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Satellite tracking the world's largest jelly predator, the ocean sunfish, *Mola mola*, in the Western Pacific

H. Dewar^{a,*}, T. Thys^b, S.L.H. Teo^c, C. Farwell^d, J. O'Sullivan^d, T. Tobayama^{e,1}, M. Soichi^e, T. Nakatsubo^e, Y. Kondo^e, Y. Okada^e, D.J. Lindsay^f, G.C. Hays^g, A. Walli^h, K. Wengⁱ, J.T. Streefman^j, S.A. Karl^k

^a National Marine Fisheries Service, Southwest Fisheries Science Center, 8604 La Jolla Shores Dr., La Jolla, California 92037-1022, USA

^b Ocean Sunfish Tagging and Research Program, 25517 Hacienda Place Suite C, Carmel California, 93923, USA

^c Department of Wildlife, Fish and Conservation Biology, University of California, Davis, California 95616, USA

^d Monterey Bay Aquarium, 866 Cannery Row, Monterey, California 93940, USA

^e International Marine Biological Research Institute, Kamogawa Sea World, 1464-18 Higashi-cho, Kamogawa, Chiba 296-0041, Japan

^f Japan Agency for Marine-Earth Science and Technology (JAMSTEC), 2-15Natsushima-cho, Yokosuka, Kanagawa 237-0061, Japan

^g Institute of Environmental Sustainability, Swansea University, Swansea SA2 8PP, UK

^h GeoVille GmbH, Museumstr. 9-11, A-6020 Innsbruck, Austria

ⁱ Pelagic Fisheries Research Program, University of Hawai'i at Manoa, Hawai'i 96822 USA

^j School of Biology, Georgia Institute of Technology, Atlanta, Georgia 30332, USA

^k Hawai'i Institute of Marine Biology, University of Hawai'i, Manoa, P.O. Box 1346, Kāne`ohe, HI, 96744, USA

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ABSTRACT

Twelve ocean sunfish, *Mola mola*, were tagged with pop-up satellite archival tags off the coast of Kamogawa, Japan during the spring of 2001 and 2003–2006. Transmitted data were obtained from seven tags. An eighth tag was recovered and provided a highly detailed four-month dataset from which several recognizable diving patterns emerged. This *M. mola* spent considerable time at the surface, possibly warming itself. These apparent basking events were punctuated by regular deep dives below the thermocline to depths as great as 600 m and temperatures as low as 2 °C. The vast majority of dives occurred during the day, with relatively little vertical movement at night. Geolocation estimates were possible between tag and release for five individuals. No large, basin-scale movements were apparent with most molas remaining relatively close to their initial tagging location over a six to nine month period. Seasonal movements were apparent for some molas and corresponded to regional shifts in oceanography. Northward movements from the Kuroshio Current into the Kuroshio–Oyashio transition zone and the Oyashio Current during the summer months coincided with an increase in temperature and reduction in chlorophyll *a* concentrations in waters near central Japan. In the fall, most molas returned inshore to the coast of Japan. Molas are targeted and incidentally captured by fishermen in these waters, and the information presented here is vital for effective fisheries management and to forecast changes in mola behaviors associated with environmental variability.

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1. Introduction

Ocean sunfish [*Mola mola* (Linnaeus, 1758)] are found in all tropical and temperate ocean basins and are the world's heaviest bony fish, reaching more than 2200 kg (Carwardine, 1995; Roach, 2003). According to fossil evidence, the family Molidae diverged from their puffer fish relatives approximately 40 million years ago, abandoned life on the reef, and took to the open sea (Tyler and Bannikov, 1992; Tyler and Santini, 2002). Currently, three species are recognized (Nelson,

1994), all of which lack a true tail (Bigelow and Welsh, 1924; Fraser-Brunner, 1951; McCann, 1961): *M. mola* (common mola), *Masturus lanceolatus* (Liénard 1840) (sharp tailed mola) and *Ranzania laevis* (Pennant 1776) (slender mola). The English common name of the group, ocean sunfish, stems from the fish's characteristic behavior of lying at the sea surface, apparently basking (Norman and Fraser, 1938).

Molas forage near the base of the food web like most of the largest whales, sharks, and rays. They may consume krill and other crustaceans (Aflalo, 1904), but their primary food source appears to be a mixed assemblage of gelatinous zooplankton, referred to here as jellies (Fraser-Brunner, 1951). One of the few large pelagic organisms that share this unique trophic niche is the leatherback sea turtle, the largest of the extant marine turtles. Jellies comprise one of the most dominant yet poorly understood assemblages of pelagic fauna (Mills,

* Corresponding author.

E-mail address: Heidi.Dewar@noaa.gov (H. Dewar).

¹ Deceased.

1995; Mills, 2001), and their global abundance and distribution may be changing due to a number of factors including climate change, pollution, and overfishing, (Brodeur et al., 1999; Purcell et al., 2007; Richardson et al., 2009). In turn, the changes in the abundance and distribution of jellies may be impacting the organisms that rely on them, such as the mola.

While general distribution patterns are known, information on the movements of *M. mola* is based on relatively few studies. In 2004, Cartamil and Lowe (2004) reported on the horizontal and vertical movements of eight acoustically tracked molas off Southern California for periods ranging from 24 to 72 h. More recently, Hays et al. (2009) published a study comparing the geographical movements and vertical tracks of four *M. mola* to those of leatherback sea turtles (*Dermochelys coriacea*) off Capetown, South Africa, with results supporting the claim that molas are deep divers (Norman and Fraser, 1938; Wheeler, 1969). In a similar study, Sims et al. (2009) provided evidence for seasonal migration of three *M. mola* in the northeast Atlantic, and highly variable dive patterns. These studies suggest that molas likely alter their vertical behavior in response to environmental conditions and prey distribution (Hays et al., 2009; Sims et al., 2009). While research to date has provided important insights into their geographic and vertical habitat use, previous studies have been limited in time, space, and/or sample size and there is currently no information available for the western Pacific where molas are captured in fisheries.

Although caught and sold in only a few locations worldwide, such as Japan and Taiwan, *M. mola* are taken incidentally in a large number of fisheries. They are the most common bycatch of the broadbill swordfish drift gillnet fishery off California and Oregon. According to reports from the National Marine Fisheries Service (NMFS) Southwest Region, between 1990 and 1998, 26.1% of the drift net catch consisted of *M. mola*. This translates to a catch of more than 26,000 individuals (Rand Rasmussen, NMFS Southwest Fisheries Science Center, pers. comm.). In the Mediterranean, *M. mola* constitute up to 90% of the catch of the illegal Spanish driftnet swordfish fishery off the Gibraltar Straits (Silvani et al., 1999). Off the coast of South Africa, ocean sunfish bycatch rates from the tuna and swordfish longline fishery are estimated at 340,000 sunfish annually (Petersen, 2005; Sims et al., 2009). Unfortunately, without even crude estimates of the population structure, connectivity, or size, the impact of these fisheries is difficult to assess. Also, while molas are considered to be highly fecund (Fraser-Brunner, 1951), recruitment is unknown.

