Research Article

Satellite Tracking and Site Fidelity of Short Ocean Sunfish, *Mola ramsayi*, in the Galapagos Islands

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Ocean sunfishes, with their peculiar morphology, large size, and surface habits, are valuable assets in ecotourism destinations worldwide. This study investigates site fidelity and long-range movements of short ocean sunfish, *Mola ramsayi* (Giglioli 1883), at Punta Vicente Roca (PVR) off Isabela Island in the Galapagos Islands. Five individuals were tracked between 32 and 733 days using ultrasonic receivers and transmitters. Two of the 5 were also tracked with towed pop-off satellite tags. One travelled to the equatorial front covering 2700 km in 53 days, with dive depths in the upper 360 m at temperatures between 9.2°C and 22°C. During its westward travel, dives extended to 1112 m (the deepest depth yet recorded for Molidae) into temperatures ranging between 4.5°C and 23.2°C. The remaining four individuals demonstrated site fidelity to PVR and were detected at the site between 128–1361 times for a total of 3557 reports. Forty-eight percent of the reports occurred during daytime hours and 52% after dark. Presumed cleaning session durations had a median of 15 minutes and a maximum of nearly 100 minutes. No other ultrasonic arrays around Galapagos or in the Eastern Pacific regional network recorded the presence of tagged individuals. These data are combined with tourist vessel sightings and submersible observations to confirm Punta Vicente Roca as an important sunfish hotspot.

1. Introduction

Ocean sunfishes, also known as mola, occupy a unique position in the marine food web as the most abundant gelativores and world's heaviest bony fish [1, 2]. Currently, four species are recognized: the common sunfish *Mola mola* (Linnaeus 1758); sharp-tailed sunfish/mola *Masturus lanceolatus* (Liénard 1840); slender sunfish/mola *Ranzania laevis* (Pennant 1776); and short sunfish/mola *Mola ramsayi* (Giglioli 1883). Two additional *Mola* species, *Mola* sp. *A* and *Mola* sp. *C*, have been suggested and await formal naming [3–5]. Despite their cosmopolitan distribution in tropical and temperate waters and large presence in bycatch worldwide [6, 7], relatively little is known of the spatial ecology and large-scale movement patterns of any ocean sunfish species.

All Molidae species are thought to be primarily pelagic and two species, *M. mola* and *M. ramsayi*, are encountered seasonally in near-shore environments worldwide. Examples include *M. mola* off California [6], United Kingdom [8], Japan [9], and South Africa [10] and *M. ramsayi* off Bali, Indonesia [11]. Such coastal forays are presumably associated with foraging and solicitation of parasite removal by resident reef cleaner fish, as Molidae are renowned for hosting substantial parasite loads [12, 13]. During cleaning sessions, opportunities for human interactions generate continued interest and revenue from ecotourism and recreational dive industries [11, 14]. Understanding site fidelity and migratory behavior of these fish is vital to sustaining and managing interactions and wellbeing of the species and tourists alike.

The only published behavioral data for *M. ramsayi* comes from Bali, Indonesia [11], and a handful of sightings from submersibles [15]. These data suggest that *M. ramsayi* has a wide thermal range with relatively even occupation of temperatures between 10 and 27.5°C and depths from the surface to 250 m. Dive depths can extend below 400 m, with the previous depth record being 483 m reported from a submersible sighting in the Indian Ocean off Australia [15]. These scant *M. ramsayi* data suggest that the species prefers the base of the mixed layer and follows frontal systems, similar to *M. mola* in other waters; however, more data are needed to confirm these preliminary patterns.

Once thought confined to the southern hemisphere [16], *M. ramsayi* are found in numerous locations north of the equator including Oman [17] and Galapagos Islands where large aggregations (10–25 individuals) are reported at cleaning stations at 10–30 m depth [14]. In Ecuador, fishermen refer to this mola as *pez borracho* (drunken fish) due to its meandering swimming movements (*pers comm* Captain Yuri Revelo, F/V Yualca). Physical similarities between *M. ramsayi* and *M. mola* have led to its misidentification and exclusion from guidebooks in the Galapagos, Bali, and other locations. These two species however can be differentiated genetically and by close examination of physical features including their clavus fin ray number, spacing and number of ossicles in the clavus, body shape, and the structure of their scales [18–20]. All tagged individuals in the current study were identified as *M. ramsayi* from visible morphology and genetics [14].

Using satellite and ultrasonic telemetry, this study tracked movements, cleaning station behavior, temperature and depth preferences, and site fidelity of *M. ramsayi* off Punta Vicente Roca (PVR) in Galapagos. These fish are a major underwater attraction for the islands, which host an increasing number of tourists each year, from 2,000 in the 1960s to 225,000 in 2015—6 per cent of which visit PVR [21]. Tagging data, coupled with sightings and predation records gathered from ships of opportunity and observations from a submersible provide the first detailed behavioral information for *M. ramsayi* in the Eastern Pacific. This baseline information is essential for comparisons between equatorial Eastern Pacific populations and populations worldwide and is vital for the informed management of this species in the protected waters of the Galapagos Marine Reserve.

