Diel movement patterns and habitat preferences of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight

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Abstract. The common thresher shark, *Alopias vulpinus*, is the basis of the largest commercial shark fishery in California waters. We used acoustic telemetry to determine the diel movement patterns and habitat preferences of this species in the Southern California Bight (SCB), where commercial fishing for the common thresher shark is concentrated. Eight common threshers (fork length: 122–203 cm) were tagged with temperature and depth-sensing acoustic transmitters and tracked for periods ranging from 22 to 49 h. Tracked sharks preferentially utilized deep offshore waters, and avoided shallower waters over the continental shelf. Mean rate of movement (ROM ± s.d.) was $2.15 \pm 0.46\,\mathrm{km\,h^{-1}}$. ROM and angular concentration (r, a measure of relative linearity) both showed a strong daytime pattern, with highest values at dawn that decreased throughout the day, whereas nocturnal ROM and r were less variable. Daytime vertical movements consisted of either vertical excursions below the thermocline or relatively level swimming within the upper portion of the thermocline. Nocturnally, all sharks remained within the mixed layer. These findings suggest that the common thresher shark is primarily a daytime predator, and have relevance for estimating how the alteration of the set depth of fishing-gear could affect catch rates of this species in the SCB.

Additional keywords: acoustic telemetry, drift gill-net, fishery management, pelagic.

Introduction

Shark fisheries have increased dramatically in scope in the past century; unfortunately, many shark fisheries around the world have proven to be unsustainable at high levels of exploitation (Walker 1998; Stevens *et al.* 2000; Baum *et al.* 2003; Dulvy *et al.* 2008). Because sharks are long-lived, slow-growing, and produce few offspring (Smith *et al.* 1998), over-harvested populations may take decades to recover, even under greatly reduced fishing pressure (Myers and Worm 2005). The life history characteristics of sharks, along with an expanding human population and corresponding demand for sharks and shark products (Clarke *et al.* 2006), pose a daunting problem for fisheries agencies charged with managing shark resources sustainably. In addition, the effectiveness of shark management strategies has been hampered by a paucity of basic biological data such as habitat utilisation and movement patterns (Wetherbee *et al.* 2001).

The common thresher shark, *Alopias vulpinus*, is a large pelagic species with a cosmopolitan distribution in subtropical and temperate seas (Compagno 2001). Off the west coast of North America, the common thresher ranges from southern Baja

California, Mexico to British Columbia, Canada (PFMC 2003). However, the highest concentrations occur in the Southern California Bight (SCB) (Hanan *et al.* 1993), a region extending from Point Conception, California (34°N) to Cabo Colonet, Mexico (31°N latitude) (Carlucci *et al.* 1986). As such, common threshers are an important secondary target species for the California drift gill-net fishery (CA–DGN) for broadbill swordfish, *Xiphias gladius*, which operates primarily within the SCB (Hanan *et al.* 1993), and constitutes the largest commercial shark fishery in California waters (CDFG 2005).

Very little is known regarding the fine-scale movement patterns or habitat preferences of the common thresher shark in the SCB or elsewhere. Telemetry tracking studies have been conducted for the less commercially important congener *A. superciliosus* (Nakano *et al.* 2003; Weng and Block 2004) in the Pacific Ocean, but such studies have not been conducted for *A. vulpinus*. The objectives of the present study were to use acoustic telemetry to collect movement pattern data and describe habitat utilisation for common thresher sharks within the SCB, and to interpret these data in terms of common thresher shark behaviour and their vulnerability to CA–DGN gear. This study

focussed on the SCB, where the CA–DGN is concentrated, and on sharks of a similar size range (fork length (FL): 120–210 cm) to those most commonly encountered in the fishery (PFMC 2003).

Materials and methods

Capture and tagging

Sharks were captured offshore of San Diego County, California, on hook and line. Heavy tackle and 80 lb. (36 kg) test monofilament line were used to reduce the interval between hooking the shark and the time it was brought alongside the tagging vessel (range 10–20 min). Once the shark was brought alongside the tagging vessel, a temperature and depth-sensing acoustic transmitter (Vemco, Halifax, Canada, Model V-22TP, 22 mm diameter × 100 mm length, frequencies 34–40 KHz) was attached to it using a stainless steel dart tag inserted into the radials at the base of the dorsal fin. Acoustic transmitters had a depth range of 680 m, and a transmitting range of ~1 km. After tagging, shark FL was measured, the hook was removed, and tracking commenced immediately upon release. Handling time at the tagging vessel was 3–5 min.

