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Movements and distribution of juvenile common thresher sharks *Alopias vulpinus* in Pacific coast waters of the USA and Mexico

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ABSTRACT: The common thresher shark *Alopias vulpinus* constitutes an important commercial fishery on the Pacific coasts of both the USA and Mexico. However, little is known about the juvenile phase of this species. This study used a combination of pop-up archival satellite tagging, tag-recapture, and fishery catch data to investigate the movement patterns, habitat preferences, ecology, and geographic distribution of juvenile common thresher sharks along the Pacific coast of the USA and Mexico. Juvenile threshers primarily utilized continental shelf waters, with a geographic range extending from Punta Eugenia in Baja California, Mexico (27.8° N) north to Morro Bay, California (35.3° N). Within this range, sharks were found at significantly lower latitudes in March and April. Satellite-tagged juvenile threshers exhibited diel patterns of vertical distribution, primarily inhabiting the upper 20 m of the water column by night, and significantly greater depths by day. In addition, juvenile threshers made frequent daytime dives to depths exceeding 50 m, with a maximum recorded dive depth of 192 m. Tracked sharks were most commonly associated with ambient water temperatures between 14 and 17°C, and inhabited significantly warmer temperatures at night than during the day. No tidal or lunar influence on vertical distribution was found, and vertical habitat utilization did not increase concomitantly with shark size. This study is the first to document movements of juvenile threshers between US and Mexican waters, highlighting the need for bi-national management strategies for this shared fishery resource.

KEY WORDS: Thresher shark · Shark nursery · Movements · Satellite telemetry · Fishery management · Zoogeography · Juvenile

INTRODUCTION

The common thresher shark *Alopias vulpinus* (Lamniformes) is a large, migratory shark ranging in size from 60 cm fork length (FL) at birth to over 300 cm FL as an adult. It inhabits subtropical and temperate seas worldwide (Compagno 2001); however, in the eastern Pacific, the population is thought to consist of a single homogenous stock (Eitner 1995, Trejo 2005) ranging from Baja California Sur, Mexico, to British Columbia, Canada (PFMC 2003). Within this region, a high population density of the common thresher occurs within the Southern California Bight (SCB) (Hanan et al. 1993), an open embayment bounded on the west by the California Current and extending along the Pacific coast from southern

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California, USA (Point Conception; 34°N), to northern Baja California (BC), Mexico (Cabo Colonet; 31°N) (see Fig. 1).

Common thresher sharks and swordfish *Xiphias gladius* are economically important target species of the California drift gillnet fishery (CA-DGF) within the SCB. Although fishery effort has been in decline over the past 25 yr, the CA-DGF constitutes the largest commercial shark fishery on the western coast of the USA (PFMC 2003). Several electronic tagging studies have been conducted in the past decade to examine thresher shark movement patterns and their fishery management implications. These studies have shown that larger thresher sharks typically inhabit waters offshore of the continental shelf, and may undertake large-scale southward movements into Mexican waters during winter months. They exhibit clear diel patterns of vertical distribution, generally remaining in the mixed layer (upper ~20 m) by night, and moving deeper by day, occasionally diving to depths exceeding 300 m (Baquero 2006, Cartamil et al. 2010a, 2011b, Heberer et al. 2010). However, these studies have focused primarily on adults and sub-adults (i.e. FL ≥ 120 cm), which are the life history stages most frequently captured in the CA-DGF (PFMC 2003).

The movement patterns and geographic distribution of juvenile (FL < 120 cm) thresher sharks in the eastern Pacific are comparatively less well known. Indirect evidence suggests that parturition occurs offshore of Baja California and southern California as adult females migrate northwards from their overwintering grounds in Mexican waters (Bedford 1992). Indeed, juvenile threshers are commonly captured in the near-shore artisanal gillnet fisheries of western Baja California (Cartamil et al. 2011a) and in gillnets off southern California (PFMC 2003). In the SCB, acoustically tracked juvenile threshers were found to prefer waters over the continental shelf, which appear to serve as a nursery area for this species (Cartamil et al. 2010b). North of the SCB, the geographic range of juvenile threshers is poorly known, although they have sporadically been reported as far north as San Francisco, CA (Bedford 1992).

Understanding the biology of both adult and juvenile life stages is necessary for the development of effective management strategies. This is particularly true for low-fecundity species such as the common thresher (Smith et al. 2008), as fishing mortality can have a more deleterious effect on these species than on those with higher fecundity (Mollet & Cailliet 2002). In the present study, we used a combination of pop-up archival satellite tag (PSAT), tag and recapture, and fishery catch data to address the following questions regarding the early life history of the common thresher shark: (1) What are the long term (i.e. several months) horizontal and vertical movement patterns and habitat preferences of juvenile threshers? (2) What is the geographic distribution of juvenile threshers in the eastern Pacific? (3) Are there predictable seasonally related migrations within this range?

MATERIALS AND METHODS

Capture and pop-up archival satellite tagging

With the exception of 1 shark captured on hook and line in October 2007, all sharks were captured and tagged during 2 separate cruises of an annual National Marine Fisheries Service (NMFS) juvenile thresher shark abundance survey aboard the FV 'Outer Banks' in September 2008 and September 2009. Briefly, sharks were targeted using a monofilament (300 lb test) longline suspended 3 m below the surface, spanning approximately 1.6 km with 100 hooks. Each 13/0 size circle hook was baited with a whole Pacific sardine and attached to the mainline by a 2.5 m stainless steel leader. The gear was set during daylight hours over the continental shelf (bottom depth range: 9 to 15 m) and allowed to soak for 2 h before retrieval.

