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Heat-seeking sharks: support for behavioural thermoregulation in reef sharks

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ABSTRACT: Most fish are ectotherms and for this reason, water temperature is thought to be one of the main physical determinants of behaviour. We tested the hypothesis that behavioural thermoregulation occurs in 4 species of reef sharks (n = 58), where water temperature influences patterns of long-term (>1 yr) movement, by analysing acoustic monitoring and environmental datasets. We also used biotelemetry to measure the body temperature of 5 adult female blacktip reef sharks *Carcharhinus melanopterus* in response to changes in water temperature, to test whether they participate in inshore aggregations potentially to increase metabolic rates. We found that water temperature had the greatest influence on shark presence at each of our study sites (deviance explained = 3.7–54.6%), when compared to other variables. On average, body temperatures of female blacktip reef sharks were consistently warmer than average (±SE) water temperature by 1.3 ± 0.57°C, providing support for behavioural thermoregulation. The maximum body temperature of blacktip reef sharks while at the aggregation site corresponded to peak daily water temperatures. The average hourly body temperature varied little among individuals. Our models showed that the relationship between water temperature and the presence of female blacktip reef sharks was strongest at the aggregation site relative to other sites. These results suggest that reef shark movements are influenced by water temperature and provide additional support for the behavioural thermoregulation hypothesis. Such data are necessary for predicting how sharks might be affected by climate change and other human modifications to water temperature patterns.

KEY WORDS: Acoustic monitoring · Water temperature · Tide height · Mixed effects models · Biotelemetry · Thermotaxis · Refuging

INTRODUCTION

Habitat use by mobile predators in both terrestrial and aquatic ecosystems is often described as a function of environmental gradients, where individuals select habitats based on biotic (prey) distributions and physiologically optimal abiotic conditions (Jaquet & Whitehead 1996, Corsi et al. 1999, Heithaus et al. 2009, Bradshaw et al. 2004, Wildhaber & Lamberson 2004, Hopcraft et al. 2005, Fukuda et al. 2008, Barnett & Semmens 2012). Understanding the relationship between the movement of marine predators and changes in the environment is vital for predicting the consequences of habitat degradation, particularly in

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areas of high human impact such as coastal marine systems (Heithaus et al. 2002, Field et al. 2009). Sharks are an important predator within the coastal marine environment and assist in maintaining ecosystem stability and prey community structure (Shepherd & Myers 2005, Myers et al. 2007). Movement patterns of sharks have been linked to various abiotic and biotic gradients such as dispersal from daytime refuges as light attenuates toward night (Klimley & Nelson 1984, McKibben & Nelson 1986, Garla et al. 2006), migrations correlated with seasonal changes in water temperature or prey movements (Heupel & Hueter 2001, Sims et al. 2003, Bruce et al. 2006, Hussey et al. 2009), tidal associations for foraging or cleaning benefits (Ackerman et al. 2000, Campos et al. 2009, Carlisle & Starr 2010, O'Shea et al. 2010) and temperature associations to maintain optimal metabolic rates (Morrissey & Gruber 1993, Economakis & Lobel 1998, DiGirolamo et al. 2012). Such studies provide valuable insight into habitat specificity, although they often lack information relating the physiological response of animals to changing environmental conditions. Using a combination of behavioural (i.e. movement) and physiological responses can provide a more complete understanding of why sharks use particular environments (e.g. Carey & Scharold 1990, Hight & Lowe 2007, DiGirolamo et al. 2012).

Because most sharks are ectothermic, there has been a tendency to focus on water temperature (Speed et al. 2010) as one of the determining factors of shark distribution and movement (Hopkins & Cech 2003, Parsons & Hoffmayer 2005, Sims et al. 2006, Vogler et al. 2008, Froeschke et al. 2010), although many of these studies also measured other environmental variables potentially influencing movements such as salinity, dissolved oxygen and current flow. An advantage of using temperature to predict shark movements (as opposed to terrestrial ectotherms), is that behaviours are more likely to be sensitive to temperature variation given its influence on activity, metabolic rates, and oxygen concentration in water (Beitinger & Fitzpatrick 1979). Indeed, many aspects of shark physiology are regulated by temperature (Sims 2003), which might explain fine-scale movement patterns and the close association with specific temperature ranges observed for some species (Simpfendorfer & Heupel 2004, Sequeira et al. 2011).

Movements to maintain body temperature within an optimal range can be explained using the hypothesis of behavioural thermoregulation, which states that fish occupy a thermal niche that maximises vital rates, such as growth, survival and reproduction (Crawshaw & O'Connor 1997, Sims 2003, Carlson et al. 2004). Some studies provide evidence to support this hypothesis by showing that sharks aggregate in warm inshore waters to raise their core temperatures (Casterlin & Reynolds 1979, Economakis & Lobel 1998, Hopkins & Cech 2003, Sims et al. 2006). The function of female shark aggregations during the middle of the day, when water temperatures are at their peak, might serve to increase embryonic development in gestating individuals (Taylor 1993, Economakis & Lobel 1998, Hight & Lowe 2007). However, few studies have demonstrated that free-ranging sharks actively select higher temperatures to optimise physiological processes (e.g. Hight & Lowe 2007). A recent study on juvenile lemon sharks *Negaprion brevirostris* showed that individuals actively selected both the warmest available habitat in the afternoon before selecting cooler-than-average temperatures during the evening and early morning (DiGirolamo et al. 2012). The investigators suggested that this behaviour acts to increase digestive efficiency, as has been suggested for other species (Wallman & Bennett 2006, Di Santo & Bennett 2011).

Previous studies have found a relationship between shark movement with tide height or currents, which are generally attributed to foraging choices (Medved & Marshall 1983, Ackerman et al. 2000, Campos et al. 2009, Carlisle & Starr 2009, 2010). In shallow coastal habitats, movements with the incoming tide potentially allow leopard *Triakis semifasciata* and brown smooth hound *Mustelus henlei* sharks to exploit areas with abundant benthic prey otherwise inaccessible during low tides (Ackerman et al. 2000, Campos et al. 2009, Carlisle & Starr 2009, 2010). Reef-associated sharks and manta rays *Manta birostris* have tide-related movement to cleaning stations, where cleaning was more frequent during ebb tides (O'Shea et al. 2010). There is some evidence that moonlight can play a minor role in shark movement, with depth and sightings of some species varying according to moon phase (Pyle et al. 1996, West & Stevens 2001, Robbins 2007, Weng et al. 2007). The presence of white sharks *Carcharodon carcharias* appears to be greatest during new moons when they are aggregating at a feeding site, which might assist in camouflaging them from their prey (northern elephant seal *Mirounga angustirostris*; Pyle et al. 1996).

