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Research Article

Tracking a Marine Ecotourism Star: Movements of the Short Ocean Sunfish *Mola ramsayi* in Nusa Penida, Bali, Indonesia

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Ocean sunfishes, Molidae, comprise the world's heaviest bony fishes. They include the short mola, *Mola ramsayi* (Giglioli 1883), an important tourist draw at Nusa Penida and Nusa Lembongan, Bali, where SCUBA divers can observe ectoparasite-laden individuals being cleaned by smaller reef fishes. Despite widespread appeal, little is known about these fishes relative to regional oceanography. We present the first behavioral information for this species anywhere in the world. Satellite tag data indicate a wide thermal range (10–27.5°C) with depth occupation mostly (95%) in the upper 250 m and habitat preference near the bottom of the warm surface layer. One tag popped off as scheduled after 6 months off Nusa Penida, <10 km from its original deployment. The 3 other tags popped off prematurely: 747 km southeast 89 days after deployment; 142 km south after 7 days of deployment; and 162 km south after 24 days of deployment. Amid mounting tourist pressures and bycatch of *M. ramsayi* in eastern regions of Indonesia, such as Alor, behavioral information of this species is essential for effective management and conservation of this valuable marine ecotourism asset.

1. Introduction

Coral reefs in and around the islands of Nusa Lembongan and Nusa Penida in Bali, Indonesia, support a thriving tourism industry with more than 200,000 tourists visiting each year [1]. From approximately June through October, Bali's south coast has strong seasonal upwelling (Figure 1) driven by winds associated with the southeast monsoon [2]. These seasonal cool currents run in close proximity to warmer waters hosting a diversity of tropical fishes (e.g., butterfly fish *Heniochus diphreutes*, *Chaetodon kleinii*; angelfish *Pomacanthus imperator*; and wrasses *Labroides dimidiatus*, *Thalassoma lunare*). SCUBA divers are attracted to this region (Figure 2(a)) to observe these smaller fishes removing ectoparasites from megafauna such as mantas *Manta birostris* (Walbaum 1792) and short ocean sunfish, *Mola ramsayi* (Giglioli 1883) [3, 4].

Little is known about the long-term movements or behavior of any species of ocean sunfish in Bali or the potentially disruptive effects of the region's growing dive tourism pressures. A 2015 survey conducted by researchers from Udayana University, Conservation International, and Oceans Initiative off Bali's southern coast from 30 Oct to 5 Nov estimates the ocean sunfish population to be 204 individuals in a survey region of 1393 km², which translates to a mean density of 1 individual per 6.8 km^{-2} (Rob Williams *pers comm*). Aside from a brief submersible encounter with *M. ramsayi* at 483 m in the Indian ocean in December 2005 [5], the present study provides the first behavioral data on *M. ramsayi* movements and diving behavior anywhere in the world using satellite telemetry, an effective technique for studying other ocean sunfish populations in California [6] and elsewhere globally (as reviewed in Pope et al. [7]).

2. Materials and Methods

In September 2004 and October 2008, 4 pop-up satellite tags (2 PAT-4 tags in 2004 and 2 MK-10 PAT tags in

Fish	Tag ID PTT	Deploy date	Pop-off date	SST (°C) Deploy depth (m)	Deploy Latitude Longitude	Pop-off Latitude Longitude	LC	TL cm	Days Dist. (km)*
А	04P0144 52918	Sep 15, 2004	Oct 9, 2004	24° 25	-8.71 115.44	-9.599 114.286	2	150	24 162
В	04P0158 52943	Oct 6, 2004	Oct 13, 2004	23° 26	8.71 115.45	-9.989 115.627	1	135	7 142
С	08A076 89297	Oct 9, 2008	Apr 15, 2009	22° 25	8.66 115.44	-8.674 115.533	3	100	188 8.4
D	08A078 89298	Oct 11, 2008	Jan 8, 2009	26° 20	8.71 115.45	-10.581 121.973	3	100	89 747

TABLE 1: Tag deployment summary. * Straight line distance between deployment and pop-off locations. PTT is platform terminal transmitter, LC is location code, TL is total length, and SST is sea surface temperature.

