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Movement patterns of the shovelnose guitarfish (Pseudobatos productus) and California bat ray (Myliobatis californica) in the Southern California Bight

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UNIVERSITY OF SAN DIEGO

San Diego

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by

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2022

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DEDICATION

To Uncle Rich, for fueling my curiosity for science and my passion for teaching.

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ABSTRACT

While the movement patterns of large elasmobranch species have been studied extensively, those of smaller, mesopredatory species remain understudied. The shovelnose guitarfish (*Pseudobatos productus)* and the California bat ray (*Myliobatis californica)* are among the least studied elasmobranchs in the Southern California Bight. This study quantified the broad- and fine-scale movement patterns of these species using passive acoustic telemetry. Twelve guitarfish were surgically implanted with coded acoustic transmitters at a known aggregation site off La Jolla (San Diego County), California, USA and tracked for 849.5 days each, on average. Six bat rays were also implanted here and tracked for 1143.8 days each, on average. These animals were detected at 187 acoustic receiver stations between Point Conception, California, and San Quintín, Baja California, Mexico. Both species exhibited annual philopatry to the La Jolla tagging site, especially during the month of July, after traveling as far north as Santa Barbara, CA (221 km away; guitarfish) and San Miguel Island, Northern Channel Islands, California (259 km away; bat rays). Of the 34 receivers off La Jolla, a mean of 84.4% of guitarfish detections and 48.4% of bat ray detections occurred at just two acoustic receivers located on a sandflat in the lee of a submarine canyon. Guitarfish had a strong preference to soft substrate off La Jolla, while bat rays utilized both soft and hard substrates. This is the longest-duration acoustic tracking study of these batoid species to date, and the first to track California bat rays using passive acoustic telemetry.

CHAPTER 1: Introduction

We are in the sixth mass extinction event on this planet which has been characterized by the loss of large fauna. Migratory species, specifically marine species whose population dynamics are already hard to predict due to their elusive nature, are particularly at risk from anthropogenic destruction and change. Large sharks are generally believed to be important mediators of ecosystem function; as the loss of apex predatory sharks increases, this may lead to trophic cascades that involve the population increase of mesopredatory (intermediate) populations of smaller sharks and rays (Myers et al. 2007).

Studies have mostly focused on the movements of highly migratory, pelagic sharks due to their trophic importance as apex predators and their significance to commercial fisheries (Block et al. 2011, Queiroz et al. 2019). By contrast, the movement ecology of smaller elasmobranch predators is understudied, despite their integral link between apex predators and lower trophic levels (Vaudo & Heithaus 2011). Mesopredatory elasmobranchs have been observed to alter biological communities through direct predation (Thrush et al. 1994) and indirect habitat alteration (VanBlaricom 1982). Thus, understanding the ecological consequences of trophic cascades, as well as preventing them in the first place, depends on detailed knowledge of the movement patterns of elasmobranch mesopredators, in addition to top predators.

Many elasmobranch mesopredators are coastal batoids (rays and skates) and smaller sharks. A location of particular interest is the Southern California Bight (SCB), which ranges from Point Conception to Cabo Colonet, Baja

California, including the offshore Channel Islands, and is home to several elasmobranch mesopredator species, such as the leopard shark (*Triakis semifasciata)* and gray smoothhound (*Mustelus californicus)*, and batoids such as the California bat ray (*Myliobatis californica)*, round stingray (*Urobatis halleri),* and shovelnose guitarfish (*Pseudobatos,* formerly known as *Rhinobatos, productus)*. The SCB also supports the largest human populations in California and Baja California, which threaten coastal elasmobranch species with fishing pressure and habitat destruction. Thus, understanding the movement patterns of these species can inform conservation and management efforts, especially across international borders, by determining when individuals are most vulnerable. Such evaluations have been made for fisheries-important pelagic sharks both worldwide (Queiroz et al. 2019) and along the Eastern Pacific Ocean (White et al. 2019), but little is known about coastal elasmobranch movement on a regional scale, specifically in the SCB.

Among the least studied coastal batoids in the SCB are the shovelnose guitarfish and California bat ray, both of which are endemic to the west coast of North America. Historically, both species, specifically bat rays, were targeted by recreational fishers in Humboldt Bay and Elkhorn Slough, California after they were alleged to pose a threat to local oyster farms (Gray et al. 1997, Carlisle et al. 2007). From the mid-1940s to the early 1990s, elasmobranch ‘derbies’ were held to control their populations, culling as many as 9,000 bat rays per year in Humboldt Bay (Gray et al. 1997, Carlisle et al. 2007). Due to derby fishing pressure and habitat alteration, bat rays showed a decrease in Elkhorn Slough derby catch from the 1980s to 1990s (68% to 57% of individuals caught; Carlisle et al. 2007). Although not targeted, shovelnose guitarfish were also caught in these derbies. In contrast to the 1950s, when 28% of the individuals caught were shovelnose guitarfish, only 5% of individuals caught in the 1970s and 3% of individuals caught in the 1990s were shovelnose guitarfish, marking a near complete disappearance from Elkhorn Slough (Carlisle et al. 2007).

Since the end of the fishing derbies, there has been some incidental commercial fishing but little to no targeted recreational fishing for bat rays or shovelnose guitarfish in California (California Department of Fish and Wildlife 2020a). Presently, bat rays and shovelnose guitarfish fall under the general category of ‘finfish’ (bony or cartilaginous) according to the California Fish and Game Commission, which sets a daily recreational catch limit of 20 finfish combined or 10 of one finfish species; however, there are no commercial limits or size restrictions for either species (California Department of Fish and Wildlife 2020b). Meanwhile, both species are taken as targeted and incidental catch in the Mexican artisanal elasmobranch fishery. Shovelnose guitarfish and bat ray landings are prominently high in fisheries along the Pacific coast of Baja California (comprising 46% and 10% of all elasmobranchs caught between 2006 and 2008, respectively; Cartamil et al. 2011) and Baja California Sur (28% and 9% of all elasmobranchs caught between 2000 and 2010, respectively; Ramirez-Amaro et al. 2013). As of 2013, bat rays are classified as ‘least concern’ by the International Union for Conservation of Nature (IUCN) (van Hees et al. 2015). However, this conservation status will soon be arbitrary if bat ray landings continue to be high in Baja California and Baja California Sur. Understanding the movement ecology of bat rays can inform sound management decisions to ensure that their populations remain stable. On the other hand, shovelnose guitarfish are classified as ‘near threatened’ by the IUCN due to their slow growth, frequent capture in artisanal gillnet fisheries, and susceptibility to bycatch by demersal shrimp trawl fisheries in Mexico (Márquez-Farías 2005). Shovelnose guitarfish fisheries remain underregulated with the lack of species-specific management efforts in both the US and Mexico.

Understanding the movement patterns of both the shovelnose guitarfish and the bat ray will further inform management and conservation of these species as well as further the knowledge of mesopredator elasmobranch movement patterns in the Southern California Bight. With their ranges spanning an international border, it is important to fully understand movement to inform species-specific management accordingly, especially for heavily targeted species like the shovelnose guitarfish (van Hees et al. 2015, Farrugia et al. 2016). In this thesis, I will explore the broad- and fine-scale movement patterns of the shovelnose guitarfish and bat ray in the SCB, as well as the environmental cues that drive their movement.

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CHAPTER 2: Movement patterns of the shovelnose guitarfish (*Pseudobatos productus*) and California bat ray (*Myliobatis californica*) in the Southern California Bight

2.1 Introduction

Elasmobranch fishes (sharks, rays, and skates) are generally believed to be important mediators of ecosystem function. Through top-down control, large predatory sharks may structure biological communities directly via predation (Baum & Worm 2009), as well as indirectly via intimidation (Heithaus et al. 2008). Thus, the loss of apex predatory sharks may lead to trophic cascades that involve the release of mesopredatory populations of rays and smaller sharks (Shepherd & Myers 2005, Myers et al. 2007). With one-third of elasmobranch species now threatened with extinction (Dulvy et al. 2021), effective conservation and management is needed to curb and reverse recent population declines to prevent detrimental consequences. These efforts rely on robust data on elasmobranch movement patterns, but are mostly limited to commercially important species of apex predators (Speed et al. 2010).

Despite their link between apex predators and lower trophic levels and their importance in understanding the ecological consequences of trophic cascades, the movement ecology of smaller, mesopredatory elasmobranch species is understudied (Vaudo & Heithaus 2011). These mesopredators are also vulnerable to direct overexploitation, as commercial fisheries deplete populations of top predators and subsequently 'fish down food webs' (Pauly et al. 1998, Pace et al. 1999). Additionally, because elasmobranch mesopredators are generally associated with coastal and benthic habitats, they are also susceptible to local artisanal and recreational fishing pressures (Pauly et al. 1998), as well as anthropogenic habitat destruction such as dredging, which can destroy elasmobranch nursery habitats such as seagrass beds (Thrush & Dayton 2002, Jennings et al. 2008). Thus, it is especially important to understand the movement patterns of elasmobranch mesopredators, particularly along coastlines with large human populations.