Captured sharks were brought on board for tagging, measurement (straight FL in cm), and sex determination. A PSAT X-Tag (Microwave Telemetry) was attached to each shark via an 8 cm monofilament tether attached to a nylon dart (Model FIM-96, Floy Tag & Mfg.) inserted into the radials at the base of the dorsal fin. Curved forceps were used to insert a plastic zip-tie under the skin at a distance of 3 cm, which was loosely cinched around the tag base to minimize lateral tag movement. Sharks were also tagged with a Floy identification tag, and some were injected with oxytetracycline (for a separate age and growth study) prior to release. Gills were kept irrigated with a seawater hose while on board; the entire tagging procedure lasted approximately 5 min. Only sharks <120 cm FL were tagged.

X-Tags measured and archived temperature (0.17°C resolution), depth (variable resolution from 0.33 to 1.34 m), and light level (arbitrary intensity units) every 2 min. Tags were programmed to detach from the sharks 3 to 6 mo after deployment, at which point they randomly transmitted raw data points (i.e. no binned data) until the battery was exhausted, resulting in 15 to 60 min data resolution depending on deployment length (i.e. the amount of archived data). After release, some transmitting tags were recovered using a Series 6000 radio direction finding system (Doppler Systems). In these cases, full archival datasets were recovered at the native 2 min resolution.

Satellite tagging data analyses

Satellite tag pop-up coordinates (deduced from class 3 or better ARGOS locations after surfacing) were plotted over bathymetric maps to determine if the shark was over continental shelf waters. Straight line distances from the point of tagging to pop-up were calculated in Arcview GIS v.3.2 (ESRI) in order to determine the minimum distance traveled during the track.

Light-based geolocation was used to reconstruct the overall tracks of the 7 sharks for which archival datasets were recovered and that were at liberty for more than 90 d. Rather than relying on sunrise and sunset times provided by the manufacturer algorithm, these times were selected following procedures in Royer & Lutcavage (2009). From these selected times, draft tracks were calculated using GeoLight (Lisovski & Hahn 2012), and refined by a state-space Kalman filter model, with sea surface temperature (SST) matching (UKFSST) (Lam et al. 2008), using the NOAA Optimum Interpolation SST V2 1° resolution imagery. The UKFSST model utilizes an underlying random walk movement model that describes the overall diffusion and advection for the entire track (Sibert et al. 2003), and provides error estimates in the form of confidence regions. Bathymetric correction was applied as a last step to prevent points being placed on land (Galuardi et al. 2010).

Pooled data obtained from all transmitters were used to construct diel (night vs. day) depth and temperature-preference histograms for juvenile threshers. A Mann-Whitney *U*-test was used to test for significant diel differences in depth and temperature preferences. Ocean Data View (Schlitzer 2014) was used to plot track depths and associated ambient temperatures for selected archival datasets.

To identify peaks in diving (vertical) activity or depth distribution over extended time scales, fast-Fourier transform, using a Hanning window function to reduce the effect of adjacent spectral components (Oppenheim & Schafer 1989, Shepard et al. 2006), was applied to full archival (i.e. recovered) datasets using Sigmaplot v.11.0 (Systat Software).

General linear models (GLMs) were used to test the hypothesis that depth utilization of individual sharks would increase with body size. First, the maximum and modal depths for each individual shark were calculated, as well as the percentage of time spent below 30 m (the approximate maximum depth of the thermocline over the SCB continental shelf). GLMs were run in R version 3.1.3 (R Development Core Team; www.r-project.org/) using these metrics as dependent variables, and body length and sex as independent variables. The residuals of each GLM model were plotted in normal Q-Q plots to ensure that linear models were appropriate.

Fishery and tag-recapture data analyses

To better understand the spatial distribution of juvenile thresher sharks in California waters, an analysis of commercial fishery thresher shark catch data was conducted using data from the NMFS Gillnet Fishery Observer Program for the 1990 to 2013 seasons. Location data for all juvenile threshers captured in the CA-DGF and in the combined small mesh gillnet fisheries targeting halibut, white seabass, and bottom sharks were plotted separately. We also examined the limited observer records for Oregon and Washington fisheries, but did not include these in our analyses due to the absence of juvenile thresher sharks in those datasets. A monthly analysis of latitudinal variability was conducted using NMFS conventional tag-recapture data from thresher sharks tagged in the SCB during research cruises over the period from 1998 to 2012. We plotted the locations of all thresher sharks <120 cm FL when recaptured. In addition, the geographic data from the satellite tags were included in the statistical analysis of monthly latitudinal variation.

RESULTS

Satellite tagging

A total of 23 juvenile thresher sharks ranging in size from 72 to 110 cm FL were satellite-tagged throughout the SCB, in locations extending from Imperial Beach, CA (32.7°N, 117.2°W) north to Point Conception (34.4°N, 120.0°W) (Table 1). Two of the tags failed to collect data and pop off, but both sharks were recaptured by fishermen (tags had monetary reward and contact information printed on the outside), providing point-to-point estimates of minimum

Table 1. Juvenile common thresher sharks tracked with pop-off satellite archival tags (PSAT) in US and Mexican waters. FL: fork length; pop-off code S: over continental shelf; O: offshore of continental shelf; ND: could not be accurately determined due to delay between pop-off and initiation of transmission; R: shark recaptured but no tag data recovered (pop-off location and date refer to recapture, days tracked refers to time at liberty). % Data: percentage of total archived data (15 min resolution) transmitted; 100% denotes that tag (and all data at 2 min resolution) was physically recovered. Dist: straight-line distance from tagging to pop-off location

