Movement and habitat use by the spine-tail devil ray in the Eastern Pacific Ocean

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ABSTRACT: The devil-ray family Mobulidae (order Myliobatiformes) comprises wide-ranging, pelagic batoids, but little is known about their basic ecology. We present the first data on the long-distance movement of mobulid devil rays. We attached pop-up archival satellite tags to 13 individuals of the spine-tail devil ray *Mobula japanica* (disk width 199.5 ± 30.0 cm; mean ± SD) off Baja California Sur to examine their habitat movement patterns. Tags remained on the rays for 83 ± 52 d (mean ± SD). Although their primary prey undergo diel migrations from depths >100 m during the day to the surface at night, tagged individuals spent the majority of their time (89.5 ± 3.1% during the day and 96.8 ± 3.5% at night; mean ± SD) near the surface at a depth of ≤50 m in 20 to 30°C water. Thus, *M. japanica* likely forages at night and remains near the surface during the day, where warmer water temperatures likely confer a physiological advantage. Most (8 of 13) individuals moved from the tagging location in the southern Gulf of California to the Pacific coast of Baja California Sur, tracking published records of seasonal patterns in euphausiid abundance, similar to other top predators in the region. The depths and geographic regions occupied by *M. japanica* coincide with the focus of artisanal and industrial fisheries. This overlap with fisheries, when combined with the delayed maturity and low reproductive rates of devil rays, raises concerns of potentially damaging high bycatch mortality.

KEY WORDS: Mobulid · *Mobula japanica* · Manta ray · Elasmobranch · Baja California · Gulf of California · Conservation

INTRODUCTION

Elasmobranchs of the devil-ray family Mobulidae (order Myliobatiformes) are wide-ranging pelagic batoids of 2 genera (*Manta* and *Mobula*), occurring throughout tropical and warm-temperate waters (Eschmeyer et al. 1983, Notarbartolo-di-Sciara 1988). They are filter feeders, using their cephalic lobes to enhance the entrance of plankton into their mouths, and feed almost exclusively on zooplankton, pelagic crustaceans and small forage fishes (Eschmeyer et al. 1983, Notarbartolo-di-Sciara 1988).

All 11 mobulid species are live bearers with low fecundity, giving birth to a single offspring per pregnancy (Notarbartolo-di-Sciara 1988). Because mobulids are taken directly or as bycatch in a range of fisheries (White et al. 2006), they are particularly vulnerable to overexploitation. Eight of the 11 mob-

ulid species reviewed on the IUCN Red List are listed as near-threatened or above, with the remaining 3 species listed as data deficient (IUCN 2012). Five mobulid species occur in the Gulf of California, Mexico and along the Pacific Coast of the Baja California, Mexico Peninsula: *Mobula japanica*, *M. munkiana*, *M. tarapacana*, *M. thurstoni* and *Manta birostris* (Eschmeyer et al. 1983, Notarbartolo-di-Sciara 1988, Villavicencio-Garayzar 1991). However, little is known about their ecology, population biology and movement patterns (Notarbartolo-di-Sciara 1988), thus limiting the ability of fishery managers to protect mobulids.

Since the early 1980s, the artisanal mobulid fishery in the Gulf of California has focussed on *Mobula japanica* (Notarbartolo-di-Sciara 1988, Serrano-López 2009). Recognizing the vulnerability of mobulids to overexploitation, the Mexican government enacted fisheries legislation prohibiting their targeted take in 2005 (NOM-029-PESC 2004); however, illegal and non-target bycatch still occurs (Bizzarro et al. 2009).

Mobula japanica has a specialized diet in the Gulf of California, comprising almost exclusively the euphausiid *Nyctiphanes simplex* (Notarbartolo-di-Sciara 1988, Sampson et al. 2010). Aggregations of *M. japanica* appear in the vicinity of La Paz, Baja California Sur, during spring, corresponding with seasonal patterns of krill abundance (Gómez-Gutiérrez et al. 2010). However, local fishers report that *M. japanica* move out of the Gulf of California by the end of summer, with large adults being rare during winter (Notarbartolo-di-Sciara 1988, Hobro 2002). Nothing is known about the seasonal distribution of these *M. japanica* from late summer through winter when they are not available to fishers. We give the first information on the seasonal migration, diel movement patterns and temperature preferences of *M. japanica*, as well as on the implications of these data for *M. japanica* fishery management.

