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Movement ecology of young-of-the-year blue sharks *Prionace glauca* and shortfin makos *Isurus oxyrinchus* within a putative binational nursery area

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ABSTRACT: Managing pelagic shark stocks requires information about the movement patterns and fisheries interactions of all age classes, including young-of-the-year (YOY; age-0), which, for many species, is particularly scant. This study investigated the vertical and horizontal movements of YOY blue sharks *Prionace glauca* and shortfin makos *Isurus oxyrinchus* in the Southern California Bight (SCB) ecoregion using pop-up satellite archival tags (PSATs) and fishery data. Geolocation estimates from PSATs (n = 5 for each species) occurred entirely within the SCB ecoregion and exclusive economic zones of the USA and México (mean tracking period: 46.1 ± 24.8 d). YOY blue sharks spent 96.4 % of their time at <40 m depth (60.4 % <2 m) and exhibited reverse diel vertical migration (greater nighttime depths). YOY shortfin makos spent 97.0 % of their time at <40 m (24.8 % <2 m) and exhibited a 'midday dip' of 5–10 m below the surface, centered around solar noon. These differences in vertical movements likely reflect foraging tactics. Additionally, observer data from the California drift gillnet fishery suggest juvenile blue sharks and shortfin makos move seasonally along the coast, northward from late summer to early fall and southward from late autumn to early winter. Age classes for both species exhibited latitudinal segregation, with smaller blue sharks and larger shortfin makos found farther north. The SCB ecoregion has long been regarded as a nursery area for both species; however, our data, in combination with previous studies, suggest this important habitat is much more extensive, comprising the highly productive continental margins spanning approximately 27.7–46.2° N for blue sharks and 23.4–34.5° N for shortfin makos.

KEY WORDS: Satellite tracking · Telemetry · Argos · PSAT · Diel vertical migration · Partial migration · Size segregation · Niche partitioning

1. INTRODUCTION

Pelagic sharks (subclass Elasmobranchii) are widely distributed throughout the upper oceanic realm, with many species ranging circumglobally (Compagno 2001). Over 60 % of these species are threatened according to International Union for the Conservation of Nature (IUCN) Red List criteria (Dulvy et al. 2008), compared to only one-quarter of all elasmobranch species (Dulvy et al. 2014), and most pelagic shark species have undergone significant population declines (Baum et al. 2003, Baum & Myers 2004, Clarke et al. 2013). On the high seas, pelagic sharks are subject to intense fishing pressure, often caught as incidental bycatch in tuna and billfish fisheries and retained for their increasingly valuable meat and fins (Clarke et al. 2007, Hareide et al. 2007, Camhi et al. 2008). Fishery management of these species is acutely

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*Corresponding author: anosal@sandiego.edu difficult because adults typically inhabit waters beyond the continental margins, and their migratory ranges fall largely outside of exclusive economic zones (EEZs) and thus the monitoring and enforcement of national jurisdictions (Harrison et al. 2018). However, the juveniles of some pelagic shark species do occupy waters above the continental margins, largely within EEZs, before recruiting offshore (Branstetter 1987, Goldman & Musick 2008, Cartamil et al. 2010). Managing juvenile stocks within EEZs can be feasible and impactful, as part of a comprehensive plan that also considers older individuals in the open ocean (Camhi et al. 2008, Kinney & Simpfendorfer 2009); however, this approach requires information about the movement patterns and fisheries interactions of juveniles, including young-of-the-year (YOY; age-0) individuals, over the continental margins.

Two common species of pelagic sharks that inhabit the continental margins as juveniles, but oceanic habitat as adults, are the blue shark *Prionace glauca* and shortfin mako *Isurus oxyrinchus* (hereafter referred to as mako shark). Blue sharks are perhaps the most widely distributed, abundant, and frequently caught shark species in the world (Walker 1998, Stevens et al. 2000, Camhi et al. 2008), while mako sharks are also widely distributed but more common at lower latitudes (Compagno 2001). Both species are major bycatch components in pelagic gillnet and longline fisheries targeting swordfish *Xiphias gladius* and tuna *Thunnus* spp. (Camhi et al. 2008, Mandelman et al. 2008, Nakano & Stevens 2008). Blue sharks are often discarded at sea, with significant mortality rates (Campana et al. 2009, Musyl et al. 2011), while mako sharks are usually retained as secondary targets due to their high-value meat (Casey & Kohler 1992, Campana et al. 2005). In addition, both species feature prominently in the international shark fin market (Clarke et al. 2006). Blue sharks are assessed globally as Near Threatened and mako sharks as Endangered under the IUCN Red List (Stevens 2009, Rigby et al. 2019).

In the eastern North Pacific, the Southern California Bight (SCB) is widely regarded as a nursery area for blue (Hanan et al. 1993, Holts et al. 2001) and mako sharks (Hanan et al. 1993, O'Brien & Sunada 1994, Taylor & Bedford 2001). By convention, the SCB commonly refers to the area above the continental margin from Point Conception, California, USA, southeast 575 km to Cabo Colonet, Baja California, México (NRC 1990). However, the SCB ecoregion, having a relatively homogenous species composition distinct from adjacent systems (Spalding et al. 2007), extends farther south, to Punta Abreojos (see Fig. 1). In this study, we used the latter, more ecologically relevant, definition of the SCB. As a result of coastal upwelling and current patterns, this region is highly productive and supports an abundance of prey species common in these sharks' diets (Bograd et al. 2009, Preti et al. 2012). According to a fishery-independent longline survey conducted in the US sector of the SCB ecoregion from 1994–2013, the overwhelming majority of blue and mako sharks caught here are immature, with 81% of blue sharks and 58% of mako sharks belonging to age classes 0–2 (Runcie et al. 2016).

Very little is known about the horizontal and vertical movements of young blue and mako sharks in the SCB ecoregion. Previous research has been limited to short-term active acoustic telemetry of larger juveniles (Holts & Bedford 1993, Klimley et al. 2002, Sepulveda et al. 2004), as well as some tag–recapture studies (Wells et al. 2013, 2017). Studies of the long-term movement patterns of juvenile blue and mako sharks, especially YOY individuals, using pop-up satellite archival tags (PSATs) have previously been unfeasible due to the large size of the tags. However, the relatively recent advent of 'miniaturized' PSATs (e.g. Microwave Telemetry X-Tag) has made this possible.

This study is the first to use PSATs to quantify the vertical and horizontal movements of YOY blue and mako sharks. Our objectives were to determine early life history behavior and habitat preferences of these 2 species, as well as the degree to which their habitats overlap. These results were analyzed in the context of historical commercial fishery data to elucidate large-scale trends in YOY distribution in the SCB ecoregion over seasonal and annual scales, and their relationship to the sustainability of pelagic fisheries.

2. MATERIALS AND METHODS

Juvenile blue and mako sharks were captured either by rod and reel or longline. Sharks caught by rod and reel (B1, B2, B3, B5, M1, and M2; Table 1) were first attracted to the fishing vessel (6 m skiff) with chum and then captured using 80 lb (36 kg) test monofilament line connected to a 5/0 circle hook baited with a whole Pacific chub mackerel *Scomber japonicus*. Fight time was typically less than 2 min. Longline-captured fish (B4, M3, M4, and M5; Table 1) were caught during NOAA's 2012 shark abundance survey (Runcie et al. 2016) using a 2 nautical mile (nmi; 3.7 km) stainless steel longline rigged with approximately 200 stainless steel leaders (5 m), each

Table 1. Young-of-the-year (except shark B-5; age-1) blue sharks *Prionace glauca* and mako sharks *Isurus oxyrinchus* tagged with pop-up satellite archival tags (Microwave Telemetry X-Tag). X-Tag was recovered for shark M-1, yielding the full archival data set at 2-min resolution. The other X-Tags were not physically recovered; however, all of the 15 min resolution transmitted data were received. FL: fork length; displacement: straight-line distance between tagging and pop-up locations

ID	Sex	FL (cm)	Tag deployment			Tag pop-off			Days tracked	Displacement (km)
			Date (dd-mo-yy)	Latitude (°N)	Longitude (°W)	Date (dd-mo-yy)	Latitude (°N)	Longitude (°W)		
Blue sharks *P. glauca*										
B-1	F	75	07-Oct-10	32.877	117.468	06-Dec-10	30.045	116.288	60	333
B-2	F	67	07-Oct-10	32.877	117.468	01-Jan-11	28.547	116.322	86	492
B-3	F	70	13-Oct-10	32.905	117.435	04-Nov-10	26.886	117.270	22	667
B-4	F	79	03-Jul-12	32.515	118.446	17-Sep-12	31.242	120.286	76	224
B-5	F	95	28-Nov-13	28.365	114.453	14-Jan-14	25.243	115.205	47	354
Mako sharks *I. oxyrhinchus*										
M-1	M	89	07-Oct-10	32.877	117.468	16-Nov-10	30.298	117.637	40	286
M-2	F	71	12-Oct-10	32.905	117.435	11-Dec-10	31.692	117.465	60	135
M-3	F	70	02-Jul-12	32.628	117.977	12-Aug-12	31.558	119.062	41	157
M-4	M	88	05-Jul-12	33.615	118.540	18-Jul-12	31.365	116.811	13	298
M-5	F	82	09-Jul-12	32.917	117.858	25-Jul-12	30.833	119.670	16	288

terminating with a 9/0 J-style hook also baited with a whole mackerel. Average soak time for the longline hooks was approximately 4 h. Sharks were only considered for tagging if hook placement was in the jaw and the shark appeared in excellent condition.

