



Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Satellite tracking of the World's largest bony fish, the ocean sunfish (*Mola mola* L.) in the North East Atlantic

David W. Sims^{a,b}, Nuno Queiroz^{a,c,d}, Thomas K. Doyle^e, Jonathan D.R. Houghton^f, Graeme C. Hays^{g,*}

^a Marine Biological Association of the United Kingdom, The Laboratory, Citadel Hill, Plymouth PL1 2PB, UK

^b School of Biological Sciences, University of Plymouth, Drake Circus, Plymouth PL4 8AA, UK

^c CIBIO-UP, Centro de Investigação em Biodiversidade e Recursos Genéticos, Campus Agrário de Vairão, Rua Padre Armando Quintas, 4485-668 Vairão, Portugal

^d School of Biological Sciences, University of Aberdeen, Tillydrone Avenue, Aberdeen AB24 2TZ, UK

^e Coastal & Marine Resources Centre, University College Cork, Lewis Glucksman Marine Facility, Haulbowline, Cork, Ireland

^f School of Biological Sciences, Queen's University Belfast, Medical Biology Centre, 97 Lisburn Road, Belfast, BT9 7BL, UK

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

ARTICLE INFO

Keywords:

Bycatch
Climate envelope
Climate warming
Gelatinous zooplankton
Leatherback
Longline

ABSTRACT

Satellite-linked archival transmitters were used to record the movements of three ocean sunfish (*Mola mola*) in the North East Atlantic. Patterns of depth use and temperature experienced by individual fish were integrated into 4-hour intervals throughout the tracking period and relayed via the Argos system. Data were recorded for 42, 90 and 54 days respectively from the three fish. The first two were tagged off southern Portugal at the end of February 2007 and travelled principally northward, while the third fish was tagged off west Ireland in August 2007 and travelled southward. These patterns are consistent with seasonal migration of ocean sunfish to high latitudes and their subsequent return south. Maximum depths recorded by the three fish were 432 m, 472 m and 320 m respectively. All three individuals showed a diel pattern in depth use, occurring deeper during the day and shallower at night, a pattern consistent with sunfish tracking normally vertically migrating prey. Sunfish sometimes remained continuously at deeper (>200 m) depths during the day, but at other times they showed extensive movement through the water column typically travelling between their maximum depth and the surface within each 4-h period. The overall pattern to emerge was that ocean sunfish travel extensively in both horizontal and vertical dimensions, presumably in search of their patchily-distributed jellyfish prey.

© 2008 Elsevier B.V. All rights reserved.

1. Introduction

The World's largest bony fish, the ocean sunfish (*Mola mola*), can grow up to 1500 kg (Freedman and Noakes, 2002). Somewhat surprisingly, little is known about the free-living behaviour of this charismatic species, most probably because ocean sunfish are neither commercially exploited nor endangered, which are two of the main drivers for work on other ocean mega-fauna such as turtles, tunas and sharks (Block et al., 2005; Shillinger et al., 2008; Sims et al., 2005). Direct observations of sunfish near the surface and bycatch reports paint a picture of the species being fairly widely distributed in the World's oceans with, for example, records from the Mediterranean, various sites in the North Atlantic, South Atlantic, Gulf of Mexico and Pacific (Lee, 1986; Silvani et al., 1999; Petersen, 2005; Houghton et al., 2006; Fulling et al., 2007). However, the overall patterns of movement across this broad range, and the extent of migrations versus year-round residence, remain unknown. For example, at relatively high latitudes, such as around the UK and Ireland, sunfish are generally

observed in the summer (Sims and Southall, 2002; Houghton et al., 2006), but it is unknown if this simply reflects their greater visibility at this time of year or their arrival from other areas.

Despite the paucity of information on their free-living behaviour, there is increasing interest in ocean sunfish for a number of reasons. First, sunfish are suffering large bycatches in commercial fisheries targeting other species (Silvani et al., 1999; Petersen, 2005). The bycatch rates are striking; for example, in the longline fishery off South Africa that targets tuna and swordfish, over a four year period (2001–2003) the estimated bycatch of sunfish was 170 individuals per 1000 hooks deployed (Petersen, 2005). Given that the domestic fishing effort alone averaged 2 million hooks per year during this time (Petersen, 2005), a simple calculation gives a total sunfish bycatch per year of around 340,000 fish. The survival rate for these fish is unknown. Therefore, these high bycatch rates indicate the need to learn more about the free-living behaviour of individuals so that bycatch mitigation strategies can be designed, as has been introduced for other groups including sea turtles and birds (Brazner and McMillan, 2008; Dietrich et al., 2008). Secondly, sunfish are unusual in that they are thought to feed primarily on gelatinous zooplankton (Thys, 1994). There is concern that as a consequence of overfishing and eutrophication,

* Corresponding author.

E-mail address: g.hays@swan.ac.uk (G.C. Hays).

Table 1
Details of the tagging locations, sunfish size and duration of the data-sets for each fish

Sunfish	Length (cm)	Tagging site	Tagging date	Duration (d)
1	70	Southern Portugal	28 Feb 2007	42
2	70	Southern Portugal	28 Feb 2007	90
3	64	Ireland	8 Aug 2007	54

the incidence of jellyfish blooms may be increasing in many areas of the world (Purcell et al., 2007). As one of the few predators able to exert top-down control on jellyfish numbers, there is a need for a better understanding of where sunfish forage in both horizontal and vertical scales. Lastly, sunfish may be a tractable group for biotelemetry studies since they are large and feed on slow moving prey. With these attributes we might expect that the impact of devices on their behaviour would be less than for smaller species and pursuit predators, where increased drag could heavily impact behaviour (Wilson and McMahon, 2006). As such, ocean sunfish may be a useful model species for exploring fundamental questions in behavioural ecology, for instance what optimal search strategy to adopt in environments like the pelagic ocean with its sparse but complex prey distributions (Sims et al., 2006, 2008).

