Seeking the sun in deep, dark places: mesopelagic sightings of ocean sunfishes (Molidae)

ARTICLE *in* JOURNAL OF FISH BIOLOGY · SEPTEMBER 2015

Impact Factor: 1.73 · DOI: 10.1111/jfb.12769

Journal of FISH BIOLOGY

Journal of Fish Biology (2015)
doi:10.1111/jfb.12769, available online at wileyonlinelibrary.com

BRIEF COMMUNICATION

Seeking the sun in deep, dark places: mesopelagic sightings of ocean sunfishes (Molidae)

N. D. Phillips*†, C. Harrod‡, A. R. Gates§, T. M. Thys|| and J. D. R. Houghton*¶

**School of Biological Sciences, Queen's University Belfast MBC Building, 97 Lisburn Road, Belfast, BT9 7BL, U.K., ‡Instituto de Ciencias Naturales Alexander von Humboldt, Universidad de Antofagasta, Avenida Angamos 601, Antofagasta, Chile, §National Oceanography Centre, University of Southampton, European Way, Southampton SO14 3ZH, U.K., ||California Academy of Science, 55 Music Concourse Drive, Golden Gate Park, San Francisco, CA, 94118 U.S.A. and ¶Institute of Global Food Security, Queen's University Belfast 123 Stranmillis Road, County Antrim, Belfast, BT9 5AG, U.K.*

(Received 27 March 2015, Accepted 30 June 2015)

Evidence is presented from publicly available remotely operated vehicle (ROV) footage that suggests deep-water ranging in ocean sunfishes (family Molidae) is more common than typically thought, including a new maximum depth recorded for the southern sunfish *Mola ramsayi*.

Key words: diving behaviour; foraging; *Mola mola*; remotely operated vehicle; SERPENT Project.

The family Molidae, or the ocean sunfishes, is currently believed to comprise four widely distributed species: the ocean sunfish *Mola mola*, (L. 1758), sharptail sunfish *Masturus lanceolatus* (Liénard 1840), southern sunfish *Mola ramsayi* (Giglioli 1883) and slender sunfish *Ranzania laevis* (Pennant 1776), although the taxonomy remains uncertain, with the possible existence of several currently undescribed species (Bass *et al.*, 2005; Pope *et al.*, 2010). Often seen basking at the surface, there was a long held perception that these species were rare, inactive drifters feeding solely on gelatinous zooplankton (Pope *et al.*, 2010). An increasing number of recent studies, however, have shown these notions to be far from accurate, with evidence of long-distance migrants travelling *c.* 27 km day^{-1} (Cartamil & Lowe, 2004), displaying deep diving behaviours (Hays *et al.*, 2009; Sims *et al.*, 2009) and consuming a mixed diet (Syväranta *et al.*, 2012; Nakamura & Sato, 2014). More specifically, there is now strong evidence of cryptic benthivory in these typically pelagic fishes (Harrod *et al.*, 2013) and records of deep-water forays to feed on colonial gelata such as siphonophores (Nakamura & Sato, 2014; Nakamura *et al.*, 2015). Taken together, a picture of an active migrant feeding broadly within marine food webs has emerged, but observational data to validate

†Author to whom correspondence should be addressed. Tel.: +44 28 9097 2620; email: nphillips01@qub.ac.uk.

behavioural studies remain difficult to come by (Houghton *et al.*, 2000). Serendipitous sightings of three sunfish species are presented here, sourced from industrial and research submersibles, providing further evidence of the deep ranging capabilities of the Molidae. More broadly, these records taken together with previous remotely operated vehicle (ROV) sightings of a hammerhead shark *Sphyrna lewini* (Griffith & Smith 1834) (Moore & Gates, 2015) add weight to the idea that mesopelagic environments may be of greater importance than thought previously for taxa often considered as epipelagic.

Sighting data were sourced primarily from the scientific and environmental ROV partnership using existing industrial technology (SERPENT) project (Jones *et al.*, 2009). As direct observations of marine life in the deep sea are often prohibitively expensive, this collaboration enables scientists to browse video footage shot by industrial ROVs, providing rare access to life in the open ocean and sightings of much understudied species *e.g.* oarfish *Regalecus glesne* Ascanius 1772 (Benfield *et al.*, 2013) and deep sea squid *Grimalditeuthis bonplandi* (Hoving *et al.*, 2013). Other data were sourced from ROV footage available online or through personal communications (see Fig. 1 and Table I).