MATERIALS AND METHODS

Capture and satellite telemetry

Mobula japanica were captured in the early summer (June) in the vicinity of La Paz, Baja California Sur, Mexico (24.8° N, 110.5° W), from 2004 to 2007. Working with local fishers, individuals were captured with encircling surface nets 150 m long, 15 m deep, with 25 cm mesh. Once captured, individuals were kept in the water alongside the skiff, and mea-

sured for length and half-width, sexed and biopsied for DNA analysis.

Pop-up satellite archival tags (PAT tag hardware version 2 during 2004–2005 and MK10-PAT tag version 10 during 2006–2007; Wildlife Computers) were secured to the dorsal surface of the ray along the pectoral fin margin using a medical-grade plastic umbrella dart with a 10 cm segment of 136 kg monofilament line applied with an aluminum pole. We applied a secondary attachment loop from the base of the PAT tag float to the dorsal surface of the animal to keep the tag flush with the surface of the animal along the margin of the pectoral fin.

PAT tags recorded temperature, depth and light intensity data while attached to the ray, and on a preprogrammed date, released to float to the surface and transmitted summary data to Argos modules on NOAA weather satellites (Block et al. 1998a). PAT tags were programmed to archive data at 30 s intervals in 2004–2005 and at 15 s intervals during 2006–2007. In the event that tags were physically recovered, this archive could be downloaded to a computer. Otherwise, tags transmitted a summary of the archival record comprising histograms of temperature and depth occupancy, depth–temperature profiles, and light curves for dawn and dusk of each day. These summaries were calculated for 12 h intervals in 2004–2005 and for 6 h intervals in 2006–2007.

Data analysis

We determined a length–width relationship for *Mobula japanica* based on our measurements. The literature on rays typically presents disc width; however, this is difficult to measure on live individuals alongside a skiff. Therefore, we either measured length (to the tip of the pelvic fin) and later estimated width using a linear regression, or we measured the half-width of the animal from the midline vertebrae to the tip of one pectoral fin.

Light levels can be used to estimate longitude (Hill 1994, Hill & Braun 2001, Ekstrom 2002), and associated latitudes can be estimated by comparing sea surface temperature (SST) recorded by tags *in situ* with that obtained from satellites (Teo et al. 2004, Nielsen et al. 2006). We used light measurements recorded by PAT tags to estimate longitude using proprietary software provided by the tag manufacturers (GPE-Suite version 1.02.0002, Wildlife Computers). To obtain associated latitudes, we used the SST-matching method of Teo et al. (2004) implemented in MATLAB (The MathWorks). Light-

and/or SST-based geolocation for free-ranging marine vertebrates provides daily positions with errors on the order of 100 km (DeLong et al. 1992, Gunn et al. 1994, Block et al. 1998b, Welch & Eveson 1999, Musyl et al. 2001, Teo et al. 2004). We estimated geolocation errors by comparing the results from light and/or SST methods with known deployment locations recorded by GPS (root mean-square [RMS] error <0.01 km; Wormley 2007), or pop-up positions obtained from Argos with location qualities of 2 or 3 (RMS error <0.35 km; www.argos-system.org).