To date there have been a few successful biotelemetry and bio-logging studies that have recorded the movement and diving behaviour of ocean sunfish (Cartamil and Lowe, 2004; Watanabe and Sato, 2008). However, these previous studies have only recorded the behaviour of individuals for a few hours or days. Hence patterns of behaviour over longer time scales remain poorly described. Given the growing interest in the free-living behaviour of ocean sunfish, here we set out to use satellite telemetry to examine the movements and diving behaviour of individuals in the North East Atlantic over periods of weeks to months. By deploying satellite-linked archival tags on sunfish at two different latitudes, our primary objective was to perform a natural experiment to establish seasonal patterns of movement. Second, we set out to identify their patterns of depth use, and lastly we aimed to establish the thermal niche occupied by these tracked fish.

2. Materials and methods

Three sunfish were each fitted with a Wildlife Computers Mk10 Pop-off Archival Transmitting (PAT) tag. In Portugal, the fish were caught in a large pound net which targeted tuna and once in the net, fish were hand caught by a snorkeller. In Ireland, the sunfish was captured by approaching slowly in a rigid inflatable boat and throwing a cast net over the fish. The total length of fish was measured. Tags were secured externally using a stainless steel T-bar anchor tag attached to the transmitter using 300 lb test monofilament line and alloy crimps. PATs were programmed to pop-off after either 2 or 3 months, whereupon depth and temperature data were relayed via Argos. Additionally each PAT had a mechanical pressure-sensitive guillotine designed to sever the tether if the depth exceeded 1800 m. This system prevents the tag from being crushed at excessive depths, with the tag being released so that it floats to the surface.

Depth and temperature were measured every 60 s by the PAT tags and then these data were binned into successive depth intervals for each 4-h period commencing at 00:00 h each day. Times are given in GMT. The depth intervals were: 0–5 m, 5–10 m, 10–20 m, 20–30 m, 30–50 m, 50–70 m, 70–100 m, 100–150 m, 150–200 m, 200–250 m, 250–400 m, 400–600 m and >600 m. The temperature intervals were –40–22 °C, –2–0 °C, 0–6 °C, 6–8 °C, 8–10 °C, 10–12 °C, 12–13 °C, 13–14 °C, 14–15 °C, 15–16 °C, 16–17 °C, 17–19 °C, 19–21 °C and >21 °C. In addition, for each 4-h integration interval the PAT tags relayed information on the minimum and maximum depth obtained and selected temperatures across this range so that temperature/depth profiles could be generated. Due to the limited bandwidth of the Argos system, not all binned depth data actually collected by the PATs were received. To calculate the mean depth occupied for each 4-h inte-

gration window we simply used the proportion of time spent in each depth bin (P_n) and assumed the mid-point of each bin (D_n), i.e. Mean depth (m) = $\sum P_n \times D_n$. Likewise we calculated the mean temperature experienced during each 4-h integration window by similarly assuming the midpoint for each temperature bin.

Geolocations of the sunfish were estimated from light level and sea surface temperature (SST) data recorded by the PAT tags as described in detail by Sims et al. (2006). In short, longitude was estimated by calculating the time of local midnight or midday from the light level data recorded by the tag using the manufacturer's software WC-GPE (v1.02.0005, Wildlife Computers, Redmond, USA). Sea surface temperature data recorded by the tags were then compared with available SSTs in the tracking areas from remote-sensing images (AVHRR, Advanced Very High Resolution Radiometer) to obtain a bias-reduced estimate of daily latitude. For a given day, or adjacent day where cloud cover did not obscure the tracking area, the latitude along the light-level-based longitude estimate at which the tag-recorded SSTs best matched the corresponding remotely sensed SSTs was considered the

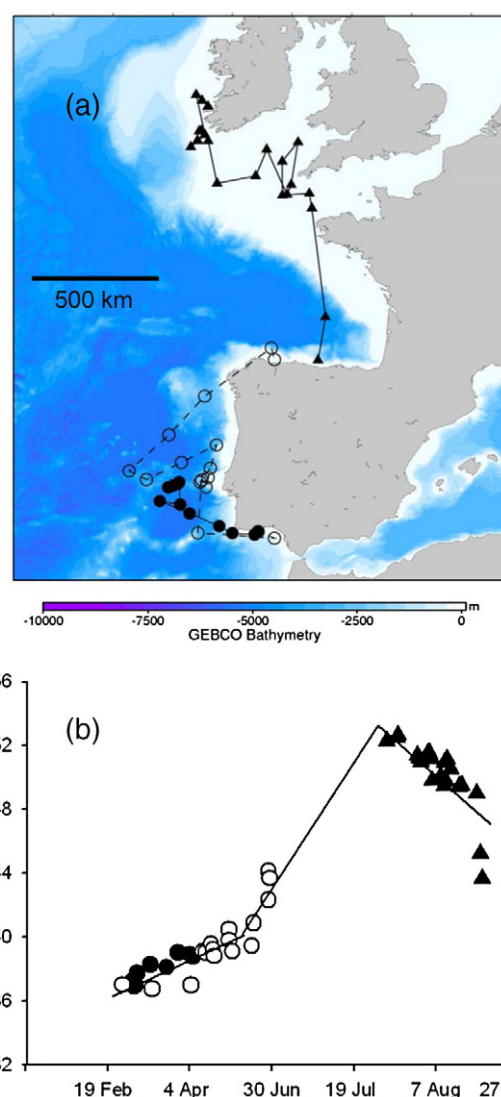


Fig. 1. (a) The tracks of three sunfish equipped with satellite tags. Start and end points are the tagging site and the pop-off location of the tag determined by multiple good quality Argos locations. Intermediate locations are based on light-based geolocation and are restricted to period prior to inferred detachment of the tags (see text for details). (b) the latitude of the three sunfish versus the day of the year. The solid line is fitted by eye simply to indicate the general pattern of spring northerly and autumn southerly movement expected for a seasonal migrant. For both (a) and (b) filled circles = sunfish 1, open circles = sunfish 2, triangles = sunfish 3.

