The biology and ecology of the ocean sunfish *Mola mola*: a review of current knowledge and future research perspectives

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Abstract Relatively little is known about the biology and ecology of the world's largest (heaviest) bony fish, the ocean sunfish *Mola mola*, despite its worldwide occurrence in temperate and tropical seas. Studies are now emerging that require many common perceptions about sunfish behaviour and ecology to be re-examined. Indeed, the long-held view that ocean sunfish are an inactive, passively drifting species seems to be entirely misplaced. Technological advances in marine telemetry are revealing distinct behavioural patterns and protracted seasonal movements. Extensive forays by ocean sunfish into the deep ocean have been documented and

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broad-scale surveys, together with molecular and laboratory based techniques, are addressing the connectivity and trophic role of these animals. These emerging molecular and movement studies suggest that local distinct populations may be prone to depletion through bycatch in commercial fisheries. Rising interest in ocean sunfish, highlighted by the increase in recent publications, warrants a thorough review of the biology and ecology of this species. Here we review the taxonomy, morphology, geography, diet, locomotion, vision, movements, foraging ecology, reproduction and species interactions of *M. mola*. We present a summary of current conservation issues and suggest methods for addressing fundamental gaps in our knowledge.

Introduction

One of the long-standing ironies within marine science remains the paucity of knowledge of many iconic and charismatic species. Gaps in our understanding may reflect a lack of commercial interest in a particular species or an exclusion from the regional and international conservation strategies that focus research efforts upon certain target groups (Sims et al. 2009a). These issues are compounded for many large vertebrates by the inherent difficulties of gathering data in remote locations or when animals are present in seemingly low abundances (Nelson et al. 1997; Doyle et al. 2008). A combination of these factors has contributed to our poor understanding of the world's heaviest bony fish, the ocean sunfish (*Mola mola* L), with outdated or loosely documented facts persisting in the literature. For example, with the possible exception of its notable size (the heaviest recorded *M. mola* measured 2.7 m in length and weighed 2.3 tonnes; Roach 2003; Fig. 1) the most obvious physical characteristic of the ocean sunfish is the degeneration of the vertebral column resulting in the replacement of the caudal fin by a broad, stiff lobe, the *clavus* (Latin: rudder; Fraser-Brunner 1951). This bizarre morphology,

Fig. 1 An ocean sunfish caught off the coast of Kamogawa, Japan in 1996 measuring 2.7 m in length and 2.3 tonnes in weight. Photograph courtesy of Kamogawa Seaworld

likened to a "swimming head" (Thys 1994), led to a perception of these animals as sluggish, inefficient swimmers that is now ceding to one of an active predator capable of protracted oceanic movements independent of prevailing current regimes (Cartamil and Lowe 2004; Sims et al. 2009a). Moreover, we now know that the unusual "basking" behaviour that so often typifies *M. mola* is only a fragment of a complex behavioural repertoire (Watanabe and Sato 2008; Houghton et al. 2009) and recent studies have shown regular deep forays into the open-ocean (Sims et al. 2009a; Hays et al. 2009). Taken together, these findings signpost the need to consolidate our understanding of this species, especially considering recent reports of substantial aggregations of ocean sunfish in coastal waters and the extremely high level of incidental bycatch in regional fisheries in Mediterranean, Californian and South African waters (Silvani et al. 1999; Cartamil and Lowe 2004; Petersen and McDonell 2007). This review attempts to identify unanswered fundamental research questions and suggest techniques for addressing them.

Phylogeny and morphology of the Molidae

Ocean sunfish belong to the family Molidae within the highly derived order Tetraodontiformes (e.g. pufferfish, triggerfish, boxfish), although Molidae's location within Tetraodontiformes is subject to controversy. It is agreed that Molidae is monophyletic (Bass et al. 2005; Santini and Tyler 2004; Yamanoue

et al. 2004, 2008) but the molids have been variously placed as a sister group to Diodontidae (porcupine-fish), Tetraodontidae (pufferfish) + Diodontidae, Ostraciidae (trunkfish) or Diodontidae + Ostraciidae (see Bass et al. 2005; Britz and Johnson 2005; Alfaro et al. 2007). Recent molecular work has suggested a basal split in Tetraodontiformes into Tetraodontoidei (Triacanthidae + Balistidae + Monacanthidae + Tetraodontidae + Diodontidae + Molidae) and Tri-acanthodoidei (Ostraciidae + Triodontidae + Tri-acanthodidae) attributable to ecological radiation into shallow (Tetraodontoidei) and deep (Triacantho-doidei) water habitats (Yamanoue et al. 2008).

The position of *M. mola* within Molidae is less contentious. In his taxonomic revision of Molidae, Fraser-Brunner (1951) identified five species divided into three genera: *Ranzania*, *Masturus* and *Mola*. The number of recognised species subsequently dwindled until each genus was considered monotypic (Santini and Tyler 2003). Fraser-Brunner's view that *Masturus* and *Mola* are more closely related to each other than to *Ranzania* is in agreement with earlier workers such as Bonaparte (1841) and Gill (1897) and has received considerable corroboration, both morpho-logically (Santini and Tyler 2002) and through molecular studies (Alfaro et al. 2007; Bass et al. 2005; Yamanoue et al. 2004).

Recent investigations into *M. mola* mitochondrial sequences have supplied compelling evidence that the genus *Mola* contains two species: *M. mola* and the resurrected southern sunfish, *M. ramsayi* (Giglioli 1883; Bass et al. 2005). Bass et al. (2005) took samples (fin clips or muscle biopsies) from 13 animals identified as *M. mola*, four as *M. lanceolatus*, and a single *R. laevis* specimen from multiple locations in the Atlantic and Pacific Oceans. The sequences of the mitochondrial DNA control region (*D-loop*) were analysed as well as any relevant GenBank sequences. The workers then assayed a subset of the individuals, chosen to represent the major clades identified by the *D-loop* analysis, for variation in the more slowly evolving cytochrome *b* gene sequence. All individual and group analyses showed high genetic divergence among *M. mola* specimens indicating two clades; one consisting of animals exclusively from the southern hemisphere and the other containing individuals from both hemispheres. This first group was suggested to be the sister species, *M. ramsayi*, previously described by Giglioli (1883). In addition, both *Mola* species appear

to be subdivided into Atlantic-Mediterranean and Indo-Pacific Ocean clades. The estimated times of divergence were of relatively recent origin (0.05–0.32 mya for *M. mola* and 1.55–4.10 mya for *M. ramsayi*) and so the isolating mechanism is unclear, although these estimates are based upon only two individuals and may be subject to further revision (Bass et al. 2005).