The geographic habitat usage of *Mobula japanica* was estimated using the kernel density technique (Silverman 1986), embedded in the Animal Movement extension (Hooge & Eichenlaub 1997) for ArcView 3.2 (ESRI). Vertical habitat use by *M. japanica* was quantified using the average distributions of time at depth and temperature transmitted by the PAT tags. Tags defined day as 06:00–18:00 h local time (GMT – 6 h) and night as 18:00–06:00 h. During the course of the study, the actual time of sunrise and sunset at the tagging location varied from 05:32– 07:05 h and 17:41–19:13 h, respectively (16 June– 26 December; US Naval Observatory, http://aa.usno. navy.mil/data/docs/RS_OneDay.html). Ocean depth at the locations where tags popped up was determined based on the ETOPO2 bathymetry data set (National Geophysical Data Center 2001) using the M_Map package (Pawlowicz 2006) for MATLAB. Results are presented as means ± SD unless otherwise stated.

RESULTS

Details of the 13 *Mobula japanica* (10 males, 3 females) tagged during June of 4 yr with PAT tags are presented in Table 1.

Length–width relationship

The length–width relationship of *Mobula japanica* was determined based on our measurements (9 males, 3 females, 50 to 104 cm disc length). The best fit (r^2 = 0.97) was obtained with a linear regression given by width = 2.1378 × length – 0.8826, and this equation was used to estimate disc width for individuals where only length was measured. Mean disc length was 93.7 ± 13.3 cm, giving an estimated mean disc width of 199.5 ± 30.0 cm (Table 1). Based upon an estimate at which the onset of sexual maturity occurs (Notarbartolo-di-Sciara 1988, Serrano-López 2009), 7 rays (5 males, 2 females) were sexually mature.

Depth and temperature utilization

The movement and depth utilization profiles of a typical *Mobula japanica* (Mx06-14) are shown in Fig. 1. Tagged *Mobula japanica* stayed almost always in the upper 50 m of the water column, 89.5 ± 3.1% of time during the day and 96.8 ± 3.5% at night (Fig. 2a), and spent over half their time in the upper 5 m, 50.5 ± 7.3% during the day and 63.3 ± 6.2% at

Table 1. *Mobula japanica*. Characteristics of tagged individuals in the southern Gulf of California. Depths at start 150 ± 87 m. ID: identification; M: male, F: female

Ray ID	Sex	Disc length (cm)	Disc width (cm)	Date Tagging	Date Pop-up	Days	Start latitude (°N)	Start longitude (°W)	End latitude (°N)	End longitude (°W)	End depth (m)
Mx04_2[a]	M	102	217[b]	17 Jun 04	31 Jul 04	44	24.83	110.53	22.56	110.12	−2990
Mx05_3[a]	F	109	232[b]	18 Jun 05	1 Dec 05	166	24.83	110.53	20.11	110.05	−2748
Mx05_5[a]	M	112	238[b]	21 Jun 05	26 Dec 05	188	24.84	110.53	20.29	111.48	−3267
Mx05_4[a]	F	103	219[b]	21 Jun 05	4 Aug 05	44	24.84	110.53	24.25	111.60	−202
Mx05_20	M	100	212[b]	23 Jun 05	23 Oct 05	122	24.84	110.53	21.89	111.19	−3242
Mx06_11	M	85	186	14 Jun 06	19 Aug 06	66	24.90	110.51	26.39	109.97	−718
Mx06_12	M	87	196	14 Jun 06	7 Aug 06	54	24.90	110.51	22.21	109.81	−3156
Mx06_14[a]	M	104	224	14 Jun 06	7 Sep 06	85	24.91	110.50	26.58	113.49	−57
Mx06_17	M	78	160	17 Jun 06	1 Jul 06	14	24.91	110.52	26.31	109.66	−390
Mx06_22	M	84	178	18 Jun 06	23 Sep 06	97	24.91	110.50	25.05	109.43	−1494
Mx07_17[a]	M	101	220	21 Jun 07	9 Sep 07	80	24.74	110.65	23.06	110.69	−1433
Mx07_32	F	86	170	25 Jun 07	21 Jul 07	26	24.75	110.65	24.38	110.68	−22
Mx07_33	M	68	142	25 Jun 07	23 Sep 07	90	24.74	110.66	26.00	111.11	−26