Shark ID#	Sex	FL (cm)	Deploy date (dd-mo-yy)	Deployment Latitude (°N)	Deployment Longitude (°W)	Pop-off date (dd-mo-yy)	Pop-off Latitude (°N)	Pop-off Longitude (°W)	Pop-off Code	Days tracked	% Data	Dist (km)
95142	F	88	06-Sep-09	34.43	119.93	06-Jan-10	34.24	119.56	S	122	75	40
95144	M	80	07-Sep-09	34.46	120.05	01-Oct-09	34.41	120.46	S	24	99	38
95145	M	81	05-Sep-09	34.33	119.42	03-Feb-10	34.33	119.69	S	151	34	25
95146	M	106	08-Sep-09	34.41	119.63	08-Feb-10	34.36	120.38	O	153	78	69
95151	F	75	06-Sep-09	34.43	119.93	06-Mar-10	32.73	117.33	S	181	77	307
95152	M	77	06-Sep-09	34.43	119.93	06-Dec-09	34.20	119.36	S	91	70	58
95153	M	82	05-Sep-09	34.41	119.57	05-Dec-09	33.94	119.58	O	122	100	52
95155	F	81	05-Sep-09	34.41	119.57	06-Mar-10	34.23	119.44	S	182	100	23
95139	F	95	05-Sep-09	34.41	119.57	05-Dec-09	34.43	120.11	S	91	100	50
95140	M	81	04-Sep-09	34.39	119.53	25-Sep-09	34.24	119.31	S	21	100	26
95141	M	92	05-Sep-09	34.41	119.57	25-Dec-09	34.92	120.78	S	111	100	125
95143	F	72	04-Sep-09	34.34	119.43	04-Jan-10	35.16	120.84	S	122	69	158
95147	M	78	05-Sep-09	34.26	119.33	08-Jan-10	33.44	118.36	ND	125	84	128
95148	F	88	04-Sep-09	34.30	119.37	22-Jan-10	31.46	116.73	S	140	83	402
95150	M	76	04-Sep-09	34.39	119.53	27-Feb-10	34.00	118.80	ND	176	100	80
95154	F	110	09-Sep-09	34.03	118.86	03-Feb-10	35.32	120.91	S	147	19	236
41494	F	86	20-Sep-08	32.60	117.16	20-Mar-09	28.69	114.85	S	181	100	490
41541	F	73	20-Sep-08	32.60	117.15	26-Sep-08	32.51	117.13	S	6	87	10
41492	F	85	20-Sep-08	32.60	117.15	05-Oct-08	34.04	118.64	ND	15	34	213
41532	F	86	20-Sep-08	32.60	117.15	20-Mar-09	32.36	117.13	S	181	32	27
41496	F	96	21-Sep-08	32.61	117.17	09-Aug-09	33.73	118.17	R, ND	322	0	157
41512	F	87	21-Sep-08	32.60	117.17	21-Mar-09	32.53	117.13	S	181	100	9
41542	F	95	03-Oct-07	32.66	117.17	10-Oct-08	30.82	116.08	R, ND	373	0	229

distance traveled. Straight-line travel distance between tagging and pop-off/recapture locations ranged from 9 to 490 km; the longest time at liberty (TAL) was 373 d. No significant correlation was found between shark size, TAL, or distance traveled (correlation analysis, $p > 0.05$).

Most tags popped off within southern California waters. However, 3 sharks traveled north of Point Conception to waters offshore of Morro Bay, CA (35.3°N), while 4 sharks traveled south into Mexican waters, one as far south as Bahia Sebastian Vizcaino (28.7°N) (Fig. 1A). Latitudinal variability in pop-off location for all satellite tagged sharks is shown in Fig. 2. Of the 18 tags for which pop-off locations could be accurately determined, 16 (89%) were in waters over the continental shelf (Table 1). Fig. 3 shows the estimated overall movement paths for the 7 sharks with full archival datasets over periods of up to 6 mo, while Fig. 4 shows the isolated latitudinal displacement for the same sharks.

Tagged juvenile threshers exhibited a diel pattern of vertical distribution. By night, tagged sharks primarily inhabited the upper 30 m of the water column, with little vertical variability. Daytime depths were significantly deeper (Mann-Whitney *U*-test, $p < 0.001$), with sharks primarily remaining in the upper 40 to 50 m of the water column (Fig. 5A). In addition, daytime depth distribution typically fell into 1 of 2 distinct modes: a 'shallow' mode, characterized by a lack of diving activity, or a 'deep' mode, characterized by frequent dives to depths that often exceeded 50 m (as previously described for adult thresher sharks in Cartamil et al. (2011b). Fig. 6 shows a representative archival dataset, illustrating typical shallow and deep mode patterns, as well as diel differences in vertical habitat utilization. The greatest depth attained by any shark was 192 m (Fig. 6A). Sharks encountered a temperature range of 9 to 21°C, but were predominantly found in ambient water temperatures of 14 to 17°C, and inhabited significantly warmer temperatures at night than during the day (Mann-Whitney *U*-test, $p < 0.001$) (Fig. 5B). Mean (±SD) SSTs (estimated from upper 5 m depth readings) during shark tracks averaged 16.1 ± 1.5°C. The fast-Fourier transform analysis indicated the presence of peaks coinciding with a

