Vol. 404: 249–258, 2010
doi: 10.3354/meps08495

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published April 8

Movement patterns and nursery habitat of juvenile thresher sharks *Alopias vulpinus* in the Southern California Bight

D. Cartamil[1,*], N. C. Wegner[1], D. Kacev[2], N. Ben-aderet[3], S. Kohin[4], J. B. Graham[1]

[1]Marine Biology Research Division, Scripps Institution of Oceanography, University of California, San Diego, 9500 Gilman Dr., La Jolla, California 92093-0204, USA

[2]Biology Department, San Diego State University, 5500 Campanile Dr., San Diego, California 92182, USA

[3]Inter-University Institute for Marine Sciences in Eilat, PO Box 469, Eilat 88103, Israel

[4]Southwest Fisheries Science Center, National Marine Fisheries Service, La Jolla, California 92037, USA

ABSTRACT: We investigated the potential use of open coastal habitat over the continental shelf as a nursery area for the common thresher shark *Alopias vulpinus*. Seven juvenile threshers were tracked using acoustic telemetry to determine their movement patterns and nursery habitat in the Southern California Bight (SCB). Tracked sharks occupied waters over the continental shelf 87% of the time. These waters had an average (± SD) sea surface temperature of 18.8 ± 1.6°C and chlorophyll concentrations that were an order of magnitude higher than in adjacent waters offshore of the continental shelf. Tracked sharks had a mean rate of movement of 1.63 ± 0.56 km h^{-1}, and some sharks exhibited high site fidelity. The vertical distribution of juvenile threshers was generally limited to the upper 20 m of the water, and most sharks showed diel depth distribution patterns, with daytime depths significantly greater than nighttime depths. An analysis of SCB commercial fishery observer data confirms that juvenile common threshers are most frequently captured over the continental shelf. This region appears to provide juvenile threshers with ample food resources and reduced predation risk relative to adult habitat, and partially satisfies more quantitative nursery area criteria recently established in the literature.

KEY WORDS: Acoustic telemetry · Shark nursery area · Southern California Bight · Thresher shark · *Alopias vulpinus*

Resale or republication not permitted without written consent of the publisher

INTRODUCTION

The young of many shark species spend the first few years of life in nursery areas that are discrete from the areas occupied by adult sharks. According to the classical paradigm, shark nursery areas appear beneficial in providing ample food resources and reduced predation risk at a vulnerable life stage (Clarke 1971, Castro 1993), and are thus seen as critical to the survival of young sharks (Medved & Marshall 1983, Carrier & Pratt 1998, Gruber et al. 2001, Heupel & Simpfendorfer 2002). Heupel et al. (2007) argued that the classical definition of a shark nursery is too vague to be useful as a management parameter, and proposed several testable criteria for a shark nursery. These are (1) that sharks are more commonly encountered in the nursery than in other areas, (2) sharks have a tendency to remain or return for extended periods, and (3) the habitat is repeatedly used across years. In view of worldwide declines in numbers of many pelagic shark species (Dulvy et al. 2008), the identification of shark nursery areas and their inclusion into fishery management plans are important for the conservation and sustainable management of sharks (Heupel & Simpfendorfer 2005, Aires-da-Silva & Gallucci 2007, Heupel et al. 2007, McCandless et al. 2007, Kinney & Simpfendorfer 2009).

*Email: dcartamil@ucsd.edu

© Inter-Research 2010 · www.int-res.com

Most documented shark nursery areas occur in bays, lagoons, and estuaries (Clarke 1971, Gruber et al. 1988, Holland et al. 1993, Heupel & Simpfendorfer 2005). Nevertheless, more open coastal habitats bordering waters along the continental shelf may also serve as nursery areas for some shark species (Hussey et al. 2009). A region containing such habitats is the Southern California Bight (SCB), an open embayment extending along the Pacific coast from Point Conception (34° N) in southern California (USA) to Cabo Colonet (31° N) in northern Baja California (Mexico), and offshore to a maximum width of approximately 300 km (Fig. 1A). The SCB has been suggested as a nursery area for various pelagic shark species, including shortfin mako shark *Isurus oxyrinchus* (Hanan et al. 1993), blue shark *Prionace glauca* (Ebert 2003), white shark *Carcharadon carcharias* (Weng et al. 2007), and common thresher shark *Alopias vulpinus* (Compagno 2001). However, no studies have addressed what nursery functions the SCB may actually provide for these species.

Here we report investigations characterizing the nursery habitat of the common thresher shark in the SCB. The common thresher is a large, highly migratory pelagic shark with a cosmopolitan distribution in subtropical and temperate waters (Compagno 2001). In the SCB, the common thresher is economically important as a secondary target of the California drift gillnet fishery (CA-DGN), and is the basis of the largest commercial shark fishery in California waters (CDFG 1999), with an average of approximately 200 t captured annually over the past decade (PFMC 2008). Fisheries data suggest that threshers make a seasonal migration from a winter habitat off Baja California to the west coast of the United States, as far north as the state of Washington (PFMC 2003). In early spring, as adult threshers travel northward, pupping is thought to occur in SCB waters. Pups are born at 60 to 70 cm fork length (FL; Smith & Aseltine-Neilson 2001).

Subadult and adult common threshers (i.e. FL > 120 cm) generally inhabit waters offshore of the SCB continental shelf (Cartamil et al. in press). However, preliminary evidence suggests that juveniles utilize the shallow waters over the SCB continental shelf. For example, one juvenile common thresher acoustically tracked by Dubsky (1974) remained in the shallow waters of Morro Bay, California. In addition, Baja California artisanal gillnet fisheries capture a substantially higher proportion of juvenile common threshers than adults over the Mexican portion of the SCB continental shelf (Cartamil 2009).

In this study, we used acoustic telemetry tracking and an analysis of commercial fishery data to test the hypothesis that the shallow, coastal waters over the continental shelf of the SCB are the preferred habitat of juvenile common thresher sharks. We describe the specific areas utilized by juveniles, their degree of short-term site specificity, and the influence of physical, temporal, and environmental variables on the movement patterns of tracked sharks. We then examine the concept of the SCB as a nursery area for the common thresher by comparing our findings to both the classical paradigm of a shark nursery and the testable shark nursery criteria proposed by Heupel et al. (2007).

