; $mlO_2\ min^{-1}$), measured using a static intermittent-flow system, was calculated during each sealed cycle of the respirometers (Fig. S2) according to Clark et al. (2013) as:

$$\dot{V}o_{2cut} = [(V_w - V_s) \times \Delta cO_2] / \Delta t \quad (1)$$

where V_w is the volume of water within the respirometer, V_s is the volume of the snake (where it was assumed that 1 g of snake displaced 1 ml of water), ΔcO_2 is the change in oxygen concentration in the respirometer water, and Δt is the change in time during which ΔcO_2 was measured.

As in Heatwole and Seymour (1978), individual breathing bouts of snakes were clearly identifiable on the recorded oxygen traces (Fig. S3). Pulmonary oxygen consumption rates ($\dot{V}o_{2pul}$; $mlO_2\ min^{-1}$), measured using a positive-pressure flow-through system, were calculated for each breathing bout according to Frappell et al. (2002) as:

$$\dot{V}o_{2pul} = flow' \times (F'IO_2 - F'EO_2) / (1 - F'IO_2) \quad (2)$$

where $F'IO_2$ and $F'EO_2$ are the fractional oxygen concentrations of incurrent and excurrent air, respectively ($F'IO_2$ was taken immediately prior to the breathing bout, and $F'EO_2$ was calculated as the mean oxygen concentration across the duration of the breathing bout). These data were standardised to the length of the breathing bout to

calculate the volume of oxygen consumed during each breathing bout (V_B; ml bout^{-1}), then divided by the time since the last breathing bout to calculate average $\dot{V}o_{2pul}$ per unit time. Measures of $\dot{V}o_{2cut}$ and $\dot{V}o_{2pul}$ were then summed to provide total oxygen consumption rates ($\dot{V}o_{2tot}$) for each individual at all four temperature treatments. The time between breathing bouts was used to calculate surfacing rate (S_r; breathing bouts h^{-1}).

Values of total mass-specific metabolic rates ($\dot{V}o_{2tot}$) and volume of oxygen consumed per breathing bout (V_B) were used to estimate theoretical maximal aerobic dive durations at all four temperature treatments. First, using blood volumes and blood-oxygen carrying capacities measured previously by Heatwole and Dunson (1987) and Pough and Lillywhite (1984), the volume of O_2 held in snakes at the start of dives in nearly-air-saturated blood was estimated (Cook and Brischoux, 2014; Rubinoff et al., 1986). As blood-oxygen carrying capacities for *Hydrophis curtus* or *H. elegans* were not measured by Pough and Lillywhite (1984), values for the closely related *Hydrophis coggeri* (identified as *Hydrophis melanocephalus*) were used [blood volume = 9.85 ± 0.48% body mass; blood-oxygen capacity = 0.108 ± 0.017 mlO_2 (ml blood)$^{-1}$]. Pough and Lillywhite (1984) also found that blood-oxygen carrying capacities for sea snakes in the *Hydrophis* group did not significantly vary between 10 – 40˚C. Therefore, applying their measured values to the monitored individuals in the present study, the theoretical volume of oxygen available in the blood at the start of dives was calculated as 10.6 mlO_2 kg^{-1}. The amount of oxygen available before a dive was calculated by adding the maximum volume of oxygen per breathing bout (V_B) and the amount of oxygen dissolved in blood, assuming negligible levels of O_2 are held in muscle. A theoretical maximal dive duration (min) was then estimated for each

species by dividing the total oxygen available before a dive ($mlO_2\ kg^{-1}$) with the average rate of mass-specific oxygen consumption ($\dot{V}o_{2tot}$; $mlO_2\ min^{-1}\ kg^{-1}$) for both species at each temperature treatment.

Temperature coefficients (Q_{10}) were calculated for $\dot{V}o_{2cut}$, $\dot{V}o_{2pul}$ and $\dot{V}o_{2tot}$ for each individual using the following equation (Dabruzzi et al., 2012; Schmidt-Nielsen, 1997):

$$Q_{10} = (K_2 / K_1)^{10 / (T2 - T1)} \quad (3)$$

where K_1 is the mean oxygen consumption rate (i.e. $\dot{V}o_{2cut}$, $\dot{V}o_{2pul}$ and $\dot{V}o_{2tot}$) at the lowest temperature treatment (T1; 21°C), and K_2 is the mean oxygen consumption rate at the highest temperature treatment (T2; 30°C).