As mentioned above, one location where molas are captured for food is in the western Pacific off the east coast of Japan. Known as 'manbou', molas occupy a special place in Japanese culture. From being a tax payment to shoguns in the 17th and 18th centuries (Jingushicho, 1910) to becoming modern day town mascots (e.g. the town of Kamogawa) and the focus of ecotourism, molas have been

revered and consumed in Japan for centuries. Currently, genetic and pop-up satellite telemetry data are being collected for *M. mola* to document movements, behaviors, population subdivision, and migratory rates and routes around the Pacific. Our objectives for this study were to examine the horizontal and vertical movements of molas in the western Pacific and relate changes in those patterns to changes in environmental parameters. Results are presented from satellite tagging efforts on *M. mola* off Japan in the spring of 2001 and 2003–2006.

2. Materials and methods

2.1. Pop-up satellite archival tags

The pop-up satellite archival tag (PSAT, Model PAT2, PAT3, PAT4 and Mk10, Wildlife Computers, Redmond, Washington USA) (Block et al., 1998; Lutcavage et al., 1999; Sedberry and Loefer, 2001) was used in this study. The precision of temperature measurements was 0.1 °C between 12 and 26.95 °C and for values outside this range was 0.2 °C. The precision in depth measurements was depth dependent and measured within 1, 2, 4, 8, and 16 m over ranges from –20 to 99.5, 100 to 199.5, 200 to 299.5, 300 to 499.5, and 500 to 979.5 m, respectively. Histograms and temperature/depth profiles (PDT's) were set at either 12- or 24-h intervals. Light intensity measurements, coupled with the internal clock, document the times of dawn and dusk and allow for calculation of local noon or midnight and subsequently longitude (Hill, 1994) using software provided by the tag manufacturer (WC-GPE v1.02.0005, Wildlife Computers). Latitude is determined using longitude and sea surface temperature (SST) transmitted by the PSAT (Teo et al., 2004). The SST reported by the tag is matched along the line of longitude to the SST obtained from satellite imagery. Root mean squared error estimates from previous studies are approximately $\pm 0.5^\circ$ for longitude and less than 2° for SST based latitudes (Hill and Braun, 2001; Musyl et al., 2001; Teo et al., 2004).

The PSAT has numerous safeguards to reduce non-reporting rates. If the tag remains at the surface or at a constant depth for a user-defined period, internal software signals the tag to release and initiate transmission. To prevent implosion at depth, a special device, the RD1500 (Wildlife Computers), severs the leader at 1500 m, releasing the tag.

2.2. Tagging

A total of 12 tags were deployed on *M. mola* off Kamogawa, Japan during April of 2001 (n = 3), 2003 (n = 2), 2004 (n = 3), 2005 (n = 2) and March 2006 (n = 2) (Table 1, Fig. 1). All molas were captured in set nets (stationary rectangular traps consisting of anchored netting)

Table 1
Summary of the deployment data for 12 pop-up satellite tags deployed off Japan between 2001 and 2006. Shown are the dates and locations of deployment and recovery when available (DR = Didn't Report), the estimated minimum distance traveled (the km between release and pop-up locations), and the total duration of the deployment.

Mola	Year	Total length of fish (cm)	PTT	Tagging latitude (°N)	Tagging longitude (°E)	Tagging date	Pop off latitude (°N)	Pop off longitude (°E)	Pop off Date	Min. Distance (km)	Duration (days)
795*	2001	93	20,020	35.01	140.17	Apr 18, 01	41.13	141.38	Oct 17, 01	689	182
758	2001	87	20,806	35.00	140.19	Apr 18, 01	36.32	146.48	May 3, 01	587	15 [#]
833	2001	112	19,748	35.00	140.19	Apr 18, 01	37.52	151.04	Jan 22, 02	1012	279 [#]
63	2003	99	40,561	34.97	140.27	Apr 17, 03	32.88	133.51	Nov 1, 03	665	197
64	2003	102	40,562	35.10	140.31	Apr 15, 03	36.30	140.73	Nov 1, 03	139	199
291	2004	97.5	41,769	35.03	140.15	Apr 22, 04	30.65	158.32	Dec 25 04	1763	247
218	2004	90	41,758	35.02	140.09	Apr 24, 04	DR	—	—	—	—
217	2004	130	41,757	35.02	140.09	Apr 24, 04	DR	—	—	—	—
41*	2005	92	40,561	35.03	140.22	Apr 09, 05	41.17	141.78	Oct 17, 05	696	191
42*	2005	87	40,562	35.03	140.22	Apr 09, 05	DR	—	—	—	—
288*	2006	133	64,264	35.05	140.15	Mar 15, 06	42.60	168.97	Oct 2, 06	2619	193
289	2006	113	64,265	35.05	140.15	Mar 15, 06	DR	—	—	—	—

*individuals held at Kamogawa Sea World prior to tag and release.

[#]tags that released early.

a few kilometers offshore. Four individuals were held at Kamogawa Sea World for a period ranging from 4 to 25 days prior to tagging and release. The remaining molas were tagged and released on the day of capture. The molas were placed in a live well on a boat, measured, and tagged at the base of their dorsal fin prior to release. Tags were secured using large nylon darts, which were attached to the tags using 300-lb test monofilament line and stainless steel crimps. A small tissue sample was taken from the pectoral fin for genetic analysis. Following tagging, the boat transported the molas offshore where they were all released at approximately the same location (Table 1). Tags were programmed to release after periods ranging from 6 to 12 months.

2.3. Data analysis

To examine the day/night differences in temperature and depth, the data from the recovered tag (no. 795) were separated using the light level curves showing the time of sunrise and sunset. The crepuscular periods during which light changed rapidly were excluded from the analysis. Data from the archival tag was combined with that obtained from tags 63 and 64 that transmitted more than

10 days of data and had 12-h bin intervals set to collect primarily daytime and nighttime periods. The remaining tags either transmitted insufficient data ($n = 4$) or the timing of the bins ($n = 1$) did not allow for the examination of day–night patterns. The approximate depth of the mixed layer (the depth at which the dramatic decrease in temperature initiated) for mola 795 was calculated from the archival record by examining temperature at depth using only the data collected on the descent. Earlier models of the PSAT tag had a thermal lag. This approach provides a conservative estimate of the mixed layer depth. Seasons were defined according to the astronomical calendar.