Depth and temperature data encoded in the acoustic transmitter signal were acquired using a rotating Vemco V10 directional hydrophone mounted on the side and extending below the keel of the tracking vessel, and decoded with a Vemco VR60 receiver. These data, along with GPS determinations of position, were recorded at 5-min intervals over the duration of each track. Water temperature profiles, down to a depth of 200 m, were determined at 2- to 3-h intervals using a bathythermograph (Seabird Electronics, Bellevue, WA, USA, Model SBE39). The tracking vessel was kept at a constant distance of ~200 m from the shark during tracking; for purposes of analysis, this was assumed to be the shark's position.

Analysis

Shark movement data were plotted over a bathymetric chart of the study area using Arcview GIS Version 3.2. Distances between successive positions were determined with the Animal Movement Analyst Extension (Hooge and Eichenlaub 2000) for ArcView GIS. Rate of movement (ROM, or speed-over-ground) was calculated by dividing distances between successive positional fixes by the sampling interval. Distances travelled within 1-h periods were summed to provide hourly ROMs, and plotted against time

of day. Fixed-effect analysis of covariance (ANCOVA) was used to investigate the relationship between ROM and time of day, with a shark effect to account for differences among sharks in individual behaviour, and hour (using 1-h bins) as a covariate. This test was also conducted to investigate the relationship between linearity and time of day. Because linearity data were bounded by 0 and 1, the significance for the relationship between linearity and time of day was also evaluated using a randomisation test (9999 randomisations: Manly 2007).

Circular statistics were performed on GPS data to determine the degree of linearity for hourly segments of each track. For these analyses, Oriana Version 2.0 was used to calculate angular concentration (r), a relative measure of linearity ranging from 0 to 1, with a value of 1 representing absolute linearity (Batschelet 1981). The equation for r is:

$$r = 1/n \left[\left(\sum \cos \varphi_i \right)^2 + \left(\sum \sin \varphi_i \right)^2 \right]^{1/2}$$

where φ is the compass bearing from one track point to the next, and n is the number of bearings. Significance of r values (i.e. linearity of movement) was tested with Rayleigh's z test.

Vertical movements were examined by plotting the depth readings for each shark against time of day and constructing a depth profile for each tracking period. Bathythermograph data were fitted over the depth profiles to evaluate the extent to which vertical movements of the shark were related to the thermal structure of the water column. Data obtained from the transmitter sensors were used to construct diel depth and temperature preference distribution histograms.

Results

Eight common thresher sharks (FL: 122–203 cm) were tracked for periods ranging from 22 to 49 h (Table 1). Most sharks exhibited a significant increase in ROM during the first 4–6 h of the track relative to ROM after 6 h (paired t-test, $P < 0.001$, see track ROM values below), and some sharks also made a deep dive immediately following release. These behaviours are consistent with short-term stress responses associated with capture and tagging that have been reported for other species (Carey and Scharold 1990; Klimley *et al.* 2002), and therefore data from the first 6 h of each track were not analysed.

Sharks tracked in this study were all caught within 20 km of the continental shelf, the offshore edge of which occurs at a

Table 1. Sex, length and track information for the eight common thresher sharks tracked in this study
FL, fork length; ROM, rate of movement

Thresher shark #	Sex	FL (cm)	Track start date	Track start location		Track duration (h)	Track distance (km)	Mean ROM
				N latitude	W longitude			
1	F	152	6 April 2005	32.84	117.44	35	57.9	1.68
2	F	179	20 April 2005	32.86	117.35	31	78.0	2.54
3	F	202	3 May 2005	32.86	117.36	40	81.4	2.04
4	F	200	11 May 2005	33.10	117.42	43	90.0	2.09
5	F	147	17 May 2005	32.83	117.36	49	94.2	1.92
6	M	132	22 May 2005	32.86	117.36	43	96.0	2.26
7	M	203	28 May 2005	32.86	117.39	26	68.9	2.65
8	F	122	5 June 2005	32.90	117.35	22	57.6	2.62

depth of ~110 m in the study area (Fig. 1). None of the tracked sharks moved inshore and over the continental shelf. Rather, they frequented waters over the continental slope and offshore basins where bottom depths ranged from 1000 to 1800 m.

