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

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Abstract The demography, spatial distribution, and movement patterns of leopard sharks (*Triakis semifasciata*) aggregating near the head of a submarine canyon in La Jolla, California, USA, were investigated to resolve the causal explanations for this and similar shark aggregations. All sharks sampled from the aggregation site ($n=140$) were sexually mature and 97.1 % were female. Aerial photographs taken during tethered balloon surveys revealed high densities of milling sharks of up to 5470 sharks ha^{-1}. Eight sharks were each tagged with a continuous acoustic transmitter and manually tracked without interruption for up to 48 h. Sharks exhibited strong site-fidelity and were generally confined to a divergence (shadow) zone of low wave energy, which results from wave refraction over the steep bathymetric contours of the submarine canyon. Within this divergence zone, the movements of sharks were strongly localized over the seismically active Rose Canyon Fault. Tracked sharks spent most of their time in shallow water ($\leq$2 m for 71.0 % and $\leq$10 m for 95.9 % of time), with some dispersing to deeper (max: 53.9 m) and cooler (min: 12.7 °C) water after sunset, subsequently returning by sunrise. These findings suggest multiple functions of this aggregation and that the mechanism controlling its formation, maintenance, and dissolution is complex and rooted in the sharks' variable response to numerous confounding environmental factors.

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Introduction

Elasmobranch fishes are vulnerable to overexploitation because of their slow growth rates, late sexual maturation, and low fecundity (Musick et al. 2000). This vulnerability is exacerbated by the aggregative tendencies of many species and the related risk of being captured *en*

masse (Jacoby et al. 2011). The leopard shark (*Triakis semifasciata*) is no exception; it is known to aggregate close to shore throughout California, USA (Smith and Abramson 1990; Ebert and Ebert 2005; Hight and Lowe 2007; Carlisle and Starr 2009), and underwent a population decline in the 1980s and 1990s because of widespread use of nearshore (within three miles) bottom-set gillnets (Pondella and Allen 2008). Although the ban of these nets in 1994 appears to have allowed the population to recover, elucidating the causes of these aggregations remains a priority to ensure this vulnerable species is managed effectively in the future (Pondella and Allen 2008).

Aggregation behavior in elasmobranch fishes can be explained evolutionarily (ultimate causes) by addressing the adaptive significance or function of the behavior, as well as mechanistically (proximate causes) by addressing the immediate environmental and physiological factors that drive the behavior. For example, aggregations of sharks and rays may result from mutual attraction to conspecifics, favorable habitat, or prey (proximate causes); however, the behavior is maintained by natural selection because individuals garner related benefits such as mating opportunities, shelter, and increased foraging efficiency (ultimate causes) (Jacoby et al. 2011). Previous studies on leopard sharks inhabiting bays and estuaries suggest aggregations may form in areas where prey is abundant (Russo 1975; Talent 1976; Webber and Cech 1998; Carlisle and Starr 2009) and water temperature is high, thus accelerating gestation in pregnant females (Manley 1995; Hight and Lowe 2007). Bays and estuaries are also believed to function as nursery and pupping grounds for leopard sharks (Ackerman 1971; Talent 1985; Carlisle et al. 2007; Carlisle and Starr 2009).

In contrast to previous work conducted in bays and estuaries, the present study is the first to investigate a leopard shark aggregation occurring along the open coast, which shows no obvious source of food, shelter, or mating benefits, and thus the ultimate and proximate causes of the aggregation are not readily apparent. To elucidate the causes of this aggregation, which forms annually off a sandy beach in southern California in the spring, summer, and autumn, the demographic composition and movement patterns of these sharks were investigated and related to potentially attractive biotic and abiotic features of the site. This provided the opportunity to evaluate the potential influences of unique bathymetric, geologic, and hydrographic features of the open-coast site in comparison to those of bays and estuaries, where most leopard shark aggregations occur, and thus refine our understanding of the ultimate and proximate factors causing leopard sharks to aggregate. In addition, because this aggregation site has been protected since 1971 by the small (2.16 km²) no-take San Diego – La Jolla Ecological Reserve, and thus was not subjected to destructive gillnet fishing in the 1980s and 1990s, it also serves as a model for evaluating the effectiveness of small no-take reserves in protecting these and similar aggregations of sharks.

Materials and methods

The leopard shark aggregation occurs at the southern end of La Jolla Shores beach (32.8525°, −117.2623°) in San Diego County, California, near the head of La Jolla Submarine Canyon and over the seismically active Rose Canyon Fault. The fault approximately separates two distinct habitats present at the aggregation site: rocky reef and sand flat (Fig. 1).

Demographic survey

To determine the demographic composition of the aggregating leopard sharks, 140 individuals were captured by hook and line from a 5 m skiff, measured for fork length (FL) and total length (TL), sexed, and tagged with a spaghetti identification tag (Floy Tag FIM-96). Sharks were released <5 min after being hooked. Seventeen female sharks were transported to Scripps Institution of Oceanography (SIO) to determine pregnancy by allowing the shark to give birth naturally, conducting an ultrasound (Philips Sonos 5500), or dissection. Five sharks that were found dead on the beach were salvaged, dissected, and included in the demographic survey. Sampling occurred in June–November of 2007–2011, when the leopard sharks were present at the aggregation site, and conducted over several years to ensure findings were representative of the aggregation and not the result of sampling during an atypical year.

