Aggregation behavior and seasonal philopatry in male and female leopard sharks *Triakis semifasciata* along the open coast of southern California, USA

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ABSTRACT: This study presents the longest uninterrupted acoustic monitoring record available to date for the leopard shark *Triakis semifasciata*, providing novel insight into the fine-scale and long-term movement patterns of this species, and demonstrating that both sexes exhibit site-specific aggregation behavior and seasonal philopatry. Twenty females and 13 males were surgically fitted with coded acoustic transmitters and tracked for over 3 yr by underwater acoustic receivers spanning 120 km of coastline from San Clemente, CA, USA to the USA-Mexico border, with 2 receivers positioned at known aggregation sites in La Jolla and Del Mar, CA. Whereas females appeared to be particularly attracted to the La Jolla site, males exhibited strong site fidelity to Del Mar. Shark abundance at both sites was higher during the day than at night, particularly in late afternoon when water temperature was highest. Female abundance in La Jolla was highest in late June through early December, and was strongly positively correlated with sea surface temperature, consistent with the hypothesis that females aggregate in warm water to accelerate gestation. In addition, seasonal arrival of females to and departure from La Jolla were highly synchronous and coincided with the summer and winter solstices, respectively. In contrast, male abundance in Del Mar was highest in late April through early October and was positively correlated with both sea surface temperature and photoperiod. Lastly, both sexes exhibited strong seasonal philopatry, with 50.0% of females and 60.0% of males returning every year to their respective aggregation sites during the 3 yr study period.

KEY WORDS: Site fidelity · Acoustic telemetry · Sexual segregation · Marine reserve · Passive acoustic tracking · Diel behavior · Water temperature · Photoperiod · Fish aggregation

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INTRODUCTION

Aggregation behavior is a common feature of elasmobranch movement patterns, having numerous proposed functions (Jacoby et al. 2012). Juveniles may reduce predation risk by aggregating in structurally complex environments (e.g. mangrove prop roots), or turbid, shallow regions of lagoons, bays, and estuaries (Holland et al. 1993, Heupel & Simpfendorfer 2005,

Duncan & Holland 2006, Guttridge et al. 2012). Increased foraging efficiency may benefit large planktivorous species that aggregate amidst zooplankton blooms and fish spawn (Sims & Quayle 1998, Heyman et al. 2001, Dewar et al. 2008), large predatory species that aggregate near pinniped haulout sites (Ainley et al. 1985, Strong et al. 1992, Klimley et al. 1996), and more generally, any species that aggregates at locations central to known foraging grounds (e.g.

Klimley & Nelson 1984, Hearn et al. 2010, Bessudo et al. 2011). Mixed-sex aggregations may facilitate courtship (Carrier et al. 1994, Pratt & Carrier 2001, Whitney et al. 2004), whereas female-dominated aggregations may reduce harassment from males in the form of excessive mating attempts (Sims et al. 2001, Jacoby et al. 2010, Wearmouth et al. 2012). Lastly, pregnant females may aggregate in nursery areas to give birth, or in warm water to reduce gestation period by accelerating embryonic development (Economakis & Lobel 1998, Wallman & Bennett 2006, Hight & Lowe 2007, Jirik & Lowe 2012, Speed et al. 2012).

The leopard shark *Triakis semifasciata* is a nearshore benthic species known to form seasonal aggregations throughout its range from Samish Bay, Washington, USA to Mazatlán, Sinaloa, México (Miller & Lea 1972, Farrer 2009, Castro 2011). These aggregations typically occur in semi-enclosed bays and estuaries such as San Francisco Bay (Smith & Abramson 1990), Tomales Bay (Hopkins & Cech 2003), Humboldt Bay (Ebert & Ebert 2005), and Elkhorn Slough (Carlisle et al. 2007), as well as in sheltered coves throughout the Channel Islands (e.g. Santa Catalina Island; Manley 1995, Hight & Lowe 2007). Nosal et al. (2013a) recently examined a novel type of aggregation that occurs along the open coast of southern California, USA, in the lee of a submarine canyon. The comparison of aggregation sites with variable hydrographic characteristics has allowed for the identification of shared habitat features and some understanding of the adaptive significance of leopard shark aggregation behavior (Nosal et al. 2013a). First, leopard sharks may benefit from increased foraging efficiency by aggregating over foraging grounds such as intertidal mudflats and eelgrass *Zostera marina* beds (Russo 1975, Talent 1976, Webber & Cech 1998, Ebert & Ebert 2005), or immediately proximal to foraging grounds such as submarine canyons, rocky reefs, and kelp forests (Manley 1995, Hight & Lowe 2007, Nosal et al. 2013a). Second, leopard sharks aggregating in warm shallows may benefit from increasing their core body temperature, thereby accelerating digestion and nutrient assimilation, somatic growth, and embryonic development in pregnant females (Hight & Lowe 2007, Nosal et al. 2013a). Finally, sites that harbor juveniles may further serve as pupping or nursery grounds (Smith & Abramson 1990, Carlisle et al. 2007, Carlisle & Starr 2009).

Despite some understanding of the putative functions of leopard shark and other elasmobranch aggregations, the biotic and abiotic factors governing aggregation behavior on daily and seasonal timescales remain less well understood. On a daily timescale, many leopard shark aggregations appear to follow the flooding and ebbing tide, possibly to forage over newly submerged intertidal mudflats that are inaccessible at lower tides, or otherwise to maintain a constant depth and perhaps temperature (Ackerman et al. 2000, Carlisle & Starr 2009, 2010). In other aggregations, diel movements have been reported where some leopard sharks disperse away from the shallows and into deeper water at night, presumably to forage (Manley 1995, Hight & Lowe 2007, Nosal et al. 2013a). However, such daily or sub-daily behaviors have usually only been observed using short-term, fine-scale monitoring techniques such as manual acoustic tracking, in which individual sharks are followed for less than 72 h (e.g. Manley 1995, Carlisle & Starr 2009, Nosal et al. 2013a); thus, the extent to which these behaviors persist over longer periods (i.e. weeks, months, and years) remains unknown.

On a seasonal timescale, factors affecting leopard shark aggregation behavior are even more nebulous. Seasonal variation in abundance has been reported at several leopard shark aggregation sites, with water temperature and salinity being suggested as the most important predictors of aggregation formation and dissolution (Hopkins & Cech 2003, Hight & Lowe 2007, Carlisle & Starr 2009). However, leopard shark aggregation behavior has never been monitored for more than 1 full year (i.e. 1 complete seasonal cycle); thus, the effect of inter-annual variability of environmental factors that potentially govern aggregation behavior has not been quantified. This limited continuous monitoring has also precluded any multi-annual determination of seasonal fidelity (philopatry) of leopard sharks to aggregation sites, which would provide insight into reported patterns of genetic divergence in their populations (Lewallen et al. 2007). Lastly, previous studies have focused primarily on female leopard sharks, and thus the long-term movement patterns of males have not been systematically examined.

The main objective of the present study is to address these voids in understanding by examining the fine-scale multi-annual movements of both female and male leopard sharks from 2 aggregation sites (La Jolla and Del Mar) along the open coast of southern California. Elucidating the spatiotemporal details of this aggregation behavior also provides needed information for the potential design and implementation of effective management strategies. Although *Triakis semifasciata* is classified as 'Least Concern' under the International Union for Conservation of Nature (IUCN) Red List, this species has a low capacity to recover from population decline

(Smith et al. 1998) and a demonstrated susceptibility to over-exploitation by bottom-set gill nets (Pondella & Allen 2008), which, when combined with sexual segregation and seasonal philopatry, may locally exacerbate the effects of overfishing and habitat destruction (Hueter et al. 2005, Wearmouth & Sims 2008, Mucientes et al. 2009).

MATERIALS AND METHODS

The daily and seasonal occurrence of male and female leopard sharks at 2 known aggregation sites along the open coast of southern California was monitored over a 3 yr period between 15 July 2009 and 4 September 2012 (1148 d). The La Jolla aggregation (32.853° N, 117.262° W), which was described by Nosal et al. (2013a), is composed primarily of pregnant females (97.1% female, 2.9% male, mean total length [TL] ± SD = 138.7 ± 10.8 cm, n = 140) and occurs over a sand flat immediately adjacent to a shallow rocky reef, just shoreward of the head of the La Jolla Submarine Canyon (Fig. 1). The Del Mar

aggregation, 12 km to the north (32.958° N, 117.277° W), forms over mixed habitat (sand patches interspersed among rocky reef) juxtaposed to a small kelp forest (Fig. 1) and was found to be mixed-sex (demography quantified by the authors at the onset of this study: 48.9% female, 51.1% male, mean TL ± SD = 130.5 ± 11.2 cm, n = 45).

Surgical implantation of acoustic transmitters

Twenty female leopard sharks (16 from La Jolla and 4 from Del Mar) and 13 males (all from Del Mar) were surgically fitted with coded acoustic transmitters (VEMCO V16-4H, 69 kHz, 60 to 180 s random transmission interval). First, each shark was captured by hook and line from a 5 m skiff and placed ventral-side-up on a custom-made surgical trough to induce tonic immobility. Next, the operating site was dried and antisepticized with povidone-iodine, and a ~3 cm longitudinal incision was made halfway between the pectoral and pelvic fins approximately 3 cm off the ventral midline. An acoustic transmitter, coated with a
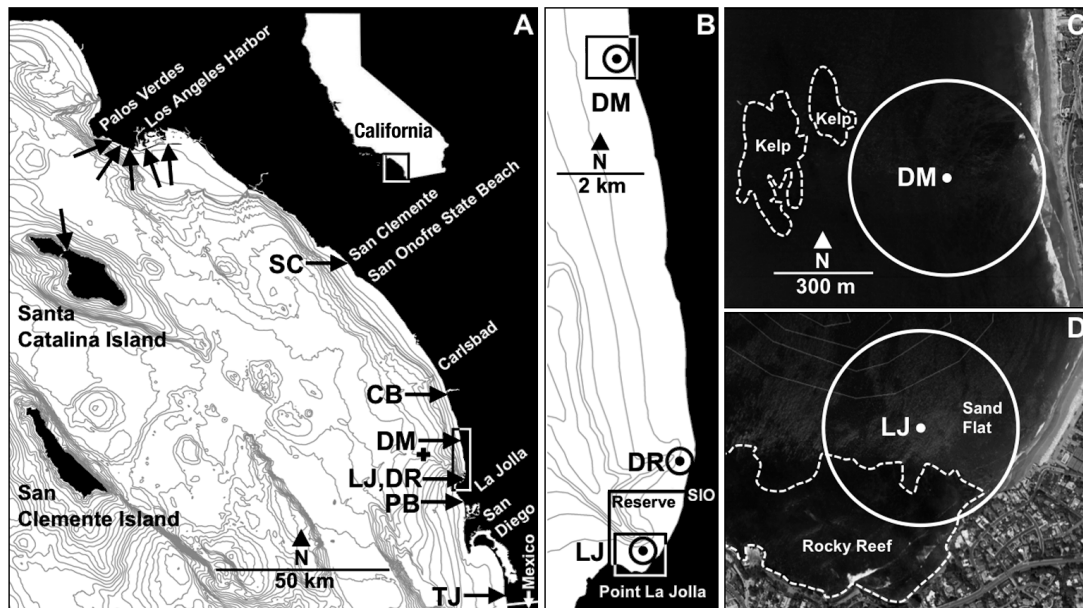