Upon capture, sharks were brought on board for tagging, measurement (straight fork length, 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, approximately 6 cm posterior to the insertion site, which was loosely cinched around the tag base to minimize lateral tag movement. The entire tagging procedure lasted approximately 5 min. Only mako sharks <90 cm FL, and blue sharks <80 cm FL (with one exception) were tagged (Table 1).

X-Tags measured and archived temperature (0.17°C resolution), depth (variable resolution from 0.33–1.34 m), and light level (arbitrary intensity units) every 2 min. Tags were programmed to detach from the sharks 3–6 mo after deployment, at which point they randomly transmitted raw data points at a 15 min resolution (i.e. no binned data) until the battery was exhausted. After release, one transmitting tag (shark M-1) was recovered using a Series 6000 radio direction finding system (Doppler Systems). In this case, the full archival data set was recovered at the native 2 min resolution. Diel differences in depth and temperature were analyzed for each species using a generalized linear mixed model (GLMM) with time (day or night; local times of sunrise and sunset from US Naval Observatory) as a fixed effect and individual shark as a random effect. The GLMM was run on a subsample of 1000 random observations from each shark to reduce the effects of temporal autocorrelation, using the 'glmmPQL' function in R 3.5.0 ('MASS' package; Ripley et al. 2018, R Core Team 2018).

X-Tag light-based geolocations were provided by the manufacturer using its proprietary algorithm in which longitude and latitude pairs are calculated based on sunrise and sunset times. These position estimates were refined using a state-space Kalman filter model with sea surface temperature (SST) matching (Ukfsst; Lam et al. 2008), using NOAA Optimum Interpolation (OI) SST V2 1° resolution imagery. The model utilizes an underlying random walk movement model that describes the overall diffusion and advection (speed, derived from velocity in the north–south and east–west directions) for the entire track (Sibert et al. 2003). Bathymetric correction was only applied for shark B-1 (Table 1) due to a small number of positions that were misplaced on land (Galuardi et al. 2010) after the initial Kalman filter correction. Minimum convex polygons (MCPs) and 95 and 50% kernel utilization distributions (KUDs) were calculated in R ('adehabitatHR' package; Calenge 2006). To calculate the KUDs, a rule-based ad hoc method was used to determine the bandwidth, or smoothing parameter, h (Kie 2013). Briefly, the reference bandwidth h_{ref} was reduced by increments of $0.05h_{\text{ref}}$ such that $h_{\text{ad hoc}}$ was the smallest increment of h_{ref} that resulted in a contiguous 95% activity space polygon with no lacunae.

In addition to tagging, shark catch data from the large-mesh drift gillnet fishery from 1990–2017 were compiled from the West Coast NOAA fishery observer database and assessed in order to examine blue and mako shark size distribution and seasonal latitudinal movements. For each age class of each species, captures were binned by month of year and by half-degree latitude, and weighted by catch per unit effort (CPUE). To calculate effort, all large-mesh gillnet sets from the database were binned by month of year and half-degree latitude. Weighting by CPUE accounted for time and area closures, which changed multiple times over the course of the data set. Because extreme outliers could drastically affect the data and lead to misleading results, the monthly weighted mean latitude of capture was calculated from the middle 95% of records (i.e. up to 2.5% of the northernmost and southernmost captures in a month were ignored). For samples of <40 captures, no records were ignored. For these and other analyses, ages were determined as follows: for mako sharks, individuals with FL < 100 cm were age-0 (YOY), 100 cm ≤ FL < 125 cm were age-1, and 125 cm ≤ FL < 150 cm were age-2 (Pratt & Casey 1983, Wells et al. 2013); for blue sharks, individuals with FL < 80 cm were age-0 (YOY), 80 ≤ FL < 105 were age-1, and 105 ≤ FL < 120 cm were age-2 (Stevens 1975, Cailliet & Bedford 1983, Blanco-Parra et al. 2008). No data were available from February–April due to the closure of the fishery within the US EEZ.

3. RESULTS

3.1. Satellite tagging

A total of 5 X-Tags were deployed on blue sharks (all females; FL mean ± SD: 77.2 ± 11.0 cm; range: 67–95 cm) and 5 X-Tags were deployed on mako sharks (2 males and 3 females; 80.0 ± 9.1 cm; range: 70–89 cm). Except for shark B-5 (a 1 yr old blue shark tagged in November 2013 in Bahía de Sebastián Vizcáino, México), the other 9 sharks were YOY and tagged in July and October of 2010 and 2012 in the SCB ecoregion between 32.515 and 33.615° N and 117.435 and 118.540° W (Table 1). Most X-Tags were shed prior to their programmed pop-off dates, averaging 58.2 ± 25.1 d (range: 22–86 d) on blue sharks and 34.0 ± 19.5 d (range: 13–60 d) on mako sharks. Net displacement (straight-line distance between tagging and pop-off locations) averaged 414.2 ± 170.6 km for blue sharks (range: 224–667 km) and 232.6 ± 79.9 km (range: 135–298 km) for mako sharks. Accounting for differences in X-Tag deployment durations, net displacement per day tracked averaged 10.4 ± 11.2 km (range: 2.9–30.3 km) for blue sharks and 10.8 ± 9.1 km (range: 2.2–22.9 km) for mako sharks (Table 1).

Geolocation estimates for tagged blue and mako sharks fell entirely within the SCB ecoregion, from just north of Catalina Island, California, USA, to just south of Punta Eugenia, México, within approximately 300 km of shore and with very few positions over the continental shelf (Fig. 1; individual tracks provided in

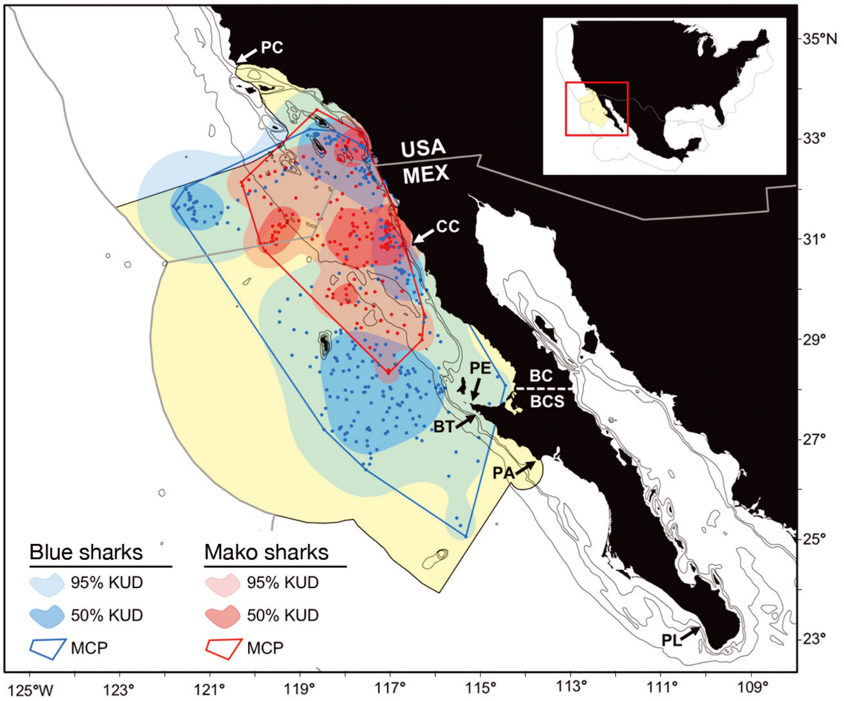

Fig. 1. Daily position estimates for 5 blue sharks *Prionace glauca* (blue dots) and 5 mako sharks *Isurus oxyrinchus* (red dots) tagged with pop-up satellite archival tags (Microwave Telemetry X-Tag). Yellow shading: Southern California Bight ecoregion (Spalding et al. 2007); gray lines: exclusive economic zones of the United States and México; white dashed line: border between the Mexican states of Baja California (BC) and Baja California Sur (BCS). Kernel utilization distributions (KUDs) are shown for each species along with minimum convex polygons (MCPs). Bathymetry is shown with 200, 500, and 2500 m isobaths. Individual tracks with error estimates are provided in Fig. S1 in the Supplement. PC: Point Conception; CC: Cabo Colonet; PE: Punta Eugenia; BT: Bahía Tortugas; PA: Punta Abreojos; PL: Punta Lobos

Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m623p099_supp.pdf). Position estimates also fell entirely within the EEZs of the USA and México. The areas of the 95 and 50% KUDs were 390 935 and 105 430 km^2 for blue sharks ($h_{\text{ad hoc}} = 0.65h_{\text{ref}} = 49\,111$), respectively, and 139 184 and 34 984 km^2 for mako sharks ($h_{\text{ad hoc}} = 0.55h_{\text{ref}} = 24\,205$), respectively. The areas of the MCPs were 322 150 and 125 146 km^2 for blue and mako sharks, respectively (Fig. 1).

Blue sharks spent most of their time near the surface, averaging 60.4 ± 2.2% of time at depths <2 m, especially during the day, when they spent 77.2 ± 5.1% of time at depths of <2 m, compared to only 45.8 ± 5.8% of time at night (Fig. 2A). On average, blue sharks spent 96.4 ± 2.9% of time at depths of <40 m (Fig. 3). Blue sharks displayed significant diel differences in depth, averaging 3.4 ± 1.2 m during the day and 11.8 ± 4.0 m at night (GLMM: slope = 6.333 ± 0.427 SE, df = 4994, t = 14.838, $p < 0.001$; Fig. 3A,B, Table 2). Diel patterns were generally robust and often persisted over several weeks; however, at times, blue sharks occupied greater depths only during crepuscular periods (Fig. 4A,B). Surrounding water temperatures averaged 17.9 ± 0.5°C during the day and 17.7 ± 0.6°C at night (GLMM: slope = −0.150 ± 0.031 SE, df = 4994, t = −4.806, $p < 0.001$; Fig. 5A, Table 2).

Compared to blue sharks, mako sharks spent less of their time near the surface (averaging 24.8 ± 8.6% of time at depths of <2 m; Fig. 2B), but a similar 97.0 ± 3.4% of time at depths of <40 m (Fig. 3C). Mako shark depth averaged 11.1 ± 2.1 m during the day and 9.2 ± 4.5 m at night (GLMM: slope = −1.614 ± 0.339 SE, df = 4994, t = −4.764, $p < 0.001$; Table 2). Mako sharks exhibited greater inter-individual variation in their depth distribution; for example, some were deeper at night, some were deeper during the day, and some showed no diel pattern at all (Fig. S2). During one track, a mako shark switched modes from swimming deeper at night to swimming deeper during the day (Fig. 4C–F). The most conspicuous feature of YOY mako shark depth distribution behavior was a 'midday dip' to depths of 5–10 m below the surface (Fig. 2B). These 'midday dips' were gradual and

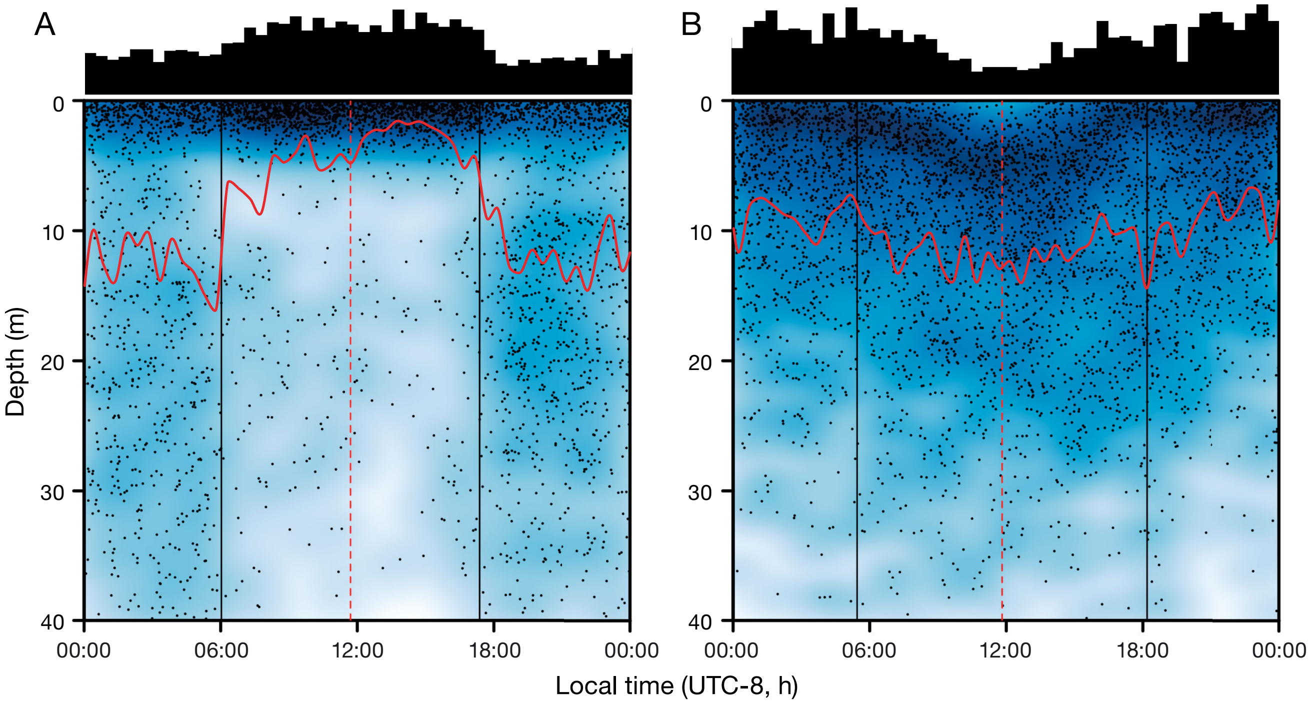

Fig. 2. Combined time series depth data for (A) 5 blue sharks *Prionace glauca* and (B) 5 mako sharks *Isurus oxyrinchus*. Each scatter plot contains 1000 randomly selected data points from every individual of that species (i.e. 5000 data points per scatter plot). Scatter plots show shark depth (m) versus time of day (UTC-8, local time) as black dots superimposed over a smoothed 2-dimensional kernel density image (shown as varyingly intense shades of blue) of the scatter plot. Only depths of <40 m are shown because these comprised 96.4 and 97.0% of the depth data for blue and mako sharks, respectively. Average depth for the entire data set (computed in 0.5 h bins) is indicated for each species by the solid red line superimposed over the respective scatter plot. Histograms above each scatter plot: relative frequency of shark depths occurring <4 m from the surface versus time of day (0.5 h bins); vertical black lines: average times of sunrise and sunset during the tracks; vertical red dashed lines: average times of local noon. Fig. S2 in the Supplement contains the scatter plots for individual sharks