Aerial photography

To observe directly the spatial distribution, abundance, and orientation of leopard sharks at the aggregation site, aerial photographs were taken automatically every 1.25 s using a digital camera (Canon Powershot SD 780 IS), mounted beneath a 1.8 m diameter helium-filled balloon (Arizona Balloon Company) tethered 45 m above the water surface. Photographs were corrected for color,
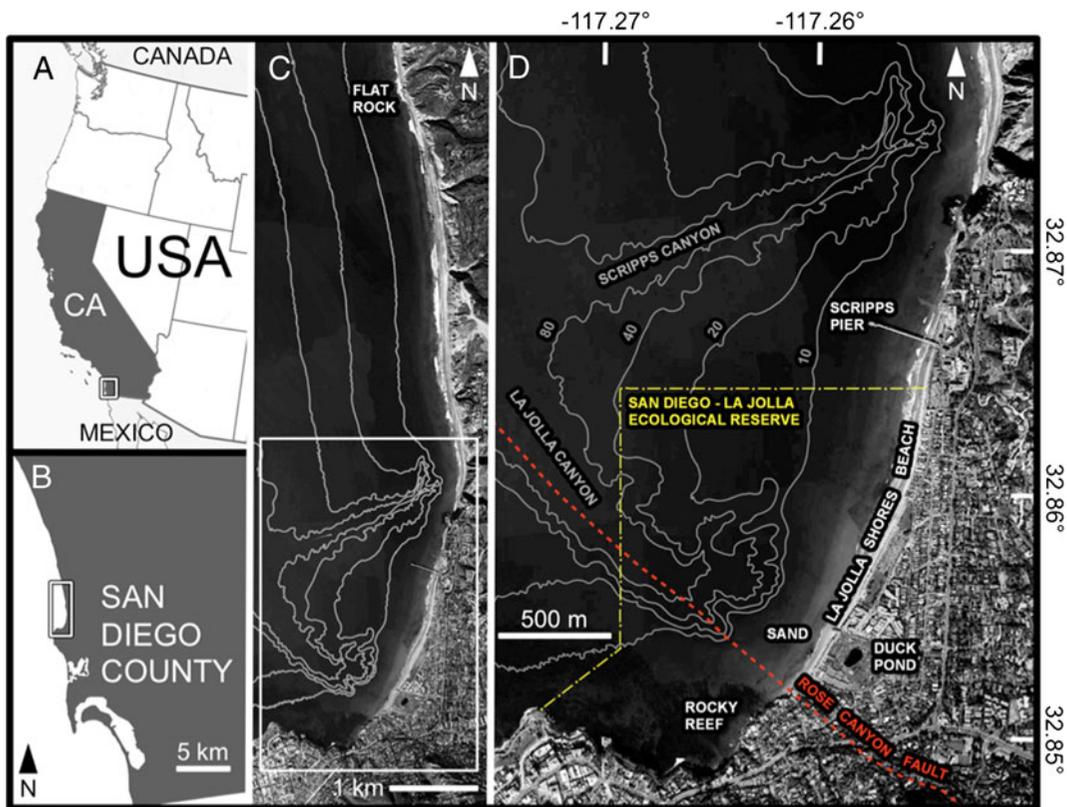
Fig. 1 Study area. **a** The western United States of America with the state of California (CA) darkened. **b** Enlarged view of the white box in A showing the coastline of San Diego County, California. **c** Enlarged view of the white box in B showing the coastline of La Jolla, California extending northward. **d** Enlarged view of the white box in C showing the study site at the southern end of La Jolla Shores Beach, La Jolla, California along with the San Diego – La Jolla Ecological Reserve boundaries and the Rose Canyon Fault. C and D are shown with the 10, 20, 40, and 80 m isobaths. Bathymetry data were acquired, processed, and distributed by the Seafloor Mapping Laboratory of California State University Monterey Bay. Aerial views in C and D are from Google Earth Pro (Imagery Date: 1 February 2008)

contrast, and exposure in Adobe Photoshop CS2 and imported into ArcMap 10 (ESRI) for scaling and spatial analysis. The geographical position of each shark was defined as the midpoint between the tips of the pectoral fins. Photographs were scaled using the shadow of the balloon on the water surface; its diameter was measured beforehand over the beach by marking the shadow's edges in the sand. Circular statistics were conducted in Oriana v. 3 (Kovach Computing Services). Approximately 5000 photographs were taken over 3 days of aerial surveys on 18 and 19 August and 27 September 2010.

Tagging and tracking

Eight leopard sharks were each externally fitted with a continuous acoustic transmitter with temperature and pressure sensors (VEMCO V16TP, 51–78 kHz, 1000 ms period) using a nylon dart (Floy Tag FIM-96) inserted into the musculature and through the radials at the base of the first dorsal fin. Active tracking commenced immediately following release from the 5 m skiff using a gunnel-mounted rotatable directional hydrophone (VEMCO VH110) coupled to an onboard acoustic receiver (VEMCO VR100), which continuously decoded and displayed water temperature and depth readings from the shark-borne transmitter. These readings, along with determinations of geographical position (Garmin GPSmap76) of the tracking vessel, which by convention were taken to be the position of the shark, were manually recorded at 5 min intervals during the tracking period. Tracked sharks 1–7 were tagged at the aggregation site and shark 8 was tagged near the head of Scripps Canyon (Fig. 1d). Tracks occurred between 4 August 2008 and 13 October 2010.

Data analyses

Positional fixes from tracked sharks were used to calculate fixed kernel utilization distributions (KUDs) (Worton 1989) in Biotas v 2.0 (Ecological Software Solutions) using the least squares cross validation (LSCV) option for the smoothing parameter, h. The 95 % probability contours (total activity space, 95 % KUD) and 50 % probability contours (core area, 50 % KUD) were calculated for each tracked shark and imported as shape files into ArcMap 10 (ESRI) for spatial analysis and map assembly. Daytime and nighttime 95 % and 50 % KUDs were calculated for each shark and the mean areas were compared between day and night (delineated by local times of sunrise and sunset, United States Naval Observatory Data Services) using a Mann–Whitney U Test. A total 95 % and 50 % KUD (KUD_{TOT}) was constructed for sharks tagged at the aggregation site by pooling the positional fixes from sharks 1–7. Rate of movement (ROM) was calculated for each shark at 5 min intervals and compared between periods of day and night using a Mann–Whitney U Test. The inherent autocorrelation of spatial observations was retained; destructive subsampling of tracking data has been shown to be an ineffective means of reducing autocorrelation and serial independence of observations is not necessary for KUD calculations (de Solla et al. 1999).

Habitat preference within the 95 % KUD_{TOT} was determined for sharks 1–7 (rocky reef vs. sand flat; habitat map layer accessed on 11 January 2011 from http://seafloor.csumb.edu). The total number of observed positional fixes over rocky reef and sand flat was compared to the expected number based on their respective areas within the available space (defined as the 95 % KUD_{TOT}) using a Chi-Squared (χ^2) Test. This analysis was repeated for positional fixes pooled hourly and by tidal height (0.2 m bins, relative to Mean Lower Low Water, MLLW) to determine whether habitat preference was affected by time of day or tide.

To relate the general alongshore distribution of positional fixes to the location of the Rose Canyon Fault (location taken from the Quaternary Faults and Folds Database of the United States Geological Survey), a best-fit line was calculated for the positional fixes inside the 95 % KUD_{TOT}. The positional fixes were then projected onto the best-fit line in 10 m bins to construct a density histogram.

The locations of the total 50 % and 95 % KUDs were also related to local wave height. The wave climate at the aggregation site and surrounding area was modeled using the SWAN (*Simulating WAves Nearshore*) wave model (Booij et al. 1999), which solves a spectral wave action balance equation to compute wave transformation from deeper water depths into the nearshore region, and produces values of significant wave height (H_S) at a resolution of 15 m alongshore and 10 m cross-shore. The effect of wave shoaling, refraction, and depth-induced wave breaking via the parameterization of Battjes (1978) with constant breaking coefficient of 0.73 were included but not the effect of non-linear wave-wave interactions. Bathymetry for the model domain was derived from multiple sources (Long and Özkan-Haller 2005) and merged using a scale-controlled interpolation routine (Plant et al. 2002). The hourly tidal elevations were obtained by the NOAA tide gauge at the SIO pier and included in each simulation. The offshore directional wave spectra used to initialize the model were taken from the Outer Torrey Pines directional wave buoy (maintained by the Coastal Data Information Program at SIO) and computed using the Maximum Entropy Method (Lygre and Krogstad 1986). Homogeneous spectra were prescribed along the western and northern model boundaries. The cross-shore variation of the incident spectra along the southern boundary of the domain is approximated assuming refraction over straight and parallel contours, which was computationally efficient and, when compared with data from previous field experiments, provided more accurate nearshore wave conditions near the aggregation site when offshore wave environments were dominated by a southerly swell. The SWAN model has been used in previous studies to estimate wave characteristics along this section of coast with favorable agreement (e.g., Gorrell et al. 2011).