Geolocations of molas over 10-day periods were plotted over 10-day averaged composites of sea surface temperature (SST) (MODIS, <http://podaac-www.jpl.nasa.gov/>) and chlorophyll *a* (SeaWiFS, <http://oceancolor.gsfc.nasa.gov/>) during the same period. This allowed us to examine the associations, if any, between the movements of the molas with changes in SST and chlorophyll *a* concentration.

3. Results

Data were collected from the eight of the 12 tags deployed (Table 1). Tag 795 was recovered by a set-net fisherman in the

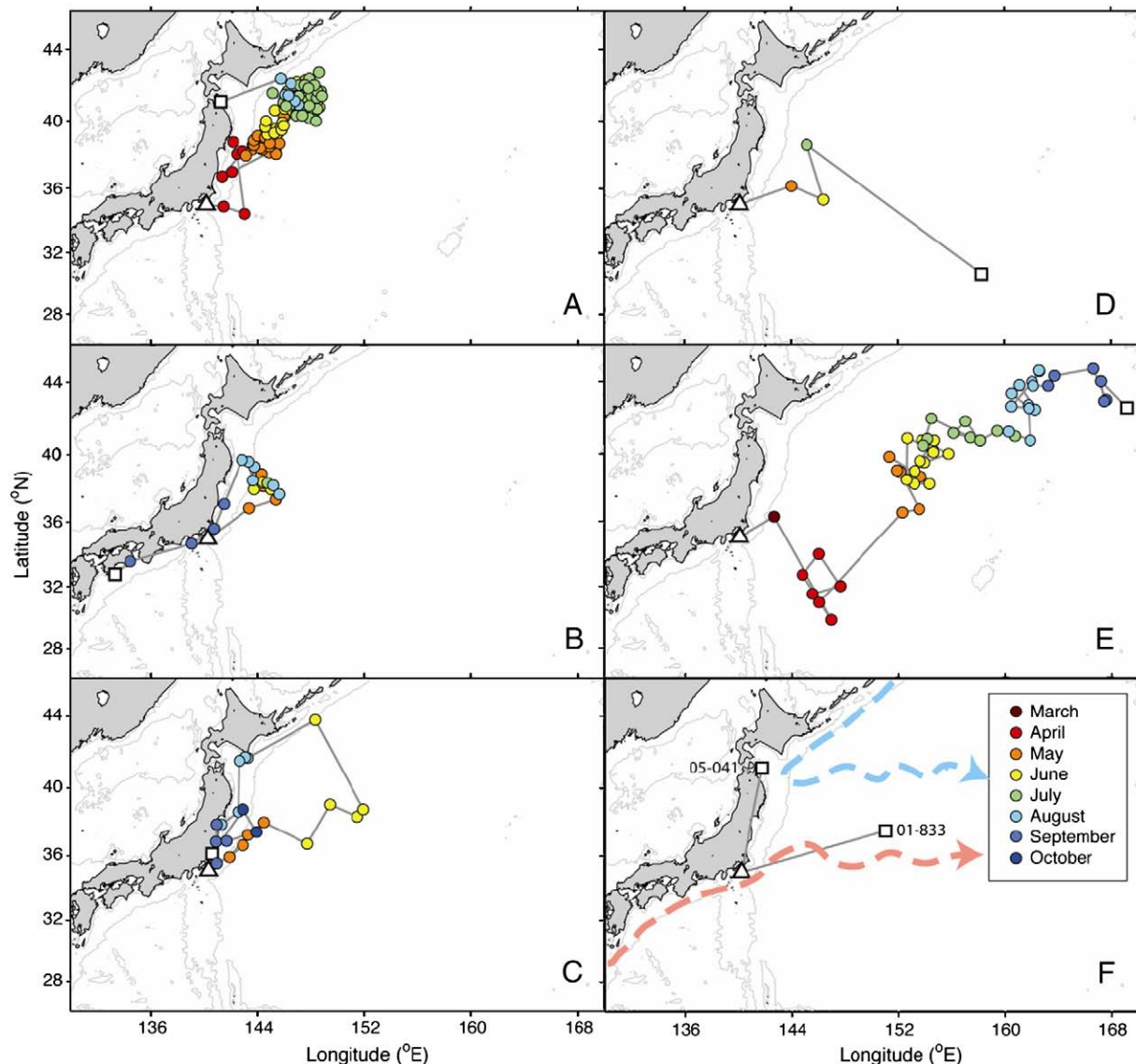


Fig. 1. Geolocations of molas A) 795, B) 63, C) 64, D) 291, E) 288, and F) 833 and 41, derived from light and sea surface temperature data from pop-up satellite archival tags. Open triangles and squares denote tagging and pop-up/recovery locations respectively. Color of circles denotes month of geolocation. Bathymetric contours (200 and 3000 m) are indicated by light grey lines. The light blue and pink lines represent a diagrammatic representation of the Oyashio and Kuroshio Currents, respectively (drawn after Sakurai, 2007).

Shiranuka Aomori Prefecture in northern Japan. Prior to the battery failing, 110 days of temperature, depth and light level data at two minute intervals were obtained. Of the remaining seven tags, two released early and all transmitted limited amounts of data. Tag 758 released when the fish went below 980 m (the depth limit of the tag), presumably triggering the RD1500 and severing the monofilament leader. Tag 833 transmitted minimal light level data and a single temperature histogram. Tag 63 transmitted between 26 and 53 out of a possible 394 temperature/depth summaries (PDT's or temperature or depth histograms). Tag 64 transmitted between 41 and 73 of a possible 398 temperature/depth summaries. Tag 291 transmitted only two to four temperature/depth summaries (all collected at night) out of a possible 494. Tag 41 provided only a pop-up location. The final tag 288 transmitted between 43 and 64 temperature/depth summaries out of a possible 386.

3.1. Geolocation

The movements of eight molas after release were based both on the pop-up location obtained from Argos (Argos, 1989) and the light and SST-based geolocation estimates when possible (Fig. 1). Given the short duration of the track, only the release and pop-up locations for tag 758 were used. For tag 833, it was only possible to estimate longitudes between tag and release because no SST data were transmitted, and for tag 41 only the pop-up location was obtained. For tags 795, 63, 64, 291 and 288, latitudes and longitudes between the release and pop-up locations were calculated.