MATERIALS AND METHODS

Tagging and tracking. Juvenile common threshers were captured by research longline or rod and reel at various coastal locations throughout the SCB (Fig. 1B). For sharks caught by rod and reel, fight time was less than 5 min. During longline operations, the line was checked hourly, and only sharks that were vigorously active and appeared free of injury when retrieved on the longline were tagged and tracked.

Captured sharks were brought alongside the capture vessel; a temperature and depth sensing acoustic transmitter (Vemco, Model V-13TP, 13 mm diameter × 45 mm length, frequencies 60 to 75 KHz, 1000 ms pulse interval) was attached to the shark with a nylon dart (Floy Tag & Mfg, Model FIM-96) inserted into the radials at the base of the dorsal fin. Each shark was then measured and sexed, the hook was removed, and tracking commenced immediately upon release. Handling time at the tagging vessel was 3 to 5 min.

Sharks were tracked from a 5 m Boston Whaler equipped with a rotating Vemco V110 directional hydrophone, mounted on the side of the tracking vessel, that extended below the keel. Depth and temperature-calibrated signals from the acoustic tags were decoded with an onboard Vemco VR100 receiver. These data, along with determinations of position (Garmin GPS 72) and bottom depth (Hummingbird Matrix 10 depth sounder), were recorded at 5 min intervals over the duration of each track. A bathythermograph (Seabird Electronics, Model SBE39) was deployed every 2 to 3 h in order to determine the thermal structure of the water column. Acoustic tags had a depth range of 200 m and a transmitting range of approximately 1 km. The tracking vessel was kept at a constant distance of approximately 100 m from the shark during tracking; for purposes of movement analyses, this was assumed to be the shark's position.

Analyses. 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 (AMAE; Hooge & Eichenlaub 1997). Dis-

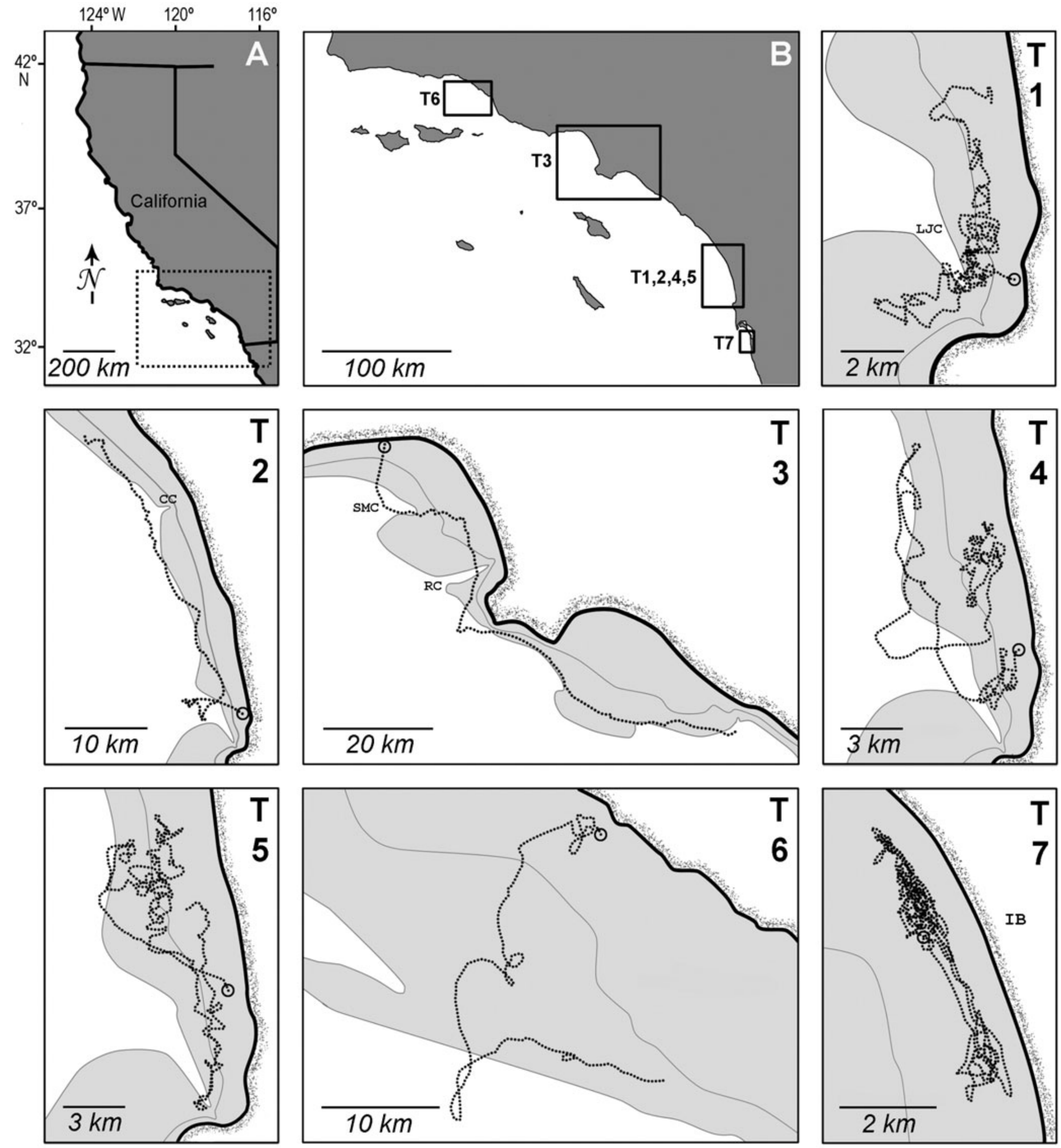

Fig. 1. (A) Coastline of California (USA), showing the Southern California Bight (SCB, dashed box), which extends into northern Baja California (Mexico). North latitude and West longitude values shown. (B) SCB; boxes show locations where juvenile thresher sharks (nos. 1 to 7) were tracked. (T1 to T7) Bathymetric maps and track records for each shark. In each map, the continental shelf (in light grey) is shown extending offshore to a depth of approximately 100 m. Depth contour lines: outer, 110 m; inner, 55 m. Shark 7 was tracked in very shallow water off Imperial Beach (IB), and only the 10 m contour is shown. Within each panel, individual tracks of juvenile common thresher sharks are shown as dotted lines (dots do not represent data collection intervals), and starting points of each track are circled. La Jolla Canyon (LJC in T1) bisects the continental shelf in T1, T2, T4, and T5. Other major canyons are labeled: CC, Carlsbad Canyon; RC, Redondo Canyon; SMC, Santa Monica Canyon

tances traveled over 1 h periods were summed to determine the hourly rate of movement (ROM), expressed in km h^{-1}.