2. Materials and Methods

2.1. Site Selection. Sightings of ocean sunfish, also referred to as mola, have been recorded at PVR by the National Geographic/Lindblad Expeditions staff members and their guests since 1999. Based on these reports and anecdotal reports from commercial dive operators, PVR was selected as the study site and two receivers were installed in the site (Figure 1(a)). The PVR receivers expand an existing regional array maintained by the MigraMar network (https://www.migramar.org) (Figure 1(b)).

2.2. Fish Handling and Tagging. On 26 September 2011, 7 tags were deployed on 5 *M. ramsayi* at Punta Vicente Roca (0.055, −91.56) between 10:30 a.m. and 16:45 p.m. local time

TABLE 1: Summary for tags deployed on Sep 26, 2011.

PVR tag deployment	MR1	MR2	MR3	MR4	MR5
Vemco Id	31739	31737	31738	31740	31741
Total length (cm)	135	98	149	142	154
Time local	10:30	13:55	14:48	15:50	16:45
MK10F ID	11A0491	11A0492			
PTT	110731	110732			
Tag off	Nov 19, 2011	*Oct 1, 2011			
Distance km	2740 km	—			

*Final report date.

(Table 1). Tagged individuals were genetically identified as *M. ramsayi* in a separate study [14]. Fish were spotted from a 4 m inflatable boat. Once within range, three snorkelers entered the water, circled the fish, brought it to the side of the vessel, assessed it for health, and measured total length to the nearest cm. If free of visible health issues and no visible parasite load, a 2 cm incision was made at the base of the fish's dorsal fin and an ultrasonic tag (V16-6H coded transmitter, 60–120 second random delay, estimated battery life 1952 d, 34 g in air, power output 158 dB, Vemco, Halifax, NS) was attached externally via an umbrella-shaped nylon anchor. Two individuals were additionally tagged with Fastloc GPS satellite tags (Wildlife Computers, Redmond, WA). These tags were placed at the base of the dorsal fin on the opposite side of the ultrasonic tag and attached via titanium darts and two lengths of leaders: 70 cm of 300 lb. monofilament for tag 0491 (PTT 110731), and 1.2 m stainless steel cable for tag 0492 (PTT 110732). Pectoral fin clippings (1 cm^2) were taken, preserved in 90% ethanol, and analyzed later genetically. Handling of live animals was under 5 minutes and no animals were sacrificed or collected. All handling was carried out under UC Davis IACUC Protocol 16022.

Wildlife Computers Fastloc GPS tags provided up to four positions per day, with no duty cycling. Depth and temperature histograms were calculated on board in 6-hour time bins for transmission to Argos.

2.3. Estimating Geopositions. Geopositions for fish MR1 were estimated from both its satellite and acoustic tags. The satellite tag provided both Argos positions as well as light and temperature data for use in geolocation. No GPS positions were received from the satellite tag. The acoustic tag provided positions when the fish was near fixed receivers. Acoustic positions are accurate to the detection distance of Vemco receivers, which is site and condition specific, and typically on the order of a few hundred meters [22]. Argos positions have errors on the order of 10 km or better [23]. Light and SST geolocations typically have errors of approximately one degree for longitude, and up to 3 degrees for latitude [24]. Where multiple methods provided positions for a given time, we selected acoustic and Argos positions over light geolocation positions, since light geolocations have much greater
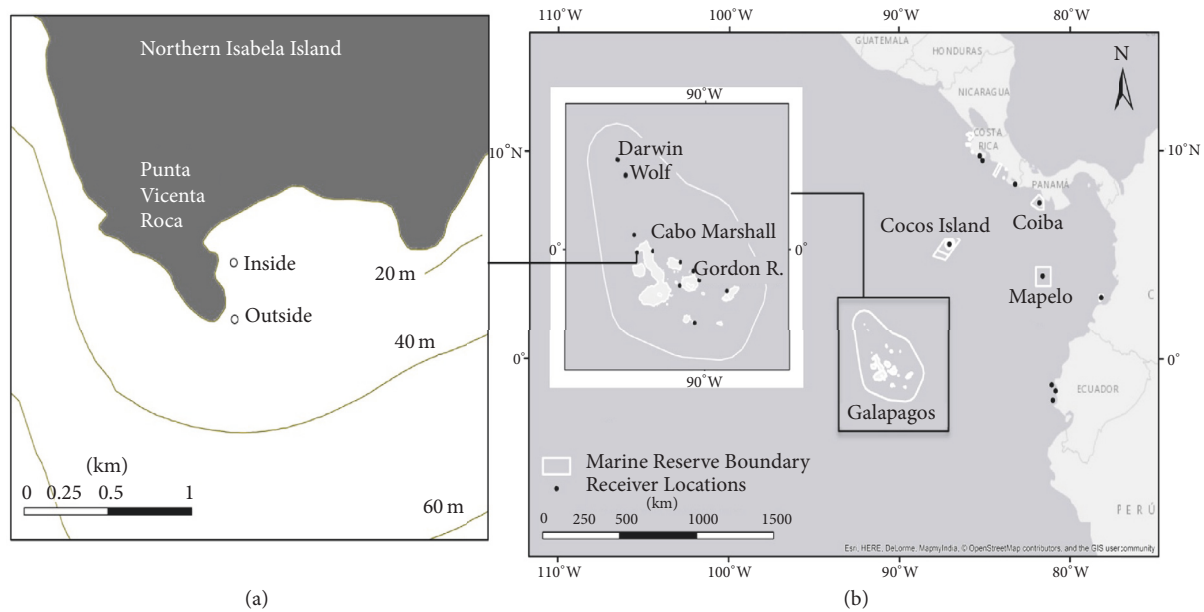
FIGURE 1: (a) Study site at Punta Vicente Roca, Galapagos, Ecuador. Open circles are the two receivers installed inside and outside the bay at PVR. (b) Black dots indicate receivers in Galapagos and the greater Eastern Tropical Pacific region from Mexico to southern Ecuador. Regional marine protected areas are shown in white outlines.

