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Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging

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ABSTRACT

Understanding animal distributions and habitat utilisation is vital for the management of populations, especially those of endangered species. However, this information is not available for the majority of marine species and is difficult to obtain for those with low population densities. The common skate, *Dipturus batis*, was once abundant and widespread in the North-East Atlantic but is now thought to be locally extinct in the Irish Sea and in the central and southern North Sea, and is listed as Critically Endangered on the IUCN Red List. The constraints of skate body morphology on locomotory mode assume low levels of activity with long periods spent resting on the seabed, therefore predicting a high degree of site fidelity. To investigate this hypothesis we tagged 8 common skate (two male and six female, mass range: 10.9–63.5 kg) with depth and temperature-logging data storage tags off the west coast of Scotland in May 2008. All 6 tags attached to females were recovered after 1–9 months at liberty. All 6 individuals exhibited pronounced site fidelity to highly localised areas. Within these local areas however, time-depth profiles were dominated by periods of high activity, with vertical movements of >100 m being conducted on a regular, sometimes daily, basis. Intra-individual plasticity was observed in vertical activity patterns with individuals switching between low and high activity patterns. Smaller skate were generally less active and occupied deeper depths. Limited short-term horizontal movements in preferred habitats supporting apparently high foraging activity highlights the need for spatial management of 'refugial' populations of this once widespread fish, that appears now largely extirpated from European waters.

1. Introduction

Animal activity patterns play a central role in their ecology. For instance, inter-specific differences in timing of activity may determine predator–prey interaction rates, while intra-specific differences in time allocated to activities, such as between the sexes, has the potential to lead to habitat sexual segregation (Wearmouth and Sims, 2008). Obtaining information on the activity patterns of free-ranging marine vertebrates is difficult, particularly for fish species which spend their entire lives submerged. However, animal-borne data-logging devices have been used to obtain information on the free-ranging movements of several marine fish species (Hobson et al., 2007; Hunter et al., 2004) as well as marine reptiles, birds and mammals.

Benthic species often exhibit crypsis (for example by covering themselves in substrate) and for flattened fishes, this characteristic, combined with their body shape, decreases their conspicuousness to predators (a detection minimisation strategy) (Gibson, 2005; Ryer, 2008). However, dorsoventral flattening of the body constrains locomotor ability and thus, whilst flatfish may periodically undertake extensive migrations between feeding and spawning grounds (Hunter et al., 2004), it is generally assumed that flattened fish, adapted for benthic living, are less active and spend long periods resting. Flattened teleost fish locomote via whole body flexure, whilst in dorsoventrally flattened elasmobranchs (batoids), the pectoral fins are used. Calcification patterns in batoid pectoral fins determine swimming mode along a continuum from undulatory (>1 wave passing along the wing) to oscillatory motion (single wave, analogous to bird flight) and as a result, oscillators (e.g. Myliobatidae) are better adapted for free-swimming than the sedentary undulators (e.g. Rajidae) (Schaefer and Summers, 2005). Propulsion by fin undulation is limited as each fin ray is attached at its base to the body, the net effect being an ability to attain only low or moderate speeds, but to achieve more precise control and manoeuvrability (Lindsey, 1978). Nevertheless, activity level is influenced by food distribution and availability and, in some habitats, benthic batoids may need to be as active as fish with a fusiform body shape in order to locate sufficient live prey or to scavenge sparse food items. This may be particularly relevant for species with a large body size, since although size-relative metabolic costs will be lower (Sims, 1996), the absolute cost of maintaining an extreme body size will be high.

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The common skate, *D. batis*, is one of the largest benthic predators in the Atlantic Ocean. It is found from inshore (30 m) to deep water (600 m) in the north-east Atlantic from Morocco to northern Norway (Wheeler, 1969). It feeds on a variety of demersal fish and crustaceans, and anecdotal accounts based on analysis of stomach contents imply some fish prey may be captured in midwater (Wheeler, 1969). Attaining lengths of up to 285 cm, it is the largest European batoid fish (Anonymous, 1999). However, this large size, combined with slow growth, late maturation and low fecundity, renders common skate particularly susceptible to overfishing. A fish described as common in south-west UK waters in the late 19th Century (Heape, 1888), *D. batis* has undergone dramatic declines in abundance over the last 100 years. Landings at Concarneau, France, decreased by 92% during the 1970s, whilst only 6 common skate were captured in UK government surveys of the Irish Sea between 1988 and 1997 (Dulvy and Reynolds, 2002). Common skate is now thought to be locally extinct in the Irish Sea (Brander, 1981), central and southern North Sea, West Baltic and western Mediteranean (Dulvy and Reynolds, 2002) and is listed as critically endangered on the IUCN Red List of Threatened Species. However, local 'remnant' populations of common skate have been found off the coast of Norway, around the Shetland Islands, off the west coast of Scotland and to the south and southwest of Ireland (Dulvy and Reynolds, 2002).

The biology of the common skate has been little studied. Mating is thought to occur during March and April as, historically, mating pairs were landed together during these months (Day, 1884). It has been suggested that skate move offshore during winter months (Wheeler, 1969), however, recent evidence from mark–recapture studies does not support this hypothesis; rather, a seasonal migration of males away from the inshore fishing grounds in summer months has been proposed (Little, 1997). These data also suggest a high level of site affinity, since the vast majority of recaptures were caught at or near the release site, and only 3% of fish moved more than 20 km after periods of liberty of up to 12 years (Little, 1998).

The purpose of this study was to test, using electronic tag recordings of the movements of free-ranging animals, whether common skate exhibit the sedentary lifestyle assumed for dorsoventrally flattened benthic species such as flatfish and rays. Secondly, by examination of the time-depth profiles of individual fish, we will describe, for the first time, the vertical activity patterns and sub-surface behaviour of common skate. Finally, the distribution of capture locations will enable re-examination of the horizontal movements and site fidelity of this critically endangered species.

2. Materials and methods

2.1. Fish capture and tagging

Fish were captured by rod-and-line angling over a six day period during May 2008. Known skate 'marks' within the vicinity of Loch Sunart, Ardnamurchan (Scottish West Coast; see Fig. 1) were fished using coalfish, mackerel or pollack baits attached to 10/0 or 12/0 hooks. To minimise capture loss resulting from bites severing the line, a 200 lb trace was used. This also reduced the chances of leaving hooks and lengths of line attached to fish.