Shark movements were mapped in relation to sea surface temperatures (SST) and chlorophyll concentrations (mg m^{-3}; spatial resolution: 1.1 km; Terrafin software: www.terrafin.com). For each shark position for which a corresponding satellite image was available, the SST and chlorophyll values were estimated, and these were used to calculate a mean for each track. A paired *t*-test was used to compare chlorophyll values for each known shark position to chlorophyll values directly offshore of the continental shelf. To determine interaction with giant kelp *Macrocystis pyrifera* beds, location and extent of kelp beds were plotted from California Department of Fish and Game survey data for the appropriate year (www.dfg.ca.gov/biogeodata/gis/mr_nat_res.asp).

A site fidelity index (SFI; modified from Zeller 1997, Bellquist et al. 2008) ranging from 0 to 1 was calculated for each shark to assess the degree to which individuals exhibited short-term site fidelity. This was calculated as:

$$1-\left(\frac{\text{distance from the first to last recorded position}}{\text{total distance traveled during the tracking period}}\right)$$

Small SFIs indicate unidirectional (linear) movements, while large SFIs indicate meandering movements over a relatively confined area (high site fidelity). Linear regression was used to determine if there was a relationship between SFI and habitat characteristics (i.e. mean SST and chlorophyll concentration) for each track.

Vertical movements were examined by plotting the depth readings of each shark against time of day. These depth profiles were then fitted over bathythermograph data to evaluate the relationship between the shark's vertical movements and the thermal structure of the water column. Data obtained from the transmitter sensors were used to construct a diel depth-preference histogram, and data from the depth sounder were used to plot a histogram of bottom depths over which the shark swam.

To examine the relationship between common thresher shark size and habitat preference on a larger spatio-temporal scale, we analyzed data from the National Marine Fisheries Service (NMFS) observer program database for the 2 main fisheries that capture common threshers in the SCB: (1) the CA-DGN (targeting primarily swordfish *Xiphias gladius* and common thresher shark, and (2) the CA setnet fishery (targeting primarily California halibut *Paralichthys californicus*). The available CA-DGN observer dataset spanned the period 1990 to 2008 and contained 4267 sets with thresher shark catch. CA setnet fishery observer data spanned the period 1990 to 1994 and contained 272 sets with thresher shark catch. The positions of sets made within the SCB that captured observer-measured common thresher sharks were plotted over a bathymetric map of the SCB. The percentage of catch over the continental shelf versus offshore of the continental shelf was then determined relative to shark size for both fisheries.

RESULTS

Seven juvenile thresher sharks (FL: 66 to 108 cm) were tracked for periods ranging from 32 to 75 h, between 9 September 2005 and 11 September 2007 (Table 1). Based upon age and growth studies by Cailliet & Bedford (1983) and Smith et al. (2008), we estimate that the smallest sharks tracked (66 and 73 cm FL) were young of the year, while larger sharks (101 to 108 cm FL) were 1 to 2 yr of age.

Mean (± SD) hourly ROM for all sharks pooled during the first 6 h following release (1.96 ± 0.51 km h^{-1}) was significantly higher than ROM values recorded beyond 6 h (1.63 ± 0.56 km h^{-1}; paired *t*-test, $p < 0.001$). This increased ROM may reflect a short-term capture-induced stress response, and thus data obtained during the first 6 h of tracking were not used for any analyses. Mean hourly ROMs for individual sharks are given in Table 1.

The continental shelf of the SCB is often less than 10 km wide and extends offshore to a bottom depth of

Table 1. *Alopias vulpinus*. Sex, length, and track details for 7 juvenile thresher sharks tracked in the Southern California Bight. F: female, M: male, FL: fork length, SFI: site fidelity index, ROM: rate of movement (km h^{-1})

Shark no.	Sex	FL (cm)	Track start date	Track duration (h)	Total track distance (km)	SFI	Mean ± SD hourly ROM
T1	F	84	9 Sep 2005	38	58.2	0.866	1.42 ± 0.31
T2	M	66	22 Jun 2006	32	60.8	0.394	1.89 ± 0.36
T3	F	78	13 Sep 2006	54	114.6	0.281	2.11 ± 0.24
T4	M	108	20 Jun 2007	67	94.1	0.864	1.32 ± 0.62
T5	M	108	25 Jun 2007	58	89.2	0.858	1.50 ± 0.45
T6	M	73	5 Sep 2007	46	82.0	0.654	1.84 ± 0.49
T7	M	101	11 Sep 2007	75	73.7	0.915	1.00 ± 0.36

approximately 110 m (Carlucci et al. 1986). Juvenile threshers occupied waters over the continental shelf almost exclusively and rarely ventured into off-shelf habitat (Fig. 1, T1–T7). Specifically, 87.0% of shark positional fixes were located over the continental shelf. Of the remaining points, most were due to sharks traversing deep submarine canyons that bisected the shelf close to shore (6.5% of total positional fixes over La Jolla canyon; 2.2% over Santa Monica, Redondo, and Carlsbad canyons). Only 4.3% of total shark positional fixes were located beyond the shelf and were unassociated with canyons. Sharks showed no preference for any particular depth zone, utilizing the entire area above the continental shelf (Fig. 2). The course of 2 tracked sharks took them within 1 km of extensive giant kelp beds near La Jolla Point, and both appeared to alter their direction in order to avoid entering this habitat (Fig. 3).