A pattern of seasonal movements was evident by examining some of the longer tracks, although some variability among individuals was apparent (Fig. 1). Following their release in the spring, all molas for which tracks were available moved northeast, north of the Kuroshio Current and into the Kuroshio–Oyashio transition zone (KOTZ) and the southern reaches of the Oyashio Current, where they remained for much of the summer. The locations, recorded SSTs and mixed layer temperature and depth are consistent with the known characteristics of these two currents (Fig. 4) (Kawai, 1969; Sakurai, 2007). In the late summer, most fish moved back towards Japan, and in the fall five fish were near the coast. This includes tags 795 and 41 that were recovered or popped up near the coast in October (Fig. 1A and F). Molas 63 and 64 moved south along the coast of Japan until their pop-up date on November 1 (Fig. 1B and C). While fish 288 showed a similar seasonal pattern through the spring and much of the summer, it did not return towards Japan in late summer and continued to progress towards the east until the tag popped up in late September (Fig. 1E). Two molas moved east into the Kuroshio extension. While mola 291 spent the summer north of the Kuroshio Current, similar to the other molas, it was ~1700 km east of its tagging location at 158°E on its January pop-up date (Fig. 1D). Data between August and December were not recovered. The longitude estimates for mola 833 reveal that by early September, when the five molas were near Japan, this individual had reached its most easterly position at 161°E. It appeared to be returning towards the west when the tag released at 151.04°E in mid October. Mola 758 had moved over 1000 km east when the tag popped up after two weeks.

Remote sensing satellite data allowed for the examination of movements in relation to SST and chlorophyll a levels, which provided a proxy for primary productivity (Fig. 2). Movements north corresponded to an increase in SST and a decrease in chlorophyll a levels off central Japan. At the same time, the temperature increased in the cooler KOTZ and Oyashio Current, and while overall chlorophyll a concentrations also dropped in this region, they were still higher than off central Japan. Satellite-derived chlorophyll a concentrations along the best track (mola 795) ranged from 0.2 to 3.1 mg m⁻³ with 80% of values falling between 0.3 and 1 mg m⁻³. These values are not precise due to the errors associated with light- and SST-based geolocation estimates.

3.2. Temperature and depth

Analyses of temperature and depth data were conducted for those molas (795, 758, 64, 63 and 288) whose tags reported 10 or more temperature or depth records (histograms or PDTs). Depth and temperature data provide the opportunity to examine the habitat, behavior and potential condition of the fish following tagging.

The general temperature and depth patterns were consistent across fish with the exception of mola 758. This individual spent the majority of its time (63%) below 20 m. While it did come to the surface each day, as indicated by 0 m minimum depth measurements, mola 758 spent only 14% of its time in the top 5 m. After two weeks it either sank or dove to 1500 m, when the tag released. This depth is over twice the maximum recorded for the other molas in this study. Mola 758 may not have recovered from tagging and was a possible mortality (see below). Given the questionable condition of this fish and short record, it is not included in subsequent analysis.

The most detailed information on diving behavior comes from the archival record (mola 795). This mola showed a consistent diel dive pattern with relatively shallow depths observed at night (Fig. 3) and deep repetitive dives during the day. Nighttime depths were generally in the top 5 m. Daytime dives ranged from 27 to 300 m and were typically punctuated by regular surface intervals. Often there was a gradual shift in depth at the beginning and end of the day. The general diel pattern was observed for the entire record except for two days when the two deepest dives were observed. Interestingly, the deepest dive to 644 m occurred near local midnight where the mola remained deep for 8 min. The second deepest dive was to 300 m and occurred near dawn.

While the diel pattern was consistent across the record, a shift in the pattern of dives was observed as the fish progressed towards the northeast (Fig. 3). For example on April 23, the mola made 12 dives to between ~100 and 200 m and 11 and 15 °C with ~1 h spent below the mixed layer on each dive (Fig. 3A). Later in the record, on August 22, the mola made more dives (43) below the mixed layer for shorter durations (~15 min) (Fig. 3B). Typical depths were 40 m and temperatures were between ~5 and 10 °C. While SST was similar on both days, depth of the mixed layer shoaled from around 60 to 20 m, with much cooler temperatures at depth (e.g. April 23 15 °C at ~100 m, August 22 15 °C at ~30 m). The pattern over the entire record for mola 795 (Fig. 4) as well as for three other molas (Fig. 5) shows the same reduction in both dive depth and temperatures as the fish moved north of the Kuroshio Current. Towards the end of the record, the SST was higher for the two fish that returned to Japan in the fall (tags 63 and 64) than for the one fish (tag 288) that was still offshore in September.

Combining data for all tags provided insight into the range of temperatures and depths experienced by *M. mola* off Japan from March through October (Table 2). The minimum dive depth for a given interval was always 0 m. The overall maximum depths for individual molas ranged from 296 to 644 m. While 644-m dives were recorded for two fish, these deep dives were anomalous and the average maximum daily depth ranged from 95 to 171 m. The minimum temperatures encountered at depth were similar, approximately 2 °C. Maximum temperature, which corresponds to SST, varied more than 16 °C, ranging from 11.3 to 27.8 °C. However, 86% of the time, SST fell between 13 and 21 °C (Fig. 6).

Temperature and depth histograms combined for three fish (nos. 795, 63 and 64) (Fig. 7) reflect the diel pattern (see Fig. 3) with deeper depths and cooler temperatures during the day. Based on the bimodal distribution, the majority of daytime dives were below 100 m. Assigning actual values to time spent in different bins day and night was not possible with the 12-h histogram intervals, as some daytime behavior was included in the nighttime bins and visa versa. Combining day and night bins, the fish spent approximately 70% of their time between 13 and 21 °C and shallower than 50 m, with 50% of