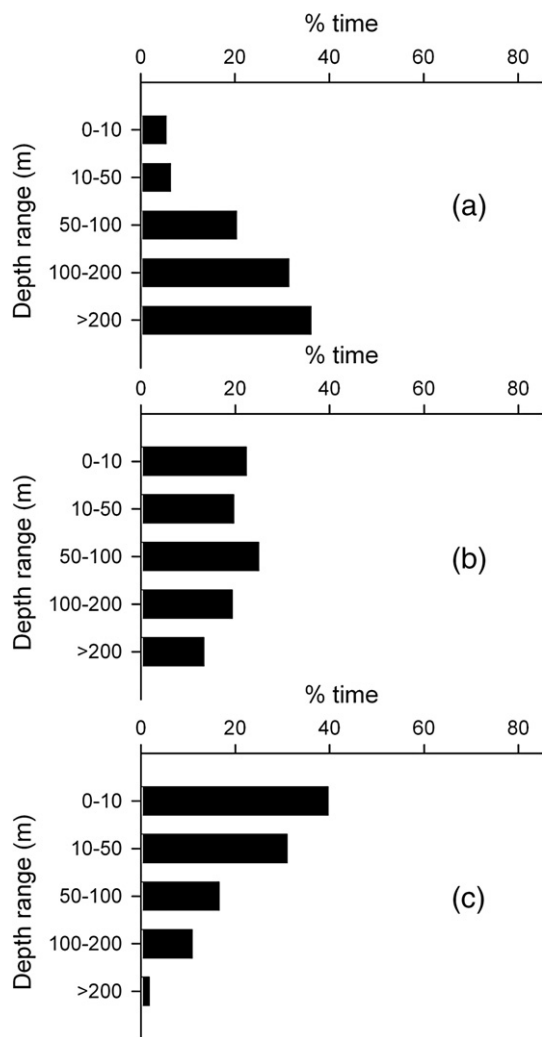


Fig. 2. Frequency distributions showing the amount of time spent in different depth zones by the three sunfish. (a–c) shows data for sunfish 1–3 respectively.

latitude estimate for the day. Maximum dive depth on the day each position was estimated was compared with available seabed depths in the vicinity of the estimated position to filter anomalous positions where the dive depth recorded was greater than the estimated seabed depth. The final estimated positions were then analysed point-to-point with a 0.25 m s^{-1} swim-speed filter (equivalent to $\sim 22 \text{ km}$ per day straight-line travel distance) that is consistent with daily distances covered by acoustic-tracked sunfish (Cartamil and Lowe, 2004). A position separated from an adjacent position by a distance too great to achieve in the speed-filter-imposed time between those positions was shifted to the location along the track where the imposed speed limit provided an acceptable distance.

3. Results

The size of sunfish tagged, dates of deployment and duration of data-sets are shown in Table 1. For sunfish 1 and 3, the depth data suggested premature detachment of the tags on 12 April and 1 October respectively. After these dates the tags were almost exclusively (generally $>99\%$ of the time within each 4-h integration window) at a depth of $<5 \text{ m}$. We therefore restricted our analysis of depth data to prior to these dates. Additionally for sunfish 1, in the three 4-h periods immediately prior to this inferred detachment of the tag, the temperature/depth data revealed the tag travelled from the surface to 1952 m. This suggests that the tag detached due to the

pressure release system. We removed these three 4-h periods from the subsequent data analysis as the fish may have died and been sinking (see Discussion). The duration of deployments shown in Table 1 refers to the time from tagging to the last depth data prior to this inferred detachment of the tags. These tags from sunfish 1 and 3 remained floating near the surface for 17 and 35 days, respectively, prior to the first Argos locations, since the tags were programmed to start transmitting only after the programmed pop-off dates. For these two tags we therefore reconstructed tracks using the initial release point and light-based geolocations determined up to four days after the inferred tag detachment date. For sunfish 2 we included all light based geolocations plus the final Argos pop-off location (Fig. 1).

The two sunfish tagged off southern Portugal on 28 February 2007 travelled westwards and northwards with final locations for the fish being 198 km and 743 km north of the tagging location. Sunfish 1 moved relatively rapidly away from the continental shelf of southern Portugal and was last located heading west towards some offshore seamounts (Fig. 1a). Similarly, sunfish 2 moved west but then northwards before being last located in the Bay of Biscay on the continental shelf off northern Spain (Fig. 1a). Converse to these patterns, the sunfish tagged off Ireland on 8 August 2007 travelled southwards, with the final location being in the Bay of Biscay, 959 km south of the tagging location (Fig. 1a). The general synopsis of fish travelling north