One such place is the Southern California Bight (SCB). This is home to several dense human populations, including the Greater Los Angeles area and the San Diego-Tijuana transborder agglomeration, as well as to various mesopredatory elasmobranch species that are endemic to the west coast of North America. These include the leopard shark (*Triakis semifasciata),* gray smoothhound (*Mustelus californicus)*, California bat ray (*Myliobatis californica;* hereafter referred to as 'bat ray'), round stingray (*Urobatis halleri),* and shovelnose guitarfish (*Pseudobatos,* formerly known as *Rhinobatos, productus*). Understanding the movement patterns of these species can inform conservation and management efforts by determining when and where individuals are most vulnerable to habitat destruction and fishing mortality (Navarro et al. 2016). Such information on movement patterns has informed management decisions for pelagic species (White et al. 2019, Queiroz et al. 2019), but far less is known about smaller coastal elasmobranchs, particularly in the SCB.

Two of the least studied mesopredatory elasmobranch species in the SCB are the shovelnose guitarfish and bat ray. Both species range from Baja California (including the Gulf of California) in the south, to San Francisco Bay, California (shovelnose guitarfish) and Oregon (bat ray) in the north (Miller & Lea 1972, Márquez-Farías 2007). The shovelnose guitarfish population is believed to be structured with at least three sub-populations: 1) Santa Catalina Island, California, 2) the mainland coast from Point Conception, California to Punta Eugenia, Mexico, and 3) the mainland coast from Punta Eugenia to Punta Abreojos, Mexico (Meyer 2020). These populations, inferred from genetic analyses, have not been confirmed directly by tagging and tracking. In contrast to the shovelnose guitarfish, much less is known about the structure of the bat ray population, although it is suspected that the Gulf of California population is distinct from the Pacific coast population (van Hees et al. 2015). Understanding population structure and home ranges is crucial for localized management to determine which sub-populations are most vulnerable and to implement regulations in certain areas accordingly.

Careful management of these species is especially important given their tendency to aggregate in certain coastal areas, including sheltered bays, coves, and estuaries, where they are vulnerable to being captured *en masse*. Pregnant females appear to be particularly attracted to these warm, shallow areas in the summer months. This ‘incubation’ behavior has been reported for other sympatric species, including the round stingray and leopard shark, and is believed to accelerate embryonic development and thus reduce gestation period (Hopkins & Cech 1994, Hight & Lowe 2007, Jirik & Lowe 2012, Nosal et al. 2014). Commercial fishery data also support the summer recurrence of shovelnose guitarfish, suspected to be mostly females, where catch per unit effort (CPUE) peaked in June in Baja California Sur (Salazar-Hermoso & Villavicencio-Garayzar 1999).

The waters off La Jolla (San Diego County), California are frequented by elasmobranch mesopredators, including summer aggregations of leopard sharks, round stingrays, bat rays, and shovelnose guitarfish (Nosal et al. 2013, 2014). La Jolla is home to four Marine Protected Areas (MPAs): the San Diego-Scripps Coastal State Marine Conservation Area (SCMA), Matlahuayl State Marine Reserve (SMR; no-take), South La Jolla SCMA, and South La Jolla SMR (no-take). The La Jolla coastline contains a variety of habitat types, including rocky reef, kelp forest, sandflat, submarine canyon, and seagrass beds. Because of its unique combination of aggregating elasmobranch mesopredators, MPAs, and diversity of habitat types, La Jolla was chosen as the tagging site for this study on the shovelnose guitarfish and California bat ray. The overall objective of this study was to quantify the broad- and fine-scale movement patterns of shovelnose guitarfish and bat rays using passive acoustic telemetry and the environmental factors underlying their movements.

2.2 Methods

Shovelnose guitarfish and bat rays were captured from a 5-m skiff off La Jolla (San Diego County), California (32.8525°N, 117.2623°W) in summer and fall of 2014–2017 (Table 1), using handlines and baited barbless circle hooks. Hooked individuals were guided into a large scoop net, transferred onto the deck of the skiff, and turned ventral side up to induce tonic immobility. Once the hook was removed, each individual was sexed, measured, and surgically implanted with a coded acoustic transmitter (Vemco V16-4H 69 kHz, 158 dB, 120 s average transmission delay, 80-160 s random transmission interval, 2440 d battery life). The transmitter, dipped in povidone-iodine, was inserted into the peritoneal cavity via a 3-cm abdominal incision made approximately 3 cm off the ventral midline. Next, the incision was closed using one continuous absorbable suture (Ethicon 2-0 VICRYL) and treated with topical antibiotic ointment (Neosporin). Finally, the animal was righted dorsal side up, externally fitted with a ‘spaghetti’ identification tag (Floy Tag FIM-96) inserted into the musculature approximately 3 cm off the dorsal midline, and released. Transmitter-implanted shovelnose guitarfish and bat rays were subsequently monitored by a coastal array of underwater acoustic receivers (Vemco VR2Tx, VR2AR, VR2W, VR2C, and VR4-UWM), through August 31, 2020 (Figure 1A, 1B). Acoustic detections were deemed spurious and removed from the dataset if they did not occur within one day of another detection of the same transmitter at the same receiver; however, no such detections were found. Detection data were also inspected for duplicate time stamps, which could occur if an animal was detected simultaneously by two or more receivers with overlapping detection ranges; however, no such duplicates were found.

The following analyses were performed in R version 4.1.0 (R Core Team 2021) and ArcMap 9.0 (Esri Inc. 2004). Given the curvature of the southern California coastline, which complicates interpretations of latitudinal seasonal movement, the location of each acoustic receiver was paired with its nearest point along the mainland coastline, and its distance from the US-Mexico border was calculated (Figure 1A). This metric of alongshore distance from the US-Mexico border, which was defined as kilometer marker 0, better approximated coastal movement patterns and was used for some analyses below. This metric is appropriate since the vast majority of receivers were near the mainland coast. The exception were the receivers located off the California Channel Islands, but due to the sparse detections there and little overlap in the metric between coastal receivers and island receivers, the acoustic receivers off the California Channel Islands were also included in this metric. Additionally, monthly sea surface temperature (SST) data were retrieved via the NOAA Multi-scale Ultra-high Resolution (MUR) SST Analysis (JPL MUR MEaSUREs Project 2015) at 0.01° resolution for the SCB between July 2014 and August 2020. A buffer line was created 5.5 km (3.0 nm) seaward from the mainland coastline and SST was obtained approximately every 10 km along this buffer line. Then, as above, the location of each SST measurement was paired with its nearest point along the mainland coastline and its distance from the US-Mexico border calculated. The alongshore distance from the US-Mexico border was then rounded to the nearest km and any gaps in SST coverage were filled via linear interpolation.

For each species, a generalized linear mixed model (GLMM) was fit to determine the significance and relative influence of environmental cues, or covariates, on coastal movement. The response variable was alongshore distance; fixed effects considered in model fitting were sea surface temperature (SST) off La Jolla, California (NOAA National Buoy Data Center; Scripps Nearshore Buoy

Station 46254), photoperiod for La Jolla (NOAA ESRL Global Monitoring Laboratory), and alongshore temperature gradient, which was calculated monthly by plotting remotely sensed SST as a function of alongshore distance from the US-Mexico border and retrieving the slope of the best fit line. Year was included as a random effect, along with individual ID by species nested within year. GLMMs were fit using the ‘lmer()’ function in the *lme4* package in R (Bates et al. 2015). Fixed effects were checked for collinearity using the ‘ggpairs()’ function in the *GGally* package (Schloerke et al. 2021). Photoperiod and the alongshore temperature gradient were deemed colinear (correlation = 0.753). For each species, a model including all fixed effects was averaged using the ‘dredge()’ function in the *MuMIn* package (Barton 2009) and the a best fit model was chosen based on AIC value. For shovelnose guitarfish, including SST and photoperiod yielded the lowest AIC value. For bat rays, including photoperiod and the alongshore temperature gradient yielded the lowest AIC value; however, due to collinearity, this model was not selected. Instead, the second best-fit model, which included SST and alongshore temperature gradient, was selected instead (ΔAIC = 5.36). Fixed effects from the best-fit model were analyzed in the *partR2* package to determine the correlation and strength of each environmental cues (Nakagawa & Schielzeth 2013). Inclusive R^2 values were used to quantify each fixed variable’s explained variance of the model. Structural coefficients were calculated to represent the correlation of each covariate with alongshore distance, where -1 represented a strong negative correlation and 1 represented a strong positive correlation. Beta weights estimated the relative significance of the environmental drivers on alongshore distance, where CIs that overlapped with 0 were not significant. The strength of influence of the driver on alongshore distance was also determined by the beta weights, where values further from 0 indicated stronger influence.

