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Diel vertical migration and central place foraging in benthic predators

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Abstract

Diel vertical migration (DVM) is a widespread behaviour among many pelagic species, from zooplankton to sharks, and has been widely studied in both marine and freshwater environments. Usually, DVM comprises repeated daily vertical movements through the water column, from shallower at night to deeper during the day. Consequently DVM is perhaps unexpected in benthic predators, nonetheless, DVM has been observed in benthic sharks and freshwater teleosts, where it comprises inshore-offshore migrations over the substrate. However there is no clear evidence of this behaviour in large temperate benthic predators, such as skates.

Here we present new observations of DVM in 4 species of skate (*Raja brachyura*, *R. clavata*, *R. microocellata* and *R. montagui*) that identify it as a general behaviour in this clade. Analysis of 89 depth recording archival tags yielded 674 clear DVM events where skate left daytime deeper waters for shallower night time areas before returning to within 2.5 m of starting depths. Interestingly, these events closely resemble those of central place foragers, where shallow areas are foraging and deeper areas are refuging locations.

Behaviour such as this has not been previously recorded in marine benthic predators and the findings suggest DVM might occur in many other benthic species. A broader understanding of DVM in benthic animals will be important in the design of effective boundaries for marine protected

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areas. These findings also have implications for trophic coupling between deep and shallow benthic zones. Further characteristics of this unexpected behaviour are presented and hypotheses for its occurrence are discussed.

Key-words

Benthic, Predator, DVM, Raja, Ray,

Introduction

The diel vertical migration (DVM) of aquatic organisms, both marine and freshwater, is a commonly observed behaviour among diverse pelagic animals from copepods to sharks (Matern et al. 2000, Hays 2003, Sims et al. 2005, Andrews et al. 2009) and has been reported as the largest daily movement of animals on the planet (Hays 2003). Typically the movement is from shallow water during the night to deeper water during the day and for smaller prey animals (copepods, krill) is hypothesised to represent a predator avoidance strategy, whereby planktonic organisms find a refuge from visual predators in darker depths during daytime (Lampert 1989, Hays 2003). The advent of electronic tagging has allowed DVM to be well studied in large pelagic vertebrates such as billfish (Goodyear et al. 2008, Evans et al. 2014), tuna (Schaefer and Fuller 2002, Walli et al. 2009, Humphries et al. 2016a) and sharks (Sims et al. 2005, Shepard et al. 2006, Queiroz et al. 2012). The principal hypothesis to explain DVM behaviour in these larger predators is foraging, with predators following vertically migrating prey (Hays 2003, Sims et al. 2005, Queiroz et al. 2010). While the adaptive significance is generally agreed to be predator avoidance or prey following, the ultimate driver of the movement is considered to be changing light levels (Lampert 1989, Mehner et al. 2007, Mehner 2012). In the case of bigeye tuna *Thunnus obesus* the behaviour has been likened to central place foraging, where the tuna forage in deep water below the thermocline during the day and return to the surface at night when light levels fall too low at depth for these obligate visual predators to hunt (Schaefer and Fuller 2010, Humphries et al. 2016a). While movement from shallow water at night to deep water during the day is that most commonly observed, and in consequence is termed normal DVM (*n*DVM), reverse DVM (*r*DVM, deep at night, shallow during the day) has also been observed in zooplankton, sharks and ocean sunfish *Mola mola* (Irigoiien et al. 2004, Sims et al. 2005, Pade et al. 2009, Queiroz et al. 2012). In basking sharks *Cetorhinus maximus* *r*DVM has been attributed to a response to *r*DVM exhibited by the copepod prey *Calanus helgolandicus* (Sims et al. 2005) which in turn were responding to the presence of chaetognath

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(arrow worm) predators in surface waters. Thus, DVM represents an often complex and flexible response to the movements of either predator or prey, most likely triggered by changing light levels.

The conventional view of DVM being restricted to pelagic animals has been extended recently to include benthic organisms, through both tagging and sampling studies. These reveal a more complex pattern of vertical migration, with some benthic animals moving into the water column (Aguzzi et al. 2015) as well as some pelagic organisms moving towards the benthos (Zouhiri and Dauvin 1996), resulting in interplay and vertical coupling between traditionally separate vertical realms (Sutton 2013, Aguzzi et al. 2015). While these studies have shown diversity and flexibility in DVM behaviour, DVM in obligate benthic predators, such as skates, is unexpected since it not obvious why animals so clearly evolved for living on the bottom should perform daily excursions into the water column. Nonetheless, DVM has previously been observed in several benthic animals, such as decapod crustaceans (Aguzzi and Company 2010), catsharks, *Scyliorhinus canicula* (Sims et al. 2006) and, in freshwater lakes, burbot *Lota lota* (Harrison et al. 2013, Cott et al. 2015). In these examples the movement does not represent a vertical displacement into the water column (i.e. from benthic to pelagic) but rather an inshore-offshore (nektobenthic displacement) movement along the sea (or lake) bed (Aguzzi and Company 2010). To differentiate between benthic and pelagic diel migrations some authors (e.g. Cott et al. 2015) have used the term diel *bank* migration (DBM), however this seems less appropriate for marine studies. Instead, to clearly distinguish the movements studied here from the more familiar pelagic DVM we will adopt the term nektobenthic DVM throughout (Aguzzi and Company 2010).

In male *S. canicula*, these nektobenthic DVM events have been attributed to behavioural thermoregulation, to improve bioenergetic efficiency (Sims et al. 2006) where the animals hunt in shallow warmer water and rest and digest in deeper cooler water. It is known from previous studies, however, that the skates studied here do not perform behavioural thermoregulation (Humphries et al. 2016b).

Skates (*Raja* spp.) are widespread around the UK coast and are strongly adapted benthic mesopredators with dorso-ventrally flattened bodies, negative buoyancy, ventrally located mouths and dorsally located gill openings (spiracles) that allow the animals to respire whilst buried in sandy or gravelly sediments. Skates, as all elasmobranchs, have electrosensitive receptors (ampullae of Lorenzini) that are used to locate cryptic benthic prey, such as sand eels (*Ammodytes* spp.) or crustaceans (Collin 2012, Wueringer et al. 2012, Kimber et al. 2013). Dietary studies further confirm the strong benthic association, with the majority of prey items being benthic invertebrates; where teleosts are found in stomach contents they are again principally benthic or demersal species,

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confirming skates to be benthophagous (Steven 1932, Ajayi 1982, Ellis et al. 1996, Farias et al. 2006, Šantić et al. 2012, Kadri et al. 2014, Pinnegar 2014). Pelagic teleosts are found in less than 2% of stomachs (Farias et al. 2006, Pinnegar 2014) and are more likely to have been scavenged, being typically very abundant species such as mackerel (*Scomber scombrus*) or sprat (*Sprattus sprattus*) which occur in fishery discards. Given these benthic specialisations it seems perhaps unlikely that DVM would be observed in skates. However, little is known regarding the fine scale movements and activity patterns in these animals, because of the difficulties of making sustained, detailed observations at depth in the turbid coastal waters which they typically inhabit. Currently all the species studied here, other than *R. montagui*, are listed as near threatened by the International Union for the Conservation of Nature (IUCN) Red List and consequently an understanding of population abundances, movements and preferred habitats is of increasing importance given documented declines in many skate populations (Genner et al. 2010, Simpson et al. 2011). Vertical movements possibly linked to DVM have previously been reported in electronically tagged common skate, *Dipturus batis*, and although only identified in half the individuals tracked and not investigated in detail (Wearmouth and Sims 2009), it is possible that nektobenthic DVM, similar to that in *S. canicula* or *L. lota*, also occur in skates. To investigate this possibility, depth time series data from 89 electronic-tagged individuals of 4 species of skate were analysed in detail to identify the presence and nature of possible DVM events and to determine possible drivers. Of particular interest was the possibility of events that suggested central place foraging, a behaviour not previously reported in temperate skates. In a pelagic setting, as with tuna, central place foraging is linked only to depth. However, the sea bed comprises a complex mosaic of habitats and if skates are returning to a preferred depth, then it is possible that this represents some favoured foraging or refuging habitat. Consequently, this paper presents new observations of DVM behaviour in four sympatric species of skates, *Raja brachyura* (blonde ray; LaFont, 1871), *R. clavata* (thornback ray; Linnaeus, 1758), *R. microocellata* (small-eyed ray; Montagu, 1818) and *R. montagui* (spotted ray; Fowler, 1910) and tests possible hypotheses to explain its occurrence. In particular this study investigates whether the observed DVM movements represent benthic rather than pelagic movements, and analyses the purpose and nature of the events in the context of central place foraging.