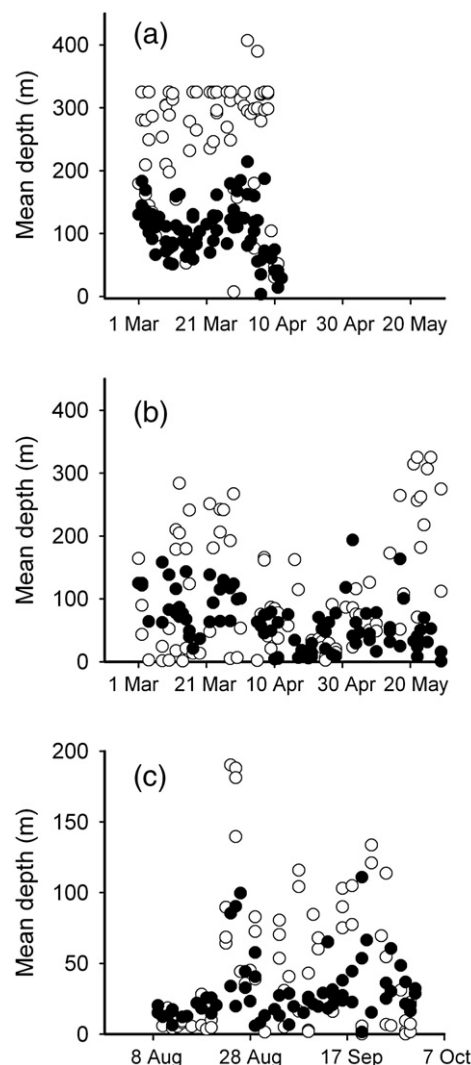


Fig. 3. The mean depth recorded within each 4-h integration window for each fish versus the date. (a–c) Fish 1–3 respectively. Filled symbols indicate 4-h integration windows beginning at 20:00, 00:00 and 04:00 (essentially night) and open symbols windows beginning at 08:00, 12:00 and 16:00 (essentially day).

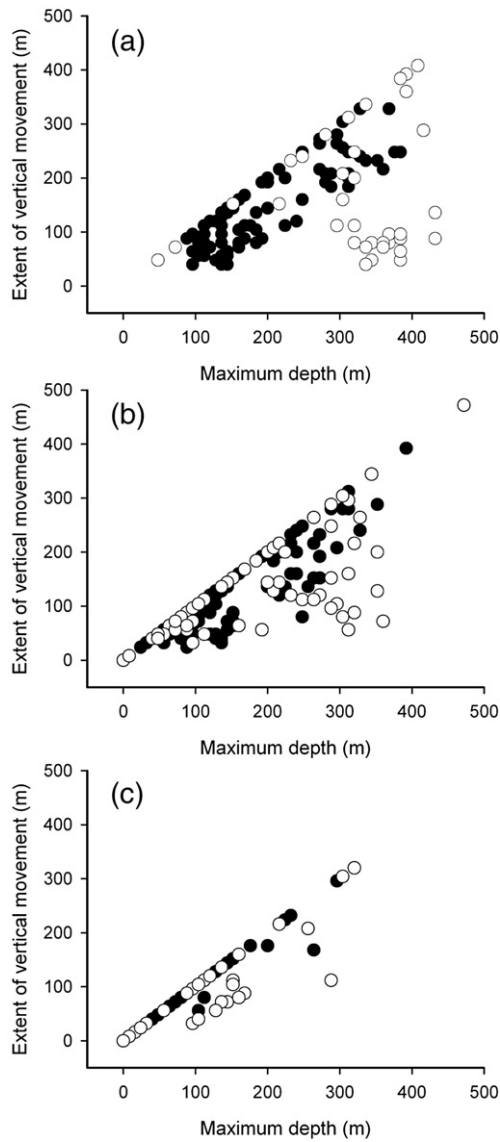


Fig. 4. The extent of vertical movement undertaken in each 4-h interval (maximum–minimum depth) as a function of the maximum depth attained in that interval. (a–c) shows data for sunfish 1–3 respectively. Filled symbols show data for individual 4-h interval commencing at 00:00, 04:00, 16:00 and 20:00. Open symbols shows 4-h interval commencing at 08:00 and 12:00.

at the end of the winter and south at the end of the summer was supported by these data. Examining the latitude of fish versus the day of the year shows a seasonal pattern, that of increasing latitude in late winter to summer and decreasing latitude from late summer into autumn (Fig. 1b).

The overall pattern of depth utilisation for each sunfish for depths less than 200 m is shown in Fig. 2 and indicates how these fish occupied a broad range of upper depths. Mean depth occupied (± 1 SE) for sunfish 1 was 172.5 m (± 8.2 m); for sunfish 2 was 89.9 m (± 5.8 m) and for sunfish 3 was 40.6 m (± 3.6 m). However, deeper depths were also occupied for appreciable amounts of time in southern tagged fish. Sunfish 1 spent 36% of its time below 200 m, with 29% in the 250–400 m range, while sunfish 2 spent 13% of the total time below 200 m. Interestingly, sunfish 3 tagged off west Ireland at 57° N spent only 2% of time below 200 m, with nearly 40% of its time spent in the top 10 m, compared with only 6 and 22% of time spent in the 0–10 m layer for sunfish 1 and 2, respectively (Fig. 2). These differences in mean depth occupied were significantly different across the three fish (One-way ANOVA on mean depths recorded in each 4-h integration window,

$F_{2,479} = 102.6, P < 0.001$). The maximum depths recorded for each fish, obtained from the temperature/depth data were 432 m, 472 m and 320 m for sunfish 1, 2 and 3 respectively.

