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Title:

Triennial migration and philopatry in the critically endangered soupfin shark (*Galeorhinus galeus*)

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Abstract:

1. Globally, one-quarter of shark and ray species is threatened with extinction due to overfishing. Effective conservation and management can facilitate population recoveries. However, these efforts depend on robust data on movement patterns and stock structure, which are lacking for many threatened species, including the Critically Endangered soupfin shark (*Galeorhinus galeus*), a circumglobal coastal-pelagic species.

2. Using passive acoustic telemetry, we continuously tracked 34 mature female soupfin sharks, surgically implanted with coded acoustic transmitters, for seven years via 337 underwater acoustic receivers stationed along the west coast of North America. These sharks and an additional six were also externally fitted with spaghetti identification tags. Our tagging site was a shallow rocky reef off La Jolla (San Diego County), California, USA, where adult females were observed to aggregate every summer.

3. Tagged soupfin sharks were highly migratory along the west coast of North America, between Washington, USA and Baja California Sur, Mexico. However, every three years, they returned to waters off La Jolla, California, where they underwent gestation. This is the first conclusive evidence of triennial migration and philopatry ('home-loving') in any animal, which is apparently driven by this species' unusual triennial reproductive cycle. Females of other shark and ray species with triennial reproductive cycles are also likely to exhibit triennial cycles of migration and philopatry.

4. At least six (15%) of our tagged soupfin sharks were killed in commercial gillnets in Mexico.

5. *Policy implications.* Identifying multiennial migratory cycles in mature female sharks can reveal hidden stock structure in the form of discrete breeding cohorts, which are spatially and temporally segregated as they cycle through different reproductive phases. Accounting for this complexity may improve the performance of spatially structured stock assessment models, particularly when fishery removals are spatially heterogeneous, as well as inform the spatiotemporal design of fishery-independent surveys. In the US, the soupfin shark is neither actively managed nor recognized as a Highly Migratory Species; however, given the highly migratory behavior we report, this designation should be revisited by the US Pacific Fishery Management Council. Finally, given the extensive fishery removals in Mexico, any future management must be internationally cooperative.

Keywords:

acoustic tracking, conservation, international fisheries management, ovarian cycle, phenology, reproductive cycle, tope, school shark

Introduction

Migration, the long-distance movement between distinct habitats for distinct purposes, is widespread among animal taxa (Dingle and Drake 2007). In long-lived, iteroparous species (i.e., most vertebrates), *loop* and *to-and-fro* migrations are most common, involving recurring round-trip journeys between breeding and nonbreeding habitats in response to seasonal changes in the environment (Ramenofsky and Wingfield 2007). Along these migratory circuits, many animals are philopatric ('home-loving'), returning to previously occupied "bottleneck sites" for feeding, mating, parturition, molting, or staging (Mayr 1963). Such predictable site fidelity can be used to monitor individual animals via automated tracking and mark-recapture methods, to study the long-term patterns of migration within an individual's lifetime. Understanding where, when, and why animals move can improve management and conservation, by identifying essential habitat, migratory corridors, and bottleneck sites, and enabling more targeted management actions that are flexible in space and time (Allen and Singh 2016).

Migration and other phenological events, such as reproduction, molting, and hibernation, usually cycle with a period of one year, regulated by endogenous circannual rhythms that are entrained to seasonally varying environmental cues such as photoperiod, temperature, and rainfall (Visser et al. 2010; Helm et al. 2013). Circannual rhythms are highly adaptive because they facilitate the anticipation of and preparation (e.g., molting, food caching or fattening, gonadal development) for seasonal changes in food and water availability, weather conditions, and associated social interactions (Dingle and Drake 2007). For these reasons, annual cycles of migration and other phenological events are nearly ubiquitous among vertebrates, whereas multiennial cycles (i.e., periods greater than one year) are rare.

One notable exception are the cartilaginous fishes (Class Chondrichthyes), in which multiennial cycles of migration and philopatry are common, at least for females. For example, white sharks (*Carcharodon carcharias*) (Domeier and Nasby-Lucas 2013), smalltooth sawfish (*Pristis pectinate*) (Feldheim et al. 2017), nurse sharks (*Ginglymostoma cirratum*) (Pratt and Carrier 2001), and lemon sharks (*Negaprion brevirostris*) (Feldheim et al. 2013) exhibit biennial cycles, in which individual females return (are philopatric) to mating or nursery areas every two years. This behavior reflects these species' biennial reproductive cycle, in which females give birth every two years. Annual migration and philopatry are also common, but in species with annual reproductive cycles: leopard sharks (*Triakis semifasciata*) (Nosal et al. 2014), Port Jackson sharks (*Heterodontus portusjacksoni*) (Bass et al. 2017), cownose rays (*Rhinoptera bonasus*) (Ogburn et al. 2018), and bonnethead sharks (*Sphyrna tiburo*) (B. Keller, unpublished data). Even triennial reproductive cycles have been reported for some species, including tiger sharks (*Galeocerdo cuvier*) (Whitney and Crow 2006), wobbegong sharks (*Orectolobus spp.*) (Huveneers et al. 2007), and dusky sharks (*Carcharhinus obscurus*) (Castro 2009). By logical extension, if annual reproductive cycles beget annual migration and philopatry, and biennial cycles beget biennial migration and philopatry, then we should expect females with triennial reproductive cycles to exhibit triennial migration and philopatry. However, conclusive evidence for such triennial movement patterns has never been produced for any animal, presumably due to the logistical challenges (e.g., large sample size, long study duration) of capturing such a pattern.

