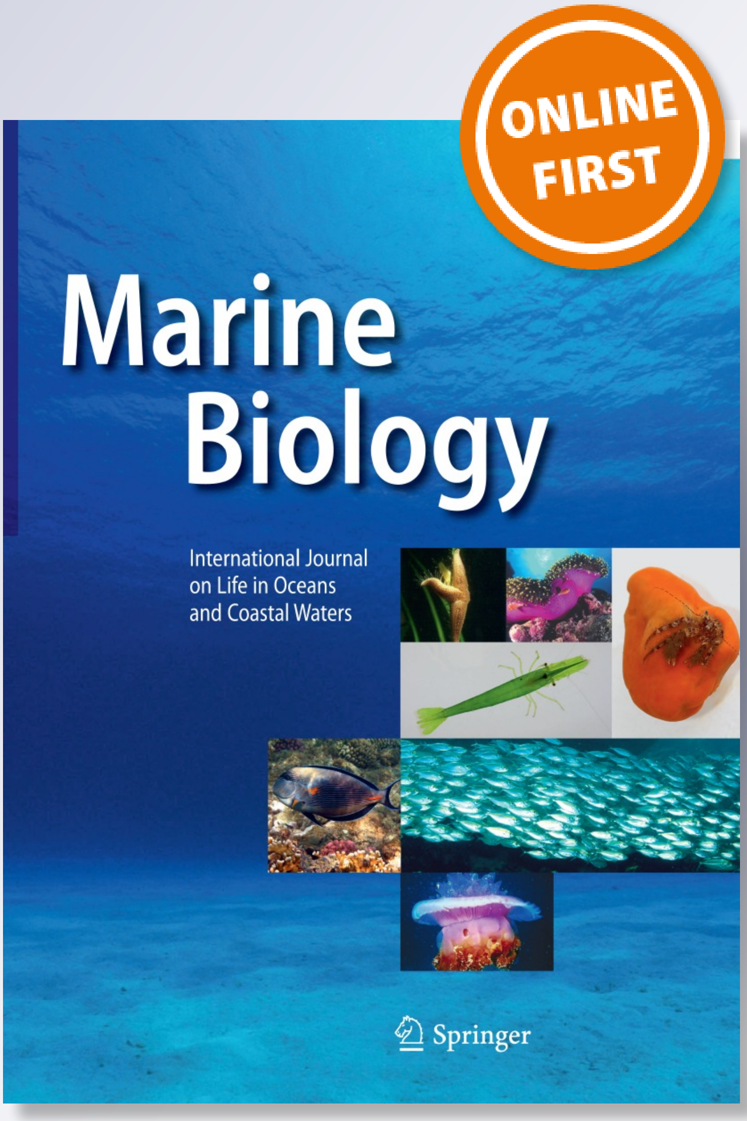
*Seasonal changes in movements and habitat preferences of the scalloped hammerhead shark (*Sphyrna lewini*) while refuging near an oceanic island*

James T. Ketchum, Alex Hearn, A. Peter Klimley, Eduardo Espinoza, César Peñaherrera & John L. Largier

Marine Biology
International Journal on Life in Oceans
and Coastal Waters

ISSN 0025-3162

Mar Biol
DOI 10.1007/s00227-013-2375-5



Springer

Mar Biol
DOI 10.1007/s00227-013-2375-5

ORIGINAL PAPER

Seasonal changes in movements and habitat preferences of the scalloped hammerhead shark (*Sphyrna lewini*) while refuging near an oceanic island

James T. Ketchum · Alex Hearn · A. Peter Klimley ·
Eduardo Espinoza · César Peñaherrera ·
John L. Largier

Received: 25 May 2013 / Accepted: 18 December 2013

Abstract Movements and habitat preferences of sharks relative to a central location are widely documented for many species; however, the reasons for such behaviors are currently unknown. Do movements vary spatially or temporally or between individuals? Do sharks have seasonal habitat and environmental preferences or simply perform movements at random at any time of the year? To help understand requirements for the designation of critical habitats for an endangered top predator and to develop zoning and management plans for key habitats, we examined vertical and horizontal movements, and determined habitat and environmental preferences of scalloped hammerhead sharks (*Sphyrna lewini*). We tracked seven hammerheads for 19–96 h at Wolf Island (1.38ºN, 91.82ºW) between 2007 and 2009 using ultrasonic transmitters with depth and temperature sensors, and we profiled temperature through the water column. Movements of individual hammerheads fell in two classes: constrained (remaining near the island) and dispersive (moving offshore to pelagic environments). The central activity space or kernel off the southeast side of Wolf Island was small and common to most, but the area varied among individuals (mean ± SE 0.25 ± 0.2 km^2), not exceeding 0.6 km^2 for any of the sharks, and not changing significantly between seasons. In general, hammerheads showed preference for the up-current habitat on the eastern side of Wolf Island in both the warm and cold seasons. However, the depth of sharks varied with season, apparently in response to seasonal changes in the vertical structure of temperature. Hammerheads performed frequent vertical excursions above the thermocline during offshore movements and, in general, were observed to prefer temperatures of 23–26 °C found above the thermocline. At times, though individuals moved into the thermocline and made brief dives below it. Our results provided evidence that hammerheads (1) are highly selective of location (i.e., habitat on up-current side of island) and depth (i.e., top of the thermocline) while refuging, where they may carry out essential activities such as cleaning and thermoregulation, and (2) perform exploratory vertical movements by diving the width of the mixed layer and occasionally diving below the thermocline while moving offshore, most likely for foraging.

Introduction

The rhythmical dispersal of groups of animals from a fixed point in space and their return to the same location

---

Communicated by J. D. R. Houghton.

J. T. Ketchum · A. Hearn · A. P. Klimley
Biotelemetry Laboratory, Department of Wildlife, Fish, and Conservation Biology, University of California, Davis, CA, USA

Present Address:
J. T. Ketchum (✉)
Centro de Investigaciones Biológicas del Noroeste and Pelagios Kakunjá, La Paz, BCS, Mexico
e-mail: jtketchum@ucdavis.edu

A. Hearn · C. Peñaherrera
Department of Marine Research and Conservation, Charles Darwin Foundation, Galapagos, Ecuador

E. Espinoza
Galapagos National Park, Santa Cruz Island, Galápagos, Ecuador

Present Address:
C. Peñaherrera
Institute for Marine and Antarctic Studies, University of Tasmania, Hobart, TAS, Australia

J. L. Largier
Bodega Marine Laboratory, University of California Davis, Bodega Bay, CA, USA

is known as central refuging (Hamilton and Watt 1970). Certain shark species stay at specific areas when not foraging forming daytime aggregations, such as the whitetip reef (*Triaenodon obesus*, Nelson and Johnson 1980), juvenile scalloped hammerhead (*Sphyrna lewini*, Holland et al. 1993), juvenile lemon (*Negaprion brevirostris*, Morrissey and Gruber 1993), and gray reef (*Carcharhinus amblyrhynchos*, Economakis and Lobel 1998) sharks. Such aggregation in core areas and dispersal into the pelagic environment represent refuging as described for scalloped hammerhead sharks, *Sphyrna lewini* (Klimley and Nelson 1984). Recent observations in the Galapagos Islands may also be suggestive of such behavior in hammerheads (Hearn et al. 2010). A number of hypotheses have been attempted to explain central refuging in sharks: to minimize energy expenditure (Klimley and Nelson 1984), predator avoidance (Morrissey and Gruber 1993), increased rate of embryonic development (Economakis and Lobel 1998), and male avoidance (Sims et al. 2001). Nevertheless, the presence and function of this behavior in predatory sharks are not well known (Sims et al. 2005), and few studies have analyzed its spatial extent and temporal effects. Spatial and temporal changes in this behavior may be occurring considering that spatial use in elasmobranchs can change daily (Cartamil et al. 2003), seasonally (Heupel et al. 2004), and ontogenetically (Grubbs 2010). Recent advances in telemetry technologies may help in understanding the spatial and temporal variability of refuging.

There is evidence of a wide range of variation in movements and space utilization of sharks. The pacific angel shark (*Squatina californica*) swims within a small area most of the day and moves over a range of 9 km at night (Standora and Nelson 1977), whereas the blue shark (*Prionace glauca*) may move throughout the whole north Atlantic gyre (Casey and Kohler 1990). Therefore, defining activity spaces or utilization distributions (UD) is important to establish the spatial extent of critical habitats and refuging grounds. Habitat preference in sharks, on the other hand, may be determined by biotic and physical factors that take place at different spatial and temporal scales (Simpfendorfer and Heupel 2012), and may be more difficult to understand due to behavioral changes associated with the variability of biophysical factors. Hence, it is essential to unravel habitat preference, horizontally and vertically, at different spatial and temporal scales, and in relation to environmental factors. Moreover, assessing habitat preference is important to predict behavior (Queiroz et al. 2012), effects of habitat changes (Arthur et al. 1996), and to determine biological requirements to support the protection of critical areas for a species (Arthur et al. 1996).