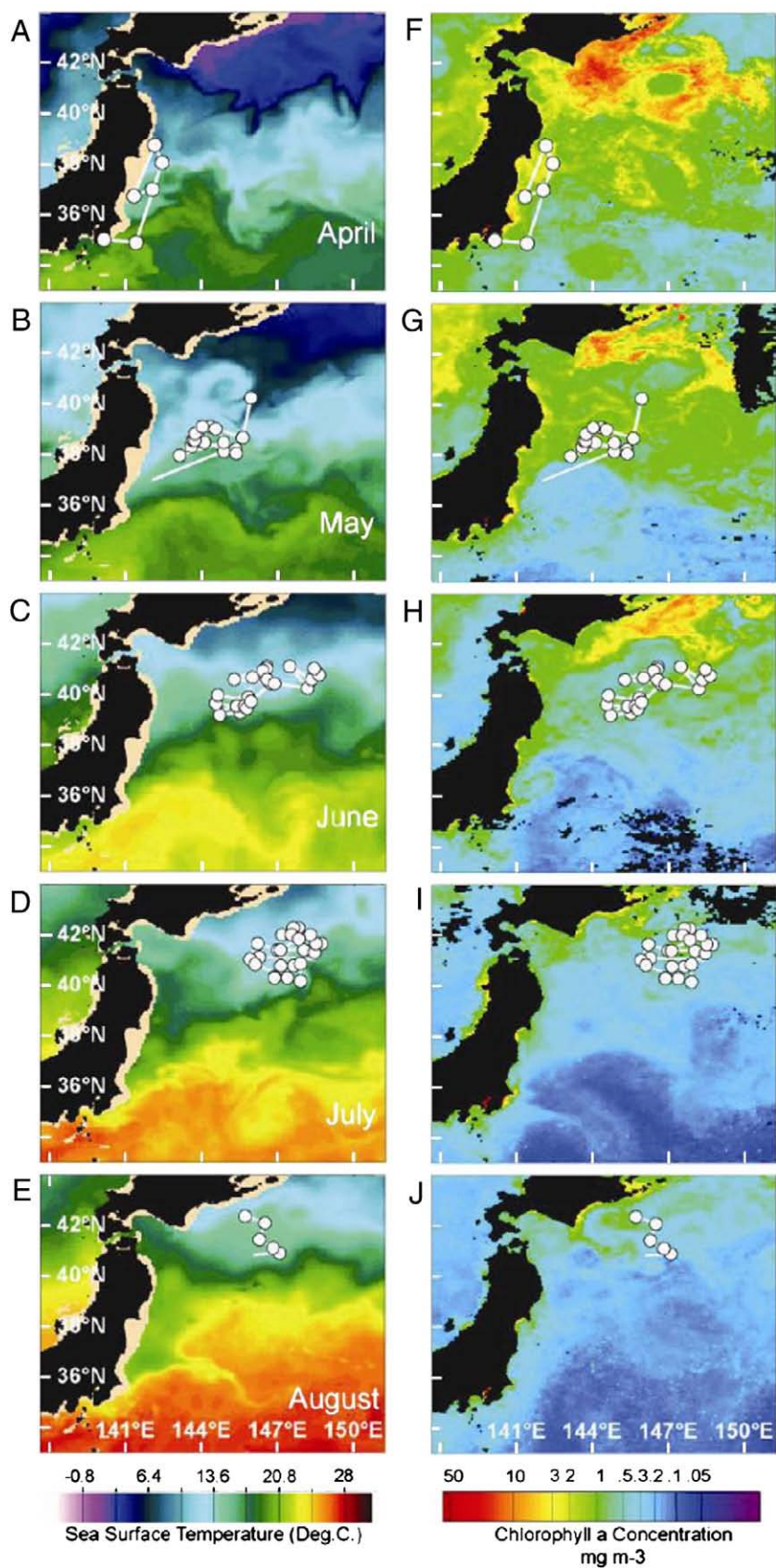


Fig. 2. Geolocations for mola 795 are shown for each month over 10 day composites of satellite imagery of sea surface temperature (MODIS) and chlorophyll *a* (SeaWiFS) from the corresponding month.

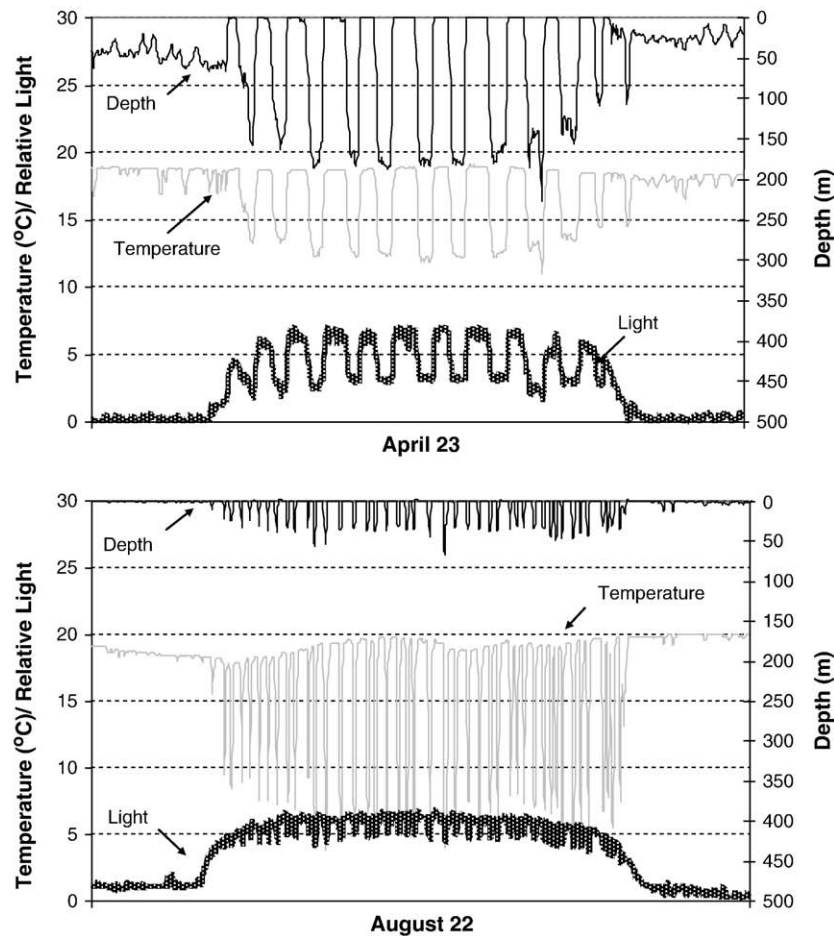


Fig. 3. Depth, temperature and light levels recorded every 2 min by the pop-up tag on mola 795 for A) April 23 and B) August 22.

their time spent in the top 10 m. Mola 288 shows a 24-h pattern closer to that exhibited at night by molas 795, 63 and 64, with more time in surface waters and less at depth. The temperatures experienced by 288 were also cooler, with a peak between 12.5° and 15 °C rather than at 15° to 17 °C.

4. Discussion

The data obtained from satellite tagging *M. mola* in Japanese waters provide new insight into this poorly understood fish. The only detailed information on behaviors of this globally distributed species comes from one acoustic telemetry study of eight individuals (Cartamil and Lowe, 2004) and two satellite-tagging studies totaling

seven individuals (Hays et al., 2009; Sims et al., 2009). This is the largest satellite tagging study to date and provides the first data on geographic and vertical movement patterns of *M. mola* in the western Pacific.

4.1. Fish condition and tag performance

While it is clear, given the long deployments, that seven of the eight molas survived the tagging process, the fate of no. 758 was uncertain. Unlike the other molas that remained predominantly in surface waters, this animal spent most of its two-week track in waters deeper than 20 m and made one final descent deeper than 1500 m. Although there is insufficient baseline information to determine

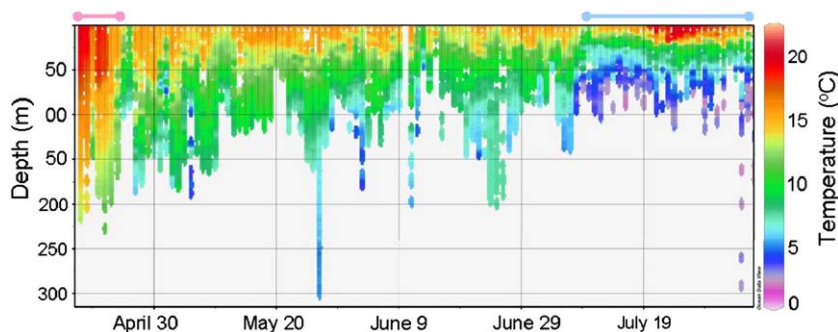


Fig. 4. Depth and temperature recorded every 2 min are shown for the archival record (mola 795) with temperature indicated in color. The pink and light blue lines indicate when the mola was in the Kuroshio and Oyashio Currents, respectively, based on location, SST and the water column thermal profile.