The effects of temperature on oxygen consumption rates and diving characteristics of both species were tested using calculated metrics. Values of $\dot{V}o_{2pul}$, $\dot{V}o_{2cut}$, S_r and V_B were compared between temperature treatments using generalised linear mixed models (GLMMs) with mass of the individual as a covariate to account for its potential influence and the individual ID as a random factor to account for the repeated measures nature of the data. Oxygen consumption rates (both $\dot{V}o_{2cut}$ and $\dot{V}o_{2pul}$) and S_r were compared before and after tagging in four individuals to test for a potential influence of the surgical procedure (paired *t*-tests; $\alpha = 0.05$). The effects of activity on bimodal oxygen consumption rates were also tested by comparing the relationships between measured body acceleration values from implanted accelerometers and each of $\dot{V}o_{2cut}$ and $\dot{V}o_{2pul}$ to assess if increased activity levels resulted in corresponding increases in aquatic or aerial oxygen uptake.

Results

Twenty-two sea snakes from two species were held in captivity and monitored within respirometers. $\dot{V}O_2$ of four individuals tested before and after tag implantation revealed no significant differences in $\dot{V}O_{2pul}$ (paired *t*-test: t = -1.11, p = 0.29) or $\dot{V}O_{2cut}$ (paired *t*-test: t = -0.47, p = 0.65). Similarly, surfacing rates (S_r) in individuals were statistically similar before and after tag implantation (paired *t*-test: t = 1.75, p = 0.12), suggesting that acclimation and recovery periods after surgical procedures were sufficient for respiration and dive behaviours to return to normal.

Measurements of dive metrics from all snakes showed a clear temperature-dependence (Fig. 1). Both species displayed reduced S_r at the lowest temperature (21˚C; *Hydrophis curtus*: 1.6 ± 0.2 breathing bouts h^{-1}; *H. elegans*: 2.7 ± 0.4 breathing bouts h^{-1}) and increased S_r at the highest temperature (30˚C; *H. curtus*: 4.5 ± 0.5 breathing bouts h^{-1}; *H. elegans*: 5.6 ± 0.5 breathing bouts h^{-1}; Fig. 1A). Consequently, both species had the longest dive durations at the lowest temperature (21˚C; *H. curtus*: mean = 39.9 ± 4.6 min, max = 152.5 min; *H. elegans*: mean = 27.3 ± 4.4 min, max = 93.6 min) and shortest dive durations at the highest temperature (30˚C; *H. curtus*: mean = 11.2 ± 0.6 min, max = 34.7 min; *H. elegans*: mean = 10.7 ± 0.7 min, max = 37.2 min; Fig. 1B). Using the estimated volume of oxygen in the blood, V_B, and mass-specific $\dot{V}O_{2tot}$ measured in each of the four temperature treatments, theoretical maximum aerobic dive durations were calculated and found to decrease with increasing temperatures for both species (Fig. 1B). The majority of dive durations observed in this study (76%) as well as dive times measured previously by Heatwole (1975) [*H. curtus*: 37 min at 21˚C, *H. elegans*: 47 min at 23˚C] were within the

estimated maximal aerobic dive durations. This suggests that the majority of diving bouts in these species are kept within aerobic limits.

Surfacing rates of the smaller *H. curtus* (SVL: 470 – 1086 mm; mass: 120 – 940 g) tended to be more frequent than those of the larger *H. elegans* (SVL: 1058 – 1738 mm; mass: 315 – 1755 g) at all four temperatures, yet the trend did not reach statistical significance ($p > 0.05$ for all comparisons, Fig. 1A). Generalised linear mixed models showed both species had significantly increased surfacing rates with increasing temperature (*H. curtus*: $p < 0.001$; *H. elegans*: $p < 0.001$) when mass was factored into models. The volume of oxygen consumed within a species at each breathing bout (V_B) was statistically similar across temperature treatments (GLMM: *H. curtus*: 29.5 ± 15.9 ml bout^{-1}, $p = 0.76$; *H. elegans*: 18.9 ± 9.4 ml bout^{-1}, $p = 0.34$), yet values for *H. curtus* were consistently higher than those for *H. elegans* across the temperature range ($p < 0.01$ for all treatments; Fig. 1C). This suggests that despite showing a trend for less frequent surfacing rates, *H. curtus* compensates by consuming proportionately larger volumes of oxygen per breathing bout to maintain longer dive durations than *H. elegans*.