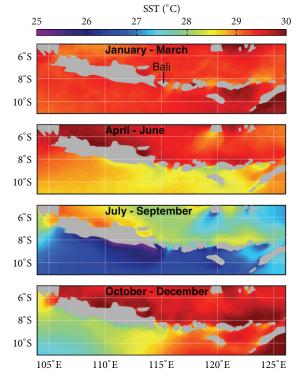


FIGURE 1: Seasonal sea surface temperature (SST) climatology of the region showing lower temperatures in the second half of the year when *M. ramsayi* reports are the highest (M. Erdmann and S. Fautz *pers comm*).

2008) were deployed on 4 *M. ramsayi* off Nusa Lembongan (Figure 3). Individuals were identified as *M. ramsayi* based on morphological observation of ossicles in the clavus that differ in number and spacing from those of the similar species the common ocean sunfish, *Mola mola* [8]. Tags had 10 cm long monofilament tethers and plastic darts and were programmed to record temperature, depth, and light intensity every 2 minutes and pop off from the animals after 6 months. Tagging was accomplished by a SCUBA diver who approached the fish during a cleaning session at 20 to 26 m depth and inserted the dart at the dorsal fin base using a modified pneumatic spear gun (Figure 2(b)).

Deployment locations were recorded with hand-held GPS units and pop-off release data were based on Argos satellite data with location classes 1–3 with reported error fields <1.5 km (anonymous, 2008; Argos User Manual; Service Argos, Inc., Largo, MD 20774).

Vertical data were analyzed using transmitted time at depth (TAD) and time at temperature (TAT) histograms and profiles of depth and temperature (PDT) data summarized at 12-hour intervals. The thermal habitat was characterized by creating a cross section of the water column traversed by the fish, while the habitat preferences were characterized by the amount of time spent in a range of depth and temperature bins. Analyses were performed in MatLab (The MathWorks, Inc., Natick, MA, USA).

To examine oceanographic variability in the greater region surrounding Bali, we examined satellite sea surface temperature (SST) data on 2 time scales: (1) a climatology based on 12 years (2004–2015) of data, binned to 3-month seasonal means, and (2) a single average for September-October 2004, when 2 tag deployments successfully returned water column data. Original SST data for these analyses were global monthly means of Advanced Very High Resolution Radiometer (AVHRR) data (http://coastwatch.pfeg.noaa.gov/erddap).

3. Results and Discussion

In 2004, Tag 52918 on Fish A popped off prematurely after 24 days of deployment and Tag 52943 on Fish B popped off after 7 days. Both tags provided pop-off locations roughly 150 km south of the deployment location in Nusa Penida. In 2008, Tag 89297 on Fish C popped off as scheduled after 188 days and surfaced less than 10 km from its initial deployment location, while Tag 89298 on Fish D popped off prematurely after 89 days, surfacing 747 km to the east. Both 2008 tags provided pop-off locations, but too little temperature and depth data to analyze (Table 1; Figure 3).

3.1. Horizontal Movements. Three of the four tags popped off in relatively close proximity to the deployment location on Nusa Penida (Figure 3). In 2004, the southerly release points of Tag 52918 (Fish A) and Tag 52943 (Fish B) suggest that, following cleaning, *M. ramsayi* move south into deeper waters near the periphery of upwelling influence (Figure 4).