error. Light geolocation was conducted using the open source R package Trackit [24]. Transmitted data were recovered from Argos and processed using Wildlife Computers software (DAP and GPE). Geoposition estimates from GPE were not used; instead, the light data from the tag were used in the Trackit package, with 95% confidence intervals computed for each position estimate [24–27].

2.4. Characterizing Thermal Habitat. Depth-temperature profile (PDT) data summaries from the Fastloc GPS tags were transmitted to Argos satellites. These data were used to construct a thermal cross section of the water column along the track of the animal using MATLAB (The Mathworks, MA, USA). Time at depth and time at temperature data were also summarized in 6-hour bins by the tags and used to characterize the temperatures and depths occupied by individuals along their tracks.

2.5. Ultrasonic Station Installment, Specifications, and Data Analysis. Two VR2W (Vemco, Halifax, NS) receivers were deployed at PVR. Each receiver was moored to a 25 kg concrete base on a 3 m buoyed rope. One receiver was placed at 30 m depth, at the point of PVR, facing out into the ocean, while the second receiver was placed inside the bay, at approximately 25 m depth on a short, flat rocky outcrop from a vertical wall (Figure 1(a)). Data were downloaded every 6–9 months and added to a regional database of detections from a large existing array of receivers: 9 around the central Archipelago, 9 at the northern islands of Darwin and Wolf, and approximately 30 more at other oceanic islands (Cocos, Malpelo) and along the coasts of Colombia, Panama, Costa Rica, and Ecuador (Figure 1).

The range for other receivers placed in similar locations around Galapagos (on rocky reefs at 30 m depth, close to steep drop-offs) has been estimated to be approximately 150 m [28]. With this range, *M. ramsayi* swimming past the receiver on the outside of the PVR study site would be detected. Assuming an average swimming speed of $1 \, \text{m s}^{-1}$ and a random pulse interval of 60–120 seconds for each tag, we defined the start of a new visit to the site as a detection occurring 5 minutes or longer after the previous detection. Visit length was then calculated from the time of the first to the last detection in a sequence of detections where the interval between individual detections was less than 5 minutes. Visit durations were tested for normality using the Shapiro-Wilk test and behavior between individuals was compared using a Kruskal-Wallis test.

2.6. Oceanography. To examine relationships between the single long individual track and sea surface temperature (SST), we obtained combined microwave-infrared maps from Remote Sensing Systems, which integrate the advantages of microwave through-cloud capabilities and higher spatial resolution from infrared sensing (http://www.remss.com/measurements/sea-surface-temperature). Mean SST for the tracking period was computed to illustrate the distributions of upwelled water and associated thermal fronts in relation to residence and movement patterns defined by the animal track. Relatively large errors in track geoposition data precluded examination of relationships between residence and small-scale features observed at high spatial resolution.

2.7. Sightings and Cleaning Behavior. To evaluate the monthly pattern of sightings, wildlife checklists were acquired from
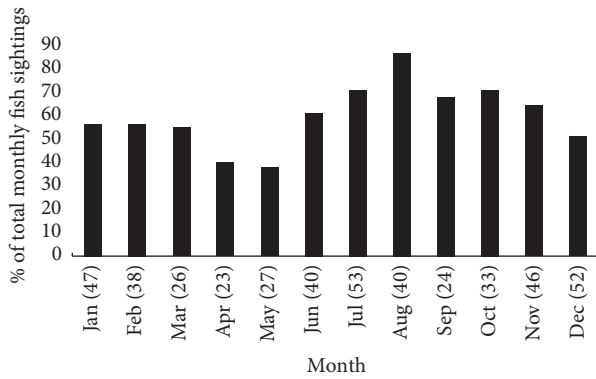
FIGURE 2: Percentage of total monthly fish sightings indicating presence of mola at PVR compiled from lists recorded aboard the National Geographic M/V Endeavor, Islander, and Polaris tourist vessels between January 2007 and January 2016. The number of available lists is in parentheses next to each month.

trained naturalist staff aboard the National Geographic Lindblad ships: M/V Polaris (January 2007–January 2009); M/V Endeavor (June 2009–November 2015); and M/V Islander (January 2009–February 2016). These tourist vessels visit PVR 3-4 times monthly throughout the year and are dry docked for several weeks in September. Given that the ship naturalists noted the presence or absence of mola and not quantities of individuals, we evaluated monthly sightings as the percentage of times mola were recorded in the wildlife checklists. Sharp-tailed mola, *M. lanceolatus*, rarely seen in Galapagos [29], is easily distinguishable from *M. mola* and *M. ramsayi*. Distinguishing between *M. mola* and *M. ramsayi* however is more challenging and requires closer morphological observation and ideally genetic confirmation. No solid evidence yet exists to confirm the occurrence of *M. mola* in Galapagos. Note that if *M. mola* do cooccur, the sightings list may mask seasonal differences in these two species.