Fig. 1. Locations of VEMCO VR2W underwater acoustic receivers. (A) Southern California; black arrows indicate receiver locations (TJ = Tijuana River; PB = Pacific Beach; LJ = La Jolla; DR = Dike Rock; DM = Del Mar; CB = Carlsbad; SC = San Clemente pier; unlabeled arrows near Los Angeles Harbor, Palos Verdes, and Santa Catalina Island indicate approximate locations of receivers, which, along with the SC receiver, were owned and operated by the Christopher Lowe Laboratory of California State University—Long Beach); ✚ indicates location of the Torrey Pines Outer Buoy where oceanographic measurements were taken. (B) Central San Diego County (enlarged view of small box in A), showing the boundary of the Matlahuayl State Marine Reserve (solid black line). Receivers and detection ranges (300 m) are shown as black dots and black circles, respectively. (C) Del Mar aggregation site (enlarged view of upper small box in B). (D) La Jolla aggregation site (enlarged view of lower small box in B). White dots and white circles indicate the position and 300 m detection range, respectively, of the DM receiver in (C) and LJ receiver in (D). Dashed white lines indicate kelp forest and rocky reef habitat in (C) and (D), respectively. All isobaths are shown at 20 m intervals to 100 m, then at 100 m intervals. Aerial views in (C) and (D) are from Google Earth Pro (imagery date: 1 Feb 2008). SIO: Scripps Institution of Oceanography

3:7 mixture of beeswax and paraffin wax and dipped in povidone-iodine to reduce the chance of immuno-logical rejection (Holland et al. 1999), was inserted into the peritoneal cavity through the incision, which was immediately closed with 1 continuous absorbable suture (2-0 Vicryl, Ethicon) and treated with a topical antibiotic (Neosporin, Johnson and Johnson Services). The shark was released by gently immersing and overturning the surgical trough in the water. Note that sharks were not anesthetized during surgical im-plantation because tricaine methanesulfonate (MS-222; the only anesthetic approved for fish by the United States Food and Drug Administration) requires a 21 d withdrawal period before human consumption. This could not be guaranteed because leopard sharks are commonly fished and consumed; holding post-op-erative sharks in captivity for 21 d was deemed im-practical and would have imposed further stress. However, no adverse effects associated with capture and transmitter implantation were observed. For shark M6 (see 'Results'), which was recaptured and re-released 61 d after surgery, the incision had healed tightly into a thin scar with no suture remnants. All procedures were approved and performed in accor-dance with Protocol S00080 of the Institutional Animal Care and Use Committee of the University of California — San Diego.

Passive acoustic monitoring

Underwater acoustic receivers (VEMCO VR2W) were mounted to dead-weight moorings deployed at the mouth of the Tijuana River (TJ; 32.554° N, 117.131° W), Pacific Beach (PB; 32.800° N, 117.265° W), La Jolla (LJ; 32.854° N, 117.265° W), Dike Rock (DR; 32.873° N, 117.255° W), Del Mar (DM; 32.958° N, 117.272° W), Carlsbad (CB; 33.078° N, 117.315° W), and San Clemente pier (SC; 33.418° N, 117.624° W) (Fig. 1). These 7 receivers were located where the au-thors had previously observed leopard sharks (though not necessarily aggregating) and spanned approxi-mately 120 km of coastline in San Diego and Orange Counties, California. The TJ, PB, LJ, DR, and DM receivers were deployed in June 2009, the CB re-ceiver in June 2010, and the SC receiver in August 2010. Each mooring consisted of tri-braid nylon rope (diam. = 2 cm), a steel clump weight (~100 kg), and a subsurface buoy (diam. = 30 cm) suspended 2 m below mean lower low water (MLLW). The receiver was attached to the nylon rope approximately 5 m be-low MLLW, yielding an acoustic detection range of approximately 300 m (determined *in situ*). Detection

data were downloaded every 3 mo from receivers *in situ* using an underwater Bluetooth cable (VEMCO), and receiver batteries were changed yearly at sea on-board the 5 m skiff. The Christopher Lowe Laboratory of California State University — Long Beach (CSULB) owned and operated the SC receiver for unrelated studies, along with an array of receivers near Los An-geles Harbor, Palos Verdes, and Santa Catalina Island (Fig. 1) that were queried for detections at the end of the monitoring period.

Spaghetti identification tags

All sharks reported by Nosal et al. (2013a) at the La Jolla site (n = 140) and at the onset of this study at the Del Mar site (n = 45), including those surgically implanted with acoustic transmitters, were externally fitted with a 'spaghetti' identification tag (Floy Tag FIM-96) inserted into the musculature and through the radials at the base of the first dorsal fin. Recap-tures of these tagged sharks are reported in this study in conjunction with movements of sharks deter-mined through acoustic monitoring.

Data analyses

To analyze temporal variation in the abundance of transmitter-implanted sharks, raw detections were converted to the number of individual sharks detected per day (abundance d^{-1}, to assess seasonal variation) and per decaminute (abundance damin^{-1}, to assess daily and tidal variation). Time of day is expressed in Pacific Daylight Time (UTC-7) and all means are given with standard error (SE) unless otherwise noted. To assess inter-annual variability in aggregation be-havior, abundance d^{-1} was compared between 2010 and 2011 (the only 2 complete calendar years for which sharks were monitored) for females and males at the LJ and DM receivers using a Mann-Whitney *U*-test.

To identify environmental correlates of aggregation behavior, the following analyses were conducted sep-arately for females and males detected by the LJ and DM receivers. Multiple regression was used to exam-ine the fine-scale seasonal relationship among shark abundance d^{-1} of one sex (the response variable) and up to 7 predictor variables: (1) daily mean sea surface temperature (SST), (2) swell height (significant wave height), (3) swell direction (variables 1, 2, and 3 were sampled twice per hour at the Torrey Pines Outer Buoy, Coastal Data Information Program; Fig. 1), (4) barometric pressure (sampled once per hour at the

Scripps Institution of Oceanography pier, NOAA Tides and Currents), (5) salinity (sampled once per day at the Scripps Institution of Oceanography pier, Southern California Coastal Ocean Observing System; Fig. 1), (6) photoperiod (United States Naval Observatory), and (7) shark abundance d^{-1} of the opposite sex. To minimize the confounding effects of high day-to-day variation in shark abundance and these environmental variables on interpreting broad seasonal relationships, regression analyses were performed by pooling and averaging the single response and 7 predictor variables in 24 half-month bins, from the 1st to 15th day of each month (15 d; 'early' month) and from the 16th to the last day of each month (13 to 16 d; 'late' month). Multiple regression analyses were performed in Minitab 16 using a best subsets regression procedure; the model with the highest adjusted coefficient of determination (R^2) was further simplified using stepwise backward elimination of predictors until all predictors in the model were significant (p < 0.05). Serial correlation was tested using a Durbin-Watson statistic (d) and multicollinearity was quantified by calculating a variance inflation factor (VIF) for each predictor in the model. Finally, the proportionate contribution of each predictor to R^2 was determined using a relative weight analysis (Johnson 2000) with modifications prescribed by Tonidandel & LeBreton (2011).

To assess diel variation in aggregation behavior, shark abundance $damin^{-1}$ was averaged across every day of the study period (n = 1148), and the resulting 144 values of mean shark abundance $damin^{-1}$ (144 damin d^{-1}) were compared between day and night (delineated by the mean times of sunrise and sunset during the study period; United States Naval Observatory) and hourly (6 damin h^{-1}) using a 1-way ANOVA and post hoc pairwise Tukey tests. To assess potential tidal influence on aggregation behavior (water level measured at the Scripps Institution of Oceanography pier, NOAA Tides and Currents; Fig. 1), shark abundance $damin^{-1}$ was pooled and averaged within ± 2 h of every high and low tide, and the resulting values were compared between high and low tide using a Mann-Whitney U-test.

RESULTS

Sexual segregation and site fidelity

The VR2W receivers recorded 777 831 detections from the 33 shark-borne transmitters (range: 7 to 109 057 detections shark^{-1}; Table 1). Females tagged in La Jolla (n = 16) were detected most often at the LJ receiver (mean ± SE = 288.4 ± 64.3 d shark^{-1}), 24.9 times more than at the DM receiver (11.6 ± 3.9 d shark^{-1}; U = 244.0, n = 32, p < 0.001). Males (n = 13) were detected most often at the DM receiver (280.8 ± 50.9 d shark^{-1}), 8.8 times more than at the LJ receiver (32.0 ± 16.4 d shark^{-1}; U = 155.5, n = 26, p < 0.001). Females tagged in Del Mar (n = 4) were detected equally at the LJ (168.8 ± 81.3 d shark^{-1}) and DM receivers (177.3 ± 94.8 d shark^{-1}; U = 9.0, n = 8, p = 0.886).

Male abundance d^{-1} was 32.6% lower in 2011 than in 2010 at the DM receiver (U = 44 629, n = 730, p < 0.001) and 2283% higher at the LJ receiver (U = 99 280, n = 730, p < 0.001). Female abundance d^{-1} was not significantly different between 2010 and 2011 at the LJ receiver (U = 71 560, n = 730, p = 0.082), but was 51.5% higher at the DM receiver in 2011 (U = 48 835, n = 730, p < 0.001). There was no significant difference between 2010 and 2011 in daily mean SST (U = 70 329, n = 730, p = 0.190), barometric pressure (U = 70 635, n = 730, p = 0.157), or swell direction (U = 68 295, n = 730, p = 0.552); however, daily mean swell height was 8.6% lower in 2011 (U = 72 910, n = 730, p = 0.026) and salinity was 0.15% lower in 2011 (U = 49 010, n = 730, p < 0.001) than in 2010.

Diel and tidal patterns of shark abundance

Mean shark abundance $damin^{-1}$ was on average 12.5% higher during the day than at night for females at the LJ receiver (F = 32.48, n = 144, p < 0.001) and 24.9% higher for males at the DM receiver (F = 136.87, n =144, p < 0.001). There was also a significant hour-of-day effect for both females at the LJ receiver (F = 139.19, n = 144, p < 0.001) and males at the DM receiver (F = 148.49, n = 144, p < 0.001); results from post hoc pairwise Tukey tests are summarized in Fig. 2. Shark abundance $damin^{-1}$ dropped at both receivers around sunset and, apart from a brief spike around sunrise, female abundance $damin^{-1}$ at the LJ receiver remained low throughout the morning hours (when water temperature was lowest), whereas male abundance $damin^{-1}$ at the DM receiver increased continuously throughout the day beginning at sunrise (Fig. 2). In addition to this general temporal trend, female abundance $damin^{-1}$ at the LJ receiver was on average 42.6% higher within 2 h of low tide than within 2 h of high tide (U = 2 032 190, n = 4349, p < 0.001); however, there was no significant difference in male abundance $damin^{-1}$ between low and high tide at the DM receiver (U = 2 386 997, n = 4331, p = 0.303).