To determine whether any individuals exhibited similar movement patterns, a cluster analysis was performed based on the co-occurrence of individuals during the tracking period. The R package *igraph* was used to create and analyze the co-occurrences, and subsequently, make a network graph to visualize the connectivity among individuals (Csardi & Nepusz 2006). A half-weighted index (w), which measures co-occurrence, was calculated according to Schilds *et al.* (2019) using the equation:

$$w = \frac{n_x}{0.5(n_a + n_b)} \qquad (1)$$

where n_x equals the number of days two individuals were detected within 20 km of each other (based on the alongshore distance metric), which was approximately the mean maximum daily displacement of individuals (Table 1), n_a equals the total days that the first individual was detected, and n_b equals the total days that the second individual was detected. The first 30 days after tagging were omitted to account for biases of co-occurrences at the tagging site. These weights were used to create a matrix and network map. A ‘fast-and-greedy’ cluster analysis was performed to determine the presence of distinct communities among the tagged individuals, which were mapped onto a dendrogram. The strength of the clusters of communities was calculated using modularity, a metric that compares the number of edges (connections) within a cluster to the expected number of edges in a random network. Modularity values range between 0 and 1; values close to 0 indicate loosely connected individuals within and between clusters, whereas values close to 1 indicate distinct, strongly connected clusters.

To quantify space use around La Jolla, CA, daily mean positions were calculated by averaging the latitude and longitude of detecting receivers in that region (Figure 1C). From these daily mean positions, kernel utilization distributions (KUDs) were computed for each species using the *adehabitatHR* package in R and the reference value ('href') for the smoothing factor *h* (Calenge 2006). Prior to KUD computation, daily mean positions that occurred on land were omitted from this analysis and daily mean positions that occurred inshore of the 5-m isobath were snapped to the nearest point along the 5-m isobath. The home range was approximated by the 95% KUD and the core area by the 50% KUD isopleths. Lastly, for each species, paired Wilcoxon rank sum tests were used to test whether there was a diel difference in when individuals were detected off La Jolla generally, and specifically, in the lee of La Jolla Submarine Canyon (the known aggregation site). A paired Wilcoxon rank sum tests were also used by species to test whether there was a diel difference in the mean distance from land of detecting receivers.

Habitat selection was calculated by collocating daily mean positions to substrate data, categorized as 'hard' and 'soft' substrate (California State Costal Conservancy & San Diego Association of Governments 2000), by species, using a habitat selection index (HSI; Meese and Lowe 2019):

$$HSI = \frac{\text{proportion of daily mean positions in a particular substrate}}{\text{proportion of area covered by that particular substrate}} \qquad (2)$$

HSI values less than 1 indicate an aversion to that substrate, whereas values greater than 1 indicate an affinity to that substrate. Substrate type (hard and soft) was determined for each daily mean position in ArcMap, with the available area defined as the over-water area inside the minimum convex polygon encompassing the circular detection ranges (estimated to be 300 m radius) of all the acoustic receivers off La Jolla. For each species, a chi-squared test was used to test whether the proportion of detections within hard and soft substrate was significantly different to the proportion of hard and soft substrate in the available area, and a Welch's two-sample t-test was used to test whether each species exhibited a significant affinity or aversion to hard and soft substrate.

2.3 Results

Twelve shovelnose guitarfish were tagged in July and August of 2014–2017 (G1–G12; Table 1); ten were mature females and two were mature males, according to the criteria of Timmons and Bray (1997). Six bat rays were tagged in July, August, and October of 2014 – 2016 (B13 – B18; Table 1); five were mature females and one was an immature female, according to the criteria of Martin and Cailliet (1998). In two of the mature female bat rays (B15 and B18), the fins of term pups were observed to be protruding from the cloaca while surgically implanting the transmitters. For shovelnose guitarfish, mean total length (TL) ± SD was 135.25 ± 7.66 cm and mean disk width (DW) was 44.79 ± 3.33 cm. For bat rays, mean TL was 88.33 ± 17.66 cm and mean DW was 108.83 ± 16.94 cm.

Known days at liberty averaged 849.5 ± 548.9 d for shovelnose guitarfish and 1143.8 ± 830.9 d for bat rays; there were no known recaptures.

Acoustic receivers that detected tagged individuals were maintained by the Brice Semmens Laboratory at Scripps Institution for Oceanography, the Christopher Lowe Laboratory at California State University, Long Beach, and the Channel Islands National Marine Sanctuary. Shovelnose guitarfish were sequentially detected along the mainland coast as far north as Santa Barbara County, CA and as far south as San Diego County, CA, at 141 acoustic receiver stations; however, no shovelnose guitarfish were detected at any receivers around the California Channel Islands. Bat rays were detected at 85 acoustic receiver stations along the mainland coast between San Diego and Los Angeles Counties (Figure 2). Although no bat rays were detected along the mainland coast of Ventura or Santa Barbara Counties, two bat rays (B13 and B17) were detected around the California Channel Islands (Figure 2). Additionally, one bat ray (B16) was detected as far south as San Quintín, Baja California, Mexico, by a receiver maintained by the Sosa-Nishizaki Laboratory at Centro de Investigacíon Científica y de Educacíon Superior de Ensenada (CISESE). No individuals of either species were detected north of Point Conception, despite widespread receiver coverage from San Luis Obispo County through San Francisco Bay Area (Nosal et al. 2021).

For shovelnose guitarfish, alongshore distance was negatively correlated with, and most strongly influenced by photoperiod from the US-Mexico border (GLMM; Table 2). SST was also a significant cue of alongshore distance with a negative correlation (Table 2). For bat rays, the alongshore temperature gradient was the strongest cue of alongshore distance, and SST had a non-significant correlation (Table 2).

Both shovelnose guitarfish and bat rays exhibited an annual summer return to La Jolla, particularly in July and August (Figure 3). After this, most shovelnose guitarfish moved north along the mainland coast and returned south to La Jolla the following summer. Except for B13, bat rays were rarely detected outside of La Jolla during non-summer months; those few detections were confined to receivers off Orange and Los Angeles Counties (Figure 2).

Of the detections by acoustic receivers off La Jolla (Figure 1C), 84.4 ± 29.8% of shovelnose guitarfish detections and 48.4 ± 40.8% of bat ray detections were made at just two receivers located in the lee of La Jolla Submarine Canyon, and 94.6% of all La Jolla detections were at acoustic receivers within the two no-take SMRs. Bat rays had a larger home range (95% KUD area = 2356 ha) and core area (50% KUD area = 152 ha) than shovelnose guitarfish (95% KUD area = 519 ha; 50% KUD area = 59 ha; Figure 4A). Shovelnose guitarfish exhibited a significant affinity to soft substrate (HSI = 2.96; 95CI: 2.10 – 3.82; one-sample t-test, $p < 0.01$) and a significant aversion to hard substrate (HSI = 0.15; 95CI: 0 – 0.52; Figure 4A; one-sample t-test, $p < 0.01$). These HSI values were significantly different from each other (Welch’s two-sample t-test, $p < 0.01$). The proportion of shovelnose guitarfish detections over a particular substrate was significantly different from the proportion of that substrate available (Chi-squared test; $X^2 = 23.094$, df = 1, $p < 0.01$). By comparison, bat rays showed only a slight affinity to soft substrate (HSI = 1.57; 95CI:1.20 – 1.94; Figure 4A) and a slight aversion to hard substrate (HSI = 0.75; 95CI: 0.268 – 1.232; Figure 4A). However, these HSI values were not significant (one-sample t-test, $p = 0.262$) nor were they significantly different from each other (Welch's two-sample t-test, $p = 0.142$). Lastly, the proportion of bat ray detections over a particular substrate was significantly different from the proportion of that substrate available (Chi squared test; $X^2 = 65.053$, df = 1, $p < 0.01$).

Of detections made by acoustic receivers off La Jolla (Figure 1C), the proportion of shovelnose guitarfish detections during the day was significantly higher than at night (paired Wilcoxon rank sum test; v = 61, $p = 0.009$). No diel pattern was apparent in detections of bat rays (paired Wilcoxon rank sum test; v = 16, $p = 0.312$). Of detections made by only the two acoustic receivers in the lee of La Jolla Submarine Canyon (Figure 1C), the proportion of shovelnose guitarfish detections made during the day was significantly higher than that at night (paired Wilcoxon rank sum test; v = 66, $p = 0.003$). A similar trend was detected for bat rays (paired Wilcoxon rank sum test; v = 15, $p = 0.057$). Neither shovelnose guitarfish nor bat rays exhibited a diel difference in the distance of detecting receivers from shore (paired Wilcoxon rank sum test; shovelnose guitarfish: v = 14, $p = 0.193$; bat ray: v = 4, $p = 0.437$).