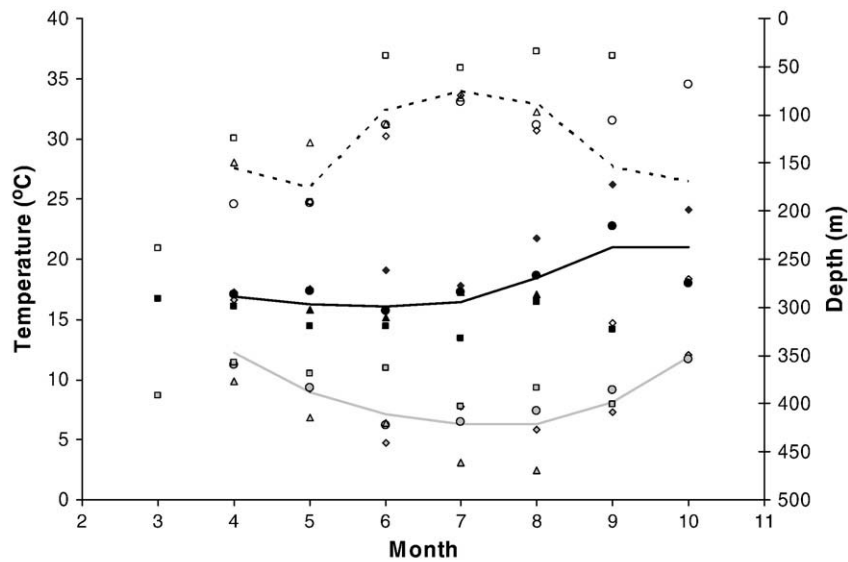


Fig. 5. The average monthly maximum (closed symbols) and minimum (grey symbols) temperature and maximum depth (open symbols) are show for four molas, 795 (triangle), 63 (diamond), 64 (circle) and 228 (square).

whether this behavior is abnormal, it is contrary to the general pattern seen for the other tagged molas in this study and those of Cartamil and Lowe (2004) and Hays et al. (2009). Shifts in vertical behavior are common in fish stressed by tagging (Gunn and Block, 2001; Arnold and Dewar, 2001), and it is possible that mola 758 did not recover from the capture and tagging event. Interestingly, the one *M. mola* that Sims et al. (2009) reported as a likely mortality also spent considerably more time below surface waters than the other molas tagged in that study.

While PSATs are a valuable tool for studying the movements and behaviors of pelagic organisms (Arnold and Dewar, 2001; Block et al., 2001; Musyl et al., 2004), the transmission of data in this study was poor; only limited temperature and depth data were transmitted even when different tag models were used. While it is not possible to determine the exact reason for this poor performance, the deployment durations were relatively long, which can increase failure rates. For example, biofouling can impact the clearance of the antennae and quality of data transmission and has been identified as a problem with other types of satellite tag (Hays et al., 2007). The tags were painted with anti-fouling paint, but it is unlikely that the paint lasted for the duration of the longer deployments. Hardware and software failures also become more likely with increased deployment duration.

4.2. Geographic movements

Historically, molas have been classified as large plankton, drifting passively with the currents (McCann, 1961; Holt, 1965; Lee, 1986). The findings from this paper counter this hypothesis, since the sunfish off Japan did not move with the prevailing currents. For example, the molas moved out of the Kuroshio Current and into the KOTZ and the southern edge of the Oyashio Current, not moving with either of these major currents. Similarly, *M. mola* tracked in the northeast Atlantic and off South Africa moved against general current patterns (Sims et al., 2009; Hays et al., 2009). These data reveal that molas can actively migrate into different water masses and consequently respond to changes in oceanography and/or prey availability.

The movements observed off Japan indicated that some molas make migrations (at least over the seasons covered in this study) corresponding to an increase in temperature and a reduction of productivity in the Kuroshio Current following the spring bloom (Fig. 2, Longhurst, 2007). From April to August, 2002, SST near the tagging location increased from around 14 °C to around 27 °C and the chlorophyll a concentration dropped. Around this time, the mola left this area for the more productive waters in the KOTZ and the southern

Table 2

Summary of the sea surface temperature (SST), minimum temperatures and maximum depths. For the four tags with sufficient data, summary statistics are provided ; for mean daily values, SD is reported. ND = No data.

Mola	SST (°C)	Average Min temp (°C)	Average Max depth (m)
795	16.3 ± 1.8 (11.3–20.7)	5.9 ± 3.0 (min = 1.0)	117 ± 69 (max = 644)
758	19.8	5.8*	(max = 448)
833	>20	<10	ND
63	20.4 ± 3.5 (15.4–27.8)	8.5 ± 4.4 (min = 2.0)	171 ± 114 (max = 432)
64	18.4 ± 2.7 (12.6–25.6)	8.3 ± 3.4 (min = 2.0)	122 ± 97 (max = 644)
291	21	<5	>400
288	14.6 ± 1.6 (12.0–19.0)	9.1 ± 2.9 (min = 2.0)	95 ± 80 (max = 296)

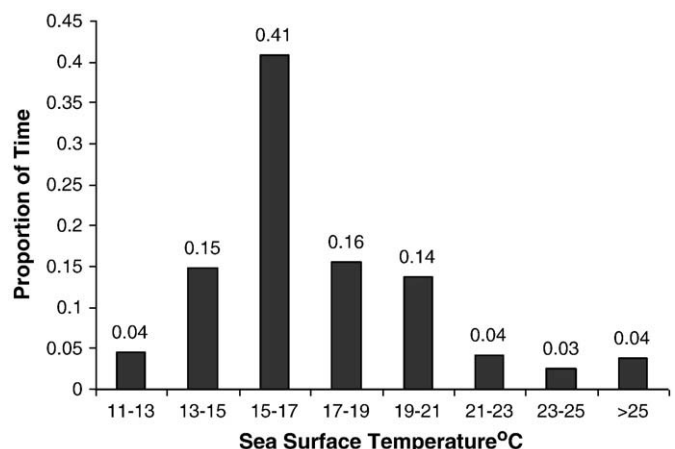


Fig. 6. Histogram of sea surface temperature experienced by molas 795, 63, 64 and 288.