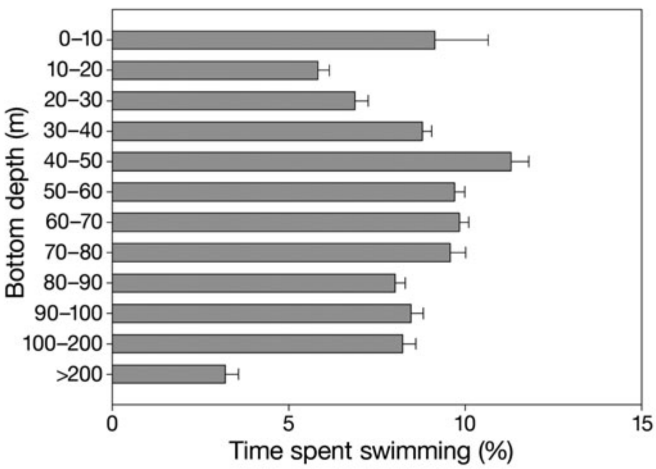

Fig. 2. *Alopias vulpinus.* Mean (± SE) percentage of time that 7 tracked juvenile common thresher sharks swam over given bottom depths (in 10 m bins)

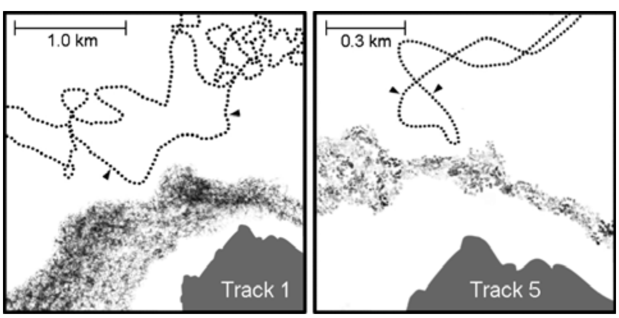

Fig. 3. *Alopias vulpinus*. Segments of juvenile common thresher Tracks 1 and 5 showing the likely influence of giant kelp beds off La Jolla Point, California, on course changes. Tracks are indicated by dotted lines, and the extent of the kelp bed is indicated by the stippled area. Arrowheads show course changes mirroring the kelp bed perimeter for durations of approximately 1 h for Track 1 and 0.5 h for Track 5

The waters occupied by tracked sharks had an average SST of 18.8 ± 1.6°C (range: 16.7 to 21.7°C). Mean chlorophyll concentration at all shark track locations for which data were available was 5.11 ± 1.27 mg m^{-3}. This was higher by 1 order of magnitude than in adjacent off-shelf habitat (0.54 ± 0.05 mg m^{-3}; $p < 0.001$, paired *t*-test).

Five of the 7 sharks exhibited high site fidelity (SFI values of 0.654 to 0.915) over the course of the tracking period (Table 1). However, SFIs were lower for sharks 2 and 3 (SFI values of 0.394 and 0.281, respectively). SFI values were not related to mean SST or mean chlorophyll levels (linear regression, $p > 0.05$).

The vertical distribution of juvenile threshers was generally limited to the upper 20 m of the water column (91.6% of shark depth readings; Figs. 4 & 5a), and temperatures encountered by sharks during vertical excursions ranged from 11 to 19°C. Most sharks showed diel depth distribution patterns, with daytime depths significantly deeper than nighttime depths ($p = 0.014$, analysis of variance [ANOVA]-type general linear model; Fig. 5b).

Analysis of commercial fishery observer data indicates that common thresher sharks captured offshore of the continental shelf were significantly larger than those captured over the shelf ($p < 0.001$, ANOVA-type general linear model). The majority (88.2%) of common threshers captured over the continental shelf were juveniles <120 cm FL and were primarily captured in the CA setnet fishery (Fig. 6A). By contrast, the majority (90.7%) of common threshers captured offshore of the continental shelf were >120 cm FL and were primarily captured in the CA-DGN fishery (Fig. 6B).

DISCUSSION

Movement patterns and habitat preferences

The track records for juvenile common threshers, obtained at several localities throughout the SCB, consistently demonstrate the preferential use of coastal waters over the continental shelf as opposed to farther offshore where larger threshers are found. Tracked juveniles were distributed over the entire continental shelf zone. For example, shark 2 spent the majority of its time near the outer edge of the continental shelf, while shark 7 never swam over waters deeper than 15 m.

Our analysis of fishery observer data shows that juveniles were frequently captured over the SCB shelf (primarily by the CA setnet fishery), while common threshers >120 cm FL were typically encountered offshore of the shelf (by the CA-DGN). These fishery-