Consistent with the increase in S_r, $\dot{V}o_{2tot}$ also increased with temperature (Fig. 2). While $\dot{V}o_{2pul}$ significantly increased with increasing water temperature (Fig. 2; GLMM: *H. curtus*: $p < 0.001$, *H. elegans*: $p < 0.001$), $\dot{V}o_{2cut}$ remained statistically similar across temperatures (GLMM: *H. curtus*: $p = 0.71$, *H. elegans*: $p = 0.32$) despite a reduction in oxygen content in the water with increasing temperature. Temperature coefficients (Q_{10}) for $\dot{V}o_{2tot}$ across the temperature range were similar for both species (*H. curtus:* 2.47 ± 0.27, *H. elegans*: 2.32 ± 0.20, Table 1). The fact that

$\dot{V}o_{2cut}$ displayed comparatively lower temperature sensitivities than $\dot{V}o_{2pul}$ in both species suggests that aquatic oxygen uptake may be diffusion-limited and have a limited capacity to be actively regulated. Increases in activity level (=body acceleration) correlated with an increase in $\dot{V}o_{2pul}$, and the slope of the relationship between body acceleration and $\dot{V}o_{2pul}$ increased with increasing water temperature in both species (Fig. 3). However, the relationship between activity and $\dot{V}o_{2cut}$ was considerably weaker, with linear models consistently close to a zero slope at all temperature treatments. Individuals displayed a 0.2% – 66% increase in oxygen uptake between periods of inactivity (minimum body acceleration) and activity (maximum body acceleration) across all temperatures. The generally limited variation in $\dot{V}o_{2cut}$ across measured values of body acceleration and temperature in the present study supports the idea of diffusion-limited aquatic oxygen uptake.

Discussion

This study quantifies for the first time how environmental temperatures and activity levels interact to modify the diving behaviours and metabolic rates of tropical sea snakes. *Hydrophis curtus* and *H. elegans* both displayed elevated metabolism, increased surfacing rates and shorter dive durations with increasing water temperatures, patterns that are consistent with reports from other diving ectotherms (e.g. *Acrochordus arafurae*: Bruton et al., 2012; Pratt and Franklin, 2010; *Laticauda colubrina*: Dabruzzi et al. 2012; *Crocodylus johnstoni*: Campbell et al. 2010a, 2010b; *Caretta caretta*: Hochscheid et al. 2004, 2005). The majority of diving animals (ectotherms and endotherms) adopt physiological strategies (e.g. diving bradycardia) to conserve oxygen stores in lungs and prolong dive durations (Andersen, 1966). In marine snakes, the combination of increased lung volume (as compared to terrestrial snakes; Wood and Lenfant, 1976), cardiorespiratory strategies (e.g. breathing tachycardia, cardiac shunting) and cutaneous gas exchange ensure that aerobic dive durations are maximised despite the increased metabolic demands elicited by warmer waters (Heatwole and Seymour, 1975a). In the present study, the volume of oxygen consumed per breathing bout did not change considerably despite the significant increase in metabolic rates between temperature treatments, which is likely the limiting factor for dive durations observed. As a group that undertakes lung-regulated buoyancy control, the amount of air inspired by individuals prior to dives is often correlated with dive depths (Graham et al., 1987), and consequently influences dive durations in their natural habitat (Hays et al., 2004). Although the species observed in the present study occupy relatively shallow near-shore habitats, pre-dive breathing patterns are an important factor in achieving longer aerobic dives with mechanisms like cutaneous gas exchange only providing a marginal supplement of oxygen. $\dot{V}o_{2cut}$

for *H. curtus* and *H. elegans* changed little with temperature (Fig. 2) and activity levels (Fig. 3), highlighting that these species have a limited capacity to increase cutaneous oxygen uptake, and may rely more heavily on other physiological strategies to maximise dive durations during periods of elevated metabolic demand.

Aerobic diving durations in most diving ectotherms decrease with increasing environmental temperature, therefore animals either accrue an 'oxygen debt' to maintain prolonged dives (Campbell et al., 2010a; 2010b), or undertake shorter dives to retain some oxygen stores and remain aerobic (Hochscheid et al., 2004; Lutz and Bentley, 1985). In the present study, the majority of the dives were within calculated aerobic limits, which is typical in marine snakes (Seymour, 1979; Seymour and Webster, 1975). However, the near-halving of maximum aerobic dive duration between 21˚ and 30˚C observed here illustrates how seasonal changes in environmental temperature may limit diving, movement patterns and access to underwater resources in the wild. The Q_{10} values for $\dot{V}o_{2tot}$ in both species in the present study were 2.3 – 2.5, which are lower than the previously reported value for closely related sea kraits (*Laticauda colubrina*, Q_{10} = 3.07; Dabruzzi et al., 2012), but similar to the value reported for file snakes (*Acrocordus arafurae*, Q_{10} = 2.52; Pratt and Franklin, 2010). High $\dot{V}o_{2tot}$ Q_{10} values are hypothesised to increase metabolic efficiency in sea kraits which are known to experience daily body temperature fluctuations exceeding 15˚C (Pough and Lillywhite, 1984). This may mean that sea kraits can maximise digestive performance on land where temperatures are high, while reducing metabolic demand and increasing submergence times in cooler aquatic habitats (Dabruzzi et al., 2012). Similarly, high Q_{10} values for $\dot{V}o_{2tot}$ have been implicated in the overwintering strategies of loggerhead turtles (*Caretta caretta*),