To identify cleaning behavior and identify cleaner species, we conducted underwater visual surveys using SCUBA (26 and 27 September 2011) and complemented this information with video footage taken from M/V Alucia's Triton 3300 submersible on 17 July 2015, 11 September 2015, and 5 September 2016.

3. Results and Discussion

3.1. Seasonality. A total of 448 wildlife checklists were examined with 269 of them listing the presence of mola at PVR. Note that these mola could be either *M. ramsayi* or *M. mola*. Since genetic confirmation was not possible from brief surface sightings, they are referred to simply as mola. This time-series of monthly sighting data (January 2007–January 2016) shows that mola are spotted year-round (Figure 2) and the percentage of visits to PVR ranged from a low of 37% in May to a high of 85% in August.

3.2. Observations of Mola at Reef Cleaning Stations

3.2.1. SCUBA. Four 30-minute SCUBA dives between 26 September and 28 September 2011 resulted in 20 min of

sunfish observation. Upon approaching the reef, groups of 1–10 *M. ramsayi* were observed at approximately 20–30 m (Figures 3(a)–3(c)). Individuals typically assumed a head-up position, after which reef fishes moved towards them and began foraging on external parasites. Reef fish involved in cleaning included female *Bodianus diplotaenia* (Mexican hogfish) and *Holacanthus passer* (king angelfish).

3.3. Submersible Sightings. Submersible dives at PVR on 17 July 2015, 11 September 2015, and 5 September 2016 (4 dives, total time approx. 10 hours) resulted in approximately 45 minutes of *M. ramsayi* observations between 30 m and 120 m. On 17 July 2015, 12 individual *M. ramsayi* (1.5–2 m TL) were observed soliciting and receiving cleaning from juvenile Mexican hogfish, *B. diplotaenia,* at 30 m. On 11 September 2015, 6 individuals (1.5–2 m TL) were observed between 80 and 120 m being cleaned by schools of *B. diplotaenia* and by an ocean whitefish, *C. affinis* (Figure 3(d)). Surface water temperature was 24°C and 20°C at 100 m, warmer than the typical average due to El Niño conditions. Outside of El Niño years, average temperatures are 21°C at the surface and 14-15°C at 100 m [30]. On 5 September 2016, two subdives, totaling 183 min, revealed 3 *M. ramsayi* (1.5–2 m TL) being cleaned by juvenile *B. diplotaenia* between 48 m and 85 m (14–16°C) for approximately 10 min and 2 other *M. ramsayi* being cleaned between 30 m and 50 m for approximately 3 minutes. This second cleaning session was interrupted by the presence of 3 Galapagos sea lions. Areas of cleaning included around the eye, head, operculum, vent, trailing edge of the anal fins, keel, and clavus (Figure 3(d)).

3.4. Long Distance Movements and Associated Diving Behavior. Tag 110731 on MR1 reported for a total of 53 days and was released prematurely where it continued to float on the sea surface with no diving for an additional 10 days before its battery was presumably depleted. This fish travelled 2740 km west-northwest (Figure 4). The second Fastloc satellite tag, 110732, deployed on MR2, reported for one week and then fell silent. This tag presumably was not released prematurely as it would have signaled from the surface. With only a week into deployment, battery failure is also unlikely. The ultrasonic tag on MR2 (a VEMCO V16-6H, depth-rated to 680 m) continued to function indicating the fish remained in the PVR vicinity, did not die, and likely did not dive past the 2000 m depth rating of the Fastloc tag. Two possible causes of malfunction may have been problems with the salt-water switch or antennae breakage, as suggested by other tag users [31].