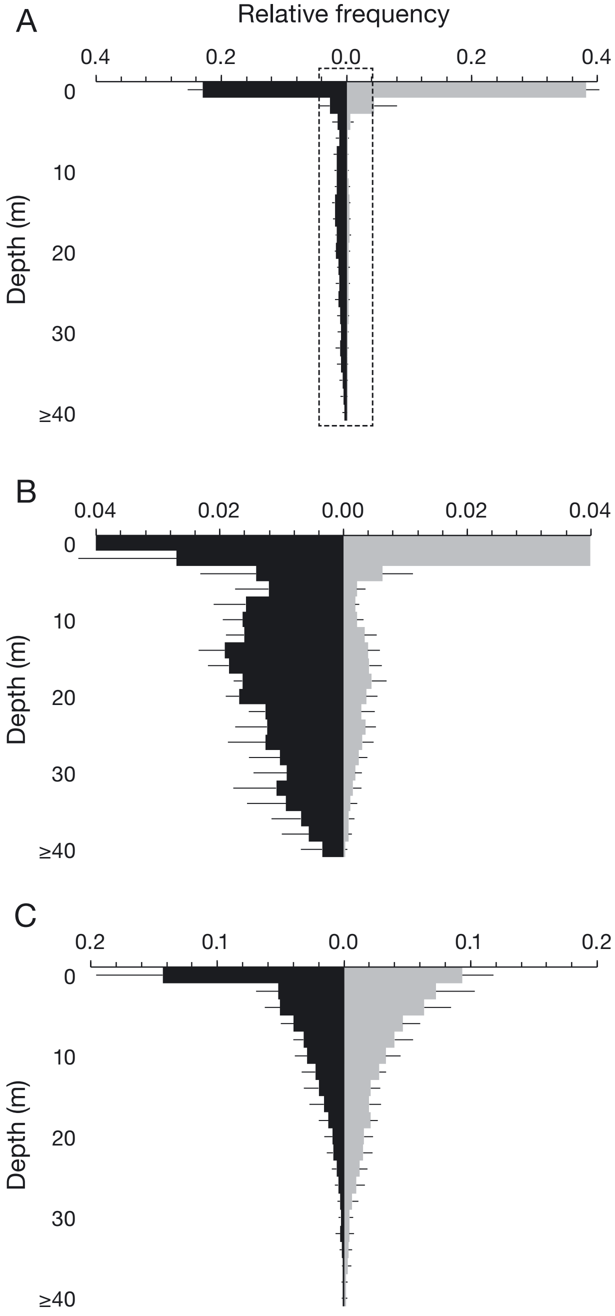

Fig. 3. Average depth–frequency distributions (2 m bins; e.g. 10 m indicates depths of ≥10 but <12 m) with standard deviation for (A,B) blue sharks *Prionace glauca* and (C) mako sharks *Isurus oxyrinchus*. (B) is a zoomed view of the box shown in (A). Gray shading: daytime distributions (sunrise to sunset); black: nighttime distributions (sunset to sunrise)

centered on the times of local noon, when the sun was highest in the sky (Figs. 2B, 4 & S2). Water temperature surrounding mako sharks averaged 17.4 ± 0.6°C during the day and 17.5 ± 0.4°C at night (GLMM: slope = 0.130 ± 0.037 SE, df = 4994, $t = 3.477$, $p < 0.001$; Fig. 5B, Table 2).

3.2. Fishery-dependent data

There were 12 509 records of blue sharks in the California drift gillnet fishery observer database. Of these, 722 records had no length measurements and 9493 records had both FL and total length (TL) measurements. The latter records were linearly regressed, yielding the equation TL = 1.1898 × FL + 3.1787 (r^2 = 0.986), which was used to convert 282 records with TL only to FL. This resulted in a total of 11 787 blue shark records with FL for use in subsequent analyses. Mean (±SD) blue shark FL was 115.2 ± 29.3 cm. There were also 7621 mako shark records in the observer database. Of these, 2180 records had no length measurements and 1933 records had both FL and TL. When linearly regressed, the latter records produced the equation TL = 1.1067 × FL + 1.5505 (r^2 = 0.988), which was used to convert 31 records with TL only to FL. This resulted in a total of 5441 mako shark records with FL for use in subsequent analyses. Mean mako shark FL was 121.5 ± 32.5 cm. Of 8882 large-mesh gillnet sets in the observer database, 15 had no latitude and 238 had no date recorded and were deleted, leaving 8629 sets with which to calculate effort.

Blue shark captures were fairly evenly distributed along the US west coast; 41.2 % of YOY (age-0) blue shark records (n = 1192) came from south of Point Conception (34.5° N), the northern boundary of the SCB ecoregion. Similarly, 36.7 % of age-1 blue sharks (n = 3294), 42.5 % of age-2 blue sharks (n = 2431), and 45.3 % of age-3+ blue sharks (n = 4870) were captured south of Point Conception (Fig. 6A–D). CPUE for age-0, age-1, age-2, and age-3+ sharks was 2.7, 3.4, 2.6, and 2.3 times higher, respectively, north of Point Conception compared to south. Unlike blue sharks, nearly all (96.2 %) of the YOY (age-0) mako shark records (n = 1559) occurred south of Point Conception. Additionally, 91.7 % of age-1 mako sharks (n = 1557), 78.2 % of age-2 mako sharks (n = 1332), and 56.7 % of age-3+ mako sharks (n = 993) were captured south of Point Conception (Fig. 6E–H). CPUE for age-0, age-1, and age-2 mako sharks was 28.7, 7.6, and 2.0 times higher, respectively, south of Point Conception compared to north. CPUE for age-3+ mako sharks was 1.4 times higher north of Point Conception compared to south. This latitudinal variation in mako shark age class, with larger individuals captured farther north, was especially strong in early autumn (September and October; Fig. 7). The distribution of blue shark age classes also exhibited latitudinal variation with a more dramatic northward shift during the summer and early autumn than makos,

Table 2. Summary depth and temperature data for young-of-the-year blue sharks *Prionace glauca* and mako sharks *Isurus oxyrinchus* tagged with pop-up satellite archival tags (Microwave Telemetry X-Tag)

ID	Overall depth (m)	Day depth (m)	Night depth (m)	Overall Depth range (m)		Overall temp. (C°)	Day temp. (C°)	Night temp. (C°)	Overall Temp. range (C°)	
	Mean ± SD	Mean ± SD	Mean ± SD	Track	Mean daily	Mean ± SD	Mean ± SD	Mean ± SD	Track	Mean daily
Blue sharks *P. glauca*										
B-1	7.8 ± 13.3	2.6 ± 7.1	12.5 ± 15.6	0–183	0–75.1	17.7 ± 1.3	18.1 ± 1.0	17.4 ± 1.4	9.5–22.2	12.9–18.7
B-2	7.8 ± 12.5	2.2 ± 6.2	12.9 ± 14.5	0–253	0–55.9	17.2 ± 1.2	17.3 ± 1.2	17.1 ± 1.2	9.2–20.7	14.2–17.9
B-3	5.2 ± 10.1	3.0 ± 8.6	7.2 ± 10.9	0–274	0–90.3	18.5 ± 0.7	18.6 ± 0.8	18.5 ± 0.7	10.1–20.7	14.2–19.2
B-4	6.2 ± 10.8	4.2 ± 9.3	8.7 ± 11.9	0–199	0–76.9	17.4 ± 1.0	17.5 ± 1.0	17.4 ± 0.9	8.9–20.0	12.8–18.0
B-5	12.1 ± 21.4	4.9 ± 22.0	17.5 ± 19.2	0–231	0–84.7	18.1 ± 1.1	18.2 ± 1.2	18.0 ± 1.1	9.6–20.9	13.7–18.7
Mako sharks *I. oxyrhinchus*										
M-1	14.3 ± 16.6	12.0 ± 14.3	16.2 ± 18.2	0–193	0–77.5	17.8 ± 1.1	17.9 ± 1.1	17.6 ± 1.0	9.8–20.2	13.7–18.7
M-2	9.9 ± 8.8	11.9 ± 9.7	8.3 ± 7.7	0–172	0–70.4	17.2 ± 1.2	17.1 ± 1.3	17.2 ± 1.2	10.1–20.0	13.2–17.8
M-3	9.4 ± 10.3	12.2 ± 11.1	5.7 ± 7.6	0–118	0–45.3	17.2 ± 1.4	17.1 ± 1.4	17.3 ± 1.2	10.1–19.9	13.8–18.1
M-4	11.3 ± 12.6	11.9 ± 13.6	10.6 ± 11.1	0–91	0–57.6	17.0 ± 1.6	16.7 ± 1.7	17.3 ± 1.6	10.7–20.4	12.3–18.3
M-5	6.3 ± 8.0	7.3 ± 9.2	5.0 ± 6.0	0–134	0–41.8	18.1 ± 1.3	18.0 ± 1.4	18.1 ± 1.3	9.8–20.2	14.0–19.2

again peaking in September and October (Fig. 7). However, unlike mako sharks, smaller blue sharks (age-0 and -1) occurred farther north.