which drastically reduces metabolic activity in cold waters and allows individuals to undertake extended dives (up to 7 hours) to hibernate (Hochscheid et al., 2005). The lower $\dot{V}O_{2tot}$ Q_{10} values in the present study may reflect the fully aquatic habit of true sea snakes, where individuals rarely experience excessive temperature fluctuations between habitats or over a diel period, and do not display overwintering behaviours.

The thermal independence of $\dot{V}O_{2cut}$ in sea snakes is similar to previous findings in other closely-related aquatic snakes (*Acrochordus arafurae*: Burton et al., 2012, Pratt and Franklin, 2010; *Laticauda colubrina*: Dabruzzi et al., 2012). Temperature sensitivities for $\dot{V}O_{2cut}$ of sea snakes examined in the present study (Q_{10} of 1.34 – 1.94) were similar to the aquatic file snake (1.18; Pratt and Franklin, 2010), which may indicate that the thermal environment has a limited effect on the mechanism driving aquatic oxygen uptake. In contrast to the findings of the present study, previous work by Heatwole and Seymour (1975b) reported that levels of activity in sea snakes can dramatically influence $\dot{V}O_{2cut}$. Heatwole and Seymour (1975b) reported that during active phases of their diel cycle, sea snakes displayed levels of cutaneous oxygen uptake that were ~14 – 120% higher than during inactive phases. In the present study, a diel pattern was not observed in the measures of $\dot{V}O_{2cut}$, with individuals only displaying limited increases in cutaneous oxygen uptake with increased activity. The use of accelerometer-derived values for activity in the present study provides empirical, quantitative evidence that this relationship may not be solely based on level of activity, but may be a combination of activity and other diel metabolic functions (e.g. digestion, reproduction). There may also be species-specific physiological attributes or methodological factors contributing to the differences between studies. Notably, while $\dot{V}O_{2cut}$ formed a significant proportion of $\dot{V}O_{2tot}$ in the present study (up

to 23%), previous work has suggested that the skin of sea snakes may play a more important role in CO_2 and N_2 elimination than oxygen uptake alone (Seymour and Webster, 1975). Indeed, studies have reported that up to 94% of total CO_2 excretion can occur via cutaneous means (Graham, 1974), and the elimination of N_2 cutaneously may allow sea snakes to conduct repeated deep dives without succumbing to decompression illness (Seymour, 1974).

As snakes in the present study were untethered, free to move, and maintained in respirometers for several days to encourage a resting state, it may be expected that if aquatic oxygen uptake was actively regulated, individuals would have increased $\dot{V}_{O_{2cut}}$ at warm temperatures to minimise surfacing frequency. The apparent lack of active regulation of $\dot{V}_{O_{2cut}}$ has implications when considering anthropogenic perturbations like trawl fishing. Indeed, an inability to up-regulate $\dot{V}_{O_{2cut}}$ during periods of stress (e.g. when trapped in trawl nets) will have important implications for survival. Elevated levels of stress experienced by individuals restrained underwater significantly influence $\dot{V}_{O_{2cut}}$, with file snakes (*Acrochordus granulatus*; Heatwole and Seymour, 1976) and pelagic sea snakes (*Hydrophis platura*; Graham, 1974) displaying considerably higher levels of cutaneous gas exchange than free-swimming individuals. The potential for active up-regulation of $\dot{V}_{O_{2cut}}$, attributed to subcutaneous capillary recruitment, has been observed in the yellow-lipped sea krait (*Laticauda colubrina*), in response to decreasing pulmonary oxygen saturation (Dabruzzi et al., in press). The authors of that study observed that sea kraits displayed steady increases in $\dot{V}_{O_{2cut}}$ as aerial oxygen decreased from 100% to 60% of air saturation, with negligible increases in $\dot{V}_{O_{2cut}}$ as saturation levels dropped below 60%. This suggests that the ability to uptake oxygen aquatically may be restricted by the capacity for

subcutaneous capillary recruitment. Dabruzzi et al. (in press) also found that sea kraits altered diving and breathing behaviours as aerial oxygen saturation levels decreased, spending more time at the surface and breathing less frequently. Although not tested in the present study, forced submergence and subsequent elevated levels of stress may play an important role in the up-regulation of cutaneous gas exchange in sea snakes. Similar effects have been observed in other air-breathing bycatch species, where forced submergence in trawl nets elevates metabolic rates and incurs high mortality rates even during short trawls (e.g. Sasso and Epperly, 2006). Elevated metabolic demand during forced submergence is likely to deplete oxygen stores within lungs quickly and induce anaerobiosis (Heatwole, 1975; Seymour and Webster, 1975), which is likely to be exacerbated by rising seasonal temperatures and further reduce survival and post-release recovery of marine snakes caught in trawl nets.