Another report by Yoshita et al. (2009) analysed the complete nucleotide sequences of *D-loop* in 101 sunfish collected from Japanese waters and published sequences in EMBL/GenBank/DDBJ from other studies. All fish were determined to belong to one of two genetically isolated clades (Groups A and B) that occurred sympatrically in Japanese waters. Group A specimens were found only on the Pacific coast of Southern Japan and other southern locations (Okinawa Island, Taiwan and Australia). Group B, on the other hand, contained specimens from various locations around the Japanese coast as well as from farther afield, including the Atlantic Ocean. When the study was expanded to use the sequences from Bass et al. (2005) all individuals identified as *M. mola* in the earlier study nested within Group B. Those identified as *M. Ramsayi* nested either within Group A or a new group (Group C) which exclusively contained animals collected in the southern hemi-sphere. They concluded that the genus *Mola* con-tained three species.

Interestingly, unlike Bass et al. (2005), who did not record any concurrent physical data, Yoshita et al. (2009) also recorded morphological differences between Groups A and B. The 15 animals comprising Group A were all large animals, with total lengths (TL) ranging from 175 to 332 cm, whilst Group B contained fish of much more varied sizes (TL range 29–277 cm) so morphometic analyses were limited to animals >180 cm TL. Specimens from Group A possessed significantly larger head bumps and deeper bodies than Group B animals. Group A sunfish also possessed a greater number of clavus fin rays (mean ± SD = 15.5 ± 1.3, range = 14–17, N = 4) than Group B (11.5 ± 1.1, 10–13, 10). This agrees with Fraser-Brunner (1951) who stated that the clavus had 16 fin rays in *M. ramsayi* and 12 in *M. mola*. In addition, all larger (TL 193.7–277.0 cm) sunfish from Group B showed a wavy edge to the clavus absent from all animals in group A and smaller (TL 28.4–155.3 cm) Group B fish.
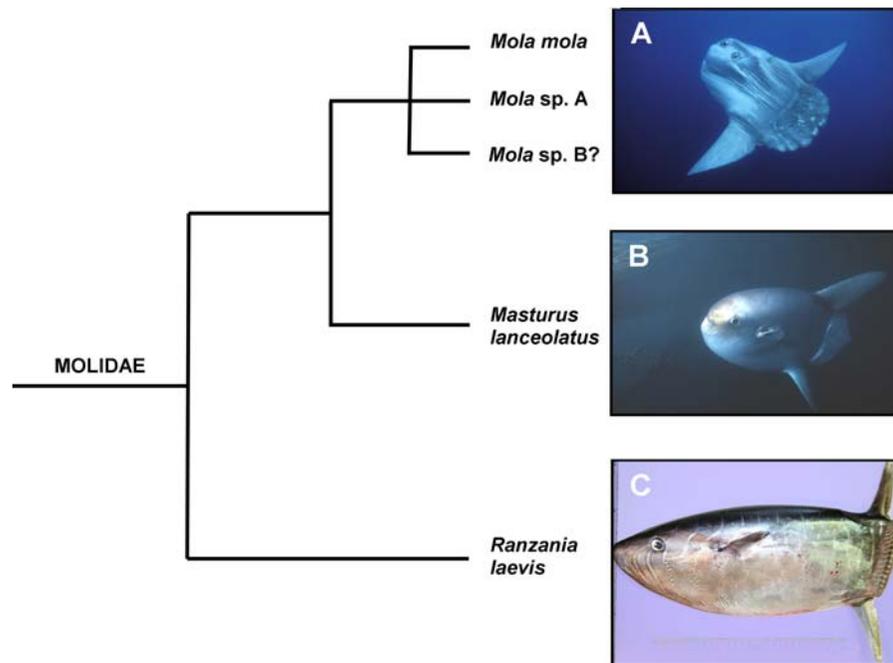
Fig. 2 The phylogeny of Molidae with illustrations of each member species. Each photograph is a lateral view. Photographs courtesy of **a** Mike Johnson, **b** Tao-Jen Kuo and **c** Wolfgang Sterrer. Redrawn with modification from Santini and Tyler (2002)

Genetic and morphological evidence strongly support the concept that *Mola* is not a monotypic genus (Bass et al. 2005; Yoshita et al. 2009; Fig. 2). More work is required, however, to clarify the interspecific relationships (Yoshita et al. 2009) so this review will concentrate on *M. mola* only, although misidentifications are possible in some of the studies cited.

Molids are distinguished from other tetraodontiforms by several distinct morphological characters, including reduced/fused caudal elements, presence of a clavus, absence of a swim bladder and a degenerate, cartilaginous skeleton. The origin of the clavus has been controversial since the earliest studies (see Johnson and Britz 2005). Fraser-Brunner (1951) argued strongly that the clavus consisted entirely of fin rays and musculature derived from the anal and dorsal fins and that the caudal fin was lost. Recently this argument has received considerable support (Johnson and Britz 2005; Nakae and Sasaki 2006). The vertebral column is severely reduced, with no ribs or pelvic fins (Cleland 1862) and the *lateralis* muscles, unable to perform their primary function of flexing the body, insert upon the deep muscles of the anal and dorsal fins (Fraser-Brunner 1951). The result

is a rigid body capable of reduced lateral flexion but with much more powerful dorsal and anal fins that become the primary means of locomotion (see Fig. 2a). Indeed, recent biotelemetry studies have shown that despite this lack of caudal propulsion, *M. mola* remains a powerful swimmer capable of highly directional horizontal movements, deep-water dives and even breaching (e.g. Cartamil and Lowe 2004; Konow et al. 2006; Watanabe and Sato 2008; Sims et al. 2009a; Hays et al. 2009). Thus the unusual morphology of *M. mola* may represent the evolutionary constraint of an already highly derived, reef dwelling tetraodontiform adopting a pelagic lifestyle.