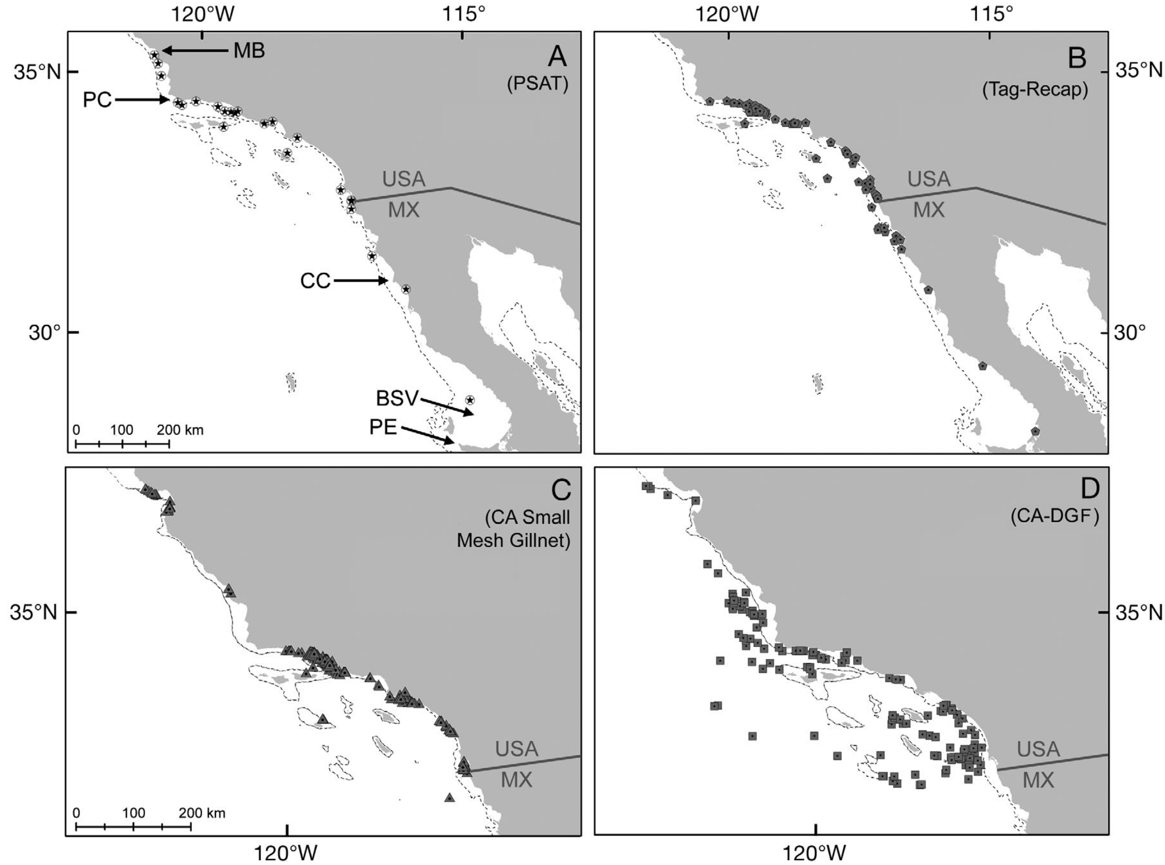

Fig. 1. Locations of juvenile thresher sharks *Alopias vulpinus* as determined by (A) pop-up archival satellite tag (PSAT) pop-off locations (n = 23) in the present study; (B) recaptures (n = 48) of juvenile threshers conventionally tagged by National Marine Fisheries Service (NMFS) research tagging cruises in the Southern California Bight (SCB) (1998 to 2012); (C) captures (n = 381) of all juvenile threshers observed in the California small mesh gillnet fisheries (1990 to 2012); (D) captures (n = 491) of all juvenile threshers observed in the California drift gillnet fishery (CA-DGF) (1990 to 2012). Dashed line indicates the outer edge of the continental shelf. MB: Morro Bay; PC: Point Conception; CC: Cabo Colonet; BSV: Bahia Sebastian Vizcaino; PE: Punta Eugenia; MX: Mexico

diel (24 h) cycle; however, no other cyclical patterns (such as lunar or tidal influence) were indicated.

For GLM analyses, normal Q-Q plots showed a linear relationship among model residuals, suggesting that the use of GLMs was appropriate. These analyses indicated that the range of vertical habitat utilized by juvenile threshers did not increase concomitantly with shark size, nor was there any difference in depth preference between male and female sharks ($p > 0.05$ in all cases).

Fisheries data

Juvenile thresher shark catch data from the NMFS Gillnet Fishery Observer Program are shown in Fig. 1C,D. There were 7215 sets observed for the small mesh gillnet fisheries (out of 103 112 sets made) and 8568 (out of 48 888 sets made) for the CA-DGF.

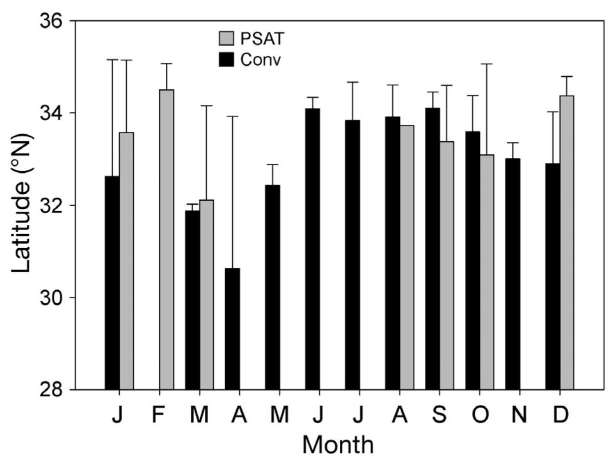

Fig. 2. Mean (±SE) monthly variability in known latitudinal position for juvenile thresher shark pop-up archival satellite tag (PSAT) pop-off locations (grey bars) and National Marine Fisheries Service (NMFS) conventional tag-recapture locations (black bars)