Co-occurrences between individuals overlapped greatly, even between species (network analysis, modularity = 0.081; Figure 5A). Eight clusters were made with the fast-and-greedy method, with only three having more than one individual; these clusters were not species-specific (Figure 5B).

2.4 Discussion

This study of shovelnose guitarfish and California bat rays represents the longest tracking period (six years) and the largest tracking scale (Southern California) for either species, as well as the first to track California bat rays with passive acoustic telemetry. Previous studies on shovelnose guitarfish and bat ray movement patterns and habitat preference had been limited to shorter monitoring periods (<1 year) and enclosed bays in California, including Tomales Bay (Matern et al. 2000, Klimley et al. 2005), Bolsa Chica Ecological Reserve (Farrugia et al. 2011), and Big Fisherman's Cove on Santa Catalina Island (Meese & Lowe 2019).

In this study, both species exhibited annual summer philopatry to La Jolla, CA, a known elasmobranch aggregation site (Nosal et al. 2013, 2014, 2021). Once summer passed, both species generally moved north and west along the southern California coast, with shovelnose guitarfish detected as far north as Santa Barbara, CA, and bat rays detected as far north as the Northern Channel Islands. These results, along with an observation of a bat ray detected off San Quintín, Baja California, Mexico, represent the farthest seasonal movements reported for either species in a single study.

2.4.1 Annual Philopatry to La Jolla, California

Both shovelnose guitarfish and bat rays exhibited annual summer philopatry to La Jolla, CA, generally returning during the months of July and August. This summer aggregation behavior is consistent with artisanal fishery data for shovelnose guitarfish off Baja California Sur, Mexico, which show higher

CPUE in summer months (Salazar-Hermoso & Villavicencio-Garayzar 1999), and elasmobranch derby capture data for both species in Elkhorn Slough and for bat rays in Humboldt Bay (Talent 1985, Gray et al. 1997, Carlisle et al. 2007).

Reproduction is a likely explanation for both species' return to La Jolla, given their annual reproductive cycles (Martin & Cailliet 1988, Márquez-Farías 2007). Tagging additional males of both species is necessary to support whether La Jolla is used as a mating ground. However, in the Gulf of California, mating in shovelnose guitarfish occurred in June and July (Márquez-Farías 2007), which is consistent with when tagged shovelnose guitarfish were present in La Jolla in this study, including the two males tagged. Additionally, mating behavior was observed in aerial drone footage over La Jolla, captured in August 2020 (A. Nosal, unpublished data).

Because shovelnose guitarfish and bat rays were mostly detected in the lee of La Jolla Submarine Canyon, behavioral thermoregulation *vis a vis* to gestation may partly explain their seasonal presence. This area was hypothesized to be a gestating ground for leopard sharks due to the divergence zone created by the canyon's bathymetry, which results in calmer, warmer water (Nosal et al. 2013). These warm conditions are hypothesized to accelerate embryonic growth in ectothermic elasmobranchs (Hight & Lowe 2007) and round sting rays (Jirik & Lowe 2012).

Juvenile shovelnose guitarfish were not observed or captured off La Jolla during our study, so it seems unlikely that La Jolla functions as a major pupping or nursery ground. Instead, female shovelnose guitarfish may move north to give birth, such as areas between Huntington Beach and Long Beach, CA, including the Bolsa Chica Ecological Reserve, which are suspected nursery areas (Martin & Cailliet 1988, Farrugia et al. 2011). Bat rays, on the other hand, may very well use La Jolla as a pupping and nursery ground. For two of the mature females tagged in this study, in July 2015 and July 2016, the fins of term pups were observed protruding from the cloaca, suggesting parturition was imminent. Drone footage in August 2019 over La Jolla has also captured aggregations of hundreds of bat rays of various sizes, including juveniles (A. Nosal, unpublished data).

Daylight is an important predictor of shovelnose guitarfish movement on both seasonal and daily timescales. For example, photoperiod was a significantly strong indicator of seasonal presence in La Jolla. This study is among the few to demonstrate the importance of photoperiod on elasmobranch movement, and only the second study to do so in the Southern California Bight. In Nosal et al. (2014), photoperiod was reported to be a strong predictor of male leopard sharks returning to an aggregation site off Del Mar, CA. Shovelnose guitarfish may use increasing photoperiod, which precedes increasing water temperature, as a cue to return to gestation grounds off La Jolla. Within the vicinity of La Jolla, shovelnose guitarfish showed diel differences in movement, as they appear to rest in the lee of the submarine canyon during the day and forage away from this area at night, outside of receiver detection range.

Around La Jolla, both shovelnose guitarfish and bat rays had a preference to soft substrate. Given that the head of the La Jolla submarine primarily consists of soft substrate, it is possible that both species do not select that substrate *per se*, but rather the temperature conditions of this area when aggregating in La Jolla. Shovelnose guitarfish had a much stronger preference for soft substrate than bat rays, which could be explained in part by coloration, with bat rays (darker) having improved crypsis over darker hard substrates such as rocky reefs and shovelnose guitarfish (lighter) having improved crypsis over soft substrate such as sand. A similar substrate preference was found during visual observation studies around Santa Catalina island, where shovelnose guitarfish preferred light colored sand over vegetated sand, whereas bat rays showed no preference (Meese & Lowe 2019). However, bat rays' equal preference to soft and hard substrate off La Jolla is contrary to Meese & Lowe (2019), in which bat rays were not observed in hard substrate at all. Bat rays may forage in the hard substrate for crustaceans and bivalves found on hard substrates; however, further investigation must be done to determine the reasons for frequenting hard substrates.

2.4.2 Seasonal Movement away from La Jolla, California

Tagged shovelnose guitarfish and bat rays moved within their previously known species ranges, from Baja California, Mexico, including the Gulf of California, north to San Francisco, CA (shovelnose guitarfish; Farrugia *et al.* 2016) and Oregon (bat ray; van Hees *et al.* 2015). Despite their consistent returns to La Jolla, both species did not have consistent movement patterns during non-summer seasons among individuals or among species, as shown by the cluster analysis (Figure 5B). The differing movement strategies among individuals within species may indicate that during non-summer months, there are multiple advantageous habitats or environmental conditions outside of La Jolla, as our tagged individuals were detected in Santa Barbara, Baja California, or even offshore near the California Channel Islands. It may be more beneficial for both shovelnose guitarfish and bat rays to disperse during non-summer months to reduce competition and return to La Jolla in the summer months for reproduction. Similar patterns have been observed in cownose rays on the Atlantic coast, in which individuals were detected in the same sites in winter, but were detected at different summer aggregations (Ogburn et al. 2018).

Movement northward by shovelnose guitarfish and some bat rays may be influenced by the Southern California Countercurrent, a counterclockwise gyre within the SCB that is characterized by its northward coastal current. It is possible that shovelnose guitarfish may follow the flow of the gyre northward during non-summer seasons and returning to La Jolla in the summer. Additionally, bat rays may depart from La Jolla with a weaker alongshore temperature gradient, which was the strongest driver of their movement. Individuals may move colder water as far north as Santa Barbara for shovelnose guitarfish, or to deeper waters out of detection range for bat rays, to slow their metabolism and conserve energy before returning to La Jolla in the summer.

Previous genetics work of the Pacific coast shovelnose guitarfish identified two geographic barriers to gene flow: 1) the San Pedro Channel and 2) Punta Eugenia, Mexico (Meyer 2020). As a strictly benthic species, it is unlikely that shovelnose guitarfish would become pelagic to cross the deep San Pedro Channel separating the California Channel Islands from the mainland, and the absence of shovelnose guitarfish detections from around the California Channel

Islands is consistent with genetically isolated island populations. However, given sparser acoustic receiver coverage in Baja California, Mexico, we could not measure the extent to which shovelnose guitarfish travel south of the US-Mexico border. On the other hand, the absence of detections from north of Point Conception, which had widespread acoustic receiver coverage from San Luis Obispo County through the San Francisco Bay area, is consistent with the well-known biogeographic boundary of Point Conception. This boundary has previously been characterized as a barrier to gene flow in other mesopredatory elasmobranchs, including brown smoothhound and leopard sharks (Chabot et al. 2015, Barker et al. 2015).