A multi-species reef shark aggregation occurs in a small bay (~5 km^2) at Ningaloo Reef, in Western Australia (Fig. 1). This aggregation is comprised predominantly of adult female blacktip reef sharks

Carcharhinus melanopterus, with grey reef *C. amblyrhynchos*, sicklefin lemon *Negaprion acutidens* and white tip reef *Triaenodon obesus* sharks also present. Spatial and temporal patterns in composition and residency of sharks in this aggregation have been described using acoustic monitoring (Speed et al. 2011), although why sharks congregate in this particular bay, one of many with similar characteristics along Ningaloo Reef, remains unknown. Speed et al. (2011) suggested that it might be used for reproduction due to observations of courtship behaviour and the presence of suspected pregnant females; no foraging behaviour or active feeding has been observed.

The long-term residency and site fidelity of reef sharks in this bay provide an ideal opportunity for testing hypotheses on how environmental cues alter movement patterns. In the first part of our study, we examined the effects of several environmental variables (tide height, water temperature, and moon illumination) on total numbers of sharks (all species combined) over each season. We hypothesised that (1) water temperature would have the greatest influence on shark presence at all sites; (2) because sharks are most common during the daytime at the aggregation site (Speed et al. 2011), nocturnal occurrence should be greatest at sites farther from shore; and (3) the probability of occurrence should not vary with tide height at the aggregation site because reef sharks do not forage with incoming tides here (Speed et al. 2011), or feed on sedentary benthic invertebrates available during high tide. Second, we tested 2 more hypotheses that relate to behavioural thermoregulation in adult female blacktip reef sharks: (4) shark body temperature should be consistently warmer on average than average water temperature and (5) sharks should actively select the warmest site and in doing so elevate their core body temperature.

MATERIALS AND METHODS

Study area

The Coral Bay region lies at the southern end of Ningaloo Reef Marine Park in north Western Australia (23° 08′ 41″ S, 113° 45′ 53″ E) (Fig. 1). Our study area was immediately north of the Coral Bay township and encompassed Skeleton Bay, a smaller bayshore where reef sharks aggregate (Speed et al. 2011). The shallow (1–3 m) lagoon of Skeleton and Coral Bay contains many small patch reefs and is bordered by fringing reef offshore. It covers an area of ~12.5 km^2 (2.5 × 5 km) (Halford & Perret 2009). Also included within the lagoon are grey reef shark and manta ray cleaning stations near Asho's Gap and Point Maud, respectively (Fig. 1).

Acoustic array and study sites

We fitted sharks with acoustic tags (see next subsection) and established an array of 9 VR2w (VEMCO) receivers to monitor individual movement patterns at Coral Bay. This array of 9 receivers is part of the Australian Animal Tagging and Monitoring System (AATAMS), which has ~100 receivers along Ningaloo Reef coastline and consists of 3 arrays and 3 curtains (www.imos.org.au/aatams). To monitor daily water temperature fluctuations in relation to shark presence, we attached temperature mini-loggers (VEMCO) to 6 receivers that took measurements at 30 min intervals for the duration of the study (463 d). Locations of receivers and mini-loggers, depths and detections of receivers are given in Table A1). Within the receiver array were 4 monitoring sites: Skeleton Bay, Point Maud, the Channel and the shark cleaning station at Asho's Gap (Fig. 1). We

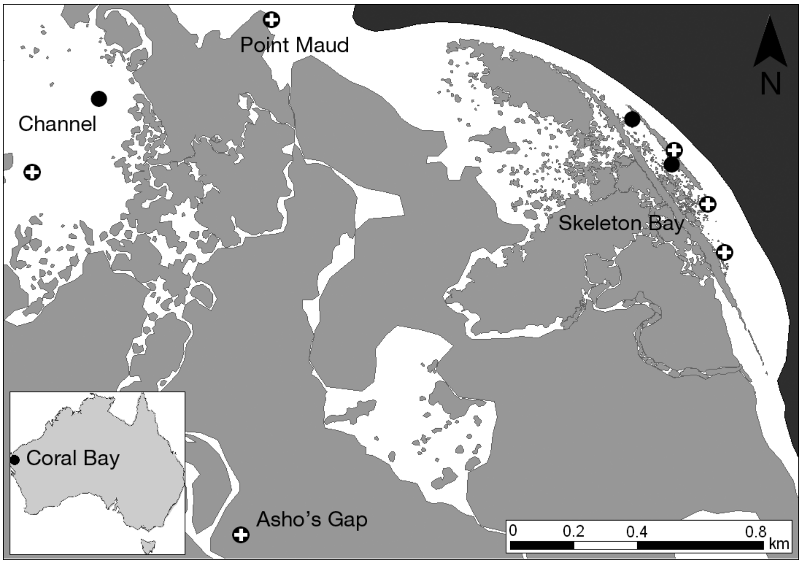

Fig. 1. Coral Bay region showing study sites within Bill's Bay. Acoustic receivers (⊕), acoustic receivers with water temperature mini-logger (●), reef (light grey), sand (white), and land (dark grey)

arranged receivers in Skeleton Bay specifically to address questions relating to shark aggregation patterns (Speed et al. 2011) and behavioural thermoregulation, at Asho's Gap to monitor visitation to the cleaning station, and receivers at the Channel and Point Maud to monitor northward movement and use of the lagoon outside of aggregation periods. We range-tested receivers by trailing a test tag (VEMCO) from a boat or person and taking GPS locations at known distances; the mean maximum detection range varied between 220 and 331 m (Speed et al. 2011).

Shark tagging

Over the 3 yr sampling period we tagged 58 sharks with acoustic transmitters, of which 36 were blacktip reef sharks, 11 were grey reef sharks, 7 were sicklefin lemon sharks, and 4 were white tip reef sharks (Speed et al. 2011). We caught all sharks on a handline with baited barbless hooks on the beach at Skeleton Bay and transported them to a holding tank using a stretcher. We made a 5 cm incision anterior to the cloaca, and inserted acoustic tags coated with beeswax (V13-1H [153dB], V16-5H [165dB], and V16-5x [165dB]; VEMCO) into the peritoneal cavity (Heupel et al. 2006). We closed the incision with dissolvable sutures (Ethicon) and did not use anaesthetics during the procedure. We also implanted V16T-5H (165 dB) temperature-recording tags using the same process above into 5 adult female blacktip reef sharks to test the hypothesis that sharks select the study site with the warmest water temperature to increase their core temperature. The range of temperature measurements for these tags was 10 to 40°C, with an accuracy of ±0.5°C (VEMCO 2011). The tagging procedure from capture to release took on average 12 min (Speed et al. 2011). We also recorded species, total length (L_T, cm) and sex. All temperature-recording tags were calibrated using the VEMCO VUE software prior to analysis to ensure there were no discrepancies in data interpretation.