Understanding how sea snakes react to different thermal conditions can provide critical information on how acute (e.g. storm events, heatwaves and cold fronts) and inter-annual (e.g. El Niño cycles, seasonal fluctuations) changes in temperature may affect metabolic requirements and behaviours (Heatwole et al., 2012). The results of the present study show that sea snakes may not have the capacity to physiologically acclimate to short-term changes in temperature, and may have to overcome increased metabolic demands in warmer waters by modifying dive behaviours in light of their limited ability to up-regulate cutaneous oxygen uptake. Modification of dive behaviours will not only influence the susceptibility of sea snakes to anthropogenic threats (e.g. trawling, targeted harvest) but will also increase their exposure to predators at the surface and reduce the time available to forage underwater.

Ultimately, this may compromise the ecological function that sea snakes provide within reef and non-reef habitats (Heatwole, 1999; Heatwole et al., 2012).

The capacity of sea snakes to acclimate to long-term, chronic changes in temperature remains understudied (Elfes et al., 2013; Heatwole et al., 2012). Thermal acclimation may play an important role in allowing air-breathing aquatic ectotherms to offset temperature effects and improve survival in thermally varied environments (Bruton et al., 2012; Campbell et al., 2010a; Clark et al., 2008). Nevertheless, previous work conducted on the pelagic sea snake *Hydrophis platura* suggests that this species may have a limited capacity to thermally acclimate to long-term increases in water temperatures (Graham et al., 1971; Heatwole et al., 2012). However, Bruton et al. (2012) demonstrated that file snakes (*Acrochordus arafurae*) that were acclimated to warm waters (32˚C) for a period of 13 weeks displayed lower $\dot{V}o_{2tot}$ (at 32˚ and 24˚C) as well as reduced thermal sensitivity of $\dot{V}o_{2tot}$ compared to snakes that were acclimated to cooler waters (24˚C). Their study showed that although warm-acclimated snakes displayed partial thermal acclimation of metabolic rates, the capacity for aquatic oxygen uptake was independent of long-term exposure to warm waters, which conferred a limited benefit to the diving abilities of warm-acclimated individuals. If long-term exposure to warm water has a similar effect on sea snakes, this may limit their capacity to cope with the projected increases in global temperatures. Given that many species of sea snakes display a high degree of fidelity towards preferred habitats (Brischoux et al., 2009; Burns and Heatwole, 1998; Lukoschek and Shine, 2012; Udyawer et al., 2016), sea snake populations may be unlikely to expand their ranges to cope with rising water temperatures, resulting in localised extinctions.

In conclusion, the present study shows that the rate of cutaneous oxygen uptake in sea snakes is largely independent of water temperature and activity, perhaps pointing to a diffusion-limited mechanism. The limited capacity to up-regulate $\dot{V}_{O_{2cut}}$ to prolong dive duration can significantly impact dive behaviours, and may in turn reduce survival of snakes trapped in trawl nets. This study also shows that metabolic rates and dive behaviours vary significantly among species, highlighting the importance of physiological characteristics in influencing the vulnerability of sea snake species to anthropogenic and natural threats. A limited capacity to physiologically acclimate to short- and long-term variations in water temperature will make sea snakes highly vulnerable to warming and extreme fluctuations in ocean temperatures, and may add increasing pressure to populations already displaying declines. Future work should explore the effect of stress or forced submergence on $\dot{V}_{O_{2cut}}$, which may provide further insight into the species-specific vulnerabilities of sea snakes caught in trawl nets and point to some mitigation strategies. Longer-term studies of this nature are also required to better understand patterns of energy expenditure in relation to other key activities including reproductive investment and postprandial processes, with an aim to understand vulnerabilities across seasons and with regard to spatial and temporal fisheries practices.

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Competing interests

The authors declare no competing financial interests.