The genetic structure of bat rays has not been investigated, but, given the absence of detections north of Point Conception, this may represent a barrier to gene flow as well. However, unlike shovelnose guitarfish, the deep channel separating the California Channel Islands does not seem to be a barrier to movement; two bat rays moved between the mainland and the California Channel Islands, with B13 making routine movements between La Jolla and the Northern Channel Islands (Figure 1). Given that another bat ray was detected off San Quintín, Mexico, these bat rays could very well comprise a single subpopulation ranging from Point Conception, California, to at least Punta Eugenia, Mexico. Additionally, despite the annual summer return to La Jolla, the absence of detections anywhere north of San Diego for B15 and B16 suggests that these individuals may have frequented Baja California, where there was sparser acoustic receiver coverage. Similar long-term, passive acoustic wide-range tracking studies should be conducted on shovelnose guitarfish and bat rays north Point Conception as well as across the US-Mexico border to understand their seasonal movement patterns and compare them to other subpopulations.

2.4.3 Conservation Implications

This study is the first to demonstrate seasonal philopatry in shovelnose guitarfish and California bat rays to La Jolla, CA, and thus also the value of the small, strategically placed Matlahuayl no-take SMR, where detections of large, possibly pregnant, females were most frequent (Figure 4A). Despite their differing individual movement patterns during the non-summer months (Figure 5), both species consistently returned to La Jolla during the summer months. This aggregation site, and therefore this no-take SMR, could be an integral site where these sub-populations converge once a year. Other locations in California and Baja California that host aggregations of shovelnose guitarfish and bat rays may similarly benefit from such reserves. Although none of our tagged shovelnose guitarfish and only one of our tagged bat rays were detected in Mexico, it is likely that both species comprise a subpopulation spanning the US-Mexico border, demonstrating the need for binational cooperation in managing these species. Disregarding the movement patterns, especially aggregation behavior, of pregnant females could lead to population declines, as was the case for the now critically endangered Brazilian guitarfish (*Rhinobatos horelii)*. In these species, pregnant females were heavily targeted in the summer months by artisanal fisheries along the coast of Brazil, which led to an estimated 85% decline in abundance from 1975 to 1990 (Casselberry & Carlson 2015). Thus, it is important to identify when and where bat rays and shovelnose guitarfish aggregate, especially when aggregations are composed primarily of pregnant females, to understand when and where individuals are most vulnerable to anthropogenic stressors.

Without species-specific conservation policies in place, bat rays and shovelnose guitarfish may be susceptible to population declines, as shovelnose guitarfish experienced in Elkhorn Slough during the elasmobranch derbies (Carlisle et al. 2007). Even the slightest exploitation rate, as small as 2 – 6%, could stop or reverse positive population trends in elasmobranchs; thus, it is important to study movements to fully understand which areas to focus conservation efforts (Ward-Paige et al. 2012). With both species' affinities to soft substrate, this leaves them vulnerable to incidental trawl catch and habitat destruction, such as dredging within the heavily anthropogenically impacted region of the SCB. Understanding the fine-scale movements of shovelnose guitarfish and bat rays provides insight into their habitat use to inform managers about where to focus restoration and preservation efforts of existing habitats.

Figure 1. (A) Coastal array of 187 acoustic receivers that passively tracked shovelnose guitarfish (*Pseudobatos productus*; G1 – G12) and California bat rays (*Myliobatis californicus*; B13 – B18) surgically implanted with coded acoustic transmitters from June 2014 through July 2020. Black dots represent acoustic receivers known to be deployed during the tracking period that did not detect shovelnose guitarfish or bat rays. Colored dots represent acoustic receivers that did detect transmitter-implanted shovelnose guitarfish or bat rays, colorized by alongshore distance from the US-Mexico border (see text for details). Percentages of raw detections are shown for five regions: San Diego County (red), mainland Orange and Los Angeles Counties (olive), Santa Catalina Island (green), mainland Ventura and Santa Barbara Counties (blue), and the Northern Channel Islands (purple). These regional percentages are separated by species, with shovelnose guitarfish above and bat rays below. (B) The Pacific coast of the United States (WA: Washington, OR: Oregon, CA: California). Black and colored dots are as described above. (C) Acoustic receivers off La Jolla, CA. Black and colored dots are as described above. The black star represents the tagging site (32.8525°N, 117.2623°W). Bathymetry is shown as 10 m isobaths (California Fish and Wildlife).

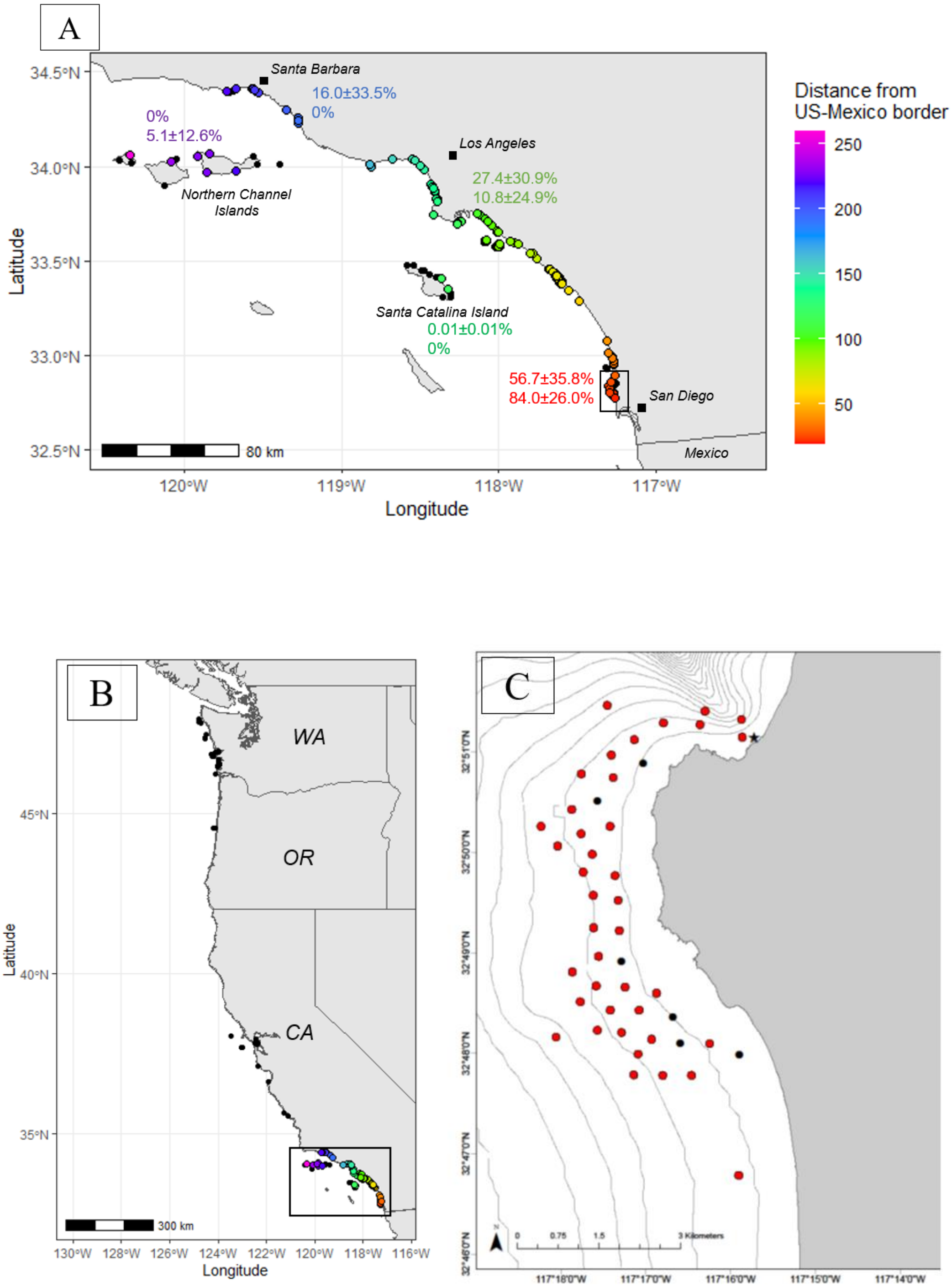
A
Santa Barbara
16.0±33.5%
0%
0%
5.1±12.6%
Los Angeles
Northern Channel Islands
27.4±30.9%
10.8±24.9%
Santa Catalina Island
0.01±0.01%
0%
56.7±35.8%
84.0±26.0%
San Diego
Mexico
80 km
34.5°N
34.0°N
33.5°N
33.0°N
32.5°N
120°W
119°W
118°W
117°W
Latitude
Longitude
Distance from US-Mexico border
250
200
150
100
50
B
WA
OR
CA
45°N
40°N
35°N
300 km
130°W
128°W
126°W
124°W
122°W
120°W
118°W
116°W
Latitude
Longitude
C
32°51'0"N
32°50'0"N
32°49'0"N
32°48'0"N
32°47'0"N
32°46'0"N
N
0
0.75
1.5
3 Kilometers
117°18'0"W
117°17'0"W
117°16'0"W
117°15'0"W
117°14'0"W

Figure 2. Diamonds representing days on which transmitter-implanted shovelnose guitarfish (G1 – G12) and bat rays (B13 – B18) were detected by acoustic receivers, colorized by daily mean alongshore distance from the US-Mexico border. The black diamond indicates the day that bat ray B16 was detected by an acoustic receiver off San Quintín, Baja California, Mexico. Asterisks indicate the time of tagging and horizontal gray lines represent known time at liberty.