As well as these differences in depth distribution between fish, there were also changes in depth distribution for individual fish over time (Fig. 3). For example, sunfish 1 showed a period of relatively shallow depth distribution during the middle of April, with many 4-h intervals where the mean depth was < 10 m, compared with March when depths > 50 m were occupied both day and night. Similarly sunfish 3 showed a shallow distribution at the start of August with the mean depth always being < 30 m between 9 and 20 August, followed by a much deeper distribution at the end of August, with, for example, a mean depth of 205 m between 08:00 and 12:00 h on 24 August. Also evident from Fig. 3 is a general tendency for a diel difference in the depth of sunfish with generally greater depths being occupied during the day. For all three fish these differences in day and night depths were highly significant: sunfish 1, occupied a mean day depth of 250.7 m, and a mean night depth of 104.7 m, ($t_{94} = 12.2, P < 0.001$), with sunfish 2 having a mean day depth of 112.1 m versus a mean night depth of 63.18 m, ($t_{148} = 4.7, P < 0.001$), and finally sunfish 3 showing a mean day depth of 50.7 m and a mean night depth of 29.9 m ($t_{92} = 3.0, P = 0.003$).

Analysis of the depth data also revealed that individual fish moved extensively through the water column. For example, using the temperature/depth profiles for individual 4-h intervals we examined the maximum depth versus the depth range occupied (i.e. maximum–minimum depth). Generally, even when the maximum depth reached was deep, the sunfish still travelled close to the surface within the same 4-h window (Fig. 4). The exception to this rule seemed to be that sometimes during the day the fish remain deep throughout a 4-h interval.

The thermal environment experienced by the sunfish varied with their location, the date and the depth. Representative temperature/depth plots at the start and end of each tracking period are shown for

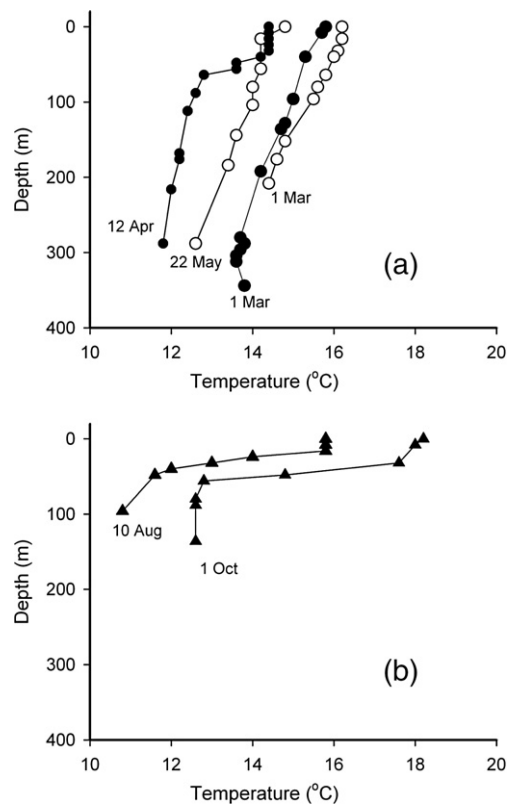


Fig. 5. Temperature depth profiles from the start and end of the tracking period for each sunfish. (a) filled circles = sunfish 1, open circles = sunfish 2. (b) triangles = sunfish 3.

each sunfish in Fig. 5. For the two fish tagged in southern Portugal, surface temperatures at the start of March were around 15.5–16 °C decreasing to around 13.5 °C at 300 m. In contrast, for the sunfish tagged off Ireland, while surface temperatures at the start of tracking (start of August) were again around 15.5 °C, temperature decreased more markedly with depth, dropping to around 10.5 °C at 100 m. By the end of the tracking period for this sunfish, when it was in the Bay of Biscay, surface temperatures had increased to around 18 °C and the temperature at 100 m was around 13 °C.

The overall patterns of time at different temperatures for the three sunfish are shown in Fig. 6. For the two fish tagged off Portugal, the majority of the time (99.2% and 95.2% respectively) was spent between 12 and 17 °C. In contrast the sunfish tagged off Ireland showed more time at colder temperatures (<12 °C) and also more time at warmer temperatures (>17 °C). When we considered the mean temperature experienced within individual 4-h intervals, there were significant differences in the temperatures experienced by the three fish (ANOVA, $F_{2,474}=15.4$, $P<0.001$) with the two fish tagged off Portugal experiencing cooler temperatures (means 14.2 °C and 14.4 °C respectively) compared to the fish tagged off Ireland (mean 15.1 °C).

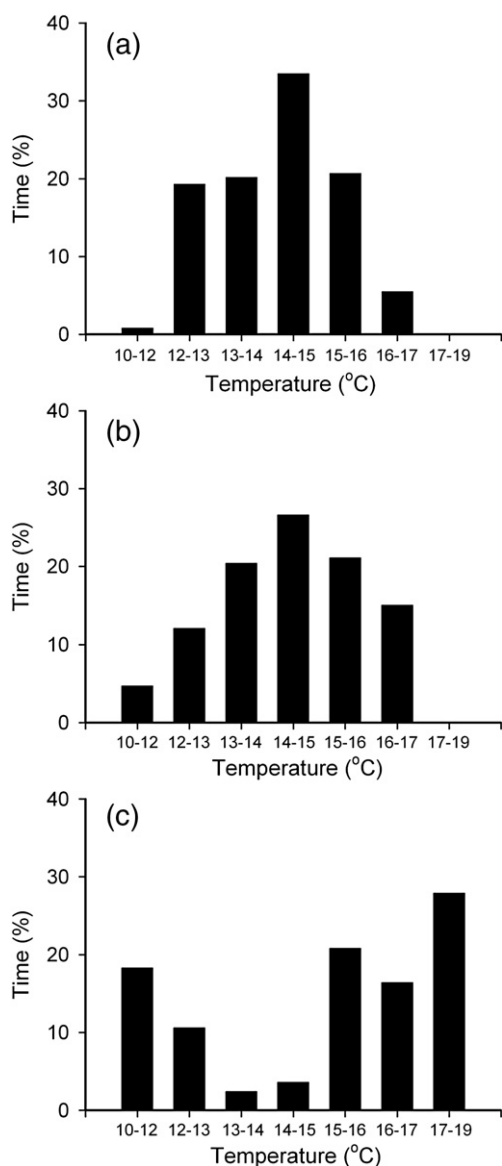


Fig. 6. The percentage of time spent within different temperature ranges. (a–c) shows data for sunfish 1, 2 and 3 respectively.