Table 1. *Triakis semifasciata*. Detection data for 33 leopard sharks surgically implanted with coded acoustic transmitters and monitored by passive acoustic telemetry between 15 July 2009 and 4 September 2012. ID: shark identification (F: female, M: male), TL: total length; receivers — TJ: Tijuana River, PB: Pacific Beach, LJ: La Jolla, DR: Dike Rock, DM: Del Mar, CB: Carlsbad, SC: San Clemente pier

ID	TL (cm)	Tagging date	Known days at liberty	Total detections at all receivers	No. of days detected at each receiver						
					TJ	PB	LJ	DR	DM	CB	SC
La Jolla											
F1	146	15-Jul-09	1148	41110	0	0	423[a]	107	53	60	0
F2	141	15-Jul-09	1138	68756	0	21	640	23	15[a]	10	0
F3	141	15-Jul-09	7	280	0	0	7[a]	1	0	0	0
F4	141	15-Jul-09	1148	72237	0	9	678[a]	36	7	5	0
F5	141	15-Jul-09	531	27878	0	0	308[a]	11	20	2	0
F6	140	15-Jul-09	1112	33170	1	46	402[a]	70	33	65	7
F7	144	15-Jul-09	361[b]	3773	0	0	54	8[a]	4	1	0
F8	140	16-Jul-09	1147	109057	0	0	784[a]	5	0	0	0
F9	145	16-Jul-09	115[c]	4168	0	0	59	11	7[a]	0	0
F10	145	16-Jul-09	1147	31206	1	5	369[a]	79	34	18	4
F11	142	16-Jul-09	152[d]	3116	0	0	40[a]	0	0	0	0
F12	150	16-Jul-09	17	359	0	0	13[a]	1	0	0	0
F13	118	23-Jun-10	803	7160	0	16	161	4	6[a]	69	0
F14	142	23-Jun-10	407	20317	0	44[a]	160	22	4	24	0
F15	142	23-Jun-10	541	43508	0	2	451[a]	15	3	4	0
F20	118	07-Sep-11	304[e]	2683	0	4	66	1	0	0	0
Del Mar											
M1	132	24-Jul-09	379[f]	3261	0	0	0	0	114	1[a]	0
M2	124	27-Jul-09	1136	26571	0	10	57[a]	11	527	2	0
M3	128	27-Jul-09	1015	34674	0	0	18	6	625[a]	1	0
M4	128	27-Jul-09	1135	27701	0	0	31	8	380[a]	8	2
M5	131	28-Jul-09	833	18519	0	0	3	4	386[a]	0	0
M6	136	28-Jul-09	421	29804	0	0	2	2	324[a]	0	0
M7	137	29-Jul-09	1	7	0	0	0	0	1[a]	0	0
M8	123	29-Jul-09	1132	33085	0	0	70	17	341[a]	0	0
M9	141	29-Jul-09	1060	6068	0	3	21	56	321[a]	2	0
M10	152	29-Jul-09	1132	2609	0	0	0	2	112[a]	24	0
M11	142	20-Jul-10	777	14626	0	0	0	0	251[a]	19	0
M12	140	20-Jul-10	167	2167	0	0	1	1[a]	37	2	0
M13	147	22-Jul-10	776	20992	0	1	213[a]	31	232	16	0
F16	126	16-Jul-10	731	818	0	1	4	0	26	19[a]	3
F17	142	20-Jul-10	778	40193	0	1	330[a]	131	301	0	0
F18	140	20-Jul-10	778	40206	1	0	285	85	377[a]	0	0
F19	122	22-Jul-10	96	7752	1[a]	0	56	5	5	0	0
				Females (mean)	0.2	7.5	264.5	30.8	44.8	13.9	0.7
				Males (mean)	0.0	1.1	32.0	10.6	280.8	5.8	0.2

[a]Last detected by array at this receiver

[b]Captured and killed by recreational fisher on north side of Scripps Institution of Oceanography pier on 10 Jul 2010; shark was in early gestation with embryos ~5 to 10 mm TL

[c]Captured and killed by recreational fisher at San Clemente pier on 7 Nov 2009; shark was in mid-gestation with embryos ~10 to 15 cm TL

[d]Detected in Big Fisherman's Cove, Santa Catalina Island, on 14 Dec 2009

[e]Detected near Los Angeles Harbor on 6 Jul 2012

[f]Captured and killed by commercial gillnet fisher off San Onofre State Beach on 6 Aug 2010

Seasonal patterns of shark abundance

Seasonal arrival of females to and departure from La Jolla were highly synchronous, coinciding with the summer and winter solstices, respectively — which delineated an apparent 6 mo 'high season' (late June to early December) during which mean shark abundance d^{-1} was 3.6 times higher ($U = 0$, n = 24, p < 0.001) than during the opposing 'low season' (late December to early June; Fig. 3). Some females were scarcely detected at the LJ receiver during the low season (e.g. sharks F1, F6, and F10 were detected on 3.8%, 2.0%, and 0.4% of low season days, respectively, compared to 64.4%, 62.6%, 59.4% of
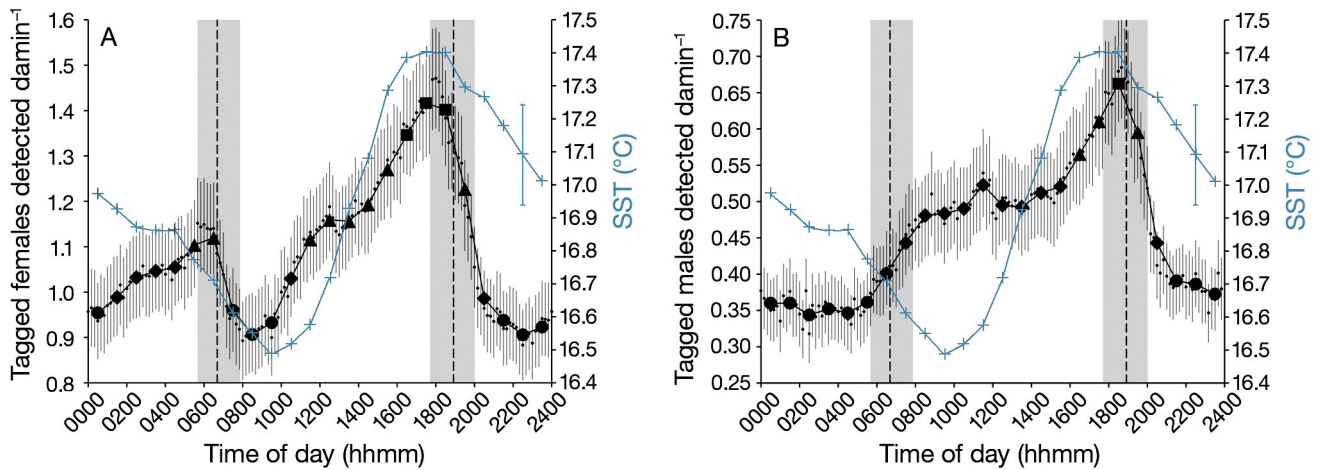
Fig. 2. *Triakis semifasciata*. Mean number of tagged sharks detected per decaminute (black dots with 95% CI shown as thin vertical black bars) during the study period for (A) females at the La Jolla receiver and (B) males at the Del Mar receiver. Mean number of tagged sharks detected h^{-1} is shown by solid black shapes (circles, diamonds, triangles, and squares) connected by a solid line. Hourly means represented by one shape are significantly different (ANOVA post hoc Tukey tests) from hourly means represented by a different shape within the same graph. Shown for reference is mean hourly sea surface temperature (SST) recorded at the Scripps Institution of Oceanography pier along with mean sunrise and sunset (vertical dashed lines) and the ranges of sunrise and sunset during the study period (thick vertical gray bars). To avoid clutter, only the largest 95% CI for mean hourly SST is shown (22:00 h)

high season days, respectively), whereas others persisted, albeit sporadically (e.g. sharks F2, F4, and F8 were detected on 39.3%, 29.4%, and 45.0% of low season days, respectively, compared to 67.1%, 86.5%, and 88.4% of high season days, respectively; Fig. 3). Those same females that were scarcely detected during the low season also made more frequent roundtrip excursions (detection at the LJ receiver, followed by detection at one or more non-LJ receivers, followed by detection at the LJ receiver) from La Jolla during the high season (75, 72, and 61 excursions detected for sharks F1, F6, and F10, respectively, compared to 14, 25, and 0 excursions detected for sharks F2, F4, and F8, respectively; Fig. 4).

Although females tagged in Del Mar (n = 4) were detected equally at both the DM and LJ receivers over the course of the study, their abundance d^{-1} was on average 53.5% higher at the LJ receiver than the DM receiver during the high season (late June to early December; $U = 75\,649$, n = 891, p < 0.001), while 215.5% higher at the DM receiver than the LJ receiver during the low season (late December to early June; $U = 100\,991$, n = 730, p < 0.001). Males were also seasonally abundant at the DM receiver (mean shark abundance d^{-1} was 2.2 times higher during high season, late April to early October [$U = 142$, n = 24, p < 0.001], compared to the opposing low season, late October to early April; Fig. 5), but gener-

ally exhibited greater inter-individual variation than females at the LJ receiver (Figs. 5 & 6).