MR1 was tracked for 50 days between 27 September 2011 and 16 November 2011 (Figure 4(a)). Following tag deployment, the individual remained near PVR through October and then moved westward more than 1000 km along the equatorial upwelling front (Figures 4(a) and 4(b)). Subsurface temperature data from the tag describes two distinct periods during which environmental conditions and diving behavior exhibited corresponding differences (Figure 4(c)). Prior to the westward movement, dives were constrained to the depth range between the surface and 400 m and the temperature range of 9.2°C to 22°C (Figures 4(b) and 4(c)). Contrary to
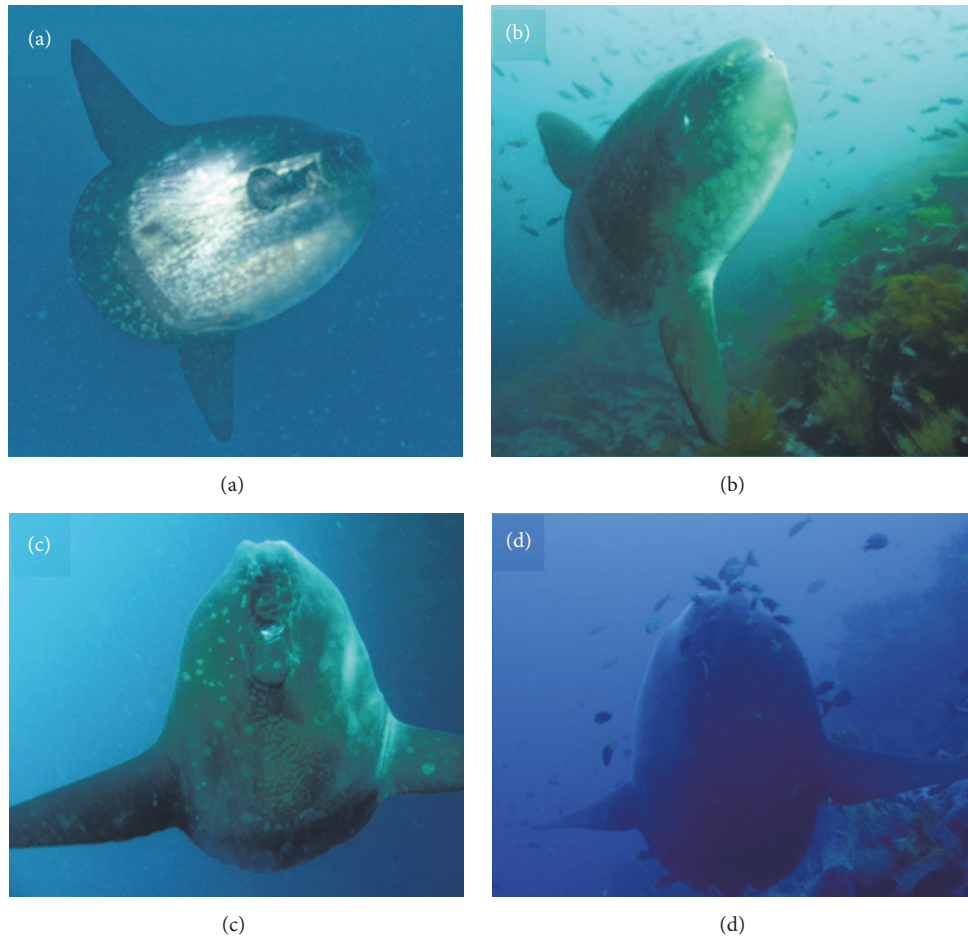
(a)

(b)

(c)

(d)

FIGURE 3: *M. ramsayi* at reef cleaning station, Punta Vicente Roca, Galapagos, Ecuador. (a) Individual approaching the reef from the pelagic environment. (b) Individual moving towards the reef and turning to a head-up position. (c) Individual in head-up position. Photos in (a), (b), and (c): K. Weng. (d) Individual being cleaned by juvenile Mexican hogfish *B. diplotaenia* and a single ocean whitefish, *Caulolatilus affinis*. Photo: frame grab from video footage taken aboard M/V Alucia's Triton 3300 submersible piloted by Mark Taylor, 11 September 2015.

this, several occasional dives extended much deeper (down to 1112 m) and within the temperature range 4.5°C to 23.2°C during the westward movement (Figures 4(b) and 4(c)). In addition to the record setting 1112 m dive, 7 dives extended deeper than 800 m on 4 of the 15 days during which westward movement was tracked. This deeper diving corresponded with a water column characterized by warmer maximum surface temperatures (>1°C) and a much thicker warm mixed layer (Figure 4(c)).

3.5. Ultrasonic Data and Site Fidelity. The receiver inside PVR was removed in September 2012, while the receiver outside PVR continued until September 2013. The PVR receivers recorded the presence of all individuals except MR5 (TL 154 cm), the largest of the tagged individuals. Overall tracking duration ranged from 32 d (MR1, which subsequently moved west as described above) to 733 d (MR4). The 4 molas were detected for a total of 3557 times, 48% of which occurred during daytime hours while 52% occurred after dark (Table 2). No diel behavior pattern was observed.

TABLE 2: Summary of acoustic detection for 4 *M. ramsayi* individuals detected at PVR.

	MR1	MR2	MR3	MR4
Track duration (d)	32	378	202	733
Total detections	128	1361	799	1269
% daytime	53	68	31	37
Total visits	21	191	92	243
# single detection visits (~1 min)	9	66	25	45
# visits < 5 min	3	32	14	112
# visits > 5 min	9	93	53	90
Sum of residency (>5 min visits)	221	2081	1289	1760
% time spent at PVR	0.48	0.38	0.44	0.17
Median length of visit (min)	15	15	14	14
Longest visit (min)	89.7	80.2	99.8	76.1