Methods

Tags and tagging

Fish were captured during routine research survey trawls in inshore waters of the Western English Channel (WEC) between Whitsand Bay (50.34 N, 4.28 W) and Bigbury Bay (50.26 N, 3.89 W) and

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between July 2008 and May 2013. Fish were tagged using either of two types of CTL G5 (www.cefastechnology.co.uk, UK), or Star Oddi (star-oddi.com; Star-Oddi, Iceland) data storage tags (DSTs). Standard G5 DSTs were 31 mm long by 8 mm diameter and weighed 1 g in water, whereas long-life DSTs measured 35.5 mm long x 11.5 mm diameter and weighed 2.1 g in water. Star Oddi DSTs were 39.4 mm by 13 mm and weighed 5 g in water. DSTs monitor temperature from 2 to 34 °C (accuracy 0.1 °C, resolution 0.03 °C) and pressure to a depth of 100 m or 200 m (accuracy 1%, resolution 0.04%). DSTs were programmed to record depth every 20 s, 30 s or 1 min intervals. All tags also recorded temperature every 10 min. DSTs were attached to skates via Peterson disc tagging using the methods described by Wearmouth & Sims (2009). Briefly, tags were mounted in a stainless steel wire cradle with a long, pointed stainless steel wire attachment. This wire was passed through a Peterson disc and then passed dorso-ventrally through the pectoral fin, taking care to avoid the abdominal cavity. A second Peterson disc was then placed onto the length of wire on the opposite (ventral) side of the animal before securing the attachment by turning a series of rounds into the length of wire remaining. Tagging was typically accomplished in less than 2 min, including the measurement of total length and body (disc) width. Animals were immediately transferred to aquaria with fresh running sea water for observation prior to release. DSTs were returned through the commercial net and trawl fisheries operating in the WEC with a reward of £50 given for return of the DST and the fish, or for information about the size of the fish and where it was captured.

Ethics statement

All tagging procedures were approved by the Marine Biological Association Animal Welfare and Ethical Review Body (AWERB) and licensed by the UK Home Office under the Animals (Scientific Procedures) Act 1986.

Data analysis

Firstly, to improve the accuracy of the depth measurements the tidal signal was attenuated by applying a correction factor to the time-series derived from the Plymouth tide gauge data recorded at Devonport (50.3684°N, 4.1852°W). At the outset the general nature of the DVM events was unknown, having been recognised in *R. clavata* through the serendipitous observation of movements such as those shown in Figure 1a. Unlike the regular and predictable DVM of pelagic predators, the events identified in skates were found to represent infrequent bouts of activity and were therefore not considered to be suitable for time-series analysis methods such as waveform analysis or hidden Markov analysis (e.g. Pinto and Spezia 2016). To confirm this assertion a spectral analysis was performed to investigate any correlation between the amplitude of the 1 cycle/day signal (indicative of DVM behaviour) and the number of events identified in each track; no significant

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correlation was found ($r^2 = 0.127$, Supplementary Table S2 and Figure S4). The activity does not therefore have a clear rhythmic component. Additionally, we performed a continuous wavelet analysis on a sample track and determined that while the analysis might indicate times when DVM activity occurred, it was largely descriptive and did not provide the detailed quantitative data required here (Supplement, Figures S6 and S7). Further, in the hidden Markov analysis performed on flapper skate (*Dipturus intermedius*) by Pinto & Spezia (2016) the analysis successfully identifies the occurrence of two behavioural modes and associates environmental covariates with these. However, here by contrast, we are interested in a detailed investigation into the nature of individual DVM events. Consequently an automated approach to their identification within the depth time series data, which would require *a priori* parameterisation or assumptions was not desirable (e.g. Adachi et al. 2016). Automatic identification of individual events would also have been hampered by the complex nature of the vertical displacements occurring during the events which make the identification of behavioural changes, such as from ascent to plateau for example, more challenging. Instead, software was developed to allow manual identification of events by using mouse clicks to mark four defining times for each event (event start time, plateau start time, plateau end time and event end time) on a display of the time series, as shown in Figure 1b. The intervals between selected times define phases referred to herein as *ascent*, *plateau* and *descent* and, overall as an *event*, with the inter event phase termed *deep*. To enable events to be viewed and marked more easily the time-series were first under-sampled to 1 in 10 by selecting every 10th data point; doing so provided a clearer view of the longer events than if the data were displayed at the original 20 s resolution, simplifying the marking of the defining times. Once the end time of an event was marked the defining times of the event were written to a Microsoft Access™ database (DB). Once all events had been identified in a given track the software used stored event times were used to perform a detailed, *post-hoc* recalculation of the events using tidally corrected but non-under-sampled time series data, to more accurately compute a range of metrics with which to describe the events: ascent/descent deltas (overall vertical displacements), speeds and durations; plateau delta, duration and activity (sum of and mean vertical displacements) and pre-event activity (activity in the hour prior to the event start). In addition a straightness index (SI) for each phase was calculated using L_0/L_1 where L_0 is the delta and L_1 is the sum of step lengths. The SI therefore gives a value in the range 0-1, where 1 represents a straight movement with low tortuosity and lower values represent reduced straightness, or increased tortuosity.

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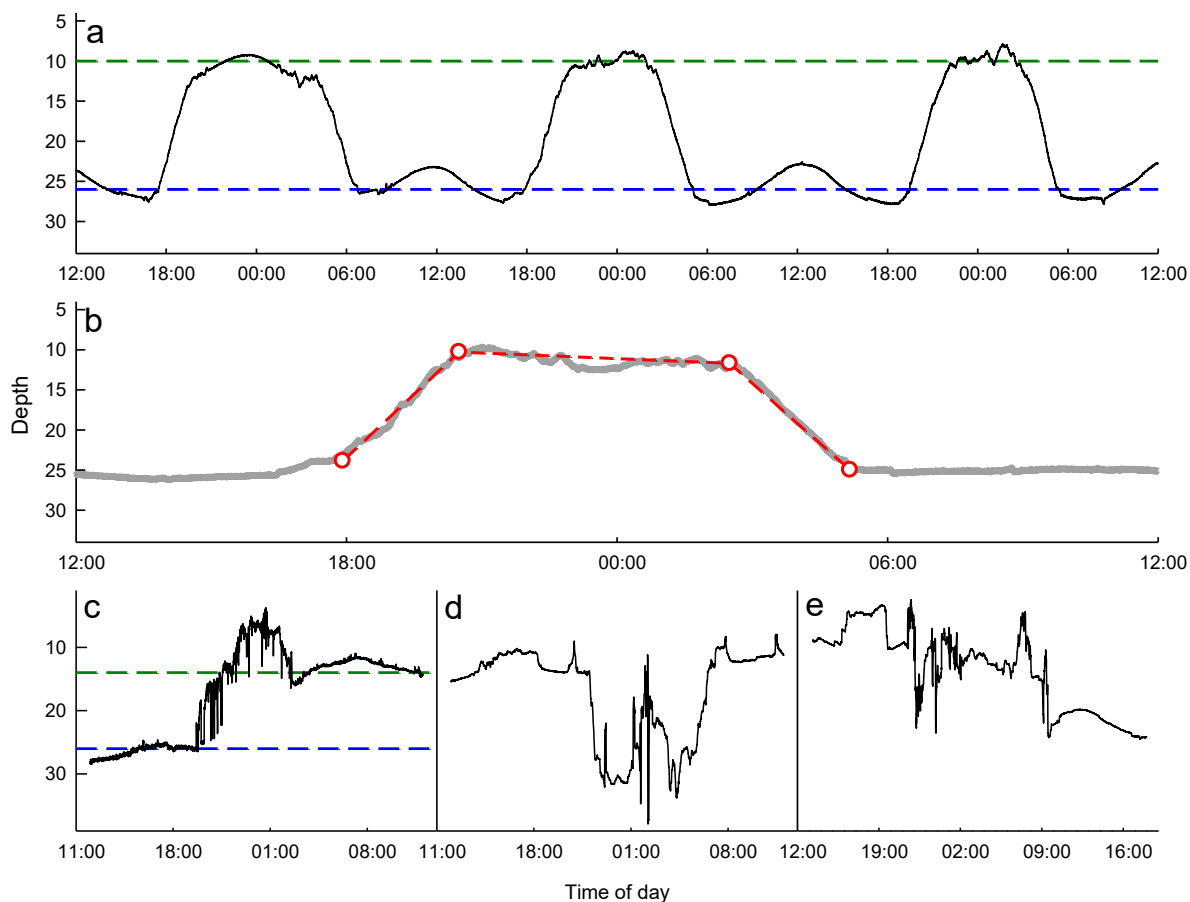