Scalloped hammerheads (*Sphyrna lewini*) inhabit waters near volcanic islands, seamounts, and lava flows in the eastern tropical Pacific. In particular, large schools are known to occur at Darwin and Wolf Islands (Hearn et al. 2010) in the northern region of the Galapagos Marine Reserve (GMR). Wolf Island is at the top of a wave-eroded volcano in the process of subsidence below the ocean surface and located very near a meridian (92°W) where the temperature and density gradients are greatest (Pak and Zaneveld 1974). The influx of up-welled waters from the Panama Bight into the northern sector of the GMR causes phytoplankton enrichment during the warm season (Palacios 2004), and possibly abundance of prey that may attract large aggregations of hammerheads to this part of the archipelago. Recent studies in the Galapagos Islands have shown that hammerheads have preference for very specific sites or “hotspots” located on the up-current side of Darwin and Wolf Islands, where they form large schools (Hearn et al. 2010). But still, little is known about the movements and habitat preferences of hammerheads in relation to such sites. This information is important to help understand requirements for the designation of critical habitats for an endangered top predator, as well as to develop zoning and management plans for key habitats within a marine-protected area. In this study, we tested (1) whether hammerhead movements vary seasonally or spatially or due to individual specialization and (2) whether hammerheads have seasonal habitat and environmental preferences about a “central location.” Hence, we examined vertical and horizontal movements of scalloped hammerheads, and determined habitat and environmental preferences near an oceanic island (Wolf Island).

Materials and methods

Study site

The Galapagos Marine Reserve (GMR) is one of the largest marine-protected areas in the world covering an area of 138,000 km^2 in the eastern tropical Pacific (Fig. 1a). The Galapagos Archipelago is composed of 13 volcanic oceanic islands and over 100 emergent rocks and islets located astride the equator and 1,000 km west from the coast of Ecuador (Snell et al. 1996). The oceanographic setting of the Galapagos Islands is of a highly dynamic nature due to the influence of many currents that converge at the archipelago (Houvenaghel 1984) and the proximity of the equatorial front (EF; Palacios 2004). The EF is the boundary of two major water masses: the Tropical Surface Waters (TSW) and the Equatorial Surface Waters (ESW). The former is warm, nutrient deficient or oligotrophic, and low salinity to the north of the EF, and the latter is cool, nutrient-enriched or eutrophic, low chlorophyll, and high salinity to the south of the EF (Palacios 2004; Sweet et al. 2007). The EF remains just north of Darwin and Wolf Islands during the coolest months, particularly in September (Palacios

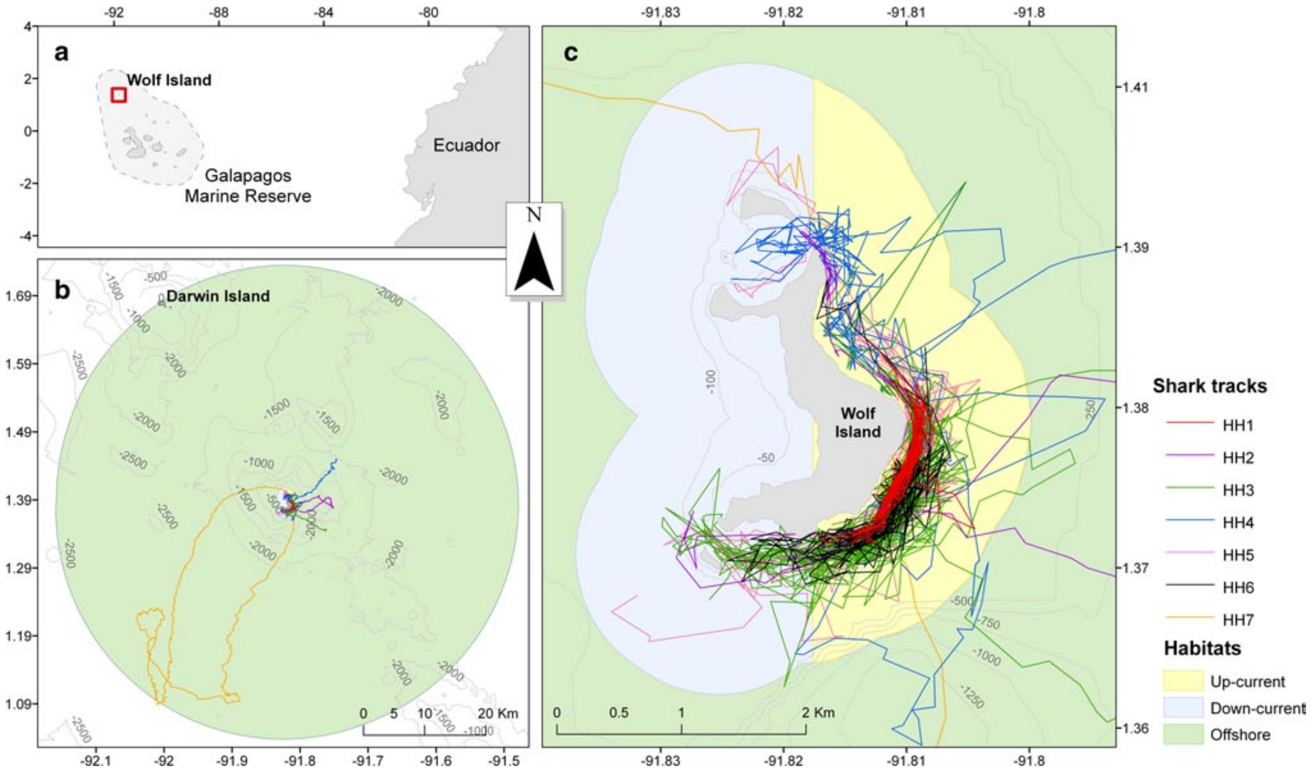


Fig. 1 **a** Location of study site (*red quad*) and Galapagos Marine Reserve (GMR boundary *dashed* and area shaded in *gray*), **b** tracks of hammerhead sharks, bathymetry, and offshore habitat, and **c** tracks of hammerhead sharks, up-current, down-current, and offshore habitats

2004), and moves south of these islands during the warmest months, especially March (Palacios 2004). Wolf Island is located in the north of the archipelago (Fig. 1a), 36 km from the nearest island (Darwin), where the influence of the EF is strongest. Sea surface temperature is higher, and salinity is lower than in the central part of the archipelago (Palacios 2004), over 100 km southward. The northern islands (Darwin and Wolf) lie at the northern edge of the EF, where TSW predominate (Sweet et al. 2007).

Tracking of sharks

Seven scalloped hammerhead sharks were fitted with external ultrasonic transmitters (120 mm long, 22 mm diameter, and 35 g weight in water; V22-TP-5XS-EP, Vemco, Ltd.) by free divers using pole spears to affix a stainless steel dart to the dorsal musculature of the shark with a tether attaching the dart to the tag. All sharks were tagged close to shore at different locations on the eastern side of Wolf Island within a radius of 1 km. Four sharks were tracked in the warm season (December–June) and three in the cold season (July–November). The transmitters were equipped with temperature and pressure sensors that transmit data at 46–50 kHz every ~3,000 ms (ms) and had a nominal life span of 10 days. We carried out shipboard tracking from a skiff followed by a larger "mother-ship" when the sharks moved away from the island more than 3–4 km, particularly at night. The skiff was outfitted with a VH110 directional hydrophone mounted on the side of the hull and a VR100 receiver to detect the data transmitted from each shark. The receiver recorded depth, temperature, and signal strength (dB) from the transmitter, and lat-long of the boat with a GPS. During each track, a dual-frequency sonar (LMS480-DF, 50/200 kHz, Lowrance, Inc.) recorded the bathymetry, sea surface temperature, speed, and location with a GPS. Additionally, characteristics of the water column (temperature and conductivity) were measured with a CTD (SBE 19plus or SBE 37 M, SeaBird, Inc.), which was lowered every hour to the current depth of the shark. The skiff was positioned as close as possible to the animals to mimic their actual movement by doing the following: (1) setting the gain of the receiver at the lowest level of 0–6 dB, (2) keeping the incoming signal strength at the highest possible level of 70–100 dB, and (3) maintaining the signal from the transmitter as omni-directional as possible. It was also important to keep the boat speed constant and similar to the speed of the shark. Sharp accelerations of the engine were avoided to minimize disturbance by the excessive noise produced by the engine. We estimated the size (total length, TL) of hammerheads visually (relative size error: ± 50 cm) and determined sex while underwater during tagging.