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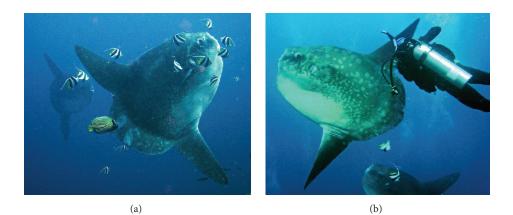
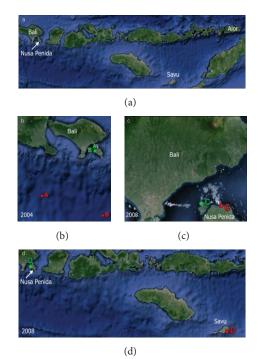
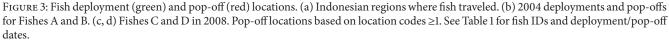


FIGURE 2: (a) 1 m TL Mola ramsayi being cleaned 25–30 m, Nusa Penida, Bali. (b) Diver, Brett Hobson, inserting satellite tag into Mola ramsayi, Crystal Bay, Nusa Penida, Bali, 11 October 2008. Photo: Sven Fautz.





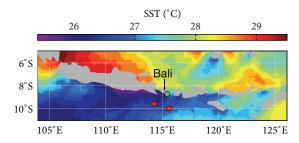


FIGURE 4: Sea surface temperature (SST) during September-October 2004, coincident with tagging period. Deployment (green) and pop-off (red) locations for Fishes A and B.

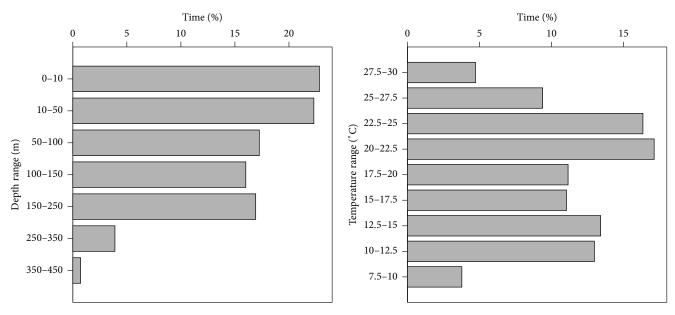


FIGURE 5: Summaries of depth and temperature range occupation based on all 2004 data from Fish A and Fish B.

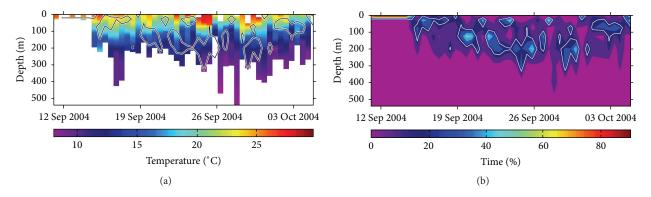


FIGURE 6: Depth occupation in relation to water column thermal structure for 2004 data from Fish A, tag 52918. (a) Thermal cross section of water column traversed by fish; each vertical bar represents a 12 hr time period, extending to the deepest point reached during the period and color-coded by temperature. Black contours define corresponding time at depth (TAD) >25%. (b) Corresponding TAD section.

These release points coincided with locally enhanced gradients along the inshore and offshore boundaries of a thermally homogeneous water mass, which suggests that these individuals were associating with offshore fronts. Studies in the California Current upwelling system have indicated that fronts in the upwelling periphery zone provide favorable foraging habitat for another species of ocean sunfish, the common mola, *M. mola* [6].

In 2008, Tag 89297 (Fish C) popped off on the north side of Nusa Penida, less than 10 km from the original deployment location, 188 days earlier. Only one of the tags, 89298 (Fish D), revealed significant movement away from the Nusa Penida region, popping up 747 km to the east of its deployment location, near the island of Savu after an 89-day deployment. Additional long-term tagging data are required to determine the degree of long-term site fidelity to the Nusa Penida region.

3.2. Vertical Movements. Combined 2004 data from Fish A and Fish B showed that the majority of time was spent in the

upper 250 m south of Bali, ~45% in the upper 50 m and 50% between 50 and 250 m (Figure 5). Maximum depth exceeded 400 m. Individuals demonstrated a wide thermal range with relatively even occupation of the temperature range 10° to 27.5°C and even occupation, above and below the thermocline (~20°C).