Figure 1: Example DVM plots

Depth time-series plots from a thornback ray (tag B0342) showing examples of typical DVM behaviour and other movements not studied here. a) Three events showing movement from deeper water (blue dashed line, 26 m, note the clear tidal signal) to a shallower depth (green dashed line, 10 m); b) A single DVM event from (a) with the tidal signal removed, showing the defining event times (red circles); c) an event representing a longer term movement from deep (blue line) to shallower water (green line); d) a reverse event, with movement from shallow to deeper water and back again; e) a complex movement pattern resulting in a transition to deeper waters. Events such as those shown in c-e, while interesting, are not classed as central place foraging events and are not further analysed in this paper.

During the manual identification step all vertical migration events that could be clearly identified and which lasted less than 24 hours were marked. This initial exploration of the data identified 2354 events with a range of characteristics as described later; however, the events of particular interest in this study were those that most resembled Figure 1a, which appear to represent clear, repeated, diel excursions from deep to shallower water and, importantly, to suggest activity similar to central place foraging, where the 'refuging' depth remains relatively constant, as does the 'foraging' depth, as would be expected with travel to and from preferred depths or habitats. These possible 'central place foraging' events were therefore identified and selected from the DB for further analysis using the following parameters: ascent delta > 5 m, overall event delta < 2.5 m and event duration between 1 and 18 hours. These parameters therefore select events where the animal moves into

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waters at least 5 m shallower, remains for between 1 and 18 hours and then returns to a depth within 2.5 m of the starting depth. Supplementary Figure S2 shows the range of values observed for the 2354 event deltas (the difference in depth between the start and end of the event) and the ascent deltas and indicates the cut off values for the events selected for further analysis.

Average temperatures for the deep phase were calculated using the tag-recorded temperatures at the event start and end times. The average temperature of the plateau phase was calculated from all data points between the plateau start and end points. Activity rates, determined as average vertical displacements (step lengths), were determined from all data points from up to 1 hour prior to the start of the event (pre-event activity) and for all points between the plateau start and end points (plateau activity). Average vertical displacements are either simply the vertical component of a 3-dimensional movement, or are the result of the interplay between horizontal movements and the complexity of the sea bed. This measure is not therefore a true measure of activity but is a reasonable proxy given that, in general, increased activity will result in increased vertical displacements. Where an event was preceded by an event within less than an hour, all available points from the end of the prior event to the start of the current were used for the pre-event activity calculation.

It is possible that a higher occurrence of events is associated with environmental factors or certain geographic locations. While the actual locations of the animals throughout the tracking period are unknown precisely off Plymouth, the depth is known accurately and can be used as a proxy for geographic location, as deeper depths are generally associated with locations further offshore in the study area. To identify peaks in the frequency of occurrence in relation to the start depth, histograms were prepared to show the count of event start depths in 10m depth bins (0-80m) by species and sex.

To investigate seasonal fluctuations in event frequency, expected seasonal counts of events by species and sex were calculated using the total number of events for the year in each category and the proportion of individuals tracked in each season. The expected counts therefore assumed an even distribution of events throughout the year, allowing for differences in the number of individuals tracked in each time frame. To provide more robust statistical analysis, counts were pooled into winter (December, January and February), spring (March to May), summer (June to August) and autumn (September to November). These months were selected using tag recorded temperatures such that winter represented the coldest three months, spring the warming months, summer the warmest and autumn the three cooling months. Using tag recorded temperatures ensures that we are using temperatures experienced by the animals to determine the warmest and

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coldest months. The statistical significance of differences between the observed and expected counts was determined using χ^2 .

All statistical tests were performed using SigmaPlot 12.5 (Systat Software, San Jose, CA) or MiniTab 15.1 (State College, PA: Minitab, Inc., www.minitab.com). Because in most cases data were found not to be normally distributed, the statistical tests employed to determine significant differences in, for example, metrics such as ascent delta, were non-parametric tests such as Mann-Whitney rank sum, or Kruskal-Wallis One Way Analysis of Variance on Ranks.

Results

Summary

Of the 179 tags deployed, 92 (51.4 %) were returned with 89 having useable data with a total of 35×10^6 data points totalling 12,585 days. A summary of the datasets available is given in Supplementary Table S1. A total of 2354 events were identified from which 674 were selected for further analysis based on the parameters described above, chosen specifically to investigate possible central place foraging events (full event details are given in the Supplementary Data spreadsheet). A summary of the number of selected events by species is shown in Table 1. The number of events recorded for each individual was found to be highly variable in all species (Figure 2a). Although *R. brachyura* and *R. montagui* have fewer individuals, fewer events and fewer days tracked, the average number of DVM events per day are very similar to the other two species, with no significant differences found (Kruskal-Wallis One Way Analysis of Variance on Ranks, $p=0.334$), suggesting an adequate sample of events had been recorded. Consequently, there is an unsurprising correlation between the number of days tracked and the number of events recorded (linear regression: *R. brachyura* $R^2=0.123$, $p=0.29$; *R. clavata* $R^2=0.313$, $p=0.002$; *R. microocellata* $R^2=0.474$, $p<0.001$; *R. montagui* $R^2=0.248$, $p=0.173$; Figure 2b-e). The correlations were strongest and significant in the two species with the most individuals and the most days tracked. Notably, the 20 tracks for which no central place events were selected (Supplementary Table S2) were generally very short, with an average length of 49 days (range 2-154), compared to an average length of 166 days (range 14-418) for those with events. Differences in the number of events for each sex, when adjusted to account for the number of days tracked were significant only in *R. brachyura* and *R. clavata*, where in both cases more events were recorded for males than females (statistical results in Table 2). No significant correlation was found between the length of the individuals and the number of events (Supplementary Figure S1).

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Table 1: Frequency of DVM events per day tracked by species

	Individuals	No with DVM	No of events	Days tracked	DVM per day tracked
<i>R. brachyura</i>	12	11	62	1215	0.051
<i>R. clavata</i>	43	28	294	5037	0.058
<i>R. microocellata</i>	24	21	240	3474	0.069
<i>R. montagui</i>	10	9	78	1795	0.043
Totals	89	69	674	11521	

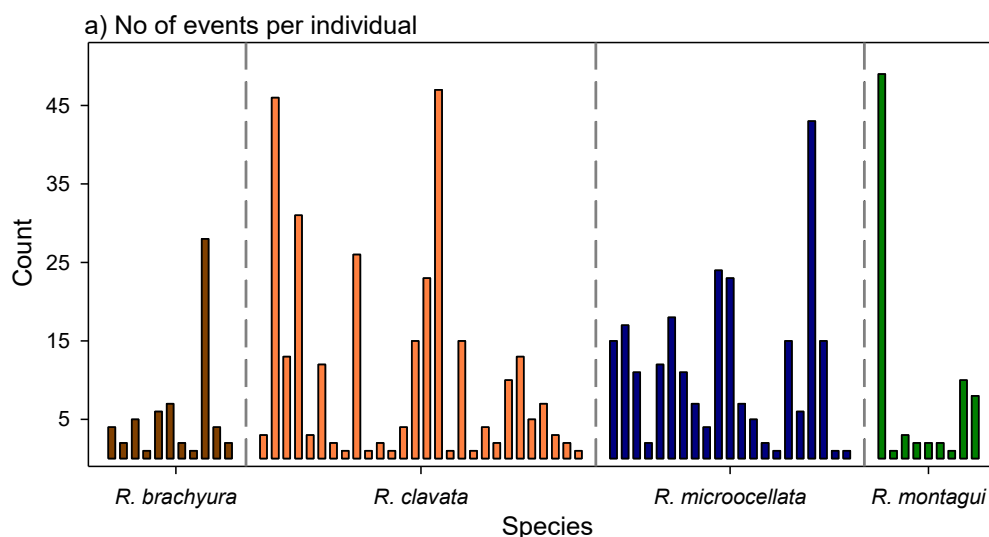


Figure 2: Frequency of events per individual

a) The histogram shows a count of the selected events recorded for each of the 69 individuals. It is clear that this behaviour is not performed consistently by all individuals. For *R. brachyura* and *R. montagui* in particular the behaviour is frequent in only a few individuals.