In this study, we overcame these challenges and tested for triennial migration and philopatry in the Critically Endangered soupfin shark (*Galeorhinus galeus*), a circumglobal, temperate coastal-pelagic species that is reported to have a triennial reproductive cycle for most of its subpopulations (Peres and Vooren 1991; Lucifora et al. 2004; Walker 2005). We used passive acoustic telemetry to track 34 adult females, tagged in five annual cohorts, for nearly seven years. Our tagging site was a shallow rocky reef off La Jolla (San Diego County), California, USA, where we had previously observed adult females aggregating every summer. Given the documented philopatry of many other shark and ray species (Hueter et al. 2004; Chapman et al. 2015; Flowers et al. 2016), we expected female soupfin sharks to be philopatric as well. Of greater interest, however, was how often they would return to this aggregation site off La Jolla. If they had an annual reproductive cycle, for example, we should expect them to return annually like the closely related (Family Triakidae) and sympatric leopard shark (*Triakis semifasciata*) (Nosal et al. 2014). However, given the triennial reproductive cycle reported for most other soupfin shark populations (Peres and Vooren 1991; Lucifora et al. 2004; Walker 2005), we hypothesized a triennial philopatric return of these tagged females. In short, our research questions were: 1) Are female soupfin sharks philopatric? 2) If so, what is the period of their return cycle? and 3) Where and why do they go beyond the aggregation site where they were tagged?

Materials and Methods

The tagging site (32.8505°N, 117.2665°W) was a shallow (3 – 6 m) rocky reef off La Jolla (San Diego County), California, USA (Fig 1). Soupfin sharks were captured from a 5-m skiff using handlines and baited barbless circle hooks. Hooked sharks were restrained alongside the skiff by cinching a 6-mm polypropylene noose around the caudal peduncle and a 19-mm nylon noose around the upper abdomen, just posterior to the pectoral fins. The free ends of each rope were then tied to opposite ends of the skiff. Sharks were measured, sexed, and, to facilitate reporting of recaptured sharks, externally fitted with a 'spaghetti' identification tag (Floy Tag FIM-96) inserted into the musculature and through the radials at the base of the first dorsal fin.

Beginning in October 2013, the restrained sharks were also rotated ventral-side up to induce tonic immobility and to facilitate surgical implantation of a coded acoustic transmitter (Vemco V16-4H, 69 kHz, 158 dB, 120 s average transmission delay, 80 – 160 s random transmission interval). During this procedure, the mouth and gills remained submerged, but the abdominal surface was kept out of the water. The surgical site was antisepticised with povidone-iodine and a 3-cm longitudinal incision was made halfway between the pectoral and pelvic fins, approximately 3 cm off the ventral midline. The transmitter, dipped in povidone-iodine, was then inserted into the peritoneal cavity via the incision, which was immediately closed with one continuous absorbable suture (Ethicon 2-0 VICRYL) and treated with topical antibiotic ointment (Neosporin). Finally, the hook was removed, shark righted dorsal-side-up, and nooses loosened to allow the shark to swim away. Transmitter-implanted sharks were subsequently monitored by a large coastal array of underwater acoustic receivers (Vemco VR2Tx, VR2AR, VR2W, VR2C, and VR4-UWM; Fig 1). Transmitter battery life was either 3.6 years (sharks 1 – 8 and 13) or 6.7 years (sharks 9 – 12 and 14 – 34; Table 1).

Pregnancy was determined for a separate sample of soupfin sharks by using a portable IBEX LITE ultrasound unit and L7HDi linear transducer (E.I. Medical Imaging). Sharks were captured, restrained, and rotated ventral-side up as described above, except the abdominal surface was kept submerged to facilitate transmission of the ultrasonic signal. The uteri were scanned beneath the ventrolateral surfaces of the abdomen, between the pectoral and pelvic fins. All procedures described above were conducted under University of California – San Diego IACUC Protocol S00080 and California Department of Fish and Wildlife Scientific Collecting Permit 183020007.

Acoustic detections were filtered for spurious detections following the manufacturer's recommendations. Briefly, detections were removed if they did not occur within 60 min (30 times the average transmission delay of 120 s) of another detection of the same transmitter at the same receiver. The remaining (non-spurious) detections were then pooled by five zones where detecting receivers were located: 1) La Jolla (San Diego County), 2) the rest of San Diego, Orange, and Los Angeles Counties (including Santa Catalina Island), 3) Ventura and Santa Barbara Counties (including the Northern Channel Islands), 4) San Luis Obispo through Sonoma Counties (including San Francisco Bay and the Farallon Islands), and 5) Oregon and Washington (Fig 1). Finally, raw detections were reduced to detection days (dates) in each zone (Fig 2).

To determine the period of the migration and philopatry cycle, the following numbers of days were subtracted from detection dates of soupfin sharks tagged in 2013: 0 d; 2014: 365 d; 2015: 730 d; 2016: 1096 d; and 2017: 1461 d. For sharks tagged in 2014 – 2017, this transformation effectively changed the detection year, but not the detection day or month, as if all sharks were tagged in 2013. The probability of presence off La Jolla was then estimated using a generalized linear mixed model (GLMM) with a binomial distribution and individual shark as a random effect via the lme4 package in R version 4.0.2 (Bates et al. 2015). The probability of presence was modeled cyclically, using the sine and cosine of transformed detection dates divided by the period (Eq. 1). We tested four *a priori* assumptions of migration cycles (annual, biennial, triennial, and quadrennial), which were compared using the AIC and relative likelihood of each model. Then, we generated a model for every possible period in one-day increments from 5 days to 5 years and compared these using the AIC and relative likelihood of each model.