Data analysis

Measurements of depth, temperature, and position were continuously recorded every 3 s during all tracks. A five-step process was applied to reduce temporal autocorrelation and remove false values. (1) Each dataset was checked with autocorrelation function estimation (ACF) of the Stats Package (R Core Team and contributors worldwide) in R version 2.15.1 (The R Foundation for Statistical Computing) to help identify whether the tracking data were temporally autocorrelated. (2) Temporal autocorrelation of the raw data was accounted for by using a resampling procedure or an optimal time interval between positions. This was determined by comparing the angular concentration of distributions of measurements (*r*) with different increasing time intervals and based on the interval producing an asymptote to the curve (see Klimley et al. 2005). Accordingly, a 5-min interval was used as the optimal time interval for all subsequent analyses of movement. Next, (3) spurious depths and temperatures not within transmitter specifications were removed, (4) spurious speeds were removed by applying a maximum over ground movement rate of 2 m s^{-1} for nondirectional and directional movements, and 2.25 m s^{-1} for highly directional movement, and (5) vertical movements were taken out if the maximum rate of depth change exceeded 2 m s^{-1}. These last two steps were based on the maximum sustained over ground speed reported for a scalloped hammerhead (Klimley and Nelson 1984), and on the knowledge of the most efficient swimming mode of fishes with a slow glide down and faster ascent rate (Weihs 1973; Klimley et al. 2002) and the mean ascent rate of tunas being similar to their slowest over ground mean speed (Block et al. 1997). We also compared shark depth with the bottom depth obtained from the sonar as well as with the bathymetry of the island. For the latter, all tracks were plotted in ArcGIS 9.3 (ESRI, Redlands, California) and overlaid on the nearshore bathymetry of Wolf Island (Peñaherrera et al. 2013) and offshore bathymetry layers (Chadwick 2007).

Shark movements were analyzed, and randomizations were performed using Animal Movement Extension to ArcView 2.0 (Hooge et al. 1999a). We used 1,000 random replicates of correlated random walks that were carried out with Monte Carlo simulations to determine whether original tracks were random, constrained, or dispersed. Activity space was examined with the (UD), and probabilities were obtained with the fixed kernel home range (KHR) and bandwidth calculated with the least-squares cross-validation, LSCV (Hooge et al. 1999a). LSCV is useful for comparing areas of use with other studies and minimizing the integrated square error (Silverman 1986). KHR is a robust and flexible method for estimating utilization distributions (UD; Worton 1989; Hooge et al. 1999b). We also used the kernel density estimator (KDE) to estimate the space used by hammerheads as a relative probability index (Geospatial Modelling Environment 0.3.3 Beta; Beyer 2009). The KDE expresses the relative probability of the presence of each shark in a particular area. Thus, KDE was used as a metric to compare the relative probability among sharks, in contrast to the UD that was applied to compare the extent of space used by different sharks. The values of KDE were first corrected for sampling effort by multiplying the maximum probability by the duration of the track (in hours), then normalizing to values from 0–1 using the largest KDE value of all sharks as unity, and finally obtaining a normalized percent area defined by a different color on a map. The latter was performed to compare the KDE of the different hammerheads. KDE bandwidth was determined manually by selecting different bandwidths and cell sizes until the most appropriate was found that could be used to compare the different kernel densities (see Silverman 1986).

In order to examine habitat preference, hammerhead activity space was separated into three habitats according to the effect of currents impinging upon the island (sensu Hearn et al. 2010), bathymetry (maximum depth), and distance from the island (based on maximum depth): (1) “up-current” inshore, 0–100 m depth, 0–1 km from east side of Wolf (2) “down-current” inshore, 0–100 m depth, 0–1 km from west side of Wolf, and (3) “offshore,” 100 to >2,000 m depth, up to 36 km (maximum straight-line distance from island travelled by any hammerhead in this study) from the outer edge of inshore habitats (Fig. 1b,c). Habitat preference was determined with the resource preference method (Johnson 1980). In this method, we quantified the measure of preference (t_{ij}) as the difference between the rank of *usage* of habitat *i* by individual *j* (r_{ij}) and the rank of *availability* of habitat *i* by individual *j* (s_{ij}).

$$t_{ij} = r_{ij} - s_{ij}$$

Usage of the different habitats by each individual shark was determined by calculating the surface area of their (1) 50 % UD overlapping the area of the different habitats and (2) 95 % UD overlapping only the offshore habitat, using the measuring tool in ArcGIS 9.3. Habitat availability was calculated from the total surface area of each habitat type measured with the same tool. Rank of usage and availability were determined by ordering habitat types from largest to smallest according to their usage surface area or total surface area, respectively. If t_{ij} was a negative number, then availability ranks lower than usage; hence, the habitat was preferred. On the contrary, if t_{ij} was a positive number, then usage ranks lower than availability; thus, the habitat was avoided. Additionally, the average of t_{ij} across individuals was calculated ($t^{\text{-}ij}$), and the resulting means were ordered in increasing values of t^{-ij} to examine the relative preference of the different habitats by the whole sample of sharks. To infer statistical significance regarding the difference among habitats, we used $\mathrm{t}_{ij} = \alpha_i - \in_{ij}$, where α_i is the effect due to habitat i and $\in_{ij}$ is the random error term (from Johnson 1980). The null hypothesis was Ho: $\alpha_i = \ldots \alpha_I$ $(= 0)$, or all habitats are equally preferred. We used ANOVA on ranks to test the null hypothesis and a post hoc Tukey test to determine the means that were significantly different from each other.

We examined vertical habitat preference with linear regressions. We also explored temporal predictors of shark depth using diel period and season (warm, cold) as fixed effects, and individual shark and ambient temperature recorded by shark as random effects. We constructed a linear mixed model (LMM) using Gaussian error and identity link implemented with the lme4 package (Bates and Maechler 2009) in R version 2.15.1 (The R Foundation for Statistical Computing). We ran different models varying the random effects. For each model, we checked for normality and homogeneity by visual inspections of plots of residuals against fitted values, and tested the significance of random effects using a chi-square distribution. We compared these models using the Akaike information criterion with a correction for finite samples (AICc) and selected the model with the smallest AICc. Lastly, the best model was compared to the null model using a chi-square to test the model's fit (e.g., Winter 2013).

We explored environmental predictors of shark depth to understand environmental effects on behavioral patterns associated with depth. A generalized linear model (GLM) was developed to examine environmental predictors of shark depth. We used different predictors such as habitat, depth of thermocline, ambient temperature recorded by shark, bottom depth, and shark individual. This model was built applying a Gamma error and identity link implemented in the glm2 package (Marschner 2009) and with the gamma shape method to estimate the dispersion parameter (Venables and Ripley 2002) also found in the R statistical software. We ran this model with different predictors, selected the best model based on the amount of deviance explained and the smallest AIC, and tested the model's fit with the analysis of deviance (Zuur et al. 2009). Finally, temperature preference was examined using the fraction of time spent at different temperatures and the relationship with the thermocline.

Results

Movements and space utilization

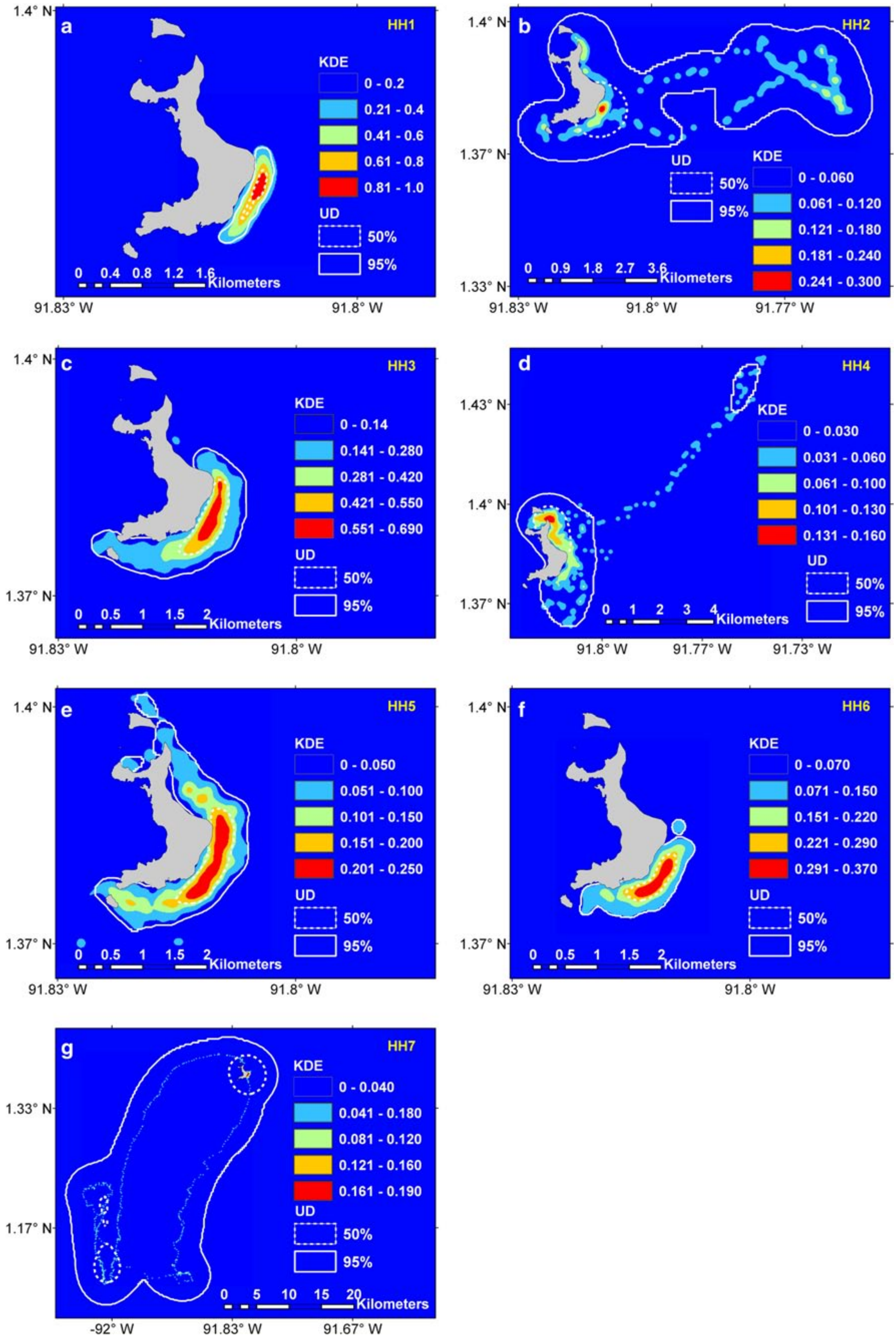
Hammerhead sharks moved in many directions away from Wolf Island. All tracks showed a great amount of variability with some sharks (HH5 and HH6) remaining day and night less than 300 m from shore, while others moving far from the island (HH2, HH7, Fig. 1b,c). Tracks of all sharks are summarized in Table 1. Most sharks spent the majority of time (69–100 %) on the eastern side of Wolf, except for HH4 that spent considerable time (46 %) at the edge of the crater on the northern end of the island, and HH2 and HH7 that remained offshore longer (64 and 99 %, respectively; Fig. 1c). Movements of hammerheads HH1, HH3, HH4, HH5, and HH6 were nonrandom and constrained (Monte Carlo random walk test, $p > 99$, % of the paths with higher mean-squared distance values), and movements of HH2 and HH7 were nonrandom and dispersed (Monte Carlo random walk test, $p > 99$, % of the paths with lower mean-squared distance values).