Once brought to the surface, fish were hoisted onto the deck using a winch with an in-line spring balance. Fish weight in air was recorded, total length and width were measured, and the fish was tagged with one or two types of electronic tags. All fish were fitted with a G5 data storage tag (Cefas Technology Limited, Lowestoft, UK) and, in all but one case, a coloured numbered T-bar anchor tag (FD-94, Floy Tag Inc., Seattle, USA). The largest fish caught (Fig. 2a) was not tagged with a number tag but with a pop-off satellite-linked archival transmitter (PSAT) (Mk 10 PAT tag, Wildlife Computers, Redmond, USA). All fish were returned to sea within 7 min of reaching the

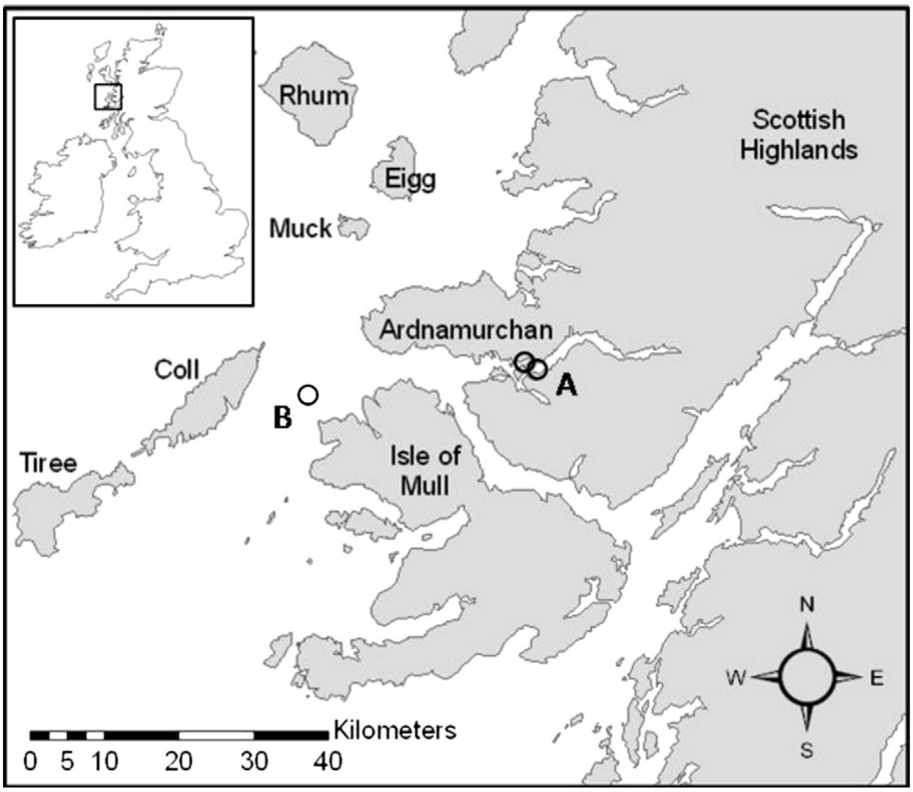

Fig. 1. Location of Scottish west coast tagging site (insert) and skate capture locations (black circles) within Loch Sunart, Ardnamurchan (A) and off Caliach Point, Isle of Mull (B).

Fig. 2. Common skate female 1 prior to release (a) showing tag positions. This female was tagged with both a data storage (insert b) and pop-off archival satellite transmitter (PSAT) (insert c).

surface. All tagging procedures were licensed by the UK Home Office under the Animals (Scientific Procedures) Act 1986.

Data storage tags (DSTs) (Fig. 2b) were cylindrical, 35.5 mm long × 11.5 mm diameter and weighed 2.1 g in water. DSTs monitor pressure to a depth of 100 m (accuracy 1 m, resolution 40 mm) and temperature from 2 to 34 °C (accuracy 0.1 °C, resolution 0.03 °C). Data logging is controlled by a temperature-compensated real-time clock and recorded data are stored to non-volatile flash memory with a data retention time in excess of 10 years. DSTs were programmed to record depth every 20 s for the first 3 months at liberty and every 2 min thereafter. The tags also recorded temperature every 10 min. The PSAT tag (Fig. 2c) archived depth (maximum depth = 1000 m, accuracy = 0.5 m), ambient temperature (−40 – 60 °C range, accuracy = 0.05 °C) and light level (at 550 nm wavelength) every second. The tag was programmed to detach by dissolving a corrodible link 90 days post-deployment, whereupon the tag should float to the surface and transmit 4-h summary histograms of parameters sampled every 10 s to Argos receivers on NOAA polar-orbiting satellites.

Data storage tags were mounted in a stainless steel wire 'cradle' (Fig. 2b) atop a long, pointed stainless steel wire. Similarly, the corrodible link of the PSAT tag was attached to a long, pointed stainless steel wire via a swivel and short length of monofilament (250 lb test) (Fig. 2c). Electronic tags were attached to the skate via Peterson disc tagging. Specifically, a numbered Peterson disc was placed on the length of pointed wire, which was then passed through the skate wing dorsoventrally at a position midway between the eye orbit and the insertion of the pectoral fin, approximately one third of the distance between the spine and the wing tip (Fig. 2a). A second Peterson disc was threaded onto the wire on the ventral side of the wing. The pointed end was then removed from the wire and its remaining length turned into a series of rounds to secure the tag in position. Number tags (or the PSAT tag) were located in a similar position on the opposite wing. On recapture by fishermen, the data storage tag was removed by snipping the wire stem and pulling the remainder back through the wing from the dorsal surface.

2.2. Data analysis

Release and recapture positions were plotted in ArcGIS (v 9.3). Distance between capture and recapture locations was calculated to the nearest metre.

Data were downloaded from all data storage tags recovered providing datasets of pressure (depth) and ambient temperature for up to 5 months post-deployment. Depth utilisation over time at liberty was summarised by plotting the proportion of time spent within 10 m depth bins. Raw depth data was plotted in relation to the light:dark cycle, where times of sunrise and sunset at the appropriate latitude (56°N) were derived from a nautical almanac. Descriptive statistics were calculated over the entire time at liberty by pooling data into both hourly and daily time bins.

For benthic species such as the skate, along substrate movements in habitats with steep bathymetry will typically result in change in depth. Therefore a time-series of changes in depth greater than 40 mm (the tag's resolution), provides a record of when fish were actively moving or resting on the seabed. Rise and fall of tidal height also influenced depth records. However, at a temporal resolution of 20 s, changes in depth attributable to tide alone did not exceed tag resolution. Calculation of relative change in depth provides a time-series of the degree of vertical activity exhibited. Rhythms in vertical activity were identified from digital signal processing. Fast Fourier Transform (FFT) with a 'Hamming' window function was applied to relative change-in-depth data using programming routines in MATLAB (for further details see Shepard et al., 2006). This analysis decomposes complex time-series data with periodic components into the underlying sinusoidal functions of particular wavelengths. A periodogram was then used to visualise the frequencies (i.e. wavelengths) and magnitude of the periodic components of the data. The chronology of significant periodicities was investigated by pooling data over the entire time at liberty into hourly time bins. The relationship between fish mass and vertical activity (median total daily change in depth over 35% of most active days) was investigated using linear regression (Minitab v 13.31).

3. Results

Six data storage tags were recovered from fish (that were then released alive) after times at liberty ranging from 29 to 281 days (Table 1). All fish were recaptured within close proximity of their release location (Fig. 3) (minimum distance moved ranged from 14 m to 1.75 km; Table 1). Fish dimensions and masses did not vary significantly over time at liberty and thus are not discussed further in this paper.

The PSAT tag detached prematurely and, presumably due to the tag lying in a horizontal position on the shore, only a small number of uncorrupted messages were received. The limited data available suggested that the tag detached sometime between the 13th and 26th June 2008. The tag's transmission signal was detected using a UHF receiver (PSR-282, General Research of Electronics Inc., Tokyo) and the signal's detectable range was identified as the 500 m section of coastline shown in Fig. 3. However, despite an extensive search of this section of coast, the tag was not recovered.

The data storage tags recorded depths to 110 m. Females 4, 5 and 6 spent 53.1, 16.9 and 66.3% of their time respectively at depths greater

Table 1
Summary details of the tagged fish.