Table 2: χ^2 results from the frequency by sex analysis

Species	χ^2	N	df	P
<i>R. brachyura</i>	12.33	62	1	<0.001
<i>R. clavata</i>	31.41	294	1	<0.001
<i>R. microocellata</i>	2.5	240	1	0.114
<i>R. montagui</i>	2.77	78	1	0.096

Movement analysis

To gain a better understanding of how the animals were moving during these events the ascent, plateau and descent phase movements were analysed for each species; the results are shown in Figure 3 and Table 3. Ascent speeds (Figure 3a) ranged from 0.53 to 3.3 cm/s; descent speeds ranged from 0.13 to 5.5 cm/s. No significant differences were found between the ascent and descent rates (see summarised statistical results in Table 3).

The results of the straightness index (SI) analysis are shown in Figure 3b. No significant differences were found between species in the ascent SI values (Kruskal-Wallis One Way Analysis of Variance on

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Ranks, $p=0.224$). A significant difference was found between the descent SI values between *R. clavata* and *R. microocellata* (Kruskal-Wallis One Way Analysis of Variance on Ranks, $p=0.012$), however, no significant differences were found between the intra-species ascent and descent values, except for *R. microocellata* (Table 3). In all cases the SI values suggest a tortuous rather than a direct movement. Other than *R. montagui* the SI index for the plateau phase was significantly lower than for the ascent or descent phases. For *R. montagui* although the median value of the plateau phase SI was comparable with the other species, there was a much greater range of values, suggesting greater individual variability. The descent phase SI for *R. montagui* also had a greater range of values and some that were much lower than the other species.

Table 3: Summarised statistical results

A summary of the statistical tests, showing the test performed for each analysis and the associated p values. LR: Linear regression; MWRS: Mann-Whitney Rank Sum. Significant p-values are highlighted.

Measure	Test	Species			
		<i>brachyura</i>	<i>clavata</i>	<i>microocellata</i>	<i>montagui</i>
Events per day tracked	LR	$R^2=0.123$	$R^2=0.313$	$R^2=0.474$	$R^2=0.24$
		$p=0.29$	$p=0.002$	$p<0.001$	$p=0.173$
Ascent vs descent rates	MWRS	$p=0.743$	$p=0.915$	$p=0.669$	$p=0.427$
Ascent vs descent SI	MWRS	$p=0.162$	$p=0.138$	$p=0.049$	$p=0.222$
Plateau vs deep activity	MWRS	$p<0.001$	$p=0.001$	$p<0.001$	$p=0.005$
Plateau vs commuting time	MWRS	$p=0.158$	$p<0.001$	$p<0.001$	$p=0.659$
Deep vs shallow temp.	MWRS	$p=0.793$	$p=0.652$	$p=0.841$	$p=0.959$

A comparison of the activity rates, computed as the average step length, for the plateau and deep phases shows significantly more vertical movement occurred during plateau phases than in deep phases (Figure 3c, Table 3). This supports the contention that the plateau phase represents active foraging in shallower water while the deep, inter-event phase represents resting or refuging.

The time spent during the plateau phase and that spent moving to and from the plateau depth were also compared (Figure 3d). In all cases more time was spent in the plateau phase than the combined ascent and descent phases, which ranged from 43% of the plateau phase (*R. microocellata*) to 73% (*R. brachyura*). Differences were significant however only for *R. clavata* and *R. microocellata* (Table 3). Average time spent in the plateau phase ranged from 4.07 to 4.89 hours which represents between 58 and 70% of the total event duration.

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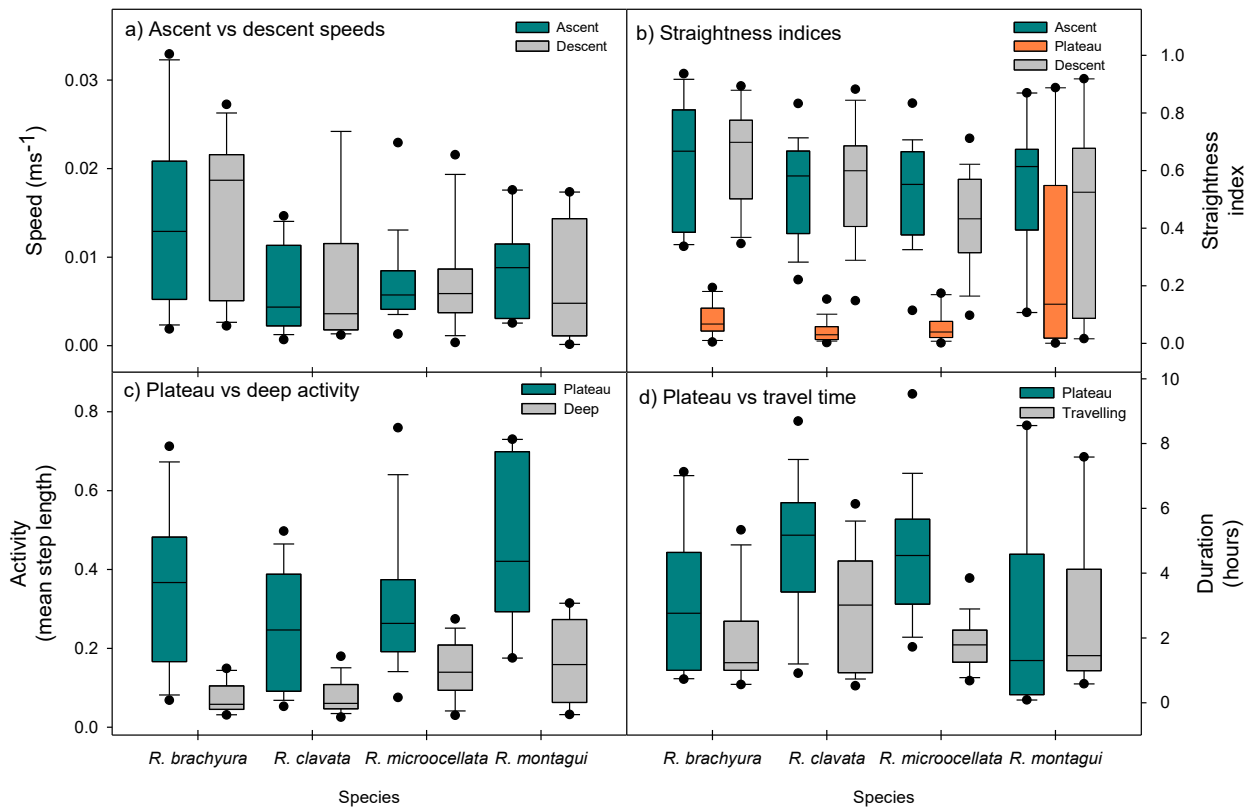


Figure 3: Event movement analysis

a) Average ascent/descent speeds. No significant differences were found between the ascent and descent speeds of any species; b) Ascent, plateau and descent straightness indices. While there are no significant differences between the ascent and descent straightness indices, differences between the ascent/descent and plateau indices are significant in all species except for *R. montagui*; c) Plateau vs deep. Activity during the plateau phase is, in all cases, significantly greater than in the deep phase; d) Plateau vs travel time. The plot shows the time spent in the plateau phase compared to the total time spent travelling between the deep and plateau depths. In all cases, except *R. montagui*, more time is clearly spent in the plateau phase than in the combined ascent and descent phases.