4. DISCUSSION

This study examined the habitat utilization of YOY blue and mako sharks by integrating PSAT tagging with fishery catch data. These data revealed interspecific differences in vertical and horizontal movements, which likely reflect different foraging tactics. YOY habitat utilization for both species was also distinct from adults; YOY vertical distribution was much more surface-oriented and geographic range apparently confined to waters over the continental margins, which appear to serve as a nursery area, spanning approximately 27.7–46.2° N for blue sharks and 23.4–34.5° N for mako sharks.

4.1. Vertical movements

The preponderance of time spent just below the surface appears to be a unique behavioral feature of YOY blue sharks, unmatched by previous studies of adults (Carey & Scharold 1990, Stevens et al. 2010, Musyl et al. 2011). This shallow depth distribution is likely related to their specialized diet; young blue sharks (<110 cm FL) off California have been found to feed almost exclusively on pelagic cephalopods, with paper nautiluses *Argonauta* spp. topping the index of relative importance (IRI) at 45.9% (Preti et al. 2012). Aggregations of argonauts are known to drift on the sea surface, constituting effective 'fish aggregating devices' (Rosa & Seibel 2010). Feeding on surface-aggregating argonauts, which would be most visible during the day, could also explain the unusual 'reverse' diel vertical migration (rDVM; shallow daytime depths and greater nighttime depths) exhibited by YOY blue sharks (Fig. 2). Larger blue sharks (Carey & Scharold 1990, Stevens et al. 2010, Musyl et al. 2011) and many other pelagic predators (reviewed by Hays 2003) most commonly exhibit 'normal' diel vertical migration (nDVM; shallow nighttime depths and greater daytime depths), apparently tracking vertically migrating prey. Correspondingly, argonauts are less important in the diets of larger blue sharks (22.1% IRI for 110 ≤ FL < 150 cm and 3.2% IRI for FL ≥ 150 cm), largely replaced by vertically migrating (Gilly et al. 2006) Humboldt squid *Dosidicus gigas* (21.9% IRI for 110 ≤ FL < 150 cm and 47.3% IRI for FL ≥ 150 cm), which are absent from the diets of individuals <110 cm FL (Preti et al. 2012).

Compared to blue sharks, YOY mako sharks spent less time near the surface (24.8 vs. 60.4% < 2 m), likely reflecting differences in their diets and foraging tactics. YOY mako sharks off California feed almost exclusively on small teleost fishes (Preti et al. 2012), especially Pacific sardine *Sardinops sagax* (40.4% IRI), Pacific chub mackerel *Scomber japonicas* (27.6% IRI), and Pacific saury *Cololabis saira* (19.8% IRI), and rarely feed on argonauts (0.15% IRI). Overall, depth distributions of YOY mako sharks in this study (70–89 cm FL) were comparable to larger juveniles (80–160 cm FL) tracked in previous studies (Holts & Bedford 1993, Sepulveda et al. 2004), but much shallower than adults (Abascal et al. 2011,

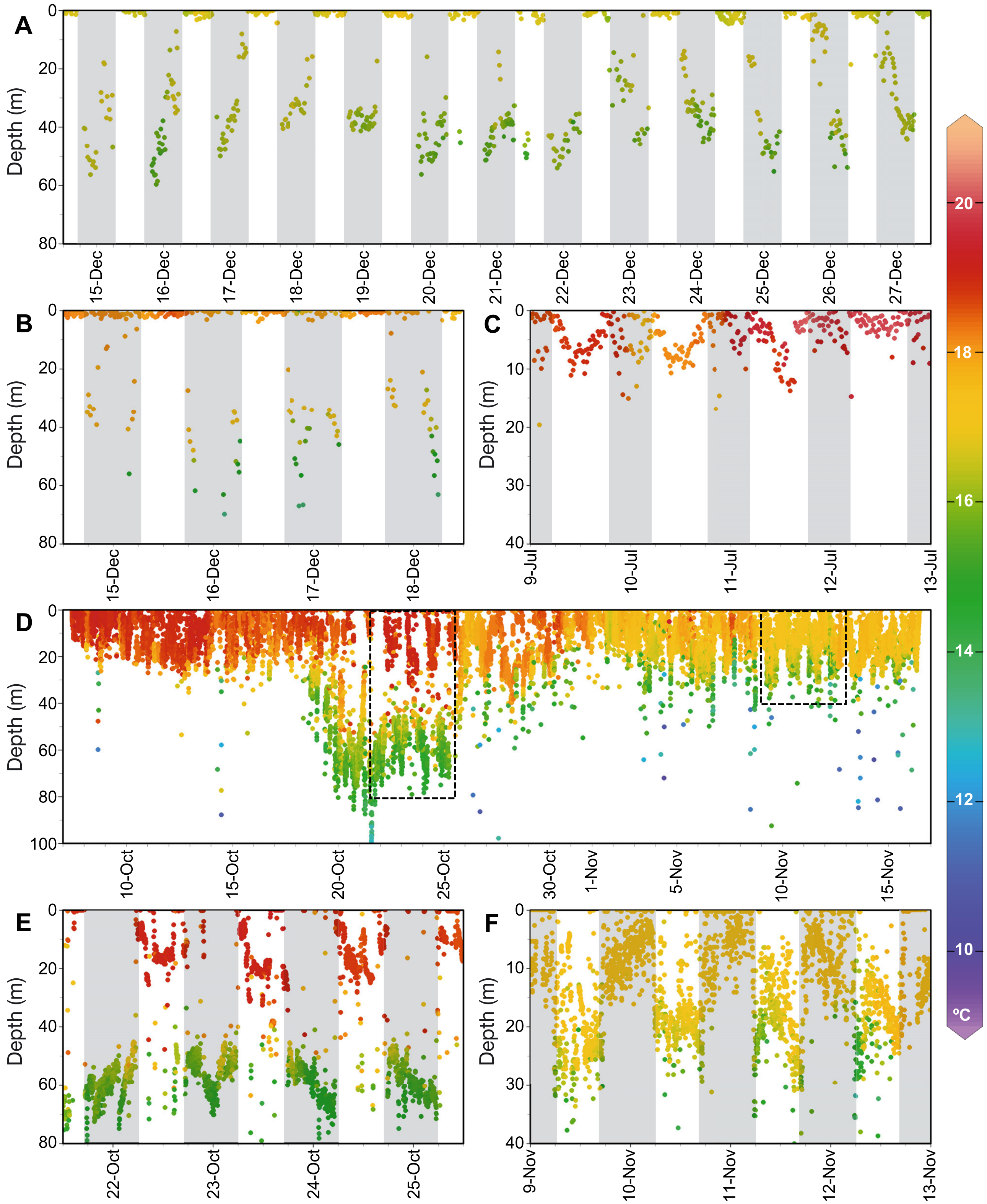

Fig. 4. Representative sections of depth and temperature time series for (A,B) blue sharks *Prionace glauca* and (C–F) mako sharks *Isurus oxyrinchus*. (A) Robust reverse diel vertical migration (rDVM) by shark B-2 in 2010; (B) crepuscular diving by shark B-5 in 2013; (C) 'midday dips' by shark M-5 in 2012; (D) switch from rDVM to normal DVM (nDVM) by shark M-1 in 2010; (E) zoomed view of large box in (D) showing rDVM; (F) zoomed view of small box in D showing nDVM. Scatter plots show shark depth (m) versus time of year; dots are colorized by water temperature (°C), indicated by the color ramp on the right. Periods of darkness (sunset to sunrise) are indicated by gray bars; these are omitted from (D) for clarity. Dates are labeled at 00:00 h