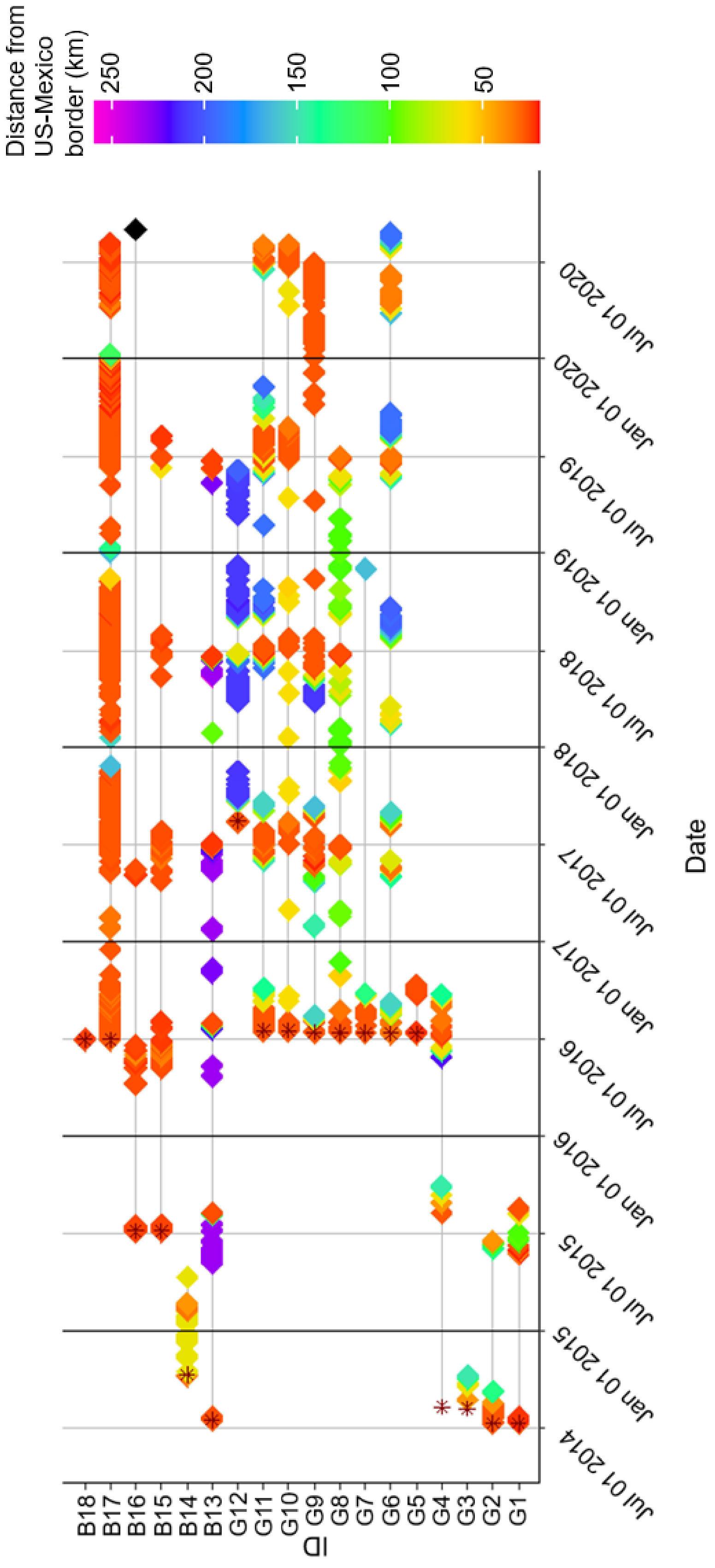
Distance from US-Mexico border (km)
250
200
150
100
50
ID
B18
B17
B16
B15
B14
B13
G12
G11
G10
G9
G8
G7
G6
G5
G4
G3
G2
G1
Jul 01 2014
Jan 01 2015
Jul 01 2015
Jan 01 2016
Jul 01 2016
Jan 01 2017
Jul 01 2017
Jan 01 2018
Jul 01 2018
Jan 01 2019
Jul 01 2019
Jan 01 2020
Jul 01 2020
Date

Figure 3. Monthly mean alongshore distance from the US-Mexico border (see text for details) of shovelnose guitarfish (GF) and California bat rays (BR) by species shown as solid black lines; the size of open circles along black lines indicates the number of unique individuals detected in that calendar month. Gray lines represent monthly mean alongshore distance by individual of each species. Dashed black lines represent the mean monthly photoperiod, for La Jolla, CA. Background raster is colorized by monthly mean SST along a buffer line created 5.5 km (3 nm) seaward from the mainland coast (see text for details).

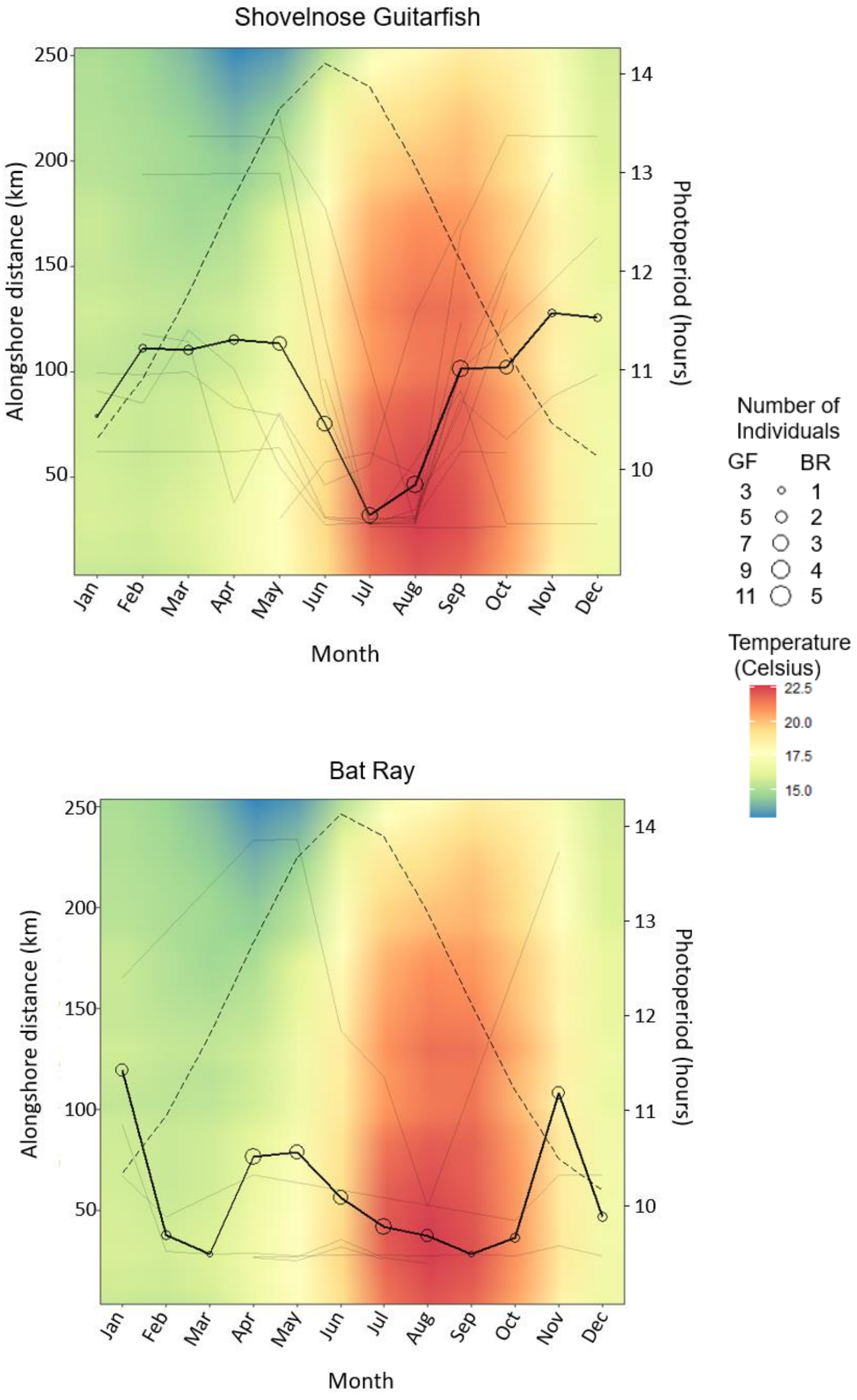Shovelnose Guitarfish
Alongshore distance (km)
250
200
150
100
50
Photoperiod (hours)
14
13
12
11
10
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month
Number of Individuals
GF
BR
3
1
5
2
7
3
9
4
11
5
Temperature (Celsius)
22.5
20.0
17.5
15.0
Bat Ray
Alongshore distance (km)
250
200
150
100
50
Photoperiod (hours)
14
13
12
11
10
Jan
Feb
Mar
Apr
May
Jun
Jul
Aug
Sep
Oct
Nov
Dec
Month