4. Discussion

Our results provide a general picture of ocean sunfish as a species that travels extensively in both horizontal and vertical dimensions. Presumably these movements reflect, at least in part, a search for gelatinous zooplankton prey. Although the spatio-temporal patterns of gelatinous zooplankton abundance are fairly poorly described, it is well known that plankton productivity in general is greatest at high latitudes in the spring and summer and exceeds that seen in more oligotrophic (nutrient poor) low latitudes (Parsons et al., 1984). This general pattern of plankton productivity accounts for some classic paradigms of ocean migration, such as baleen whales moving to the poles to feed in summer before moving to warmer tropical areas to over-winter. Similarly, evidence from long-term satellite tracking as well as direct observation, suggests that another predator of gelatinous zooplankton, the leatherback turtle (*Dermochelys coriacea*), is a seasonal visitor to high latitudes (McMahon and Hays, 2006). Our preliminary data suggests that ocean sunfish also conform to this classic paradigm, moving north at the end of winter and south at the end of summer.

As well as undertaking extensive horizontal movements, it was clear that ocean sunfish also exhibit marked vertical movements. A diel pattern in depth use pervaded across all the individuals we tracked with deeper daytime distribution. These observations fit the classic pattern of normal diel vertical migration (DVM), whereby zooplankton occur deeper in the water column during the day and shallower at night (Hays, 2003). It is well known that this pattern of DVM may interact with the physiology of predators to influence their diving behaviour and patterns of depth use. For example, penguins may dive deeply during the day to feed on deeply distributed krill and then cease feeding when their prey is closer to the surface at night because ambient light levels are too low for sensory perception of prey (Wilson et al., 1993). In contrast, when their prey are exhibiting DVM, the pattern of behaviour for leatherback turtles is for shallow diving at night when prey are near the surface and then a lack of diving during the day when prey are deep (Hays et al., 2006). Our results imply that ocean sunfish may simply track their vertically migrating prey and continue to feed both day and night. Similar conclusions have been reached for megamouth sharks and basking sharks over at least shorter term periods of several days to weeks (Nelson et al., 1997; Sims et al., 2005). It seems that freed from the need to surface to breathe, planktivorous fish are more readily able to exploit deeply distributed prey.

Yet, while we saw a generalised diel pattern of depth use by ocean sunfish, it was also evident that within each 4-h interval, individuals were often moving extensively through the water column. These movements might reflect prey searching (Sims et al., 2008). It was interesting that between 08:00 and 16:00 h, sunfish often remained continuously at depth, whereas the extensive vertical movements were more evident at other times. During the daytime zooplankton might already be resident at their daytime depths and so it may be that vertical movements by sunfish occur when prey are ascending or descending, with the sunfish attempting to locate maximum prey concentrations at these times. Alternatively there are other possibilities for why sunfish might regularly surface. For some fish, marked vertical movements are sometimes linked to re-warming at the surface or to fish only being able to spend limited time in deep sub-oxic waters (Carey and Robison, 1981; Holland et al., 1992; Dagorn et al., 2000). These remain possibilities for surfacing by sunfish (Cartamil and Lowe, 2004). In addition it has been suggested that sunfish may periodically surface to solicit birds and other fish to remove parasites from their skin (Thys, 1994; Konow et al., 2006). Teasing apart these various hypotheses for surfacing in sunfish will benefit from tracking fish over a broad range of conditions as well as obtaining continuous (archival) records of depth and temperature. Unfortunately due to the limited bandwidth of the Argos system most remotely recovered data-sets, like ours, have gaps in the data record.

While high prey densities may be the ultimate reason for migration of ocean sunfish to high latitude, the question remains as to why fish do not remain at high latitudes during the winter. For example, some fish that feed during the summer around the UK and Ireland may remain at high latitudes during the winter. Examples include mackerel (*Scomber scombrus*) and basking sharks (Sims et al., 2003, 2006). Southerly movements by sunfish at the end of the summer are presumably linked to the more restricted thermal tolerances of this species. The thermal envelope occupied by the three individuals we tracked was essentially encompassed by the range 10–19 °C (>99% of time). It may be that sunfish are unable to spend long periods below this range, or without at least prolonged re-warming in surface waters. In the winter sea surface temperatures to west of Ireland typically drop to around 8–10 °C (Boelens et al., 1999) and this might be too low for ocean sunfish. However, it should be noted that water temperatures in the North East Atlantic, as elsewhere in the World's oceans, are changing and the last two decades have seen a progressive warming (Hobson et al., 2008). If ocean sunfish are indeed thermally constrained to the time of year they can occur at high latitude, we would expect that this seasonal thermal window of favourable conditions is currently expanding in the North Atlantic. It should also be noted that the individuals we equipped were fairly small with predicted weights (using length/weight relationships in Watanabe and Sato (2008)) ranging from 14.1 kg to 18.1 kg. For a wide range of species, size plays a key role in influencing distribution and vertical movements (e.g. Eckert, 2002; Fowler et al., 2006). Clearly equipping larger sunfish would be very useful to investigate how behaviour varies with size in this species.