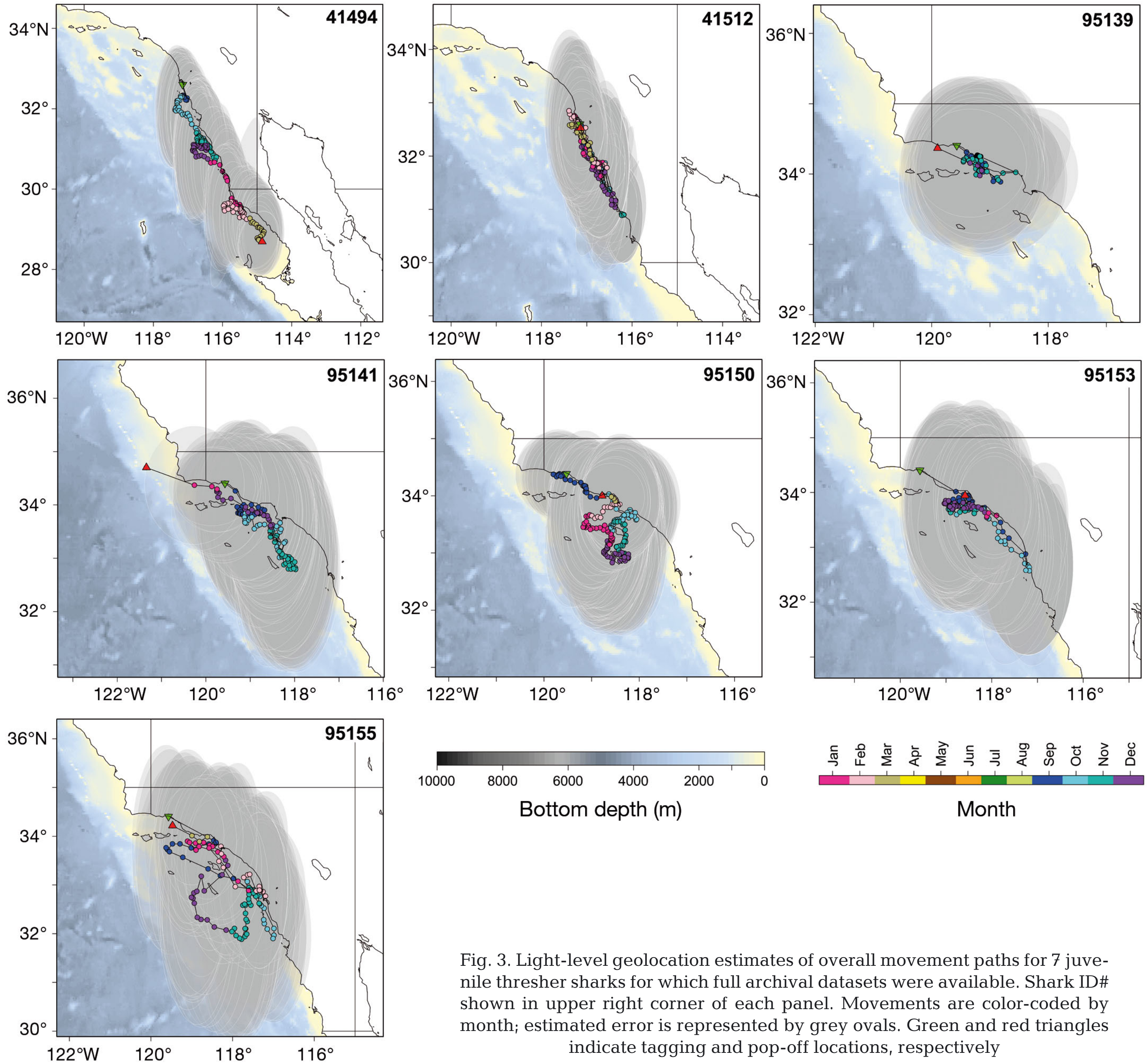

Fig. 3. Light-level geolocation estimates of overall movement paths for 7 juvenile thresher sharks for which full archival datasets were available. Shark ID# shown in upper right corner of each panel. Movements are color-coded by month; estimated error is represented by grey ovals. Green and red triangles indicate tagging and pop-off locations, respectively

Both plots suggest similar geographic distributions, with catch ranging from the US/Mexican border (the southern limit of both fisheries) to offshore of Morro Bay, CA, with some sporadic captures as far north as Monterey Bay, CA (~37°N). However, the proportion of juveniles to larger size classes was considerably different between fisheries. Juvenile threshers comprised 90.7% (381 of 420) of the total observed thresher catch for the small mesh gillnet fisheries, and only 9.7% (491 of 5086) for the CA-DGF.

SSTs (when available) for fishery-captured juvenile thresher sharks averaged 16.5 ± 1.9°C.

Tag-recapture data

Juvenile thresher recapture data from NMFS conventional tagging efforts in the SCB (n = 48; Fig. 1B) reveal a geographic distribution markedly similar to that suggested by satellite tagging results, with recaptures ranging from offshore of Morro Bay, CA to Bahia Sebastian Vizcaino, BC (Fig. 1B). The majority of recaptures, however, occurred between Point Conception and the US/Mexican border. The longest straight-line distance traveled by recaptured sharks was 856 km; the longest TAL was 571 d. Temporal

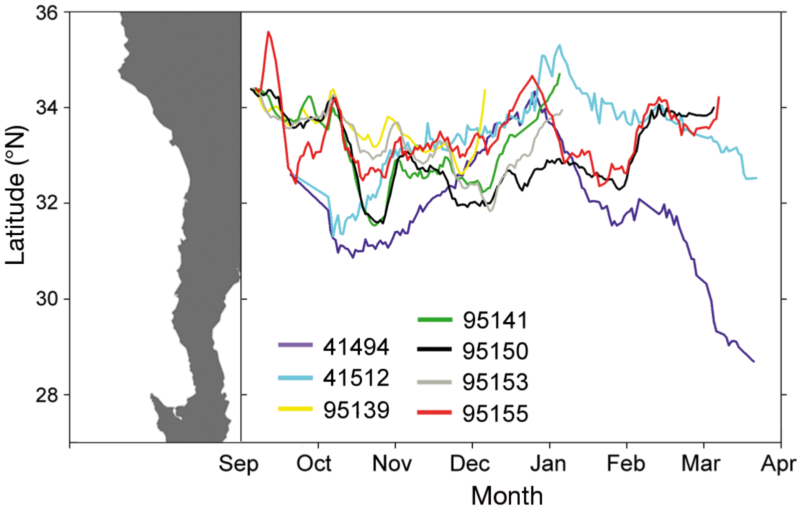

Fig. 4. Geolocation estimates of latitudinal movements for 7 juvenile thresher sharks for which full archival datasets were available. Latitude (*y*-axis) coincides with the inset figure showing those latitudes intersecting the west coast of California (USA) and Baja California (Mexico). Each colored line indicates the latitudinal movement of an individual shark (ID# shown) over the tag deployment period (up to 6 mo). For clarity, error estimates are not shown