Pooled and averaged on a half-month basis, female abundance d^{-1} at the LJ receiver was positively correlated with SST and photoperiod, which accounted for 91.3% (95% CI: 81.4 to 97.6%) and 8.7% (95% CI: 3.7 to 16.5%) of the variation explained by the multivariate model, respectively ($R^2 = 0.941$; Fig. 7, Table 2). Male abundance d^{-1} at the DM receiver was also positively correlated with SST and photoperiod; these predictors accounted for 46.5% (95% CI: 25.7 to 64.5%) and 53.4% (95% CI: 24.4 to 75.9%) of the explained variation, respectively ($R^2 = 0.787$; Fig. 7, Table 2). Logistic regression of female abundance d^{-1} at the LJ receiver (normalized to % of yearly max.) with SST estimated the threshold value (inflection point of the fitted sigmoid curve: $y = 0.709 - 0.567 / \{1 + \exp[(x - 17.616) / 1.023]\}$) to be 17.6°C (95% CI: 17.3 to 17.9°C). The threshold SST value for males at the DM receiver ($y = 0.531 - 0.453 / \{1 + \exp[(x - 16.316) / 1.664]\}$) was 16.3°C (95% CI: 14.6 to 18.0°C). VIF did not exceed 1.462 for the half-month models (Table 2); these are well below even the most conservative recommended threshold value of VIF = 4 (reviewed by O'Brien 2007), above which multicollinearity among predictors would require attention and possibly correction. Autocorrelation was not detected in the half-month models (Table 2).
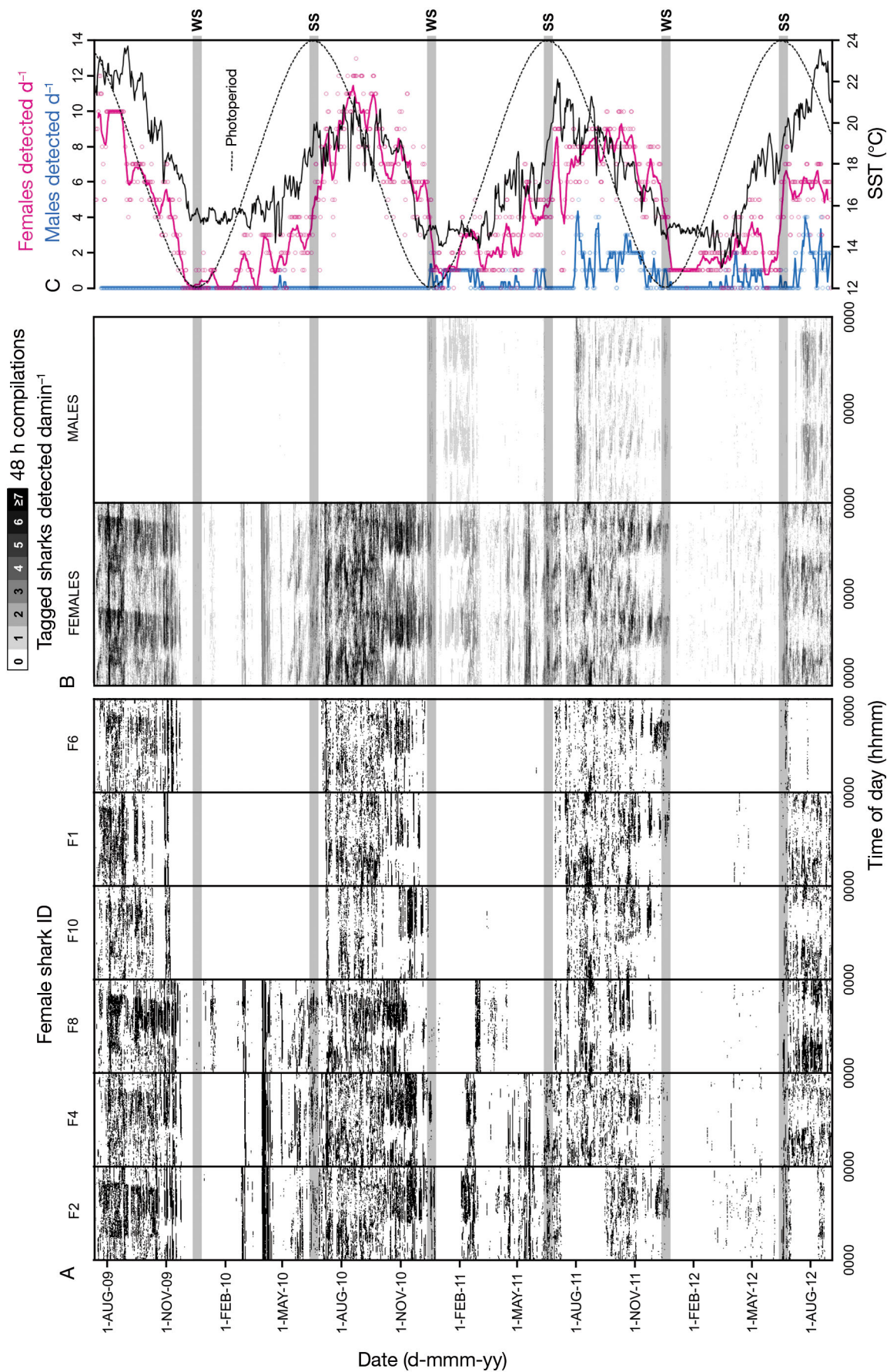
Fig. 3. *Triakis semifasciata.* (A) The 6 longest detection records for females at the La Jolla (LJ) receiver. Each record goes from midnight to midnight (Pacific Daylight Time) and for 1148 d (duration of monitoring period, from 15 Jul 2009 to 4 Sep 2012). Each black pixel is a 10 min time bin (damin) in which that female was detected at the LJ receiver. (B) Compilation records generated from detections of all tagged females (n = 20) and males (n = 13), showing the number of sharks detected damin⁻¹ at the LJ receiver in 48 h (to show the night period uninterrupted). (C) Number of tagged females (pink) and males (blue) detected per day (open circles, with 15 and 3 d centered moving average as solid pink and blue lines, respectively) at the LJ receiver, along with mean daily sea surface temperature (SST; solid black line) and photoperiod (dotted black line; no units). Horizontal gray bars = summer and winter solstices (±1 wk); WS = winter solstice (9 h 59 min), SS = summer solstice (14 h 19 min)
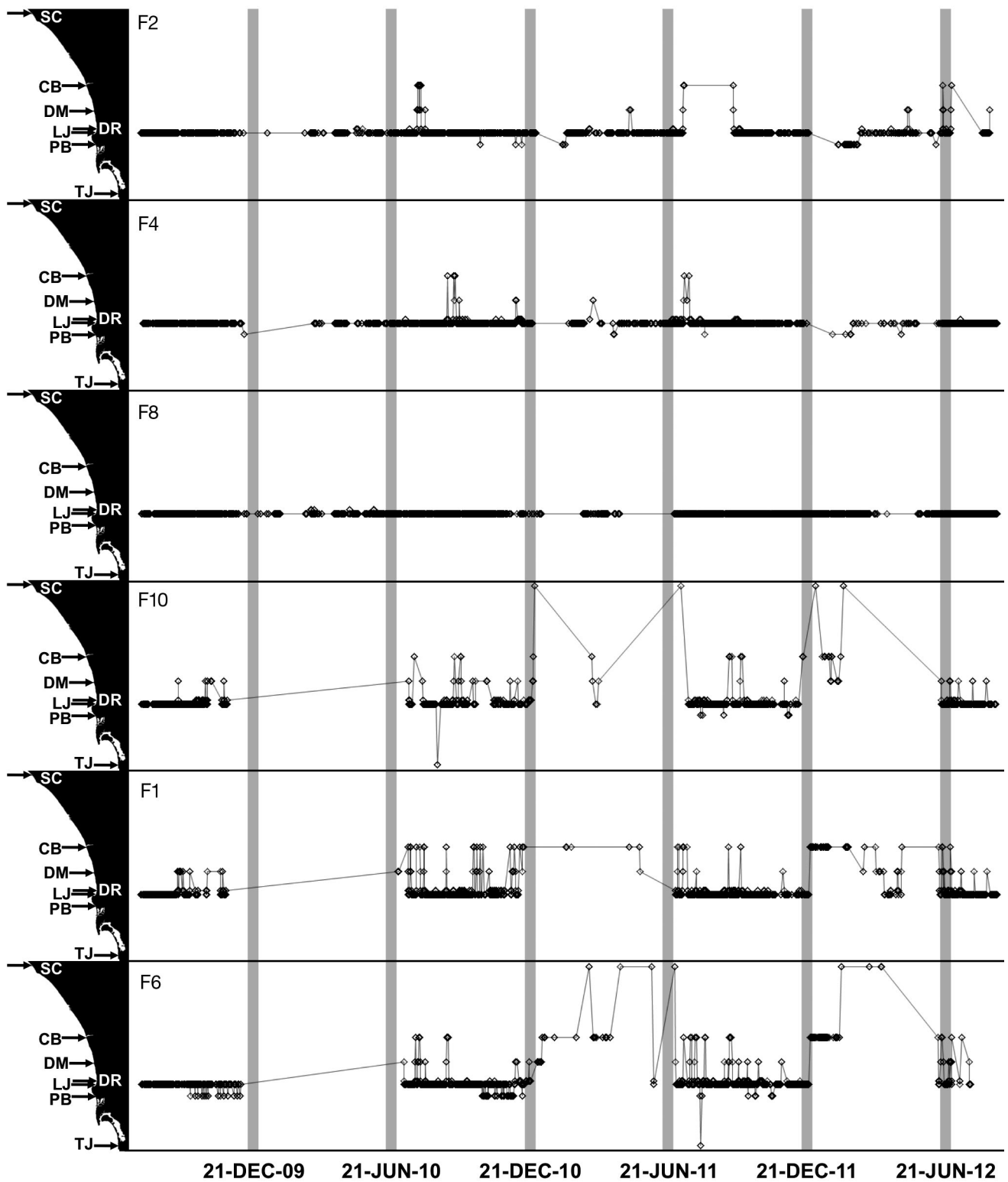
Fig. 4. *Triakis semifasciata*. Detection locations (black diamonds; thin gray lines connect consecutive detections) for the 6 females with the longest detection records over the 3 yr study. The location of the detection is indicated by the latitude of the detecting receiver shown on the stylized maps (see Fig. 1A for details). The times of the summer and winter solstices (±1 wk) are shown for reference as vertical gray bars. TJ = Tijuana River; PB = Pacific Beach; LJ = La Jolla; DR = Dike Rock; DM = Del Mar; CB = Carlsbad; SC = San Clemente pier
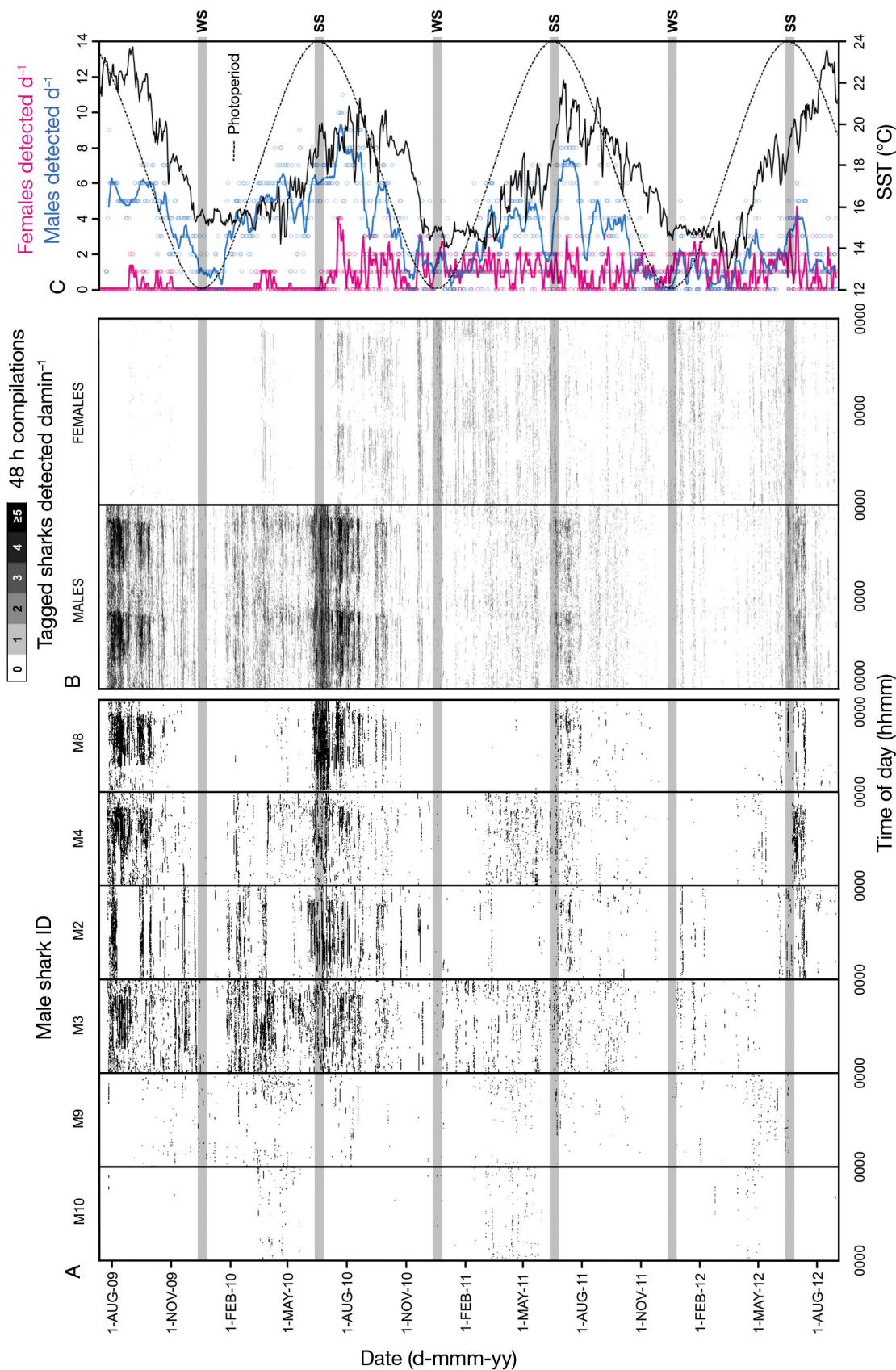
Fig. 5. *Triakis semifasciata*. (A) The 6 longest detection records for males at the Del Mar (DM) receiver. (B) Compilation records generated from detections of all tagged males (n = 13) and females (n = 20) at the DM receiver, along with mean daily sea surface temperature (SST; solid black line) and photoperiod (dotted black line; no units). Horizontal gray bars = summer and winter solstices. For details, see Fig. 3
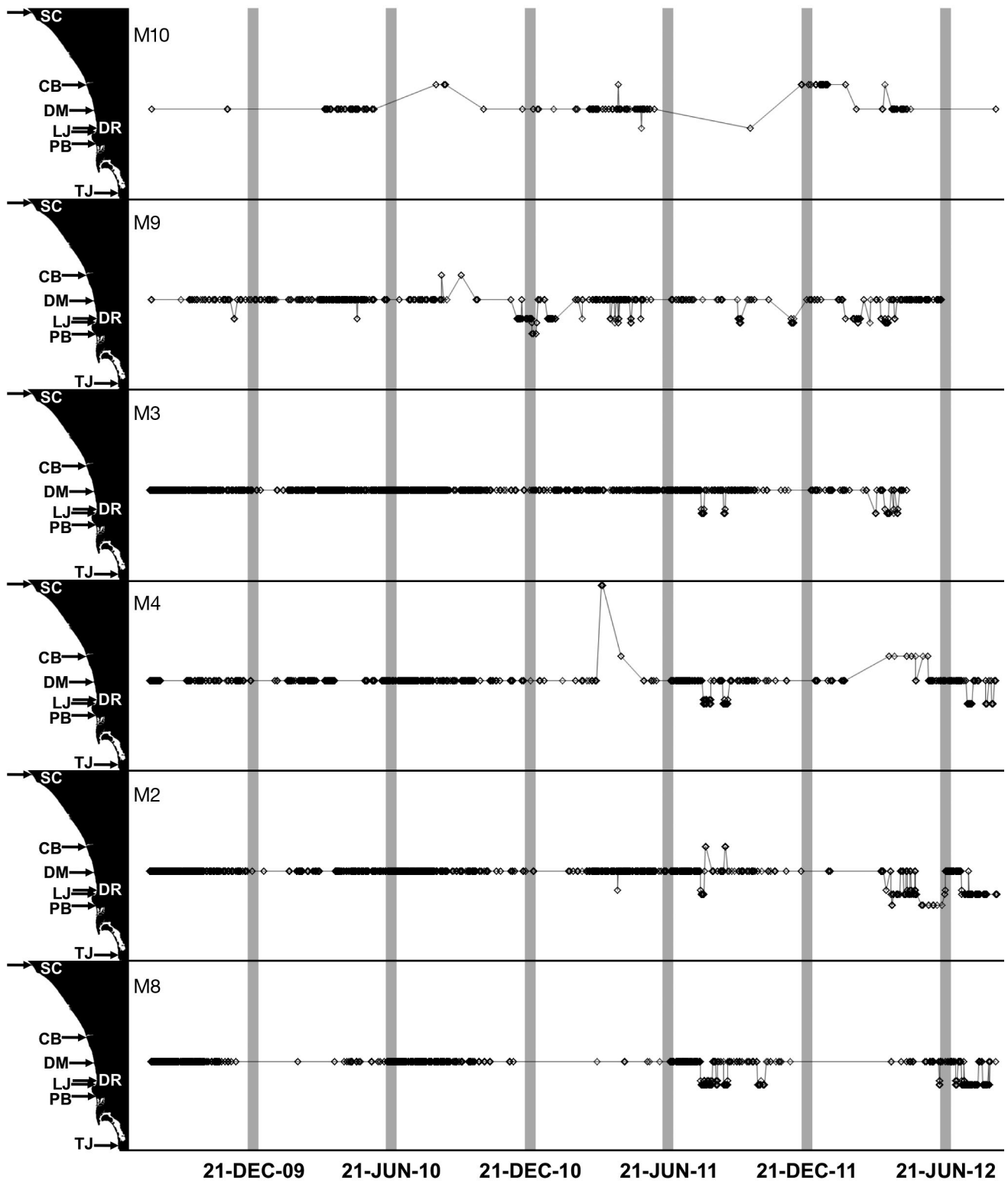
Fig. 6. *Triakis semifasciata*. Detection locations (black diamonds; thin gray lines connect consecutive detections) for the 6 males with the longest detection records over the 3 yr study. Location of the detection is indicated by the latitude of the detecting receiver shown on the stylized maps (see Fig. 1A for details). Times of summer and winter solstices (±1 wk) are shown for reference as vertical gray bars. TJ = Tijuana River; PB = Pacific Beach; LJ = La Jolla; DR = Dike Rock; DM = Del Mar; CB = Carlsbad; SC = San Clemente pier
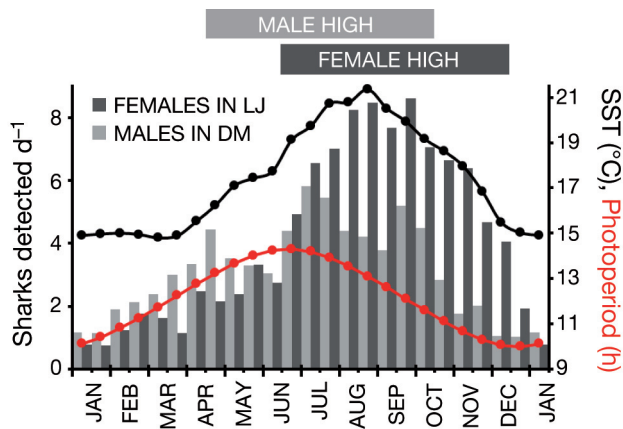
Fig. 7. *Triakis semifasciata*. Mean number of tagged females (dark gray) and males (light gray) detected d⁻¹ at the La Jolla and Del Mar receivers, respectively, pooled and averaged in 24 half-month bins and plotted with half-month variation in sea surface temperature (SST) and photoperiod (the 2 predictor variables explaining the most variation in shark abundance). Duration of the high seasons for females at the La Jolla receiver (late June to early December; FEMALE HIGH) and males at the Del Mar receiver (late April to early October; MALE HIGH) shown for reference