Geographical range

Records from the Mediterranean (Silvani et al. 1999; Dulčić et al. 2007), North Atlantic (Sims and Southall 2002; Houghton et al. 2006a), South Atlantic (Petersen 2005), Gulf of Mexico (Fulling et al. 2007), East Pacific (Cartamil and Lowe 2004) and West Pacific (Sagara and Ozawa 2002; Liu et al. 2009) indicate a wide-ranging distribution for *M. mola*. Figure 3 illustrates ocean sunfish sightings, redrawn from OBIS data with additional sightings from literature
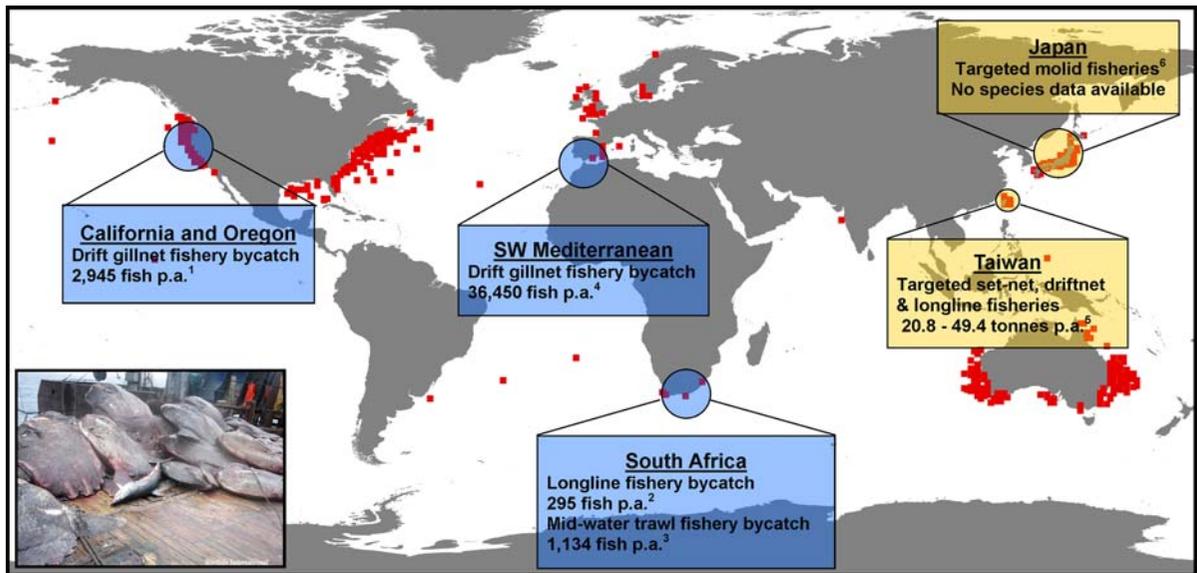
Fig. 3 World map showing locations of *Mola mola* sightings (*red squares*) redrawn from OBIS data (www.fishbase.org, accessed 18th February 2009) with additional sightings from literature and personal communications to www.oceansunfish.org. Commercial fisheries targeting *M. mola* are highlighted in *gold*, those known to experience considerable levels of *M. mola* bycatch are highlighted in *blue*. *Inset* shows *M. mola* bycatch on a horse mackerel trawler off South Africa (photograph courtesy of Birdlife International).[1] Rand Rasmussen, personal communication, Southwest Fisheries Science Center (based upon observed drift net fishery catch for 1990–1998). [2] Petersen (2005). [3] Petersen and McDonell (2007). [4] Crude estimate from Tudela et al. (2005). [5] Estimate from Liu et al. (2009). [6] Sagara and Ozawa (2002)

and personal communications. It should be noted, however, that such maps based on sighting and catch data, whilst a best estimate, suffer from various reporting biases. First, the map is constructed from recorded occurrences and may include aberrant observations of individuals outside of a species' typical range (as discussed in McMahon and Hays 2006). Second, a lack of records may not reflect a lack of occurrence of *M. mola* in particular areas but rather a lack of rigorous sampling. More accurate estimates of range are obtained for many fish species from commercial catch data. Such anecdotal data are not readily available for ocean sunfish, however, because there are few dedicated fisheries.

Diet

Ocean sunfish are often referred to as obligate or primary feeders on gelatinous zooplankton (Fraser-Brunner 1951; MacGinitie and MacGinitie 1968; Hooper et al. 1973; Bass et al. 2005). The importance of this group of animals in the diet of *M. mola* is far from clear, however, and most fish that eat gelatinous prey are known to have broad diets (Purcell and Arai 2001). There are several eyewitness accounts of *M. mola* surface predation on gelatinous zooplankton (MacGinitie and MacGinitie 1968; Thys 1994) but caution is necessary when interpreting near-surface feeding events, especially in a species now known to show deep diving behaviour (Hays et al. 2009; Sims et al. 2009a; see "Foraging ecology" section) and the relatively small gape of *M. mola* does not appear well adapted for capturing and ingesting large scyphozoan jellyfish (*cf.* the large gape of the leatherback turtle).

The diet of *M. mola* has not been investigated by any dedicated study to our knowledge and the literature on this subject is sparse. To illustrate this, a recent review that included a list of fish known to predate pelagic coelenterates based upon stomach contents data did not include *M. mola*, one of the few fish frequently cited as an obligate gelativore, because no quantitative data were available for this species (Arai 2005). Field guides and reference books mention varied stomach contents for ocean sunfish including algae, crustaceans, ophiuroids, molluscs, hydroids and fish (Norman and Fraser 1949; Clemens

and Wilby [1961]; Hart [1973]), although how these observations were obtained is unknown. Schmidt ([1921]) stated that the ocean sunfish was known to feed on small forms of pelagic life, including large numbers of leptocephalus eel larvae. Fraser-Brunner ([1951]) made reference to a 60 cm ling (*Molva macrophthalma*) found in an individual's stomach, although whether this represented active predation or opportunistic scavenging is unknown. The general impression of an omnivore is supported by the capture of ocean sunfish on pelagic long-line hooks (Petersen [2005]) baited with either squid, or a combination of squid and fish (pilchard, mackerel). Alternatively, it is possible that *M. mola* is attracted to the highly visible light sticks used in conjunction with the bait (Petersen [2005]) which may mimic the appearance of bioluminescent gelatinous zooplankton, or they may simply be foul-hooked rather than actively taking the bait.