For tracks 1–7, the modeled hourly wave conditions were averaged to generate track-specific mean wave climates, which were then averaged to generate a mean wave climate for all tracks. The 95 % KUD_{TOT} and 50 % KUD_{TOT} were georeferenced and superimposed over this overall mean wave climate. Modeled H_S values were isolated and averaged in each of the following areas: 1) inside the 50 % KUD_{TOT}, 2) inside the 95 % KUD_{TOT} but outside the 50 % KUD_{TOT}, and 3) in the "vicinity" surrounding the 95 % KUD_{TOT} bounded by the 10 m isobath between Point La Jolla and SIO pier.

Results

Demographic survey

Of the 140 sharks sampled, 97.1 % were female and 2.9 % were male. Mean TL±SD was 138.9±10.6 cm for females (range: 110–164 cm) and 130.7±15.6 cm for males (range: 116–147 cm); all sharks were sexually mature according to Kusher et al. (1992). When pregnancy was ascertained (n=22), all females were found to be pregnant.

Aerial survey

Aerial photographs showed that the aggregation typically consisted of distinct high-density and low-density areas (Fig. 2a), with the former often occurring near or inshore of the surf line (Fig. 2b). Using Fig. 2a as an example, the minimum convex polygon (MCV) comprising the high-density area contained 92 sharks at 5470 sharks ha^{-1}, of which 87.0 % were <1 mean body length (L=138.9 m) from their nearest neighbor. In contrast, the MCV comprising the low-density area contained only 20 sharks at 581 sharks ha^{-1}, of which none were <1L from their nearest neighbor. The largest shark count in any single photograph was 125, however, additional sharks were likely outside the field of view. Sharks were in constant motion and exhibited very few conspicuous formations or behaviors except for brief bouts (a few seconds, visible in no more than 5–10 sequential photographs) of circling, following, and occasionally turning over to expose their white ventral surfaces (see Klimley 2003, Smith 2005; Fig. 2c). The sharks' movements are best described as milling, lacking any obvious unimodal polarization (i.e., sharks were not oriented in the same direction). However, the distribution of shark headings was bimodal and significantly oriented to the axis parallel to the swell (Rao's Spacing Test, $p<0.05$).

Active tracking

In total, leopard sharks were tracked for 272.4 h and 223.3 km (Table 1). Sharks 1 and 8 traveled north along the coast to Flat Rock; shark 1 later returned to the aggregation site (Fig. 3a–b). Sharks 2, 3, 6, and 7
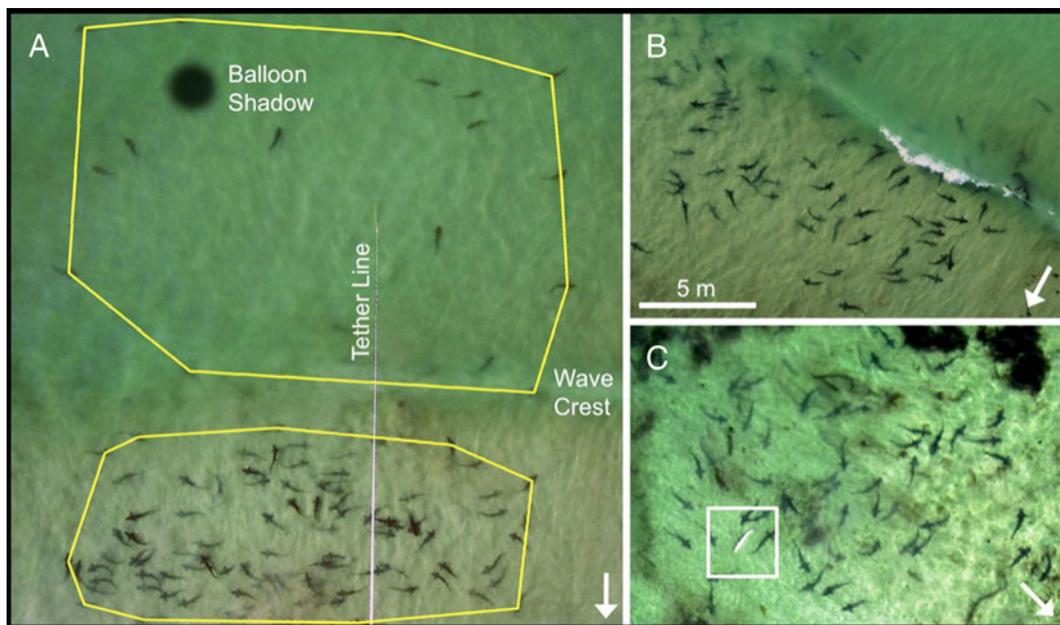

Fig. 2 *Triakis semifasciata*. Aerial photographs of the leopard shark aggregation in La Jolla, California. **a** High- and low-density areas of the aggregation, approximately separated by the incoming wave crest, each bounded by minimum convex polygons. Visible are the tether line and the shadow of the balloon, which was used to scale the photograph. **b** Aerial photograph showing a wave about to break over the leopard shark aggregation. **c** Aerial photograph showing a shark ventral-side-up, enclosed by a white box. Arrows in A, B, and C indicate the direction of the shoreline. The scale bar in B is applicable to the entire figure

Table 1 Summary information for eight leopard sharks (*Triakis semifasciata*) actively tracked using acoustic telemetry

Shark ID	Sex (M/F)	Length FL TL (cm)	Tagging Latitude Longitude (D.d°)	Tracking Period (mo/d/yr 24 h UTC-7)	Total Contact Time (hh:mm)	Longest Continuous Track (hh:mm)	Mean Depth±SD (RANGE) (m)	Mean Temp± SD (RANGE) (°C)	Area 50 % KUD 95 % KUD (km²)	Total Distance Traveled (km)
1	F	140 157	32.85323 −117.26234	08/25/08 0625 - 08/30/08 1550	41:35	20:45	2.6±2.4 (0.0–13.4)	21.8±1.0 (17.5–23.5)	0.073 0.366	43.2
2	F	124 142	32.85270 −117.26246	09/09/08 0810 - 09/11/08 0940	49:30	49:30	1.2±0.4 (0.8–4.2)	22.7±0.5 (20.5–23.9)	0.009 0.073	34.2
3	F	116 132	32.85297 −117.26299	09/16/08 1000 - 09/17/08 1005	24:05	24:05	0.8±0.5 (0.0–3.9)	19.1±0.6 (17.9–19.9)	0.025 0.120	16.8
4	F	128 147	32.85258 −117.26182	09/29/09 0910 - 10/01/09 0910	48:00	48:00	6.5±11.7 (0.4–53.9)	20.3±2.5 (12.7–22.4)	0.005 0.242	41.9
5	F	122 140	32.85283 −117.26182	10/06/09 1005 - 10/08/09 1005	48:00	48:00	3.4±7.3 (0.1–41.3)	18.7±1.1 (12.9–20.2)	0.021 0.218	40.2
6	M	131 147	32.85388 −117.26182	09/26/10 1355 - 09/27/10 2225	32:30	32:30	1.4±0.7 (0.0–5.5)	17.4±0.6 (15.7–19.3)	0.016 0.087	23.2
7	F	128 147	32.85296 −117.26182	10/13/10 1015 - 09/27/10 2225	03:05	03:05	0.9±0.5 (0.1–1.9)	19.3±0.2 (18.8–19.9)	0.015 0.077	2.1
8	F	95 112	32.87335 −117.25323	08/04/08 1100 - 08/07/08 1200	25:40	24:30	3.8±2.0 (0.0–7.7)	22.2±0.9 (19.9–23.7)	0.035 0.330	21.7