Site fidelity, defined as the number of days an individual was detected at least once at PVR, is expressed as a percentage of the total tracking duration. All 4 individuals had similar
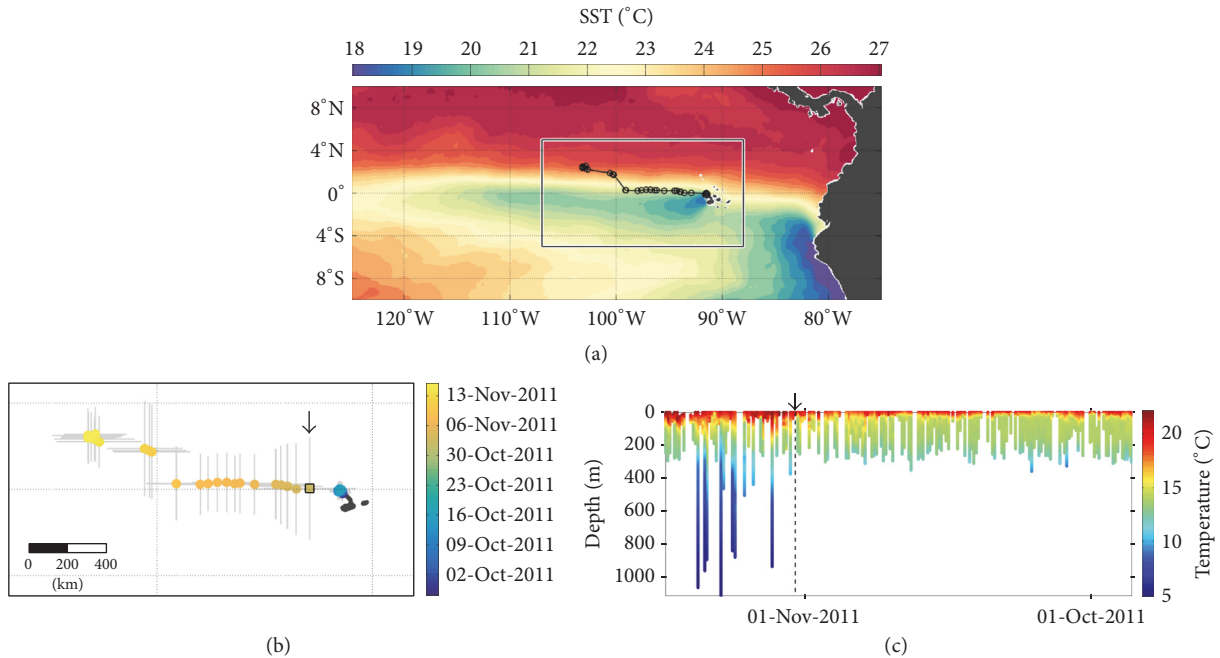
FIGURE 4: Spatial occupancy and diving behavior of MR1 (tag 110731). (a) Average sea surface temperature (SST) during the tracking period, with the track overlaid in black. (b) Track timing (color) and 95% confidence interval of positions (gray lines) are represented for the inset region of (a). The black square identifies the start of the westward migration along the equatorial upwelling front. (c) Temperature profiles along the track; time progresses from right to left for consistency with (b), and the vertical dashed line marks the time of the position marked by the black square in (b).

site fidelity (10–15%); however, MR1 was only detected over two 48-hour periods, on October 7-8 and later on October 27-28. The 3 molas that did not move away (MR2, MR3, and MR4) remained close to PVR until April 2012, at which point all 3 left the site (Figure 5). Two of the individuals (MR2 and MR4) returned to PVR after a two-month absence. MR2 continued at the site until the track ended in October 2012, while MR4 left the site again during the same period of the following year, returning again in June and continuing at PVR until the receiver was removed in September 2013. Overall, absences (time elapsed between visits) ranged from 5 minutes to 78 days, but 77% of absences from the site were less than a day, with only 5% of absences of two weeks and greater, and only 1.8% greater than 30 days. Three of the longest absences occurred in the months of April–June: MR4 was absent for 59 and 54 days, respectively, in June 2012 and 2013, while MR2 had been absent for 67 days when it returned to the site on 27 June 2012.

Visit lengths were nonnormally distributed and varied between individuals (Kruskal-Wallis Chi-sq = 9.6089, df = 3, p = 0.0222, Figure 6), although median length of visits (excluding single detections) was remarkably consistent among each individual (14-15 minutes). Visits ranged from a few minutes to 99.8 minutes (MR3), while the cumulative time spent at the site in relation to the entire track period ranged from 0.17% to 0.48% (Table 2).

3.6. Beyond PVR. No tagged individuals were detected at any of the other 18 listening stations located throughout Galapagos including Darwin, Wolf, Cabo Marshall, and Gordon
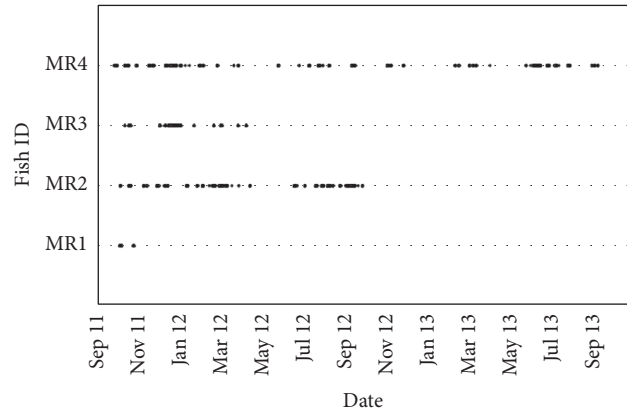

FIGURE 5: Daily detection of *M. ramsayi* at PVR from 11 September 2011 to 13 September 2012.