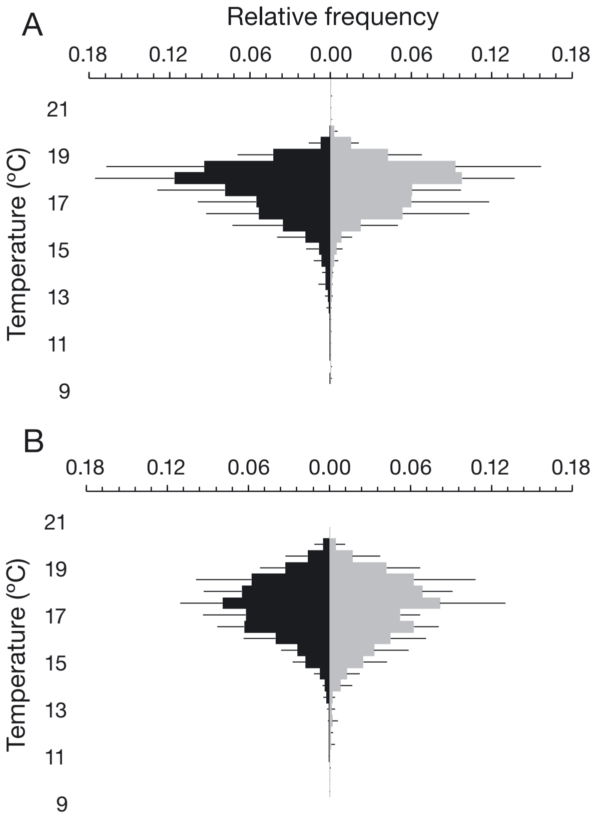

Fig. 5. Average temperature–frequency distributions (0.5°C bins; e.g. 17 indicates temperatures ≥17 but <17.5°C) with standard deviation for (A) blue sharks *Prionace glauca* and (B) mako sharks *Isurus oxyrinchus*. Gray shading: daytime distributions (sunrise to sunset); black: nighttime distributions (sunset to sunrise)

Musyl et al. 2011, Vaudo et al. 2016). Some YOY mako sharks displayed oscillatory 'yo-yo' or 'bounce' diving, a behavior widely reported for larger makos (Sepulveda et al. 2004, Abascal et al. 2011, Vaudo et al. 2016), and often attributed to foraging, but may also be associated with behavioral thermoregulation, energy conservation, and navigation (Klimley et al. 2002, Sepulveda et al. 2004, Bernal et al. 2010). Lastly, compared to blue sharks, YOY mako sharks displayed a weaker pattern of DVM (nDVM overall), with one individual switching between rDVM and nDVM during the tracking period (Fig. 4D–F). Previous studies have also reported weak patterns of DVM for both juvenile and larger mako sharks (Holts & Bedford 1993, Abascal et al. 2011, Musyl et al. 2011) as well as intra- and interindividual plasticity in DVM for other lamnid sharks (Pade et al. 2009, Coffey et al. 2017).

A subtle, but notable feature of YOY mako shark behavior was an apparent midday withdrawal below the surface, manifested as a 'dip' of 5–10 m in the depth profile. This behavior has not been explicitly described previously, although it is evident in the depth profiles of larger juveniles manually tracked in previous studies (see Fig. 3 in Holts & Bedford 1993 and Figs. 3B & 3F in Sepulveda et al. 2004). These daytime dips appear to correspond to solar elevation angle, with the center of each dip occurring around solar noon, when the sun is highest in the sky. Because their small teleost prey tend to school near the surface during the day (Kaltenberg & Benoit-Bird 2009), we hypothesize that as the sun climbs in altitude, YOY mako sharks may dip down to optimize their angle to best align the silhouettes of their prey against the sun, akin to how white sharks *Carcharodon carcharias* exploit the sun during predatory approaches (Huveneers et al. 2015). Larger mako sharks off California may not exhibit this behavior because small schooling fishes are less important in their diets (~70 % IRI for 110 ≤ FL < 150 cm and ~11 % IRI for FL ≥ 150 cm), apparently replaced by Humboldt squid (22.6 % IRI for 110 ≤ FL < 150 cm and 84.0 % IRI for FL ≥ 150 cm; Preti et al. 2012), which would best be pursued via nDVM (Gilly et al. 2006).

4.2. Horizontal movements and geographical distribution

Although geolocation estimates for our PSAT-tagged YOY blue and mako sharks occurred entirely within the SCB ecoregion (Fig. 1), these results are likely biased by the tagging locations (all within the SCB ecoregion), small sample sizes (n = 5 for each species), and relatively short tracking periods (mean = 46.1 ± 24.8 d; Table 1). The observer data examined from the California drift gillnet fishery show that YOY blue sharks are commonly encountered north of Point Conception, well into waters off Oregon and Washington (Fig. 6). In contrast, YOY and age-1 mako sharks were captured almost exclusively south of Point Conception in the drift gillnet fishery, consistent with PSAT geolocation estimates. However, makos appear to expand their northward range as they grow, with catch rates north of Point Conception increasing with size (Fig. 7). This suggests the importance of the SCB ecoregion for the youngest mako sharks, but its waning role as they age. In Mexican waters, juvenile blue and mako sharks are commonly caught in artisanal gillnet and longline fisheries along the entire west coast of the Baja California peninsula, including south of Punta Abreojos and the SCB ecoregion (Blanco-Parra et al. 2008, Cartamil et al. 2011, Ramírez-Amaro et al. 2013).

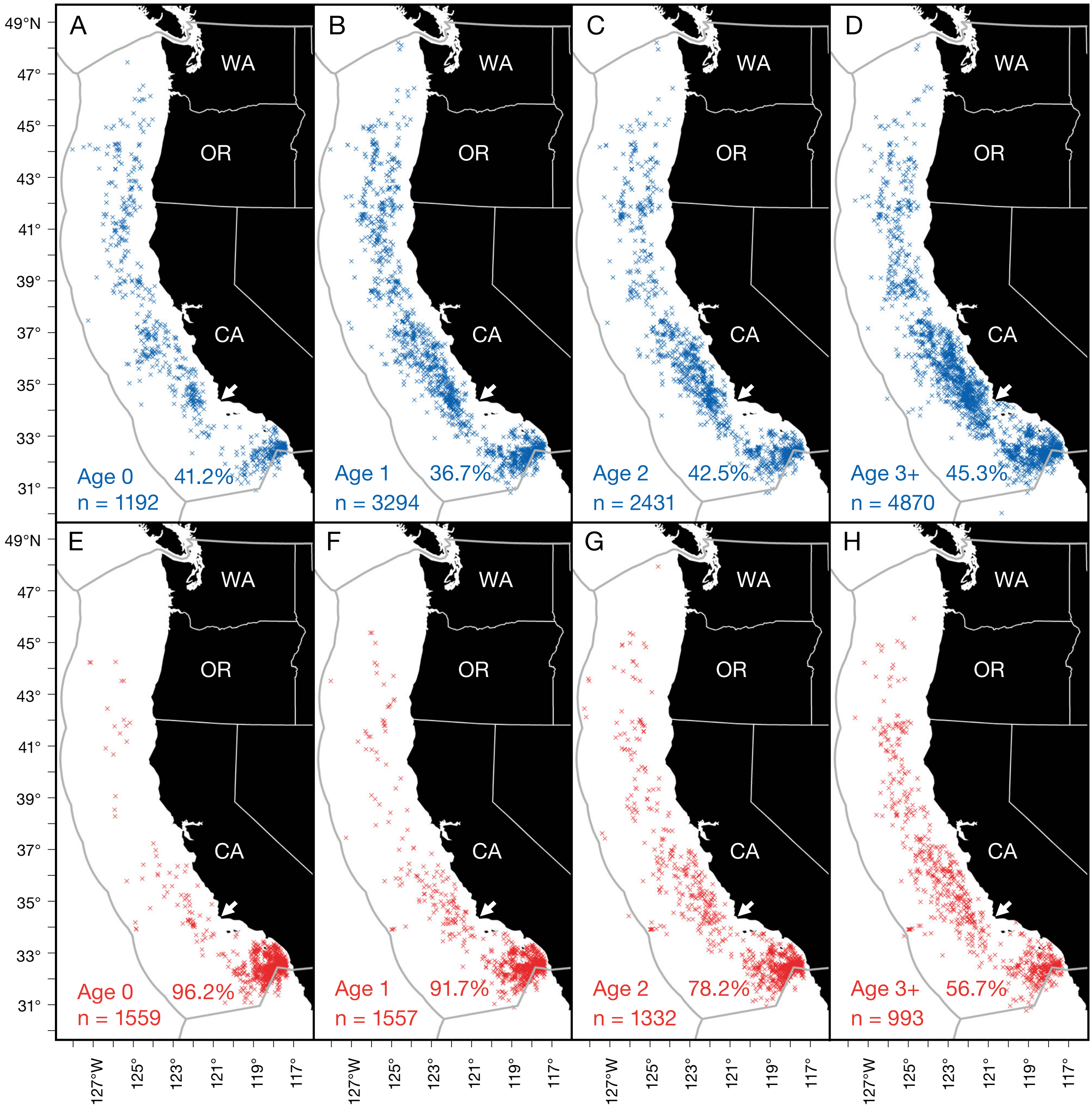

Fig. 6. NOAA observer database records of (A–D) blue sharks *Prionace glauca* and (E–H) mako sharks *Isurus oxyrinchus* captured in the California drift gillnet fishery from 1990–2017. (A) Age-0 blues (young-of-the-year [YOY]; fork length [FL] < 80 cm); (B) age-1 blues (80 ≥ FL < 105 cm); (C) age-2 blues (105 ≥ FL < 120 cm); (D) age-3+ blues (FL ≥ 120 cm); (E) age-0 makos (YOY; FL < 100 cm); (F) age-1 makos (100 ≥ FL < 125 cm); (G) age-2 makos (125 ≥ FL < 150 cm); (H) age-3+ makos (FL ≥ 150 cm). White arrow: Point Conception (34.5° N latitude), the northern boundary of the Southern California Bight. The percentage of sharks of each age class captured south of 34.5° N is indicated in each panel. Gray lines: exclusive economic zones of the USA and México