The mean hourly ROM ($\pm$ s.d.) for all eight sharks was 2.15 ± 0.46 km h^{-1} (range: 0.99–4.42 km h^{-1}), which for an average shark with a FL of 167.1 cm is equivalent to 0.41 ± 0.09 FLs s^{-1}. No relationship was found between shark size (FL) and mean hourly ROM (linear regression, $r^2 = 0.2$, $P = 0.92$). There was a significant daytime pattern in hourly ROM, which was highest at dawn and generally decreased throughout the day until sunset (ANCOVA, $P < 0.001$); a similar daytime pattern was found for angular concentration (ANCOVA, $P = 0.004$)

(Fig. 2a). In contrast, nocturnal ROM remained relatively constant and was similar to the mean overall ROM. The maximum hourly ROM determined for an individual shark was 4.42 km h^{-1}. No consistent overall directional trend was seen (Fig. 1).

Figures 3 and 4 detail diel effects on the depth of occurrence and ambient temperatures experienced by the tracked sharks. Nocturnally, common threshers remained in the mixed layer 88.4% of the time. Based upon examination of the bathythermograph data, the lower limit of the mixed layer (and thus the upper limit of the thermocline) occurred at a depth of 15–20 m during tracks (Fig. 3). Daytime movement patterns were more variable. Sharks 2, 3, 4 and 5 made very few vertical movements during the day, but remained deeper than their nocturnal depths,
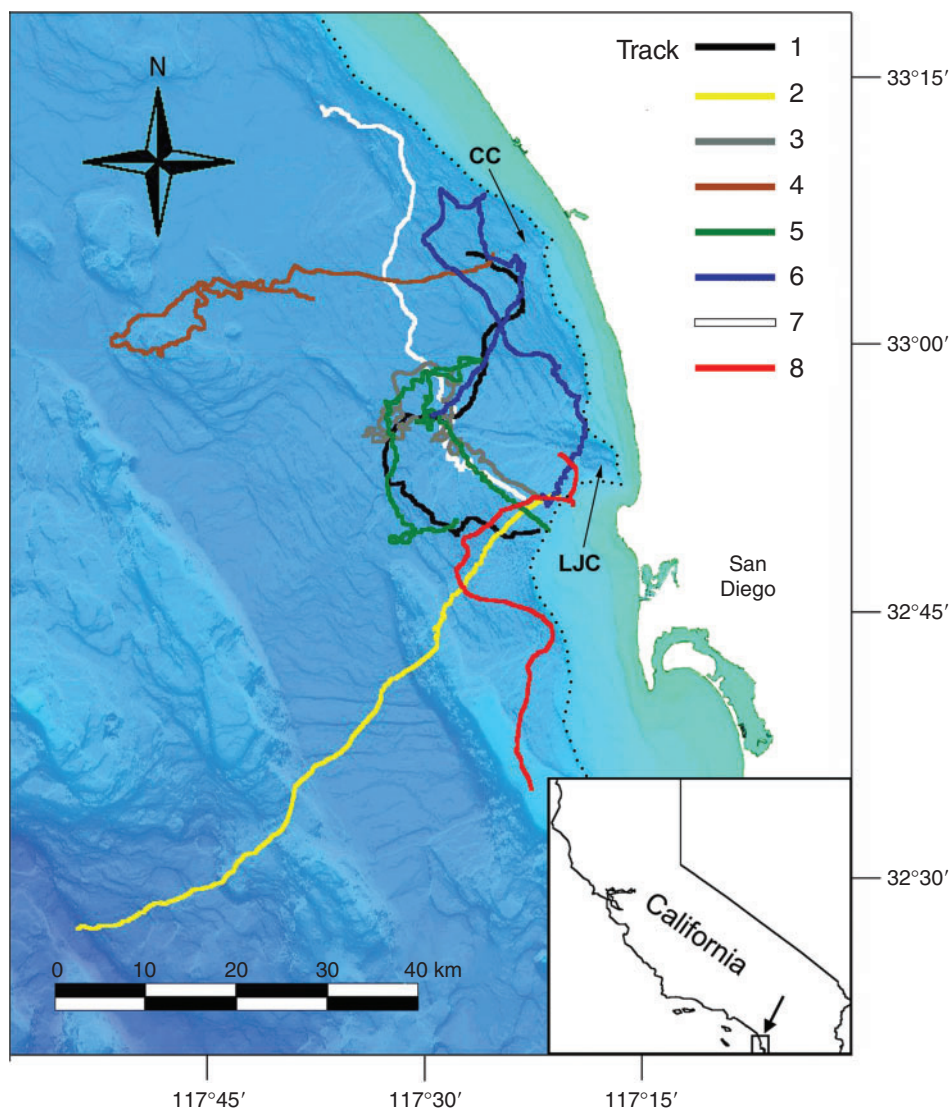