Eq. 1 $$P(T) = C + A\cos\frac{2\pi T}{Period} + B\sin\frac{2\pi T}{Period}$$

T is the transformed detection date; C is the intercept representing the baseline probability; A and B are coefficients that contribute to the magnitude and phase shift of the wave.

Lastly, to visualize the general migratory patterns in relation to likely reproductive phase (Fig 3), zones 1 and 2 above were combined into the 'Southern California' region and zones 3 – 5 were combined into the 'Central Coast' region. Transformed detection days were reduced to detection months in each of these two regions.

Results

From 2013 to 2017, 34 soupfin sharks were surgically implanted with Vemco V16 coded acoustic transmitters (2013: N=8; 2014: N=5; 2015: N=6; 2016: N=11; 2017: N=4) as well as externally tagged with identifying 'spaghetti' tags (sharks 1 – 34; Table 1). Six additional sharks were tagged from 2010 to 2013 with only 'spaghetti' tags (sharks A – F; Table 1). All 40 sharks tagged were female; no males were ever caught or observed. Mean total length ± SD was 178 ± 10 cm (range: 152 – 198 cm). Most, if not all, of these tagged females were sexually mature, based on a total length of 158 cm for 50% female maturity in southern California (Ripley 1946). Lastly, there was no significant difference in total length among the five tagging cohorts (2013 – 2017) of transmitter-implanted sharks ($F_{4,29} = 1.77$, $p = 0.16$, one-way analysis of variance).

Six of the 40 tagged soupfin sharks (15%) were recaptured in commercial gill nets in Mexico: sharks B, 7, 8, and 10 near Bahía Sebastián Vizcaíno and sharks 22 and 25 within 50 km of the US-Mexico border. Additionally, shark C was recaptured in a Washington Department of Fish and Wildlife gillnet in Grays Harbor, Washington, USA (Table 1, Fig 1).

Pregnancy was determined opportunistically for an additional (non-tagged) sample of 21 female soupfin sharks from San Diego County, via dissection of dead sharks that washed ashore or were captured by local fishers ($N = 8$), or ultrasound examination of live sharks ($N = 13$). Mean total length ± SD was 176 ± 9 cm (range: 163 – 198 cm). All these sharks were gravid with visible embryos (see Table S1 and Videos S1 – S3 in Appendix S1 of the Supporting Information) and there was no significant difference in total length between these confirmed pregnant females and the forty tagged soupfin sharks ($t_{59} = 0.966$, $p = 0.34$, independent-samples t-test).

The transmitter-implanted soupfin sharks were detected at 337 receiver stations along the US west coast: 45 off La Jolla (San Diego County), 121 off the rest of San Diego, Orange, and Los Angeles Counties (including 14 around Santa Catalina Island), 33 off Ventura and Santa Barbara Counties (including 13 around the Northern Channel Islands), 109 off San Luis Obispo through Sonoma Counties (including San Francisco Bay and the Farallon Islands), and 29 off Oregon and Washington (Figs 1, 2). Known days at liberty averaged 904 ± 606 d (range: 1 – 2199 d). On average, sharks were detected on 173 ± 134 (30.5 ± 26.0%) of their known days at liberty (range: 1 – 628 d). Sharks were highly mobile, swimming at speeds of up to 73.7 km d^{-1}; the most distant detection or recapture event for each shark averaged 427 ± 464 km (range: 1 – 1796 km) from the tagging site.

Based on a logistic sinusoidal regression of individuals' days detected off La Jolla over time, a triennial cycle of return (i.e., period of the fitted sine wave) best explained the detection patterns, with a relative likelihood exceeding 0.999. This far exceeded the next best model (ΔAIC = 2106), with a quadrennial cycle of return and a relative likelihood less than 0.001. The models with annual (ΔAIC = 4117) and biennial cycles (ΔAIC = 5377) were even less likely. When testing for every possible period in one-day increments from 5 days to 5 years, the dominant period was 1130 days or 3.094 years (95% CI = 3.083 – 3.127 years; Figure S1 in Appendix S1).

In summary, transmitter-implanted sharks generally remained in southern California (San Diego, Orange, and Los Angeles Counties) through the fall or winter post-tagging (Year 0; Figs 2, 3). Four of these sharks were recaptured off Mexico within one year of tagging, thus precluding further detections (sharks 7, 10, 22, 25; Fig 2). Of the remaining 30 sharks, 21 (70%) were detected off the Central Coast of California (Ventura through Sonoma Counties) during the next two years (Year 1 and 2 post-tagging; Figs 2, 3). Three of these made excursions as far north as

Oregon and Washington (Figs 1, 2). Of these 21 sharks, 12 (57.1%) returned to the La Jolla aggregation site in Year 3, thus exhibiting triennial philopatry (Figs 2, 3). One of these (shark 12), which was tagged in 2014 and returned in 2017 (Year 3), also returned in 2020 (Year 6), thus completing two full triennial cycles (Fig 2). None of the sharks tagged in 2013 could have been detected in Year 6 post-tagging (2019) because their transmitters had battery lives of only 3.6 years. The transmitters implanted into the other sharks (except shark 13) had longer battery lives of 6.7 years. Of the remaining 9 of 21 sharks that were detected along the Central Coast of California, four never returned to La Jolla and five returned, but with patterns resembling annual (sharks 23 and 28) and quadrennial (sharks 8, 24, and 27) philopatry (Fig 2).