A total of 13 anecdotal sightings of Molidae were obtained at depths of up to 550 m (Table I). Eleven animals were recorded from depths of >160 m, with eight of these individuals exceeding 200 m. Aside from the general pattern of mid-water ranging, the Australian sighting of a *M. ramsayi* at 483 m probably constitutes the deepest record for this species to date. The only previous record of depth use for this species came from the Sea of Oman (Sea & Bejgan, 2014) where an individual was caught in a trawl at 85 m. For context, the maximum depths previously recorded from sunfishes were 844 m for *M. mola* (Potter & Howell, 2011) and 670 m for *M. lanceolatus* (Harbison & Janssen, 1987), which suggests that 483 m is unlikely to represent a maximum for *M. ramsayi* given the gross morphological similarities between these species.

Previous studies have intimated that such movements of Molidae into deeper water may be a means of locating deep or vertically migrating zooplankton prey (Cartamil & Lowe, 2004; Sims *et al.*, 2009; Dewar *et al.*, 2010; Nakamura *et al.*, 2015). Typically, such forays to depth constitute daytime bouts of V-shaped dives punctuated by periods at the surface (Cartamil & Lowe, 2004; Dewar *et al.*, 2010). Recently, Nakamura *et al.* (2015) verified that the main function of surfacing is the recovery of body temperature, with the fish increasing heat gain from the warm surface water by physiological regulation (Hays, 2015). The data presented here may be aligned with such behaviour given that the greatest depths of sunfishes recorded from the ROV footage (Table I) occurred during the day (0600 to 1800 hours) but with some diving activity at night (with maximum depth of 306 m recorded at 0130 hours). Such daytime excursions to mesopelagic depths (albeit rarely) have also been documented in leatherback turtles *Dermochelys coriacea*, with the overall assertion that individuals were speculating for vertically ascending gelatinous zooplankton, rather than feeding at depth (Houghton *et al.*, 2008). From the ROV footage (Fig. 1), no comment can be made on whether these observations constituted brief (*i.e.* speculative), or prolonged (*i.e.* feeding) excursions to depth or the behaviour prior to or following such events. These data, however, can provide visual observations over a broad geographical range to support the notion that ocean sunfishes routinely dive below the epipelagic zone.