Temperature as a possible driver

Given that temperature was found to be a driver for the diel migrations of small spotted catsharks, *Scyliorhinus canicula* (Sims et al. 2006) the average deep and plateau temperatures were analysed to determine whether the skates were migrating to deeper colder waters for energetic advantages (Figure 4a). However, no significant temperature differences were found in any case (**Table 3**). Interestingly, *R. clavata* experienced significantly warmer temperatures during both the plateau and deep phases (Kruskal-Wallis One Way Analysis of Variance on Ranks, $p=0.009$).

Depth ranges

The average depths of the deep and plateau phases were analysed in order to identify species differences in the putative refuge and foraging areas (Figure 4b). Significant differences were found

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in the deep phase across species (Kruskal-Wallis One Way Analysis of Variance on Ranks, $p < 0.001$). A pairwise multiple comparison (Dunn's method) indicated significant differences ($p < 0.05$) between the two pairs *R. brachyura* / *R. montagui* and *R. clavata* / *R. microocellata*. However, differences in the shallower, plateau depth, although significant (Kruskal-Wallis One Way Analysis of Variance on Ranks, $p = 0.04$) were less pronounced, with pairwise comparisons only being significant between *R. montagui* and *R. clavata* / *R. microocellata*. There was therefore more overlap in plateau depths between *R. brachyura* and *R. clavata* / *R. microocellata*, with *R. montagui* occupying deeper depths during the plateau phase.

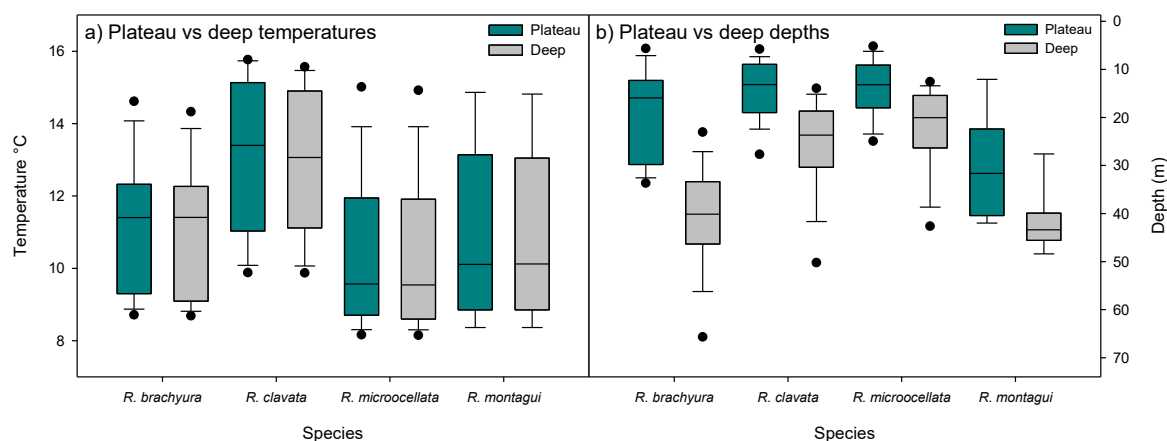


Figure 4: Plateau vs deep temperatures and depths

a) Plateau temperature vs deep temperatures. No significant differences were found except for *R. clavata* where both temperatures were significantly higher than the other species; b) Differences in the deeper depths are as expected from Humphries *et al.* (2016b). Differences in the shallower, plateau depths are less pronounced, suggesting a greater overlap in putative foraging depths than expected.

The analysis of event frequency and start depth showed no clear overall pattern (Figure 5). However, significant differences were found between male and female start depths in both *R. montagui* and *R. clavata* ($p < 0.001$ in both cases, Kruskal-Wallis One Way Analysis of Variance on Ranks). In *R. montagui*, females started events from deeper depths than males, while *R. clavata* females started events shallower than males. In *R. brachyura* and *R. clavata* the peak in events coincides with the preferred depth, as identified by Humphries *et al.* (2016b), however with *R. microocellata* and *R. montagui* the peak in event frequency occurs in shallower waters. These plots also show a significantly greater propensity for DVM in male *R. brachyura* and *R. montagui* ($N=674$, $df=1$, $\chi^2=26.47$, $p < 0.001$).

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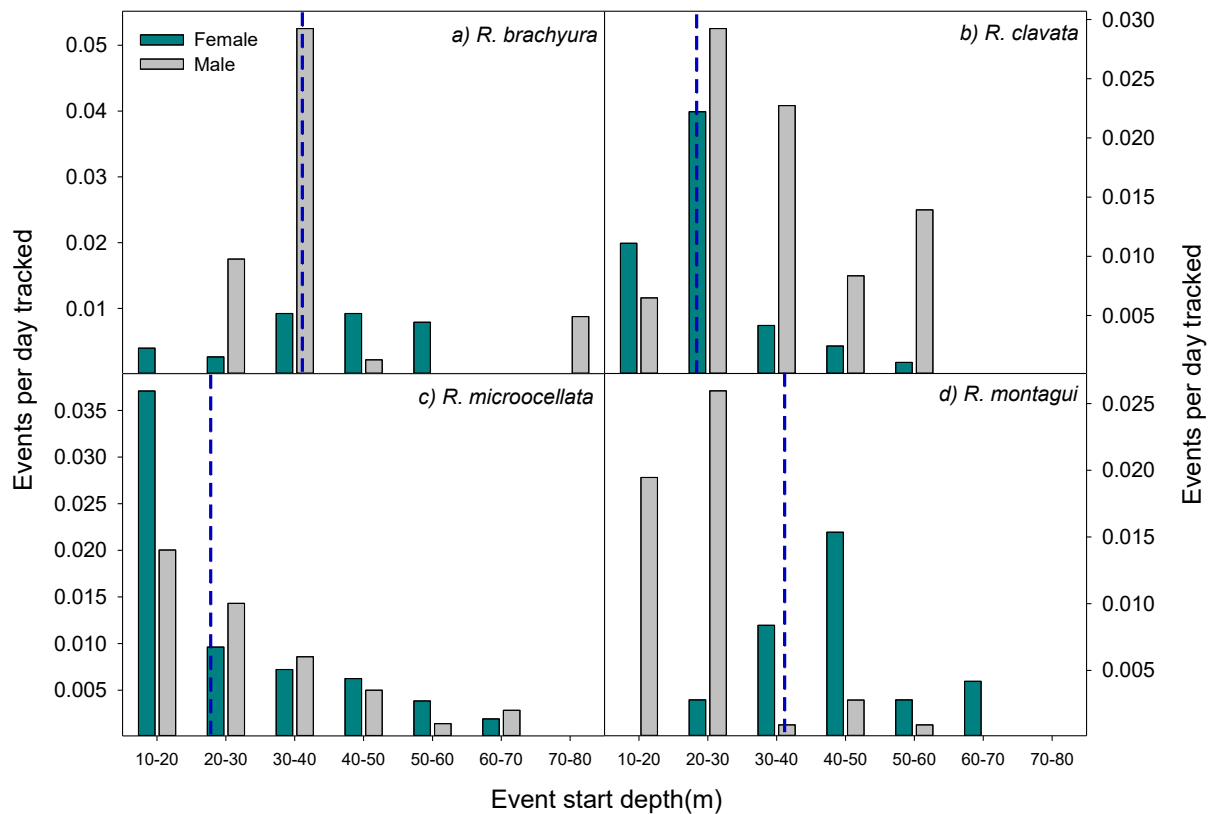


Figure 5: Frequency of events by start depth for species and sex.

The vertical dashed line indicates the preferred mean depth for each species (from Humphries et al. 2016b).