Discussion

We discovered that soupfin sharks exhibit a triennial cycle of migration and philopatry, which is not known for any other animal. Of the 34 soupfin sharks implanted with acoustic transmitters over five consecutive years (i.e., five independent tagging cohorts), we found at least two sharks per cohort (except 2017) exhibited a clear triennial cycle, returning to waters off La Jolla (San Diego County) from as far north as Oregon and Washington, USA (Figs 2, 3). Most compelling was a shark tagged in 2014 (shark 12) that completed two triennial return cycles (Fig 2). The most likely explanation for this three-year movement pattern in adult female soupfin sharks is a triennial reproductive cycle. Given that some other animal species also have triennial reproductive cycles, we suggest that triennial migration and philopatry may be more common, however not yet reported, due to relatively short study durations and small sample sizes that heretofore have not been able to capture these patterns conclusively.

Probable Triennial Reproductive Cycle

In Chondrichthyan females, the reproductive cycle consists of a series of events including follicle development and ovulation (i.e., the ovarian cycle), mating, sperm storage, fertilization, embryo gestation and parturition in viviparous species, egg case formation, retention, and oviposition in oviparous species, and a possible resting period before the start of the next ovarian cycle (Awruch 2018). In most soupfin shark populations, such as Australia and South America, the reported reproductive cycle is triennial, as evidenced by three distinct reproductive phases co-occurring within the population of sexually mature females: 1) Gravid, 2) Non-Gravid-1 (early vitellogenesis with small ovarian follicles, 0.5 – 2.5 cm diameter; oviduct in resting stage), and 3) Non-Gravid-2 (late vitellogenesis with large ovarian follicles, 3.5 – 5.5 cm diameter; dilated oviducal gland preparing for ovulation) (Peres and Vooren 1991; Lucifora et al. 2004; Walker 2005). By contrast, an annual reproductive cycle has been repeatedly asserted for the Eastern North Pacific population (Holts 1988; Peres and Vooren 1991; Capapé et al. 2005; COSEWIC 2007), citing Ripley's (1946) analysis of the California soupfin shark fishery during World War II. However, although Ripley (1946) referred to the "annual reproductive cycle of female soupfin," he never explicitly concluded an annual ovarian or parturition cycle. Furthermore, given the reported 12-month gestation period for soupfin sharks (Ripley 1946; Peres and Vooren 1991; Lucifora et al. 2004; Walker 2005) and our finding of triennial migration and philopatry in Eastern North Pacific females, an annual reproductive cycle seems unlikely. In Appendix S1, we explain Ripley's (1946) widely misunderstood use of "reproductive cycle" and show how Ripley's data do not in fact preclude a triennial reproductive cycle. Resolving the period of the reproductive cycle has major conservation implications because an overestimated parturition frequency (i.e., annual instead of triennial) can lead to an overestimated intrinsic population growth rate (r_{max}) and thus an underestimated extinction risk (Cortés 2016).

In short, the best explanation for the triennial migration and philopatry observed in this study is that female soupfin sharks in the Eastern North Pacific have a triennial reproductive cycle, as reported for other subpopulations of this species. This could be confirmed by observing a bimodal length frequency distribution of ovarian follicles in mature, non-gravid females (i.e., Non-Gravid-1 and -2 phases) along the Central Coast of California.

Although philopatry to the La Jolla aggregation site predominantly cycled with a period of three years, some sharks tagged in 2016 exhibited annual (sharks 23 and 28), biennial (shark 21), and quadrennial (sharks 24 and 27) cycles (Fig 2). Some of this variation is likely due to plasticity in the reproductive cycle, particularly the onset and duration of vitellogenesis, which depend on how effectively the mother can sequester in her liver energy from the environment and transfer that energy to the developing oocytes (Castro 2009). To that end, Baremore and Hale (2012) suggested that differences in food availability and energetic condition could explain the plasticity (biennial or triennial) of the sandbar shark (*Carcharhinus plumbeus*) reproductive cycle. In this study, the soupfin sharks tagged in 2016 may have experienced varied energy intake due to the strong 2015/2016 El Niño event, which affected resource availability unevenly along the west coast of North America. For example, giant kelp (*Macrocystis pyrifera*) forests and their associated fish and invertebrate assemblages declined drastically off central Baja California due to heat stress, but were largely unaffected or even increased off northern Baja California and southern California (Reed et al. 2016; Arafeh-Dalmau et al. 2019). Similarly, bull kelp (*Nereocystis luetkeana*) forests were decimated off northern California, but remained intact or even increased off Oregon (Rogers-Bennett and Catton 2019; Hamilton et al. 2020). Thus, depending on their location and resource availability therein, the soupfin sharks tagged in 2016 could have experienced either higher-than-average energy intake (accelerated vitellogenesis; biennial reproductive cycle), average energy intake (normal vitellogenesis; triennial reproductive cycle), or lower-than average energy intake (slowed or delayed vitellogenesis; quadrennial reproductive cycle). However, not even the highest possible energy intake could result in an annual reproductive cycle, given the 12-month gestation period with consecutive, not concurrent, vitellogenesis. Thus, the sharks exhibiting annual philopatry to La Jolla likely employ a different migration strategy, returning to La Jolla for purposes in addition to gestation, such as feeding.

Reproductive Phenology, Migration, and Philopatry to Gestating Grounds

Given the abundance of mature pregnant females, but lack of mature males and juveniles, we conclude that the waters off La Jolla function primarily as a gestating ground for soupfin sharks, but not a mating or nursery ground. Philopatry to gestating grounds is not unusual in sharks and rays (Chapman et al. 2015), with pregnant females commonly showing affinity to warm water, which is hypothesized to accelerate embryonic development and minimize gestation period (Economakis and Lobel 1998; Hight and Lowe 2007; Jirik and Lowe 2012). This likely explains the strong latitudinal sexual segregation reported in Ripley's (1946) analysis of the California soupfin shark fishery: sharks caught in southern California (San Diego through Los Angeles Counties; $N = 5020$) were 97.8% females, in northern California (Mendocino through Del Norte Counties; $N = 5724$) were 2.5% females, and along the Central Coast (Ventura through Sonoma Counties; N=2699) were 46.5% females (Fig 1). Southern California, including Santa Catalina Island, is warmed by the north-flowing Southern California Counter Current, whereas northern California and the Central Coast, including the Northern Channel Islands, are characterized by persistent upwelling and cooling by the south-flowing California Current (Watson et al. 2011). Given that the timing of acoustic detections off San Diego, Orange, and Los Angeles Counties clustered together (Figs 2, 3), other localities off southern California, besides La Jolla, likely also serve as gestating grounds, including the waters off Santa Catalina and San Clemente Islands.