Following tagging, Fish A stayed in warm, shallow (<40 m) waters during the first few days and then began much deeper dives, to 200–400 m, consistent with its movement offshore into deep water (Figure 6(a)). The rapid changes in the water column thermal structure along the deep water portion of this individual's track suggest it moved across frontal zones perhaps generated by the coastal upwelling known to occur south of Bali (Figure 4). Taken together, the TAD and PDT data indicate the fish's depth range occupation correlated with the water column thermal structure. Specifically, Fish A spent the majority of time near the bottom of the warm surface layer, the depth of which varied significantly on short time scales (Figures 6(a) and 6(b)). For example, during

24–30 September 2004, depth occupation oscillated between deep and shallow twice, in relation to corresponding water column thermal structure.

Previous observations on *M. ramsayi* in these waters by recreational SCUBA divers (above 30 m) suggest the species is most commonly sighted during spring tides of July through October, when cold-water upwelling drops sea surface temperatures (Figure 4) (M. Erdmann *pers obs*). Deeper diving (50–70 m) at Nusa Penida by one of the coauthors suggests short ocean sunfish may in fact be present year-round but inhabit deeper cooler waters (20–24°C) beyond recreational SCUBA depth limits (M. Erdmann *pers obs*). Additional long-term tagging will reveal further details of the seasonal patterns of *M. ramsayi* habitat occupation and if individuals are remaining in the vicinity of Nusa Penida outside of peak upwelling season at depths not frequented by recreational divers (Figure 1).

In comparison, *M. mola*, the only other ocean sunfish species with published behavioral data, show similar dive behaviors in the temperate and subtropical regions of the Atlantic and Pacific. *M. mola* have been recorded in temperatures as low as 1.8° C off Japan [9] and as high as 30° C off the southeastern coast of the U.S. and Bahamas [10]. Recent studies of *M. mola* habitat use in the California Current [6] and northeastern Atlantic reveal satellite tagged individuals are strongly influenced by temperature, avoiding higher temperatures ($\geq 25^{\circ}$ C) [11] and preferring frontal areas [6].

Additional site fidelity and behavioral data of *M. ram-sayi* are essential to management authorities of the Nusa Penida Marine Protected Area, who are currently developing species-specific tourism management guidelines for megafauna including the short ocean sunfish and manta ray, *Manta birostris* (Walbaum, 1792). Moreover, additional tracking data and genetic analyses will further elucidate if the short ocean sunfish caught as bycatch in shark fisheries of Alor are confluent with the populations of short ocean sunfish around Nusa Penida. If so, a strong economic argument for conservation measures to protect the species throughout Indonesia could be made given their economic value as tourism assets in Nusa Penida.

4. Conclusions

The short ocean sunfish *Mola ramsayi* off Bali attract SCUBA divers from around the world and provide a significant tourism asset for this popular Indonesian island. Pop-off satellite tags on 4 individuals revealed these individuals to have a wide thermal range $(10-27.5^{\circ}C)$ with a preferred habitat in the upper 250 m near the base of the warm surface layer. Following a 6-month deployment, the tag from one individual, Fish A, popped off at Nusa Penida (<10 km from the initial tagging location) and may be suggestive of site fidelity to this area. Tags from Fish B and Fish C popped off prematurely approximately 150 km south from their original tagging locations following a 7-day and 24-day deployment, respectively. Temperature and depth data from these tags suggest these individuals were seeking southern frontal zones

for potential foraging opportunities. Fish D's tag popped off more than 700 km east from its tagging location after 89 days and suggests that the Nusa Penida short ocean sunfish populations could be confluent with those in Alor where anecdotal reports of bycatch are on the rise. Data presented here provide the first behavioral and movement information for this species. As tourism, numbers of divers and fisheries pressures increase off Bali, behavioral information is essential for the effective management and conservation of this valuable marine ecotourism asset throughout Indonesian waters.

Competing Interests

The authors declare that they have no competing interests.

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