The extent of space used (KHR) did not differ significantly between sharks in the cold versus warm times of the year (Mann–Whitney U test, $U = 6$, $\mathrm{N}_1 = 3$, $\mathrm{N}_2 = 4$, $p > 0.05$), and neither did their UD (Mann–Whitney U test, $U = 4$, $\mathrm{N}_1 = 3$, $\mathrm{N}_2 = 4$, $p > 0.05$). KUDs ranged from 0.29–798 km^2. The size of the core area where hammerheads concentrated their activities at the southeast end (see orange and red kernels, Fig. 2) varied from 0.05 to 0.55 km^2, including

Table 1 Summary of sizes, sex, dates tracked, duration, mean speed, mean depth, minimum, and maximum depth

Shark ID	Total length (cm)	Sex	Dates tracked	Track duration (h:m:s)	Total distance (km)	Mean speed, SE (m s^{-1})	Mean depth, SE (m)	Min. depth (m)	Max. depth (m)
HH1	200	M	2–4 Nov 07	43:15:01	52	0.3 ± 0.01	30.9 ± 0.5	3.3	272
HH2	200	F	18–19 Nov 08	19:25:15	34	0.5 ± 0.02	38.8 ± 3.7	3.1	377
HH3	170	M	9–20 Feb 09	96:03:51	197	0.6 ± 0.01	20.3 ± 0.7	0.2	256
HH4	180	F	13–20 Feb 09	31:24:58	79	0.7 ± 0.02	20.3 ± 1.5	0.4	227
HH5	200	F	18–20 Feb 09	48:09:59	109	0.7 ± 0.02	20.9 ± 0.8	0.4	175
HH6	180	U	16–17 Mar 09	33:20:28	64	0.6 ± 0.02	14.0 ± 0.5	0.2	68
HH7	180	M	9–11Aug 09	51:19:56	178	0.9 ± 0.02	48.4 ± 4.1	0.2	892

U undetermined sex


a
HH1
KDE
0 - 0.2
0.21 - 0.4
0.41 - 0.6
0.61 - 0.8
0.81 - 1.0
UD
50%
95%
0 0.4 0.8 1.2 1.6 Kilometers
1.4° N
91.83° W
91.8° W
b
HH2
KDE
0 - 0.060
0.061 - 0.120
0.121 - 0.180
0.181 - 0.240
0.241 - 0.300
UD
50%
95%
0 0.9 1.8 2.7 3.6 Kilometers
1.4° N
1.37° N
1.33° N
91.83° W
91.8° W
91.77° W
c
HH3
KDE
0 - 0.14
0.141 - 0.280
0.281 - 0.420
0.421 - 0.550
0.551 - 0.690
UD
50%
95%
0 0.5 1 1.5 2 Kilometers
1.4° N
1.37° N
91.83° W
91.8° W
d
HH4
KDE
0 - 0.030
0.031 - 0.060
0.061 - 0.100
0.101 - 0.130
0.131 - 0.160
UD
50%
95%
0 1 2 3 4 Kilometers
1.43° N
1.4° N
1.37° N
91.8° W
91.77° W
91.73° W
e
HH5
KDE
0 - 0.050
0.051 - 0.100
0.101 - 0.150
0.151 - 0.200
0.201 - 0.250
UD
50%
95%
0 0.5 1 1.5 2 Kilometers
1.4° N
1.37° N
91.83° W
91.8° W
f
HH6
KDE
0 - 0.070
0.071 - 0.150
0.151 - 0.220
0.221 - 0.290
0.291 - 0.370
UD
50%
95%
0 0.5 1 1.5 2 Kilometers
1.4° N
1.37° N
91.83° W
91.8° W
g
HH7
KDE
0 - 0.040
0.041 - 0.180
0.081 - 0.120
0.121 - 0.160
0.161 - 0.190
UD
50%
95%
0 5 10 15 20 Kilometers
1.33° N
1.17° N
-92° W
91.83° W
91.67° W

◀ **Fig. 2** Space use by hammerhead sharks shown with a relative probability index (kernel density estimator, KDE) and the utilization distribution (UD). KDE probabilities are color-coded (*red* = highest and *blue* = lowest), and UD probabilities are 50 % (*dotted line*) and 95 % (*solid line*). **a** HH1, **b** HH2, **c** HH3, **d** HH4, **e** HH5, **f** HH6, **g** HH7

the sharks with dispersed movements. KDEs probabilities also varied between individuals. HH1 exhibited a 100 % probability (maximum value = 1) of being present at the southeast end of Wolf, evident as small kernels centered at this location (Fig. 2a), whereas HH4 had the lowest probability of occurrence because its kernels were centered on the edge of the crater to the north of the island (Fig. 2d). The core area of HH4 was similar in size to the other sharks (0.4 km^2), but at a different location. HH7 was five times less likely than HH1 to be seen at the southeast end, and it spent 23 % of the time at two locations 31–37 km southwest of Wolf, clearly spending more time offshore (Fig. 2g).

Horizontal and vertical habitat preference

Ranking of habitats for all sharks, from most to least preferred (after Johnson 1980), showed the up-current as the most preferred habitat (Table 2; Fig. 1c). We also performed this ranking for each season, where only the up-current habitat was preferred and the other two habitats were avoided (Table 2). There was significant difference between habitats (Kruskal–Wallis test, $H_2 = 14.11$, $p < 0.001$). The up-current habitat was significantly different from offshore (Tukey test, $q = 5.02$, $p < 0.05$), whereas the other comparisons were not significant. Hammerheads 3, 4, 5, and 6 tracked in the warm season (December–June) had similar mean depths and the shallowest maximum depths, and hammerheads 1, 2, and 7 tracked in the cold season (July–November) had different mean depths and the deepest maximum depths (see Table 1). Furthermore, hammerheads tracked during the warm period dived shallower (median (IQR): 15.8 [10.3–23.8] m) and spent more time at shallower depths (<20 m), while those in the cold season dived deeper (31.7 [23.9–37.6] m) and spent more time at deeper depths (>30 m), particularly at nighttime (Fig. 3). The depth of the thermocline was marked by a "critical isotherm depth" (22 °C) observed on contour plots of temperature (Fig. 4b–f). When plotting depth of all sharks versus thermocline depth, the number of points below a 1:1 regression line was three times greater than the points above the line (Fig. 4a), i.e., hammerheads preferred to remain at depths above the thermocline (22 °C)—but still remain close to the thermocline. When plotting depth of sharks located offshore versus thermocline depth, all of the points (black triangles), except one, were below the regression line (see Fig. 4a), also remaining above the thermocline but evidently moving between thermocline and the surface.