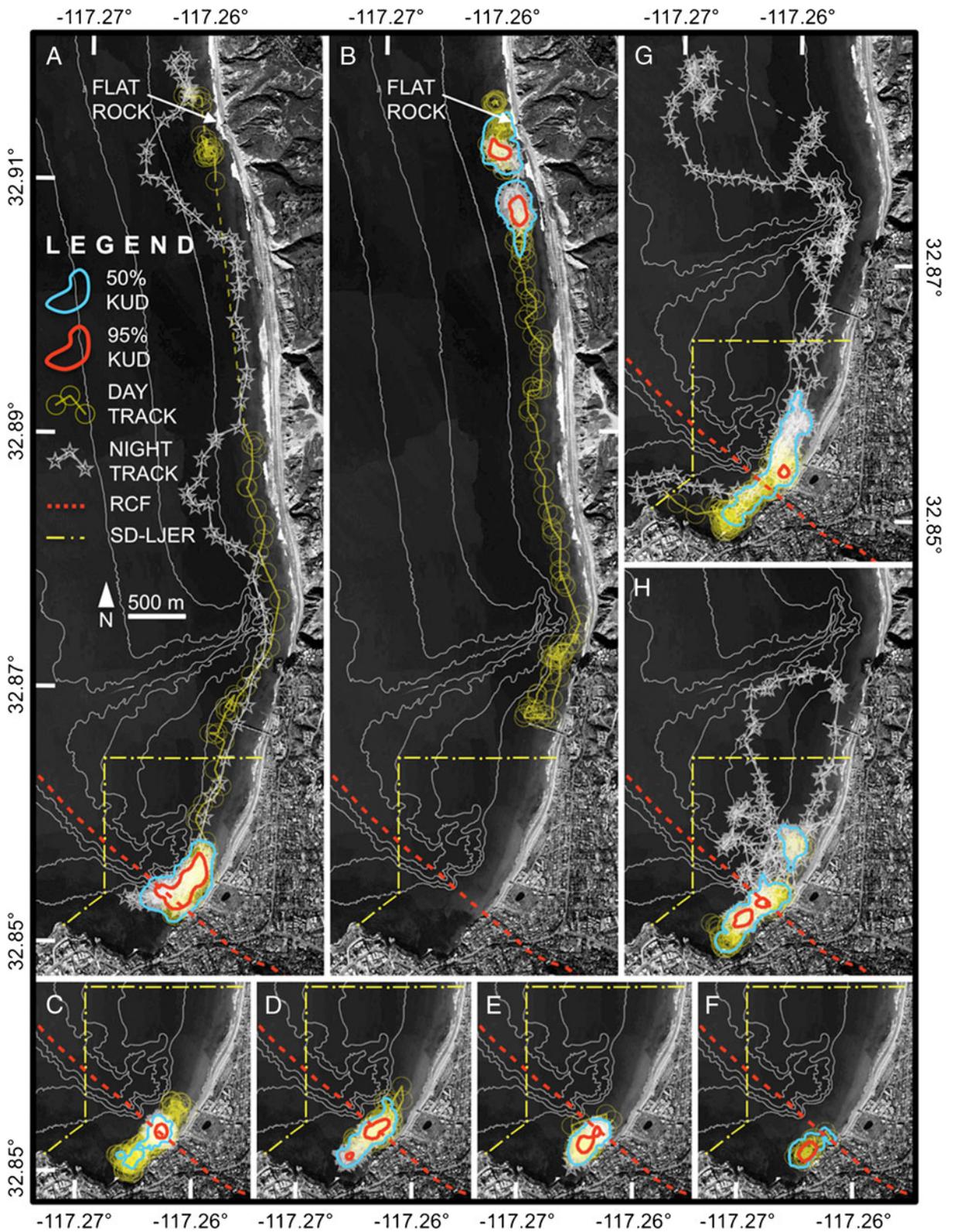*FL* fork length; *TL* total length, *KUD* kernel utilization distribution

remained near the aggregation site for the entire track (Fig. 3c–f). Sharks 4 and 5 dispersed from the aggregation site at sunset (Fig. 3g–h), traveling along the bottom to the deeper and cooler water of the submarine canyons (Fig. 4a–b), before returning to the aggregation site by sunrise. Mean 5-min ROM pooled for all sharks was significantly higher at night (0.86±0.61 kmh^{-1}) than during the day (0.77±0.46 kmh^{-1}) (Mann–Whitney U Test, $p < 0.05$), however, the mean areas of individual 95 % and 50 % KUDs did not differ significantly between day and night (Mann–Whitney U Test, $p > 0.05$). The sharks spent most of their time in shallow water (71.0 %≤2 m, 95.9 %≤10 m), more so during the day (80.0 %≤2 m, 99.8 %≤10 m) than at night (61.4 %≤2 m, 91.7 %≤10 m), and were located significantly deeper in the water column at night (mean ± SD= 4.24±8.14 m) than during the day (mean ± SD=1.55± 1.62 m) (Mann–Whitney U Test, $p < 0.05$).

The areas of the total 95 % and 50 % KUDs (KUD$_{TOT}$), calculated from positions pooled from sharks 1–7 (shark 8 was excluded because it was not tagged at the aggregation site), were 0.347 km² (28.7 % located over rocky reef and 71.3 % over sand flat) and 0.038 km² (17.0 % over rocky reef and 83.0 % over sand flat), respectively (Fig. 5a). The times at which positions were recorded over rocky reef and sand flat were significantly oriented (Rayleigh Test, $p < 0.05$); mean circular time ± SD was 09:00±05:19 h for rocky

reef and 18:26±08:23 h for sand flat (Fig. 5b), approximately coinciding with the times of mean daily minimum (09:00 h) and maximum (17:00 h) sea surface temperature measured at SIO pier for the months of August–October from 2008 to 2010 (archived data from NOAA Tides and Currents). Sharks were significantly biased toward the rocky reef between 07:00 and 12:00 h and toward the sand flat between 16:00 and 21:00 h (Chi-Squared Test, $p < 0.05$; Fig. 5c). Sharks were also significantly biased toward the rocky reef at intermediate tides (1.0–1.4 m above MLLW) and toward the sand flat at high (1.6–2.0 m above MLLW) and low tides (0.0–0.6 m above MLLW) (Chi-Squared Test, $p < 0.05$).