Hooper et al. ([1973]) used thin layer chromatography and gas liquid chromatography to analyse the lipids extracted from various tissues (connective tissues, white muscle, dark muscle, liver and intestinal contents) from four ocean sunfish. They identified two unusual component fatty acids: *trans*-6-hexadecenoic acid and 7-methyl-7-hexadecenoic acid. *Trans*-6-hexadecenoic acid was known to comprise 2% of the total fatty acids in the moon jellyfish *Aurelia aurita* (Hooper and Ackman [1972]). In addition, both of these fatty acids had previously been isolated from tissues of the leatherback turtle, *Dermochelys coriacea* (Hooper and Ackman [1970]), an animal known to be an obligate gelatinous zooplanktivore (Houghton et al. [2006c]). Thus the presence of these fatty acids in both leatherback turtles and ocean sunfish was taken as an indicator of a diet containing jellyfish (Ackman [1997]). The role of jellyfish in the diet of *M. mola* remains unclear, however, since the study that identified *trans*-6-hexadecenoic acid in *D. coriacea* also identified it in two other turtle species: the loggerhead *Caretta caretta* and Kemp's Ridley *Lepidochelys kempii* (Hooper and Ackman [1970]), both of which are omnivorous, not obligate feeders on jellyfish (Bjorndal [1997]). A proposed link between these fatty acids and predation on jellyfish becomes less certain when subsequent studies also identified both fatty acids in the liver oil of the reef-dwelling Atlantic spadefish *Chaetodipterus faber* (Pearce and Stillway [1976]) and

7-methyl-7-hexadecenoic acid as a constituent of sperm whale oil (Pascal and Ackman [1975]).

Locomotion

Cartamil and Lowe ([2004]) showed conclusively that *M. mola* is an active swimmer capable of highly directional movements. Eight individuals equipped with acoustic transmitters off southern California were shown to move greater distances (mean 26.8 km day^{-1}) than they could possibly accomplish through simply planktonic passive drifting. It was also demonstrated that these horizontal movements were highly directional and independent of the prevailing current regime.

Further insights into *M. mola* locomotion were achieved when Watanabe and Sato ([2008]) used high-resolution multi-channel data loggers to record the movements of three individuals in Otsuchi Bay, Japan under natural conditions. The fish undertook frequent vertical movements and swam at continuous speeds of 0.4–0.7 m s^{-1} (similar to records of other large fishes such as salmon, marlins and pelagic sharks). It was also confirmed that ocean sunfish stroke their dorsal and anal fins synchronously (dominant frequency 0.3–0.6 Hz) to generate a lift-based thrust that was likened to the symmetrical flipper beats of penguins (Watanabe and Sato [2008]). Essentially, *M. mola* uses its anal and dorsal fins as a pair of wings. It is worth noting that this is the only animal known to use two fins for this purpose that are not originally bilaterally symmetrical (Watanabe and Sato [2008]). Watanabe and Sato ([2008]) argued that the symmetrical pair of dorsal and anal fins are well suited for cruising because they are mechanically more efficient (Walker and Westneat [2000]) and give more thrust per stroke at high speed (Vogel [1994]) compared to the drag-based swimming of other Tetraodontiform fishes (e.g. pufferfish, Gordon et al. [1996]; box fish, Hove et al. [2001] and burrfish, Arreola and Westneat [1996]).

The same study also demonstrated that the aspect ratio (length to mean width) of the anal and dorsal fins dramatically decreases with age, with an expected concomitant decrease in swimming efficiency. Watanabe and Sato ([2008]) hypothesised that mechanical strength was of more importance than efficiency in larger fish. This decrease in expected

efficiency with increasing size may explain why a similar study observed that the allometry of fin-beat frequency is reversed in ocean sunfish (Houghton et al. 2009). In other words, large ocean sunfish have a faster fin beat frequency than smaller sunfish. This is in contrast to most fish with a lateral propulsive system where larger individuals show slower fin-beat frequencies than smaller ones (Bainbridge 1958; Gleiss et al. 2009). This later study by Houghton et al. (2009) demonstrated the use of a new low-impact harness with an automated release mechanism to attach multi-channel data loggers ('daily diaries'; see Wilson et al. 2008; Shepard et al. 2008 for full descriptions) to three ocean sunfish off the coast of County Kerry, Ireland. It was discovered that ocean sunfish roll far more extensively than would be expected for a teleost during typical locomotion and body roll was intrinsically linked with vertical velocity, with highest roll angles recorded at relatively slow vertical velocities (Houghton et al. 2009). *M. mola* also showed an unusual decrease in the amplitude of body sway with increasing frequency (mean frequency and amplitude of body sway were taken as a proxy for timing and magnitude of fins strokes) as higher frequencies would be expected to have larger amplitudes (Gleiss et al. 2009).

The study by Watanabe and Sato (2008) also examined the internal and external morphologies of 49 ocean sunfish (body mass ranging from 2 to 959 kg) collected from local fish markets. It was demonstrated that despite the missing swim-bladder, ocean sunfish are neutrally buoyant (mean body density $1,027 \pm 4$ kg m^{-3}, $N = 20$) in seawater (density *ca.* 1,026 kg m^{-3}) and that a thick layer of low-density, subcutaneous, gelatinous tissue plays a major role providing this buoyancy (Watanabe and Sato 2008). The degenerate, cartilaginous skeleton of *M. mola* (Cleland 1862) also likely contributes to buoyancy (Davenport and Kjørsvik 1986). Importantly, the gelatinous tissue is incompressible, enabling rapid depth changes without the changes in buoyancy that would be experienced by fish possessing swim-bladders (Yancey et al. 1989). This combination of a lift-based swimming mode and neutral buoyancy from incompressible, gelatinous tissue appears to allow *M. mola* to move over considerable distances, despite its unusual morphology.