Seasonal philopatry and recaptures of tagged sharks

Females returned annually to the LJ receiver; 50.0% of females tagged in 2009 (n = 12) were detected in each of the following 3 yr (during the high season, late June to early December), 52.6% of females tagged in 2009 and 2010 (n = 19) were detected in at least each of the following 2 yr, and

70.0% of females tagged between 2009 and 2011 (n = 20) were detected in at least the following 1 yr (Table 3). Similarly, males returned annually to the DM receiver; 60.0% of males tagged in 2009 (n = 10) were detected in each of the following 3 yr (during the high season, late April to early October), 69.2% of sharks tagged in 2009 and 2010 (n = 13) were detected in at least each of the following 2 yr, and 84.6% of sharks tagged in 2009 and 2010 (n = 13) were detected in at least the following 1 yr (Table 3).

Only 1 shark (F20) was detected along the mainland coast north of the SC receiver at CSULB receivers around Palos Verdes and Los Angeles Harbor (Fig. 1); these receivers were in continuous operation from July 2010 through the end of this study. Two sharks were also detected by another CSULB receiver in Big Fisherman's Cove (BFC), Santa Catalina Island (Fig. 1): shark M6 in November 2009 and shark F11 in December 2009 (this receiver was only in operation from October 2009 until March 2010). Whereas shark F11 was not detected back along the mainland coast, shark M6 was detected at the DM receiver 49 h and 4 min after being last detected in BFC (125 km away), suggesting an average swimming speed of 2.55 km h⁻¹ or 0.54 body lengths s⁻¹ (assuming a straight course between the 2 points).