Figure 4. Habitat use off La Jolla, CA, USA, by shovelnose shovelnose guitarfish (*Pseudobatos productus*) and California bat rays (*Myliobatis californicus*), surgically implanted with coded acoustic transmitters. (A) 50 and 95% Kernel Utilization Distributions (KUDs) of shovelnose guitarfish (blue) and bat rays (red) over substrate type: hard substrate (brown), soft substrate (tan), and no data (purple). Non-faded habitat colors represent the area of the minimum convex polygon used for habitat selection index (HSI) analysis (see text for details). Crosses indicate the locations of acoustic receivers and dark gray polygons indicate the boundaries of no-take State Marine Reserves (SMRs): Matlahuayl SMR (northernmost) and South La Jolla SMR (southernmost). Bathymetry is shown as 10 m isobaths (California Department of Fish and Wildlife). (B) Habitat selection index (HSI) of hard and soft substrate of shovelnose guitarfish and bat rays in La Jolla, CA. Error bars are the 95% confidence intervals.

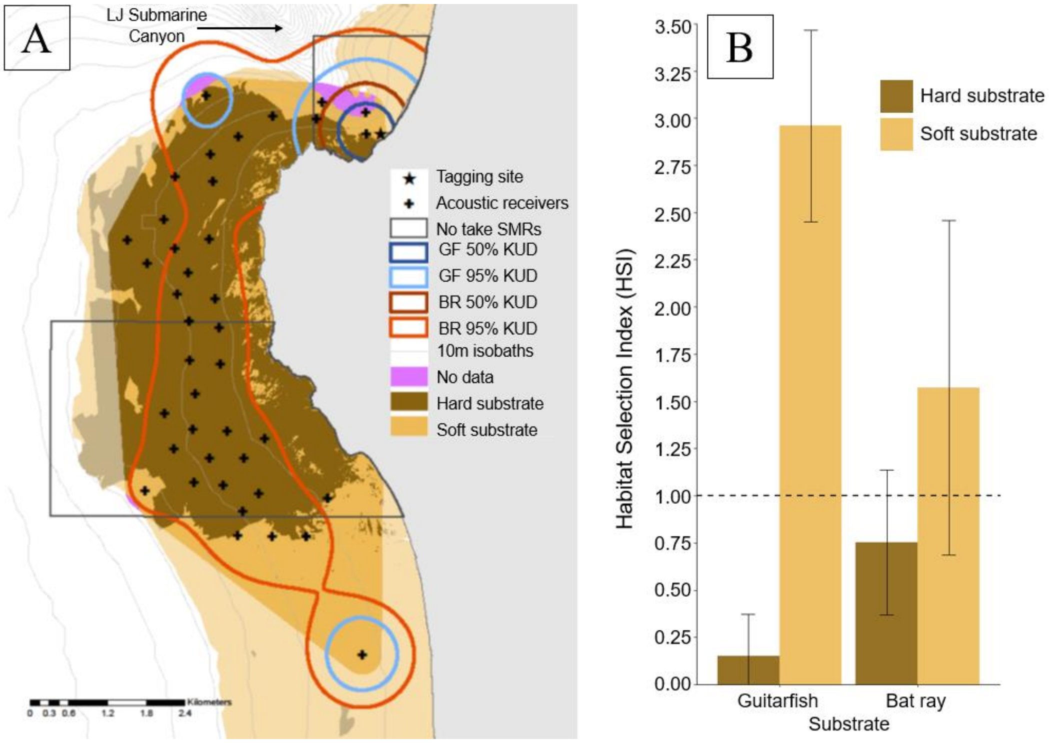
A
LJ Submarine Canyon
Tagging site
Acoustic receivers
No take SMRs
GF 50% KUD
GF 95% KUD
BR 50% KUD
BR 95% KUD
10m isobaths
No data
Hard substrate
Soft substrate
0 0.3 0.6 1.2 1.8 2.4 Kilometers
B
Hard substrate
Soft substrate
Habitat Selection Index (HSI)
3.50
3.25
3.00
2.75
2.50
2.25
2.00
1.75
1.50
1.25
1.00
0.75
0.50
0.25
0.00
Guitarfish
Bat ray
Substrate

Figure 5. Network analysis of shovelnose guitarfish (*Pseudobatos productus*; G1 – G12) and California bat rays (*Myliobatis californicus*; B13 – B18), surgically implanted with coded acoustic transmitters. (A) Network graph of individuals based on the half weight index of connected daily detections (see text for details) with the first 30 days after tagging omitted. Circle nodes represent females and square nodes represent males. The thickness of the lines indicates the value of the half weight index, where values closer to 1 have thicker lines. (B) Dendrogram with individuals grouped by a fast and greedy cluster analysis based on the half weight index of connected daily detections. Red boxes indicate clusters consisting of more than one individual.

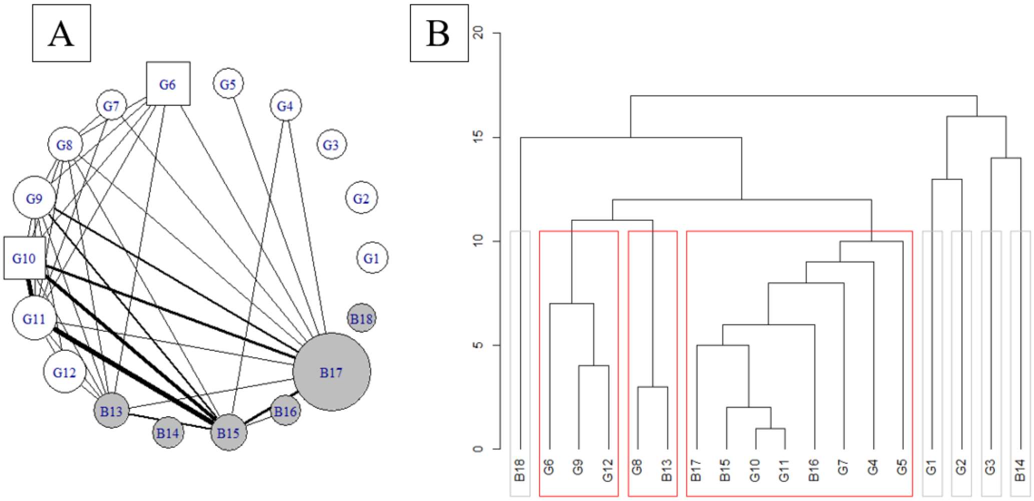
A
G6
G5
G7
G4
G8
G3
G2
G9
G10
G1
G11
B18
G12
B17
B13
B16
B14
B15
B
20
15
10
5
0
B18
G6
G9
G12
G8
B13
B17
B15
G10
G11
B16
G7
G4
G5
G1
G2
G3
B14

Table 1. Shovelnose guitarfish (*Pseudobatos productus*; G1 – G12) and California bat rays (*Myliobatis californicus*; B13 – B18) surgically implanted with coded acoustic transmitters off La Jolla, California, USA (32.8525°N, 117.2623°W) and subsequently tracked by passive acoustic telemetry. Known days at liberty are the number of days between the dates of tagging and last detection (there were no known recaptures). Farthest distance is the linear distance between the tagging site and the farthest detecting receiver. For each individual, maximum daily displacement was calculated between sequential detections separated by at least one day; the linear distance between those two detecting receivers in km was divided by the time in days (including fractions thereof) between sequential detections. From these average cruising speeds, the fastest cruising speed is reported. Cumulative daily displacement is the cumulative linear distance between daily mean positions of detecting receivers. *Bat ray B17 was immature according to criteria from Martin and Cailliet (1998). Abbreviations: DW, disk width; TL, total length.