Vision

A recent study by Kino et al. (2009) investigated the eyes of three immature *M. mola* from Japanese waters. They found a region of high retinal ganglion cell density that implied a main visual axis directed towards the lower frontal portion of the visual field (10–20° below horizontal; Kino et al. 2009). High-density areas are indicative of a well-developed visual system and also require the ability to move the eye to direct this region of more acute vision to objects of interest (Fritsches et al. 2003). Such eye movements, especially in the ventral plane, were documented in live specimens by Kino et al. (2009). Visual acuity, calculated from peak ganglion cell densities, was between 3.51 and 4.33 cycles per degree, comparable to adult sharks (2.8–3.7 cycles per degree; Kino et al. 2009) but much lower than adult blue marlin, *Makaira nigricans* (8.5 cycles per degree; Fritsches et al. 2003). It should be noted, however, that these were very small ocean sunfish and visual acuity typically increases as fish grow (Fritsches et al. 2003). The study also suggested that this angled visual axis indicated that *M. mola* detected its prey items mainly whilst descending or foraging near the sea bottom. The recent work showing that *M. mola* rolls extensively when swimming (i.e. it swims at an angle; Houghton et al. 2009) and its observed ability to direct its vision weaken this view.

Published eyeball size data for *M. mola* are all from juvenile animals less than 1 m TL but ocean sunfish appear to possess large eyes; a 97 cm TL specimen possessed an eye >38 mm in diameter (Cleland 1862) and the three fish described by Kino et al. (2009; TL 42.3–45.5 cm, 3.3–3.5 kg) had eyeballs with diameters ranging from 33.3 to 35.4 mm. Eye size usually reflects the importance of vision in animals (Walls 1942) and many deep ranging species simply possess large eyes able to accommodate more retinal photoreceptive cells and acquire more light per solid angle of image space (Motani et al. 1999). For example, billfish are known to possess very large eyes (Fritsches et al. 2003) with brain and eye heaters for maintenance of function in deep, cold waters (Carey 1982). Whilst eyeball size is a crude estimate of visual acuity, it is worth noting that ocean sunfish have been tracked targeting depths of greater than 200 m for protracted periods (Hays

et al. 2009) and undertake deep dives to nearly 500 m depth (Sims et al. 2009a).

Horizontal movements

Sightings of *M. mola* at temperate latitudes are more common in summer months (Sims and Southall 2002; Houghton et al. 2006a), a phenomenon seen with other large marine vertebrates, such as the leatherback turtle (Brongersma 1972; Houghton et al. 2006a) and the basking shark, *Cetorhinus maximus* (Sims et al. 2003). Leatherback turtles migrate seasonally into higher latitudes once water temperatures are warm enough (McMahon and Hays 2006), presumably to take advantage of the greater plankton productivity in spring and summer at these latitudes (Parsons et al. 1984). Conversely, basking sharks, in the North East Atlantic at least, remain in temperate waters during the winter months with increased sightings during the summer simply reflecting increased visibility of the species at this time of year (Sims et al. 2003).

Recent tracking studies have provided valuable insights into the seasonal horizontal movements of ocean sunfish. Sims et al. (2009a) attached satellite-linked archival transmitters to ocean sunfish in the North East Atlantic in 2007; two fish in the waters of southern Portugal in February and a third off southwest Ireland in August. The animals were tracked for between 42 and 94 days. *M. mola* tagged in the waters off southern Portugal in February moved in northerly and westerly directions whilst the animal equipped in Irish waters in August moved southerly to the Bay of Biscay, North Spain, 959 km south of the tagging location (Fig. 4). This pattern of increased latitude in late winter to summer and decreasing latitude from late summer to autumn is consistent with a model of northerly travel at the end of winter and movement south at the end of summer.

Sims et al. (2009b) equipped three ocean sunfish with fast-acquisition Global Positioning System (Fastloc GPS) tags off southern Portugal in the first long-term GPS tracking study of a large pelagic fish. These tags produce very low spatial errors for geolocations (between *ca*. 26–64 m) and are thus able to resolve behaviour on a much finer scale. Two animals were tagged in May 2008 for 5 and 15 days whilst a third, larger (1.0 m TL) animal was tracked
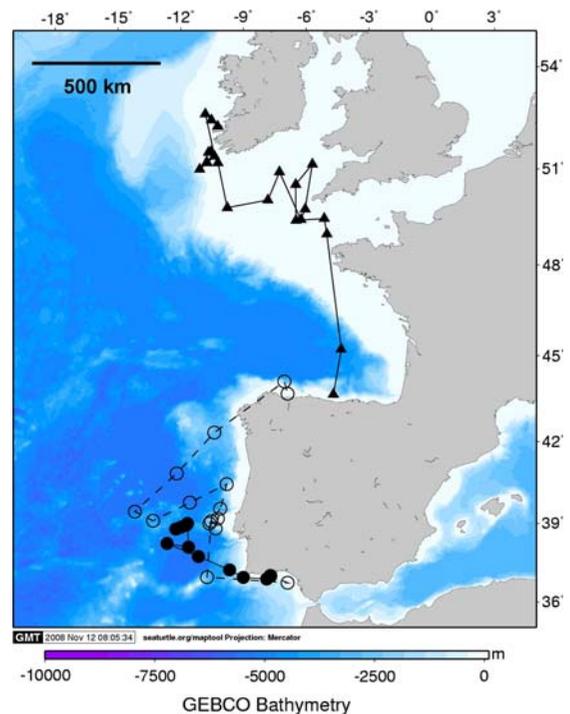

Fig. 4 Movements of three ocean sunfish, *Mola mola*, equipped with satellite tags in the North-East Atlantic in 2007. The first two fish (*filled circle* and *open circle*) were tagged off southern Portugal at the end of February and travelled in a predominantly northerly direction whilst the third animal (*filled triangle*) was tagged off west Ireland in August 2007 and travelled southward. These movements are consistent with the seasonal migration of ocean sunfish to higher latitudes and their subsequent return south. Start and end points are the tagging site and the pop-off location of the tag determined by multiple good quality Argos locations. Intermediate locations are based on light-based geolocation and are restricted to period prior to inferred detachment of the tags (see Sims et al. 2009a for details). From Sims et al. (2009a)

for 92 days between early November 2008 and early February 2008. The larger animal travelled an estimated 1,819 km, moving at a mean speed of 19.8 km day^{-1}, proceeding south-westerly and then south-easterly into the warmer waters of the gulf of Cadiz as winter developed (Sims et al. 2009b). The rates of travel were comparable to those of pelagic sharks and GPS track integration showed that this fish often swam into and across prevailing currents and showed intermittent periods of reduced movement in localised areas and faster, directional movements. It was hypothesised that these 'stopovers' in localised areas represented encounters with patches of preferred prey (Sims et al. 2009b).