illustration of these data (Fig. 2) indicates that conventionally tagged juveniles were generally recaptured farther south during the spring (March through May). When these data were pooled with the PSAT location data (Fig. 2), the mean latitude occupied by these juvenile threshers was significantly lower (i.e. farther south) during March and April than during other months (ANOVA, $p < 0.01$).

DISCUSSION

Geographic distribution and large-scale movement patterns

Our analysis of multiple datasets (satellite tagging, conventional tag-recapture, fishery capture data) converges upon a markedly similar pattern. These data indicate a larger 'core' geographic range for juvenile common thresher sharks than was previously reported (PFMC 2003), extending from Morro Bay, CA, at the northern boundary to Bahia Sebastian Vizcaino, BC, at the southern boundary (Fig. 1).

Point Conception (~34.5°N) likely plays a major zoogeographic role in limiting the northern distribution of juvenile thresher sharks, due to rapid water temperature declines that occur north of this point (Horn et al. 2006, Kennedy 2013). Based on satellite pop-off locations, only 3 sharks were observed north of Point Conception, and only as far as Morro Bay (100 km to the north). Observer data from the small mesh gillnet fisheries and CA-DGF also document the presence of juvenile threshers between Point Conception and Morro Bay, albeit fewer relative to the number in the SCB. Thus, the occurrence of juveniles north of Point

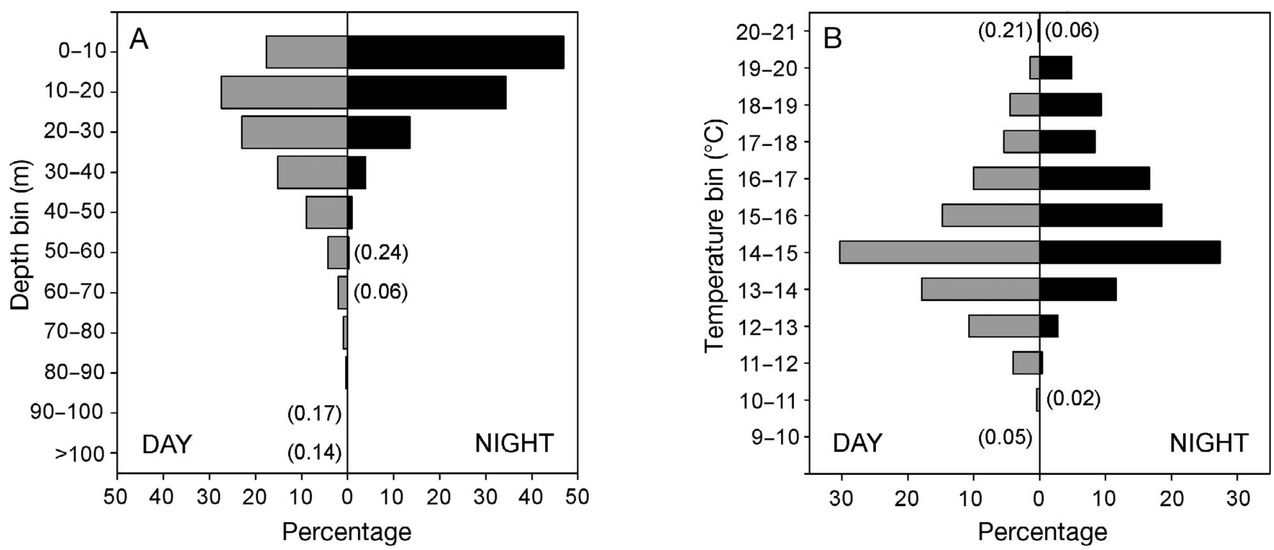

Fig. 5. Pooled juvenile common thresher shark (A) depth distributions (% frequency) in 10 m bins during day (grey) and night (black), and (B) temperature distributions (% frequency) in 1°C bins. For clarity, numbers in parentheses indicate bars with values <0.3