We had evidence that tags detached prematurely in two cases and that one fish might have died and sunk to the seabed. Inferring the fate of both tags and tagged animals is a perennial challenge in long-term tracking studies where both animals and tags are rarely re-sighted (Hays et al., 2007). For birds, altitude and location data have been used to infer mortality (Combreau et al., 2001), while for sea turtles capture of tagged individuals has been inferred by tags coming out of the water and travelling inland (Hays et al., 2003). The descent of one of our tags to almost 2000 m when the tag had previously only been to a maximum of 432 m in the preceding 42 days of tracking, suggests that this fish had died for reasons unknown and sunk to the seabed. Similar conclusions have been reached using depth data for other fish equipped with satellite tags (Graves and Horodysky, 2008). That the event occurred 42 days after the sunfish was equipped, suggests that the tagging procedure was not the cause, although there might possibly have been some longer-term effect of tagging. In addition to high bycatch mortality, small sunfish are also consumed by sharks (Fergusson et al., 2000), so there are various possibilities for why this fish might have died. In particular, small sunfish are preyed upon by the blue shark (*Prionace glauca*), being present in their stomach contents from this region (N. Queiroz, unpublished data). However, as with all biotelemetry work, future studies should clearly aim for least invasive attachment procedures as well as longer term data sets. For a complete understanding of seasonal patterns of behaviour we should aim for studies lasting up to one year and certainly these types of data records have been attained with other species and remain a realistic goal.

In conclusion, we have provided here an initial descriptive account of some of the key movement patterns, in both horizontal and vertical dimensions, for sunfish tagged in the North East Atlantic. Clearly this work is only a starting point and yet even with the preliminary nature of our work it is clear that ocean sunfish move actively in both horizontal and vertical dimensions and appear to be seasonal migrants to high latitudes.

Acknowledgements

This research was facilitated through the European Tracking of Predators in the Atlantic (EUTOPIA) programme in the European

Census of Marine Life. Funding was provided by the UK Natural Environment Research Council (NERC) through the NERC Oceans 2025 Strategic Research Programme theme 6 (Science for Sustainable Marine Resources). DWS and NQ thank FlyingSharks and especially Tunipex for providing access and logistical support at the tuna pen. Fieldwork in Ireland was supported by Údarás na Gaeltachta, Taighde Mara Teo, and the Marine Institute. We would like to thank Vincent Roantree, Mark Norman, Martin Lilley and Pádraig Frank O'Súilleabháin for the fieldwork assistance in Ireland. All tagging procedures conformed to UK Home Office standards. The NERC Remote Sensing and Data Analysis Service are thanked for provision of AVHRR images and we acknowledge use of the Maptool program for some analysis and graphics in this paper. N. Humphries is thanked for geolocation programming code. GCH was supported by a Ray Lankester Investigatorship from the Marine Biological Association of the UK, NQ by a Fundação para a Ciência e a Tecnologia (FCT) grant (SFRH/BD/21354/2005), TKD by an IRCSET Fellowship, and DWS by a NERC-funded MBA Senior Research Fellowship. [SS]

References

- Block, B.A., Teo, S.L.H., Walli, A., Boustany, A., Stokesbury, M.J.W., Farwell, C.J., Weng, K.C., Dewar, H., Williams, T.D., 2005. Electronic tagging and population structure of Atlantic bluefin tuna. *Nature* 434, 1121–1127.
- Boelens, R.G.V., Maloney, D.M., Parsons, A.P., Walsh, A.R., 1999. Ireland's marine and coastal areas and adjacent seas: an environmental assessment. Marine Institute Report. Department of Environment and Local Government and Department of Marine and Natural Resources, Ireland. 388pp.
- Brazner, J.C., McMillan, J., 2008. Loggerhead turtle (*Caretta caretta*) bycatch in Canadian pelagic longline fisheries: relative importance in the western North Atlantic and opportunities for mitigation. *Fisheries Research* 91, 310–324.
- Carey, F.G., Robison, B.H., 1981. Daily patterns in the activities of swordfish, *Xiphias gladius*, observed by acoustic telemetry. *Fishery Bulletin* 79, 277–292.
- Cartamil, D.P., Lowe, C.G., 2004. Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Marine Ecology Progress Series* 266, 245–255.
- Combreau, O., Launay, F., Lawrence, M., 2001. An assessment of annual mortality rates in adult-sized migrant houbaru bustards (*Chlamydotis [undulata] macqueenii*). *Animal Conservation* 4, 133–141.
- Dagorn, L., Bach, P., Josse, E., 2000. Movement patterns of large bigeye tuna (*Thunnus obesus*) in the open ocean, determined using ultrasonic telemetry. *Marine Biology* 136, 361–371.
- Dietrich, K.S., Meluin, E.F., Conquest, L., 2008. Integrated weight longlines with paired streamer lines – best practice to prevent seabird bycatch in demersal longline fisheries. *Biological Conservation* 141, 1793–1805.
- Eckert, S.A., 2002. Distribution of juvenile leatherback sea turtle *Dermochelys coriacea* sightings. *Marine Ecology Progress Series* 230, 289–293.
- Fergusson, I.K., Compagno, L.J.V., Marks, M.A., 2000. Predation by white sharks *Carcharodon carcharias* (Chondrichthyes: Lamnidae) upon chelonians, with new records from the Mediterranean Sea and a first record of the ocean sunfish *Mola mola* (Osteichthyes: Molidae) as stomach contents. *Environmental Biology of Fishes* 58, 447–453.
- Fowler, S.L., Costa, D.P., Arnould, J.P.Y., Gales, N.J., Kuhn, C.E., 2006. Ontogeny of diving behaviour in the Australian sea lion: trials of adolescence in a late bloomer. *Journal of Animal Ecology* 75, 358–367.
- Freedman, J.A., Noakes, D.L.G., 2002. Why are there no really big bony fishes? A point-of-view on maximum body size in teleosts and elasmobranchs. *Reviews in Fish Biology and Fisheries* 12, 403–416.
- Fulling, G.L., Dagmar, F., Knight, K., Hoggard, W., 2007. Distribution of Molidae in the northern Gulf of Mexico. *Gulf and Caribbean Research* 19, 53–67.
- Graves, J.E., Horodysky, A.Z., 2008. Does hook choice matter? Effects of three circle hook models on postrelease survival of white marlin. *North American Journal of Fisheries Management* 28, 471–480.
- Hays, G.C., 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* 503, 163–170.
- Hays, G.C., Broderick, A.C., Godley, B.J., Luschi, P., Nichols, W.J., 2003. Satellite telemetry suggests high levels of fishing induced mortality for marine turtles. *Marine Ecology Progress Series* 262, 305–308.
- Hays, G.C., Hobson, V.J., Metcalfe, J.D., Righton, D., Sims, D.W., 2006. Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* 87, 2647–2656.
- Hays, G.C., Bradshaw, C.J.A., James, M.C., Lovell, P., Sims, D.W., 2007. Why do Argos satellite tags deployed on marine animals stop transmitting? *Journal of Experimental Marine Biology and Ecology* 349, 52–60.
- Hobson, V.J., McMahon, C.R., Richardson, A., Hays, G.C., 2008. Ocean surface warming: the North Atlantic remains within the envelope of previous recorded conditions. *Deep-Sea Research Part 1* 55, 155–162.
- Holland, K.N., Brill, R.W., Chang, R.K.C., Sibert, J.R., Fournier, D.A., 1992. Physiological and behavioral thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature* 358, 410–412.
- Houghton, J.D.R., Doyle, T.K., Davenport, J., Hays, G.C., 2006. The ocean sunfish *Mola mola*: insights into distribution, abundance and behaviour in the Irish Sea and Celtic Seas. *Journal of the Marine Biological Association of the United Kingdom* 86, 1237–1243.