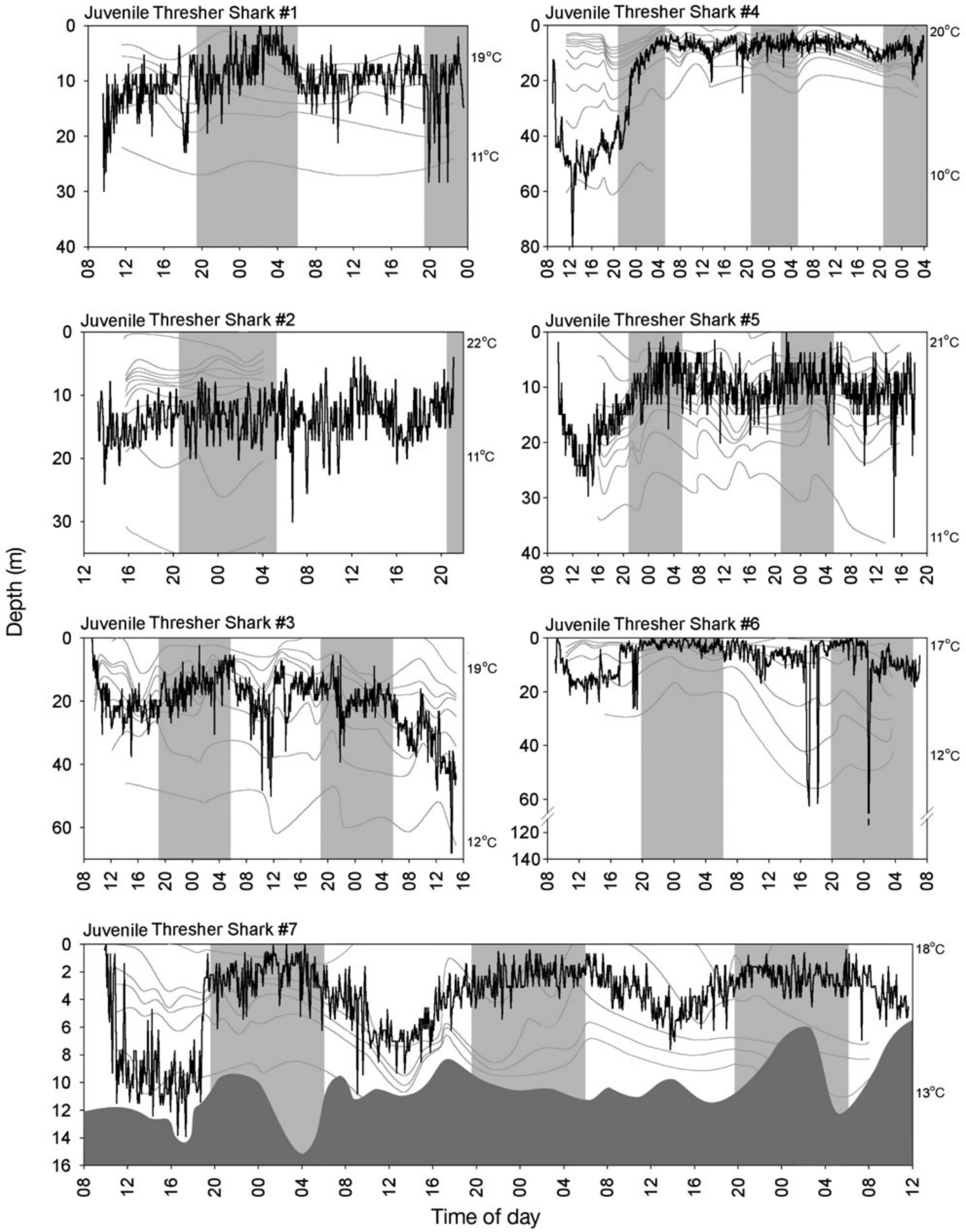

Fig. 4. *Alopias vulpinus.* Dive profiles of juvenile common thresher sharks 1 through 7. Shaded areas indicate nighttime hours. Gray lines represent 1°C isotherms; maximum and minimum isotherm temperatures are given on the right. For Track 7, the bottom contour is shown in dark grey

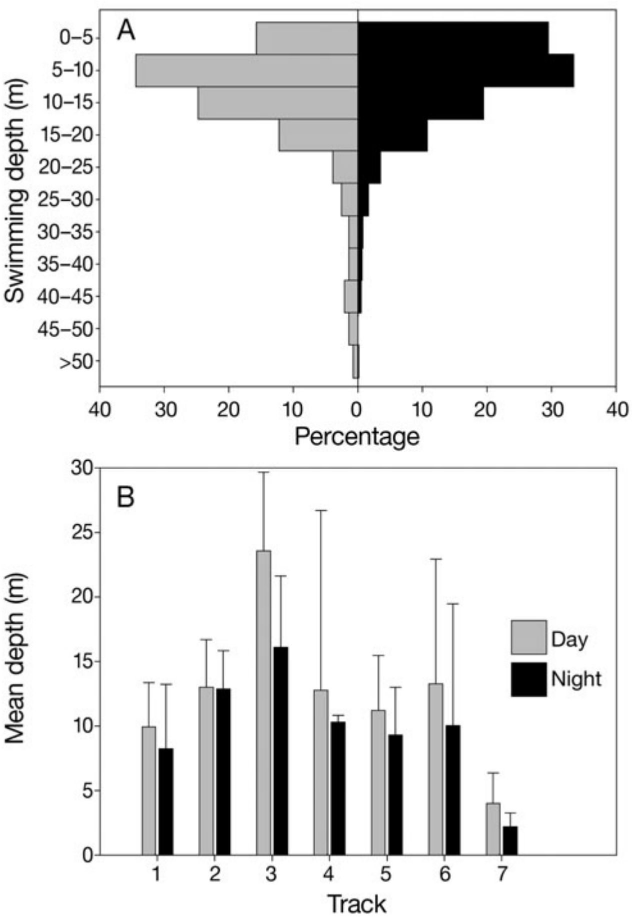

Fig. 5. *Alopias vulpinus*. (A) Percentage of time spent at swimming depths (in 5 m bins) for juvenile common thresher sharks during day (grey) and night (black). (B) Mean (± SD) swimming depths of sharks 1 to 7 during day (grey) and night (black)

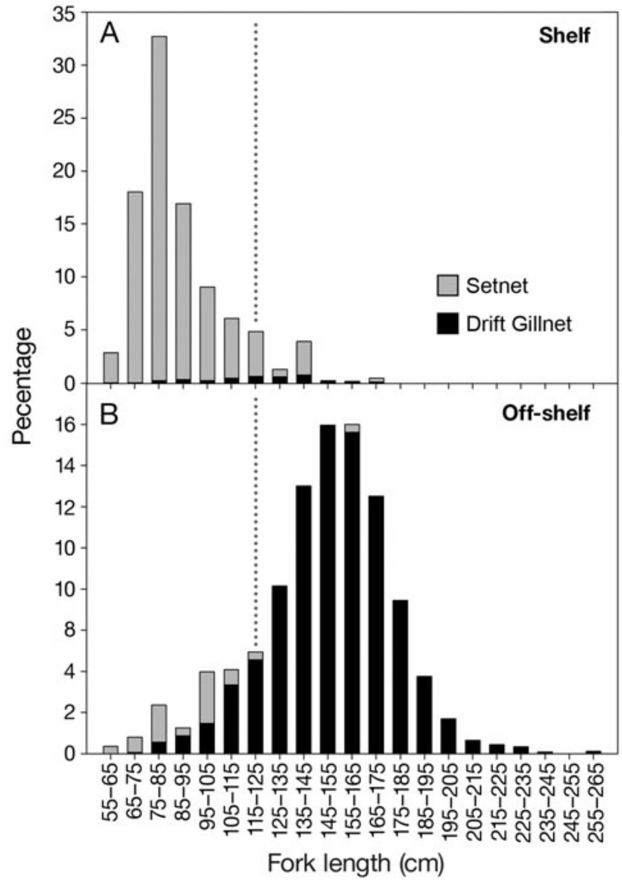

Fig. 6. *Alopias vulpinus.* Size distribution of common thresher sharks captured in both the California setnet fishery (grey portion of bars) and California drift gillnet fishery (black portion of bars) relative to: (A) waters over the continental shelf and (B) waters offshore of the continental shelf. The dotted gray line represents 120 cm fork length, the approximate size at which common threshers appear to switch from on-shelf to off-shelf habitat

dependent data are potentially biased by differences in fishery selectivity. For example, the CA setnet fishery operates year-round and mesh size averages approximately 22 cm, while the CA-DGN operates from August through January and mesh size averages approximately 50 cm. Nevertheless, they provide additional evidence of a habitat disjuncture between juvenile and adult common threshers.