[a]Sexual maturity based on Notarbartolo-di-Sciara (1988) and Serrano-Lopez (2009).
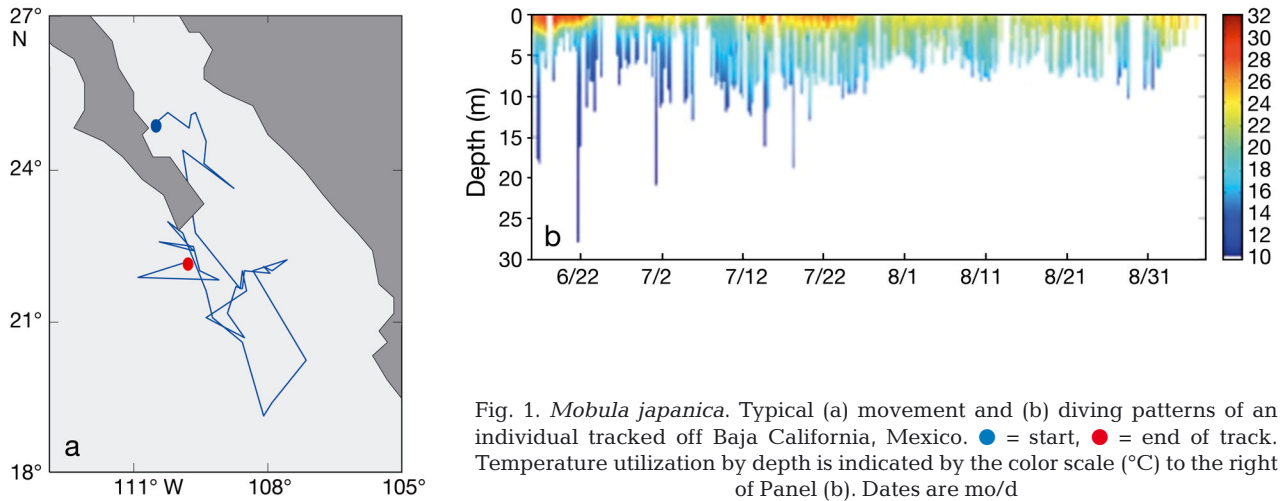[b]Estimated using length–width equation (see 'Results')

Fig. 1. *Mobula japanica*. Typical (a) movement and (b) diving patterns of an individual tracked off Baja California, Mexico. ● = start, ● = end of track. Temperature utilization by depth is indicated by the color scale (°C) to the right of Panel (b). Dates are mo/d

night. As a result, *M. japanica* spent 80.7 ± 1.8% of daylight and 87 ± 2.8% of nighttime hours in relatively warm water between 20 and 30°C (Fig. 2b).

Geographic movements

The tracking periods averaged 83 ± 52 d, with a maximum of 188 d, for a total of 1076 d. Most individuals moved from the southern Gulf of California (where tagging occurred) to the Pacific coast of Baja California Sur as summer progressed. The mean depth of the water where rays were tagged was 150 ± 87 m; at the end of their tracks it was 1515 ± 1378 m depth, indicating that the individuals tended to move from nearshore coastal habitat in the Gulf to offshore neritic or pelagic habitat on the Pacific side during the tracking period. Three rays ended their tracks in shelf waters shallower than 200 m, 3 on slope waters of 200 to 1000 m and 7 in pelagic waters deeper than 1000 m. Dispersal from the tagging location was not rapid. Kernel density analysis shows that the 50% core region of occupancy was centered in the La Paz area during June, with the individuals slowly moving out of the Gulf of California, west around the Baja California Peninsula and then north into Bahia Ulloa as the summer progressed (Fig. 3).