Rocks (Figure 1(b)). No detection was recorded in any other ultrasonic arrays run by Migramar—a regional project aimed at understanding the migratory dynamics of large pelagics (https://www.migramar.com) within the Tropical Eastern Pacific Seascape (Figure 1(b)). No sightings of any ocean sun-fish species were recorded at any other Galapagos site aside from PVR by the National Geographic/Lindblad vessels. Ocean sunfish however have been sighted at Cabo Douglas on the northwestern point of Fernandina Island (*GMR, Pelagic surveys*; Hearn A/CDF-UCD-DPNG, *unpublished data*), Punta Albemarle on the north tip of Isabela during the months of September-December (Thys *pers obs*), and Kicker
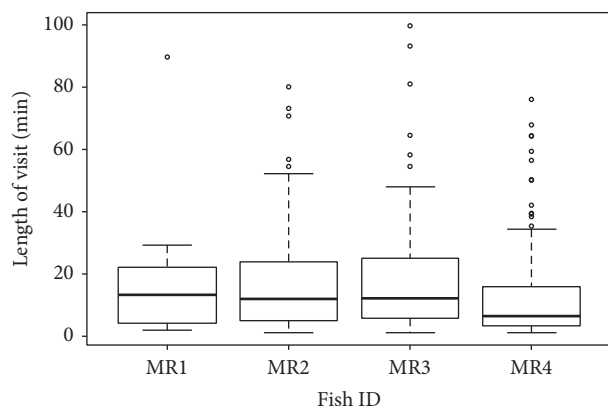
FIGURE 6: Length of *M. ramsayi* visits to PVR by each individual. Boxplots show medians and interquartile range, with whiskers denoting upper and lower quartiles. Open circles denote outliers. Note that single detections were removed from the analysis on the assumption that these corresponded to fish passing through the range of the receivers.

Rock off the NW corner of San Cristobal in March (K. Khoo, *pers comm*). Since 2013, molas are increasingly being reported by recreational dive operators off North Seymour Island and at Gordon Rocks, a dive site off the east coast of Santa Cruz Island (Figure 1(b), Scuba Iguana Galapagos Dive Center *pers comm*).

3.7. Past Studies. To date, the only published study on the ecology of *M. ramsayi* comes from 4 individuals fitted with satellite tags and tracked in Bali, Indonesia [14]. Although one of those tags placed on *M. ramsayi* detached 188 days later, only 8.4 km away from the original tagging location, no locations during the deployment period were estimated so the degree of site fidelity remains unquantified.

More comprehensive spatial ecology data come from tagging studies conducted on common mola, *M. mola*, using pop-up satellite archival tags and Fastloc GPS tags in the Eastern Pacific off California [6] and Eastern Atlantic off the UK and Europe [8, 32, 33]. These studies report that *M. mola* engage in latitudinal movements correlated with seasonal changes in temperature and productivity linked with favorable thermal conditions (10–20°C), foraging areas, and frontal systems. Vertical migrations feature a diel pattern with individuals occurring deeper during the day engaging in repeated dives to 150–200 m and remaining shallower at night [6, 9]. Off the coast of South Africa, *M. mola* demonstrate prolonged residence and less latitudinal migration presumably due to the region's abundant year-round food supply [10].

Less is known about other Molidae species, for example, sharp-tailed mola, *M. lanceolatus,* which do not appear to surface-bask regularly, preferring depths below 200 m [34]. No behavioral studies have been published for *R. laevis*. The current study provides the first evidence of consistent site fidelity for *M. ramsayi* and suggests a seasonal absence in the months of April-May.

3.8. Cleaning Stations. Data from ultrasonic tracking and underwater visual survey data suggest PVR is a year-round cleaning station for *M. ramsayi*. The shallow protected reefs and close proximity to deep (>2000 m) productive waters appear to provide favorable conditions as a safe haven and cleaning station. Cleaner fish species include predominately juvenile hogfish *(B. diplotaenia)* followed by king angel *(H. passer)*. In July 2015, ocean whitefish, *C. affinis,* was also observed acting as a cleaner. To the best of our knowledge, this is the first time this species has been observed acting as a cleaner. In other regions of the world, for example, Bali, Indonesia, *M. ramsayi* can attract atypical cleaner species presumably due to their plentiful parasite load [35]. While *M. ramsayi* are occasionally sighted at other sites in Galapagos, for example, Gordon Rocks and Kicker Rock, both in the central Archipelago, compiled sightings from commercial dive operators, tourists, and citizen scientists indicate PVR as the most important and consistent hotspot for mola throughout the Galapagos Archipelago, with sightings peaking in July–November (Figure 2). (Note that past sightings lists identify the mola species as *M. mola;* however, to date, the only genetically verified species of the *Mola* genus in the Galapagos is *M. ramsayi,* which is easily mistaken for *M. mola.)*

Observations of any Molidae cleaning stations are rare and the present study provides the first such observations in Galapagos and the Humboldt Current system. The importance of cleaning stations to the overall health of reef animals and reef systems is well documented [36–39]. Having access to such stations may be crucial for the proper growth of individual client fish. For example, a cleaner fish exclusion study on Lizard Island in the Great Barrier Reef, Australia, found that the removal of one species of cleaner, *Labroides dimidiatus,* led to a 37% decrease in remaining client fish sizes [40]. Establishing a baseline of understanding and quantifying the role of megafaunal cleaning stations is a useful component in the assessment of ecosystem health in this protected region.