PSAT geolocations and California drift gillnet catch data indicate that YOY blue and mako sharks spend most of their time over the continental margin, but off the continental shelf, well within the EEZs of the USA and México (Figs. 1 & 6). This pattern is supported by longer-term tag–recapture studies of juveniles for both species (Wells et al. 2013, 2017). Additionally, mako sharks off California and Baja California exhibit greater westward (offshore) movements with size, likely associated with the inclusion of larger and often deeper dwelling prey (e.g. Humboldt squid) in their diet (Nasby-Lucas et al. 2019).

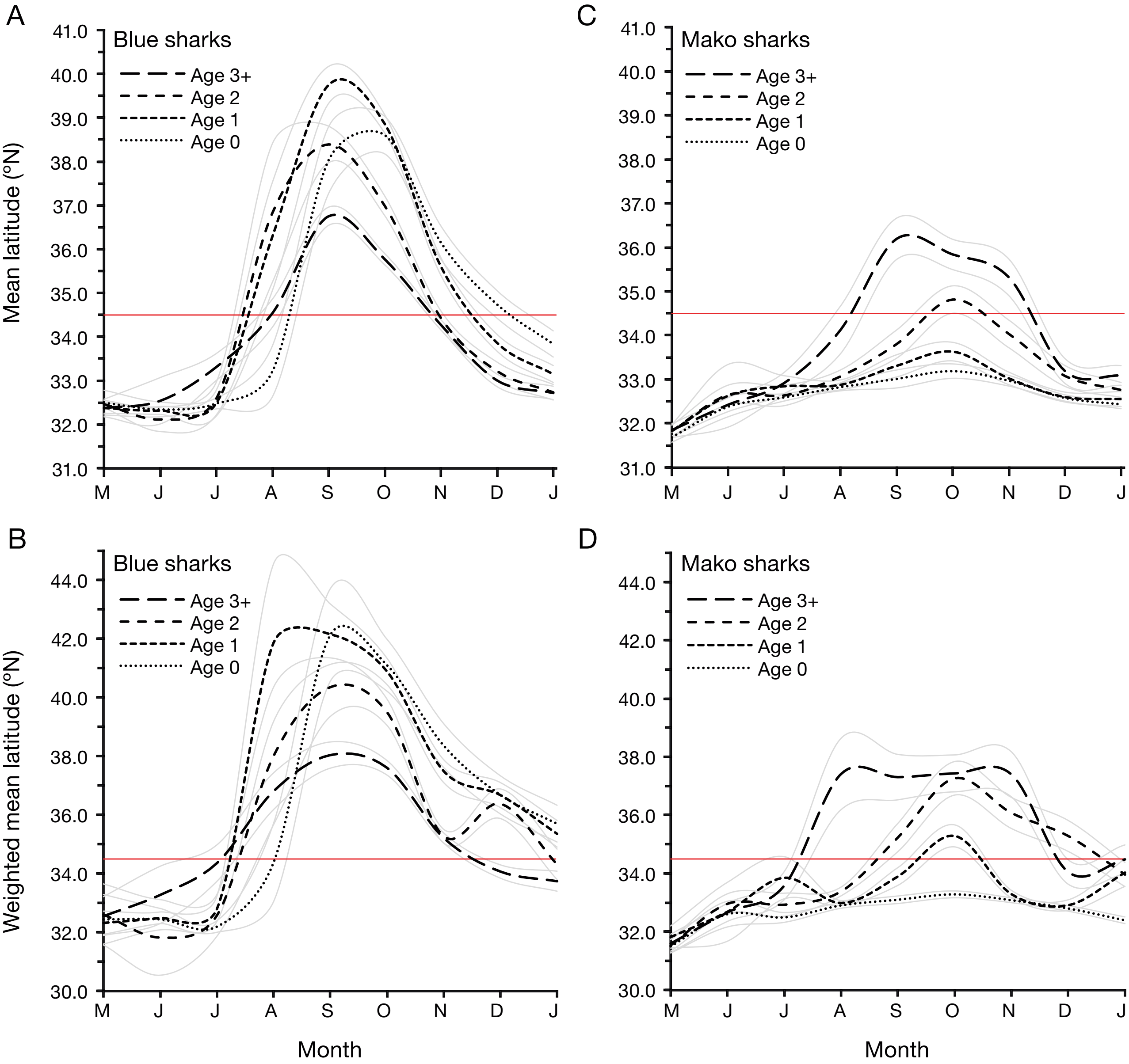

Fig. 7. Mean monthly capture latitude for (A,B) blue sharks *Prionace glauca* and (C,D) mako sharks *Isurus oxyrinchus* in the California drift gillnet fishery between May and January (NOAA observer database records; no records from 1 Feb to 30 April due to seasonal closure). Mean capture latitudes are shown (A,C) unweighted and (B,D) weighted by catch per unit effort. Mean capture latitudes are separated by age class (thick dashed black lines) with 95% confidence intervals (thin solid gray lines). (A,B) Blue sharks: age-0 (young-of-the-year [YOY]; fork length [FL] < 80 cm), age-1 (80 ≥ FL < 105 cm), age-2 (105 ≥ FL < 120 cm), age 3+ (FL ≥ 120 cm); (C,D) mako sharks: age-0 (YOY; FL < 100 cm), age-1 (100 ≥ FL < 125 cm), age-2 (125 ≥ FL < 150 cm), age-3+ (FL ≥ 150 cm). Red line: the latitude of Point Conception (34.5° N latitude), the northern boundary of the Southern California Bight

The primary use of continental margin but not shelf waters by YOY blue and mako sharks differs from other prominent coastal pelagic sharks in the region such as the common thresher *Alopias vulpinus* and white shark *C. carcharias*, whose YOY movements are almost entirely over (common thresher) or split over and off (white shark) the continental shelf (Dewar et al. 2004, Weng et al. 2007, Cartamil et al. 2010, 2016). Limited diet data from common thresher and white sharks suggest juveniles and subadults of these species incorporate some demersal fishes and continental shelf species into their diets (Preti et al. 2001, 2004, 2012, A. Preti unpubl. data), which may explain their affinity to waters above the shelf and reduce interspecific competition with juvenile blue and mako sharks.

4.3. Seasonal movements

Observer data from the California drift gillnet fishery indicate juvenile blue and mako sharks are most concentrated in the US sector of the SCB ecoregion (i.e. south of Point Conception) in the late spring and early summer, and tend to move north along the California coast from late summer to early autumn, finally returning south from late autumn to early winter (Fig. 7). For blue sharks, these latitudinal movements are greatest for age-0 and -1 individuals, which exhibit the highest mean capture latitude in late summer to early autumn (Fig. 7). Similar patterns of latitudinal segregation of blue shark age classes (smaller individuals caught at higher latitudes) have been reported in the Indian Ocean (Coelho et al. 2015), Atlantic (Carvalho et al. 2011, Joung et al. 2017), and other regions of the Pacific (Nakano 1994, Stevens & Wayte 1999, West et al. 2004). In contrast, mako shark latitudinal movements appear to increase with size, as YOY makos showed little northward movement, remaining the farthest south, well within the SCB ecoregion even during the late summer and autumn when older makos were often captured north of Point Conception (Fig. 7). Such strong latitudinal segregation of mako shark age classes has not been reported previously.