Skate sex and number	Length (m)	Disc width (m)	Weight (kg)	Release date	Capture (and release) location	Recapture date	Days at liberty	Minimum distance moved (m)
Female 1	2	1.55	63.5	04/05/08	Sunart	02/08/08	90	14
Female 2	1.65	1.3	33.6	04/05/08	Sunart	04/06/08	31	50
Female 3	1.62	1.13	25.4	06/05/08	Sunart	11/02/09	281	305
Female 4	1.32	1.06	16.3	06/05/08	Sunart	04/06/08	29	1749
Male 1	1.25	0.97	10.9	06/05/08	Sunart			
Female 5	1.65	1.21	24.5	07/05/08	Sunart	08/07/08	62	210
Female 6	1.6	1.27	33.1	07/05/08	Sunart	07/07/08	61	169
Male 2	1.95	1.5	58.1	08/05/08	Caliach			

than 110 m (Fig. 4) and thus a relatively high proportion of movements were missed. In contrast, females 1, 2 and 3 spent only 4.3, 6.6 and 1.6% of their time respectively at depths greater than 110 m (Fig. 4). This pattern of depth use may be related to fish size, with smaller females spending a greater proportion of their time at depth. Mean depth over entire time at liberty was 63.2 and 78.1 m for the two largest females, females 1 (2.00 m TL) and 2 (1.65 m TL), whilst the mean depth of the two smallest females, females 4 (1.32 m TL) and 6 (1.60 m TL), was 105.8 and 106.2 m respectively. As the depth time-series of females 1–3 were more complete (i.e. the fish remained within the depth limit of the tag for a greater proportion of the time), only these data were analysed in detail. However, sections of depth data recovered from fish 4–6 were examined to compare inter-individual activity patterns.

On four separate occasions, females 3 (one occasion), 4 (two occasions) and 5 (one occasion) ascended rapidly to the sea surface, where they remained for several minutes before undertaking a rapid descent to depth. These behaviours are not illustrated here as they are not thought to represent natural behaviours (see Discussion).

Fig. 5 shows the 90-day time-depth profile and daily temperature range for female 1. During the first two weeks at liberty, this female remained at depths >40 m and, although active, did not range widely through the water column on a daily basis (daily depth range: 6.6 to 40.9 m). In contrast, towards the end of May (3–4 weeks post-tagging), the degree of vertical ranging exhibited by this female increased, with the fish regularly ranging from relatively shallow water (minimum recorded depth between release and recapture was 4.7 m) to beyond 110 m within a 24 h period (maximum daily depth range, at least 105.3 m). The limited PSAT tag data retrieved from the same fish recorded a maximum depth of 128 m, suggesting that daily depth ranges of over 120 m may have occurred. This vertical ranging behaviour, interspersed by periods of more modest ranging,

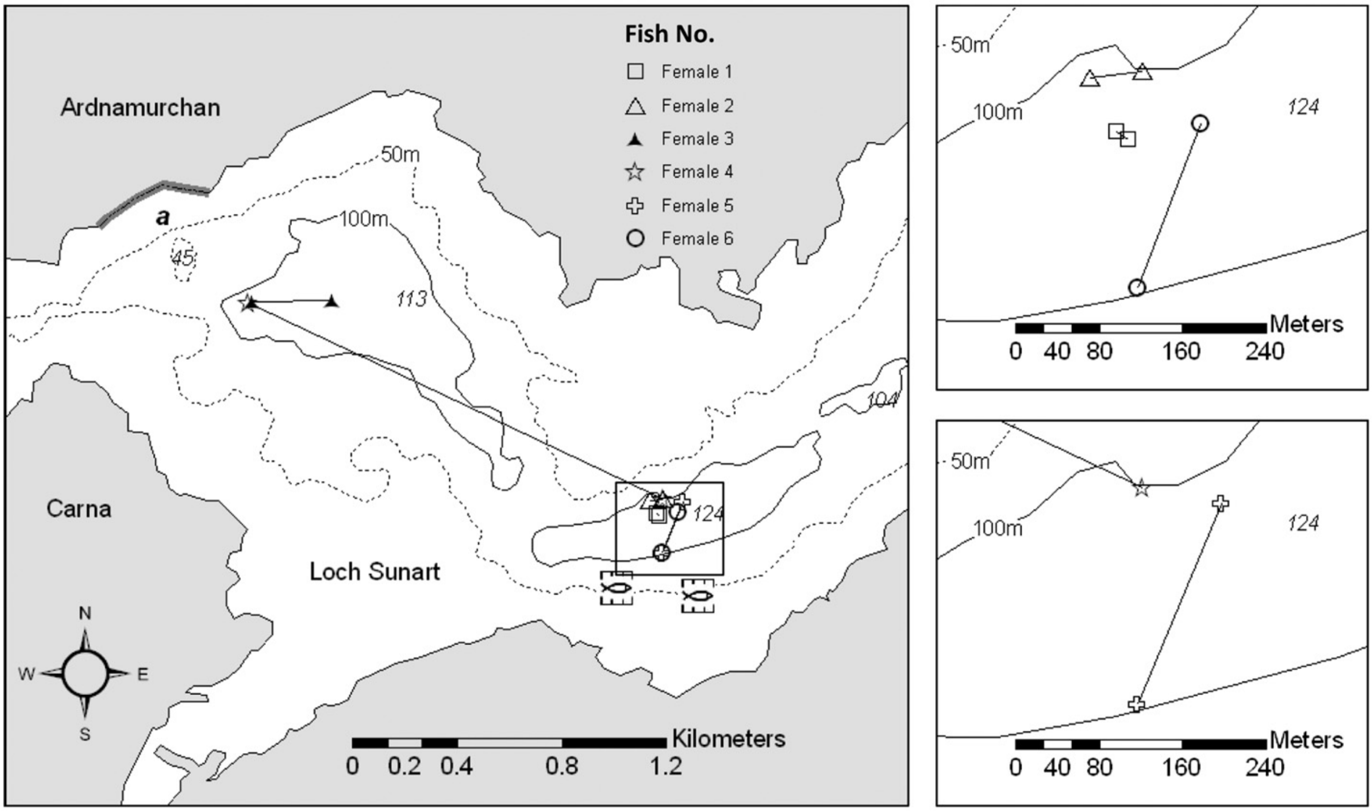

Fig. 3. Bathymetric map of skate capture locations with Loch Sunart (area A in Fig. 1) indicating the capture and recapture locations of the 6 data storage-tagged female skates, where numbers in italics denote maximum seabed depths. Solid black lines join capture and recapture locations for each individual to indicate minimum distances moved. The highlighted section of coast labelled *a.* illustrates the transmission detection range of the beached pop-off satellite archival transmitter (PSAT). The locations of two salmon cages are shown as boxed fish symbols.