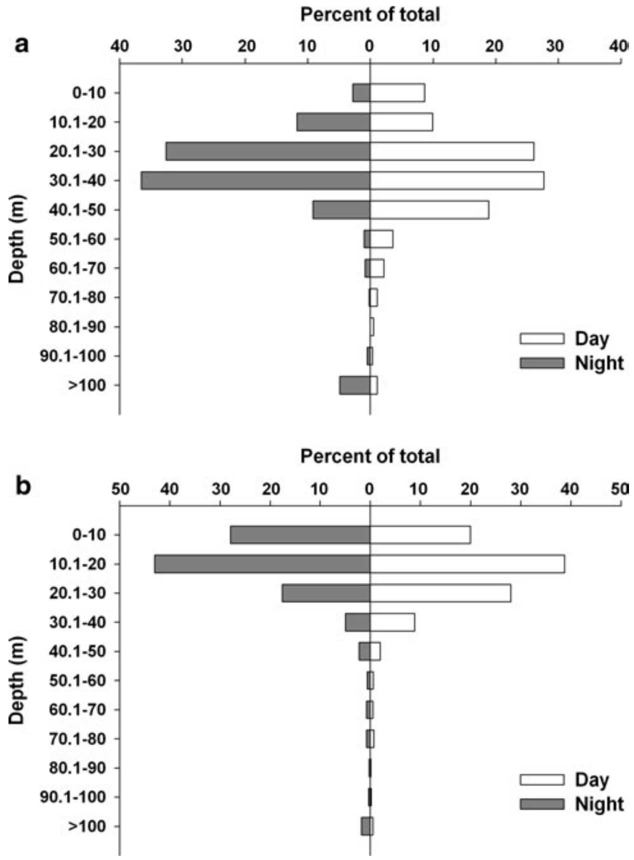


Fig. 3 Diel depth preference of sharks tracked in the **a** cold and **b** warm season

Predictors of depth

A LMM (Model 1) fit by residual maximum likelihood (REML) with the lowest AICc was selected. Of the fixed

Table 2 Habitat preference analysis by rank difference

	Rank difference							Warm sharks		Cold sharks	
Habitat	HH1	HH2	HH3	HH4	HH5	HH6	HH7	Mean	Habitat preference	Mean	Habitat preference
Up-current	−2	−1	−2	−2	−2	−2	0	−2.0	preferred	−1.0	preferred
Down-current	0	1	0	1	0	0	0	0.3	avoided	0.3	avoided
Offshore	1	0	2	1	2	2	0	1.8	avoided	0.3	avoided

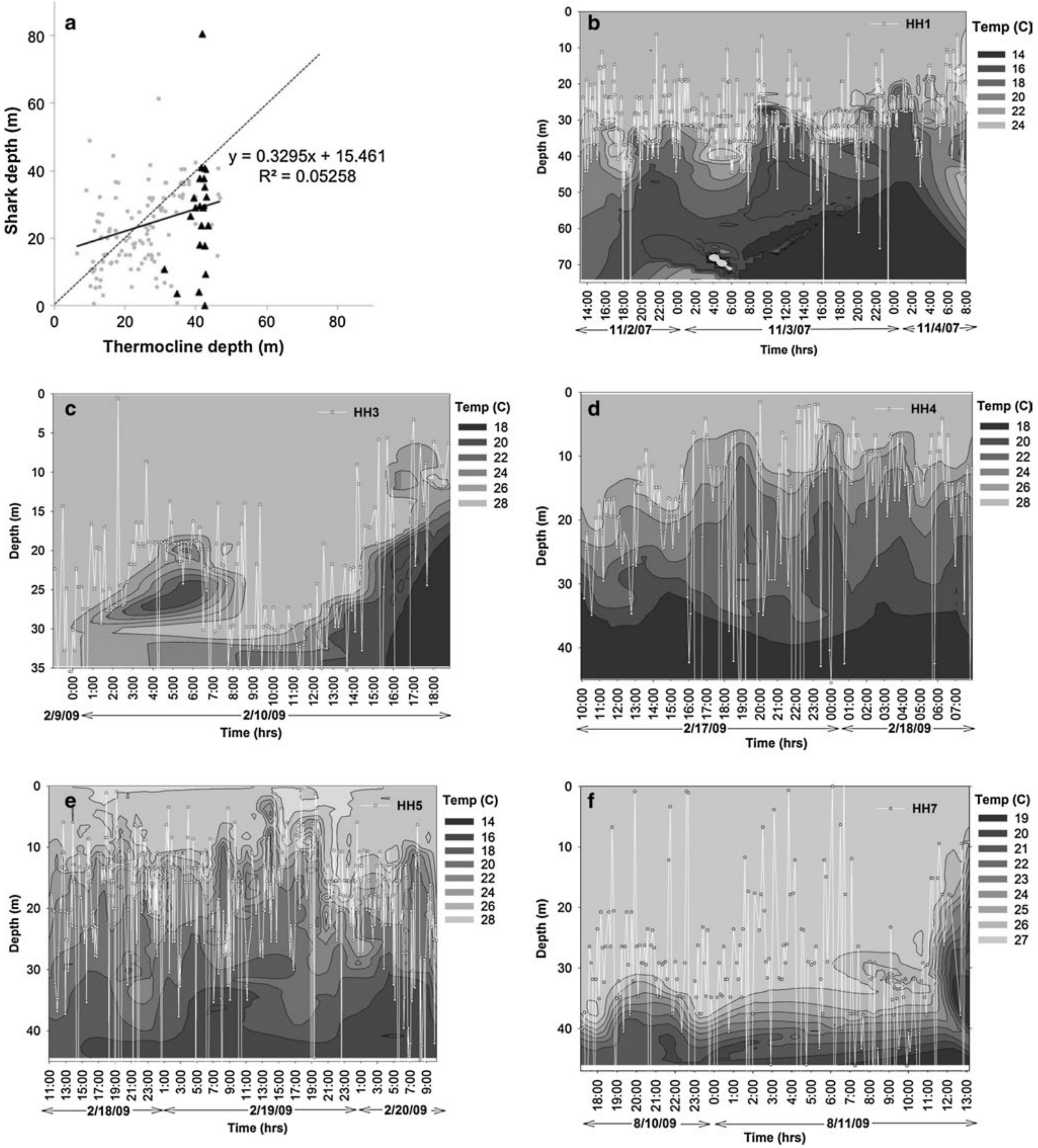


Fig. 4 **a** Regression of shark depth and thermocline depth, *gray circles* denote inshore locations, *black triangles* indicate offshore locations, *dotted line* is the regression line with slope of 1, and *solid line* is the regression line for all data points. (b–f) Temperature profiles and vertical movements of hammerheads

factors, season had a significant effect on shark depth ($p < 0.0001$) and diel period was not significant ($p > 0.05$) (Table 3), and of the random effects, ambient temperature recorded by shark contributed 99 % of the total variance. Hence, the depth of hammerheads was strongly determined by season (cold or warm) and ambient temperature of water (above/below thermocline). A GLM (Model 2) fit by iteratively reweighted least squares (IWLS) was run separately

Table 3 Fixed effects of a linear mixed model (LMM) of temporal predictors of shark depth

Coefficient	Estimate	SE	DF	*t*	*p* (two-tailed)
Intercept	87.235	11.308	3,005	7.715	<0.0001
Season	−14.470	1.636	3,005	−8.844	<0.0001
Diel period	0.403	0.611	3,005	0.660	0.5093

Table 4 Generalized linear model (GLM) of environmental predictors of shark depth

Term	Estimate	SE	*Z*	*p*
Intercept	93.188	11.443	8.143	0.000
Habitat	−6.299	1.343	−4.692	0.000
Thermodepth	0.253	0.087	2.903	0.004
Sharktemp	−2.863	0.413	−6.927	0.000
Bottom	0.002	0.026	0.088	0.930
Intercept	181.513	42.513	4.270	0.000
Thermodepth	0.357	0.294	1.213	0.225
Sharktemp	−6.914	1.876	−3.685	0.000
Bottom	0.006	0.003	2.403	0.016

Shaded area corresponds to warm-season sharks

Thermodepth = depth of thermocline, Sharktemp = telemetered temperature from sensor

for sharks in the cold and warm season, and selected the models with the lowest AIC. The best model for warm-season sharks showed three variables with significant effect on shark depth (Table 4): ambient temperature recorded by shark (highly significant, $p < 0.001$), habitat (highly significant, $p < 0.001$), and thermocline depth (significant, $p < 0.01$). The best model for cold season sharks had two variables that were significant: ambient temperature (highly significant, $p < 0.001$) and bottom (significant, $p < 0.05$, Table 4).