Fig. 1.   Movement data for eight common thresher sharks tracked by acoustic telemetry off San Diego County, California. Inset shows the tracking area in relation to California. Dotted line indicates the offshore edge of the continental shelf (shelf shown in light blue), which occurs at a depth of ~110 m. Beyond the shelf, the bottom depth drops off quickly to a maximum of 1800 m. All tracks were initiated immediately (within 20 km) southwest of La Jolla Canyon (LJC), except for track 4, which was initiated over Carlsbad Canyon (CC).
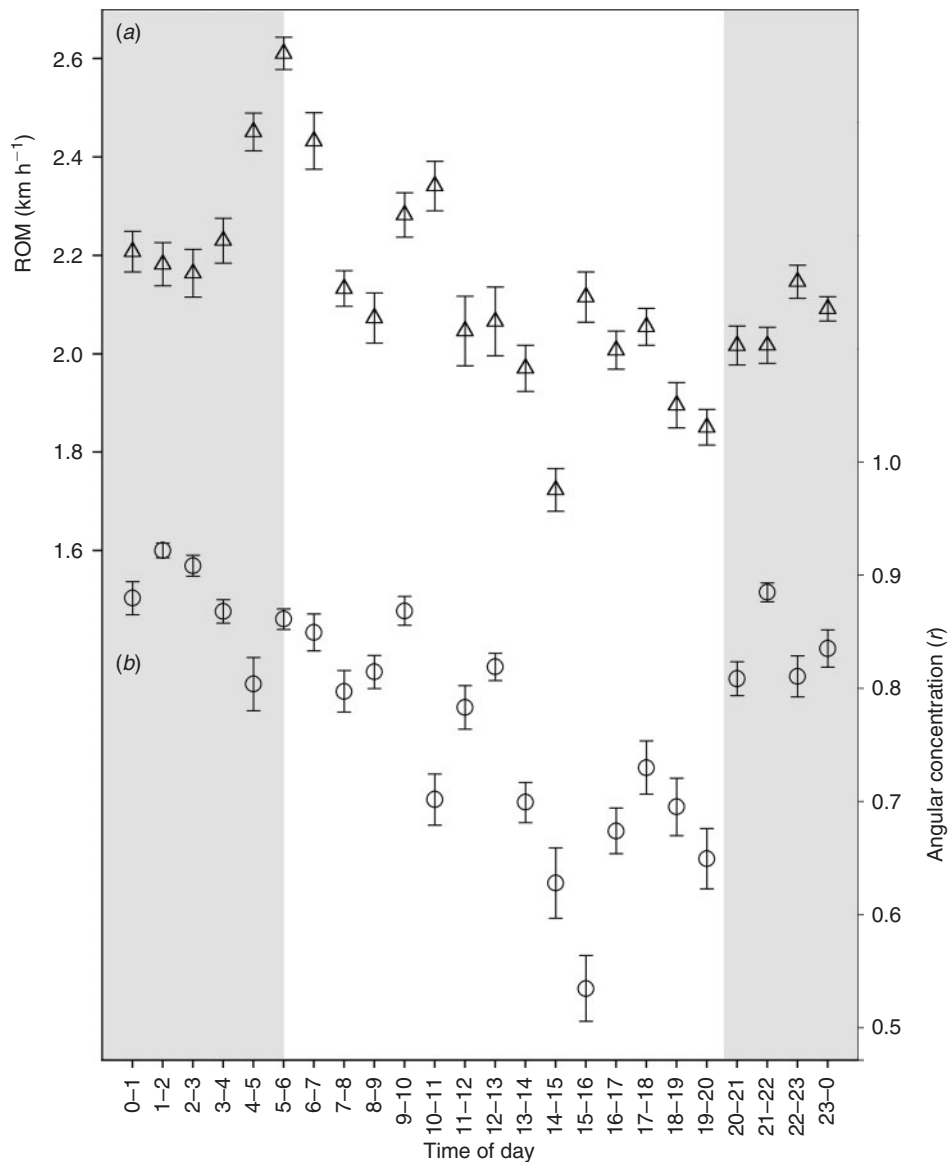
Fig. 2. (*a*) Open triangles: hourly rates of movement (ROM: km h^{-1}, mean ± s.e.) of common thresher sharks tracked over the diel cycle. Gray shaded areas are nocturnal hours, unshaded areas are daylight hours. (*b*) Open circles: corresponding hourly angular concentration (*r*) values.

typically residing within the thermocline. However, sharks 1, 6, 7 and 8 made extensive daytime vertical excursions below the thermocline; these excursions often commenced at first light and ranged in duration from several minutes to over 10 h. Maximum dive depth was 217 m, and the minimum temperature experienced at depth was 9.4°C, corresponding to a differential of approximately 10°C from sea surface temperature.