The 95 % KUD$_{TOT}$ was bounded in the cross-shore direction by the shoreline and the rim of La Jolla Canyon and alongshore by the divergence (shadow) zone of smaller wave height caused by bathymetric refraction of wave rays away from the canyon head (Fig. 6). Mean significant wave height (H_S) ± SD was 41.5±2.6 cm (range: 33.7–47.0 cm) inside the 50 %

Fig. 3 *Triakis semifasciata*. Movements of eight leopard sharks in relation to the aggregation site in La Jolla, CA as determined through active acoustic telemetry. **a** Shark 1. **b** Shark 8. **c** Shark 2. **d** Shark 3. **e** Shark 6. **f** Shark 7. **g** Shark 4. **h** Shark 5. See Table 1 for a summary of tracking details for each shark. Abbreviations: RCF, Rose Canyon Fault; SD-LJER, San Diego – La Jolla Ecological Reserve. *Semi-transparent dashed lines* indicate temporary signal loss with subsequent reacquisition
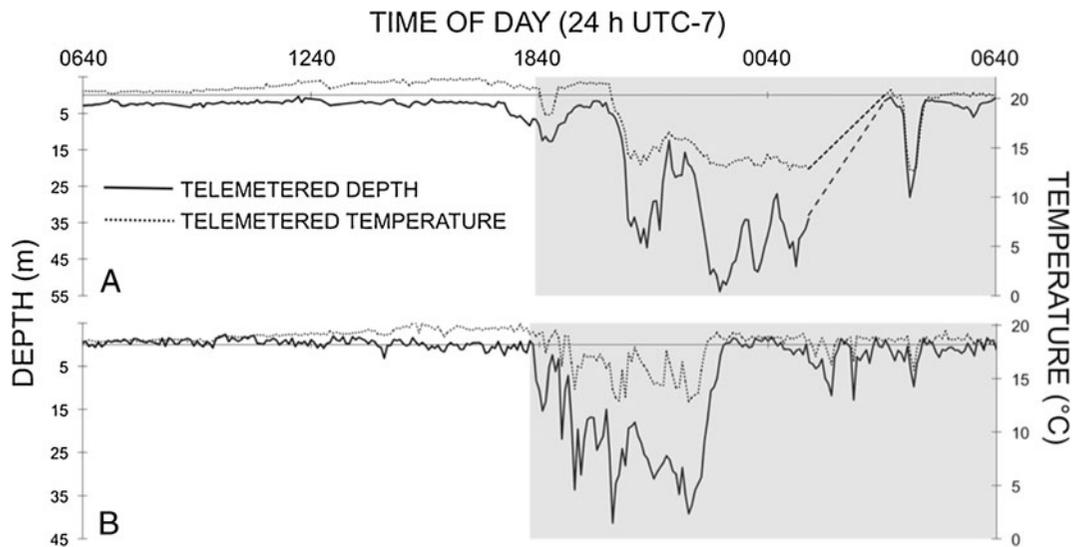
Fig. 4 *Triakis semifasciata*. Telemetered depth and temperature profiles from a representative 24 h tracking period for sharks 4 (**a**) and 5 (**b**). The dashed line in (**a**) corresponds to a temporary loss of signal between 01:45 and 03:45 h. The night period is indicated in gray

KUD_{TOT}, 47.1±12.2 cm (range: 22.5–86.7 cm) inside the 95 % KUD_{TOT} but outside the 50 % KUD_{TOT}, and 66.9±14.0 cm (range: 11.6–113.9 cm) in the vicinity (from Point La Jolla to the SIO pier, inshore of the 10 m isobath) surrounding the 95 % KUD_{TOT}, indicating a bias toward the areas with the lowest wave height.

The best-fit line through the 2596 acoustic tracking positional fixes within the 95 % KUD_{TOT} was oriented 41.3° from north and had a coefficient of determination (R^2) of 0.753 (Fig. 5a). Figure 7 shows the largest peak of the density histogram along this line occurred at a distance of 510.0 m from the southwestern endpoint, <1 m from where the Rose Canyon Fault intersected the line at 510.6 m at a nearly perpendicular angle of 88.8°.

Discussion

This study suggests various ultimate and proximate causes for the La Jolla open-coast leopard shark aggregation, some of which resemble previously proposed causes for aggregations in bays and estuaries, while others appear unique to this site. These putative explanations for the leopard shark aggregation, taken together with the movement patterns of individuals in relation to the boundaries of the San Diego – La Jolla Ecological Reserve, provide compelling evidence for the effectiveness of small reserves in protecting leopard sharks and other aggregating species.

Ultimate causes

The aggregation is site-specific and appears to function as a "home base" to which leopard sharks return regularly to exploit unique environmental features of the site and its proximity to foraging grounds. The head of La Jolla Canyon and the adjacent sandy shelves are known spawning grounds for market squid (*Loligo opalescens*) (McGowan 1954), which dominated the diet of leopard sharks sampled non-destructively from the aggregation site during the course of the study (M. Royer unpubl. data). Tracking data for sharks 4 and 5 (Figs. 3g–h, 4) showed nocturnal excursions into deeper water presumably to feed on this abundant prey item. This concept of returning to a "home base" near foraging grounds has been suggested for other elasmobranch species, including scalloped hammerheads (*Sphyrna lewini*) that aggregate at seamounts and oceanic islands (Klimley et al. 1988; Hearn et al. 2010; Bessudo et al. 2011).