Finally, 12 of the 185 sharks (6.5%) equipped with spaghetti identification tags, including 3 sharks implanted with acoustic transmitters, were recaptured (n = 9) or found dead (n = 3) along the coast of southern California and northern Baja California, Mexico. Three were captured in commercial bottom-set gillnets: 1 male (shark M1; August 2010) and 1 female (April 2011) 5 km off San Onofre State Beach

Table 2. *Triakis semifasciata*. Multiple regression of shark abundance d⁻¹ pooled and averaged in half-month bins (females detected at the La Jolla receiver = FEMALES LJ; males detected at the Del Mar receiver = MALES DM) with sea surface temperature (SST) and photoperiod (PP). For each model, variance inflation factors (VIF) are given for each predictor as well as the Durbin-Watson statistic (*d*). RI: relative importance; rescaled RI weights are expressed as a percentage of the total variance explained by the model (coefficient of determination, R²)

Response	Predictor	Coefficient ± SE	t	p	VIF	Raw RI weights (95% CI)	Rescaled RI weights (95% CI)
FEMALES LJ	CONST	−11.883 ± 1.298	−9.15	<0.001			
	SST	1.34 ± 0.077	17.39	<0.001	1.462	0.859 (0.766–0.918)	91.3% (81.4–97.6%)
	PP	−0.594 ± 0.116	−5.12	<0.001	1.462	0.082 (0.035–0.155)	8.7% (3.7–16.5%)
	R² = 0.941, adjusted R² = 0.935, S = 0.695, F = 167.0, p < 0.001, d = 1.412 (p > 0.05)						
MALES DM	CONST	−8.269 ± 1.307	−6.33	<0.001			
	SST	0.294 ± 0.078	3.79	0.001	1.462	0.366 (0.202–0.508)	46.5% (25.7–64.5%)
	PP	0.518 ± 0.117	4.44	<0.001	1.462	0.420 (0.192–0.597)	53.4% (24.4–75.9%)
	R² = 0.787, adjusted R² = 0.766, S = 0.700, F = 38.7, p < 0.001, d = 1.277 (p > 0.05)						

Corrected after publication (marked by red square)

Table 3. *Triakis semifasciata*. Seasonal philopatry for females detected at the La Jolla receiver and males detected at the Del Mar receiver. Diamonds (◆) indicate the years in which individuals were detected during the high season (late June to early October for females and late April to early October for males). The number of consecutive annual returns following the year of transmitter implantation is indicated to the right. Shark F7 was captured and killed in 2010, shark F9 in 2009, and shark M1 in 2010

Sex	Shark ID	2009	2010	2011	2012	Annual returns
FEMALES	F1	◆	◆	◆	◆	3
	F2	◆	◆	◆	◆	3
	F3	◆				0
	F4	◆	◆	◆	◆	3
	F5	◆	◆			1
	F6	◆	◆	◆	◆	3
	F7	◆	◆			1
	F8	◆	◆	◆	◆	3
	F9	◆				0
	F10	◆	◆	◆	◆	3
	F11	◆				0
	F12	◆				0
	F13		◆	◆	◆	2
	F14		◆	◆		1
	F15		◆	◆		1
	F16		◆	◆	◆	2
	F17		◆	◆	◆	2
	F18		◆	◆	◆	2
	F19		◆			0
	F20			◆		0
MALES	M1	◆	◆			1
	M2	◆	◆	◆	◆	3
	M3	◆	◆	◆	◆	3
	M4	◆	◆	◆	◆	3
	M5	◆	◆	◆		2
	M6	◆	◆			1
	M7	◆				0
	M8	◆	◆	◆	◆	3
	M9	◆	◆	◆	◆	3
	M10	◆	◆	◆	◆	3
	M11		◆	◆	◆	2
	M12		◆			0
	M13		◆	◆	◆	2

(Fig. 1) and 1 female (August 2011) off Puerto Nuevo, Baja California, Mexico (40 km south of the USA-Mexico border). Recreational fishers captured 1 female (shark F9) off the San Clemente pier in November 2009, 2 females from the beach immediately north of the SIO pier in July (shark F7) and August 2010, and 1 male (shark M6; released) in Del Mar in September 2009. The authors also recaptured and released 1 female at the Del Mar aggregation site in July 2010 and 1 female at the La Jolla site in July 2011. Lastly, 3 females were found dead in the water or on the beach near the La Jolla aggregation site in September 2010 and December 2011, with injuries attributable to fatal attacks by California sea lions *Zalophus californicus*.

DISCUSSION

This study presents the longest uninterrupted acoustic monitoring record of male and female leopard sharks (3.15 yr), providing novel insight into the long-term movement patterns of this species and demonstrating that both sexes exhibit site-specific aggregation behavior and seasonal philopatry — which have important conservation implications. On both daily and seasonal timescales, leopard shark aggregation behavior appears to be most strongly influenced by temperature and light. The former is not unexpected, given that water temperature is known to influence the behavior and physiology of elasmobranch fishes (Economakis & Lobel 1998, Matern et al. 2000, Wallman & Bennett 2006, Hight & Lowe 2007); however, photoperiod has only recently been recognized as a potential cue associated with long-term movement patterns in elasmobranchs (e.g. Dudgeon et al. 2013).

Sexual segregation and site fidelity

In general, tagged leopard sharks showed strong fidelity to their capture sites; the females tagged in La Jolla frequented the LJ receiver but were rarely detected at the DM receiver only 12 km away (Fig. 4, Table 1), whereas the males clearly preferred Del Mar (Fig. 6, Table 1). Sexual segregation in marine vertebrates generally results from a combination of sex-specific habitat selection and social segregation (reviewed by Wearmouth & Sims 2008), and leopard sharks appear to be no exception; individuals are likely attracted to site-specific factors that may contribute to the observed sexual segregation in aggregation behavior. Although access to nearby foraging grounds (rocky reef and submarine canyon in La Jolla and kelp forest in Del Mar) is likely an attractive feature of both aggregation sites, the La Jolla site, being located in the lee of a submarine canyon, is the calmest and warmest site along the immediate coastline (Kobayashi 1979, Nosal et al. 2013a, E. Parnell unpubl. data).

As proposed for other shallow, female-dominated elasmobranch aggregations (Economakis & Lobel 1998, Wallman & Bennett 2006, Hight & Lowe 2007, Jirik & Lowe 2012, Speed et al. 2012), Nosal et

(2013a) hypothesized the warm water in La Jolla to be of particular benefit to pregnant female leopard sharks by potentially accelerating embryonic development. The female high season at the LJ receiver (late June to early December) begins just after leopard shark pupping season (April and May). Given this timing and the annual reproductive cycle and 10 to 11 mo gestation period reported for this species (Ebert 2003, Castro 2011), female *Triakis semifasciata* aggregating at the La Jolla site are likely in the early stages of pregnancy. Thus, the seasonal timing of the aggregation appears largely unrelated to parturition and may be a means of reducing harassment by males after mating elsewhere. Although females tagged in Del Mar were detected equally at the LJ and DM receivers during this study, their increased preference for the La Jolla site during the high season, when the local temperature anomaly is likely greatest due to seasonally smaller waves and increased thermal stratification, is consistent with warm temperatures being particularly attractive to females.

Putative effects of temperature and light on aggregation behavior

In addition to its likely role as an attractant, temperature (along with light) appears to influence both diel and seasonal movement patterns of leopard sharks. On a daily timescale, shark abundance was highest at the aggregation sites during daylight hours, which has emerged as a common feature of elasmobranch aggregation behavior (Klimley et al. 1988, Economakis & Lobel 1998, Hight & Lowe 2007, Speed et al. 2011), and peaked in late afternoon when water temperature was highest—consistent with behavioral thermoregulation functions proposed for other shark aggregations (Economakis & Lobel 1998, Hight & Lowe 2007, Speed et al. 2012). The recurring morning dip in female leopard shark abundance near the LJ receiver (Figs. 2 & 3) was consistent with actively tracked sharks (Nosal et al. 2013a) being biased toward the warmer rocky reef (largely outside detection range; Fig. 1) during the coldest morning hours of 07:00 h to 11:00 h (the rocky reef is warmer due to topographical trapping of warm surface water and increased absorption of light and radiation of heat by the darker substrata; Kobayashi 1979, E. Parnell unpubl. data), and shifting toward the sand flat area (within detection range; Fig. 1) later in the day. Hight & Lowe (2007) also reported a late-afternoon peak in leopard shark abundance in BFC, Santa Catalina Island, where

sharks selectively occupied the warmest areas of the cove throughout the day. Similarly, fewer sharks were detected at the LJ receiver around the time of high tide than at low tide, which likely reflects their movement shoreward (outside detection range) with the flooding tide to remain in warm, shallow water, or else to reduce predation risk, as suggested for juvenile lemon sharks *Negaprion brevirostris* (Guttridge et al. 2012). The latter seems less likely, however, because male California sea lions *Zalophus californianus* and broadnose sevengill sharks *Notorynchus cepedianus* have been known to drive leopard sharks against the beach during predation events (Ebert 1991, Hight & Lowe 2007).

Similar tidal movements have been reported previously for leopard sharks (Ackerman et al. 2000, Carlisle & Starr 2010) as well as for the related brown smoothhound *Mustelus henlei* (Campos et al. 2009), which were attributed to benthic foraging over intertidal mudflats during the flooding tide. Although high tide may also allow sharks at the La Jolla site to forage over newly submerged intertidal areas of the rocky reef, the addition of accessible habitat is limited due to the steep bathymetry of the reef. Rather, both female and male leopard sharks appear to forage primarily at night, away from their aggregation sites and independent of tide. The onset of these nocturnal foraging excursions (e.g. to the submarine canyon near La Jolla and to the kelp forest near Del Mar) appears to be triggered by sunset, as evidenced by the concomitant drop in shark abundance at both aggregation sites (Fig. 2) and supporting active tracking results by Nosal et al. (2013a). Leopard sharks in BFC, Santa Catalina Island, were also observed to disperse from the aggregation site at night (Manley 1995, Hight & Lowe 2007), whereas leopard sharks aggregating in Elkhorn Slough showed little diel pattern in movement, which likely reflects the abundance of food available throughout the local intertidal mudflats, thus producing little incentive to leave the aggregation site (Carlisle & Starr 2010).

Seasonal movement patterns also appear to be influenced primarily by water temperature and light. The most important predictor of female aggregation behavior was SST, explaining 85.9% of the half-month variation in female abundance at the LJ receiver (Fig. 7, Table 2). Previous work in central California suggested a temperature of 10 to 12°C might cue the seasonal arrival and departure of leopard sharks in Tomales Bay (Hopkins & Cech 2003) and Elkhorn Slough (Carlisle & Starr 2009), which is considerably different from the threshold temperature of 17.6°C found in the present study; it thus

appears that leopard shark aggregation behavior is not triggered by some absolute value of SST. Rather, the synchronous year-to-year formation and dissolution of the leopard shark aggregations may be driven by seasonally changing SST and possibly supplemented by responses to yearly maximum and minimum values of photoperiod (i.e. the summer and winter solstices; Fig. 3). The seasonal 'attractiveness' of the La Jolla site is likely also defined by the seasonality of swell height and direction, which affect local water turbulence and temperature. The female high season in La Jolla (late June to early December) is delineated by a lull in swell height and a shift in swell direction to the southwest (the aggregation site is sheltered from southwest swells by the Point La Jolla promontory; Fig. 1B), which results in lower wave energy causing localized warming (Nosal et al. 2013a).