Temporal datasets

We calculated the total number of individuals of all species present at each of the 4 study sites per hour from detections at the acoustic receivers. We considered an individual as 'present' at one of the sites per hour if at least 1 detection was received within that hour. We obtained tide height data from the Government of Western Australia Department of Transport (www.transport.wa.gov.au). Data were recorded hourly at a tide station in Carnarvon (24° 53′ 26″ S, 113° 39′ 26″ E). We estimated tide height for Coral Bay by subtracting 48 min from each datum. Water temperature was recorded by mini-loggers at acoustic receiver stations at 30 min intervals and averaged for hourly periods at each of the 4 sites (Fig. A1). We obtained daily moon illumination data from the US Naval Observatory (www.usno.navy.mil/USNO/astronomical-applications/data-services/frac-moon-ill). We adjusted all datasets to Western Australian Standard Time (UTC +8 h).

Environmental association analysis

We used generalised linear models to determine the relationship between shark distribution (all individuals of all species combined) and environmental variables at each site. Total shark presence/absence h^{-1} at each site was the response variable, while water temperature, tide height, and moon phase were the explanatory variables. We initially measured autocorrelation among the data using correlograms (Burnham & Anderson 2002); however, due to the inherent autocorrelation structure present in our dataset (presence or absence over time), the assumption of temporal independence was violated. We accounted for this autocorrelation by using matched-block sampling with replacement (Carlstein et al. 1998, Politis & White 2004). This method sub-samples and replaces optimum block lengths from the dataset that maintain the autocorrelation structure. We resampled blocks of data randomly with replacement from the original time series and then joined them in a random order to create the uncorrelated bootstrapped sample (Carlstein et al. 1998, Politis & White 2004, Patton et al. 2009). The block bootstrap method is a compromise between preserving some of the dependence structure and corrupting it by assuming the data are independent (Carlstein et al. 1998). We then applied the model-fitting process to 100 bootstrapped samples and used the median and 95% bootstrapped confidence intervals (2.5 and 97.5 percentiles) of the small sample-corrected Akaike's information criterion (Burnham & Anderson 2002) test statistics: AIC_c, ΔAIC_c, $wAIC_c$ and percent deviance explained (%DE) to rank and weight models. We ran models separately for each site rather than including 'site' as part of an interaction term due to the large size of datasets.

Behavioural thermoregulation

To test the hypothesis that adult female blacktip reef sharks actively select the warmest site to raise their body temperature, we examined the relationship between the number of 'presence events' (>1 detection h^{-1}) of each of the 5 individuals with average water temperature h^{-1} at each site. We used a $\log_{10}$ transformation to ensure data were approximately Gaussian and then applied linear mixed-effects models to assess the strength of the relationship between average water temperature and the total number of presence events at each of the 4 sites (Zuur et al. 2009). A bootstrap sub-sampling technique was not necessary to account for temporal autocorrelation because the mixed-effects model can include correlation structure directly. Because of the considerable differences in the number of presence events among locations, we included multiple intercepts within some models. Models were ranked using AIC_c and $wAIC_c$ (Burnham & Anderson 2002).

To assess the extent to which body temperatures of sharks were determined by water temperatures in Coral Bay, we averaged daily water temperature from all 6 mini-loggers and compared these to average daily body temperatures of the 5 sharks tagged with temperature sensors in the mixed-effects models. This should indicate whether shark body temperatures were consistently warmer than the surrounding water temperatures, and whether any bias observed depended on the temperature range. Our prediction here is that at lower ambient temperatures, the difference between shark body and ambient temperatures should be highest such that the animals experience a more stable thermal environment internally. We then calculated the average difference between the combined body temperatures of all 5 blacktip reef sharks and water temperature for each of the 4 sites when sharks were present. If sharks moved into Skeleton Bay to warm their core temperatures, we expected to observe the greatest difference between body and water temperatures at this site. We also determined the difference in body temperature among the 5 adult female blacktip reef sharks while in Skeleton Bay by calculating the mean hourly temperature for each individual. We did all analyses using the software R (R Core Development Team 2009).

Table 1. *Carcharhinus melanopterus*. Adult female blacktip reef sharks (T1 to T5) implanted with acoustic tags and temperature sensors. Note: detections and temperature values are from when sharks were detected in Skeleton Bay only. L_T: total length. Date: dd/mm/yyyy

Date tagged	Tag ID	Sensor ID	L_T (cm)	Temperature detections	Average body temperature (°C)
19/11/2008	14501	T1	131	560	26.17 (±0.11)
24/11/2008	14502	T2	144	1491	26.98 (±0.06)
20/11/2008	14503	T3	142	1353	26.88 (±0.06)
16/11/2008	14504	T4	134	268	25.92 (±0.15)
22/11/2008	14505	T5	141	1278	26.76 (±0.07)

RESULTS

Shark tagging

We tagged all 5 adult female blacktip reef sharks fitted with body temperature sensor tags during November 2008; all individuals were between 131 and 144 cm L_T (Table 1), which we considered to be sexually mature on the basis of size (i.e. size at maturity L_T > 95–110 cm) (Last & Stevens 2009) and the presence of healed mating scars on pectoral fins and the dorsal surface. One of these sharks also had a distended abdomen, which suggests it was gravid.

Environmental association analysis

Prior to running the generalised linear models to test for influences of shark presence with environmental variables, we determined that the optimum block-size length to be sub-sampled prior to bootstrapping for each site ranged between 225 and 243 h. Some of the temporal autocorrelation was maintained within each block sampled for the response and explanatory variables (Fig. A2). The model that provided the top-ranked ($wAIC_c \geq 0.99$ at all sites) fit for all sites was one that included water temperature as a covariate and season as a factor (Table 2), and explained most of the deviance (Skeleton Bay = 17.6%, Asho's Gap = 3.8%, Point Maud = 33.9%, and Channel = 54.6%). Furthermore, examination of the coefficients showed that the presence of individuals increased in summer at Skeleton Bay (0.8 ± 0.02 SE), Asho's Gap (0.2 ± 0.04), and at Point Maud (0.5 ± 0.03). We were unable to estimate coefficients for the Channel due to a lack of water temperature records during summer (Dec–Feb 2008/09) (Fig. A1). The models that included only tide height and moon illumination

Table 2. Results of generalised linear models with bootstrap sampling for hourly presence events (all shark species combined) with environmental variables. Model comparison was based on Akaike's information criterion corrected for small samples (AIC_c). Best model is in **bold**. For each of the models contrasted: number of parameters (k), maximum log-likelihood (LL), AIC_c, AIC_c weight ($w\text{AIC}_c$), and the % deviation explained (%DE)