In addition, the aggregation site is located in a wave divergence, or "shadow" zone, due to wave refraction over the La Jolla Canyon (Munk and Traylor 1947; Magne et al. 2007; Fig. 6). The locally reduced wave action and mixing results in a higher water temperature than other areas along the coast (e.g., the aggregation site is on average ~0.5 °C warmer than 1.8 km north at the SIO pier; Kobayashi 1979). The exceptionally warm water and predominance of pregnant females at this site are consistent with the "incubation
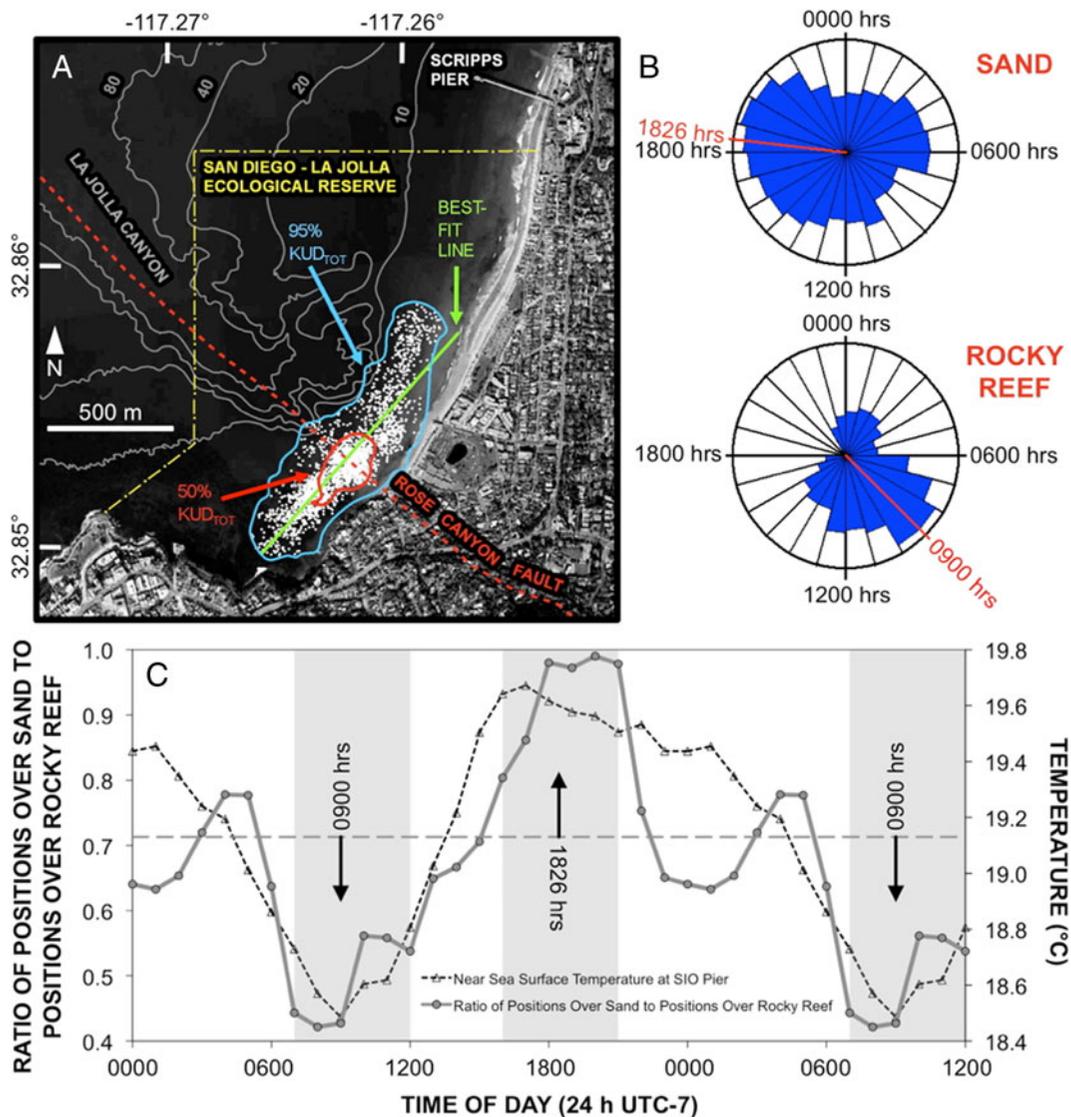
Fig. 5 *Triakis semifasciata*. (**a**) Best-fit line through the 2,596 positional fixes (*white dots*) that occurred inside the total 95 % kernel utilization distribution (KUD$_{TOT}$). (**b**) Circular histograms showing the distribution of times of positional fixes that occurred over sand (above) and over rocky reef (below). Circular mean time of positions over each habitat is shown as a red line. (**c**) Hourly changes in habitat preference throughout the day as shown by the observed ratio of positions over sand to positions over rocky reef (*solid grey line*). The expected ratio of positions over sand to positions over rocky reef based on the areas of these habitats within the total 95 % KUD (sand: 71.3 %, rocky reef: 28.7 %) is shown by the *horizontal dashed grey line*. *Grey areas* indicate the hours when the observed ratio is significantly different from the expected ratio (χ^2, $p < 0.05$). Mean circular times of positions over sand (09:00 h) and rocky reef (18:26 h) are shown. Mean hourly sea surface temperature from SIO pier, averaged for the months of August–October 2009–2010 is shown as a *dashed black line*

hypothesis," that female elasmobranch fishes behaviorally thermoregulate to accelerate embryonic development (Economakis and Lobel 1998; Hight and Lowe 2007; Mull et al. 2010; Jirik and Lowe 2012). Aggregating in calm surf might also allow the sharks to conserve energy, requiring fewer locomotory adjustments in response to breaking waves and turbulence. The sharks' bias toward the rocky reef when overall water temperature was coldest (~09:00 h) and toward the sand flat when overall water temperature was warmest (~17:00 h) suggests they may be exploiting the thermal heterogeneity of this area to maintain an optimal
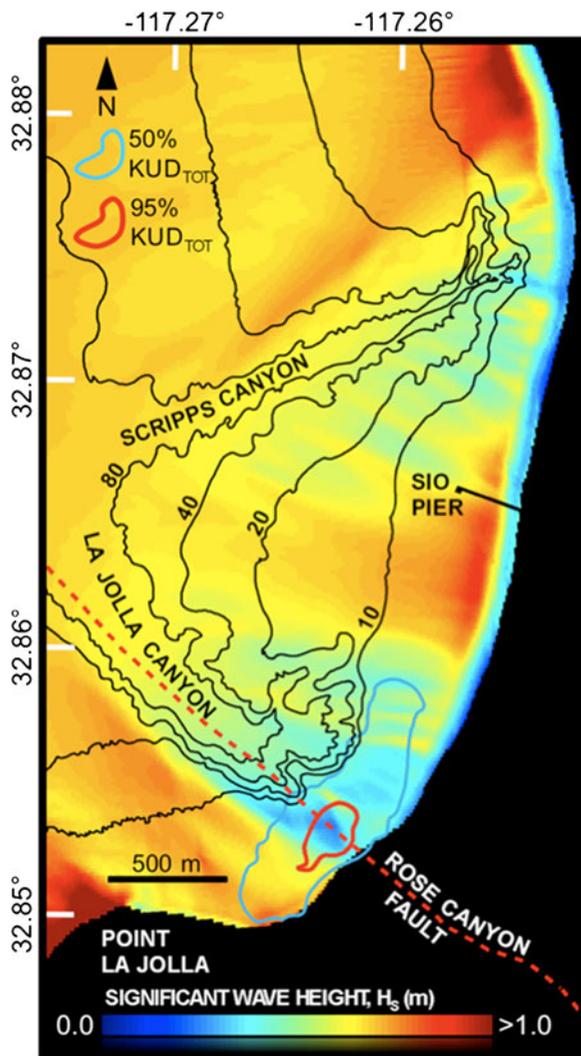
Fig. 6 *Triakis semifasciata*. Total leopard shark 50 % and 95 % kernel utilization distributions (KUD$_{TOT}$) overlaid on the modeled overall mean wave climate for all tracking periods

courtship, allowing mate selection for females, and increasing copulatory success for males) do not seem to apply (Carrier et al. 1994; Economakis and Lobel 1998; Pratt and Carrier 2001; Whitney et al. 2004). The absence of juvenile leopard sharks in the demographic survey is consistent with aerial surveys and *in situ* snorkeling observations that individuals under 1 m TL are uncommon at the aggregation site. However, neonate sharks could be highly cryptic and able to hide amongst the rocks and surf grass of the rocky reef. Thus, although other leopard shark aggregations have been hypothesized to serve as pupping grounds (Ackerman 1971; Russo 1975; Talent 1985; Carlisle and Starr 2009), the extent to which the La Jolla site serves as such remains unknown, requiring more extensive sampling and exploration of the rocky reef.