DISCUSSION

Vertical habitat and behavior

Mobula japanica inhabits tropical and subtropical waters, such that its surface environment is primarily warmer than 20°C. Notarbartolo-di-Sciara (1988)

found that *M. japanica* feed almost exclusively upon the euphausiid *Nyctiphanes simplex*. As most euphausiids, *N. simplex* undergoes a diel migration: grazing at the surface at night and aggregating at depths >50 m during the day (Brinton 1967). Although *M. japanica* occasionally made short daytime excursions to deeper depths where it encountered waters in the range of 12°C, individuals spent the majority of their time well above the deep scattering layer both day and night, at depths <50 m. Thus, it is likely that *M. japanica* feeds primarily at night when their prey undergo a diel migration to the surface (Brinton 1967, Gómez-Gutiérrez et al. 2010). This contrasts with the diving depth of other *N. simplex* predators in the Gulf of California such as Humboldt squid *Dosidicus gigas* and fin whales *Balaenoptera physalus*, which consistently dive to depths >100 m (Croll et al. 2001, Gilly et al. 2006) to feed on euphausiids during the day.

It is less clear why *Mobula japanica* spent extensive periods during the day in waters <5 m, where their prey are largely absent. Generally these waters are >25°C, perhaps providing a thermal advantage for metabolic processes. Mobulid rays have a cranial rete system that likely serves as a counter-current heat exchanger to warm the brain, indicating physiological adaptation for temperature control (Alexander 1996). Temperature can profoundly affect physiological processes in poikilotherms (Hochachka & Somero 2002) such that behavioral preferences for warmer waters in the upper few meters of the surface have the potential to provide significant physiological advantages to mobulid rays, especially during the daytime when prey are not available in surface waters.

Alternatively, *Mobula japanica* may have been limited by oxygen availability. The eastern margin of the
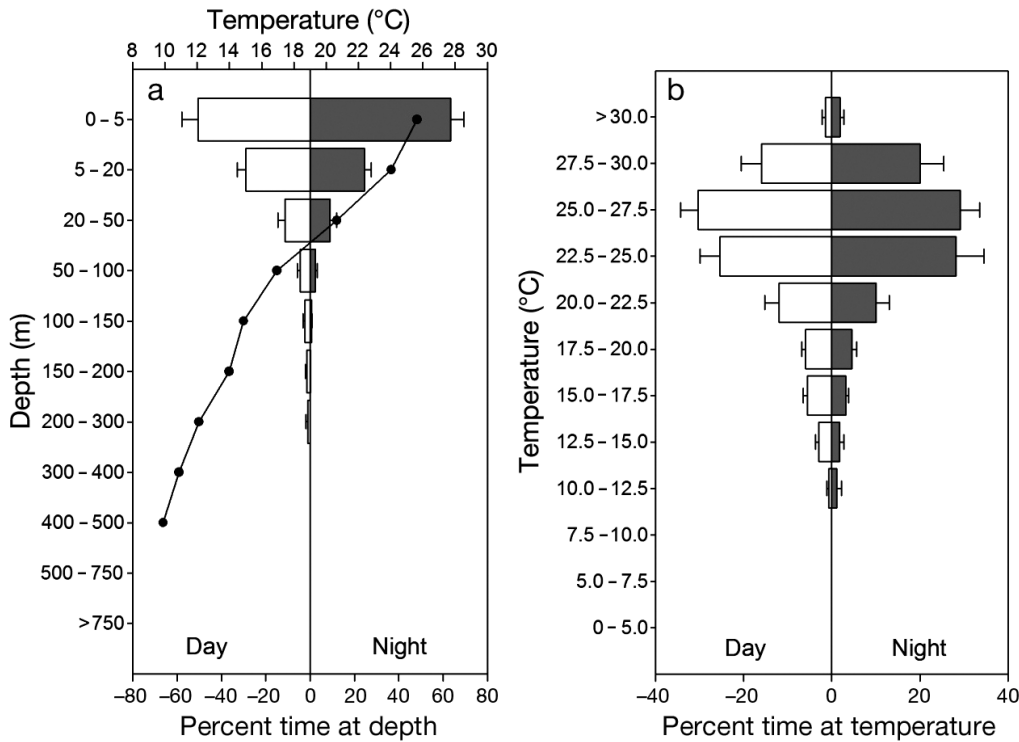
Fig. 2. *Mobula japanica*. Depth and thermal habitat off Baja California, Mexico. (a) Percent time at depth (bars) during the day (white) and night (gray), and mean temperature at depth (line). (b) Percent time at temperature (°C) during the day (white) and night (gray). Mean + SE