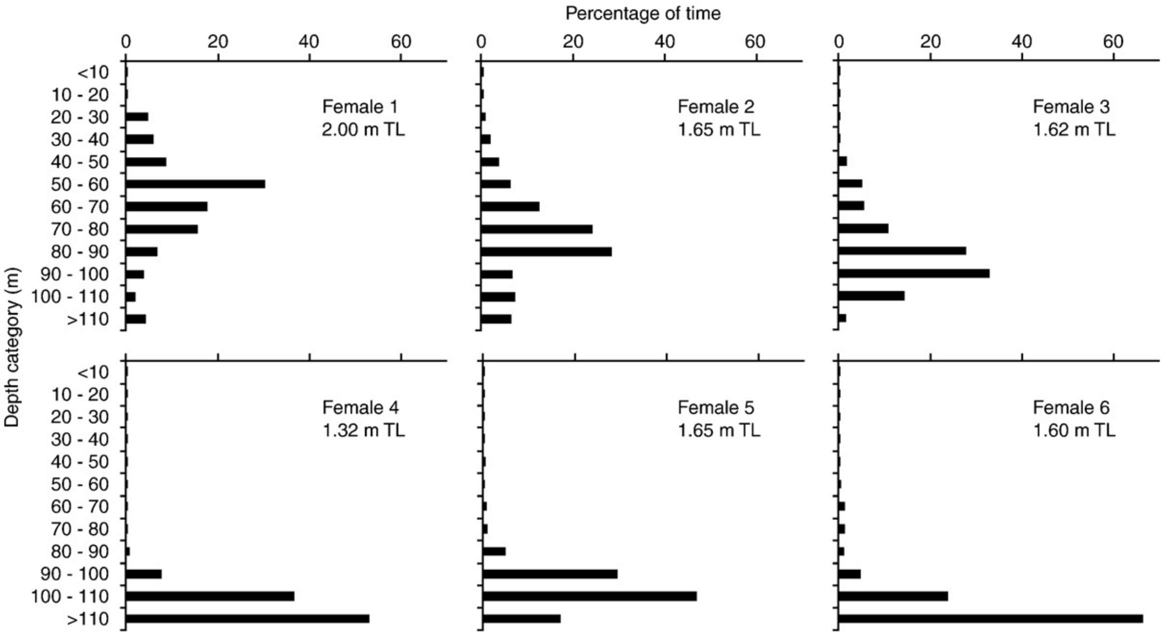

Fig. 4. Percentage of time each tagged female skate spent within 10-m depth categories over the entire times at liberty.

continued throughout the entire time at liberty. Daily mean depth varied between 26.6 m and 108.4 m, with a mean daily depth range of 53.8 m. The ambient temperature experienced by this fish increased from a daily mean of 8.3 °C on the 5th May to 13.1 °C on the 30th July. The daily temperature range increased with the degree of vertical ranging (maximum daily temperature range = 1.1 °C, mean daily range = 0.5 °C).

The 31-day and 147-day time-depth profiles of females 2 and 3 were broadly consistent with that of female 1, indicating periods of vertical ranging interspersed by more limited vertical movements (daily depth range: 12.1 to >106.6 m and 3.2 to >88.1 m; mean daily depth range = 55.8 and 43.3 m respectively). However, unlike female 1, vertical activity in these females closely followed the light: dark cycle, with large vertical ascents and descents predominantly

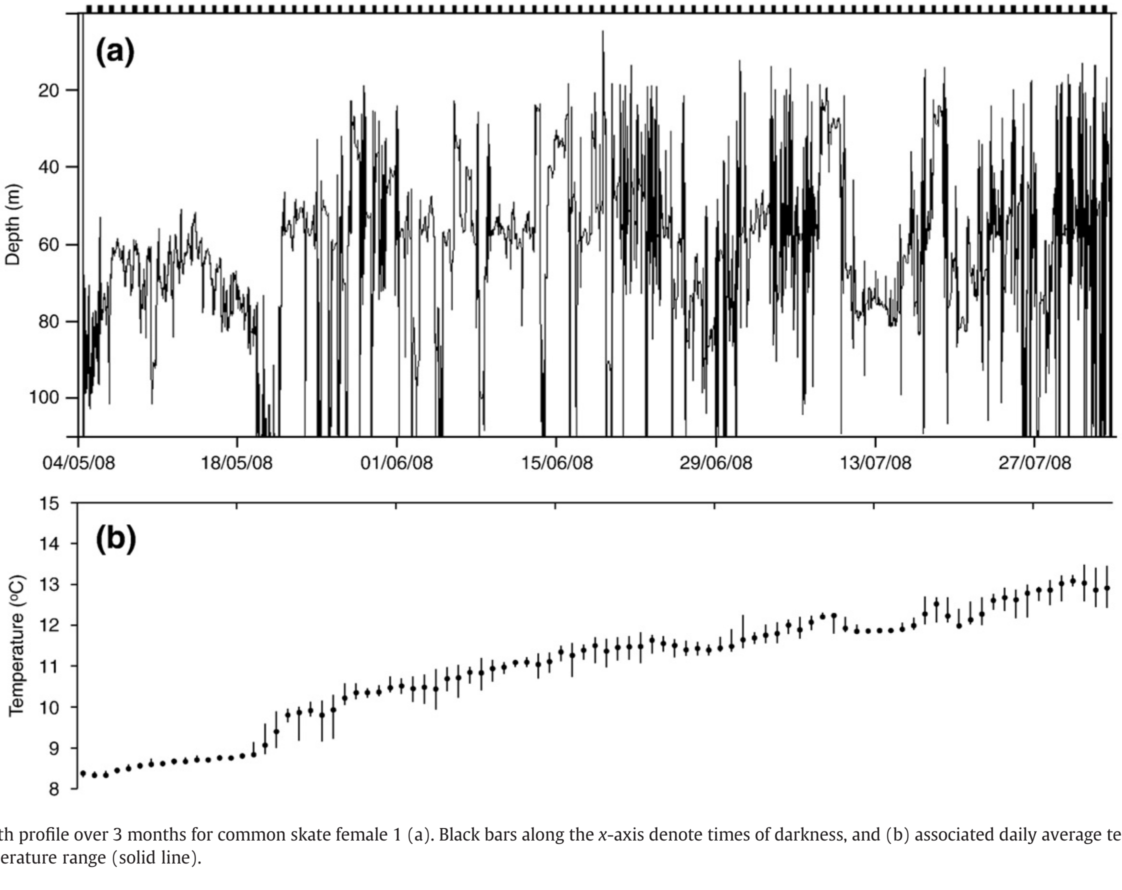

Fig. 5. Time-depth profile over 3 months for common skate female 1 (a). Black bars along the *x*-axis denote times of darkness, and (b) associated daily average temperature (black circle) and temperature range (solid line).

occurring nocturnally. The minimum depth recorded between release and recapture was 1.9 m for female 2 (daily mean depth: 50.9 to 102.8 m) and 13.6 m for female 3 (daily mean depth: 49.8 to 103.5 m). As seen for female 1, ambient temperature increased during time at liberty for females 2 (mean daily temperature ranged from 8.3 °C on 5th May to 10.4 °C on 2nd June) and 3 (8.7 °C on 11th May to 14.1 °C on 9th September). Daily temperature range increased with higher levels of vertical movement (maximum daily temperature range = 1.2 °C and 2.0 °C, mean = 0.4 °C and 0.3 °C for females 2 and 3 respectively).