Historically, a sheltered estuarine lagoon existed at the aggregation site, which likely provided additional benefits of shelter, warmth, and food for the sharks. Evidence for this lagoon is a ~10 m thick deposit of estuarine material throughout the head of La Jolla Canyon, containing finely laminated mud, silt, clay, and gypsum, mingled with driftwood, reeds, fibrous root material, and fossils of the brackish water ostracod (*Perissocytheridea meyerabichi*) (Shepard and Dill 1966; Holden 1968; Judy 1987; Le Dantec et al. 2010). Historical photographs from the early 1900s show this lagoon (Moriarty 1964), which has since been reduced to a small duck pond (Fig. 1a). Although this location once resembled the sheltered bays and estuaries where leopard shark aggregations usually occur (Smith and Abramson 1990; Ebert and Ebert 2005; Hight and Lowe 2007; Carlisle and Starr 2009), it is unlikely that the current aggregation is merely a vestige of sharks still "searching" for an ancient lagoon; rather, the present-day open-coast site continues to attract sharks because it provides the aforementioned benefits to those aggregating there.

For aggregation behavior at this site to be maintained, the benefits should outweigh the costs, namely predation risk. Hight and Lowe (2007) suggested that aggregating might make leopard sharks more susceptible to predation by male California sea lions (*Zalophus californicus*), which are known to capture and eviscerate sharks to consume their fatty visceral organs. We observed three such mortalities at the La Jolla aggregation site in November 2009. Nevertheless, the yearly occurrence of this aggregation suggests the cost of predation does not outweigh the benefits, and certain features of

body temperature. Preliminary water temperature data indicate the rocky reef habitat is consistently warmer (>0.2 °C) than the sand flat due to the topographical trapping of warm surface water by prevailing onshore winds, decreased mixing because of the complex rocky bathymetry, and increased absorption of light and radiation of heat by the darker substrata.

The scarcity of males at the site suggests the aggregation could function as a refuge for females by reducing physically costly superfluous mating attempts (Pratt and Carrier 2001; Sims et al. 2001; Ebert and Ebert 2005; Hight and Lowe 2007). Thus, mating-related functions proposed for other shark aggregations (i.e., facilitating
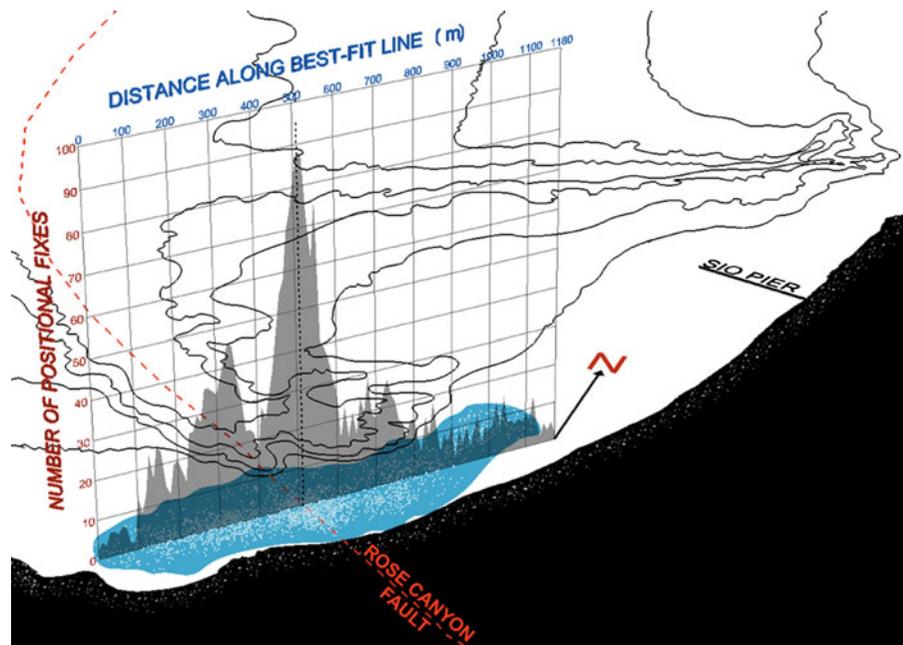
this site may actually mitigate predation risk (e.g., access to hiding places in the rocky reef and surf zone).

Proximate causes

The mechanism governing the formation, maintenance, and dispersion of the leopard shark aggregation is rooted in the interaction between environmental stimuli that elicit the behavior and the responsiveness of the sharks to those stimuli. For example, sunlight appears to be an important extrinsic stimulus, particularly sunset, which elicits some leopard sharks to disperse from the aggregation site (Fig. 3g–h). The aggregation could also form and be maintained through mutual attraction to favorable environmental conditions and avoidance of unfavorable conditions. For example, rip currents forced by wave divergence over La Jolla Canyon are generated at the approximate northern boundary of the 95 % KUD_{TOT} (Shepard and Inman 1950; see Fig. 8-6 in Komar 1998). Thus, the greater water turbulence adjacent to the aggregation may have a confining effect contributing to the location and size of the home range.

However, being attracted to warm, calm water is inadequate to explain the highest concentration of shark movements directly above the Rose Canyon Fault (Fig. 7), which may bear an attractive feature, such as a magnetic anomaly or groundwater discharge.

Cross-strike anomalies in total magnetic intensity have been reported for other intrasedimentary faults, attributable to tectonic juxtaposition of sedimentary layers with differing magnetic properties (Gunn 1997; Grauch et al. 2001; Grauch et al. 2006), and sharks are known to detect magnetic fields (Kalmijn 1982) and have long been hypothesized to use geomagnetic cues as referential landmarks (Klimley 1993). Sharks could also cue into groundwater discharge, which is visible throughout the study area as a blurry mixing of fresh and saltwater (E. Parnell, pers. comm.), and can likely locally depress salinity. However, the extent of submarine groundwater discharge and geomagnetic anomalies in this area has not been quantified.

Summary of ultimate and proximate causes of leopard shark aggregations

Previous studies of leopard shark aggregations reveal their formation in calm, warm water near productive foraging grounds in sheltered bays and estuaries (Smith and Abramson 1990; Ebert and Ebert 2005; Hight and Lowe 2007; Carlisle and Starr 2009). The La Jolla aggregation site is thus unique in being located on the open coast; however, it is similarly sheltered by wave divergence in the lee of a submarine canyon, which results in the calmest and warmest water along the immediate coastline. The demographic composition

Fig. 7 *Triakis semifasciata*. Density histogram (semi-transparent grey) of 2,596 positional fixes falling within the total 95 % KUD (*solid blue area*) projected onto the best-fit line of these fixes. Land is indicated as solid black with white stippling along the coastline. Isobaths shown are 10, 20, 40, and 80 m. The intersection of the best-fit line and Rose Canyon Fault is extended upward by a *dashed black line* to show the relation of the fault line to the largest peak of the histogram

and movement patterns of leopard sharks aggregating in La Jolla closely resemble those of another aggregation that forms in a sheltered cove on Santa Catalina Island, California (Manley 1995; Hight and Lowe 2007), where mature females also spend the day in warm, shallow water and often disperse at night, presumably to forage. Similar to the present study, Hight and Lowe (2007) observed that leopard sharks at their site selectively occupy the warmest water in the cove, suggesting these females might also be regulating their body temperature to accelerate gestation. Other leopard shark aggregations, such as in Elkhorn Slough and San Francisco Bay, California, likely also function as nursery and mating areas, where both males and females occur along with immature individuals (Smith and Abramson 1990; Carlisle et al. 2007; Carlisle and Starr 2009). The congregation of these sharks on intertidal mudflats also suggests their potential exploitation of rich on-site foraging grounds (Carlisle and Starr 2009), consistent with the proposed function of the La Jolla site serving as a central location close to abundant food sources (e.g., the submarine canyon).