Species	ID	Sex	DW (cm)	TL (cm)	Date Tagged (dd-mmm-yy)	Known Days At Liberty	Farthest Distance (km)	Maximum Daily Displacement (km)	Cumulative Daily Displacement (km)
P. productus	G1	F	44	142	11-Jul-14	404	124	12.6	352
	G2	F	43	132	11-Jul-14	343	155	29	298
	G3	F	39	123	07-Aug-14	63	178	11.2	168
	G4	F	44	131	10-Aug-14	776	286	17.3	786
	G5	F	47	136	13-Jul-16	91	39	13.1	64
	G6	M	41	124	14-Jul-16	1505	252	29.8	2224
	G7	F	46	140	14-Jul-16	873	192	22.5	199
	G8	F	48	147	14-Jul-16	1082	124	31.8	995
	G9	F	50	136	15-Jul-16	1445	275	20.9	1182
	G10	M	42	135	18-Jul-16	1477	68	8.3	565
	G11	F	48	146	18-Jul-16	1475	273	35.2	2285
	G12	F	46	131	15-Aug-17	660	283	35	766
M. californicus	B13	F	114	84	17-Jul-14	1804	316	43.2	3031
	B14	F	120	87	10-Oct-14	184	72	30.5	209
	B15	F	124	99	07-Jul-15	1495	61	7.7	380
	B16	F	99	99	08-Jul-15	1881	284	4.2	382
	B17*	F	79	59	01-Jul-16	1497	313	33.5	1764
	B18	F	117	102	01-Jul-16	2	18	4.6	8

Table 2. General Linear Mixed Models (GLMMs) fitted for shovelnose guitarfish (*Pseudobatos productos*) and California bat rays (*Myliobatos californica*) to model the environmental covariates (sea surface temperature (SST) of La Jolla, photoperiod, and alongshore temperature gradient (see text for details) of alongshore distance from the US-Mexico border, with individuals nested in year as a random effect (see text for details). Inclusion R^2 represents the variance that each covariate explains. Structural coefficients represent a fixed effect's correlation, irrespective of other fixed effects. Beta weights with confidence intervals that do not overlap 0 represent significance of that environmental covariate on the predictor variable, and relative beta weights represent strength of correlation with the overall model prediction.

Guitarfish alongshore distance ~ La Jolla SST + photoperiod + (1 | year/ID)

Intercept = 358.021 ± 20.476

AIC = 10783.66

Adjusted R^2 = 0.679 (CI: 0.627 – 0.749)

Environmental covariate	Regression coefficient (unstandardized)	Inclusive R^2	Structure Coefficients	Beta Weights
La Jolla SST	-2.715 ± 0.628	0.254 (0.208 – 0.362)	-0.611 (-0.720 – -0.546)	-0.096 (-0.178 – -0.088)
Photoperiod	-16.994 ± 1.291	0.615 (0.508 – 0.680)	-0.952 (-0.973 – -0.896)	-0.249 (-0.324 – -0.235)

Bat ray alongshore distance ~ La Jolla SST + alongshore temperature gradient + (1 | year/ID)

Intercept = 56.711 ± 6.415

AIC =1873.01

Adjusted R^2 = 0.611 (CI: 0.561 – 0.716)

Environmental covariate	Regression coefficient (unstandardized)	Inclusive R^2	Structure Coefficients	Beta Weights
La Jolla SST	-0.595 ± 0.295	0.34 (0.163 – 0.467)	-0.754 (-0.815 – -0.521)	-0.090 (-0.088 – 0.001)
Alongshore temperature gradient	-642.205 ± 153.202	0.554 (0.540 – 0.621)	-0.952 (-0.996 – -0.917)	-0.194 (-0.223 – -0.102)

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CHAPTER 3: Conclusion

Understanding the movement patterns of coastal mesopredatory elasmobranchs is crucial for managing populations before they are exploited and for preserving habitats that are susceptible to destruction. This was the first passive acoustic telemetry study conducted on bat rays, and on adult shovelnose guitarfish, with the only other tracking studies conducted over in short periods of time and within small areas to characterize habitat preference (Matern et al. 2000, Hopkins & Cech 2003, Farrugia et al. 2011, Meese & Lowe 2019).

In Chapter 2, general seasonal movement patterns were discussed; however, individuals had distinct movement patterns that were not similar to others. Studies on cownose rays along the Atlantic coast observed similar timing of arrival to differing summer aggregations from the same overwintering sites (Ogburn et al. 2018), indicating that cownose rays may base movement from overwintering regions on environmental cues such as sea surface temperature. The same behavior may be occurring in our bat rays, with La Jolla being the shared summer aggregation site that unites individuals from this subpopulation. For instance, bat ray B13 was the only individual to be detected in the Channel Islands, with sparse detections along the coast. Its arrival off the Channel Islands aligns with other bat rays' arrivals in La Jolla, and its detections in La Jolla is near the time of departure from La Jolla for other individuals. Additionally, bat ray B17, which was the only non-mature individual tagged according to criteria from Martin and Cailliet (1998), resided in La Jolla for most of the year during its tracking period. If La Jolla does serve as a nursery ground for bat rays as discussed in Chapter 2, this bat ray's longer residency is consistent with this claim. Bat ray maturity occurs around 5-6 years, so it is likely that B17 reached maturity age within its tracking period. B17 was also the only tagged individual to be detected off Santa Catalina Island–it is unlikely immature bat rays are strong enough to cross the San Pedro Channel and might have been of maturity when these detections occurred.

Sea surface temperature had significant influence on shovelnose guitarfish movement, both on a broad and fine scale, but this was not observed in bat rays. Although little is known about preferential temperature ranges, shovelnose guitarfish in Bolsa Chica were detected in temperatures around 22^{o}C, which aligns with the temperature in which shovelnose guitarfish were at peak abundance in La Jolla (Farrugia et al. 2011). For bat rays, there may have not been enough detection data outside of La Jolla as it is possible that bat rays, may seek refuge in warmer waters south of La Jolla in Baja California, Mexico. In previous studies, bat rays in Tomales Bay, CA were found to have an increase in metabolism in temperatures ranging from 14-20^{o}C, with high metabolisms peaking at around 25^{o}C (Hopkins & Cech 1994). Regarding movement off La Jolla, this temperature range aligns with the temperature range of La Jolla during peak bat ray abundance in this study of 20-23°C. However, bat rays in Tomales Bay utilized the extreme heterogenized temperature distribution in the bay to regulate their internal temperature, foraging heavily in warm, prey-rich mudflats and resting in the colder, deeper waters (Matern et al. 2000). This behavior, dubbed 'shuttling,' optimizes net energy gain by hunting in warm, soft substrates, and resting in colder, hard substrates; the bat rays tagged did not display such behavioral thermoregulation. This may be in part due to the openness of La Jolla, and therefore, lack of a strong temperature gradient. Additionally, it is possible that these bat rays are of two different populations and have differing behaviors due to the conditions they live in, such as drastic temperature differences between the California Countercurrent system and the California Current system. On the other hand, it is possible that bat rays in La Jolla may move to the darker, cooler hard substrate more often to thermoregulate, regardless of time of day. Unlike bat rays in Hopkins & Cech (1994) which behaviorally thermoregulated by moving within a more stagnant bay based on diel patterns, La Jolla bat rays may move freely between soft and hard substrate because water temperature of a circulating cove is more consistent throughout the day.

Reproduction is undoubtedly a reason for seasonal philopatry to La Jolla. Bat rays have an annual reproductive cycle and mature ova are present in females in the late gestation stages (Martin & Cailliet 1988). In Martin & Caillet (1988), ovulation was only observed in June (7% of 28 individuals) and birthing began around May and went as late as November. Similarly, shovelnose guitarfish embryonic growth peaks in May and June, with birth from June to October in the Gulf of California (Márquez-Farías 2007). In this study, shovelnose guitarfish abundance peaked during June and July; however, there were no juvenile shovelnose guitarfish captured or tagged. This may be due to the type of bait and hooks that were used and could bias larger animals. It is also possible that the gestation period of this population of shovelnose guitarfish is delayed to that of the Gulf of California population due to slightly colder waters, causing embryonic growth to be slower in Southern California and birthing elsewhere, such as Bolsa Chica Ecological Reserve (Farrugia et al. 2011). However, gestation remains a strong reason for philopatry to La Jolla in both species given the evidence discussed in Chapter 2.

Using passive acoustic telemetry to infer movement is integral for fully understanding species' ranges and the environmental cues that may influence movement. As anthropogenic intervention continues to impact habitats and species of the SCB, it is increasingly more necessary to study when and where species will be most affected and to anticipate how current non-threatened or declining species will be impacted in the future.

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