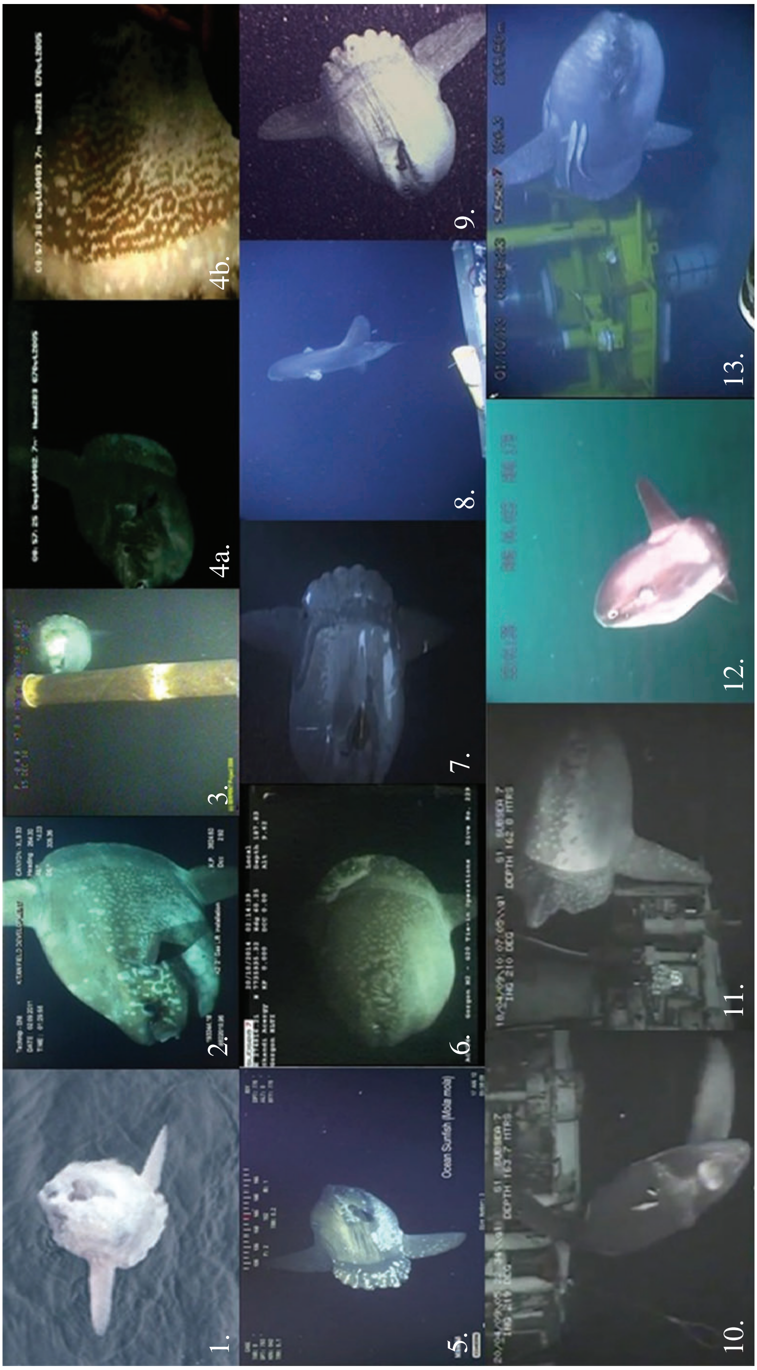

FIG. 1. Incidental sightings of ocean sunfishes; photographs and stills from remotely operated vehicle (ROV) video footage. The number on figures refers to individuals in Table I (see Table I for location and depth data also). The footage of individuals was clear enough for reliable identification of species. For example, the image of individual 11 clearly shows the distinctive sharp tail that is diagnostic of *Masturus lanceolatus*, whilst images 4(a) and 4(b) show the increased band of denticles with closely situated ossicles that are indicative of *Mola ramsayi*. Interesting behaviours were also identified from these brief encounters such as for individual 10 which can be clearly seen in the video footage scratching itself against the rig structure.

Table I. Observation records of ocean sunfishes. Full co-ordinates are given, where known, otherwise general location is stated

Observation number	Date	Local time (hours)	Location: geographical co-ordinates	Species	Depth (m)	Reference
1	10 September 2004	–	North Sea, west of Shetland, U.K. 60° 20′ 03″ N; 4° 05′ 56″ W	*Mola mola*	0	SERPENT Archives (Jones *et al.*, 2009)
2	2 September 2011	0129	Indian Ocean, Timor, Western Australia 10° 38′ 37″ S; 126° 11′ 50″ E	*Mola mola*	305	SERPENT Archives (Jones *et al.*, 2009)
3	15 December 2010	2215	South Atlantic, Congo, West Africa	*Mola mola*	110	SERPENT Archives (Jones *et al.*, 2009)
4	7 December 2005	0857	Indian Ocean, Australia 18° 30′ 00″ S; 115° 30′ 00″ E	*Mola ramsayi*	483	SERPENT Archives (Jones *et al.*, 2009)
5	17 August 2012	0558	North Atlantic, Gulf of Mexico	*Mola mola*	242	SERPENT Archives (Jones *et al.*, 2009)
6	20 October 2014	0213	Indian Ocean, Australia 20° 28′ 53·2″ S; 114° 24′ 37·6″ E	*Mola mola*	193	SERPENT Archives (Jones *et al.*, 2009)
7	10 November 2002	0922	North Atlantic, Florida 27° 44′ 8″ N; 91° 13′ 3″ W	*Mola mola*	401	2002 R.V. *Seward Johnson II* Fall Cruise (Cordes, 2009)
8	19 May 2007	1417	North Atlantic, Gulf of Cadiz 35° 17′ 914″ N; 6° 38′ 709″ W	*Masturus lanceolatus*	348	Tyler (pers. comm.) JC10 R.V. *James Cook* cruise 2009
9	1 July 2001	–	North Atlantic, Dry Tortugas, Florida Keys 24° 43′ N; 82° 52′ W	*Mola mola*	550	Thys (pers. comm.) 2001 Islands in the Stream Expedition S. A. Earle/Sustainable Seas Expedition
10	20 April 2009	1008	Location unknown	*Masturus lanceolatus*	167	SERPENT Archives (Jones *et al.*, 2009; Subsea, 2009*b*)