Timing of events

To determine whether light was a possible driver for the movements the event start and end times were analysed to give counts of event starts and ends per hour. The results (Figure 6) were plotted together with the local times of sunrise and sunset. A clear correlation was observed between the time of sunset and the start of the events, with event start times being in most cases just after sunset. Event end times were correlated with dawn and occurred predominantly shortly after sunrise.

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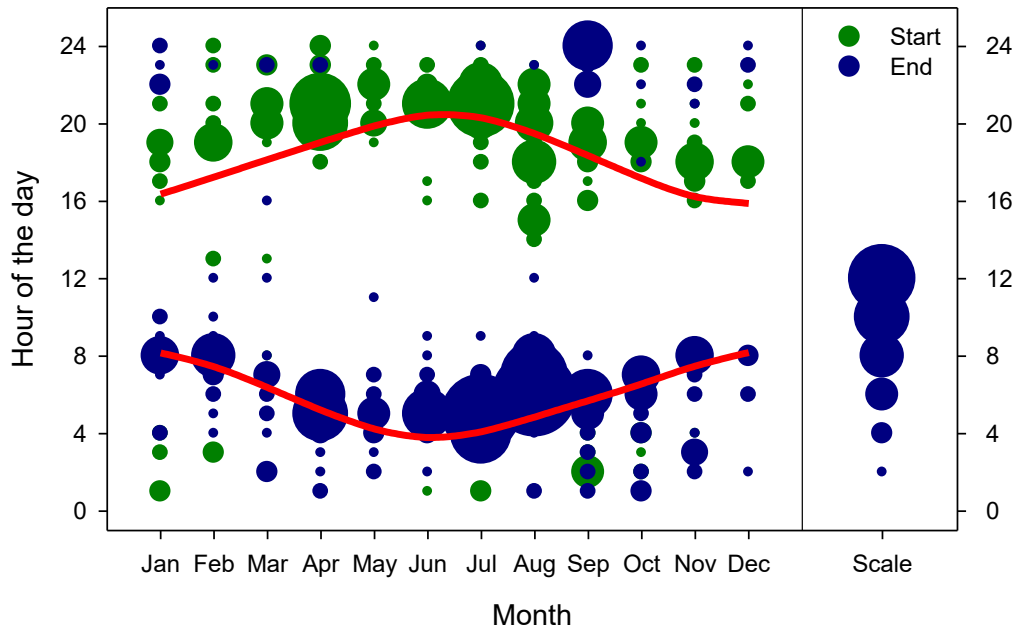


Figure 6: Timing of events in relation to sunrise and sunset times

Throughout most of the year events can be seen to start (green circles) just after sunset and to end (blue circles) just after sunrise. Bubble size indicates the number of events recorded, single events have been omitted for clarity.

Seasonality of events

The seasonal event frequency differed significantly from the expectation of randomness in all but three cases (female *R. brachyura* and *R. microocellata* and male *R. montagui*); statistical results are given in Table 4. The plot in Figure 7 shows the differences between observed and expected event frequencies by species, sex and season. Peaks in event frequency occur throughout the year for different species and sexes; in particular in spring for *R. brachyura* males, summer for *R. clavata* (male and female) and *R. microocellata* males and autumn for *R. montagui* females. It is interesting that peaks do not occur in winter in any case and that lows occur in spring for *R. microocellata* females and *R. montagui* males. Female *R. brachyura* and *R. montagui* and male *R. microocellata* exhibit the most consistent event frequency throughout the year.

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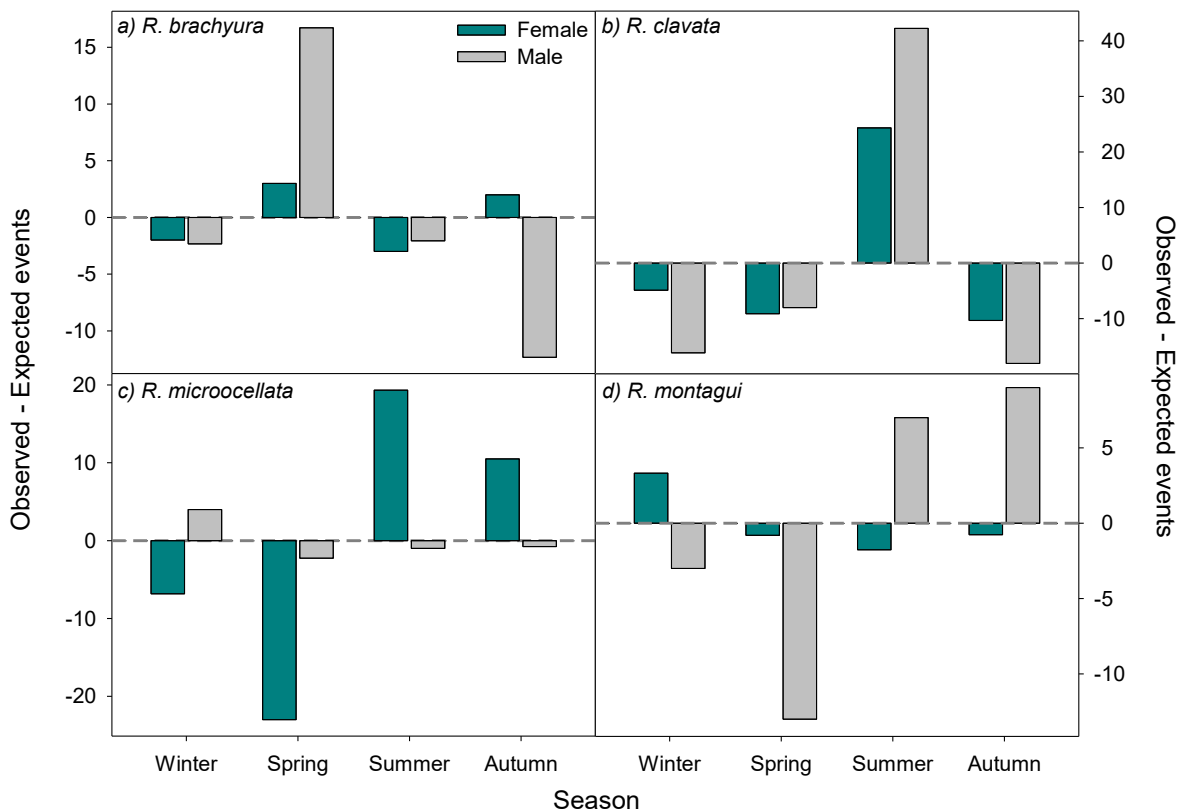


Figure 7: Observed – Expected event counts by species, sex and season

The plot highlights the differences between the observed and expected seasonal frequency of events, where bars above the line indicate higher, and below the line lower, frequencies than expected if there was no seasonal pattern. The expected counts are those determined by the χ^2 analyses.

Table 4: χ^2 results from the seasonal analysis, significant results highlighted

The results confirm that in most cases the event frequency has seasonal highs and lows that differ significantly from the expectation of randomness.

Species	Sex	χ^2	N	df	P
<i>R. brachyura</i>	Female	4.3667	25	3	0.224
<i>R. brachyura</i>	Male	42.0378	37	3	<0.001
<i>R. clavata</i>	Female	21.2486	120	3	<0.001
<i>R. clavata</i>	Male	80.8832	174	3	<0.001
<i>R. microocellata</i>	Female	34.9508	156	3	<0.001
<i>R. microocellata</i>	Male	0.8225	84	3	0.844
<i>R. montagui</i>	Female	2.2066	24	3	0.531
<i>R. montagui</i>	Male	21.5625	54	3	<0.001

Discussion

While exploratory movements, including longer term shifts in depth to areas further inshore or offshore, are expected in active benthic predators such as skates as part of seasonal migrations (Hunter et al. 2005a, Hunter et al. 2005b), regular diel vertical migrations (DVM) from deep resting

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or refuging areas to shallow foraging areas are unexpected. Nonetheless it is clear that all the species in this study do so with a similar propensity and in a similar fashion. This analysis of the 89 depth time-series datasets identified 2354 events that represented diel inshore-offshore movements of which 674 were selected as being those most similar in character to the DVM of pelagic predators. In pelagic predators, such as bigeye tuna (*Thunnus obesus*) DVM represents a form of commuting, or central place foraging, where either the animals are only able to forage efficiently in the colder deeper waters during daylight and consequently return to the warmer surface water during the night, or alternatively, follow vertically migrating prey (Vaske et al. 2012). The ecological and physiological drivers for this behaviour are well understood in predators such as *T. obesus* (Schaefer and Fuller 2010, Fuller et al. 2015, Humphries et al. 2016a). Consequently, the purpose of the work presented here was to investigate the occurrence of the DVM events that most closely suggest central place foraging, to test the hypotheses that the movements are benthic rather than pelagic, that the purpose of the events is foraging and to explore possible drivers and motivations for a behaviour that must incur a metabolic cost of transport, yet reduces foraging time.