Two tracked sharks appeared to alter their direction to avoid entering dense kelp beds near La Jolla Point. While this does not provide definitive evidence of kelp habitat avoidance, corroborative evidence comes from Hubbs Sea World Research Institute (HSWRI) gillnet survey data, which show an extremely low catch per unit effort (CPUE) of juvenile threshers in kelp beds relative to other shark species commonly found on the SCB continental shelf, such as soupfin shark *Galeorhinus galeus* and leopard shark *Triakis semifasciata* (L. Belquist pers. comm.). This may be related to prey availability; past and ongoing studies of juvenile thresher shark stomach contents (Preti et al. 2001, 2004, A. Preti unpubl. data) indicate that they feed primarily on northern anchovy *Engraulis mordax* in the SCB. Although the northern anchovy is occasionally observed in kelp *Macrocystis* forests, it is generally a pelagic schooling species and is more commonly found in open waters over soft bottom (Stephens et al. 2006). Additionally, kelp habitat may physically inhibit thresher shark movement or predation.

Other facets of juvenile common thresher shark behavior appear consistent with predation on northern anchovy. Anchovy normally school in near-surface waters during the day (PFMC 1998), but may disperse at night (Allen & DeMartini 1983). Juvenile threshers occupy the upper 20 m of the water column, but are slightly deeper during the day, which may enable detection of schools of anchovy silhouetted by downwelling light. Good agreement also exists between the

SST range (16.7 to 21.7°C) where the tracked juvenile common threshers occurred, the SST range (15 and 22°C) yielding the highest catch rates of larger (mainly subadult and adult) common threshers in the CA-DGN (PFMC 2003), and the SST preference of northern anchovy in the SCB (Checkley et al. 2000). This is perhaps not surprising given that adult common threshers also prey largely on northern anchovy, although they apparently have a greater dietary diversity than juveniles (Preti et al. 2001, 2004).

Three of the 4 common threshers tracked off La Jolla and the individual tracked at Imperial Beach all showed high SFIs, implying that generally favorable habitat conditions prevailed in the areas occupied by those sharks during the tracking period. However, SFI values were not related to SST or chlorophyll levels, and were likely not related to bottom substrate due to the sharks' preference for the upper water column. It is possible that SFIs may have been affected by factors that could not be quantified during the present study, such as prey abundance and local ocean currents.

Are the continental shelf waters of the SCB a nursery area for the common thresher?

The findings for habitat preference support the hypothesis that juvenile common threshers primarily utilize the continental shelf area of the SCB. Here we analyze the potential link between habitat preference and a nursery area function by considering the 2 key features of the shark nursery area concept: access to ample food resources and reduced predation (Clarke 1971, Castro 1993). We then consider the more quantitative criteria for shark nursery areas proposed by Heupel et al. (2007).

(1) Ample resources: Prey resources appear to be abundant for juvenile common threshers in the SCB, where continental shelf waters are more productive than offshore waters (Hardy 1993). Indeed, our determinations during the period when tracking was done show that there was a 10-fold greater chl *a* concentration in shelf waters than in offshore waters. A higher productivity can support a larger biomass of planktivorous northern anchovy. During favorable conditions, the northern anchovy can be the most abundant fish species over the SCB continental shelf (Allen & DeMartini 1983). In addition, ichthyoplankton surveys conducted by the CalCOFI program during the time of this tracking study indicate that the highest concentration of northern anchovy eggs (and, by extension, spawning biomass) was in nearshore waters of the SCB (Goericke et al. 2007, McClatchie et al. 2008).

(2) Decreased predation risk relative to adult habitat: The offshore pelagic habitat of adult common threshers is also inhabited by large, abundant predators such as adult blue and shortfin mako sharks. By contrast, in the continental shelf habitat occupied by juvenile threshers, co-occurrence with these pelagic predators is minimal (Casey & Kohler 1992, Nakano 1994, Compagno 2001). Nevertheless, some potential for predation exists. For example, juvenile white sharks in the SCB may utilize habitat similar to that of juvenile threshers (Dewar et al. 2004, Weng et al. 2007); other predators with the capacity to feed on small sharks include the sevengill shark *Notorhynchus cepedianus* (Lucifora et al. 2005, Braccini 2008) and California sea lion *Zalophus californianus* (Lowry et al. 1990). However, none of these species has been documented to prey on *Alopias vulpinus*. Therefore, relative to the pelagic environment, the continental shelf habitat used by juvenile threshers in the SCB likely decreases predation risk.

Life history traits of the common thresher shark may also contribute to reduced juvenile mortality. Branstetter (1990) noted that large neonatal size is an important attribute contributing to early survival of shark species such as sand tiger *Odontaspis taurus* and dusky sharks *Carcharhinus obscurus*, whose juveniles inhabit shallow, coastal waters. The low fecundity of the thresher shark (2 to 4 pups litter^{-1}, 2 yr cycle; PFMC 2003) may directly contribute to reduced predation by allowing for a relatively large pup size of 60 to 70 cm FL (Smith & Aseltine-Neilson 2001). Moreover, neonatal size is markedly accentuated by an elongate tail, resulting in a total length (TL) of 114 to 156 cm (Smith et al. 2008). Finally, the relatively rapid growth rate of juvenile threshers may also make them less vulnerable to predation. Estimated values of k, the growth coefficient in the von Bertalanffy curve describing the time to reach maximum length (Pauly 1983), reported for this species are relatively high compared to other sharks, ranging from 0.12 to 0.19 yr^{-1} (Smith et al. 2008).

Heupel et al. (2007) noted that the traditional assumptions of shark nursery areas are difficult to quantify accurately and may not hold true for all nurseries. Thus, these authors proposed 3 specific criteria to more quantitatively assess shark nursery areas; below we address each criterion individually with respect to the designation of the SCB continental shelf as a nursery area for the common thresher shark.