After leaving La Jolla, most of the transmitter-implanted soupfin sharks were detected for the next two years along California's Central Coast, between the Northern Channel Islands and San Francisco Bay area (Fig 3). This region likely serves as a pupping and nursery ground, consistent with Ripley's (1946) finding that only 58.4% of soupfin sharks caught along the Central Coast were sexually mature, compared to 97.1% and 97.3% of soupfin sharks caught in northern and southern California, respectively. Mating likely also occurs there during females' second non-gravid year (Non-Gravid-2 phase), consistent with the approximately 1:1 sex ratio found by Ripley (1946). Lastly, spermatophores have been found in the oviducal glands of mature females, up to five months before ovulation, indicating the potential for long-term sperm storage (Peres and Vooren 1991).

One area of further study is the apparent cross-border connection to Mexican waters, which was never addressed by Ripley (1946). At least four of our tagged soupfin sharks were captured around Bahía Sebastián Vizcaíno, approximately halfway down the Baja California peninsula (Fig 1). Based on a sample of 407 soupfin sharks caught in artisanal gill nets in this region (Cartamil et al. 2011; Ramirez-Amaro et al. 2013), 68.8% were immature, of which 55.4% were female. Of the mature individuals caught, 81.9% were female. Therefore, this region may be another pupping and nursery ground, and, even a mating ground given the presence of mature males, resembling in many ways the Central Coast of California. However, given the scarcity of acoustic receivers in this region during our study (none of these detected any of our transmitter-implanted sharks), the magnitude of the connection between California and Mexico, and thus the potential for multiple substocks, remains unclear.

Conservation Implications

Due to decades of heavy fishing pressure and steep population declines worldwide, the conservation status of the soupfin shark was elevated to Critically Endangered globally in 2020 by the IUCN (Walker et al. 2020). In the Eastern North Pacific, the population declined sharply in the 1940s due to a fishery boom that targeted soupfin sharks for their livers, which were valued for their rich vitamin A content (COSEWIC 2007). Only after nearshore gillnets were banned in southern California in 1994 did the population begin to recover (Pondella and Allen 2008). However, artisanal fisheries in Mexico continue to capture soupfin sharks in gillnets (Cartamil et al. 2011; Ramirez-Amaro et al. 2013), demonstrating the importance of cooperative international management of this species.

In the US, the soupfin shark fishery has not undergone a stock assessment or been subject to a Fishery Management Plan (FMP), unlike in Australia (Punt and Walker 1998; Punt et al. 2000), South Africa (Winker et al. 2019), and Canada (Fisheries and Oceans Canada 2012). Instead, soupfin sharks are merely classified as an Ecosystem Component (EC) species of the Pacific Coast Groundfish Fishery, and therefore not actively managed by the corresponding FMP. The soupfin shark is also not currently recognized as a Highly Migratory Species (HMS), a designation that would require stock assessments by the US Pacific Fishery Management Council (PFMC). In 2020, however, the soupfin shark was added to Appendix II of the United Nations Convention on the Conservation of Migratory Species (CMS), joining the common thresher shark (*Alopias vulpinus*), shortfin mako shark (*Isurus oxyrhinchus*), and blue shark (*Prionace glauca*), which are already managed as HMS by the US PFMC. Given the recent CMS listing and IUCN status elevation to Critically Endangered globally, as well as the highly migratory nature we report along the west coast of North America, the designation of HMS for the soupfin shark should be revisited by the US PFMC.

Finally, accounting for the triennial migration and philopatry of discrete female breeding cohorts may improve the performance of spatially structured stock assessment models, particularly when fishery removals are spatially heterogeneous (Walker et al. 2008). For example, unsustainable removals of gravid females off La Jolla in one year may not be detected in catch-per-unit-effort at the same location until three years later, when that same breeding cohort returns. The triennial movement patterns are also important to consider in the spatiotemporal design of fishery-independent surveys. For example, a summer survey conducted annually off La Jolla would sample a different female breeding cohort every year and the same cohort every three years, whereas a biennial survey would sample a different cohort every two years but the same cohort only every six years. A triennial survey would sample the same cohort every three years but ignore the other two. These considerations are of course dependent on the stability of female breeding cohorts, which is not currently known; plasticity in the reproductive cycle could be a destabilizing factor.

Triennial Migration and Philopatry in other Taxa and Future Directions

It was only possible to capture this triennial pattern of migration and philopatry in soupfin sharks because of a large sample size, five independent tagging cohorts (2013 – 2017), and a long (7-year) tracking period. Multiennial patterns are likely underreported in the literature because most animal tracking studies have lasted only a few years due to technological (e.g., transmitter battery life) and logistical constraints (e.g., pressure to publish within graduate degree timelines, grant funding windows, and probationary employment periods). Other animals likely also exhibit triennial movement patterns, which could be captured by robust, long-term studies.