Site	Model	k	LL	AIC_c	$w\text{AIC}_c$	%DE
Skeleton Bay	~1 (Intercept only)	1	−20 006.65	40 015.29	<0.0001	0.00
	~Temp	5	−17 446.40	34 896.80	<0.0001	12.80
	~Tide	5	−19 826.76	39 657.52	<0.0001	0.90
	~Moon	5	−19 971.93	39 947.86	<0.0001	0.17
	~Temp + factor (Season)	**6**	**−16 490.87**	**32 991.75**	**>0.9999**	**17.57**
	~Tide + factor (Season)	6	−16 984.14	33 978.28	<0.0001	15.11
	~Moon + factor (Season)	6	−17 096.54	34 203.08	<0.0001	14.55
Channel	~1 (Intercept only)	1	−15 243.40	30 488.79	<0.0001	0.00
	~Temp	5	−8503.67	17 011.34	<0.0001	44.21
	~Tide	5	−15 140.22	30 284.44	<0.0001	0.68
	~Moon	5	−15 242.60	30 489.20	<0.0001	0.01
	~Temp + factor (Season)	**6**	**−6916.86**	**13 841.72**	**>0.9999**	**54.62**
	~Tide + factor (Season)	6	−12 901.39	25 812.78	<0.0001	15.36
	~Moon + factor (Season)	6	−12 876.16	25 762.33	<0.0001	15.53
Asho's Gap	~1 (Intercept only)	1	−8438.86	16 879.73	<0.0001	0.00
	~Temp	5	−8173.45	16 350.91	<0.0001	3.15
	~Tide	5	−8376.49	16 756.97	<0.0001	0.74
	~Moon	5	−8436.67	16 877.34	<0.0001	0.03
	~Temp +f actor (Season)	**6**	**−8121.76**	**16 253.53**	**>0.9999**	**3.76**
	~Tide + factor (Season)	6	−8150.55	16 311.10	<0.0001	3.42
	~Moon + factor (Season)	6	−8147.21	16 304.43	<0.0001	3.46
Point Maud	~1 (Intercept only)	1	−12 562.55	25 127.09	<0.0001	0.00
	~Temp	5	−8671.16	17 346.33	<0.0001	30.98
	~Tide	5	−12 428.59	24 861.17	<0.0001	1.07
	~Moon	5	−12 488.47	24 980.93	<0.0001	0.59
	~Temp + factor (Season)	**6**	**−8297.18**	**16 604.35**	**>0.9999**	**33.95**
	~Tide + factor (Season)	6	−10 917.56	21 845.12	<0.0001	13.09
	~Moon + factor (Season)	6	−10 878.83	21 767.67	<0.0001	13.40

were not ranked highly for any of the 4 sites, which suggests that tide height and moon illumination have much less of an influence on shark presence in Coral Bay than water temperature.

Overall, total hourly presence events (all individuals of all species grouped) were greatest at Skeleton Bay and peaked at 14:00 h (Fig. 2A). This coincided with a drop in total hourly presence events at the Channel site. There were also fewer presence events during daytime hours at Point Maud than at night (Fig. 2B). There was a bimodal peak in tag detections at Asho's Gap at 08:00 and again at 13:00 h (Fig. 2C), which consisted predominantly in detections of blacktip reef sharks and grey reef sharks. In general, blacktip reef sharks and grey reef sharks were present regularly at all 4 sites; however, whitetip reef sharks were only present regularly at Point Maud and the Channel sites, while sicklefin lemon sharks were mostly present at Skeleton Bay.

Behavioural thermoregulation

Most (58%) presence events for the 5 blacktip reef sharks were at Skeleton Bay, when compared to the other 3 sites (Fig. 3). Furthermore, individuals were most frequently present at Skeleton Bay between 11:00 and 15:00 h throughout the study (Fig. 3A). Mean water temperature at Skeleton Bay followed a similar trend to the presence events and peaked between 14:00 and 16:00 h. Although sharks were much less frequently present at the other 3 sites, weak patterns were still evident. Troughs in shark presence occurred between 12:00 and 16:00 h at both the Channel and Point Maud sites, whereas we observed a distinct peak in presence at Asho's Gap at 14:00 h (Fig. 3B–D). The model that provided the top-ranked fit between presence events and average water temperature was the multiple-intercept model at Skeleton Bay ($w\text{AIC}_c = 0.31$, %DE = 41.4) (Table 3). There was also evidence for reasonable fit of the