A number of characteristic behaviours were identified from the time-depth profiles of all fish (Fig. 6). These behaviours were exhibited by all five females at some point during liberty and can be broadly categorised into 3 types based on the degree of activity exhibited: resting behaviour, low activity, and high activity. Resting behaviour (Fig. 6a) was characterised by a smooth sinusoidal wave in the fish's depth record, consistent with the rise and fall of tidal height as the fish remained at the same depth. In the example shown in Fig. 6a, female 4 remained stationary for over 30 h (more than 2 full tidal cycles), the longest rest period identified from the <110 m depth data of all 5 fish. Tidal rhythms were also evident in low activity behaviours (Fig. 6b and c), although small peaks and troughs in the time-depth profile representing vertical excursions indicated some activity periodically over the five day period shown. The low activity

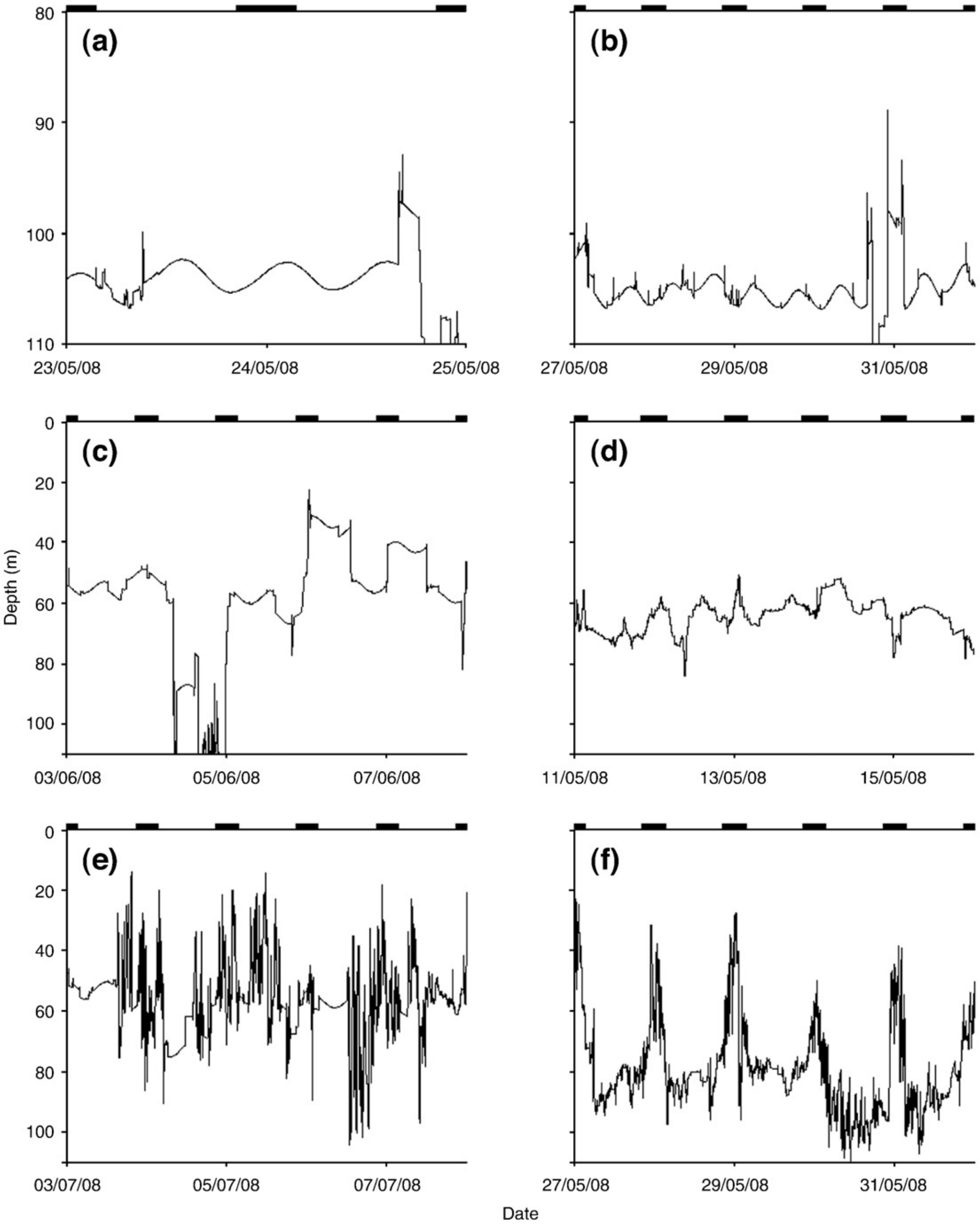

Fig. 6. Examples of characteristic behaviours identified within the time-depth profiles of electronically tagged common skates: (a) seabed resting (female 4); (b) low activity: seabed resting interspersed with brief activity bouts (female 5); (c) low activity: seabed resting interspersed by changes in depth (female 1); (d) high activity: active within a narrow range of depths (female 1); (e) high activity: vertical ranging (female 1); and (f) high activity: vertical ranging with nocturnal ascent (female 2). Black bars along the *x*-axis denote times of darkness.

behaviour exhibited by female 5 (Fig. 6b) differs from that shown by female 1 (Fig. 6c) in that the latter fish frequently undertook large depth changes between successive resting periods. In contrast, little tidal rhythm was evident during high activity behaviours (Fig. 6d–f). Over the five day period shown in Fig. 6d, the time-depth profile of female 1 appeared irregular, suggesting that the fish moved constantly and therefore overall exhibited a high level of activity. A similar pattern of high activity is apparent in Fig. 6e (also female 1) albeit over a much greater range of depths and interspersed by a few short periods of resting on the seabed. Female 2 also exhibited pronounced vertical ranging behaviour (Fig. 6f), although in this example, vertical ranging is combined with nocturnal ascent (movement into shallower water shortly after the onset of darkness and return to depth pre-dawn). Nocturnal ascent was also exhibited by females 3 and 6.

To further illustrate the degree of vertical ranging exhibited, Fig. 7 shows female 1's depth profile over a 24-h period during which time a high activity vertical ranging strategy was adopted. Over this 24-h period, female 1 utilised the entire water column, ranging from depths of 13.7 m to beyond 110 m. However, it is evident from this figure that multiple, wide ranging (>50 m) vertical ascents and descents were undertaken over this time, that these movements were relatively rapid compared to other vertical movements exhibited (maximum rate of change = 12.9 m min^{-1}) and occurred predominantly at night. Consequently, a considerable total change in depth was evident in such cases: in this example, a total vertical movement of 1846.5 m over 24-h.

There is some evidence to suggest that vertical ranging may be more predominant in larger females. Regression analysis revealed a significant relationship between fish mass and degree of vertical ranging when active (median total daily change in depth over 25% of most vertically active days), with larger animals ranging more than smaller females ($r^2 = 0.586$, $F = 8.07$, $P = 0.047$; Fig. 8).

Fast Fourier transform of the change in depth data for females 1, 2 and 3 revealed large spectral peaks near zero (Fig. 9a–c). Peaks at zero frequency represent unchanging data such as the mean change in depth, therefore only peaks following the descent of this initial slope were interpreted as periodic signals in the change in depth data. The periodograms of all fish were curtailed at 6 cycles per day as there were no significant peaks beyond this value. There is some evidence of an influence of the tidal spring/neap cycle (spectral peak at a periodicity of ~12 d) in the depth record of female 1 (Fig. 9a). However, the dominant periodic component within the change in depth data for all 3 females was a diel rhythm (peak at 1 cycle per day). Small spectral peaks at multiples of 1 cycle per day represent harmonics of the only true periodic component in the data (a diel rhythm) and were ignored. Examination of the hourly average change in depth data (Fig. 10a–c) reveals lower vertical activity levels during early morning to mid-afternoon (~05:00–17:00; minimum average change in depth for females 1, 2 and 3 were 0.061, 0.050 and 0.034 m and occurred within 0800, 1000 and 1100 time windows respectively) and higher vertical activity during late afternoon and during the night (~17:00–05:00; maximum average change in depth for females 1, 2 and 3 were 0.308, 0.360 and 0.267 m and occurred within 0100, 2200 and 2200 time windows respectively). Thus, the periodic behaviour identified through periodogram analysis represents the diel cycle between relatively low vertical activity during daylight hours and high vertical activity nocturnally.