Among the tetrapods, we are unlikely to find triennial migration and philopatry in amphibians and birds, which mostly reproduce annually (Morrison and Hero 2003; Helm et al. 2013; Williams 2018). In contrast, triennial reproduction is common in some species of snakes, lizards, and turtles (Blackburn 2018). However, most of these reptiles undertake only short-distance migrations, so any triennial movement patterns associated with reproduction would occur only on small scales (Russel et al. 2005). An exception to this are marine turtles, which, being highly migratory and having multiennial reproductive cycles (Carr and Ogren 1960; Hirth 1971; Rivalan et al. 2005), may show triennial migration and philopatry to nesting beaches. Lastly, although many mammals have protracted gestation periods and multiennial reproductive cycles (Renfree and Shaw 2018), most still migrate annually (seasonally) to increase food and water intake, escape predators, and avoid harsh weather conditions (Avgar et al. 2014).

Among the iteroparous bony fishes with synchronous reproduction, spawning mostly occurs on an annual cycle, except for ‘skipped spawning’ as a facultative response to environmental constraints, which may manifest itself as an irregular multiennial cycle (Rideout and Tomkiewicz 2011). In contrast, many cartilaginous fishes appear to have evolved an obligate multiennial reproductive cycle, which presumably maximizes their lifetime reproductive success. In highly migratory species with triennial reproductive cycles, such as the tiger shark (*Galeocerdo cuvier*) (Whitney and Crow 2006), future long-term tracking studies are likely to uncover robust triennial cycles of migration and philopatry in mature females, which have been postulated for tiger sharks off the Hawaiian Islands (Papastamatiou et al. 2013) and in the Coral Sea (Werry et al. 2014). In other threatened species, whose reproductive cycles have been described as biennial or triennial, such as the grey nurse shark (*Carcharias taurus*) (Bansemer and Bennett 2009), sandbar shark (*Carcharhinus plumbeus*) (Baremore and Hale 2012), and several species of mobulid rays (*Mobula spp*.) (Rambahiniarison et al. 2018), long-term tracking studies of mature females may clarify any apparent discrepancies or confirm inherent plasticity in the reproductive cycle.

In summary, we have demonstrated the value of long-term, highly collaborative animal tracking studies in revealing unexpected movement patterns, and their implications for wildlife conservation and management. Rapidly advancing tracking technologies (e.g., transmitter and receiver battery lives, miniaturization, data management and sharing) have eroded most of the technological constraints precluding long-term tracking studies (Hussey et al. 2015; Kays et al. 2015). Such long-term tracking studies should be widely incorporated into research programs, at least as 'side projects' to circumvent any remaining 'pressure-to-publish' logistical constraints. Obtaining these long-term animal movement data will enable managers to implement conservation actions that are flexible and targeted, thereby minimizing conflicts among stakeholders (Allen and Singh 2016).

Authors' Contributions:

APN conceived the research idea and led the writing of the manuscript; APN, DPC, AJA, LFB, NJB, KMB, ESB, EDC, RMF, RKL, and CFW collected and analyzed the data. All authors contributed critically to the drafts and gave final approval for publication.

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Data Availability Statement:

Data available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.1jwstqjtp (Nosal et al. 2021).

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Table and Figure Legends:

Table 1. Soupfin sharks (*Galeorhinus galeus*) tagged off La Jolla, California, USA. Sharks 1 – 34 were each surgically implanted with a Vemco V16 coded acoustic transmitter (estimated battery life = 1327 d for sharks 1 – 8, 13, and 2440 d for sharks 9 – 12, 14 – 34), whose

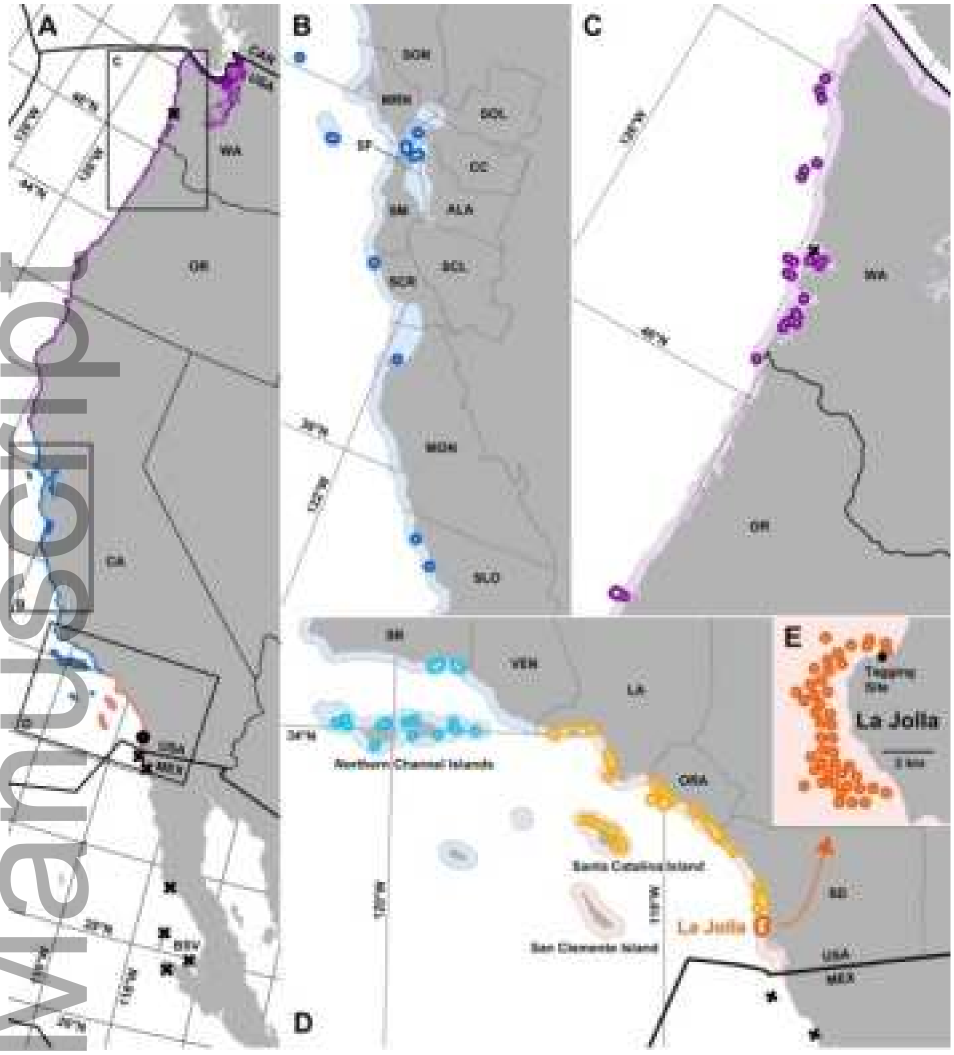
subsequent movements were monitored by underwater acoustic receivers. Sharks A – F were tagged only with an external 'spaghetti' identification tag. Known days at liberty is the time between the date of tagging and date of last detection or recapture. Total detection days are the number of days a shark was detected at any acoustic receiver. Farthest distance traveled is between the tagging site (32.8505°N, 117.2665°W) and the latitude and longitude of the farthest detecting receiver or recapture. Abbreviations: FL (fork length), TL (total length)