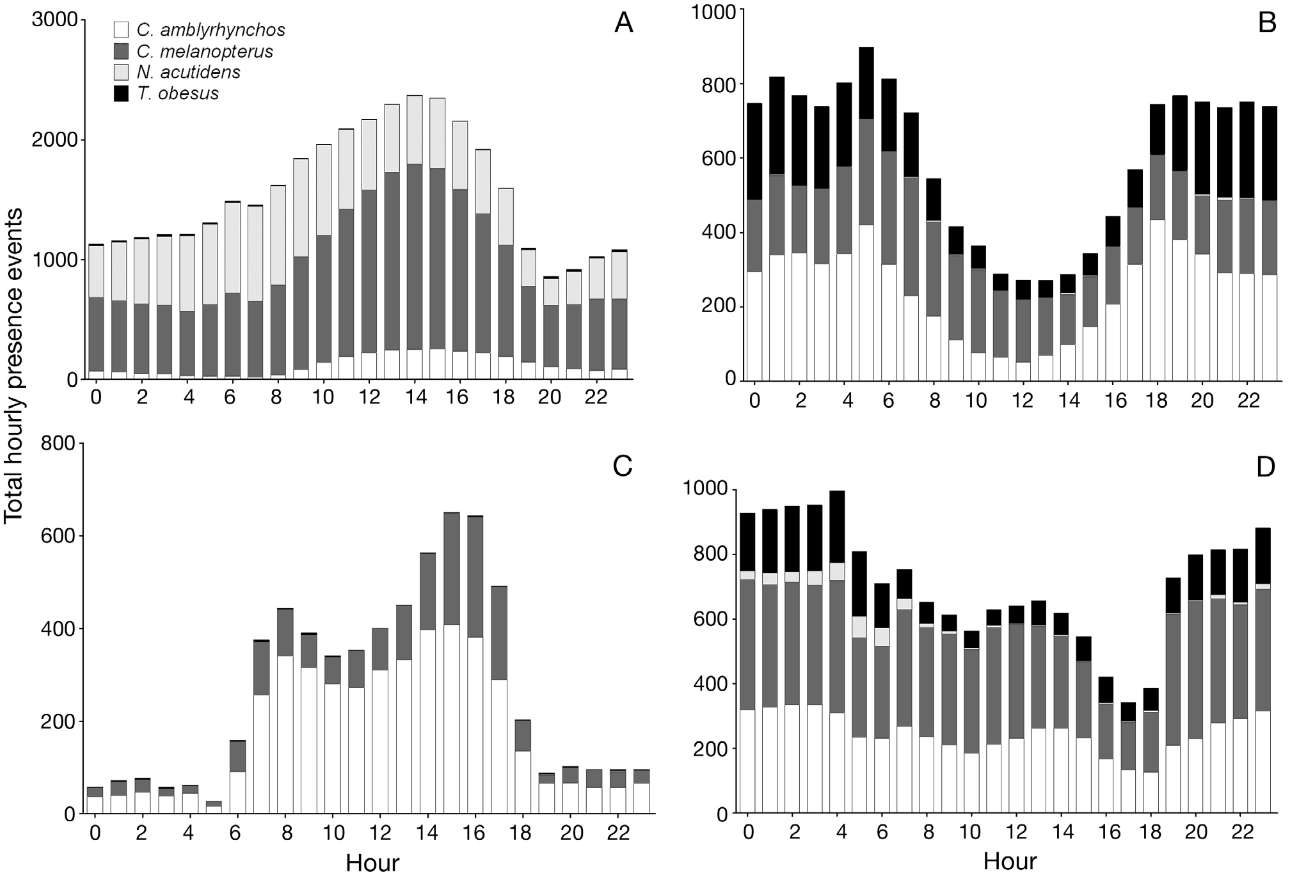

Fig. 2. *Carcharhinus melanopterus*, *C. amblyrhynchos*, *Negaprion acutidens* and *Triaenodon obesus*. Total hourly presence events (>1 detection h^{-1}) of all reef sharks tagged with acoustic pingers at (A) Skeleton Bay, (B) Channel, (C) Asho's Gap, and (D) Point Maud. Note *y*-axis scale differences

single-intercept model (Presence ~ Temperature + Site) ($wAIC_c = 0.22$, %DE = 38.4).

The average body temperatures for the 5 blacktip reef sharks while in Skeleton Bay ranged between 25.92 (±0.15) and 26.98°C (±0.06). The highest body temperature recorded in Skeleton Bay was 32°C, while the lowest was 20.6°C. Average hourly body temperatures while in Skeleton Bay peaked between 16:00 and 18:00 h (Fig. 4). Shark T4 consistently had the lowest mean body temperature throughout the 24 h cycle; however, it also had the fewest number of detections overall (268). Similarly, shark T1 also had relatively low mean body temperatures, particularly outside of peak temperatures (14:00 to 18:00 h) and also had relatively few detections (560) compared to sharks T2 (1491), T3 (1353), and T5 (1278) (Table 1). The mean body temperatures of Sharks T2, T3, and T5 were similar throughout the 24 h cycle.

We were able to compare body temperatures of the 5 tagged sharks with average water temperature in Coral Bay (data from all 6 mini-loggers combined) from 19 November 2008 to 25 February 2010 (463 d). The slope and intercept model ($wAIC_c = 0.87$, %DE = 12.93) was ranked above the zero-intercept model ($wAIC_c = 0.13$, %DE = 13.73) (Table 4). Based on model coefficients, body temperature of these sharks was 1.3°C warmer on average than water temperature (SE ±0.57). There was also no change in this pattern with increasing water temperature (slope = 0.99, ±0.02), indicating that body temperature was always consistently and invariably warmer than average water temperature.

The greatest difference in water and body temperatures was observed at Skeleton Bay, where the average body temperature was >1°C (±0.02) warmer than average water temperature (Fig. 5). There was also a >0.5°C (±0.01) difference at the other inshore site at Point Maud, and smaller differences at sites farther out in the lagoon at Asho's Gap (0.27 ± 0.03°C) and Channel (0.03 ± 0.01°C) sites. The greatest positive difference was recorded for shark T4 on 26 September 2009 in Skeleton Bay, where the body temperature was >6°C warmer than the water temperature.

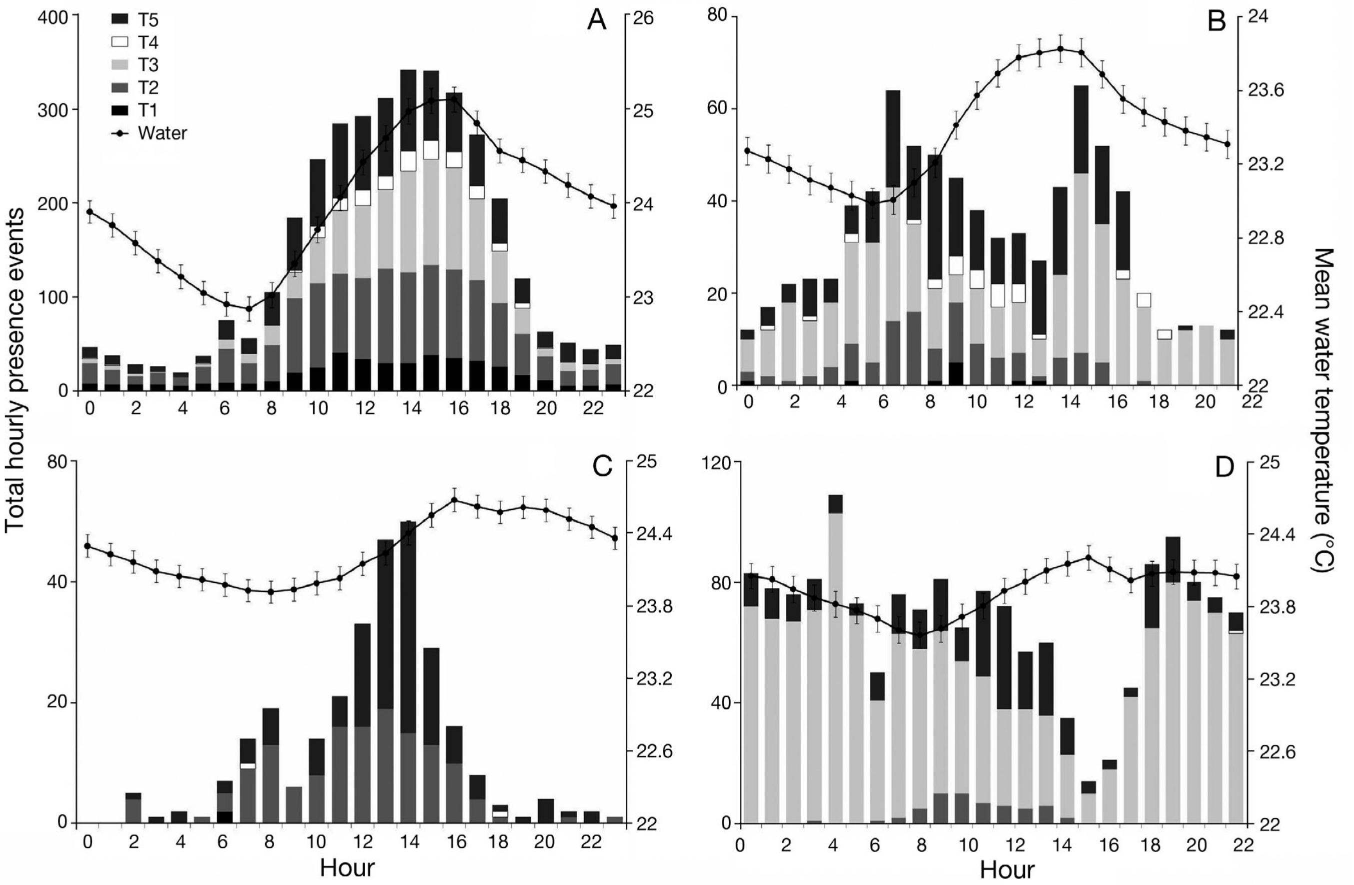

Fig. 3. *Carcharhinus melanopterus*. Total hourly presence events (>1 detection h^{-1}) of 5 female blacktip reef sharks (T1 to T5) tagged with acoustic pingers and temperature sensors, compared to average (±SE) water temperature at (A) Skeleton Bay, (B) Channel, (C) Asho's Gap, and (D) Point Maud. Note *y*-axis scale differences