In contrast to females at the La Jolla site, seasonally changing SST and photoperiod were equally important predictors of male aggregation behavior in Del Mar, explaining 36.6 and 42.0% of the half-month variation in male abundance (Table 2). This is one of only a few studies to demonstrate the importance of photoperiod in predicting elasmobranch movement patterns. Previously, Grubbs et al. (2007) found that photoperiod was the environmental trigger most likely to initiate the seasonal migration of juvenile sandbar sharks *Carcharhinus plumbeus* to and from Chesapeake Bay, and that water temperature likely caused the sharks to enter the shallow estuaries that serve as nursery grounds. Most recently, Dudgeon et al. (2013) showed that seasonal abundance of the zebra shark *Stegostoma fasciatum* at an aggregation site in southeast Queensland, Australia, was highest between November and February, when photoperiod is longest in the Southern Hemisphere. Similar to male leopard sharks in Del Mar, peak abundance of zebra sharks did not coincide with peak SST; SST accounted for only about one quarter of the variation explained by month of year (a proxy for photoperiod). Numerous studies have demonstrated the importance of photoperiod in regulating elasmobranch hormone levels (Heupel et al. 1999, Mull et al. 2008, 2010), which in teleost fishes are known to govern certain migratory behaviors (e.g. smoltification in salmonid fishes; Wagner 1974, Folmar & Dickhoff 1980, Björnsson 1997), and may also elicit aggregation and migratory behavior in elasmobranch fishes.

The discrepancy between the sexes in the importance of photoperiod to seasonal aggregation behavior in leopard sharks remains unclear, but may simply reflect the phenological timing of life history events and the concomitant availability of environ-

mental cues. For example, mating begins in April (Castro 2011), which coincides with the onset of the high aggregation season for males in Del Mar and the most rapid increase in photoperiod (around the vernal equinox; Fig. 7). Thus, changing photoperiod may be the most readily perceptible environmental cue for male leopard sharks at that time, eliciting aggregation behavior in Del Mar (perhaps to mate; the sex ratio at the Del Mar site was approximately 1:1). After the mating season ends in May (Castro 2011), females (at or soon to be in early gestation) begin aggregating in La Jolla, when water temperature is most rapidly increasing (Fig. 7). Thus, changing water temperature may be the most readily perceptible environmental cue for females at that time, and the particularly high predictive value of temperature is consistent with its suspected importance to females in accelerating gestation. Hormone levels likely mediate these differences, and sex-specific effects of photoperiod on sex steroid levels in elasmobranch fishes are not unprecedented. For example, in male round stingrays *Urobatis halleri*, plasma testosterone and 11-ketotestosterone concentrations are correlated with photoperiod (Mull et al. 2008), whereas estradiol levels in females are not (Mull et al. 2010). As photoperiod is the most predictable environmental cue for animals residing in middle and high latitudes, and along with temperature, the most powerful environmental regulator of seasonal life-history events such as gametogenesis, mating, and migration in other organisms (Bradshaw & Holzapfel 2007, Milner-Gulland et al. 2011), its documentation here and in previous studies (Grubbs et al. 2007, Dudgeon et al. 2013) suggests future research should also consider the influence of photoperiod on the long-term movements of other elasmobranch species.

Seasonal philopatry and recaptures of tagged sharks

Leopard sharks exhibited strong long-term philopatry to the La Jolla and Del Mar aggregation sites with 50% of females and 60% of males tagged in 2009 returning every year of the study period (2009 to 2012; Table 3); actual philopatry may have been higher because at least 3 of the 22 sharks tagged in 2009 were recaptured and killed and thus could not have returned. Short-term (1 yr) philopatry in this study (70% of females and 84.6% of males detected 1 yr after tagging) was higher than that observed for female leopard sharks in BFC, Santa Catalina Island

(50.0%, n = 10; Hight & Lowe 2007), and Elkhorn Slough (7.7%, n = 13; Carlisle & Starr 2009). Whereas the lower rate of philopatry in BFC and Elkhorn Slough is likely due to the availability of alternative aggregation sites in surrounding areas, the higher yearly rate of return of females to La Jolla could reflect a lack of other sheltered areas along the mainland coast of southern California that provide the desired warm temperature and proximity to foraging grounds.

Males also exhibited high seasonal philopatry, despite the only readily apparent feature defining the Del Mar site being the adjacent kelp forest — which is hardly unique to the region. Nevertheless, the importance of giant kelp *Macrocystis pyrifera* appeared to be evidenced by a significant decline in male abundance at the DM receiver and increase at the LJ receiver in 2011 and 2012 compared to 2009 and 2010 (Figs. 4 & 6), which coincided with a massive die-off of the adjacent kelp forest due to turbidity stress and strong storms during the winter of 2010–2011 (no concomitant change in any of the measured environmental variables readily explained this shift in shark behavior). Permanent band transect surveys indicated a 23-fold decline in annual mean density of *M. pyrifera* in the Del Mar kelp forest, from 0.095 and 0.105 plants m^{-2} in 2009 and 2010, respectively, to 0.035 and 0.005 plants m^{-2} in 2011 and 2012, respectively (E. Parnell unpubl. data). This drastic decline in canopy-forming kelp likely changed the local community composition and may have reduced local prey abundance, which suggests changes to the local environment may alter shark aggregation behavior and movement patterns and may also have wider-reaching biological consequences. Specifically in this case, the percentage of leopard shark litters having multiple fathers was significantly higher in pregnant females sampled from the La Jolla site in 2011 (83.3%) than in 2010 (20.0%; Nosal et al. 2013b) possibly due to the influx of males to the La Jolla site in 2011.

The high philopatry exhibited by male leopard sharks in this study was unexpected, given previous work on other shark species reporting discordance in population structure based on analyzing nuclear DNA (biparentally inherited; less structure) and mitochondrial DNA (maternally inherited; more structure) — which suggest gene flow is largely male-mediated, and thus male sharks are generally more dispersive and less philopatric than females (Feldheim et al. 2002, 2004, Keeney et al. 2005, Portnoy et al. 2010, Karl et al. 2011). However, we found no evidence of sex-specific philopatry in the

leopard shark, which suggests both sexes have limited dispersal. In addition to high seasonal philopatry, limited dispersal in leopard sharks is further evidenced by tagged sharks not being detected or reported captured north of Palos Verdes, CA or south of Puerto Nuevo, Baja California, Mexico, which is consistent with the southern California leopard shark population being a distinct genetic unit with little gene flow beyond this region (Lewallen et al. 2007).

The longest known movement away from the aggregation sites was to BFC, Santa Catalina Island (Fig. 1). This, along with similar movements of leopard sharks between the mainland and Channel Islands reported by Hight & Lowe (2007), supports other evidence suggesting a panmictic southern California population (Lewallen et al. 2007). In addition, its demonstrated ability to enter the pelagic environment offers an interesting contrast to the general supposition that the leopard shark is a 'nearshore benthic' species (Ebert 2003, Castro 2011). In fact, because the average swimming speed of shark M6 returning to Del Mar from Santa Catalina Island (0.54 body lengths s^{-1}) was already faster than the theoretical optimal cruising speed determined for other sharks species (0.40 body lengths s^{-1}; Weihs 1975), this shark likely swam a rather direct route (~125 km) and thus spent approximately 2 full days in the open ocean. Similar 'uncharacteristic' pelagic migrations between islands in French Polynesia have recently been reported for the comparably sized blacktip reef shark *Carcharhinus melanopterus*, apparently for the purpose of giving birth (Mourier & Planes 2013). The scarcity of detections at CSULB receivers around Palos Verdes and Los Angeles Harbor is consistent with leopard sharks transiting offshore (e.g. to Santa Catalina Island) south of Los Angeles, or may indicate that leopard sharks also overwinter along the mainland coast south of Los Angeles. Why some sharks were more transient than others remains unknown; however, Carlisle & Starr (2009) reported a similar finding for leopard sharks in Elkhorn Slough.

Conservation implications

The strong philopatry demonstrated in this study indicates the leopard shark, like other philopatric species, is susceptible to localized stock depletions resulting from fishing mortality or habitat destruction (Hueter et al. 2005). This vulnerability is likely exacerbated by the aggregation behavior and sex-

ual segregation reported in this study due to the risk of sharks being captured en masse and the threat of sex-biased mortality (Wearmouth & Sims 2008, Jacoby et al. 2012). The predominantly female aggregation in La Jolla clearly benefits from the small no-take Matlahuayl State Marine Reserve. Individual females spent up to 68.3% of the study period (1148 d) and up to 98.8% of the high season (183 d) within range of the LJ receiver, and therefore well within the reserve (Fig. 1). This suggests that even modestly sized reserves are effective at protecting leopard sharks on both a short- and long-term basis, and that other leopard shark aggregations would also benefit from small, strategically placed protected areas. Given that some sharks were detected at the TJ receiver, and likely crossed the international border, and that at least 1 shark was confirmed killed in a commercial gillnet in Baja California, Mexico (these incidents were likely underreported), there is clearly a need for binational conservation efforts to protect this and other trans-border species by identifying and protecting aggregation sites on both sides of the border.