Thermal preference

During the warm season, hammerheads spent 16 and 22 % of their time at temperatures of 24 and 26 °C, respectively (see the two peaks in frequency at 24 and 26 °C, Fig. 5a), with a broad preference for temperatures from 23 to 27 °C. These sharks remained above the 22 °C critical isotherm depth 79 % of time (and 95 % of time above 19 °C). In contrast, during the cold season, hammerheads spent 36 and 29 % of their time at temperatures of 23 and 26 °C, respectively (see two peaks in frequency, Fig. 5b), and these data from a limited number of individuals suggest a similar broad thermal preference (and again, sharks are above 19 °C for 95 % of their time). The peak preference for 23 °C during the cold season was primarily due to HH1 that had a strong predilection for remaining inshore and swimming near the thermocline, whereas the preference for 26 °C was dominated by HH2 and HH7, sharks that remained mostly offshore. Overall, during the cold season, sharks remained above the themocline 84 % of their time. These temperature and depth preferences with respect to the thermocline can be observed in detail on the vertical movements of each individual shark (see Fig. 4b–f). HH7, in particular, upon approaching the island was possibly affected by a very shallow thermocline and a change in the vertical structure of the water column (Fig. 4f).

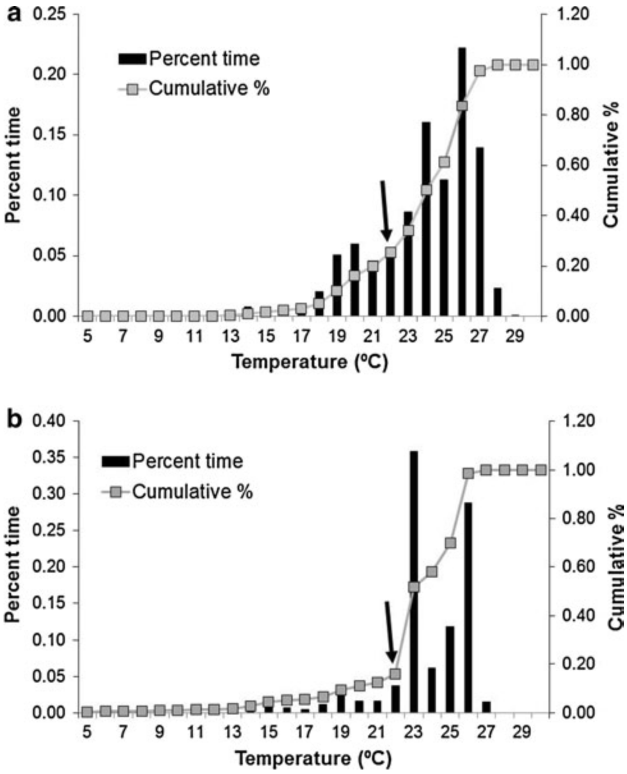


Fig. 5 Temperature preference of hammerheads. Ambient temperatures recorded by all hammerheads and the cumulative frequency in the **a** warm and **b** cold season. *Arrows* indicate the 22 °C critical isotherm

Discussion

Movements and space utilization

Movements of all scalloped hammerheads tracked in this study were centered near Wolf Island with several offshore excursions into the pelagic environment. Most of those dispersive movements were carried out around dusk similar to what was observed in the Gulf of California in earlier studies (Klimley and Nelson 1984; Klimley 1993); however, they occurred in different directions and distances from the island. In addition, three of the sharks tracked in this study did not move more than 500–700 m away from Wolf. Hence, these sharks with constrained movements remained along the east coast, up-current of the island all the whole time, unlike at El Bajo Seamount (EBS), where nightly excursions were observed for all sharks (Klimley 1993). Locally constrained movement as in this study has been reported also from Malpelo Island (Bessudo et al. 2011). During February (warm season), we observed some hammerheads at the island moving rapidly in bursts and in many directions near the surface at night. Overall, sharks in this study used a very small activity space on the south-eastern side of Wolf Island. Other species of sharks also exhibit very small core activity spaces that they use on a daily basis, such as the gray reef shark (Nelson and Johnson 1980) and juvenile lemon (Morrissey and Gruber 1993) and prickly sharks (*Echinorhinus cookei*, Dawson and Starr 2009). The use of a small central space by hammerheads at Wolf Island is an example of a refuging system, originally characterized for this species in the Gulf of California (Klimley and Nelson 1984). The intensity of use of this refuge as shown by the KDE in all tracks is remarkable, considering the amount of space available around the rest of the island and elsewhere. Possible reasons for the intensity of use of a central place or hotspot were reduced currents (relative to offshore) and vantage location for foraging excursions into open waters (Hearn et al. 2010)—hammerheads may reduce energy costs by milling slowly at a central place with reduced currents. Similarly, bat rays (*Myliobatis californica*) minimize metabolic costs when in their refuge, but they do so by thermoregulating in cool and deep water (Hopkins and Cech 1994). Other central places were identified at Wolf Island. For example, the use of the outer-eastern edge of the northern crater by several hammerheads and the high occurrence of one hammerhead there may indicate another important activity space at the island. Activity spaces did not vary between seasons, but did vary between individuals; hence, differences in movement and spatial use may be due to individual variability in behavior and possible individual diet specializations. Individual specialization is widespread in a broad range of taxa (Bolnick et al. 2003), and in some shark, species may be enhanced by resource limitation in oligotrophic environments, intraspecific competition, food-predation risk trade-offs, and spatial overlap of food webs (Matich et al. 2011).

Habitat preference

Hammerheads preferred the up-current habitat near Wolf Island while refuging during day and night. The up-current side of the island receives a steady flux of planktonic food particles that supports a large number of planktivorous pelagic and reef fishes that, in turn, constitute an abundant food source for secondary consumers and top marine predators (Hearn et al. 2010). Hammerheads have been successfully caught with bait nearshore at Wolf and Darwin islands; nevertheless, it has not been possible to attract them with chum or catch them elsewhere with bait such as at EBS (Klimley and Nelson 1981) or Cocos Islands (Klimley, Hearn, Hoyos-Padilla, Arauz, pers. comm. 2011). The avoidance of the down-current habitat by hammerheads in both warm and cold seasons is noteworthy. The leeward/down-current side of the island is sheltered from wind, and currents are slow. While pelagic larvae and other plankton may be retained and even accumulate in island wakes (Boehlert et al. 1992; Swearer et al. 1999), the flux of plankton to wakes is slow. Clearly, these down-current waters do not constitute optimal habitat for large pelagic species and top predators, as observed in this study and Hearn et al. (2010). On the other hand, offshore habitats are characterized by increased current velocities (e.g., Barton 2001) and are undesirable as refuging habitat. Although feeding was not observed during this study, there is evidence indicating that hammerheads may be feeding in offshore areas—specifically during dives below the thermocline. In other studies, (1) the most important prey items of hammerheads in Ecuadorian waters (mostly in the GMR area) were oceanic cephalopods (Castañeda-Suárez and Sandoval-Londoño 2007), (2) hammerheads tracked to the pelagic offshore environment away from EBS in the Gulf of California were found to feed on pelagic fish and cephalopods (Klimley 1987), and (3) shark movements away from core areas often involve in feeding (Sundstrom et al. 2001). If dispersive sharks are indeed foraging offshore, this would represent island–ocean coupling and transfer of biomass by hammerheads, e.g., sharks feed offshore and return to the refuge to be cleaned by reef fishes. Cleaning stations are quite common at Wolf Island, occurring at different locations around the island, where hammerheads and other shark species (e.g., Galapagos sharks, *Carcharhinus galapagensis*) are cleaned (pers obs.; Hearn et al. 2010).

Depth preference

Vertical habitat preference varied significantly between the cold and warm seasons. The seasonal change in hammerhead depth distributions is likely associated with seasonal changes in the vertical structure of water column temperature around Wolf Island. The water column is strongly stratified during March when the EF moves to the south of Wolf Island bringing warm oligotrophic waters (TSW) to the area (Palacios 2004). In contrast, during the cold season, hammerheads may be less affected by the weaker stratification of the water column in the cooler months. The finding that thermocline depth influences the depth of warm-season hammerheads further substantiates the importance of seasonal changes in water column stratification on the vertical distribution of hammerheads. The gray reef shark (*C. amblyrhynchos*) also shows well-defined seasonal patterns of depth preference, using shallower waters in the winter and an increase in depth range in spring when the thermocline is displaced to deeper waters (Vianna et al. 2013). On the other hand, tropical instability waves (TIW), or Kelvin waves, occur in the equatorial eastern Pacific from July to February in normal and La Niña years (Sweet et al. 2009), which causes large vertical displacements of the thermocline in the Galapagos Islands (Palacios et al. 2006). This phenomenon could have a significant effect on the distribution of hammerheads in the water column considering their preference for depths above the thermocline. Furthermore, evidence shows that the effect of TIW is enhanced at Wolf Island: Records from temperature sensors placed at different locations around the island show sharp temperature changes over very short periods of time (Hearn et al. in prep).