In conclusion, ultimate causes of leopard shark aggregations appear related to 1) behavioral thermoregulation, 2) maintaining a "home base" close to nearby foraging grounds, and 3) reproduction (avoiding harassment from males in female-dominated aggregations, finding mates in mixed-sex aggregations, or pupping). In addition to sunlight, which may govern the daily formation and dissolution of some leopard shark aggregations, the most likely proximate cause is mutual attraction to 1) low water turbulence, 2) warm water temperatures, 3) food, and, possibly, 4) other unique stimuli associated with local bathymetry or other site-specific features (e.g., magnetic anomalies, salinity gradients).

Conservation implications

This study demonstrates that leopard shark aggregations can be densely populated and occur very close to shore, making them extremely vulnerable to overexploitation. Given the demographic composition of mostly pregnant females at sites such as the one described in this manuscript, local, concentrated extirpation could negatively affect the wider population. The individual and total 95 % KUDs of all tracked sharks tagged at the La Jolla open-coast aggregation site fell within the boundaries of the no-take San Diego – La Jolla Ecological Reserve, suggesting this small (2.16 km^2) sanctuary is effective at protecting the aggregation, at least in the short term, and that other leopard shark aggregations throughout California and Baja California could similarly benefit from small, strategically placed no-take reserves.

References

Ackerman LT (1971) Contributions to the biology of the leopard shark, *Triakis semifasciata* (Girard) in Elkhorn Slough, Monterey Bay, California. MA Thesis. Sacramento State College, California

Battjes JA (1978) Ocean Wave Statistics for 1961 North-Atlantic Storm - Discussion. J Waterw Port Coast Ocean Eng 104:461–462

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 Fish 91:165–176

Booij N, Ris RC, Holthuijsen LH (1999) A third-generation wave model for coastal regions. Model description and validation. J Geophys Res 104:7649–7666

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 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

De Solla SR, Bondurianski R, Brooks RJ (1999) Eliminating autocorrelation reduces biological relevance of home range estimates. J Anim Ecol 68:221–234

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

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

Gorrell L, Raubenheimer B, Elgar S, Guza RT (2011) SWAN predictions of waves observed in shallow water onshore of complex bathymetry. Coast Eng 58:510–516

Grauch VJS, Hudson MR, Minor SA (2001) Aeromagnetic expression of faults that offset basin fill, Albuquerque basin, New Mexico. Geophysics 66:707–720

Grauch VJS, Hudson MR, Minor SA, Caine JS (2006) Sources of along-strike variation in magnetic anomalies related to intrasedimentary faults: a case study from the Rio Grande Rift, USA. Explor Geophys 37:372–378

Gunn PJ (1997) Application of aeromagnetic surveys to sedimentary basin studies. J Aust Geol Geophys 17:133–144

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

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

Holden JC (1968) Brackish water ostracods from La Jolla Submarine Canyon 7200±500 years before present. University of California Berkeley Museum of Paleontology, Berkeley, CA

Jacoby DMP, Croft DP, Sims DW (2011) Social behaviour in sharks and rays: analysis, patterns and implications for conservation. Fish Fish. doi:101111/j1467-2979201100436x

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

Judy TC (1987) Reconnaissance geology of Holocene lagoonal deposits in the La Jolla Submarine Canyon and their relationship to the Rose Canyon Fault. Department of Geological Sciences, San Diego State University

Kalmijn AJ (1982) Electric and magnetic field detection in elasmobranch fishes. Science 218:916–918

Klimley AP (1993) Highly directional swimming by scalloped hammerhead sharks, *Sphyrna lewini*, and subsurface irradiance, temperature, bathymetry, and geomagnetic field. Mar Biol 117:1–22

Klimley AP (2003) The secret life of sharks: a leading marine biologist reveals the mysteries of shark behavior. Simon and Schuster, New York

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

Kobayashi BN (1979) California Marine Waters Areas of Special Biological Significance Reconnaissance Survey Report, San Diego-La Jolla Ecological Reserve, San Diego County. Water Quality Monitoring Report No. 79-1

Komar PD (1998) Beach processes and sedimentation. Prentice Hall, Upper Saddle River

Kusher DI, Smith SE, Cailliet GM (1992) Validated age and growth of the leopard shark, *Triakis semifasciata*, with comments on reproduction. Environ Biol Fish 35:187–203

Le Dantec N, Hogarth LJ, Driscoll NW, Babcock JM, Barnhardt WA, Schwab WC (2010) Tectonic controls on nearshore sediment accumulation and submarine canyon morphology offshore La Jolla, Southern California. Mar Geol 268:115–128

Long JW, Özkan-Haller HT (2005) Offshore controls on nearshore rip currents. J Geophys Res 110:C12007. doi:10.1029/2005JC003018

Lygre A, Krogstad HE (1986) Maximum-entropy estimation of the directional distribution in ocean wave spectra. J Phys Oceanogr 16:2052–2060

Magne R, Belibassakis KA, Herbers THC, Ardhuin F, O'Reilly WC, Rey V (2007) Evolution of surface gravity waves over a submarine canyon. J Geophys Res 112:C01002. doi:10.1029/2005JC003035

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

McGowan JA (1954) Observations on the sexual behavior and spawning of the squid, *Loligo opalescens*, at La Jolla, California. Calif Fish Game 40:47–54

Moriarty JR (1964) The use of oceanography in the solution of problems in a submarine archaeological site. In: Miller RL (ed) Papers in marine geology. Macmillan, New York

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

Munk WH, Traylor MA (1947) Refraction of ocean waves: a process linking underwater topography to beach erosion. J Geol 55:1–26

Musick JA, Burgess G, Cailliet G, Camhi M, Fordham S (2000) Management of sharks and their relatives (Elasmobranchii). Fisheries 25(3):9–13

Plant NG, Holland KT, Puleo JA (2002) Analysis of the scale of errors in nearshore bathymetric data. Mar Geol 191:71–86

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

Pratt HL, Carrier JC (2001) A review of elasmobranch reproductive behavior with a case study on the nurse shark, *Ginglymostoma cirratum*. Environ Biol Fish 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

Shepard FP, Dill RF (1966) Submarine Canyons of the La Jolla, California Area. In: Shepard FP, Dill RF (eds) Submarine canyons and other sea valleys. Rand McNally, Chicago

Shepard FP, Inman DL (1950) Nearshore water circulation related to bottom topography and wave refraction. Trans Am Geophys Union 31:196–212

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 (2005) Leopard shark mating observed off La Jolla, California. Calif Fish Game 91:128–135

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

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

Talent LG (1985) The occurrence, seasonal distribution, and reproductive condition of elasmobranch fishes in Elkhorn Slough, California. Calif Fish Game 71:210–219

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

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

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home range studies. Ecology 70:164–168