Table 3. Results of the relationship between the presence of blacktip reef sharks *Carcharhinus melanopterus* and water temperature at each study site based on general linear mixed-effects model comparison based on Akaike's information criterion corrected for small samples (AIC_c). All models include the random effect 'Individual'. Best model is in **bold**. For each of the models contrasted: maximum log-likelihood (LL), AIC_c, AIC_c weight ($wAIC_c$), and the % deviation explained (%DE)

Model	df	LL	AIC_c	$wAIC_c$	%DE
Intercept-only (Presence ~ 1)	4	−44.93	97.85	0.00	0.00
Slope-only (Presence ~ Temp)	5	−40.71	91.42	0.00	9.38
Site only (Presence ~ Site)	7	−30.56	75.12	0.03	31.98
Own intercept (Presence ~ Temp + Site)	8	−27.66	71.32	0.22	38.43
Full model (Presence ~ Temp + Site + Temp : Site)	11	−26.16	74.32	0.05	41.77
Multiple intercept models (Presence ~ Temp + Intercepts + Temp × Site)					
Skeleton Bay	**9**	**−26.32**	**70.63**	**0.31**	**41.42**
Point Maud	9	−27.11	72.21	0.14	39.67
Asho's Gap	9	−27.53	73.06	0.09	38.72
Channel	9	−27.08	72.17	0.15	39.71

DISCUSSION

Understanding how abiotic and biotic gradients influence distribution and movement of elasmobranchs is a necessary precursor for predicting how they might respond to rising water temperature and altered salinity regimes associated with climate change (Field et al. 2009, Chin et al. 2010), thermal discharges from coastal electrical plants (Vaudo & Lowe 2006), ocean farming (Papastamatiou et al.

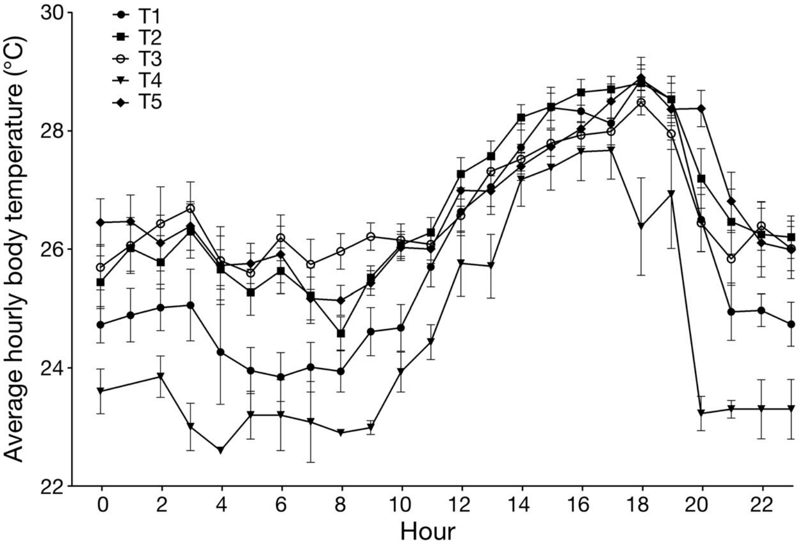

Fig. 4. *Carcharhinus melanopterus*. Average (±SE) hourly body temperatures for 5 female blacktip reef sharks (tags: T1 to T5) implanted with temperature sensors at Skeleton Bay

Table 4. Comparison results of mean water temperature and mean shark body temperature contrasted using general linear mixed-effects models. For each of the models contrasted: number of parameters (*k*), maximum log-likelihood (LL), Akaike's information criterion corrected for small samples AIC_c, AIC_c weight ($wAIC_c$), and the % deviation explained (%DE)

Model	*k*	LL	AIC_c	$wAIC_c$	%DE
slope and intercept ($y \sim x$)	5	−1897.88	3805.77	0.87	12.93
slope and zero-intercept ($y \sim 0 + x$)	4	−1900.79	3809.58	0.13	13.73

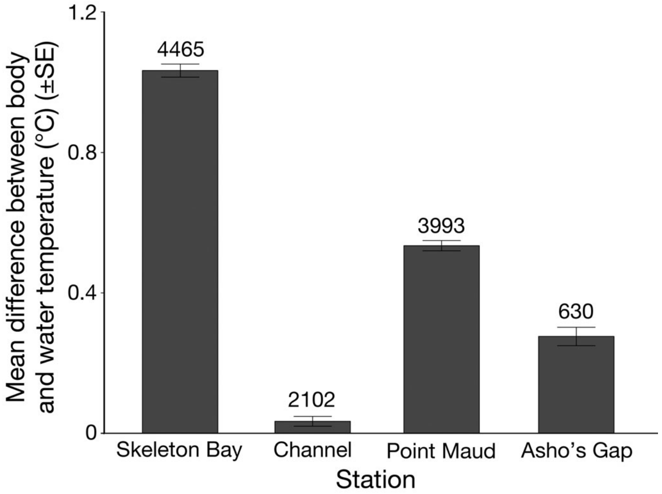

Fig. 5. *Carcharhinus melanopterus*. Mean (±SE) difference between average water temperature at each site and average body temperature of 5 female blacktip reef sharks (all data combined). Numbers above columns: counts of temperature recordings

2010) and food provisioning by ecotourism operators (Laroche et al. 2007, Semeniuk & Rothley 2008, Clua et al. 2010, Fitzpatrick et al. 2011). Previous studies of movements and habitat selection of coastal sharks in relation to environmental conditions have focussed on water temperature, and concluded that it has a major influence on distribution (Morrissey & Gruber 1993, Economakis & Lobel 1998, Hight & Lowe 2007, DiGirolamo et al. 2012). However, few studies have attempted to study fine-scale (<10 km^2) patterns.