The preference for depths near the upper layers of the thermocline may be related to foraging. Plankton tends to accumulate at density gradients at the base of the mixed layer (e.g., Lande and Wood 1987), such that potential prey for sharks may also be more abundant at these depths. Moreover, these food-rich thermocline waters are preferentially delivered to the up-current side of the island, yielding a low-current environment with at least moderate food availability. A different pattern was observed for individuals with dispersive movement, which were observed diving through the thermocline into deep colder waters, presumably also for foraging. Yo-yo deep dives were carried out during offshore tracks, deep enough to feed on the jumbo squid, *Dosidicus gigas*, which occur in the hypoxic zone—as suggested for the Gulf of California (Jorgensen et al. 2009). Such behaviors seemed to be more common when sharks moved offshore (HH2, HH4, HH7 dived to depths >200 m—and HH7 to a maximum of 900 m), but data are limited and remain inconclusive. Nevertheless, even when offshore, hammerheads remained mostly above the thermocline (see Fig. 4a), but here they seem to move more actively between the surface and the thermocline (see Fig. 4f) as if searching for prey. Similarly, the dolphinfish (*Coryphaena hippurus*) performs repeated dives within the mixed layer to maximize the probability of encountering prey (Furukawa et al. 2011). In contrast, hammerheads in inshore waters associated with the upper layers of the thermocline and exhibited less vertical movement to the surface and down (see Fig. 4b–d).

Thermal niche

The vertical dimensions of the activity spaces of hammerheads can be understood as "thermal niches" given the well-defined thermal structure and strong association of sharks with specific temperatures (Fig. 5). Occurrence in a preferred density/temperature layer has also been described as a thermal niche for other species, e.g., yellowfin tuna (*Thunnus albacares*) have a particular preference for the surface mixed layer, which expands or narrows depending on the latitude (Block et al. 1997), in gray reef sharks vertical movements are driven by an optimum thermal habitat in the surface layer (Vianna et al. 2013), and shortfin makos (*Isurus oxyrinchus*), white (*Carcharodon carcharias*) and whale sharks (*Rhincodon typus*) remain in warm shallow waters for long times between deep foraging dives (Sepulveda et al. 2004; Weng et al. 2007; Thums et al. 2013). In contrast, salmon sharks (*Lamna ditropis*) have a broad thermal niche from subartic to subtropical waters (Weng et al. 2005). The scalloped hammerhead shark is a tropical species that physiologically may need to remain in near-surface warmer waters to maintain body temperature, consistent with observed preference for warmer waters above the thermocline. Other shark species use warm surface waters as well to thermoregulate (Economakis and Lobel 1998; Speed et al. 2012; Howey-Jordan et al. 2013). A preference of hammerheads for warmer water has been observed in the Gulf of California, where shark emigrations occurred in response to cooler water masses over EBS, and immigrations in response to warmer water masses (Klimley and Butler 1988). Similarly, gray reef sharks respond behaviorally to water temperature shifts in order to maintain an optimum body temperature (Vianna et al. 2013). Yet, hammerheads may be exposed to strong thermal gradients in the vertical that would help with the ability to choose temperatures while refuging at Wolf Island due to a shallower thermocline (observed during this study) and subject to warm and cool temperatures when offshore above the thermocline or when performing deep dives. Accordingly, hammerheads may conform to a "hunt cool/warm—rest warm" strategy, where the "rest" phase occurs in shallower water than the "hunt" period. This is similar to the "hunt cool—rest warm" (Di Santo and Bennett 2011) strategy of other tropical sharks, but with a possible "hunt warm" phase.

Temperature changes or gradients may also function as an important navigation mechanism for hammerheads returning to refuges at islands or seamounts. Movements in relation to gradient layers have been demonstrated for olfactory orientation in salmon, but fish could use other properties of the thermal vertical structure to navigate (Westerberg 1982). Fish can orient by using the composition and structure of the water column, and yo–yo dives are performed to determine the chemical composition of the gradient layers and guide movement homeward (Westerberg 1982). In the present study, one of the hammerheads (HH7) seemed to orient to a shallow thermocline during its ascent to the surface upon approaching Wolf Island. In this regard, hammerheads could be using temperature gradients for homing after long offshore excursions into the pelagic environment.

Our results provide evidence that hammerheads are (1) highly selective of location (i.e., habitat on up-current side of island) and depth (i.e., base of mixed layer) while refuging, where they may carry out essential activities such as cleaning and thermoregulation, including energy cost reduction, and (2) perform exploratory vertical movements by diving the width of the mixed layer or at times below the thermocline while moving offshore, most likely for foraging. These observations of hammerhead movements and habitat preference provide baseline information for the management and zoning of waters of the northern Galapagos Islands.

Acknowledgments We thank the Galapagos National Park Service and the crews of the M/N Sierra Negra and B/I Tiburón Martillo for providing crucial logistical support for tracking sharks near Wolf Island and in the open ocean. Thanks to the Charles Darwin Research Station and staff of Biomar, especially Matthias Wolff, Roberto Pépolas, and Julio Delgado. Many thanks to Cap. Tito Franco for his dedication, long hours at the helm, and appreciation of our study. Many thanks to Cap. Peter Castillo of the F/M Arrecife, Cap. Andy Angermeyer of the Sea Ranger, and to all tracking volunteers: J. Delgado, R. Pépolas, G. Soler, R. Nebot, M. Calvopiña, P. Martínez, G. Vázquez, N. Trivedi, P. Acosta, Y. Mascarell, V. Linares, Y. Llerena, and T. Chapple. Thanks are due to Hawthorne Beyer (geospatial modeling) for his assistance in the use of the kernel density tool and to E. Melcon for her help on statistical analyses. We would also like to thank the Associate Editor and two anonymous reviewers for their constructive comments and suggestions that greatly improved earlier versions of this manuscript. This work was funded by WWF-Galapagos, Conservation International, Galapagos Conservation Trust, Galapagos Conservancy, Lindblad Expeditions, AeroGal, and Shark Diver. JTK was awarded a UC MEXUS-CONACYT fellowship that supported part of his work. Special thanks to Karina Busto for her help in the final edition of this manuscript.

References

Arthur SM, Manly BFJ, McDonald LL, Garner GW (1996) Assessing habitat selection when availability changes. Ecology 77:215–227

Barton ED (2001) Turbulence and diffusion: island wakes. In: Steele J, Thorpe S, Turekian K (eds) Encyclopedia of ocean sciences I. Academic Press, London, pp 1397–1403

Bates D, Maechler M (2009): linear mixed-effects models using S4 classes. R Package Version 0.999375-32 http://cran.r-project.org/web/packages/lme4/

Bessudo S, Soler G, Klimley AP, Ketchum JT, Arauz R, Hearn A (2011) Residency of the scalloped hammerhead shark (*Sphyrna lewini*) at Malpelo Island and evidence of migration to other islands in the Eastern Tropical Pacific. Environ Biol Fishes 91:165–176

Beyer HL (2009) Geospatial modelling environment (version 0.3.3 Beta)

Block BA, Keen JE, Castillo B, Dewar H, Freund EV, Marcinek DJ, Brill RW, Farwell C (1997) Environmental preferences of yellowfin tuna (*Thunnus albacares*) at the northern extent of its range. Mar Biol 130:119–132

Boehlert GW, Watson W, Charles Sun L (1992) Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific. Deep-Sea Res 39:439–466

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161:2–28

Cartamil DP, Vaudo JJ, Lowe CG, Wetherbee BM, Holland KN (2003) Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. Mar Biol 142:841–847

Casey JG, Kohler NE (1990) Long distance movements of Atlantic sharks from the NMFS cooperative shark tagging program. In: Gruber SH (ed) Discovering sharks. Underwater Naturalist, Highlands, pp 87–91

Castañeda-Suárez JD, Sandoval-Londoño LJ (2007) Hábitos alimentarios del tiburón martillo, *Sphyrna lewini* (Griffith & Smith, 1834) en el Pacífico Ecuatoriano. In: Martínez-Ortiz J, Galvan-Magana F (eds) Tiburones en el Ecuador: casos de estudio. EPESPO-PMRC, Manta, pp 66–76

Chadwick B (2007) Galapagos bathymetry. http://www.pmel.noaa.gov/eoi/staff/chadwick/galapagos.html

Dawson CL, Starr RM (2009) Movements of subadult prickly sharks *Echinorhinus cookei* in the monterey canyon. Mar Ecol Prog Ser 386:253–262

Di Santo V, Bennett WA (2011) Is post-feeding thermotaxis advantageous in elasmobranch fishes? J Fish Biol 78:195–207

Economakis AE, Lobel PS (1998) Aggregation behavior of the grey reef shark, *Carcharodon amblyrhynchos*, at Johnston Atoll, Central Pacific Ocean. Environ Biol Fishes 51:129–139

Furukawa S, Kawabe R, Ohshimo S, Fujioka K, Nishihara GN, Tsuda Y, Aoshima T, Kanehara H, Nakata H (2011) Vertical movement of dolphinfish *Coryphaena hippurus* as recorded by acceleration data-loggers in the northern East China Sea. Environ Biol Fishes 92:89–99

Grubbs RD (2010) Ontogenetic shifts in movements and habitat use. In: Carrier J, Musick JA, Heithaus MR (eds) Sharks and their relatives II: biodiversity, adaptive physiology, and conservation. CRC Press, Boca Raton, pp 319–350