Author contributions

VU: designed the study, conducted field and lab work, analysed data, drafted the manuscript and created the figures; CAS: provided materials and field resources, assisted in drafting of the manuscript; MRH: designed the study, provided materials and field resources, assisted in drafting of the manuscript; TDC: designed the study, provided lab equipment and resources, assisted with lab work, analysed data, assisted in drafting of the manuscript.

Ethics and funding statement

This research was conducted with the approval of the Animal Ethics Committee of James Cook University (A1799) and in accordance with the Great Barrier Reef Marine Park Authority (G14/36624.1) and the Queensland Department of Environment and Heritage Protection's Scientific Purposes Permit (WISP11923512). This project was funded by the Australian Government's National Environmental Research Program (Tropical Ecosystems Hub) and the School of Earth and Environmental Sciences (SEES), James Cook University.

Data Accessibility

Data used for all analyses are available as electronic supplementary materials and upon request from the authors.

List of symbols and abbreviations

AIMS	Australian Institute of Marine Science
RMS	Root mean square value representing body acceleration from all three axes (Acceleration; m s^{-2})
$\dot{V}o_2$	Oxygen consumption rate (mlO_2 min^{-1} kg^{-1})
$\dot{V}o_{2cut}$	Mass-specific oxygen consumption rate through cutaneous means (aquatic oxygen uptake; mlO_2 min^{-1} kg^{-1})
$\dot{V}o_{2pul}$	Mass-specific oxygen consumption rate through pulmonary means (aerial oxygen uptake; mlO_2 min^{-1} kg^{-1})
$\dot{V}o_{2tot}$	Total mass-specific oxygen consumption rate ($\dot{V}o_{2cut}$ + $\dot{V}o_{2pul}$; mlO_2 min^{-1} kg^{-1})
V_w	Volume of water within respirometer (ml)
V_s	Volume of individual sea snake (ml)
ΔcO_2	Change in oxygen concentration in respirometer water (mlO_2 min^{-1})
Δt	Period between respirometer flush cycles (min)
$F'IO_2$	Fractional oxygen concentration of incurrent air into respirometer (mlO_2 min^{-1})
$F'EO_2$	Fractional oxygen concentration of excurrent air from respirometer (mlO_2 min^{-1})
V_B	Oxygen consumed during each breathing bout (ml $bout^{-1}$)
S_r	Surfacing rate (breathing bouts h^{-1})
Q_{10}	Temperature coefficient
K_1	Mean oxygen consumption rate at lowest temperature treatment (mlO_2 min^{-1} kg^{-1})
K_2	Mean oxygen consumption rate at highest temperature treatment (mlO_2 min^{-1} kg^{-1})
T1	Lowest temperature treatment (˚C)
T2	Highest temperature treatment (˚C)
GLMM	Generalised linear mixed model

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Table

Table 1. Summary of morphometrics, oxygen consumption rates and temperature coefficients for both species of sea snake tested.

Species	Snout-vent Length range (mm)	Body mass range (g)	Oxygen consumption ($\dot{V}O_2$)	Mean metabolic rate at 21˚C ($mlO_2\ min^{-1}\ kg^{-1}$)	Mean metabolic rate at 30˚C ($mlO_2\ min^{-1}\ kg^{-1}$)	Q_{10} (±SE)
Hydrophis curtus	470 – 659	120 – 300	Cutaneous ($\dot{V}O_{2cut}$)	0.03 ± 0.003	0.05 ± 0.007	1.94 ± 0.203
			Pulmonary ($\dot{V}O_{2pul}$)	0.19 ± 0.023	0.41 ± 0.045	2.54 ± 0.349
			Total ($\dot{V}O_{2tot}$)	0.21 ± 0.022	0.46 ± 0.049	2.47 ± 0.271
Hydrophis elegans	1058 – 1738	315 – 1755	Cutaneous ($\dot{V}O_{2cut}$)	0.05 ± 0.008	0.07 ± 0.016	1.34 ± 0.221
			Pulmonary ($\dot{V}O_{2pul}$)	0.63 ± 0.227	1.18 ± 0.269	2.51 ± 0.238
			Total ($\dot{V}O_{2tot}$)	0.65 ± 0.198	1.24 ± 0.281	2.32 ± 0.182

Note: Mean temperature coefficients (Q_{10}) were calculated for all forms of oxygen consumption rate using mean values measured at the lowest (21°C) and the highest (30°C) temperature treatments according to equation 3 in the text.