Discussion

The common thresher shark is a highly migratory species and its range in the north-eastern Pacific extends well into Mexican waters (Eitner 1995). It is thought that this species overwinters offshore of Baja California, and migrates north to the SCB

(or farther in the case of larger sharks) in the spring (Smith and Aseltine-Neilson 2001). This purported northward migration is strongly supported by fisheries data (Hanan *et al.* 1993), and the appearance of common threshers in large numbers offshore of San Diego County beginning in early spring (typically April or May) is a phenomenon well known to commercial and sport fishermen. It is during this period that we used acoustic telemetry to track common threshers in the SCB, and thus fine-scale movement patterns are described within the overall context of a generally northward migration. However, the movements of sharks tracked in this study were generally not to the north. Rather, no consistent directional pattern in the movements was observed. Therefore, while a northward trend on the seasonal scale is probable, fine-scale movements appear to be more
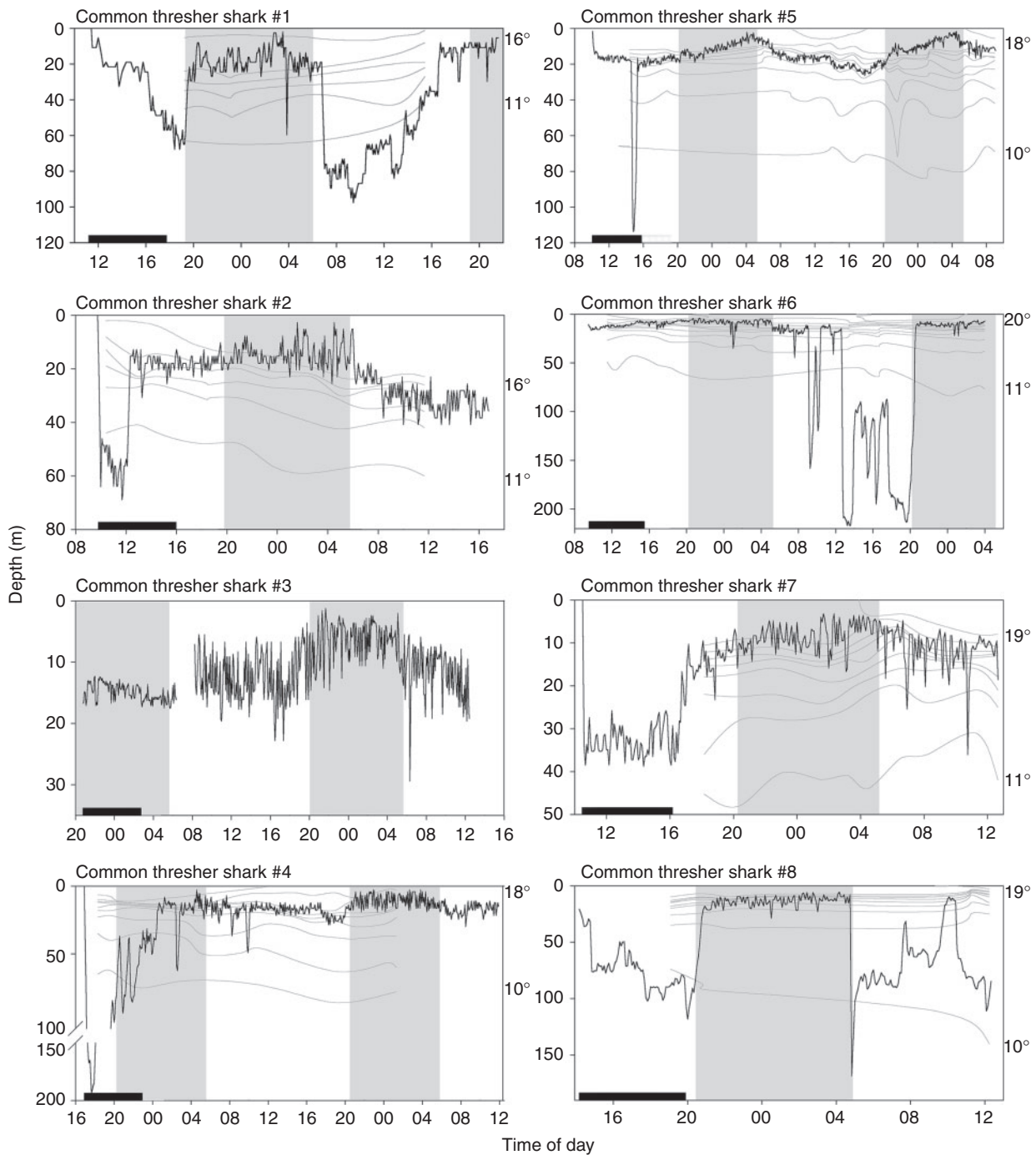
Fig. 3. Dive profiles of common thresher sharks 1 through 8. Shaded areas indicate night-time hours. Gray lines represent 1°C isotherms; maximum and minimum isotherm temperatures are given on the right. Where not shown (shark #3 and sections of other tracks), water temperature data were not collected. Black bars on the *x*-axis of each track denote the first 6 h of data, which were not used in analyses.