The classic migratory paradigm illustrated by Sims et al. (2009a, b) may not be geographically uniform, however. Hays et al. (2009) attached satellite-linked archival transmitters to four *M. mola* in the waters of South Africa, obtaining data spanning January to August 2004 and March to August 2006. Interestingly, the tracks of all these ocean sunfish showed prolonged residence off South Africa from the austral summer to winter. Presumably, the waters off South Africa must represent a suitable year-round habitat for these fish (Hays et al. 2009), although it would be useful to determine whether migratory behaviour differs between *M. mola* and the putative southern hemisphere species, *M. ramsayi* (see "Phylogeny and morphology of the Molidae").

Foraging ecology

Ocean sunfish occupy a broad range of depths and move extensively throughout the water column (Sims et al. 2009a; Hays et al. 2009). Cartamil and Lowe (2004) observed a diel pattern in depth utilisation, with fish residing in the warmer mixed layer above or within the thermocline at night and repeatedly diving beneath the thermocline into cooler water during the day (Californian waters, July–September 2001). Sims et al. (2009a) tracked sunfish in the North-East Atlantic in late winter to early spring and late summer to early autumn and observed all three study animals occupying significantly ($P < 0.003$) greater depths during the day (mean diurnal depths of 250.7, 112.1 and 50.7 m versus mean nocturnal depths of 104.7, 63.18 and 29.9 m for each fish, respectively). This behaviour matches the strategy of normal diel vertical migration (DVM) and has been attributed to a strategy of near continual feeding on vertically migrating prey (Sims et al. 2009a; Hays et al. 2009) although concurrent data on the distribution of potential prey have not yet been analysed. Hays et al. (2009) again saw DVM with sunfish in South African waters, although this was not an invariant behaviour with individuals sometimes not displaying vertical movements.

Despite showing normal DVM when it occurs, ocean sunfish repeatedly return to the surface during the day and do not simply remain at depth (Cartamil and Lowe 2004; Hays et al. 2009). Cartamil and Lowe (2004) observed that daytime periods were characterised by short (mean dive duration 11.2 ± 9.5 min) repeated dives below the thermocline (40–150 m). Hays et al. (2009) also noted that although individual sunfish showed a range of preferred depth that altered over time, they were still moving up and down the water column and regularly returning to close to the surface. Similar behaviour has been observed in a variety of fish species such as swordfish *Xiphias gladius* (Carey and Robison 1981), blue shark *Prionace glauca* (Carey and Scharold 1990) and bluefin ((*Thunnus thynnus*) and bigeye (*T. obesus*) tuna (Dagorn et al. 2000; Kitagawa et al. 2007). Although its exact function has yet to be resolved, Cartamil and Lowe (2004) proposed that periodic returns to the surface in *M. mola* may imply some form of behavioural thermo-regulation i.e. prolonged time in cold waters necessitates time spent at the surface to re-warm. They recorded *M. mola* diving into water with a temperature of 6.8°C, well below the thermal range recorded for ocean sunfish in the North East Atlantic of 10–19°C (>99% of time; Sims et al. 2009a) and identified a significant relationship between time spent in the cold water and the ensuing post-dive surface period. This may

Fig. 5 The ocean sunfish, *Mola mola*, showing characteristic basking behaviour. Photograph courtesy of Mike Johnson

explain the frequent observations of ocean sunfish observed 'basking' or swimming on their sides at the surface during the day (Cartamil and Lowe 2004; Fig. 5). Conversely, Sims et al. (2009a) argued that extensive vertical movements may simply reflect a crepuscular searching strategy when prey are descending or ascending, with sunfish attempting to locate maximum prey abundances at this time. It has been also been suggested more generally that large amplitude dives or ascents of large pelagic fish and other vertebrates during prey tracking may represent prey searching behaviour (Shepard et al. 2006) characterised by extensive movements to new locations (Sims et al. 2008).

Hays et al. (2009) subsequently proposed that individual ocean sunfish respond to patchily distributed plankton prey with differing levels of DVM. This pattern may mirror the behavioural plasticity noted in leatherback turtles, whereby individuals are thought to shift predation from seasonally abundant surface medusae in summer months towards vertically migrating deep-water gelatinous species during the winter (Houghton et al. 2008).

Reproductive biology

Very few studies have been conducted on the reproductive biology of ocean sunfish. The spawning period of *M. mola*, in Japanese waters at least, is estimated as between August and October and the same study also identified asynchronous egg development, suggesting they are multiple spawners (Nakatsubo et al. 2007). Average sea-surface temperature (SST) around this study region of Japan between August and October 1982–2006 was 25.52 ± 0.58°C (Mean ± 1 SD, using NOAA NCDC ERSST version 2, 32–36E, 136–142N, http://www.cdc.noaa.gov/). Reproductive seasonality for *M. mola* in other locations is less well documented. Although the central gyres of the North and South Atlantic, North and South Pacific and Indian Oceans have been suggested as spawning areas (Bass et al. 2005) evidence in support of this concept is sparse. The means by which adult fish aggregate for spawning also remain unclear, as does the link between open ocean habitats and the large groupings of *M. mola* observed in many coastal areas worldwide (Silvani et al. 1999; Cartamil and Lowe 2004). A recent study did not identify any

chromosomal or morphometric sexual dimorphism in *M. mola* other than in TL (Nakatsubo 2008). Females were larger than males, with all animals larger than 250 cm TL being female (Nakatsubo 2008).

The lifespan or reproductive age of *M. mola* under natural conditions is unknown, although captive animals have been maintained for more than 8 years (Nakatsubo et al. 2007). A growth curve derived from repeated measurements of captive specimens estimated an individual with a total length of 3 m would be about 20 years old (Nakatsubo 2008). Nevertheless, caution is prudent in comparisons between wild animals and those in captivity. Recent work used growth band pairs in vertebrae to age the closely related sharptail mola *M. lanceolatus* caught in the eastern Taiwan fishery (Liu et al. 2009). The age estimates ranged between >2 and >23 years for females and >1 and >16 years for males (Liu et al. 2009). A similar approach may be more suitable for ageing *M. mola* than using their anatomically primitive otoliths (Gauldie 1990).