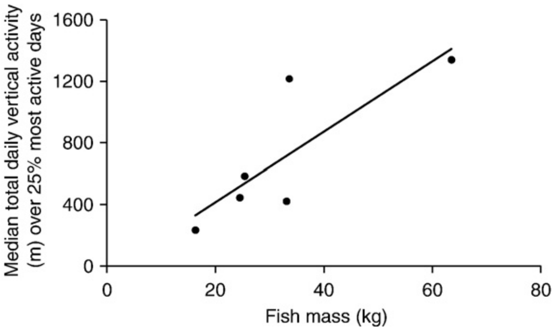

Fig. 8. Relationship between fish mass and degree of vertical activity when active (median total daily change in depth over 25% of most vertically active days) (linear regression analysis: median daily activity = −43.7495 + 22.8847 * mass, r^2(adj.) = 0.59, $F = 8.07$, $P = 0.047$).

4. Discussion

This is the first study to track the movements of common skate, *D. batis*, using electronic tags and as such provides the first insights into the subsurface behaviour and vertical activity patterns of this, the largest batoid species in European waters. The results indicate that: (1) female common skate exhibit extreme site fidelity, apparently remaining within small geographical areas over medium temporal scales (months); (2) skates exhibited high rates of vertical activity with a predominant diel rhythm, indicating higher rates of vertical movement nocturnally; and (3) inter- and intra-individual variation in vertical movements were evident, with some (smaller) individuals

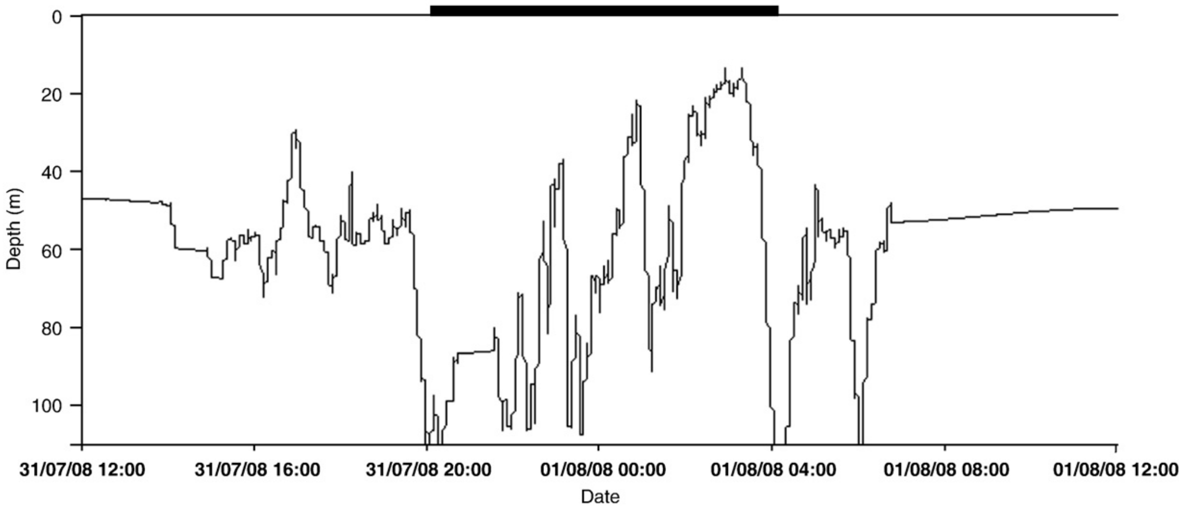

Fig. 7. Example of high rate of nocturnal vertical activity exhibited by female skate 1 over a 24-h period in summer.

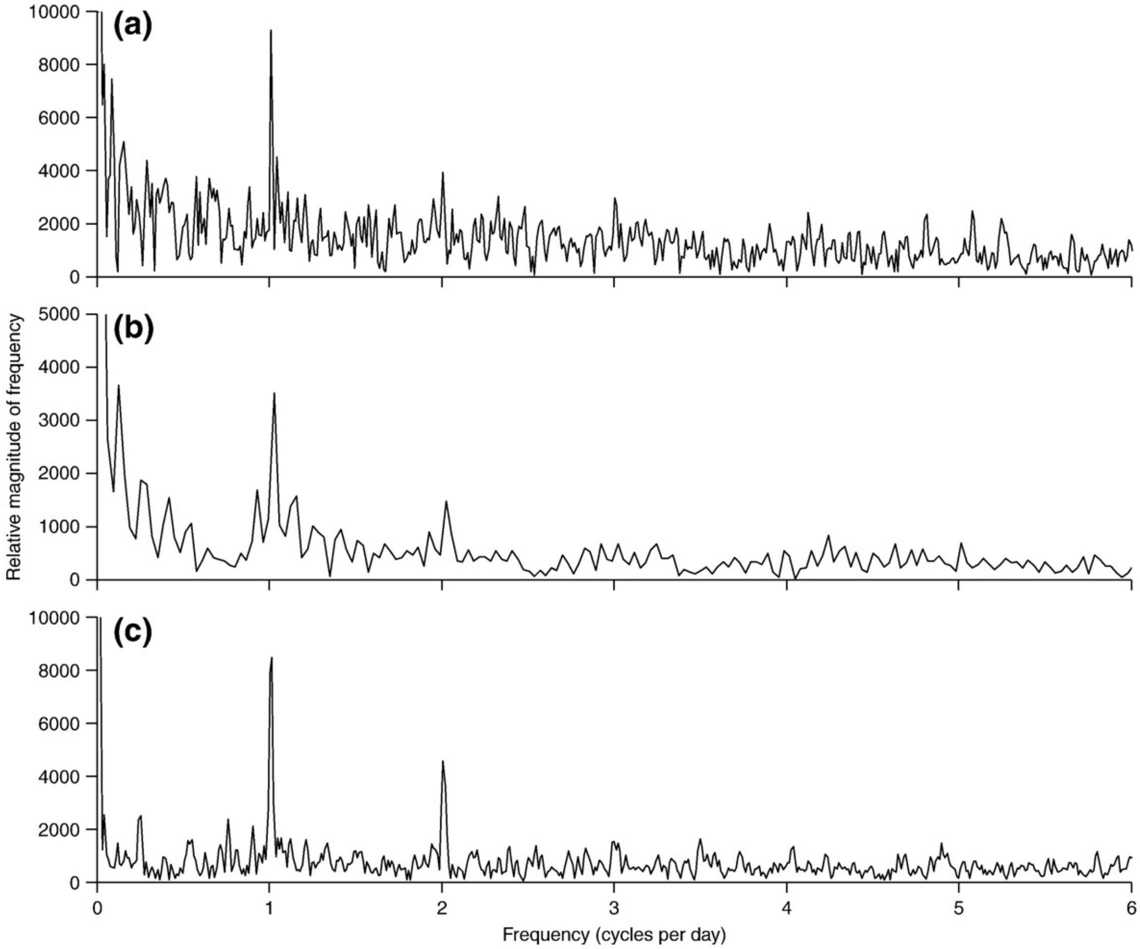

Fig. 9. Fast Fourier Transform-generated periodogram analysis for the time-series of change in depth for (a) female 1, (b) female 2 and (c) female 3. High amplitude peaks at 1 cycle per day denote significant diel rhythms in common skate vertical movement.

remaining at depth (>100 m) for the major part of the time at liberty. Several characteristic behaviours could be identified in the time-depth profiles of recaptured fish, ranging from inactivity (resting on the seabed) to vertical ranging behaviour, where daily depth range frequently exceeded 100 m. Individual fish exhibited a range of these behaviours at apparently irregular times.