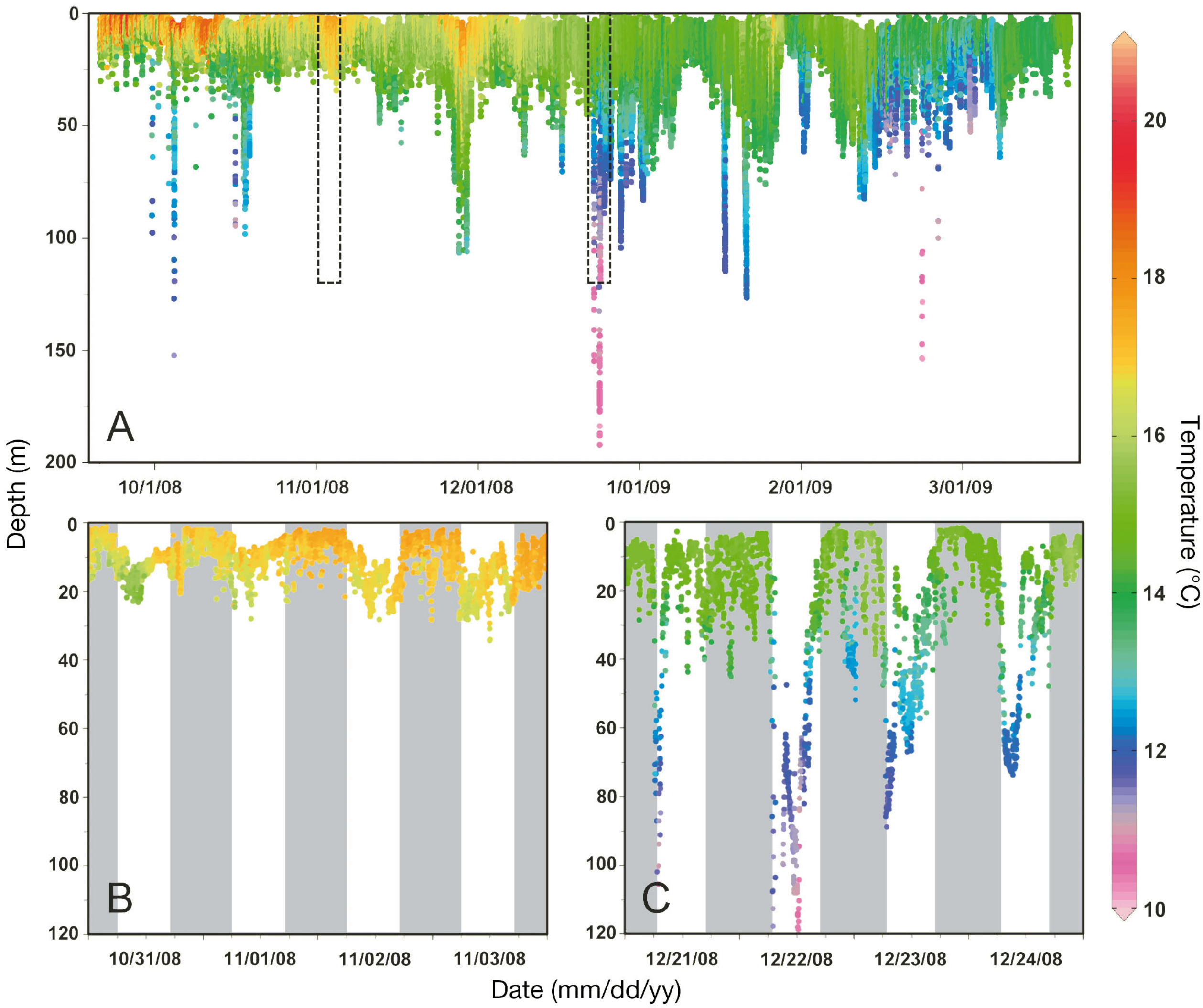

Fig. 6. (A) Representative archival time series of vertical movements and water column thermal structure for common thresher shark ID# 41494 over a 6 mo tag deployment period. Color denotes ambient water temperature. Dashed boxes in (A) indicate representative 4 d periods of typical (B) 'shallow' and (C) 'deep' mode behaviors. Grey shading in (B) and (C) represents nighttime hours

Conception may represent 'spillover' from warmer SCB waters. However, this habitat boundary could shift farther north in warm water years. In addition, fishery records indicate the occasional catch of juvenile threshers in the vicinity of Monterey Bay, CA (~37°N). The extent to which juvenile threshers utilize this area is unclear, and should be further investigated with survey and tagging efforts specific to this region.

Near the southern boundary of the juvenile thresher shark geographic range, satellite-tagged juveniles traveled as far south as Bahia Sebastian Vizcaino, the southern limit of which is demarcated by Punta Eugenia (Fig. 1A). Like Point Conception, Punta Eugenia is a major zoogeographic landmark, and the distribution of many fish species is thought to be limited by rapid increases in water temperatures south of this point (Lluch-Belda et al. 2003). This is consistent with NMFS conventional tagging results (Fig. 1A), as well as Cartamil et al. (2011a), who documented frequent catch of juvenile thresher sharks in Bahia Sebastian Vizcaino's artisanal gillnet fishery. In addition, a survey of artisanal elasmobranch fisheries south of Punta Eugenia by Ramirez-Amaro et al. (2013) did not report catch of any juvenile threshers. Thus, rather than being limited to the SCB, juvenile thresher core range is contained within the larger 'Californian' zoogeographic province, which extends from Point Conception, CA to Punta Eugenia, BC (Kennedy 2013). The boundaries of this core range, however, are likely highly variable, and influenced by large-scale environmental conditions and prey distribution.

In the eastern Pacific, a seasonal migration cycle has been suggested in which thresher sharks migrate southward from the SCB into warmer waters offshore of BC in the winter (Bedford 1992, Smith et al. 2008). However, this has not been conclusively demonstrated for either juvenile or adult threshers. In our PSAT study, most juvenile threshers did not migrate but rather remained within the SCB, and geolocation estimates of the 7 sharks with complete archival datasets did not reveal an obvious temporal pattern (Figs. 3 & 4) Our combined analysis of PSAT and conventional tag-recapture data suggests that juvenile threshers may travel farther south in March and April (Fig. 2), soon after water temperatures have reached their minimum in BC and southern California waters (Lluch-Belda 2000). However, the sample size for this analysis may not be sufficient to reliably define the full distribution by season, and further electronic studies are needed. Furthermore, a southward migration from the SCB would not necessarily result in warmer water temperatures, as the waters of BC's Pacific coast are highly influenced by upwelling (Lluch-Belda 2000), and may be colder than nearshore waters of the SCB at any given time. Thus, we suggest that juvenile threshers roam throughout the California province, opportunistically exploiting areas of increased prey density. Juvenile thresher shark diet is primarily composed of small coastal pelagic fishes, particularly northern anchovy *Engraulis mordax* and Pacific sardine *Sardinops sagax* (Preti et al. 2001, 2004, 2012), both of which are abundant within the California province region and themselves exhibit highly variable migratory behavior (Demer et al. 2012).