At all 4 of our study sites, shark presence was strongly correlated with water temperature and season. This result, when combined with a predominance of individuals during the middle of the day at Skeleton Bay and an increase in the number of individuals during summer, provides further support for shark movement being largely driven by water temperature. This corroborates previous findings of shark attendance at Skeleton Bay, where blacktip reef sharks and grey reef shark adults displayed diel cycles of attendance, being most frequent during summer between 13:00 to 14:00 h (Speed et al. 2011), and a similar peak in reef attendance patterns for some grey reef sharks at the Rowley Shoals, atoll reefs in the far north-west of Australia (Field et al. 2011). We found that these 2 species were more frequently present at the Channel site during periods of darkness than at Skeleton Bay. This supports the daytime refuge hypothesis, where sharks disperse farther out into the lagoon at night, possibly to forage (Klimley & Nelson 1984, McKibben & Nelson 1986, Garla et al. 2006, Papastamatiou et al. 2009, Speed et al. 2011). However, bimodal daytime peaks of attendance at the reef shark cleaning station Asho's Gap are perhaps more closely associated with diurnal patterns in cleaning behaviour (O'Shea et al. 2010, Oliver et al. 2011) than changes in water temperature.

Inshore daytime aggregations and habitat selection associated with raised water temperature have been observed in other species of elasmobranchs such as leopard shark *Triakis semifasciata*, grey reef sharks (Economakis & Lobel 1998, Hight & Lowe 2007), juvenile *Negaprion brevirostris* (DiGirolamo et al. 2012), as well as bat rays *Myliobatis californica* (Matern et al. 2000). Our findings are similar to those of Hight & Lowe (2007) and DiGirolamo et al. (2012) who found that the core temperatures of sharks reached their peak during the afternoon/early evening and that these animals showed site fidelity to thermal refuges during the day before dispersing at night. Hight & Lowe (2007) hypothesised that *T. semifasciata* might have been aggregating to increase core body temperature for reproductive reasons, which was also suggested for aggregations of adult female grey reef sharks (Economakis & Lobel 1998). Another potential explanation for this behaviour is that individuals make use of warmer waters to increase their metabolic rate while feeding and then retreat to cooler water to slow digestion and evacuation rates, which might aid in nutrient uptake efficiency (Matern et al. 2000, Carlson et al. 2004, Sims et al. 2006, Di Santo & Bennett 2011, DiGirolamo et al. 2012). Evidence to support both of these hypotheses was provided by a thermal preference experiment on the Atlantic stingray *Dasyatis sabina*, where pregnant and unfed individuals selected warmer temperatures than non-pregnant and fed individuals (Wallman & Bennett 2006). We did not observe any daytime foraging in blacktip reef sharks, although we have noted courtship behaviour and the presence of pregnant individuals in Skeleton Bay (Speed et al. 2011). Therefore, the most plausible explanation is that female blacktip reef sharks use the increased water temperature of this site to aid in reproduction, possibly by increasing embryonic development. However, male blacktip reef sharks and other species and size classes are also common in this site, which suggests that higher temperatures might provide additional benefits for digestion or growth. For example, movement into warmer water after feeding has been hypothesised to elevate evacuation rates for species that feed frequently ('hunt cool – rest warm') (Di Santo & Bennett 2011), and has been suggested previously for captive *Carcharhinus melanopterus* (Papastamatiou et al. 2007).

The body temperatures of female blacktip reef sharks while in Skeleton Bay were highest during the afternoon between 16:00 and 18:00 h, which coincided with the maximum average daily water temperature at this site (16:00 h). Furthermore, these individuals were most often present at this time and consistently had body temperatures >1°C warmer than the average water temperature. Matern et al. (2000) also observed this pattern in bat rays, where the body temperature of rays in shallow water (<1 m depth) were always warmer than at other sites, particularly during the afternoon. They suggested that this was due to the influence of solar radiation, as was also suggested for raised temperatures of leopard sharks when in shallow areas (Hight & Lowe 2007). Furthermore, leopard sharks can darken their skin colour, which might serve to increase heat uptake and in doing so raise metabolic rates (Hight & Lowe 2007). Solar warming might have had the greatest influence on shark body temperature at Skeleton Bay due to sharks aggregating in the shallow water of the bay during midday. Unfortunately, we were unable to monitor water temperature with mini-loggers close to shore at the southern end of Skeleton Bay due to the water level often being <0.5 m, or even completely dry during spring low tides. However, visual censuses identified that aggregations were common in this area of the site (Speed et al. 2011), so it is possible that water temperature and shark body temperatures are even higher when individuals aggregate in shallow water outside of detection range of receivers/mini-loggers in Skeleton Bay.

Tide height had little influence on the presence of reef sharks at any site in our study. In contrast, tide can have an important influence on the movement of other species (Medved & Marshall 1983, Ackerman et al. 2000, Dewar et al. 2008, Campos et al. 2009, Carlisle & Starr 2009, 2010), which seems to be related mostly to foraging (but see O'Shea et al. 2010). Because reef sharks are primarily piscivores (Cortés 1999) and we had no evidence of foraging within Skeleton Bay (Speed et al. 2011), we did not expect to see an effect of tide height on the presence of sharks at this site, where foraging opportunities on benthic invertebrates would be increased with rising tide height. Our results confirm this hypothesis, and suggest that shark aggregations in Skeleton Bay are not influenced by tide height. Furthermore, our study sites were all within the Coral Bay lagoon, and therefore largely protected from prevailing currents by the reef, which is exposed on spring low tides. The daily tidal range of Coral Bay is small (~1.5 m), and therefore tide height appears to have minimal influence on shark movement patterns, although spring low tides preclude sharks from entering the shallowest areas within Skeleton Bay. Moon illumination also had minimal influence on the presence of reef sharks at Skeleton Bay.

CONCLUSION

We found evidence that adult female blacktip reef sharks visit Skeleton Bay during the warmest parts of the day and season and in doing so elevate their body temperatures. This provides support for behavioural thermoregulation in this species, whereby individuals are able to increase their metabolic rates through thermotaxis, possibly for reproductive advantages. However, the extent to which metabolic rates changes with water temperature (Q_{10}) is still unknown for this species. Future research should include a variety of species, over both sexes and differing size classes, to provide a better overview of how changes in water temperature influence the physiology of reef sharks. Furthermore, testing progesterone concentrations in females to assess reproductive status would assist in the classification of gravid individuals, which might behave differently in response to ambient temperature fluctuations.