variable, and are likely to be influenced by factors such as local prey dynamics and oceanographic features (discussed below).

Offshore habitat preference and prey availability

The sharks tracked in this study showed a strong preference for waters over the continental slope, offshore basins and submarine

canyons, although shallower inshore habitat over the continental shelf was readily accessible. It is likely that prey distribution, predation risk, and physical habitat characteristics may be important driving mechanisms for this preference.

Common threshers can attain large sizes (to at least 5.7 m TL: Compagno 2001) on a diet consisting largely of small schooling fish. Dominant prey include northern anchovy, *Engraulis mordax*,

Pacific sardine, *Sardinops sagax*, and Pacific mackerel, *Scomber japonicus* (Preti *et al.* 2001, 2004); species that are commonly observed in near-surface waters both offshore and over the continental shelf. Because of the unique mode of predation used by the common thresher, wherein prey are struck with the elongate upper lobe of the caudal fin before capture (Gubanov 1972), predation is likely to require adequate light levels. Thus, the higher turbidity found in nearshore waters (Eganhouse and Venkatsen 1993) might inhibit predatory efficiency (Abrahams and Kattenfield 1997), contributing to an offshore habitat preference.

Another factor that may influence the offshore habitat preference of the common thresher is an ontogenetic increase in dietary scope. As they increase in size, common thresher sharks become more generalised predators, and demersal species form an additional component of the diet of larger sharks (Preti *et al.* 2001, 2004; A. Preti, pers. comm.). For example, Pacific hake, *Merluccius productus*, a demersal species that commonly occurs beyond the continental shelf at depths of up to 500 m (Ressler *et al.* 2007), was found to be a frequent food item of larger common threshers by Preti *et al.* (2001). The terminal depth of some daytime dives (specifically, for sharks 6 and 8) was within 100 m of the continental slope bottom, suggesting that larger common threshers may exploit the increased availability of alternative prey in deeper waters.

Interestingly, neonatal and juvenile common threshers appear to preferentially utilise shallower waters over the continental shelf (Cartamil *et al.* 2010), and might be inhibited from venturing offshore owing to the presence of large and abundant predators, such as adult shortfin mako, *Isurus oxyrhinchus*, and blue shark, *Prionace glauca*. Common threshers over 120 cm FL (such as those tracked in this study) are presumably large enough to inhabit offshore pelagic waters with minimal predation risk, although they might encounter increased competition for food resources from other large pelagic sharks.

Daytime movement patterns and foraging

Although feeding periodicity is not known, distinct diel patterns in vertical movement, swimming speed, and path linearity suggest that common thresher sharks are more active by day and are relatively quiescent at night. Evidence for daytime activity comes from the correlation between ROM and angular concentration, both of which had highest values at dawn, decreasing throughout the day, and were generally lowest at sunset. (The low mean values in Fig. 2 between 1400 and 1600 hours were not a consistent pattern across all sharks, but rather reflect the influence of outlying points.) The increased speed of sharks at first light, coupled with highly linear movement, suggests a foraging behaviour that maximises the probability of encountering patchily-distributed prey (e.g. sardine schools). When an area of high prey density is encountered, ROM and *r* would be expected to decrease as the shark remained to feed in a relatively small area. Similarly, greater linearity was found to coincide with non-foraging migratory behaviour and foraging was accompanied by convoluted (i.e. lower *r* value) movements for the white shark, *Carcharodon carcharias* (Weng *et al.* 2007), salmon shark, *Lamna ditropis* (Weng *et al.* 2008), and narwhal, *Monodon monoceros* (Laidre *et al.* 2004).