4.1. Horizontal movements

All six fish were recaptured less than 2 km from their release site, and five were recaught within 300 m of the point of release. Whilst these results appear to suggest that common skate do not move far, the tags used in this study do not reveal where the animal travelled whilst at liberty. Thus it is feasible that the skate tagged in our study exhibit an affinity to sites to which they repeatedly return, rather than in which they remain. However, all 6 tracked fish spent a large proportion of their time at depth, with 3 spending the vast majority (63–90%) of their time below 100 m. Examination of the bathymetry of the surrounding waters reveals only three areas (other than those shown in Fig. 3) where water depth exceeds 100 m within 10 km of the main release site. In addition, the location of the PSAT tag coming ashore, which detached from female 1 between the 13th and 16th June, suggests that this fish was within the study site at least a month after tagging, and then again upon recapture in August. Thus, overall it appears likely that tracked fish did not move far whilst at liberty, perhaps even remaining in the localised region of Loch Sunart for the entire time. One reason why skate may frequent this area is the presence of two aquaculture cages containing salmon (shown in Fig. 3). High densities of large rays have been documented at fish farms in other locations, presumably, together with other aggregating wild fish, to take advantage of the persistent supply of food available in terms of unused feed, dead cultured fish (Dempster et al., 2005) and abundant benthic infauna (Brown et al., 1987).

Our results support the hypothesis that individual skate may associate with specific sites for long periods. It is possible that skate in Loch Sunart may not be an exception; the Sound of Mull also appears to hold a relatively small, localised and mainly resident population of skate. In a mark–recapture study around the Isle of Mull, 75% of recaptured skate were caught at or near their release site (Little, 1995), with 100% of recaptures tagged in the Sound, being recovered from within the Sound (Little, 1997). Large scale migrations appear rare for common skate. Only 3% of fish tagged in the mark–recapture study moved more than 20 km from the site of release, with only one female moving further, some 900 km from the west coast of Scotland to south west Norway (Little, 1995, 1998). Mark–recapture studies of thornback ray (*Raja clavata*), in the Thames Estuary, UK (Hunter et al., 2005b; Walker et al., 1997), as well as acoustic tracking of giant manta rays, *Manta birostris*, in the Komodo Marine Park, Indonesia (Dewar et al., 2008), also indicate high levels of site fidelity, which suggests that this could be a common feature within batoid populations.

Neither of the two males tagged during May 2007 were recaught in the period to March 2009. Failure to recapture the male tagged off Caliach point, Isle of Mull, may reflect the lower fishing effort in this area. However, that male 1, released in Loch Sunart was not recaptured despite a recapture rate of 100% for females tagged in the same area, implies that males disperse. Having tagged only two males

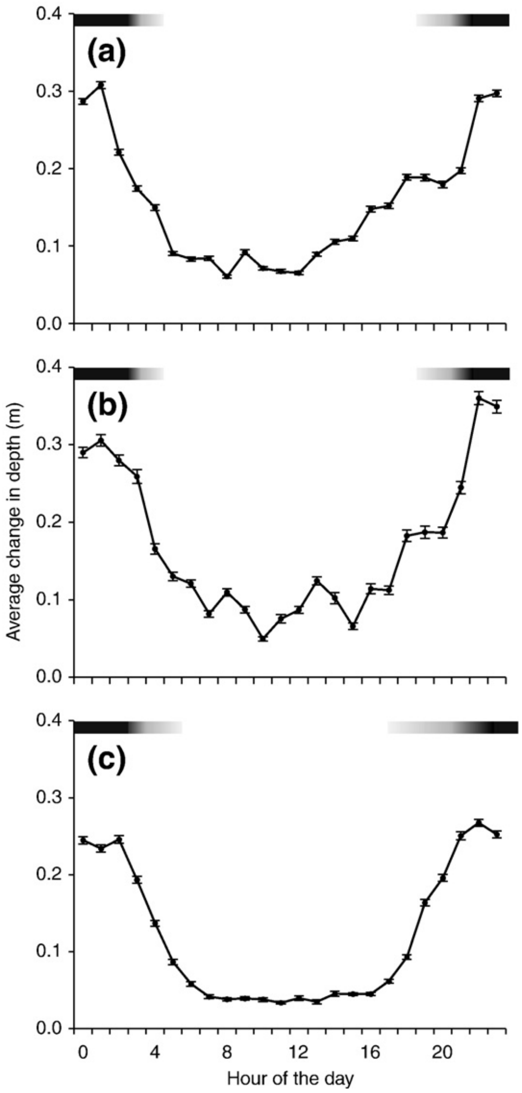

Fig. 10. Average rate of change in depth within hourly time bins (a: female 1; b: female 2; c: female 3) show increased vertical activity by night, where hours of darkness are indicated by black bars on the *x*-axis. Error bars indicate standard error.

in the current study, further work is required to elucidate the movements of male fish, however a previous study suggested that, whilst males and females were found in fairly equal numbers in the Sound of Mull during the spring and autumn, males moved out of the area during the summer months (Little, 1997). Sex-differences in behaviour, particularly where differences in space use (sexual segregation) result, has the potential to lead to sex-biased exploitation (Mucientes et al., 2009; Wearmouth and Sims, 2008). Although common skate are protected under UK law, returning animals alive is complicated by their large size and animals are often injured in the process. If females are exposed to higher rates of capture related mortality than males, this could have major consequences at the population level.

4.2. Vertical activity patterns

Female common skate tracked in the current study spent periods of up to 30 h resting on the seabed. However, in the majority of cases, seabed resting was frequently interspersed by brief periods of vertical activity and fish rarely remained stationary for a full tidal cycle. Low activity behaviours may represent opportunistic feeding (ambush predators forage by jumping off the seabed and over their prey; Heithaus, 2004; Motta, 2004) or, where changes in depth occur, disturbance events. Inactivity at or close to the seabed is a common feature of dorsoventrally flattened (Hunter et al., 2004) as well as fusiform benthic fish species (e.g. cod; Hobson et al., 2007). It is their propensity to spend long periods resting with the tag recording change in tidal height and range that enables tidal geolocation (for further details see Hunter et al., 2005b).

In addition to the low activity behaviours described above, three categories of high activity behaviour were also identified: high activity within a limited range of depths, vertical ranging, and diel vertical migration (DVM) (nocturnal ascent). Vertical activity in benthic teleosts is commonly attributed to migratory movements (Hobson et al., 2007; Hunter et al., 2004). However, as the skates we tagged exhibited limited horizontal movements whilst at liberty, the patterns of vertical activity observed are more likely to represent foraging behaviour. High activity within a narrow range of depths may represent benthic foraging of common skate, which are known to prey upon benthic crustaceans and fish (Wheeler, 1969). To maximise the probability of prey encounter and capture, speculative foragers search an area where they expect to find prey (Heithaus, 2004; Motta, 2004). In areas of steep seabed topography, this foraging mode is likely to result in small scale changes in depth over time similar to those seen in Fig. 6d. Larger scale vertical movements may also represent searching behaviour. Extensive, ballistic-like movements typify behaviours shown by marine predators when searching for new prey patches (Hobson et al., 2007; Sims and Quayle, 1998; Sims et al., 2008). Repeated large-scale vertical oscillations have been identified in the swimming behaviour of several pelagic fish species, including ocean sunfish, *Mola mola* (Cartamil and Lowe, 2004; Sims et al., 2009), billfishes (e.g. yellowfin tuna, *Thunnus albacares*, Schaefer et al., 2007) and predatory and plantivorous sharks (e.g. shortfin mako, *Isurus oxyrinchus*, and basking shark, *Ceterohinus maximus*, Schaefer et al., 2007; Shepard et al., 2006; Sims et al., 2003), with dives from the surface to 100+ m occurring over the course of minutes to several hours. However, to date, only pelagic species have been documented to regularly undertake large-scale vertical movements over the course of relatively short time periods as we now show for common skate.