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Appendix 1. Additional data

Table A1. Acoustic receiver and water temperature mini-logger information for Coral Bay study sites. NA: not applicable

Station	Site	Latitude (°S)	Longitude (°E)	Depth (m)	Receiver deployment (dd/mm/yyyy)	Total detections	Mini-logger	Mini-logger deployment
Asho's Gap	Asho's Gap	23.13587	113.7537	9.5	21/01/2008	36 682	Yes	07/04/2008
Maud VR2a	Channel	23.12282	113.75152	3	21/01/2008	56 220	No	NA
Maud VR2b	Channel	23.1246	113.7491	3	21/01/2008	16 214	Yes	07/04/2008
Point Maud	Point Maud	23.12137	113.75722	7	18/11/2007	77 653	Yes	07/04/2008
Skeleton South	Skeleton Bay	23.13008	113.76998	3	18/11/2007	129 937	Yes	26/08/2008
Skeleton Inner	Skeleton Bay	23.12693	113.76896	3	18/11/2007	69 597	Yes	26/08/2008
Skeleton Mid 1	Skeleton Bay	23.12863	113.76971	3	18/11/2007	92 210	Yes	26/08/2008
Skeleton Mid 2	Skeleton Bay	23.12733	113.7688	3	18/11/2007	51 027	No	NA
Skeleton North	Skeleton Bay	23.12588	113.76782	3	18/11/2007	97 434	No	NA

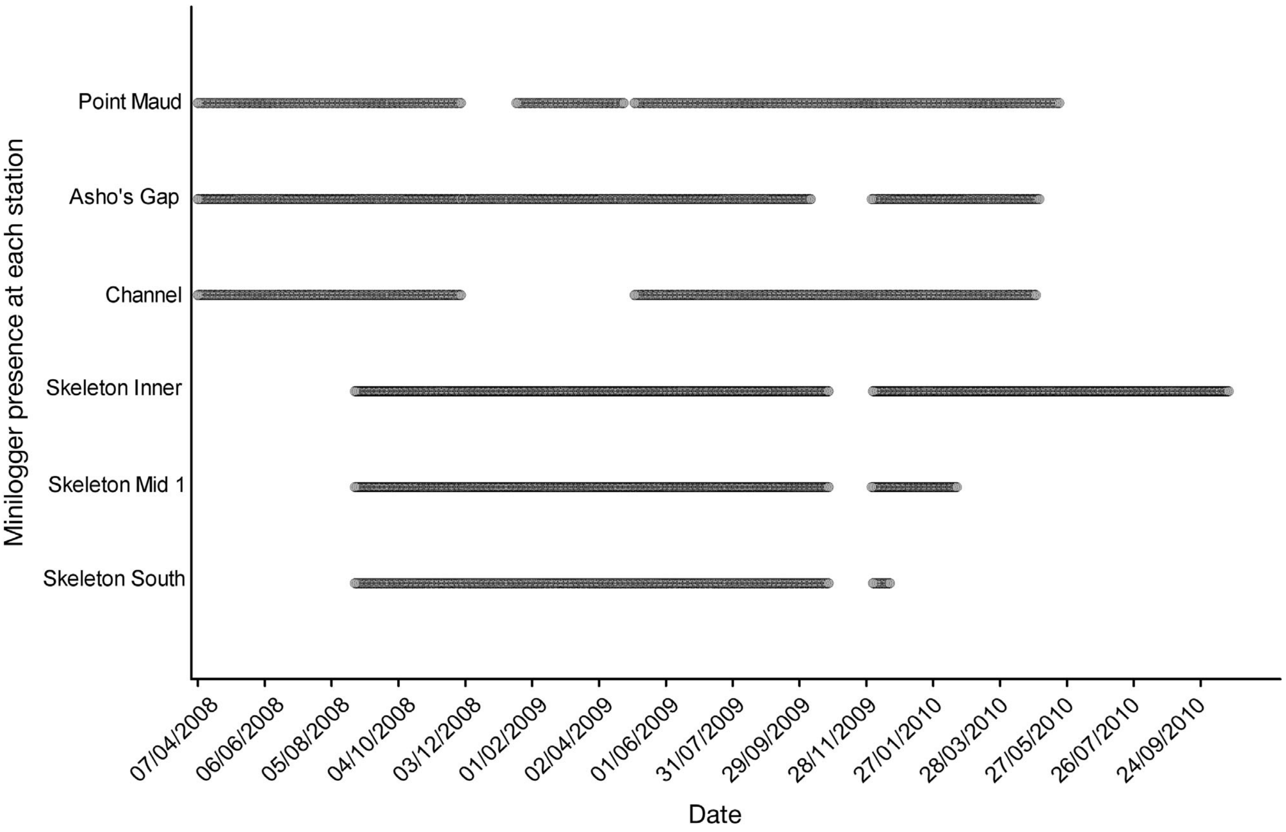

Fig. A1. Presence of water temperature mini-loggers at acoustic receivers in Coral Bay throughout the study. Date: (dd/mm/yyyy)

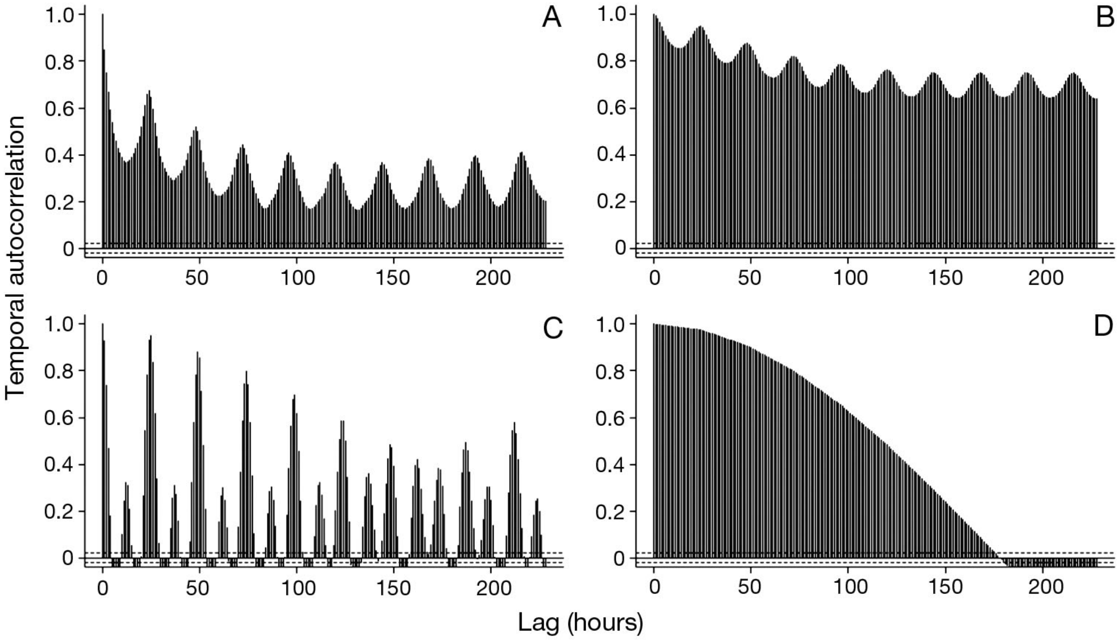

Fig. A2. Temporal autocorrelation present within subsampled blocks from the Skeleton Bay dataset. (A) Number of individuals (response variable), (B) water temperature, (C) tide height, and (D) moon illumination

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