Less is known about seasonal latitudinal movements of juvenile blue and mako sharks south of the USA–México border. Juveniles of both species are captured year-round off the northern half of the Baja California peninsula (north of Punta Eugenia), but the seasonality of these capture rates has not been examined (Cartamil et al. 2011). Along the southern half of the peninsula (south of Punta Eugenia), CPUE for both species is highest in winter, followed by the spring (63.6% of winter CPUE for blue sharks, 66.6% for mako sharks) and lowest in summer (18.8% of winter CPUE for blue sharks, 19.5% for mako sharks) and autumn (28.0% of winter CPUE for blue sharks, 40.3% for mako sharks; Ramírez-Amaro et al. 2013). By extension, this correlates with juvenile blue and mako shark CPUE in Southern California being highest in summer and autumn (Hanan et al. 1993, O'Brien & Sunada 1994). Geolocation estimates for YOY blue and mako sharks tagged during the autumn appear to have captured the southward phase of this movement cycle, with sharks moving southward along the Baja California peninsula (Fig. 1, Fig. S1). Previous blue and mako shark tag–recapture (Wells et al. 2013, 2017) and satellite tagging studies on larger juveniles (Block et al. 2011, Nasby-Lucas et al. 2019) have also captured this seasonal movement cycle, which is also common for other predatory fishes off the west coast of North America, including bluefin *Thunnus orientalis* and yellowfin tunas *T. albacares*, white sharks, and salmon sharks *Lamna ditropis*, and appears to be strongly correlated with seasonally changing SST (Block et al. 2011).

Despite the evidence for seasonal latitudinal movements, some juvenile blue and mako sharks are caught year-round off the west coast of California (present study) and the Baja California peninsula (Cartamil et al. 2011, Ramírez-Amaro et al. 2013), suggesting considerable variation in the timing and extent of movement, including the possibility that some individuals remain locally resident. Seasonal movement by only a fraction of a population (e.g. partial migration) is ubiquitous among animal groups (Chapman et al. 2011), including predatory fishes such as sharks (Chapman et al. 2012, Papastamatiou et al. 2013, Espinoza et al. 2016), and may be driven in part by individual condition and intraspecific competition (Chapman et al. 2012).

4.4. Nursery habitat

The SCB ecoregion has long been considered a pupping and nursery area for blue sharks (Hanan et al. 1993, Holts et al. 2001) and mako sharks (Hanan et al. 1993, O'Brien & Sunada 1994, Taylor & Bedford 2001), based primarily on the prevalence of juveniles in this region. However, our data, in combination with previous studies, suggest that the nursery areas for blue and mako sharks in the eastern North Pacific extend along the continental margins far beyond the SCB ecoregion. Specifically, the blue shark nursery appears to extend along the continental margins of the SCB ecoregion, north through Oregon (approximately 27.7–46.2° N), while the mako shark nursery extends along the continental margins of the SCB ecoregion, south to the tip of the Baja California peninsula (approximately 23.4–34.5° N). Thus, the SCB ecoregion likely constitutes the overlapping region between 2 nurseries that extend farther along the Pacific coasts of the USA and México.

However, the high abundance of YOY and juvenile sharks does not alone warrant a definitive classification as a nursery area. While YOY habitat within the SCB ecoregion and adjacent waters apparently adheres to conventional shark nursery area theory (e.g. high productivity, low exposure to potential predators; Branstetter 1990), and appears to be discrete from adult habitat (more oceanic than coastal), we considered 3 testable criteria from Heupel et al.

(2007) for an area to be considered a shark nursery: (1) higher than average density of YOY sharks in the area, (2) tendency for YOY sharks to remain or return to the area for extended periods, and (3) the area is used repeatedly across years.

The first of the 3 nursery criteria is partially supported by fishery data, indicating that subadult and adult blue and mako sharks are caught more often in the north Central Pacific and juveniles are caught more often in coastal areas of the Northeast and Northwest Pacific (Semba et al. 2011, Sippel et al. 2015, 2016). In the fishery-independent longline survey that operated in the US sector of the SCB ecoregion from 1994–2013, <8% of the blue sharks and <4% of mako sharks caught were mature (Runcie et al. 2016). This is consistent with the California drift gillnet fishery data examined in this study, which showed <12% of blue sharks and <6% of mako sharks caught were mature. Further evidence of differences in adult and juvenile habitat is seen in various tagging studies such as Nasby-Lucas et al. (2019), who found that small mako sharks (FL < 165 cm) tagged in the SCB ecoregion with PSATs generally stayed within several hundred km of shore, whereas larger individuals (FL ≥ 165 cm) readily utilized the oceanic habitat of the north Central Pacific. Additionally, tag–recapture data showed that YOY and older juvenile blue and mako sharks were tagged and recaptured within the SCB ecoregion (Wells et al. 2013, 2017). These data, along with the present study, also lend support to the second nursery criterion, that YOY blue and mako sharks remain within the putative nursery for extended periods of time. Finally, the third nursery criterion is supported by high catch rates of multiple juvenile age classes (age-0, -1, and -2) of both species across multiple years in the California drift gillnet fishery data (Figs. 6 & 7), Mexican artisanal fishery data (Cartamil et al. 2011, Ramírez-Amaro et al. 2013), and in the fishery-independent survey data reported by Runcie et al. (2016).

Water temperature appears to play an important role in defining the putative nursery habitat of YOY blue and mako sharks. Based on the California drift gillnet fishery data (Figs. 6 & 7), the northern boundary of the mako shark nursery is Point Conception (34.5° N), which coincides with a sharp transition between the Warm Temperate North Pacific and Cold Temperate North Pacific marine provinces (Spalding et al. 2007). This transition is marked by a difference in temperature regimes that is driven by strong upwelling north of Point Conception (Parrish & Tegner 2001). On the other hand, juvenile blue sharks are not deterred from the colder waters north of Point Conception (Figs. 6 & 7), where average CPUE for age-0, -1, and -2 was more than double that south of Point Conception. These findings, along with the observation that YOY and age-1 blue sharks ranged the farthest north (Fig. 7), through at least the Oregon–Washington border (46.2° N), suggest the SCB ecoregion is no more important to juvenile blue sharks than areas north of Point Conception. South of the USA–México border, juvenile blue sharks, including YOY, are captured along the entire western coast of the Baja California peninsula (Cartamil et al. 2011, Ramírez-Amaro et al. 2013, F. Galván-Magaña unpubl. data); however, YOY individuals are common only to Bahía Tortugas (27.7° N), which coincides with another transition zone at Punta Eugenia, with warmer and less productive waters to the south (Durazo 2015). Lastly, juvenile mako sharks, including YOY, appear common to Punta Lobos (23.4° N), near the southern tip of the Baja California peninsula, which coincides with yet another major transition, between the Temperate Northern Pacific and Tropical Eastern Pacific marine realms (the highest bioregional classification; Spalding et al. 2007). South of Punta Lobos, juvenile blue and mako sharks are very rarely caught by artisanal fisheries along the coasts of the central Mexican states of Sinaloa (Bizzarro et al. 2009a) and Nayarit (Pérez-Jiménez et al. 2005), nor along the eastern coast of Baja California Sur (Bizzarro et al. 2009b).

4.5. Fisheries management

Stock assessments conducted for blue and mako sharks in the eastern Pacific indicate that neither species is currently overfished (ISC 2017, 2018), and in the US sector of the SCB ecoregion, fishing effort and catch rates of commercial fisheries targeting pelagic sharks (e.g. the California drift gillnet fishery) have decreased significantly over the past several decades (PFMC 2018). However, as demonstrated in the current study, juvenile blue and mako sharks undertake cross-boundary movements into Mexican waters, where they are vulnerable to capture in often more intense artisanal and commercial longline fisheries (Cartamil et al. 2011, Ramírez-Amaro et al. 2013, Castillo-Geniz et al. 2014), in which fishing effort and catch rates are not consistently monitored. Because these highly migratory species are a shared resource between the USA and México, binational monitoring and management strategies would be advisable. Specifically, there is a need for accurate estimates of juvenile blue and mako shark catch in Mexican artisanal fisheries, as well as estimates of the total annual landings in commercial longline fisheries based out of Ensenada, Bahía Magdalena, and Cabo San Lucas. These data could be incorporated into future binational stock assessments that take into account fishery mortality incurred in both countries. In addition, there may be juvenile pelagic shark aggregation areas (e.g. Bahía Sebastián Vizcaíno; Cartamil et al. 2011, Santana-Morales et al. 2012, Oñate-González et al. 2017) within the larger context of the nursery area. These 'hotspots' deserve further study and may benefit from localized management to afford protection to this vulnerable life history stage.

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