- 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.
- Lee, D.S., 1986. Seasonal, thermal and zonal distribution of ocean sunfish, *Mola mola* (Linnaeus), off the North Carolina Coast. *Brimleyana* 12, 75–83.
- McMahon, C.R., Hays, G.C., 2006. Thermal niche, large scale movements and implications of climate change for a critically endangered marine vertebrate. *Global Change Biology* 12, 1330–1338.
- Nelson, D.R., McKibben, J.N., Strong Jr, W.R., Lowe, C.G., Sisneros, J.A., Schroeder, D.M., Lavenberg, R.J., 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes* 49, 389–399.
- Parsons, T.R., Takahashi, M., Hargrave, B., 1984. *Biological oceanographic processes*, 3rd edition. Pergamon Press. 330pp.
- Petersen, S., 2005. Initial bycatch assessment: South Africa's domestic longline fishery, 2000–2003. Domestic pelagic longline fishery: Bycatch Report 2000–2003. BirdLife South Africa. 45 pp.
- Purcell, J.E., Uye, S., Lo, W.-T., 2007. Anthropogenic causes of jellyfish blooms and their direct consequences for humans: a review. *Marine Ecology Progress Series* 350, 153–174.
- Shillinger, G.L., Palacios, D.M., Bailey, H., Bograd, S.J., Swithenbank, A.M., Gaspar, P., Wallace, B.P., Spotila, J.R., Paladino, F.V., Piedra, R., Eckert, S.A., Block, B.A., 2008. Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biology* 6, e171. doi:10.1371/journal.pbio.0060171.
- Silvani, L., Gazo, M., Aguilar, A., 1999. Spanish driftnet fishing and incidental catches in the western Mediterranean. *Biological Conservation* 90, 79–85.
- Sims, D.W., Southall, E.J., 2002. Occurrence of ocean sunfish, *Mola mola* near fronts in the western English Channel. *Journal of the Marine Biological Association of the UK* 82, 927–928.
- Sims, D.W., Southall, E.J., Richardson, A.J., Reid, P.C., Metcalfe, J.D., 2003. Seasonal movements and behaviour of basking sharks from archival tagging: no evidence of winter hibernation. *Marine Ecology Progress Series* 248, 187–196.
- Sims, D.W., Southall, E.J., Tarling, G.A., Metcalfe, J.D., 2005. Habitat-specific normal and reverse diel vertical migration in the plankton-feeding basking shark. *Journal of Animal Ecology* 74, 755–761.
- Sims, D.W., Witt, M.J., Richardson, A.J., Southall, E.J., Metcalfe, J.D., 2006. Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society B* 273, 1195–1201.
- Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K., Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J., Metcalfe, J.D., 2008. Scaling laws of marine predator search behaviour. *Nature* 451, 1098–1102.
- Thys, T., 1994. Swimming heads. *Natural History* 103, 36–39.
- Watanabe, Y., Sato, K., 2008. Functional dorsoventral symmetry in relation to lift-based swimming in the ocean sunfish *Mola mola*. *PLoS ONE* 3 (10), e3446. doi:10.1371/journal.pone.0003446.
- Wilson, R.P., Putz, K., Bost, C.A., Culik, B.M., Bannasch, R., Reins, T., Adelung, D., 1993. Diel dive depth in penguins in relation to diel vertical migration of prey: whose dinner by candlelight? *Marine Ecology Progress Series* 94, 101–104.
- Wilson, R.P., McMahon, C.R., 2006. Measuring devices on wild animals: what constitutes acceptable practice? *Frontiers in Ecology and the Environment* 4, 147–154.