Daytime movements often featured repeated dives of up to 10 h in duration and occasionally reaching depths in excess of 200 m. Other sharks, such as the shortfin mako, have been shown to feed during diving episodes (Sepulveda *et al.* 2004). Carey and Scharold (1990) suggested that vertical movement of blue sharks through the water column might increase prey encounter rates, and this could also be true for common threshers, particularly on dives of short duration.

Some sharks did not dive by day, and instead remained at depths of 15–40 m, near the upper limit of the thermocline. A vantage point at these depths might assist in location of schooling near-surface prey by silhouetting them against downwelling light. It is also possible that higher prey density may be found at these depths, although this could not be quantified during the study. Alternatively, the sharks could have been using the thermocline as a vertical reference point, as suggested by Holland *et al.* (1999) for tiger sharks, *Galeocerdo cuvier*, or maintaining their position within a preferred temperature range.

Nocturnal movements

The characteristic high variability in daytime movement patterns (suggestive of foraging behaviour) is absent by night, and nocturnal movements were instead characterised by lower variability in all measured movement parameters. Specifically, both ROM and angular concentration were more constant at night (nocturnal ROM usually ranged from 2.05 to 2.25 km h^{-1} and *r* ranged from 0.8 to 0.9). In the presumed reduction of feeding activity, this constancy of nocturnal ROM may indicate an optimal cruising speed (U_0) that would minimise the energy required per unit distance travelled (Weihs 1984), while still maintaining ram-ventilatory efficiency. Indeed, the measured nocturnal ROM translates to ~0.6 m s^{-1}, which falls within the uncertainty estimates of U_0 (0.5–0.75) calculated by Weihs (1984) for the size class of sharks tracked in this study.

There was also little variation in swimming depth by night, and tracked sharks were located in the mixed layer 88.4% of the time during night-time hours. A nocturnal preference for the mixed layer after daytime predatory activity could be a form of post-feeding thermoregulation; common threshers might benefit from warmer temperatures in the mixed layer by increased digestive rate and assimilation efficiency (Wurtsbaugh and Neverman 1988). However, common threshers could be opportunistic feeders, and the possibility of nocturnal predation cannot be excluded. Feeding periodicity data are needed to validate these findings, and are a logical next step for common thresher shark research.

Fishery management implications

Catch rates of common threshers in the CA–DGN peaked in 1982 at over 1000 tonnes (t) (Hanan *et al.* 1993); however, commercial landings in 2004 totalled only 67 mt (CDFG 2005). This marked decline in landings is partially attributable to a reduction in thresher shark population size following severe fishing pressure in the late 1970s and early 1980s. Other factors affecting this discrepancy in landings include increased regulatory measures and a decrease in the CA–DGN fleet size (PFMC 2003).