southern Gulf of California has an oxygen minimum as shallow as 150 m (Lluch-Cota et al. 2007). Air-breathing species such as whales are not limited by the oxygen minimum layer, and some gill-ventilating organisms such as the Humboldt squid have apparently adapted to low oxygen conditions (Gilly et al. 2006). Tagged *M. japanica* frequently undertook dives deeper than this oxygen minimum layer, indi-

cating that they may be tolerant to limited hypoxia. However, these dives were shorttime, suggesting that they may have incurred an oxygen debt. Temperature at these depths was typically <15°C, which may also have been a factor limiting the duration. Whale sharks *Rhincodon typus* tracked in the Gulf of California similarly spent the majority of their time in waters shallower than 10 m, infrequently diving to depths >200 m (Eckert & Stewart 2001), perhaps related to constraints imposed by the oxygen minimum layer.
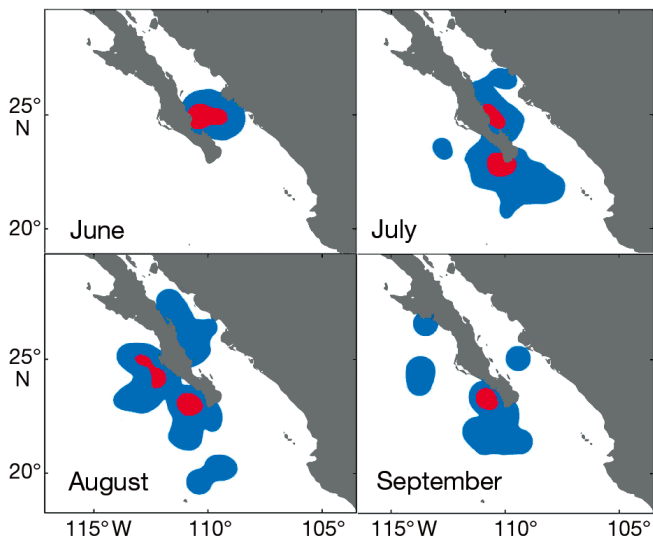
Geographic range

Mobula japanica utilizes a broad geographic range including both coastal and pelagic waters. The most important habitats for the tagged *M. japanica* were the southern Gulf of California, the Pacific coastal waters of Baja California Sur and the pelagic waters between the Revillagigedos Islands and Baja California. These waters are also a focal area for a number of top predators including sharks, whales, sea turtles and tuna (Block et al. 2011). The co-occurrence of vulnerable top predators and commercial species has also led to a concentration of artisanal and industrial purse-seine fisheries in the region. These fisheries have been shown to affect other wide-ranging species such as

Fig. 3. *Mobula japanica*. Weighted fixed-kernel density distributions (blue: 95%; red: 50%) of 13 tagged individuals, June–September

sea turtles (Seminoff et al. 2002, Peckham et al. 2008). Mobulid fisheries data from this area are lacking, but similar fisheries in the Gulf of California have been shown to impose directed and by-catch mortality of mobulids (Notarbartolo-di-Sciara 1988, Bizzaro 2001, Chong-Robles 2006, Sampson et al. 2010).

The large home range and global distribution of *Mobula japanica* indicates that it is less susceptible to extirpation than geographically restricted species from the Gulf of California such as the totoaba *Totoaba macdonaldi* or vaquita *Phocoena sinus* (Lluch-Cota et al. 2007). However, their large home range and migratory lifestyle also means that *M. japanica* cannot be protected by means of small marine reserves and managed areas (Woodroffe & Ginsberg 1998). Detailed genetic analysis of the global population structure of *M. japanica* is a next step towards informing the global conservation of this species.