TABLE I. Continued

Observation number	Date	Local time (hours)	Location: geographical co-ordinates	Species	Depth (m)	Reference
11	18 April 2009	0849	Location unknown	*Masturus lanceolatus*	164	SERPENT Archives (Jones *et al.*, 2009; Subsea, 2009*b*)
12	17 October 2008	2201	Location unknown	*Mola mola*	50	Californian District Fisheries and Wildlife Archives (CDFW, 2008)
13	1 October 2013	0158	Location unknown	*Mola mola*	206	SERPENT Archives (Jones *et al.*, 2009)

With respect to prey acquisition at depth, low levels of mesopelagic light suggest that the Molidae possess adequate visual acuity at depth to hunt mobile prey, potentially in combination with other senses such as olfaction, (Hara, 1994). Visual acuity, determined from immature *M. mola*, was calculated at 3·5–4·3 cycles per degree (Kino *et al.*, 2009), similar to values recorded from some adult sharks [*e.g.* 3·8: *Galeus melastomus* Rafinesque 1810 and 2·8: *Etmopterus spinax* (L. 1758); Bozzano & Collin, 2000] and higher than those from adult cetaceans (*e.g.* 2·7: *Lagenorhynchus obliquidens* and 2·6: *Delphinapterus leucas*; Murayama & Somiya, 1998). As visual acuity typically increases over the lifetime of an individual (Fritsches & Marshall, 2003), this value is likely to increase for mature sunfishes. Eye size usually reflects the importance of vision to a species (Walls, 1942) and the large eyes of the Molidae support the suggestion by Hays *et al.* (2003) that ambient light levels at prey field depths may be important in determining foraging success in marine predators. Ocean sunfish eyeball diameter data have only been published from juveniles (total length, L_T, <1 m), with maximum eye diameter of 38 mm (Cleland, 1862). This is comparatively large when considering other pelagic predators [*Carcharodon carcharias* (L. 1758) 37·1 mm and *S. lewini* 25·5 mm; Lisney & Collin, 2007] with the overall inference that Molidae are well adapted to foraging at depth. Moreover, as gelatinous zooplankton may be difficult to locate while looking down through the water column, diving to depth may allow such species to be silhouetted against down-welling light during re-ascent.

Alternatively, prey densities at depth may simply be sufficient to warrant exploration in low-light conditions, although the mechanisms for detection are not yet fully understood. Davenport (1988) and Davenport & Balazs (1991) suggested that the Molidae and leatherback turtles may use luminescence to help in their search for deep prey (*e.g.* pyrosomes); however, as such behaviour was not observed here, it is not possible to comment further. The potential for the ROV lights themselves to attract sunfishes must also be acknowledged, given that baited remote underwater video systems (BRUVS) routinely employ illumination to entice animals closer to the camera (Harvey *et al.*, 2012; Fitzpatrick *et al.*, 2013; De Vos *et al.*, 2014). This matter aside, gelata are certainly present at depth in open water and can constitute 50–80% of the integrated standing crop by volume (Angel & Pugh, 2000; Houghton *et al.*, 2008). Qualitatively, there is evidence of putative prey in the Gulf of Mexico from the SERPENT archives (corresponding geographically to the 2012 *M. mola* sighting; Table I) including the scyphomedusa *Stygiomedusa gigantean* (Benfield & Graham, 2010), *Aurelia aurita*, narcomedusae (*Solmissus* spp.), salps and ctenophores, suggesting deep-water feeding behaviour warrants further investigation.