Figures

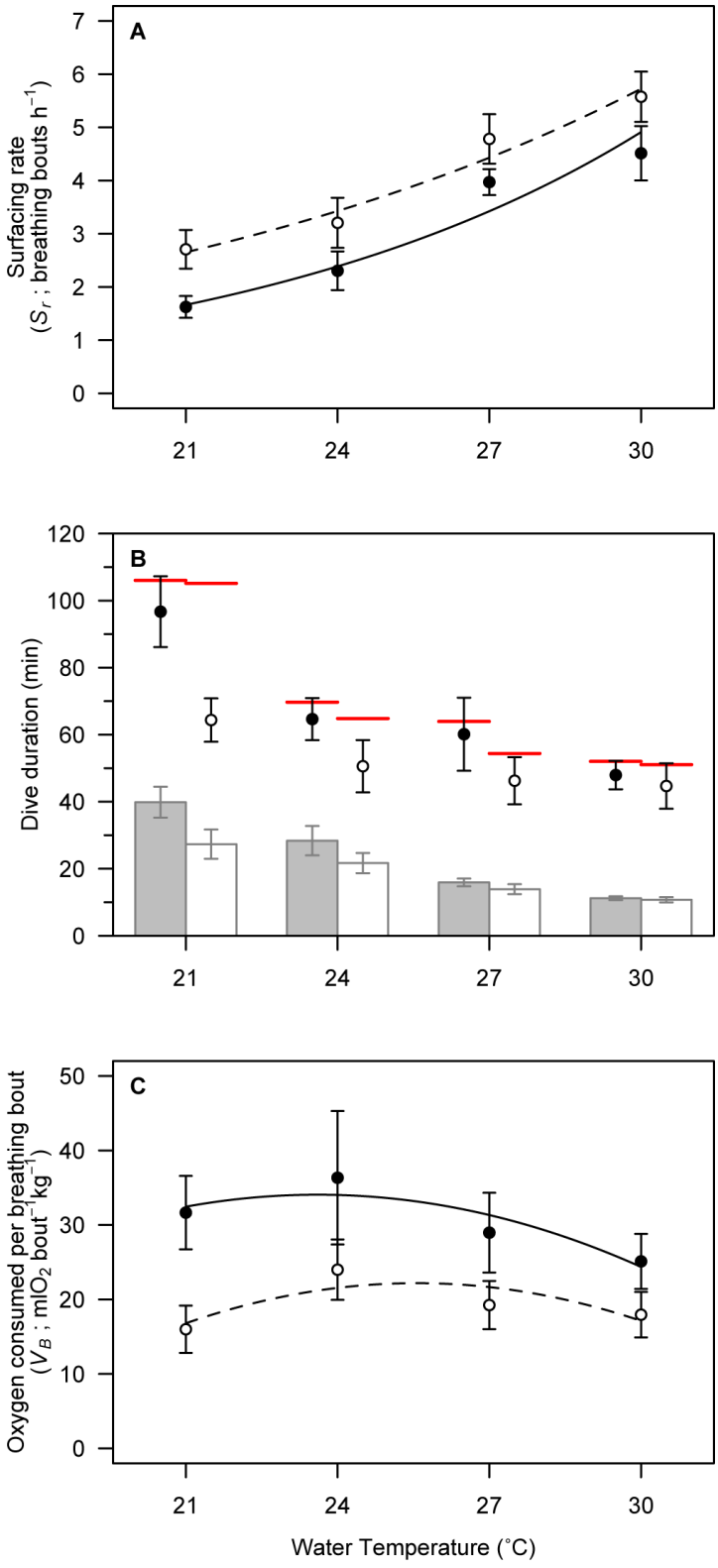

Figure 1. Metrics of dive behaviours of *Hydrophis curtus* (n = 11; solid circles, filled bars) and *H. elegans* (n = 10; open circles, white bars). (A) increased surfacing rate (S_r) with increased water temperature. (B) decreasing mean dive durations with increasing temperature (bar plot), points represent mean maximum dive durations among all observed individuals with red lines indicating theoretical maximum aerobic dive duration. (C) relatively constant volumes of oxygen consumption per breathing bout (V_B) across temperatures. Mean values displayed with standard error bars.