M. mola is famously the most fecund of all vertebrates (Carwardine 1995) with a 137 cm female containing an estimated 300 million eggs (Schmidt 1921). By necessity, these eggs are very small (mean diameter 0.13 cm; Gudger 1936) and so *M. mola* growth is staggering. For the 0.25 cm larva to grow to a 3 m adult requires an increase in mass of 60 million times (Gudger 1936). An individual in captivity at the Monterey Bay Aquarium gained 373 kg in just 15 months (454 days, 0.82 kg day^{-1}; Powell 2001) although more typical captive growth rates have been found to be between 0.02 and 0.49 kg day^{-1} in weight (M. Howard, personal communications. Monterey Bay aquarium, 800 Cannery Row, Monterey CA 93490; T. Nakatsubo, personal communications. International Marine Biological Institute, Kamogawa Sea World, Kamogawa, Chiba 296-0041, Japan) and on average 0.1 cm day^{-1} TL (Nakatsubo and Hirose 2007). These rates are also highly dependent on the starting TL of the captive animal (Nakatsubo and Hirose 2007).

Predators and parasites

There are several documented accounts of predation on *M. mola* by sealions (T. Thys, unpublished observations), orcas (Gladstone 1988) and large

Fig. 6 *Mola mola* remains found in the stomach of a sub-adult blue shark *Prionace glauca* (168 cm TL) captured on a longline near the Azores in 2006. Photograph from Nuno Queiroz

sharks (Fergusson et al. 2000). For example, ocean sunfish have repeatedly been found in the stomachs of blue sharks (N. Queiroz, unpublished observation; Fig. 6) and a white shark, *Carcharodon carcharias* measuring over 5 m (TL) that was harpooned near the Italian port of Messina in Sicily was found to include the fresh remains of a large adult *M. mola* (Fergusson et al. 2000). The fish had been bitten into three sections that when combined indicated a TL of around 2 m (Fergusson et al. 2000). It should be noted, however, that the accuracy of this account by Fergusson et al. (2000) has been contested (Celona et al. 2001). Californian sea lions, *Zalophus californianus*, have been observed biting the fins off ocean sunfish during the autumn months in Monterey, California and beating the dismembered bodies against the sea surface, presumably to tear through *M. mola*'s tough skin (T. Thys, unpublished observations).

Another possible explanation for the basking behaviour of ocean sunfish may relate to the substantial infestations of parasites observed in some individuals (Fraser-Brunner 1951; Konow et al. 2006). A report by the National Marine Fisheries Service (National Oceanic and Atmospheric Administration) lists 54 species of parasitic organisms found on *M. mola* (Love and Moser 1983). More than half of these species are members of Platyhelminthes, with cestodes (7 species), monogeans (8 species) and especially digeneans (16 species) found in the

intestines, liver, gills, muscle connective tissue and skin (Love and Moser 1983). Crustaceans, especially copepods (14 species) but also isopods, cirripedes and branchiurans have been found on the skin, gills, buccal cavity and operculum (Love and Moser 1983). Other parasites are nematodes, protozoans and members of Acanthodephala (Love and Moser 1983). There is growing evidence to support the long-held view that *M. mola* may reside at the surface to solicit cleaning by seabirds or fish (Thys 1994; Konow, et al. 2006). This is supported by the association of *M. mola* with kelp beds that has been linked with parasite elimination through the action of cleaner fish (Cartamil and Lowe 2004; Hixon 1979). An Indonesian study observed ocean sunfish being cleaned by five different species of fish and also witnessed breaching events that were suggested as a possible means of decreasing parasite load (Konow et al. 2006).

The heavy parasite loads observed in *M. mola* may support the hypothesis that gelatinous zooplankton are a preferred prey group as such animals are known to be intermediate hosts for trematode, cestode and nematode larvae (Purcell and Arai 2001). There is also evidence that hydromedusae and ctenophores show greater incidence of trematode infection than other zooplankton (Purcell and Arai 2001). Many of these parasites are larval forms of species where the definitive hosts are fish (Arai 2005). Unfortunately, we know very little about interactions between fish and gelatinous zooplankton (Purcell and Arai 2001) but a better understanding of ocean sunfish parasite associations will also provide insights into potential prey types. Molecular analyses of the parasites may also reveal connectivity between *M. mola* populations and overall movements.

Conservation issues: *Mola mola* in a changing ocean environment

It has been contended that 90% of all large predatory fish have disappeared from the oceans (Myers and Worm 2003) since the arrival of industrialised fishing and there is substantial evidence that sharks, one of the known predators of *M. mola*, are declining worldwide at an alarming rate (Baum et al. 2003; Myers et al. 2007; Heithaus et al. 2008). Whilst trophic cascades are hard to predict, any reduction in

top–down control may have significant effects on *M. mola* populations globally (Heithaus et al. 2008). Insightful data have already emerged from the North West Atlantic where the decline of 11 species of large sharks has resulted in an increase in 12 out of 14 investigated prey species (Myers et al. 2007), although it should be noted that many of these predatory species have not been associated with *M. mola*. In addition, there is evidence that over-fishing can be correlated with a concomitant increase in gelatinous zooplankton numbers (Mills 2001; Lynam et al. 2006) as the removal of large numbers of fishes makes food resources available to jellyfish (Mills 2001). The increased water temperatures and water column stratification associated with climate warming may also favour outbreaks of gelatinous fauna, although attributing such instances to climate change alone is highly problematic (Richardson et al. 2009). Nonetheless, a merger of reduced top–down control and increased prey availability in certain locations may provide conditions favourable for *M. mola* population growth.