Within this collection of mesopelagic encounters, there was one sighting of specific interest where an *M. lanceolatus* was filmed interacting with the physical structure of the rig itself. Given that the Molidae can be highly parasitized (Fraser-Brunner, 1951) and have been observed undertaking many behaviours suggested to reduce parasite loads (*e.g.* attracting sea birds; Abe *et al.*, 2012, aggregating at reef cleaning stations and breaching; Konow *et al.*, 2006), the rig structure may offer a hard surface to rub against. In the relatively featureless open ocean, such opportunities are lacking which may explain the behaviour of the 2009 *M. lanceolatus* sighting at 167 m (see Table I; Subsea, 2009*a*). The video footage here clearly shows the *M. lanceolatus* using the platform's framework to scratch itself, suggesting that such structures might provide a service for sunfishes throughout the water column.

Another sighting of specific interest was recorded in 2004 to the west of Shetland (Table I). This record was not collected from great depth, but in surface waters, where an *M. mola* was observed at 60° N, close to the reported northerly limit of the *M. mola* range, where they are sighted rarely. This northerly boundary may be temperature constrained as *M. mola* in the north-east Atlantic Ocean have been recorded spending 99% of the time in water temperatures between 10 and 19° C (Sims *et al.*, 2009). Despite its northerly location, this individual was sighted in September when the average sea surface temperature off Shetland is 12·7° C (World Sea Temperatures, 2015), well within the stated *M. mola* temperature range. Consequently, it is unlikely that the scarcity of *M. mola* sightings in this area reflects thermal tolerances alone.

In conclusion, this paper provides repeated evidence of mid-water ranging in the Molidae using anecdotal sightings from publicly available ROV footage. These data suggest that sunfishes are more common in the mesopelagic zone than previously thought, in line with deep-water forays of other typically epipelagic species. A new depth record is also presented for the *M. ramsayi* sighted at 483 m and a rare observation of an *M. mola* north of 60° N. These data show the importance of collaborations between commercial enterprises and academics, providing access to anecdotal sightings that have the potential to significantly increase the understanding of rarely encountered fish species. Such evidence also serves to highlight the increasing realization that the Molidae are far more complex in their ecology than previously thought.

The authors would like to thank E. Egbore and H. Escott from Subsea 7 and M. Benfield from Louisiana State University, along with P. Tyler from the National Oceanography Centre Southampton for their contribution of sunfish sightings and videos. Thanks also to L. Eagling for proof-reading the manuscript on more than one occasion. We would like to thank the three reviewers and Associate Editor for their comments which improved this manuscript.

References

Abe, T., Sekiguchi, K., Onishi, H., Muramatsu, K. & Kamito, T. (2012). Observations on a school of ocean sunfish and evidence for a symbiotic cleaning association with albatrosses. *Marine Biology* **159,** 1173–1176.

Angel, M. V. & Pugh, P. R. (2000). Quantification of diel vertical migration by macroplankton and micronektonic taxa in the northeast Atlantic. *Hydrobiologia* **440,** 161–179.

Bass, A. L., Dewar, H., Thys, T., Streelman, J. T. & Karl, S. A. (2005). Evolutionary divergence among lineages of ocean sunfish family, Molidae. *Marine Biology* **414,** 148–405.

Benfield, M. C. & Graham, W. M. (2010). *In situ* observations of *Stygiomedusa gigantean* in the Gulf of Mexico with a review of its global distribution and habitat. *Journal of the Marine Biological Association of the United Kingdom* **90,** 1079–1093.

Benfield, M. C., Cook, S., Sharuga, S. & Valentine, M. M. (2013). Five *in situ* observations of live oarfish *Regalecus glesne* by remotely operated vehicles in the oceanic waters of the northern Gulf of Mexico. *Journal of Fish Biology* **83,** 28–38.

Bozzano, A. A. & Collin, S. P. (2000). Retinal ganglion cell topography in elasmobranchs. *Brain, Behavior and Evolution* **55,** 191–208.

Cartamil, D. P. & Lowe, C. G. (2004). Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Marine Ecology Progress Series* **266,** 245–253.

Cleland, J. (1862). On the anatomy of the short sunfish (*Orthragoriscus mola*). *Natural History Review* **2,** 170–185.

Davenport, J. (1988). Do diving leatherbacks pursue glowing jelly? *British Herpetological Society Bulletin* **24,** 20–21.