LITERATURE CITED

Ackerman JT, Kondratieff MC, Matern SA, Cech JJ (2000) Tidal influence on spatial dynamics of leopard sharks, *Triakis semifasciata*, in Tomales Bay, California. Environ Biol Fishes 58:33–43

Ainley D, Henderson R, Huber H, Boekelheide R, Allen S, McElroy T (1985) Dynamics of white shark/pinniped interactions in the Gulf of the Farallones. Mem South Calif Acad Sci 9:109–122

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

Björnsson BT (1997) The biology of salmon growth hormone: from daylight to dominance. Fish Physiol Biochem 17: 9–24

Bradshaw WE, Holzapfel CM (2007) Evolution of animal photoperiodism. Annu Rev Ecol Evol Syst 38:1–25

Campos BR, Fish MA, Jones G, Riley RW and others (2009) Movements of brown smoothhounds, *Mustelus henlei*, in Tomales Bay, California. Environ Biol Fishes 85:3–13

Carlisle AB, Starr RM (2009) Habitat use, residency, and seasonal distribution of female leopard sharks *Triakis semifasciata* in Elkhorn Slough, California. Mar Ecol Prog Ser 380:213–228

Carlisle AB, Starr RM (2010) Tidal movements of female leopard sharks (*Triakis semifasciata*) in Elkhorn Slough, California. Environ Biol Fishes 89:31–45

Carlisle A, King A, Cailliet G, Brennan J (2007) Long-term trends in catch composition from elasmobranch derbies in Elkhorn Slough, California. Mar Fish Rev 69:25–45

Carrier JC, Pratt HL, Martin LK (1994) Group reproductive behaviors in free-living nurse sharks, *Ginglymostoma cirratum.* Copeia 1994:646–656

Castro JI (2011) The sharks of North America. Oxford University Press, New York, NY

Dewar H, Mous P, Domeier M, Muljadi A, Pet J, Whitty J (2008) Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo Marine Park, Indonesia. Mar Biol 155:121–133

Dudgeon CL, Lanyon JM, Semmens JM (2013) Seasonality and site fidelity of the zebra shark, *Stegostoma fasciatum*, in southeast Queensland, Australia. Anim Behav 85: 471–481

Duncan KM, Holland KN (2006) Habitat use, growth rates and dispersal patterns of juvenile scalloped hammerhead sharks *Sphyrna lewini* in a nursery habitat. Mar Ecol Prog Ser 312:211–221

Ebert DA (1991) Observations on the predatory behaviour of the sevengill shark *Notorynchus cepedianus.* S Afr J Mar Sci 11:455–465

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

Ebert DA, Ebert TB (2005) Reproduction, diet and habitat use of leopard sharks, *Triakis semifasciata* (Girard), in Humboldt Bay, California, USA. Mar Freshw Res 56: 1089–1098

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

Farrer DA (2009) Northern range extension of the leopard shark, *Triakis semifasciata.* Calif Fish Game 95:62–64

Feldheim KA, Gruber SH, Ashley MV (2002) The breeding biology of lemon sharks at a tropical nursery lagoon. Proc R Soc Lond B 269:1655–1661

Feldheim KA, Gruber SH, Ashley MV (2004) Reconstruction of parental microsatellite genotypes reveals female polyandry and philopatry in the lemon shark, *Negaprion brevirostris.* Evolution 58:2332–2342

Folmar LC, Dickhoff WW (1980) The parr–smolt transformation (smoltification) and seawater adapation in salmonids. A review of selected literature. Aquaculture 21: 1–37

Grubbs RD, Musick JA, Conrath CL, Romine JG (2007) Longterm movements, migration and temporal delineation of a summer nursery for juvenile sandbar sharks in the Chesapeake Bay region. Am Fish Soc Symp 50: 87–107

Guttridge TL, Gruber SH, Franks BR, Kessel ST and others (2012) Deep danger: intra-specific predation risk influences habitat use and aggregation formation of juvenile lemon sharks *Negaprion brevirostris.* Mar Ecol Prog Ser 445:279–291

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

Heupel MR, Simpfendorfer CA (2005) Quantitative analysis of aggregation behavior in juvenile blacktip sharks. Mar Biol 147:1239–1249

Heupel MR, Whittier JM, Bennett MB (1999) Plasma steroid hormone profiles and reproductive biology of the epaulette shark, *Hemiscyllium ocellatum.* J Exp Zool 284: 586–594

Heyman WD, Graham RT, Kjerfve B, Johannes RE (2001) Whale sharks *Rhincodon typus* aggregate to feed on fish spawn in Belize. Mar Ecol Prog Ser 215:275–282

Hight BV, Lowe CG (2007) Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? J Exp Mar Biol Ecol 352:114–128

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

Holland KN, Wetherbee BM, Lowe CG, Meyer CG (1999) Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. Mar Biol 134:665–673

Hopkins TE, Cech JJ (2003) The influence of environmental variables on the distribution and abundance of three elasmobranchs in Tomales Bay, California. Environ Biol Fishes 66:279–291

Hueter RE, Heupel MR, Heist EJ, Keeney DB (2005) Evidence of philopatry in sharks and implications for the management of shark fisheries. J Northwest Atl Fish Sci 35:239–247

Jacoby DMP, Busawon DS, Sims DW (2010) Sex and social networking: the influence of male presence on social structure of female shark groups. Behav Ecol 21:808–818

Jacoby DMP, Croft DP, Sims DW (2012) Social behaviour in sharks and rays: analysis, patterns and implications for conservation. Fish Fish 13:399–417

Jirik KE, Lowe CG (2012) An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. J Fish Biol 80:1227–1245

Johnson JW (2000) A heuristic method for estimating the relative weight of predictor variables in multiple regression. Multivariate Behav Res 35:1–19

Karl SA, Castro ALF, Lopez JA, Charvet P, Burgess GH (2011) Phylogeography and conservation of the bull shark (*Carcharhinus leucas*) inferred from mitochondrial and microsatellite DNA. Conserv Genet 12:371–382

Keeney DB, Heupel MR, Hueter RE, Heist EJ (2005) Microsatellite and mitochondrial DNA analyses of the genetic structure of blacktip shark (*Carcharhinus limbatus*) nurseries in the northwestern Atlantic, Gulf of Mexico, and Caribbean Sea. Mol Ecol 14:1911–1923

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

Klimley AP, Butler SB, Nelson DR, Stull AT (1988) Diel movements of scalloped hammerhead sharks, *Sphyrna lewini* (Griffith and Smith), to and from a seamount in the Gulf of California. J Fish Biol 33:751–761

Klimley AP, Pyle P, Anderson S (1996) The behavior of white sharks and their pinniped prey during predatory attacks. In: Klimley AP, Ainley D (eds) Great white sharks: the biology of *Carcharodon carcharias*. Academic Press, San Diego, CA, p 175–191

Kobayashi BN (1979) California marine waters: areas of special biological significance reconnaissance survey report. San Diego-La Jolla Ecological Reserve, Water Quality Monitoring Report No. 79-1. San Diego, CA

Lewallen EA, Anderson TW, Bohonak AJ (2007) Genetic structure of leopard shark (*Triakis semifasciata*) populations in California waters. Mar Biol 152:599–609

Manley J (1995) Diel movement patterns and behaviors of leopard sharks, *Triakis semifasciata*, at Santa Catalina Island, California. MS thesis, California State University, Long Beach, CA

Matern SA, Cech JJ, Hopkins TE (2000) Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: evidence for behavioral thermoregulation? Environ Biol Fishes 58:173–182

Miller DJ, Lea RN (1972) Guide to the coastal marine fishes of California. Fish Bull Calif Dep Fish Game 157:1–249

Milner-Gulland EJ, Fryxell JM, Sinclair ARE (2011) Animal migration: a synthesis. Oxford University Press, New York, NY

Mourier J, Planes S (2013) Direct genetic evidence for reproductive philopatry and associated fine-scale migrations in female blacktip reef sharks (*Carcharhinus melanopterus*) in French Polynesia. Mol Ecol 22:201–214

Mucientes GR, Queiroz N, Sousa LL, Tarroso P, Sims DW (2009) Sexual segregation of pelagic sharks and the potential threat from fisheries. Biol Lett 5:156–159

Mull CG, Lowe CG, Young KA (2008) Photoperiod and water temperature regulation of seasonal reproduction in male round stingrays (*Urobatis halleri*). Comp Biochem Physiol A Mol Integr Physiol 151:717–725

Mull CG, Lowe CG, Young KA (2010) Seasonal reproduction of female round stingrays (*Urobatis halleri*): steroid hormone profiles and assessing reproductive state. Gen Comp Endocrinol 166:379–387

Nosal AP, Cartamil DP, Long JW, Lührmann M, Wegner NC, Graham JB (2013a) Demography and movement patterns of leopard sharks (*Triakis semifasciata*) aggregating near the head of a submarine canyon along the open coast of southern California, USA. Environ Biol Fishes 96: 865–878

Nosal AP, Lewallen EA, Burton RS (2013b) Multiple paternity in leopard shark (*Triakis semifasciata*) litters sampled from a predominantly female aggregation in La Jolla, California, USA. J Exp Mar Biol Ecol 446:110–114

O'Brien R (2007) A caution regarding rules of thumb for variance inflation factors. Qual Quant 41:673–690

Pondella DJ, Allen LG (2008) The decline and recovery of four predatory fishes from the Southern California Bight. Mar Biol 154:307–313

Portnoy DS, McDowell JR, Heist EJ, Musick JA, Graves JE (2010) World phylogeography and male-mediated gene flow in the sandbar shark, *Carcharhinus plumbeus*. Mol Ecol 19:1994–2010

Pratt HL Jr, Carrier JC (2001) A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. Environ Biol Fishes 60: 157–188

Russo RA (1975) Observations on the food habits of leopard sharks (*Triakis semifasciata*) and brown smoothhounds (*Mustelus henlei*). Calif Fish Game 61:95–103

Sims DW, Quayle VA (1998) Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. Nature 393:460–464

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

Smith SE, Abramson NJ (1990) Leopard shark (*Triakis semifasciata*) distribution, mortality rate, yield, and stock replenishment estimates based on a tagging study in San Francisco Bay. Fish Bull 88:371–381

Smith SE, Au DW, Show C (1998) Intrinsic rebound potentials of 26 species of Pacific sharks. Mar Freshw Res 49: 663–678

Speed CW, Meekan MG, Field IC, McMahon CR and others (2011) Spatial and temporal movement patterns of a multi-species coastal reef shark aggregation. Mar Ecol Prog Ser 429:261–275

Speed CW, Meekan MG, Field IC, McMahon CR, Bradshaw CJA (2012) Heat-seeking sharks: support for behavioral thermoregulation in reef sharks. Mar Ecol Prog Ser 463: 231–244

Strong WR, Murphy RC, Bruce BD, Nelson DR (1992) Movements and associated observations of bait-attracted white sharks, *Carcharodon carcharias*: a preliminary report. Aust J Mar Freshwater Res 43:13–20

Talent LG (1976) Food habits of the leopard shark, *Triakis semifasciata*, in Elkhorn Slough, Monterey Bay, California. Calif Fish Game 62:286–298

Tonidandel S, LeBreton JM (2011) Relative importance analysis: a useful supplement to regression analysis. J Bus Psychol 26:1–9

Wagner HH (1974) Photoperiod and temperature regulation of smolting in steelhead trout (*Salmo gairdneri*). Can J Zool 52:219–234

Wallman HL, Bennett WA (2006) Effects of parturition and feeding on thermal preference of Atlantic stingray, *Dasyatis sabina* (Lesueur). Environ Biol Fishes 75: 259–267

Wearmouth VJ, Sims DW (2008) Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. Adv Mar Biol 54:107–170

Wearmouth VJ, Southall EJ, Morritt D, Thompson RC, Cuthill IC, Partridge JC, Sims DW (2012) Year-round sexual harassment as a behavioral mediator of vertebrate population dynamics. Ecol Monogr 82:351–366

Webber JD, Cech JJ (1998) Nondestructive diet analysis of the leopard shark from two sites in Tomales Bay, California. Calif Fish Game 84:18–24

Weihs D (1975) An optimum swimming speed of fish based on feeding efficiency. Isr J Technol 13:163–167

Whitney NM, Pratt HL, Carrier JC (2004) Group courtship, mating behaviour and siphon sac function in the whitetip reef shark, *Triaenodon obesus*. Anim Behav 68:1435–1442