Benthic rather than pelagic movement

Both the specialised morphology and the benthophagous diet indicate that skates are strongly adapted to a benthic lifestyle. While foraging, skates have been observed using their crura to 'walk' along the sea bed and manoeuvre with precision to search for buried prey using their electroreceptive sense and only to resort to swimming as an escape response when alarmed (Lucifora and Vassallo 2002, Koester and Spirito 2003). At high swimming speeds (around 2 body lengths/s) the energetic costs increase significantly (Di Santo et al. 2017) and consequently sustained high speed swimming, as might be required for pelagic hunting, is unlikely. The lower energetic cost of 'walking', in comparison to even slower (1 BL/s) swimming explains why most observed movements along the bottom involve walking using crura rather than swimming using undulations of the pectoral fins (Macesic and Kajiura 2010, Di Santo et al. 2017). Additionally, as walking involves fewer muscles, it therefore provides a quieter electrical environment while foraging (Macesic and Kajiura 2010, Di Santo et al. 2017).

The speed of the ascent and descent phases also suggests that the inward and outward migrations are likely the result of skates traversing the sea bed at 'walking pace'. Firstly, the speeds, in terms of vertical displacements, are in all cases very low, with median ascent and descent speeds being < 1 cm/s (Figure 3a). Median 'walking' speeds have been shown to be around 14.5 cm/s, or about one third body length per second (Koester and Spirito 2003). If the skates studied here are moving over the sea bed it is expected that the maximum rate of vertical displacement would be significantly less

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than the rate of horizontal displacement. The low measured speeds are therefore expected, however at more than an order of magnitude less than 'walking' speed the results do suggest that the skate's horizontal speeds are also slow, suggesting not only that the migrations are benthic but also that they may be meandering rather than directed. Further evidence in support of the low speed of movement can be drawn from a comparison with the free fall rate of descent, measured at ~ 13.6 cm/s, which is again an order of magnitude greater than the ascent and descent speeds measured here.

The analysis of tortuosity (SI index) of the ascent and descent phases again suggests that the skates are not frequently making directed movements typical of the DVM of pelagic predators (Shepard et al. 2006, Schaefer and Fuller 2010, Humphries et al. 2016a). Instead, the high tortuosity suggests benthic movement over a complex sea bed topology, possibly searching and foraging opportunistically *en route*. In this respect the movements differ from the DVM of pelagic predators and clearly resemble those of other benthic predators such as burbot *Lota lota* or catsharks *Scyliorhinus canicula* (Sims et al. 2006, Gorman et al. 2012, Harrison et al. 2013, Cott et al. 2015).

Finally, it is worth noting that the average duration of a DVM event is 7.3 hours, which would represent a considerable expenditure of energy if the entire event was pelagic rather than benthic.

Consequently, the majority of movements, in the form of vertical displacements, recorded by the tags are most likely induced by the interaction between horizontal benthic movements and the complex topology of the sea floor and therefore it is reasonable to refer to the events subsequently as nektobenthic DVM.

Nektobenthic DVM as possible central place foraging

Central place foraging is typically observed when animals have conflicting requirements for foraging and other activities. A common example is nesting sea birds, such as northern gannets, *Morus bassanus* or black browed albatross, *Diomedes melanophrys*, where provisioning birds need safe terrestrial locations for nesting, yet often forage in open seas at long distances from the colony (Weimerskirch et al. 1997, Patrick et al. 2014). In other cases, foraging areas can only be visited temporarily, as is the case with air breathing marine predators such as seals (Burns et al. 2008) or penguins (Wilson et al. 1993) or in ectothermic predators such as bigeye tuna, *Thunnus obesus*, diving into cold waters below the thermocline (Fuller et al. 2015, Humphries et al. 2016a). For many animals, for example Cape fur seals, *Arctocephalus pusillus pusillus* (De Vos et al. 2015) it is predation risk that affects foraging behaviour. In all such cases animals are driven to forage in areas in which they cannot permanently reside and therefore must bear the often significant cost of movement between these areas or the risk of predation. The skates studied in this work are

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temperate benthic mesopredators that are unlikely, as adults, to be subject to significant predation pressure in the area studied (Scharf et al. 2000) and it was therefore expected that the depths or habitats occupied would be those that offer the best feeding opportunities (Krebs and Davies 1997). While considerable movement resulting from exploration was expected, and observed, it was not expected that skates would vacate productive foraging areas and return to apparent refuge areas in the way frequently observed with known central place foragers (e.g. Lawton 1987).

Given the similarity between the subset of events selected and the DVM of pelagic predators the principal hypothesis explored here is that these movements represent a form of central place foraging and several lines of evidence support this contention. For example, the difference in activity between the deep and plateau phases suggests that during the deep phase skates exhibited limited or no movement and were resting, while during the plateau phase they were more actively exploring the sea bed. Although only vertical movements were recorded by the tags in this study, the greater vertical displacements observed in depth time-series from the shallower plateau phase were consistent with skates moving much more actively across the sea bed, with differences in sea bed topography generating more vertical movements, in addition to any active swimming above the substrate the animals might perform. Further support for central place foraging is provided by the presence of a clear tidal signal observed in the deep phase of many of the tracks but which is rarely evident in the plateau phase. A clear tidal signal indicates that the animal is remaining at a relatively constant depth on or close to the sea bed. Some teleosts, such as cod, *Gadus morhua*, can effectively remain neutrally buoyant at the same distance above the sea bed, allowing a tidal signal to be detected by tags attached to individual fish (Pedersen et al. 2008). Skates however lack swim bladders, are negatively buoyant and therefore cannot maintain a depth above the seabed without active swimming. During the deeper phase the skates are therefore most likely resting on the sea bed and, if they are moving, it is with considerably less activity than during the shallow plateau phase. Given a skate's propensity to bury itself in the bottom substratum (Kotwicki and Weinberg 2005), resting on the sea bed would seem to be the most likely behaviour to be occurring during the low activity deep phase observed between nektobenthic DVM events. Consequently it seems reasonable to conclude that the deep phase represents resting or refuging behaviour, while the plateau phase represents foraging.

Potential drivers of nektobenthic DVM

There are several hypotheses that could be considered as possible drivers of the nektobenthic DVM behaviour, for example, behavioural thermoregulation, predator avoidance, prey tracking or simply the avoidance of light. A potential driver for the nektobenthic DVM behaviour observed in skate

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appears to be threshold levels of natural light, with the majority of events beginning just after sunset and ending shortly after sunrise (as shown in Figure 6). There is little direct evidence in the literature for nocturnal activity patterns in skates, except for Hove and Moss (1997), Auster (1995) and some trawling studies (e.g. Appa Rao and Krishnamoorthi 1982, Casey and Myers 1998) where catches of skates were greater at night. Given the difficulties of observing the detailed movements of free-ranging skates the lack of detailed studies is not surprising. However, it is clear from this study that the nektobenthic DVM events, and the higher rates of activity associated with them, occur predominantly during night time hours. Casey and Myers (1998) suggest that the increased catchability of skates at night is possibly due to them being unable to visually detect the oncoming trawl net. However, skate eyes are well adapted for low light and nocturnal activity (Murphy and Howland 1990) and therefore it is perhaps more likely that day time catches are lower as skates are buried in substrata while during the night they are actively moving across the sea bed and consequently more vulnerable to capture in a bottom trawl net. Further evidence for this is provided by observations of the behaviour of skates during trawling, where a frequent response to the presence of a trawl is to attempt to bury in the substrate (Queirolo et al. 2012). A further possibility, suggested by this study, is that skates performing nektobenthic DVM are moving to areas for daytime resting where trawling is not undertaken. Indeed, diel differences in distribution have been previously recorded by video transect survey in the little skate *Raja erinacea*, with microhabitat association being observed during the day but with more random and dispersed distributions being seen during the night, consistent with resting or refuging during daylight and active foraging and searching during the night (Auster et al. 1995).