Davenport, J. & Balazs, G. H. (1991). “Fiery Bodies” -are pyrosomes an important component of the diet of leatherback turtles? *British Herpetological Society Bulletin* **37**, 33–38.

De Vos, L., Gotz, A., Winker, H. & Attwood, C. G. (2014). Optimal BRUVs (baited remote underwater video system) survey design for reef fish monitoring in the Stilbaai Marine Protected Area. *African Journal of Marine Science* **36,** 1–10.

Dewar, H., Thys, T., Teo, S. L. H., Farwell, C., O'Sullivan, J., Tobayama, T., Soichi, M., Nakatsubo, T., Kondo, Y., Okada, Y., Lindsay, D. J., Hays, G. C., Walli, A., Weng, K., Streelman, J. T. & Karl, S. A. (2010). Satellite tracking the world's largest jelly predator, the ocean sunfish, *Mola mola*, in the Western Pacific. *Journal of Experimental Marine Biology and Ecology* **393,** 32–42.

Fitzpatrick, C., McLean, D. & Harvey, E. S. (2013). Using artificial illumination to survey nocturnal reef fish. *Fisheries Research* **146,** 41–50.

Fraser-Brunner, A. (1951). The ocean sunfishes (Family Molidae). *Bulletin of the British Museum (Natural History) Zoology* **1,** 87–121.

Fritsches, K. A. & Marshall, N. J. (2003). Retinal specializations in the blue marlin: eyes designed for sensitivity to low light levels. *Marine and Freshwater Research* **4,** 333–341.

Hara, T. J. (1994). The diversity of chemical stimulation in fish olfaction and gustation. *Reviews in Fish Biology and Fisheries* **4,** 1–35.

Harbison, G. R. & Janssen, J. (1987). Encounters with a swordfish (*Xiphias gladius*) and sharptail mola (*Masturus lanceolatus*) at depths greater than 600 meters. *Copeia* **1987,** 511–513.

Harrod, C., Syväranta, J., Kubicek, L., Cappanera, V. & Houghton, J. D. R. (2013). Reply to Logan & Dodge: "Stable isotopes challenge the perception of ocean sunfish *Mola mola* as obligate jellyfish predators". *Journal of Fish Biology* **82,** 10–16.

Harvey, E. S., Butler, J. J., McLean, D. L. & Shand, J. (2012). Contrasting habitat use of diurnal and nocturnal fish assemblages in temperate Western Australia. *Journal of Experimental Marine Biology and Ecology* **426,** 78–86.

Hays, G. C. (2015). New insights: animal-borne cameras and accelerometers reveal the secrets of cryptic species. *Journal of Animal Ecology* **84,** 587–589.

Hays, G. C., Broderick, A. C., Godley, B. J., Luschi, P. & Nichols, W. J. (2003). Satellite telemetry suggests high levels of fishing-induced mortality in marine turtles. *Marine Ecology Progress Series* **262,** 305–309.

Hays, G. C., Farquhar, M. R., Luschi, P., Teo, S. L. H. & Thys, T. M. (2009). Vertical niche overlap by two ocean giants with similar diets: ocean sunfish and leatherback turtles. *Journal of Experimental Marine Biology and Ecology* **370,** 134–143.

Houghton, J. D. R., Woolmer, A. & Hays, G. C. (2000). Sea turtle diving and foraging behaviour around the Greek Island of Kefalonia. *Journal of the Marine Biological Association of the United Kingdom* **80,** 761–762.

Houghton, J. D. R., Doyle, T. K., Davenport, J., Wilson, R. P. & Hays, G. C. (2008). The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*). *Journal of Experimental Biology* **211,** 2566–2575.

Hoving, H. J. T., Zeidberg, L. D., Benfield, M. C., Bush, S. L., Robison, B. H. & Vecchione, M. (2013). First in situ observations of the deep-sea squid *Grimalditeuthis bonplandi* reveal unique use of tentacles. *Proceedings of the Royal Society B* **280,** 1769.

Kino, M., Miayzaki, T., Iwami, T. & Kohbara, J. (2009). Retinal topography of ganglion cells in immature ocean sunfish, *Mola mola*. *Environmental Biology of Fishes* **85,** 33–38.