There are signs that this population might be slowly recovering, including increased catch-per-unit-effort (CPUE) and average fish size (Smith and Aseltine-Neilson 2001) in the
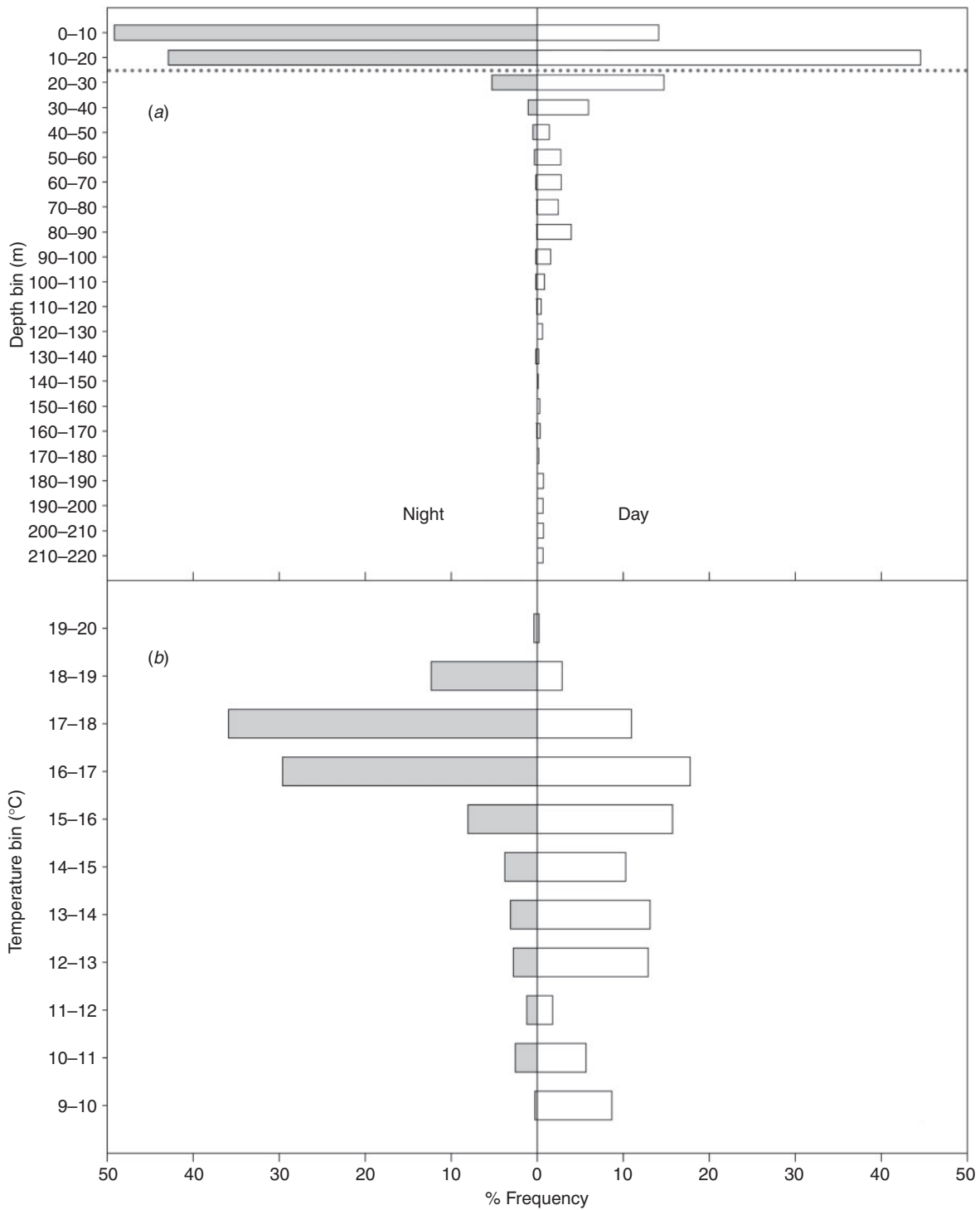
Fig. 4. (*a*) Pooled depth distributions (% frequency) for all tracked common thresher sharks in 10-m bins, during night (shaded bars) and day (unshaded bars). Dotted line represents the depth of the thermocline averaged across all tracks. (*b*) Pooled temperature distributions (% frequency) for all tracked common thresher sharks in 1°C bins.

CA–DGN. This is largely attributable to a seasonal closure (within 75 miles (120.7 km) of the coast from 1 May to 14 July), enacted subsequent to the crash and designed to protect vulnerable aggregations of threshers during their spring migration northward along the California coast. Our tracking data support

this closure, in that they show the habitat of subadults and adults during this period to include the area immediately offshore of the continental shelf.

In addition to seasonal and area closures, gear parameters (e.g. net dimensions, mesh size, and deployment time and depth)

of drift gill-nets can be manipulated for management purposes in the CA–DGN. For example, Sepulveda *et al.* (2004) stated that drift gill-net deployment depths in the CA–DGN probably lead to a reduced catch of juvenile mako shark. Typically, drift gill-net gear consists of a 2.2-km (length) × 30–40-m (depth) large-mesh (≥35.6 cm) gill-net that hangs vertically in the water column at a legally mandated minimum depth of 6 fathoms (~11 m). Nets are set at dusk and retrieved before dawn, and therefore it is the nocturnal depth distribution of the common thresher that largely determines its susceptibility to DGF gear. Based upon data shown in Fig. 4, 50.5% of nocturnal depth readings exceeded 6 fathoms, and common threshers were thus within 'capture range' a substantial portion of the time. These data indicate that increasing the legally mandated minimum net depth would have the effect of decreasing catch rates of this species. Additionally, it appears that the depth of the thermocline has a strong influence on nocturnal vertical distribution of the common thresher. Thus, the incorporation of thermocline depth (among other oceanographic variables), habitat preferences and movement patterns into habitat-based fisheries models (e.g. Brill *et al.* 2005) could result in more efficient management of the common thresher and other pelagic fishery resources in the SCB.

Acknowledgements

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