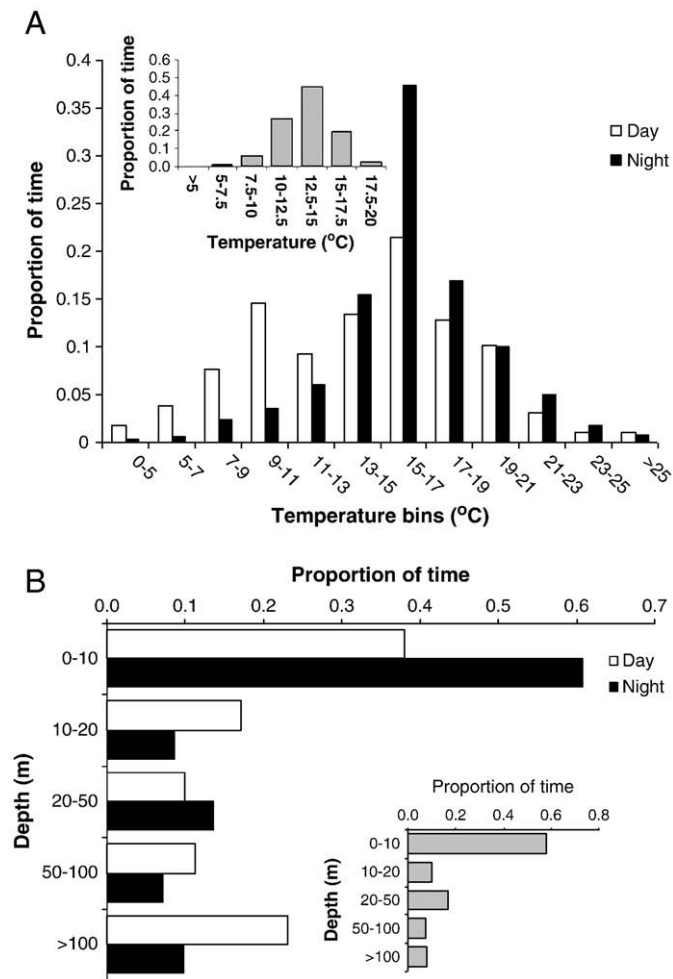


Fig. 7. Temperature (A) and depth (B) histograms for day (open bars) and night (black bars) for tags 795, 63 and 64. The data for 288 are shown in each inset.

reaches of the Oyashio Current. Here, meso-scale eddies and warm-core rings enhance the regional productivity resulting in a large forage base for a range of species including anchovy, salmon, mackerel and skipjack tuna (Minoda, 1989; Yasuda and Kitagawa, 1996). The tracks that continued into the fall show the mola returning to the waters off Japan and the Kuroshio Current when there is typically a second annual peak in productivity (Longhurst, 2007). Better information on the fine-scale seasonal patterns of abundance and distribution of jellies is needed to accurately define the links between the molas, their prey, and regional oceanography.

While there are few comparative data available, movements to higher latitudes as temperatures increase in the summer is consistent with patterns reported by others for this species around the globe. Off Japan, the general pattern of moving progressively northward as the temperatures warm is supported by catch rates of *M. mola* in fish markets along the Japanese coast (Sagara and Ozawa, 2002). This trend has also been suggested for molas on both the east and west coast of the United States. It is primarily in the summer months that molas are seen at the northern extent of their range off Nova Scotia, Oregon, Washington state and Alaska (Thys unpublished data). Similar to a large number of other species, including whales, turtles, and bluefin tuna (Mate et al., 2000; Block et al., 2001; Houghton et al., 2006a,b), it is likely that some molas are taking advantage of the pulse of high productivity at high latitudes while the surface waters are warm and then returning south when temperatures cool. All molas tagged in this study were likely immature, and thus it is unlikely that their movements were associated with spawning. Maturity is presumably

reached between 3 and 4 years (150–180 cm TL) and spawning is thought to occur from August to October (Nakatsubo et al., 2007; Nakatsubo, 2008).

The data obtained in this study provide no indication that *M. mola* from Japan are making basin-scale movements or large-scale migrations, at least in the months from March through October. Even no. 833, which moved past 160 E, appeared to be returning towards Japan when the tag released in January. Relatively small-scale movements were also observed for molas tagged off both South Africa and in the northeast Atlantic (Hays et al., 2009; Sims et al., 2009). This limited movement by molas contrasts with extensive, sometimes basin-wide, movements seen in leatherback turtles (Hays et al., 2006; Benson et al., 2007; Bailey et al., 2008) and is interesting given the similar jelly diets of these species. It has been suggested that the ability of sunfish to exploit deeper prey might remove the necessity for extended migrations (Hays et al., 2009), although differences in their reproductive life histories likely also play a role.

Our findings on both vertical and geographic movements have important implications for management of this species. Information on vertical habitat use in relation to regional oceanography could be used to reduce bycatch. Geographically, if movements are limited, population separation within the Pacific is possible. Population structure within the Pacific has been reported for a range of large pelagic fish including some highly migratory tunas, sharks, and billfishes (Graves and McDowell, 1994; Reeb et al., 2000; Graves and McDowell, 2003; Block et al., 2005; Michaud, 2009). If there is a separate stock of *M. mola* in the western Pacific, regional over-exploitation could lead to local depletion and loss of genetic diversity. Given that little is known about the standing stock size for this species, the probability of local depletion is difficult to determine. To contribute to management efforts, additional information on longer-term migrations over a range of life history stages is necessary to quantify the variability and relative importance of the molas' migratory patterns and inform stock structure.

4.3. Behaviors and the environment

The habitat of molas off Japan encompasses a broad range of temperatures and depths. Molas can descend to as deep as 644 m, expanding the known depth range for this species (S. Earle pers comm., R and T Kemper, pers comm., T. Thys unpublished data, Sims et al., 2009; Hays et al., 2009), yet most dives were much shallower and the majority of time during both day and night was spent in surface waters. This is similar to reports from other regions (Cartamil and Lowe, 2004; Sims et al., 2009; Hays et al., 2009). During dives, molas off Japan encountered the coldest temperatures reported for this species, demonstrating an impressive thermal tolerance. Diving into very cold water (0.4 °C) has also been reported for leatherback turtles on their foraging grounds (James et al., 2006). However, as with sunfish, such descents into cooler water can only be tolerated for short periods and only occur where the surface water is much warmer.

The highest temperatures were encountered in surface waters, which spanned the range of values reported in other areas for this species. For example, 93% of surface sightings of *M. mola* in the western English Channel were in temperatures between 13° and 17 °C (Sims and Southall, 2002). Based on the data from our study, 11 °C likely represents the lower bound of the SST habitat envelope for relatively small molas. This is similar to the 8–10 °C and suggested by Sims et al. (2009) as a limit to lower SST. As indicated by the seasonal movement patterns apparent from this and other studies, SST likely plays a large role in the abundance and distribution of molas, similar to other pelagic fish, mammals, and turtles. Understanding links to SST will help predict potential distributional shifts associated with climate change. For example, McMahon and Hays (2006) report a northward range expansion of the summer foraging grounds of leatherback sea turtles in association with an increase in SST at higher latitudes.