Then again, any such amelioration of conditions for ocean sunfish may be offset by anthropogenic mortality. *M. mola* is not a commercially important fish (Fulling et al. 2007; Silvani et al. 1999) although there is some market for it in Japan (Sagara and Ozawa 2002; Watanabe and Sato 2008) and Taiwan (20.8–49.4 tonnes *per annum*, Liu et al. 2009). Ocean sunfish populations may still be vulnerable to fishing activity nonetheless because of the high levels of bycatch observed in many fisheries (Silvani et al. 1999; Cartamil and Lowe 2004; Fulling et al. 2007, Petersen and McDonell 2007). For example, the South African longline fishery for tuna and swordfish was estimated to have annually caught between 0.08 and 0.29 sunfish for every 1,000 hooks set (1.6–2.7 million hooks per year) in the 4 years between 2000 and 2003 (Petersen 2005). Furthermore, *M. mola* was by far the most common bycatch species in the Cape horse mackerel (*Trachurus trachurus capensis*) mid-water trawl fishery in the same region (Petersen and McDonell 2007; see Fig. 3) representing 51% of the total bycatch between 2002 and 2005 (Petersen and McDonell 2007). This fishery caught predominantly large individuals (172 ± 1.66 cm, mean ± SD, $N = 581$) and observed a significant decline in ocean sunfish catch rates during the study period, with other bycatch species remaining comparatively stable

(Petersen and McDonell 2007). Similarly, *M. mola* comprised between 70 and 93% of the total fish catch in Spanish drift gillnet fisheries within the Mediterranean between 1992 and 1994 (Silvani et al. 1999) and bycatch estimates from the Californian swordfish fishery suggest ocean sunfish make up 29% of all bycatch; far outnumbering the target species (Cartamil and Lowe 2004). Whilst the Spanish fishery was closed in 1994 (Silvani et al. 1999; Tudela et al. 2005), an illegal Moroccan driftnet fleet continued to operate until the Moroccan government passed a law in 2007 intended to phase out the use of driftnets. A crude calculation using values from a recent study of the Moroccan fleet (Tudela et al. 2005) suggests an annual bycatch of 36,450 ocean sunfish. Whilst the majority of *M. mola* are returned to the water alive (Silvani et al. 1999), they often show varying levels of trauma (Cartamil and Lowe 2004) and post-catch survival data are lacking. If *M. mola* exist as discrete populations, even within ocean basins, as has been proposed (Bass et al. 2005) then these isolated populations may be more prone to local depletion, or even extinction, than the previously envisioned pan-global population. The broader ecological implication of removing such large numbers of predatory fish with a poorly resolved diet is even less clear.

Future research perspectives

In order to make absolute comment on possible effects of climate change in this species, it is essential that we gather more robust data on seasonal abundances in specific locations. One suggestion is to incorporate ocean sunfish into existing surveys already looking for marine megafauna (Houghton et al. 2006a) or gelatinous zooplankton (Houghton et al. 2006b). The advent of chemical and molecular techniques is also helping unravel long-distance movements and ontogenetic habitat shifts in fish populations and may prove useful for molid studies. For example, the use of stable isotopes has answered key questions about the relationships between Atlantic bluefin tuna populations (Rooker et al. 2008) whereby the otoliths in yearlings from regional nurseries were used as natural tags to assess natal homing and mixing. Significant trans-Atlantic movement (East to West) was detected, with individuals of

Mediterranean origin mixing with the western population in the U.S. Atlantic (Rooker et al. 2008). Additionally, genetic markers have been used to unravel protracted movements in fish such as the coastal migration of juvenile Coho (*Oncorhynchus kisutch*) and Chinook Salmon (*O. tshawytscha*; Trudel et al. 2004). The combination of these techniques with additional satellite tracking efforts should further our knowledge of sunfish population ecology, although structures such as fin rays (Arai et al. 2002) may be substituted for otoliths for reasons stated previously.

It is clear that more work is required to resolve the fundamental question of diet. Future studies are warranted that complement analytical techniques with studies simultaneously tracking *M. mola* and gelatinous zooplankton in the field (Hays et al. 2008). Stomach content investigations using appropriate fixation for gelatinous animals (Arai 2005) may yield valuable data and putative food groups for stable isotope and fatty acids analyses. The use of stable isotope ratios will prove more useful in identifying predator trophic levels rather than the species composition of a diet (Iverson et al. 2004) but may help to pinpoint the relative importance of gelatinous zooplankton in *M. mola* diet. Although not directly relevant to studies of gelatinous zooplankton, such a combination of stable isotope analysis and stomach contents has recently been used to identify a marked ontogenetic shift in prey types amongst yellowfin tuna, *Thunnus albacares* (Graham et al. 2007). Alternatively, techniques such as quantitative fatty acid signature analysis (QFASA; see Iverson et al. 2004) can provide more detailed information on particular prey items and their relative importance.

More detailed work on the overall visual acuity of ocean sunfish at depth may shed further light on their basic foraging strategies. Recent detailed retinal studies of blue marlin have shown that their eyes are specifically adapted to cope with low light levels, such as those experienced when diving (Fritsches et al. 2003). Conversely, similar studies of leatherback turtles revealed that they have small eyes in comparison with their biomass that are not well adapted to dim light (Brudenall et al. 2008), even though this species is known to engage in deep diving behaviour (Houghton et al. 2008). It was concluded that marlin are able to hunt visually at depths greater than 200 m (Fritsches et al. 2003) whilst leatherbacks predominantly feed at the surface, or during shallow dives below 150 m (Brudenall et al. 2008).

Further deployments of multi-channel data-loggers will provide greater understanding of specific behaviours such as basking. Further knowledge of the thermal conditions and depths sunfish experience prior to this behaviour may prove illuminating. In addition, no studies so far have tracked larger animals (>2 m TL) which may display markedly different behaviour to smaller fish, which appear to be coastal in nature. Finally, the likelihood of sympatric sister species to *M. mola*, especially in the southern hemisphere, needs to be acknowledged. Future studies will benefit greatly from careful identification in the field, the recording of morphometric data for each individual used, including detailed descriptions or photographs of the clavus and the acquisition of blood or tissue samples.

In conclusion, a number of key foci are emerging for future research, namely deep-diving behaviour and long-distance migrations, population structure, foraging ecology and the effects of incidental bycatch. The technology and techniques required to address these questions are now largely in place as described above, allowing us to move away from an incidental, slow accumulation of data towards collaborative, international efforts targeted to understand the ecological importance of this charismatic, yet poorly understood species.

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