Hamilton WJ, Watt KE (1970) Refuging. In: Johnston RF, Frank PW, Michener CD (eds) Annu Rev Ecol Syst 1:263–287

Hearn A, Ketchum JT, Klimley AP, Espinoza E, Peñaherrera C (2010) Hotspots within hotspots? Hammerhead shark movements around Wolf Island, Galapagos Marine Reserve. Mar Biol 157:1899–1915

Heupel MR, Simpfendorfer CA, Hueter RE (2004) Estimation of shark home ranges using passive monitoring techniques. Environ Biol Fishes 71:135–142

Holland KN, Wetherbee BW, Peterson JD, Lowe CG (1993) Movements and distribution of hammerhead pups on their natal grounds. Copeia 1993:495–502

Hooge PN, Eichenlaub W, Solomon E (1999a) The animal movement program. USGS, Alaska Biological Science Center

Hooge PN, Eichenlaub WM, Solomon EK (1999b) Using GIS to analyze movements in the marine environment. Unpublished Report

Hopkins TE, Cech JJ (1994) Effect of temperature on oxygen consumption of the bat ray, *Myliobatis californica* (Chondrichthyes, Myliobatidae). Copeia 1994:529–532

Houvenaghel GT (1984) Oceanographic setting of the Galápagos Islands. In: Perry R (ed) Galapagos (key environments). Pergamont Press, Oxford, pp 43–54

Howey-Jordan LA, Brooks EJ, Abercrombie DL, Jordan LK, Brooks A, Williams S, Gospodarczyk E, Chapman DD (2013) Complex movements, philopatry and expanded depth range of a severely threatened pelagic shark, the oceanic whitetip (*Carcharhinus longimanus*) in the Western North Atlantic. PLoS ONE 8:e56588

Johnson DH (1980) The comparison of usage and availability measurements for evaluating resource reference. Ecology 61:65–71

Jorgensen SJ, Klimley AP, Muhlia-Melo AF (2009) Scalloped hammerhead shark *Sphyrna lewini*, utilizes deep-water, hypoxic zone in the Gulf of California. J Fish Biol 74:1682–1687

Klimley AP (1987) The determinants of sexual segregation in the scalloped hammerhead shark, *Sphyrna lewini*. Environ Biol Fishes 18:27–40

Klimley AP (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Mar Biol 117:1–22

Klimley AP, Butler SB (1988) Immigration and emigration of a pelagic fish assemblage to seamounts in the Gulf of California related to water mass movements using satellite imagery. Mar Ecol Prog Ser 49:11–20

Klimley AP, Nelson DR (1981) Schooling of the scalloped hammerhead shark, *Sphyrna lewini*, in the Gulf of California. Fish Bull 79:356–360

Klimley AP, Nelson DR (1984) Diel movement patterns of the scalloped hammerhead shark (*Sphyrna lewini*) in relation to El Bajo Espiritu Santo: a refuging central position social system. Behav Ecol Sociobiol 15:45–54

Klimley AP, Beavers SC, Curtis TH, Jorgensen SJ (2002) Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. Environ Biol Fishes 63:117–135

Klimley AP, Kihslinger RL, Kelly JT (2005) Directional and non-directional movements of bat rays, *Myliobatis californica*, in Tomales Bay, California. Environ Biol Fishes 74:79–88

Lande R, Wood AM (1987) Suspension times of particles in the upper ocean. Deep-Sea Res Pt I 34:61–72

Marschner I (2009) glm2: fitting generalized linear models. R Package Version 1.1.1. http://cran.r-project.org/web/packages/glm2/

Matich P, Heithaus MR, Layman CA (2011) Contrasting patterns of individual specialization and trophic coupling in two marine apex predators. J Anim Ecol 80:294–305

Morrissey JF, Gruber SH (1993) Home range of juvenile lemon sharks, *Negaprion brevirostris*. Copeia 1993:425–434

Nelson DR, Johnson RH (1980) Behavior of the reef sharks of Rangiroa, French Polynesia. National Geographic Research Report 12:479–499

Pak H, Zaneveld RV (1974) Equatorial front in the eastern Pacific Ocean. J Phys Oceanogr 4:570–578

Palacios DM (2004) Seasonal patterns of sea-surface temperature and ocean color around the Galapagos: regional and local influences. Deep-Sea Res Pt II 51:43–57

Palacios DM, Bograd SJ, Foley DG, Schwing FB (2006) Oceanographic characteristics of biological hotspots in the North Pacific: a remote sensing perspective. Deep-Sea Res Pt II 53:250–269

Peñaherrera C, Harpp K, Banks S (2013) Rapid seafloor mapping of the Northern Galapagos Islands. Darwin and Wolf, Galapagos Research 68

Queiroz N, Humphries NE, Noble LR, Santos AM, Sims DW (2012) Spatial dynamics and expanded vertical niche of blue sharks in oceanographic fronts reveal habitat targets for conservation. PLoS ONE 7:e32374

Sepulveda C, Kohin S, Chan C, Vetter R, Graham J (2004) Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrhinchus*, in the Southern California Bight. Mar Biol 145:191–199

Silverman BW (1986) Density estimation for statistics and data analysis. Chapman & Hall, Boca Raton

Simpfendorfer CA, Heupel MR (2012) Assessing habitat use and movement. In: Carrier J, Musick JA, Heithaus MR (eds) Biology of sharks and their relatives. CRC Press, Boca Raton, pp 579–601

Sims DW, Nash JP, Morritt D (2001) Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation. Mar Biol 139:1165–1175

Sims DW, Southall EJ, Wearmouth VJ, Hutchinson N, Budd GC, Morritt D (2005) Refuging behaviour in the nursehound *Scyliorhinus stellaris* (Chondrichthyes:elasmobranchii): preliminary evidence from acoustic telemetry. J Mar Biol Assoc UK 85:1137–1140

Snell HL, Stone PA, Snell HL (1996) A summary of the geographic characteristics of the Galapagos Islands. J Biogeogr 23:619–624

Speed CW, Meekan MG, Field IC, McMahon CR, Bradshaw CJA (2012) Heat-seeking sharks: support for behavioural thermoregulation in reef sharks. Mar Ecol Prog Ser 463:231–245

Standora EA, Nelson DR (1977) A telemetric study of the behavior of free-swimming Pacific angel sharks, *Squatina californica*. Bull South Calif Acad Sci 76:193–201

Sundstrom LF, Gruber SH, Clermont SM, Correia JPS, de Marignac JRC, Morrissey JF, Lowrance CR, Thomassen L, Oliveira MT (2001) Review of elasmobranch behavioral studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. Environ Biol Fishes 60:225–250

Swearer SE, Caselle JE, Lea DW, Warner RR (1999) Larval retention and recruitment in an island population of a coral-reef fish. Nature 402:799–802

Sweet WV, Morrison JM, Kamykowski D, Schaeffer BA, Banks S, McCulloch A (2007) Water mass seasonal variability in the Galapagos Archipelago. Deep Sea Res Part 1 Oceanogr Res Pap 54:2023–2035

Sweet WV, Morrison JM, Liu KM, Kamykowski D, Schaeffer BA, Xie L, Banks S (2009) Tropical instability wave interactions within the Galapagos Archipelago. Deep-Sea Res Pt I 56:1217–1229

Thums M, Meekan M, Stevens J, Wilson S, Polovina J (2013) Evidence for behavioural thermoregulation by the world's largest fish. J R Soc Interface 10:20120477

Venables WN, Ripley BD (2002) Modern applied statistics with S. Statistics and computing, 4th edn. Springer, New York

Vianna GMS, Meekan MG, Meeuwig JJ, Speed CW (2013) Environmental influences on patterns of vertical movement and site fidelity of grey reef sharks (*Carcharhinus amblyrhynchos*) at aggregation sites. PLoS ONE 8:e60331

Weihs D (1973) Mechanically efficient swimming techniques for fish with negative buoyancy. J Mar Res 31:194–209

Weng KC, Castillo PC, Morrissette JM, Landeira-Fernandez AM, Holts DB, Schallert RJ, Goldman KJ, Block BA (2005) Satellite tagging and cardiac physiology reveal niche expansion in salmon sharks. Science 310:104–106

Weng KC, O'Sullivan JB, Lowe CG, Winkler CE, Dewar H, Block BA (2007) Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. Mar Ecol Prog Ser 338:211–224

Westerberg H (1982) Ultrasonic tracking of Atlantic salmon (*Salmo salar*). II. Swimming depth and temperature stratification. Inst Freshw Res Drottningholm 60:102–120

Winter B (2013) Linear models and linear mixed effects models in R with linguistic applications. arXiv:1308.5499. http://arxiv.org/pdf/1308.5499.pdf

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70:164–168

Zuur AF, Ieno EN, Walker NJ, Saveliev AA, Smith GM (2009) Mixed effects models and extensions in ecology with R. Springer, New York