(1) Juvenile sharks are more commonly encountered in the area than in other areas: Analysis of commercial fishery observer data clearly indicates that juvenile threshers in the SCB are more frequently encountered over the continental shelf than offshore of the shelf.

(2) Sharks have a tendency to remain or return for extended periods: Tracked juvenile threshers occupied waters over the SCB shelf and shelf-contiguous habitat 95.7% of the time, and it is likely that juveniles re-

mained in this habitat for longer than any individual tracking period. However, for constantly moving, wide-ranging sharks such as juvenile common threshers, tag-and-recapture, satellite tagging studies, and fishery-independent surveys may be more suitable to address this criterion, and are in progress.

(3) The habitat is repeatedly used across years: The commercial fishery observer data analyzed in this study span an 18 yr period (1990 to 2008), and show a consistent pattern of increased juvenile catch over the SCB continental shelf. Thus, this habitat is used repeatedly by juvenile threshers across years.

In conclusion, this study shows that juvenile common thresher sharks preferentially utilize open coastal habitat, specifically the upper 20 m of the water column over the continental shelf, in the SCB. We provide evidence that this habitat conforms to the classical nursery area paradigm, as well as more quantitative criteria proposed by Heupel et al. (2007). Juvenile threshers are also common below the SCB along the Pacific coast of Baja California to as far south as 28° N latitude (Cartamil 2009), and occur north of the SCB to a lesser extent (PFMC 2003). Thus, the SCB represents one component of a potentially vast nursery area within which juvenile threshers likely undertake large-scale migratory excursions (D. Cartamil unpubl. data). Future studies should focus on determining the full geographic extent of juvenile thresher shark habitat, seasonal shifts in abundance, and the impacts of commercial fisheries on juvenile threshers throughout their nursery range.

Acknowledgements. Funding for this study was provided by California Sea Grant, the Ocean Protection Council, the Moore Family Foundation, the William H. and Mattie Wattis Harris Foundation, the Tinker Foundation, the Save Our Seas Foundation, and U.C. Mexus-CONACYT. D.C. was supported by a California Sea Grant traineeship, and the Tuna Industry Endowment Fund at Scripps Institution of Oceanography. We acknowledge the following individuals for assistance with fieldwork: E. Kisfaludy, P. Pelzer, S. Aalbers, D. Ramon, H. Dewar, S. Snyder, R. Runcie, M. Olvera, O. Santana, C. Sepulveda, M. Musto, A. Nosal, J. Schram, and H. Selbie. SST and chlorophyll maps were kindly provided by Terrafin Software (www.terrafin.com). We also thank D. Checkley, P. Hastings, C. Lennert, R. Rosenblatt, D. Woodruff, and 3 anonymous referees for reviewing and commenting on this manuscript. All procedures were performed under the guidelines of the Institutional Animal Care and Use Committee of the University of California, San Diego (protocol S00080).

LITERATURE CITED

Aires-da-Silva AM, Gallucci VF (2007) Demographic and risk analyses applied to management and conservation of the blue shark (*Prionace glauca*) in the North Atlantic Ocean. Mar Freshw Res 58:570–580

Allen LG, DeMartini EE (1983) Temporal and spatial patterns of nearshore distribution and abundance of the pelagic fishes off San Onofre-Oceanside, California. Fish Bull 81: 569–586

Bellquist LF, Lowe CG, Caselle JE (2008) Fine-scale movement patterns, site fidelity, and habitat selection of ocean whitefish (*Caulolatilus princeps*). Fish Res 91:325–335

Braccini JM (2008) Feeding ecology of two high-order predators from south-eastern Australia: the coastal broadnose and the deepwater sharpnose sevengill sharks. Mar Ecol Prog Ser 371:273–284

Branstetter S (1990) Early life history implications of selected carcharhinoid and lamnoid sharks of the northwest Atlantic. NOAA Tech Rep 90 NMFS:17–28

Cailliet GM, Bedford DW (1983) The biology of the three pelagic sharks from California waters and their emerging fisheries: a review. Calif Coop Ocean Fish Invest Rep 24: 57–69

Carlucci AF, Eppley RW, Beers JR (1986) Introduction to the Southern California Bight. In: Eppley RW (ed) Plankton dynamics of the Southern California Bight. Springer-Verlag, New York, p 1–12

Carrier JC, Pratt HL (1998) Habitat management and closure of a nurse shark breeding and nursery ground. Fish Res 39:209–213

Cartamil D (2009) Movement patterns, habitat preferences, and fisheries biology of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. PhD dissertation. University of California, San Diego, CA

Cartamil D, Wegner NC, Aalbers S, Sepulveda CA, Baquero A, Graham JB (in press) Diel movement patterns and habitat preferences of the common thresher shark (*Alopias vulpinus*) in the Southern California Bight. Mar Freshw Res

Casey JG, Kohler NE (1992) Tagging studies on the shortfin mako shark (*Isurus oxyrinchus*) in the western North Atlantic. Mar Freshw Res 43:45–60

Castro JI (1993) The shark nursery of Bulls Bay, South Carolina, with a review of the shark nurseries of the southeastern coast of the United States. Environ Biol Fishes 38:37–48

CDFG (California Department of Fish and Game) (1999) Review of some California fisheries for 1998: Pacific sardine, Pacific mackerel, Pacific herring, market squid, sea urchin, groundfishes, swordfish, sharks, nearshore finfishes, abalone, Dungeness crab, prawn, ocean salmon, white seabass, and recreational. Calif Coop Ocean Fish Invest Rep 40:9–24

Checkley DM Jr, Dotson RC, Griffith DA (2000) Continuous, underway sampling of eggs of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*) in spring 1996 and 1997 off southern and central California. Deep-Sea Res II 47:1139–1155

Clarke TA (1971) The ecology of the scalloped hammerhead shark *Sphyrna lewini* in Hawaii. Pac Sci 25:133–144

Compagno LJV (2001) Sharks of the world: an annotated and illustrated catalogue of shark species known to date. Vol 2: bullhead, mackerel and carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO, Rome

Dewar H, Domeier M, Nasby-Lucas N (2004) Insights into young of the year white shark, *Carcharodon carcharias*, behavior in the Southern California Bight. Environ Biol Fishes 70:133–143