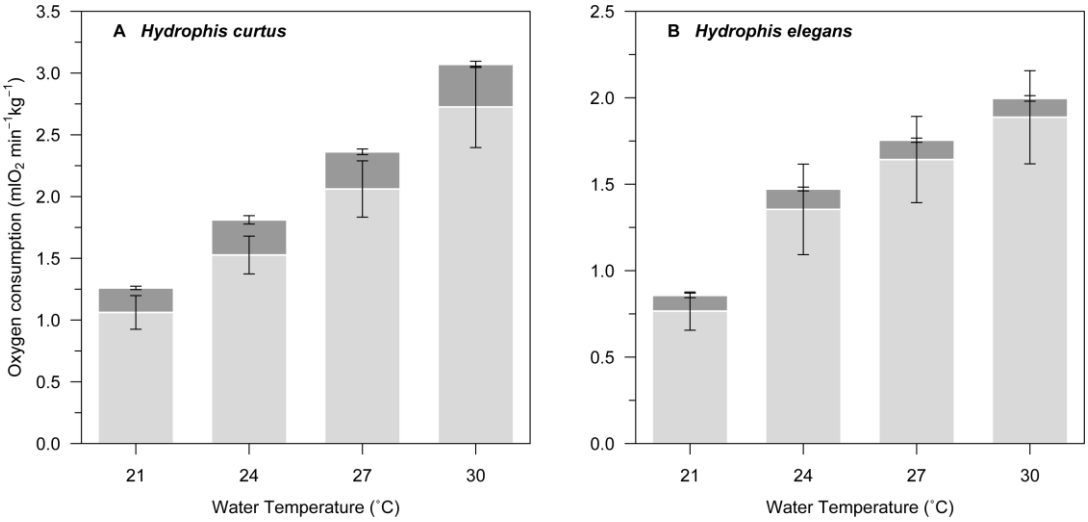

Figure 2. Patterns in mean oxygen consumption rates (with standard errors) via pulmonary ($\dot{V}o_{2pul}$; light gray) and cutaneous ($\dot{V}o_{2cut}$; dark gray) pathways in (A) *Hydrophis curtus* (n = 11) and (B) *H. elegans* (n = 10) across the four temperature treatments. Note the difference in scale of the vertical axes, whereby the absolute values are consistently higher for *H. curtus*.

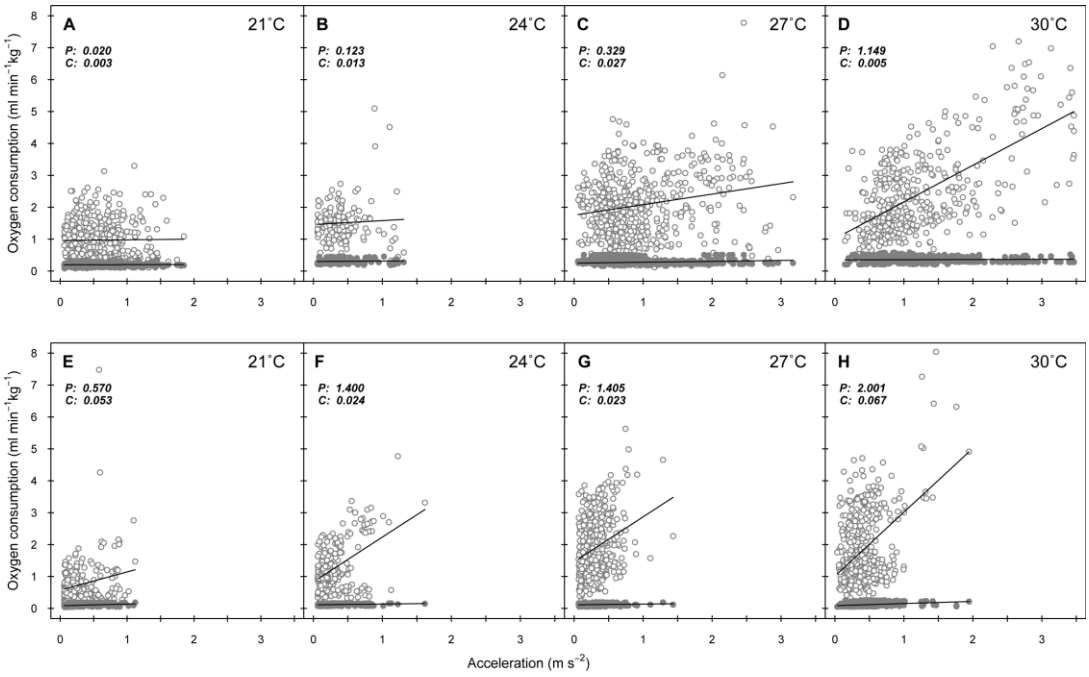

Figure 3. Effect of activity levels (body acceleration) on bimodal oxygen consumption rates over the four temperature treatments in *Hydrophis curtus* (A-D) and *H. elegans* (E-H). Open circles and trendlines represent relationships between pulmonary oxygen consumption ($\dot{V}o_{2pul}$) and body acceleration, and closed grey circles with trendlines represent relationships between cutaneous oxygen consumption ($\dot{V}o_{2cut}$) and body acceleration. The slope of each relationship is displayed in each plot (P: pulmonary; C: cutaneous).