3.9. Horizontal Movements. Satellite tag data for a single individual (MR1) reveals that, approximately 5 weeks following tagging, this fish travelled westward along the equatorial front at an average speed of approximately 50 km/day. This travel speed is much faster than speeds reported in other regions of the Eastern Pacific for *M. mola*, the only Molidae for which travel speed data exist, for example, 20–27 km/day in the California Current [6]. This individual however was in the region of the westward flowing equatorial currents, which likely increased the rate of westward movement. Planktivorous whale sharks *(Rhincodon typus)* tracked from Galapagos display a similar behavior by associating with the equatorial front at certain times of year and moving at higher rates than displayed elsewhere [41].

After beginning westward movement in early November 2011, the individual exhibited deeper diving behavior to 1112 m—the deepest recorded depth for a Molidae species. This behavior is presumably related to foraging. Additional tagging with a camera [42] and or submersible coupled with sampling could lend further insight into foraging habits.

Diet studies on a close relative, *M. mola,* indicate small individuals (<50 cm) feed on benthic crustaceans and other neritic prey, while larger individuals (>200 cm) focus more on gelatinous zooplankton [43]. Individuals in this study were

between 98 and 154 cm TL. Tracking data on *M. ramsayi* off Bali Indonesia indicate that this species may seek out upwelling fronts, similar to behavior displayed by *M. mola*, in the California Current [6] and eastern Atlantic [8]. Our data presented here suggest a similar pattern in Galapagos.

3.10. Limitations of Study and Future Work. Additional tagging, with both ultrasonic and high resolution Fastloc GPS satellite tags, will lend further insight into these preliminary findings and allow for greater correlation of behaviors with oceanographic features. Exploring the genomics of this population could also lend insight into differentiating between *M. ramsayi* and its morphologically similar relative *M. mola* and determine if *M. mola* occurs in Galapagos. Comparative genetics with other mola populations abroad could also reveal biogeographic origins and linkages to mola bycatch reported from Peruvian fisheries [44] while stable isotope analyses could provide useful information on diet preferences [43].

Another potentially fruitful investigation would be comparing large *M. ramsayi* (>200 cm) with other large gelativores, namely, leatherback sea turtles, *Dermochelys coriacea*. Migration studies have revealed markedly different foraging behaviors and recovery rates for Pacific and Atlantic leatherback populations with Pacific populations faring worse than those in the Atlantic. These differences suggest measurable differences in the availability of gelatinous prey between ocean basins, at least at the times of the studies. Such differences could also affect large molas and influence movements [45].

Comparative parasitology may also yield insight between predators and prey since numerous parasites require multiple hosts to complete their lifecycles. A variety of monogenes, digenes, cestodes, copepods, and trematodes have been documented on *M. ramsayi* in Peruvian and Chilean waters [46, 47]. How these assemblages differ between locations and the role cleaners play in governing these assemblages are unknown. We did note however an apparent lack of visible external parasites on the Galapagos mola, especially in comparison with the high parasite loads of *M. mola* in the California Current system [T. Thys *pers obs*].

Investigation and quantification of predation pressures and overall population size are also recommended. The western region of the Galapagos Islands is characterized by cool, productive upwelling waters, which likely provide a food source for much of the year. This, combined with the availability of the cleaning station at PVR, may explain the long-term residency found in this study. Seasonal aerial surveys could offer insight into population size and predation events. *M. ramsayi* here are harassed by Galapagos sea lions and occasionally eaten by orcas. Six orca predation events were reported between 2005 and 2016 (Judith Denkinger, *pers comm*) with at least one witnessed by the tourist vessel M/V Polaris on 23 August 2005. This sighting indicated a pod of 7 orcas, 2 adults and 5 juveniles, which attacked a mola (approx. 2 m TL) at PVR. The pod repeatedly brought the fish to the surface. One adult orca first appeared to be using the mola as a prey-capture teaching tool for an accompanying juvenile orca before the mola was eventually eaten. Further work on the interactions between food availability, cleaning services,

and potential threats may help further elucidate movement patterns.

4. Conclusions

The current study provides the first and most comprehensive behavioral data for *M. ramsayi* in the Eastern Tropical Pacific and offers a foundation for more in-depth investigations of this species worldwide. Additionally, it highlights the importance of the Galapagos Marine Reserve for wide-ranging pelagic species. While the value of the reserve for the protection of coastal marine and terrestrial species is well documented (e.g., [48, 49]), its contribution towards the conservation of migratory marine species within a regional context is less understood and is the focus of current research efforts [50].

Conflicts of Interest

The authors declare that there are no conflicts of interest regarding the publication of this paper.
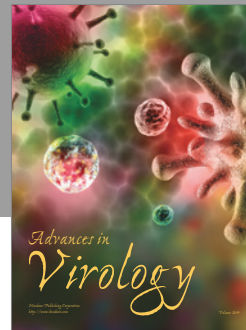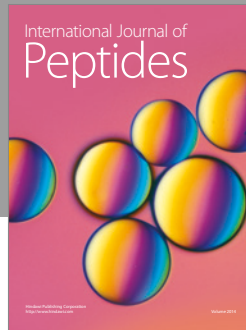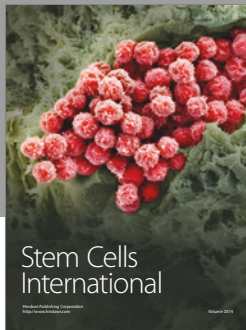
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