Figure 1. West coast of North America, where 34 adult female soupfin sharks (*Galeorhinus galeus*) were tracked by passive acoustic telemetry between 2013 and 2020. Lines of latitude (°N) and longitude (°W) are given in 2-degree increments. US state waters (out to 5.6 km) are color-coded by region, as defined by Ripley (1946). Southern California (CA) waters are colored orange: San Diego (SD), Orange (ORA), and Los Angeles (LA) Counties; California Central Coast waters are colored blue: Ventura (VEN), Santa Barbara (SB), San Luis Obispo (SLO), Monterey (MON), Santa Cruz (SCR), Santa Clara (SCL), San Mateo (SM), San Francisco (SF), Alameda (ALA), Contra Costa (CC), Solano (SOL), Marin (MRN), and Sonoma (SON) Counties; and Northern California (Mendocino, Humboldt, and Del Norte Counties; not shown), Oregon (OR), and Washington (WA) waters are colored purple. The black circle indicates the tagging site off La Jolla (San Diego County), CA. The locations of acoustic receivers that detected soupfin sharks are indicated by white dots with color-coded halos by zone: 109 receivers off SLO through SON are haloed dark blue (B), 29 off OR and WA purple (C), 45 receivers off La Jolla in SD dark orange (E), 121 off the rest of SD, ORA, and LA light orange, and 33 off VEN and SB light blue (D). Black X's indicate recapture locations of tagged soupfin sharks (BSV = Bahía Sebastián Vizcaíno). Thin gray lines indicate CA county borders, medium black lines state borders, and thick black lines international borders, including exclusive economic zones.

Figure 2. Days on which 34 adult female soupfin sharks (*Galeorhinus galeus*), surgically implanted with coded acoustic transmitters from 2013 to 2017, were detected by acoustic receivers between 2013 and 2020. Days detected off La Jolla in San Diego (SD) County, California are indicated by dark orange diamonds; off the rest of SD, Orange (ORA), and Los Angeles (LA) Counties (including Santa Catalina Island) by light orange diamonds; off Ventura

(VEN) and Santa Barbara (SB) Counties (including the Northern Channel Islands) by light blue diamonds; off San Luis Obispo (SLO) through Sonoma (SON) Counties (including San Francisco Bay and the Farallon Islands) by dark blue diamonds; and off Oregon and Washington by purple diamonds. Black X's indicate days on which sharks were killed in commercial gillnets in Mexico and gray lines indicate when shark-borne acoustic transmitters could potentially transmit (i.e., before estimated battery life expired or shark mortality confirmed).

Figure 3. Triennial cycle of migration and philopatry determined from passive acoustic tracking of 34 adult female soupfin sharks (*Galeorhinus galeus*) between 2013 and 2020. One, two, three, or four years were subtracted from all detection dates of sharks tagged in 2014, 2015, 2016, and 2017, respectively, to enable the comparison of all five tagging cohorts relative to a single reference tagging year (Year 0). Thus, time on the x-axis is relative time after tagging. The number of unique sharks detected per month (not cumulative) following this date transformation is pooled by region and plotted on the y-axis. Sharks detected in Southern California (San Diego, Orange, and Los Angeles Counties) are shown in orange and those detected along the California Central Coast (Ventura through Sonoma Counties) are shown in blue. For this analysis, sharks detected off Oregon and Washington were pooled with the Central Coast region. The notes about reproductive phenology (ovulation, birth, mating, vitellogenesis) are taken from Peres and Vooren (1991) and Ripley (1946). Lastly, the black line indicates the maximum possible number of sharks at liberty that month. This line increases when new sharks are implanted with acoustic transmitters and declines when these sharks are captured and killed, transmitter battery life ends, or sharks in later tagging cohorts (2015, 2016, and 2017) reach the end of the tracking period.