Konow, N., Fitzpatrick, R. & Barnett, A. (2006). Adult emperor angelfish (*Pomacanthus imperator*) clean giant sunfishes (*Mola mola*) at Nusa Lembongan, Indonesia. *Coral Reefs* **25,** 208.

Lisney, T. J. & Collin, S. P. (2007). Relative eye size in elasmobranchs. *Brain, Behavior and Evolution* **69,** 266–279.

Moore, A. & Gates, A. R. (2015). Deep-water observation of scalloped hammerhead Sphyrna lewini in the western Indian Ocean off Tanzania. *Marine Biodiversity Records* **8,** 91–95.

Murayama, T. & Somiya, H. (1998). Distribution of ganglion cells and object localizing ability in the retina of three cetaceans. *Fisheries Science* **64,** 27–30.

Nakamura, I. & Sato, K. (2014). Ontogenetic shift in foraging habit of ocean sunfish *Mola mola* from dietary and behavioral studies. *Marine Biology* **161,** 1263–1273.

Nakamura, I., Goto, Y. & Sato, K. (2015). Ocean sunfish rewarm at the surface after deep excursions to forage for siphonophores. *Journal of Animal Ecology* **83,** 1365–2656.

Pope, E. C., Hays, G. C., Thys, T. M., Doyle, T. K., Sims, D. W., Queiroz, N., Hobson, V., Kubicek, L. & Houghton, J. (2010). The biology and ecology of the ocean sunfish *Mola mola*: a review of current knowledge and future research perspectives. *Reviews in Fish Biology and Fisheries* **20,** 471–487.

Potter, I. F. & Howell, W. H. (2011). Vertical movement and behavior of the ocean sunfish, *Mola mola*, in the northwest Atlantic. *Journal of Experimental Marine Biology and Ecology* **396,** 138–146.

Sea, N. O. & Bejgan, N. (2014). The first record of Southern Ocean sunfish, *Mola ramsayi* from Northern Oman Sea, Iran. *Iranian Journal of Fisheries Sciences* **13,** 242–246.

Sims, D. W., Queiroz, N., Doyle, T. K., Houghton, J. D. R. & Hays, G. C. (2009). Satellite tracking of the World's largest bony fish, the ocean sunfish (*Mola mola*) in the North East Atlantic. *Journal of Experimental Marine Biology and Ecology* **370,** 127–133.

Syväranta, J., Harrod, C., Kubicek, L., Cappanera, V. & Houghton, J. D. R. (2012). Stable isotopes challenge the perception of ocean sunfish *Mola mola* as obligate jellyfish predators. *Journal of Fish Biology* **80,** 225–231.

Walls, G. L. (1942). The vertebrate eye and its adaptive radiation. *Optometry and Vision Science* **20,** 30–32.

Electronic References

CDFW (2008). *The California Department of Fish and Wildlife ROV Footage*. Available at https://www.youtube.com/watch?v=ETbF_UTzKqs/ (last accessed 10 March 2015).

Cordes, E. (2009). *2002 Seward Johnson II Fall Cruise Report*. Available at http://deepseanews.com/2009/06/reflections-on-the-johnson-sea-link-dr-cordes/ (last accessed 10 March 2015).

Jones, D. O. B., Gates, A. R., Curry, R. A., Thomson, M., Pile, A. & Benfield, M. (Eds) (2009). *SERPENT Project Media Database Archive*. Available at http://archive.serpentproject.com/ (last accessed 12 March 2015).

Subsea (2009a). *Subsea 7 Sunfish Sighting ROV Footage*. Available at https://www.youtube.com/watch?v=2iwnvXCXEeY/ (last accessed 10 March 2015).

Subsea (2009b). *Subsea 7 Sunfish Sighting ROV Footage*. Available at https://www.youtube.com/watch?v=WNNDeM-1heg/ (last accessed 10 March 2015).

World Sea Temperatures (2015). *World Sea Temperatures*: *Shetland Average September Sea Temperatures*. Available at http://www.seatemperature.org/europe/united-kingdom/shetland-september.htm/ (last accessed 10 March 2015).