Similarly, the DVM pattern of vertical activity exhibited by three of the tagged skate is also a strategy more commonly seen in the pelagic marine environment. Nonetheless, DVM has been documented in the benthic marine environment, and its occurrence has been attributed to thermoregulatory behaviour in California cleftnose eagle rays, *Myliobatis californica*, (Matern et al., 2000) and male lesser spotted dogfish, *Scyliorhinus canicula*, (Sims et al., 2006), and to local differences in bathymetry and habitat in Atlantic cod, *Gadus morhua* (Neat et al., 2006). However, as only three of the individuals we tagged exhibited this behaviour whilst all six remained within a small core area whilst at liberty, a more likely explanation for DVM in common skate is foraging. Females 2, 3 and 6 may have exploited vertically migrating prey or, alternatively, these individuals may have ascended into shallower water at night to exploit nocturnally active, shallow water prey species. Individual-specific patterns of DVM have been attributed to differences in foraging ecology in the short-tailed stingray, *Dasyatis brevicaudata*. One of two individuals tracked in the latter study exhibited DVM and it was suggested that this individual foraged in the water column whilst the other foraged in benthic habitats (Le Port et al., 2008).

Inter-individual differences were also observed in the depth use and degree of vertical activity exhibited by the tagged female common skate. These differences appeared to be size-dependent, with larger females generally utilising a wider range of depths and exhibiting higher vertical activity rates than smaller females, which tended to remain at deeper depths. These body-size relationships may reflect ontogenic changes in performance (i.e. swimming speed), behaviour, dietary preferences or perhaps age-related foraging experience.

Smaller, younger individuals may be more opportunistic and rely on more easily obtainable food sources such as benthic fish and invertebrates, whereas larger, more experienced animals may be more capable of and spend more time actively pursuing a wider range of prey, including large fish. Whilst these results are based on a small number of animals and further trackings are required to determine whether size-segregation by water depth is a general feature of common skate, similar patterns have been documented in thorny skate, *Amblyraja radiata*, in the northeastern North Sea and Skagerrak. In the latter species, occupation of intermediate depths by the largest individuals corresponded to an ontogenic dietary shift from benthic animals such as polychaetes to benthopelagic animals such as gadoid fishes (Skjaeraasen and Bergstad, 2000). Ontogenic dietary shifts have also been documented in the mobulid bat ray, *Myliobatis californica* (Gray et al., 1997), whilst inter-individual differences in activity patterns have been suggested to reflect age-related foraging in basking sharks (Shepard et al., 2006).

Diel rhythms in activity are a common feature of fish populations (Reebs, 2002) and elasmobranchs, in general, exhibit nocturnal activity. Data from the current study suggests that common skate are no exception to this general rule as the observed diel rhythms in the vertical activity patterns of all but one female (female 4 which did not exhibit DVM and spent more than 50% of its time at depths >110 m) corresponded to elevated vertical activity nocturnally.

Contrary to our general expectation of low activity in dorsoventrally flattened benthic predators however, the common skates tracked in the current study exhibited high levels of vertical activity and undertook repeated, large-scale vertical movements totalling up to 1.8 km on a daily basis. Thus, it appears that, despite limited horizontal movements, common skate is not a sedentary species, but rather an active forager on benthic, and possibly, pelagic prey. Despite a recent surge in tagging studies, our knowledge of the movements and behaviour of batoids is poor, particularly in the vertical dimension. In demersal teleost fishes, high levels of vertical activity are generally associated with migration (Hunter et al., 2004; Righton et al., 2007), yet this does not appear to be the case for the common skates we tagged. To our knowledge, the only other batoid species for which detailed vertical movement patterns have been determined is the smaller bodied thornback ray. Tagging studies in the Thames Estuary revealed that this species was also capable of exhibiting periods of high vertical activity and individuals would periodically spend over 10 h a day swimming in midwater (Hunter et al., 2005a,b). Together with our study, this would appear to suggest that, despite calcification patterns conferring morphological adaptation to slow swimming and a sedentary lifestyle in batoid undulators (Schaefer and Summers, 2005), rays such as common skate are capable of active swimming and movement patterns more akin to those expected for oscillators.

4.3. Conservation implications

The slow life-history characteristics of elasmobranchs, including a late age at maturity, slow growth, low fecundity and long gestation period, result in low rates of population increase (Stevens et al., 2000). Due to recent declines in abundance, coupled with their inherent vulnerability to extinction, common skate are listed as Critically Endangered on the IUCN Red List of Threatened Species. Common skate were protected by a zero total allowable catch (TAC) in European waters, and new regulations now prevent them being retained by commercial vessels necessitating the prompt release of unharmed fish. However, there is currently no spatial protection for this species in European seas.

Prior to this study, little was known about the behaviour and habitat use of common skate. The techniques employed in this study did not pose an exceptional risk to the animals involved: sustainable fishing practices were used and fish were returned to sea as quickly as possible. Tag attachment procedures were non-invasive and all fish resumed normal movement patterns within an estimated 48 h of release. Interestingly, three of the skate spent time at the surface on two (female 4) and on a single occasion(s) (females 3 and 5). However, the vertical ascents and descents associated with these surface movements did not differ significantly from the depth traces associated with original release and subsequent recapture and thus cannot be attributed with any certainty to natural behaviour. The waters around the Isle of Mull represent one of the last known refuges of the common skate and, as such, are popular with sports anglers. Therefore, it is entirely feasible that the tagged skates were hooked, brought near the surface, then lost. Clearly, as population estimates are generally based on catch per unit effort, repeated recapture of individual animals at rates of up to 4 times per month has the potential to lead to gross overestimation of population sizes.

Whilst female common skate tracked in the current study exhibited high degrees of vertical ranging, utilising almost the entire extent of the water column available to them, they did not range widely horizontally. However, all but one female common skate tagged in the current study were recaptured within 3 months of deployment. Seasonal changes in distribution have been noted in other species of rajid ray (Hunter et al., 2005b), stingray (Le Port et al., 2008), and mobulid ray (Dewar et al., 2008; Notarbartolo-di-Sciara, 1988), as well as in other demersal fish species (e.g. cod, Righton et al., 2007). In addition, animals from different areas may behave in different ways (Dewar et al., 2008; Righton et al., 2007). Tagging of skates in other areas, as well as obtaining data over a longer time at liberty and from males would all contribute to further our understanding of the behavioural ecology of this species.

Nonetheless, it is likely that common skate form discrete local populations of relatively limited geographic range between which there may be limited mixing. As extinction vulnerability is linked to geographic range (Dulvy and Reynolds, 2002), the extreme site fidelity demonstrated by female common skate likely explains historical local extinctions and further suggests that there is little capacity for recolonisation of depleted areas since juvenile recruitment to new areas would be dependent on adult female dispersal and egg-laying. Our research therefore highlights the need for spatial management of these 'refugial' populations across their entire range.

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