Dubsky PA (1974) Movement patterns and activity levels of fishes in Morro Bay, California, as determined by ultrasonic tagging. MS thesis, California Polytechnic State University, San Luis Obispo, CA

Dulvy NK, Baum JK, Clarke S, Compagno LJV and others (2008) You can swim but you can't hide: the global status and conservation of oceanic pelagic sharks and rays. Aquat Conserv 18:459–482

Ebert DA (2003) Sharks, rays and chimaeras of California. University of California Press, Berkeley, CA

Goericke R, Venrick E, Koslow T, Sydeman WJ and others (2007) The state of the California Current, 2006–2007: Regional and local processes dominate. Calif Coop Ocean Fish Invest Rep 48:33–66

Gruber SH, Nelson DR, Morrissey JF (1988) Patterns of activity and space utilization of lemon sharks *Negaprion brevirostris* in a shallow Bahamian lagoon. Bull Mar Sci 43:61–76

Gruber SH, de Marignac JRC, Hoenig JM (2001) Survival of juvenile lemon sharks at Bimini, Bahamas, estimated by mark-depletion experiments. Trans Am Fish Soc 130: 376–384

Hanan DA, Holts DB, Coan AL Jr (1993) The California drift gillnet fishery for sharks and swordfish, 1981–1982 through 1990–1991. Calif Fish Game Bull 175:1–95

Hardy JT (1993) Phytoplankton. In: Dailey MD, Reish DJ, Anderson JW (eds) Ecology of the Southern California Bight: a synthesis and interpretation. University of California Press, Berkeley, CA, p 233–265

Heupel MR, Simpfendorfer CA (2002) Estimation of mortality of juvenile blacktip sharks, *Carcharhinus limbatus*, within a nursery area using telemetry data. Can J Fish Aquat Sci 59:624–632

Heupel MR, Simpfendorfer CA (2005) Using acoustic monitoring to evaluate MPAs for shark nursery areas: the importance of long-term data. Mar Technol Soc J 39:10–18

Heupel MR, Carlson JK, Simpfendorfer CA (2007) Shark nursery areas: concepts, definition, characterization and assumptions. Mar Ecol Prog Ser 337:287–297

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

Hooge P, Eichenlaub E (1997) Animal movements extension to Arcview. Alaska Biological Center, US Geological Survey, Anchorage, AK

Hussey NE, McCarthy ID, Dudley SFJ, Mann BQ (2009) Nursery grounds, movement patterns and growth rates of dusky sharks, *Carcharhinus obscurus*: a long-term tag and release study in South African waters. Mar Freshw Res 60: 571–583

Kinney MJ, Simpfendorfer CA (2009) Reassessing the value of nursery areas to shark conservation and management. Conserv Lett 2:53–60

Lowry MS, Oliver CW, Macky C, Wexler JB (1990) Food habits of California sea lions *Zalophus californianus* at San Clemente Island, California, 1981–1986. Fish Bull 88: 509–521

Lucifora LO, Menni RC, Escalante AH (2005) Reproduction, abundance and feeding habits of the broadnose sevengill shark *Notorynchus cepedianus* in north Patagonia, Argentina. Mar Ecol Prog Ser 289:237–244

McCandless CT, Kohler NE, Pratt HL Jr (eds) (2007) Shark nursery grounds of the Gulf of Mexico and the east coast waters of the United States. Symp 50. American Fisheries Society, Bethesda, MD

McClatchie S, Goericke R, Koslow JA, Schwing FB and others (2008) The state of the California Current, 2007–2008: La Niña conditions and their effects on the ecosystem. Calif Coop Ocean Fish Invest Rep 49:39–76

Medved RJ, Marshall JA (1983) Short-term movements of young sandbar sharks *Carcharhinus plumbeus*. Bull Mar Sci 33:87–93

Nakano H (1994) Age, reproduction and migration of blue shark in the North Pacific Ocean. Bull Nat Res Inst Far Seas Fish 31:141–256

Pauly D (1983) Some simple methods for the assessment of tropical fish stocks. FAO Fish Tech Pap 234

PFMC (Pacific Fishery Management Council) (1998) Essential fish habitat: coastal pelagic species. Available at: http://swr.ucsd.edu/hcd/cpsefh.pdf

PFMC (2003) Fishery management plan and environmental impact statement for U.S. West Coast fisheries for highly migratory species. Pacific Fishery Management Council, Portland, OR

PFMC (2008) Status of the U.S. West Coast fisheries for highly migratory species through 2008. Pacific Fishery Management Council, Portland, OR

Preti A, Smith SE, Ramon DA (2001) Feeding habits of the common thresher shark (*Alopias vulpinus*) sampled from the California-based drift gill net fishery, 1998–1999. Calif Coop Ocean Fish Invest Rep 42:145–152

Preti A, Smith SE, Ramon DA (2004) Diet differences in the thresher shark (*Alopias vulpinus*) during transition from a warm-water regime to a cool-water regime off California-Oregon, 1998–2000. Calif Coop Ocean Fish Invest Rep 45: 118–125

Smith SE, Aseltine-Neilson D (2001) Thresher shark. In: Leet WS, Dewees CM, Klingbeil R, Larson EJ (eds) California's living marine resources: a status report. University of California, Sacramento, CA, p 339–341

Smith SE, Rasmussen RC, Ramon DA, Cailliet GM (2008) The biology and ecology of thresher sharks (Alopiidae). In: Camhi MD, Pikitch EK, Babcock EA (eds) Sharks of the open ocean: biology, fisheries and conservation. Blackwell Science, Ames, IA, p 60–68

Stephens JS, Larson RJ, Pondella DJ (2006) Rocky reefs and kelp beds. In: Allen LG, Pondella DJ, Horn MH (eds) The ecology of marine fishes: California and adjacent waters. University of California Press, Berkeley, CA, p 227–252

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

Zeller DC (1997) Home range and activity patterns of the coral trout *Plectropomus leopardus* (Serranidae). Mar Ecol Prog Ser 154:65–77

Editorial responsibility: Matthias Seaman, Oldendorf/Luhe, Germany

Submitted: July 3, 2009; Accepted: January 13, 2010
Proofs received from author(s): March 18, 2010