Juvenile threshers showed a strong habitat preference for continental shelf waters, as evidenced by the fact that 89% of satellite tags popped off over the continental shelf. These results are similar to those described by Cartamil et al. (2010b), who reported that 87% of positional fixes for acoustically tracked juvenile threshers were located over the continental shelf. Although the estimated movement paths shown in Fig. 3 suggest that 2 sharks (ID#s 95150 and 95155) may have made offshore excursions, these apparent movements may be spurious artefacts of the light-level geolocation estimation process, since the latitudinal confidence intervals for the estimated movements are extremely large. In addition, satellite-tagged juvenile threshers never attained depths greater than 200 m, the approximate maximum depth of the continental shelf in the California province region. A continental shelf habitat preference is also strongly corroborated by fishery catch data. In the CA setnet fishery, where set gillnets are deployed over the continental shelf, 90% of captured threshers were juveniles. By contrast, in the CA-DGF where drift gillnets are deployed offshore of the continental shelf, only 10% of captured threshers were juveniles. Although these 2 fisheries are not directly comparable in terms of shark catchability (mesh size in the CA setnet fishery averages approximately 22 cm and nets are set near the bottom, while the CA-DGF utilizes average mesh sizes of 50 cm and nets are set at depths ranging from 11 to 50 m below the surface), they provide additional evidence of a habitat disjuncture between juvenile and adult threshers.

Diel depth and temperature preferences

Satellite-tagged juvenile thresher sharks exhibited a distinct diel vertical distribution pattern, wherein sharks inhabited the upper 30 m of the water column by night, and moved into slightly deeper waters during the day (Figs. 5 & 6b). These patterns are consistent with previous electronic tagging studies of both juvenile (Cartamil et al. 2010b) and sub-adult and adult threshers (Cartamil et al. 2010a, 2011b), which suggested that thresher sharks are primarily daytime foragers, inhabiting deeper waters by day to more easily detect and approach schools of prey silhouetted by downwelling light.

All satellite-tagged sharks exhibited both deep and shallow modes of depth distribution (Fig. 6) at various points over their tracks. Shallow and deep modes, which have also been noted in previous studies of thresher sharks (Cartamil et al. 2011b) and other large marine fishes (e.g. Schaefer et al. 2007, Sepulveda et al. 2010), likely reflect the vertical distribution and abundance of prey. In the eastern Pacific, northern anchovy range in depth from 0 to 200 m, while Pacific sardine are found from 0 to 100 m (but more commonly from 0 to 50 m) (Demer et al. 2012, Zwolinski et al. 2012). Thus, sharks likely exhibit shallow mode behavior when these prey species are abundant near the surface, while a switch to the deep mode of vertical distribution may occur when their prey move into deeper waters.

Throughout the size range corresponding to the juvenile life history phase of threshers (FL < 120 cm), we found that the depth utilization of individual sharks did not increase as a function of size. However, the overall depth range of juvenile threshers (Cartamil et al. 2010b, present study) is generally truncated relative to the larger depth range exhibited by sub-adult and adult threshers (max. depth: 192 vs.

560 m; Baquero 2006, Cartamil et al. 2010a, 2011b, Heberer et al. 2010). This may reflect a greater capacity for heat retention and red muscle endothermy (Bernal & Sepulveda 2005) in sub-adult and adult sharks. As a thresher shark grows, the surface area-to-volume ratio of its body decreases and the heated medial red muscle becomes more insulated from ambient water, increasing its capacity for retention of metabolic heat. Thus, larger sharks may be better physiologically equipped to exploit greater depths. Indeed, thresher shark gill surface area in relation to body mass has a higher scaling exponent than that of most other fishes, likely associated with an increased capacity for endothermy with size (Wootton et al. 2015). This may also provide a physiological explanation for the expanded northward range of adult threshers into colder waters as far north as British Columbia, Canada (PFMC 2003).

Management implications

This study documents, for the first time, the movements and geographic range of juvenile thresher sharks in US and Mexican waters. Similar movements have been documented for juvenile white sharks (Weng et al. 2007). Our research highlights a potential conservation concern, in that juvenile threshers (as well as other shark species) in western BC continental shelf waters are highly vulnerable to capture in artisanal set gillnet fisheries, which target teleosts and elasmobranchs (Cartamil et al. 2011a). There have been recent efforts by Mexican fishery authorities to protect elasmobranch species subject to fishing pressure. Since May 2007, regulation NOM-029 restricts fishing activity in order to protect elasmobranchs within coastal waters and allow them to attain sexual maturity (DOF 2007). More recently, a seasonal (May through August) ban on directed fishing for elasmobranchs was instituted across Mexico (DOF 2012).

Although thresher sharks are considered to be sustainably managed in US waters (PFMC 2003), preliminary genetic analyses indicate that thresher sharks in the eastern Pacific belong to one large undifferentiated stock (D. Kacev unpubl. data). Thus, juvenile threshers are a 'shared resource' between the USA and Mexico, highlighting the need for binational management strategies. Specifically, there is a need for accurate estimates of juvenile thresher shark catch in Mexican waters, as well as estimates of the total annual landings of larger (sub-adult and adult) threshers captured in the Ensenada, BC, longline fishery (O. Sosa-Nishizaki unpubl. data). These data could be incorporated into binational stock assessments that take into account fishery mortality incurred in both countries.

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