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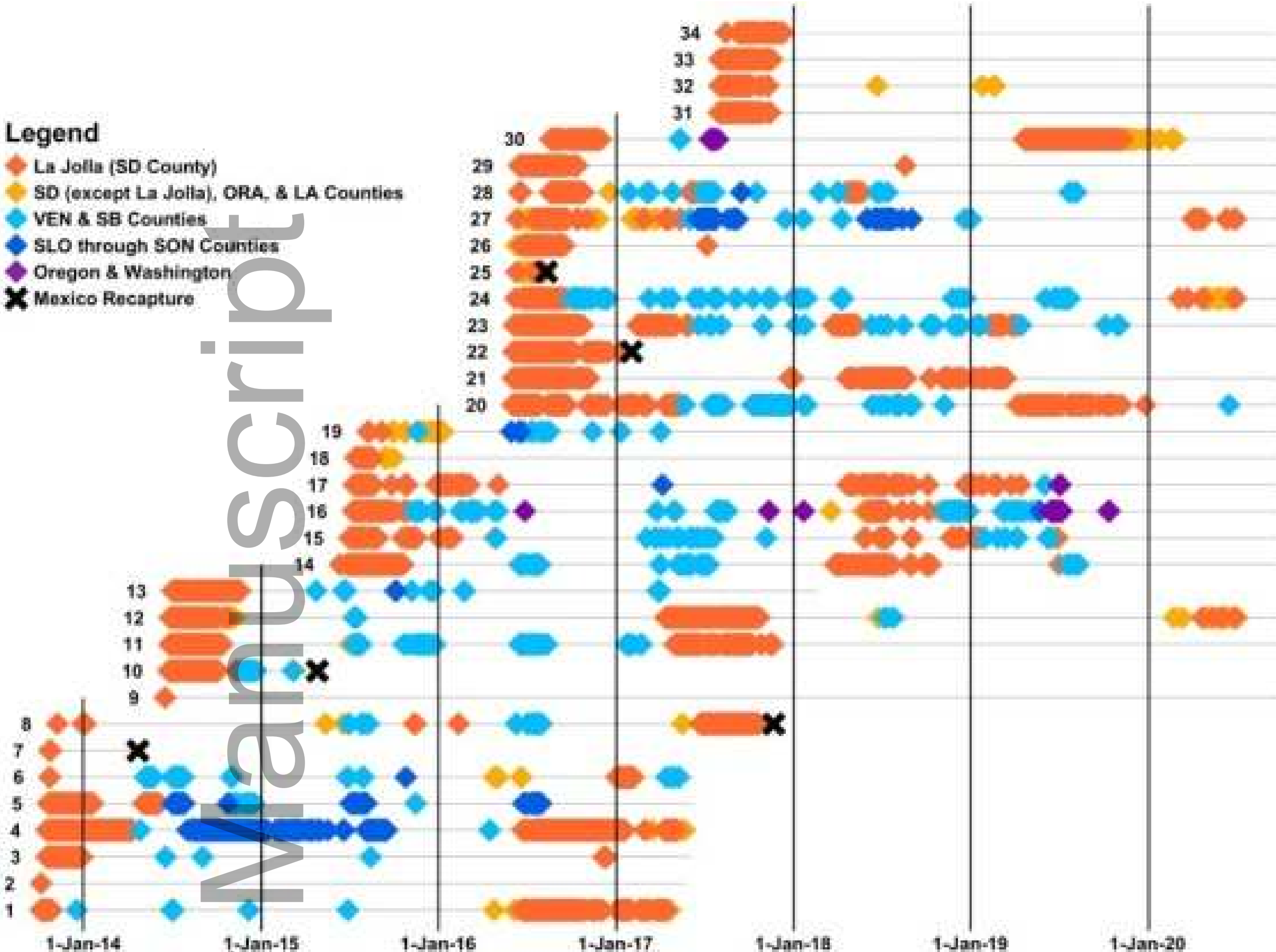

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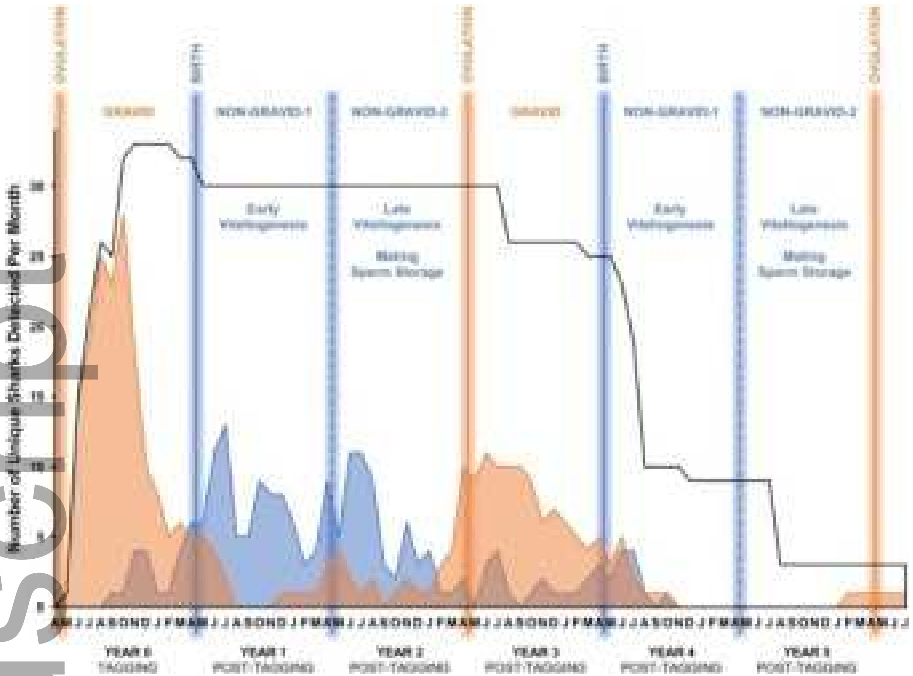

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