The broad range of temperatures and depths experienced by molas are linked to their diel vertical movement patterns, best observed in the archival dataset. A diel pattern was also observed in the acoustic tracks for molas off Southern California (Cartamil and Lowe, 2004), although the dives in this study tended to be less regular with less surface behavior than observed off Japan. The summarized data provided by Hays et al. (2009) and Sims et al. (2009) also suggest a diel pattern. Diel vertical movements through the mixed layer are common among a large number of active, pelagic teleosts (Carey and Scharold, 1990; Holland et al., 1992; Musyl et al., 2004; Weng et al., 2007; Schaefer et al., 2007). As with most fish, the repeated dives of molas are presumed to be associated with foraging at depth (Carey and Robison, 1981; Carey and Scharold, 1990; Musyl et al., 2004; Schaefer et al., 2007). The comparatively low activity levels of the mola's prey may facilitate foraging, especially in light of the mola's unconventional form, which is not well suited for extended pursuits (Fish and Lauder, 2006).

The similarity in the diel behavior and regular dive patterns between molas and a number of other active pelagic fish is interesting for numerous reasons: first, it indicates a relatively high level of activity for molas, which have traditionally been considered slow moving and lethargic. The mola's ability to make 40 or more dives a day underscores this activity level. Second, the regularity of the dives and the reduced time at depth in cooler waters supports the hypothesis that their surface behavior is associated with behavioral thermoregulation. Returning to warm waters between dives has been demonstrated to be thermoregulatory for both sharks (Carey and Scharold, 1990; Dewar et al., 2004) and tuna (Holland et al., 1992; Schaefer and Fuller, 2002). Cartamil and Lowe (2004) came to a similar conclusion for molas tracked off California. As seen in bigeye tuna, larger molas will likely spend more time at depth due to their increased thermal inertia, which will slow the rate of cooling during dives (Holland et al., 1992; Dagorn et al., 2000; Schaefer and Fuller, 2002). Third, the occurrences of a gradual increase and decrease in dive depths at sunrise and sunset suggest that molas may be following prey that is vertically migrating. Similar foraging behavior has been widely reported for a range of vertebrates including fish, turtles, and birds that are foraging on vertically migrating prey (Carey and Robison, 1981; Hays, 2003; Musyl et al., 2004).

Although, diel vertical movements were consistent throughout the record, the pattern of movements changed seasonally. The most dramatic change was observed during the summer when dives were much shallower and shorter. While the shift in depth could be linked to changes in prey distribution, the reduced dive time is likely related to thermal constraints. Due to the shallow and extreme thermocline in the Oyashio Current in particular, very cold waters were encountered close to the surface. Sims et al. (2009) reported a similar pattern where the mola with the shallowest depth distributions was in waters with the steepest thermocline. Thus, in colder regions, time at depth and associated foraging activity appear to be reduced, a pattern also noted for yellowfin tuna (Weng et al. 2009). This may represent a trade-off while foraging in the productive waters north of the Kuroshio Current.

Possible prey items for the molas off Japan are suggested from transects conducted with remotely operated vehicles and towed cameras operated by the Japan Agency for Marine–Earth Science and Technology. In March 2006, salps were abundant during the day in the area off Kamogawa from 50 to 550 m with the maximum abundance between 200 to 350 m. At night, the maximum abundance was from 0 to 80 m. Salps were also the most abundant gelatinous macroplankton in the upper 200 m in September in a warm-core ring and in the KOTZ, while they were not observed in the surrounding colder waters (see Fig. 1D in Lindsay et al., 2008). A similar pattern was seen in the physonect siphonophore, *Nanomia bijuga*, during April–May 2006. In colder surrounding waters or below the thermocline, the following species have been observed in the same depth layers where *M. mola* foraging seems to predominately occur: *Aglantha digitale*, *Bolinopsis*

infundibulum, *Mertensia ovum*, Euplokaamid cydippid ctenophores, *Beroe abyssicola* and the krill, *Euphausia pacifica*. Other large jellyfishes known to occur in this area include *Aurelia limbata* (moon jelly), *Cyanea capillata* (lion's mane) and *Chrysaora* sp. (sea nettle).

4.4. Inter-specific comparisons

Satellite tag data recorded for 61 days from a single sharp-tailed mola in the Gulf of Mexico provides interesting comparisons (Seitz et al., 2002) to vertical and thermal habitat use of *M. mola* off Japan. The *M. lanceolatus* showed little of the apparent basking behavior prevalent in *M. mola* and spent only 2.7% of its time in the top 5 m. These observations are similar to reports of Taiwanese fishermen who indicate *M. lanceolatus* are rarely encountered on the surface and captured primarily in set nets (Huang Brothers, Hua Lien, Taiwan, pers. comm.). *M. lanceolatus* also occupied deeper waters in the Gulf of Mexico (Seitz et al., 2002) spending approximately 25% of its time between 10 and 50 m and nearly 50% of its time between 50 and 100 m. Despite these relatively deep depths, most of its time (86%) was spent at temperatures above 20 °C. The coldest temperature encountered was 6 °C. Similar to *M. mola*, there was an apparent diel pattern with the deepest dives (exceeding 700 m) observed during daylight hours. While the data suggest there may be differences in the thermal habitats of *M. mola* and *M. lanceolatus*, comparisons are confounded by the differences in the water column thermal structure. The Gulf of Mexico has considerably warmer SST and a deeper thermocline than recorded in this study.

5. Conclusion

The data collected on the movement, behaviors, and habitats encountered by *M. mola* off Japan provide important insights into their vertical and geographic movements. These molas do not appear to make basin-scale migrations. If movements are indeed localized, over-exploitation off the Japanese coast may result in a loss of genetic diversity and potentially the loss of a discrete population. However, it should be noted that the molas in this study are juvenile fish and mature fish may make larger-scale migrations. Molas appear to be relatively active predators that are capable of migrating moderate distances most likely in response to shifts in regional productivity and temperature. From this initial baseline information, it may be possible to use the abundance and distribution of molas as an indicator of jelly abundance and distribution, especially for jellies that are diel migrators and only occur on the surface at night. More tracks for a greater size range of individuals over a longer time scale are required to confirm the overall movement patterns of molas. Additional information on diet, possibly incorporating molecular techniques, will also be important for defining trophic links. Establishing these links will greatly enhance the utility of the mola as an indicator species for gelatinous zooplankton.

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