Trophic dynamics and foraging ecology

Mobula japanica is a stenophagous predator, feeding almost exclusively upon the subtropical euphausiid *Nyctiphanes simplex* (Notarbartolo-di-Sciara 1988, Sampson et al. 2010). Thus, the movements of *M. japanica* are likely largely driven by seasonal and geographic patterns in the availability of *N. simplex* which show strong correlations with the warmer sub-tropical to tropical water masses along the Pacific Coast of Baja Peninsula year-round (Brinton & Townsend 2003). Inside the southern Gulf of California, *N. simplex* abundance peaks during spring with wind and tidally driven upwelling, and then decreases into summer (Brinton & Townsend 1980, de Silva-Dávila & Palomares-García 1998). In the Pacific, on the coastal shelf of Bahia Magdalena, *N. simplex* abundance also peaks during late spring and summer during enhanced coastal upwelling and declines when temperatures increase during autumn (Gómez-Gutiérrez et al. 1996). *M. japanica* have largely moved out of the Gulf of California by July, corresponding of the seasonal decline to *N. simplex* in the Gulf late in the spring and increasing abundance off southwestern Baja California in June and July (Gómez-Gutiérrez et al. 1996, de Silva-Dávila & Palomares-García 1998). Warm tropical water intrudes into the southwestern Baja California region in late summer or early fall, leading to steep declines in *N. simplex* abundance (de Silva-Dávila & Palomares-García 1998). Our tags were not retained long enough on the rays to track their response to these declines, but we speculate that they move to other regions of higher local productivity at that time.

In filter-feeding vertebrates, the energetics of foraging requires prey organisms to exceed threshold densities to make foraging profitable (Sims 1999). Basking sharks facultatively seek out habitats in which prey densities are likely to be higher (Sims et al. 2006), whereas whale sharks have been shown to feed on high densities of copepods in the Gulf of California (Clark 1997, Hacohen-Domene et al. 2006) as well as high densities of fish spawn in Belize (Heyman et al. 2001). Blue whales *Balaenoptera musculus* are able to access high densities of euphausiids in regions where upwelling occurs near steep topographic relief (Croll et al. 1998). Although estimates of this density threshold have not been made for mobulid rays, it is likely that they cannot sustain themselves where zooplankton occur at low densities and must take advantage of regions where physical or biological processes aggregate their prey. Anderson et al. (2011) found that migrations of *Manta alfredi* in the Maldives are driven by zooplankton abundance, supported by seasonal increases in primary production on the downstream sides of the atolls, which is driven by annual patterns of monsoon-driven currents. Thus, the large-scale movement patterns of *Mobula japanica* are likely best explained by seasonal patterns in euphausiid availability combined, perhaps, with limitations imposed by water temperature in the upper 5 to 10 m of the water column.

Conservation and management

The Gulf of California and the adjacent Pacific coastal waters of Baja California Sur comprise a highly complex system with a diversity of fisheries presenting multiple challenges for management (Lluch-Cota et al. 2007). Both small-scale artisanal and large-scale commercial fisheries in the region induce extensive directed or bycatch mortality on a range of long-lived species susceptible to overexploitation (Chong-Robles 2006, Peckham et al. 2008, Bizzarro et al. 2009, Galván-Magaña 2009). *Mobula japanica* is exceptionally vulnerable to fisheries over-exploitation because of its delayed maturity and low reproductive rates (White et al. 2006). Although their targeted take is prohibited in Mexico (NOM-029-PESC 2004), illegal artisanal-targeted mortality as well as substantial artisanal and large-scale fisheries bycatch mortality persist (D. A. Croll pers. obs.). Our

information on the seasonal movements and habitat preferences of mobulid rays provides data needed for the development of effective fisheries management policies for mobulids. There are a number of marine protected areas in the Gulf of California (Lluch-Cota et al. 2007), but these are far smaller than the home range of *M. japanica* as demonstrated by our study. Therefore, marine protected areas are unlikely to provide significant protection from fisheries. Instead, the enforcement of current for the rays species-based protection combined with additional policies that reduce mobulid bycatch are likely to be the best policies to avoid catastrophic decline of this charismatic species.

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