It is interesting that the regularity of the nektobenthic DVM events observed here is quite unlike that frequently observed for pelagic marine predators, such as swordfish (e.g. *Xiphius gladius*) or bigeye tuna (*Thunnus obesus*) where it is usual for DVM to be performed by every animal every day (Schaefer and Fuller 2010, Evans et al. 2014). By contrast, the skates studied here performed nektobenthic DVM for only a part of the time they were tracked. As an example a daily minimum-maximum depth plot is shown for *R. clavata* B0334 (Figure 8). The selected 'central place foraging' nektobenthic DVM events occur for a relatively short period of time, during which the animal is residing in deep water during the day yet moving to much shallower water during the night. At the beginning of August the skate then relocates into shallower water but can be seen to still be moving over a range of depths each day. Following the relocation in August the deeper resting depth is around 12-13 m and the shallower, foraging, depth is around 9-10 m. Observations such as this illustrate the complex nature and apparent flexibility of the behaviour of these predators. In this

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case it seems possible that the animal moved to a geographic area where preferred foraging and resting habitats were in closer proximity, making any diel differences less marked.

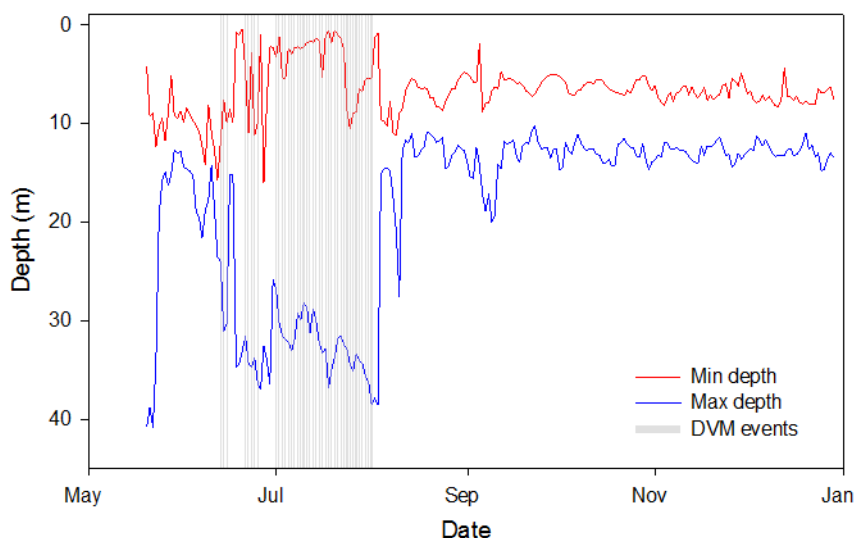


Figure 8: Min-max depth plot for thornback ray B0334

Red line shows daily minimum depth, blue line shows daily maximum depth, grey vertical lines indicate the occurrence of nektobenthic DVM events.

From the sporadic nature of the events it would appear that while light is a trigger for the onset or end of the movements, it may not be the causal driver (Ringelberg and Van Gool 2003). In other words, while changing light levels might trigger the start or end of an event, the causal factor (or underlying motivation) is more likely to be the need to find more suitable foraging habitat (at the start of event) or refuging habitat (at the end). The skates may therefore be responding to changing needs for environmental conditions (prey availability, substrate type) or internal states (hunger, satiation, exhaustion) on an *ad-hoc* basis, with the timing of the response triggered by a light level threshold. There must therefore be a mismatch, at times, between the area in which the animals prefer to forage and areas they prefer when resting, with this mismatch providing the motivation to move. One possibility is that the animals prefer a particular substrate (sand, mud or gravel) when resting, one in which they are able to partially bury themselves but which offers few opportunities for foraging. However, little is known regarding preferred substrates, as skates are reported as being found in a range of habitat types from mud and sand through to coarse gravel (Wheeler 1969, Fock 2014). Precisely which habitats are preferred for specific activities remains unknown. Further research into identifying habitat preferences is currently hampered by a lack of horizontal fine-scale movement data, with this study being typical in having detailed depth records, but no precise geographical locations. The complex heterogeneity of the sea floor in the study area (see Supplementary Information) means that depth alone is a very poor indicator of likely substrate.

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Indeed, for example, even though it is well known that *R. clavata* frequently makes use of estuarine habitats (Hunter et al. 2005a, Hunter et al. 2005b) it is not yet possible to determine such movements from the depth records of the skates in this study.

While no common seasonal driver for the onset of nektobenthic DVM behaviour was identified, there is less activity in winter for all species and increased activity for *R. clavata*, *R. microocellata* and *R. montagui* in the warmer months of summer and autumn. Indeed for *R. clavata* nektobenthic DVM is principally observed in summer months which most likely explains the higher overall temperatures recorded for the events in this species (Figure 4a). With the exception of *R. brachyura*, where the peak in activity is in spring, it is possible that the observed increase in nektobenthic DVM is a result of the animals being more active overall in warmer water. Warmer water temperature will increase metabolic rate of ectothermic skates and consequently increase the requirement for food if growth rates are to be maintained, possibly driving increased foraging activity. However, it is not clear why large predators such as skates should choose not to remain in favourable foraging grounds, but instead return each day to deeper waters.

One possible explanation for the spatial separation between foraging and resting phases could be energy conservation through behavioural thermoregulation. In the catshark *Scyliorhinus canicula* behavioural thermoregulation was proposed to account for the observed nektobenthic DVM behaviour (Sims et al. 2006). It was found that catsharks hunted in warmer, shallow waters at night, but returned to deep, cooler waters at night to rest and digest, with an estimated energetic saving of around 4% by adopting nektobenthic DVM compared to isothermal, non-migratory behaviour (Sims et al. 2006). In contrast, blacktip reef sharks, *Carcharhinus melanoptis*, inhabiting warmer tropical areas than *S. canicula*, have been found to move into shallower water during daytime low tides in order to warm and possibly increase rates of digestion, but hunt during early evening having cooled, but while still warmer than their prey (Papastamatiou et al. 2015). Temperatures recorded for the skates studied here however showed no significant differences between the deep and shallow areas occupied (Figure 4a). The reason for a lack of a relation between temperature and depth is most likely the strong tidal mixing that occurs in these coastal waters, making them quite different from stratified pelagic waters (Pingree and Griffiths 1978). Therefore, behavioural thermoregulation is unlikely to be a driver for the activity observed here.

The return to deeper, darker waters during daylight hours could be motivated by predator avoidance, as is the case with many pelagic fish (e.g. Sutton and Hopkins 1996). Typically, pelagic prey with visual predators, avoid day time predation by diving to deeper depths where the lower light levels afford some protection. However, the four skates studied here are considerably larger

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than any other benthic predators in this coastal assemblage (Ellis et al. 2005b) and are unlikely to be subject to significant, if any, predation in the area studied. Consequently they are less likely to choose protection from predators over foraging. Over the last 100 years populations of other elasmobranchs, including possible predators of skates (such as the common skate, *Dipturus* spp.) have declined precipitously (Dulvy et al. 2000, Ellis et al. 2005a) so although predator avoidance seems unlikely it is possible that the observed nektobenthic DVM represents an historic behavioural trait evolved to anticipate the risk of predation (Mehner et al. 2007). However, as discussed by Mehner (2007), such behaviour would be expected to produce a more stable and consistent pattern of movement than is observed here, being generated by an intrinsic driver rather than representing an ad hoc response to changing environmental variables.

Given that the skates are essentially apex predators in this coastal, demersal ecosystem, a further possibility is that the migrations are being performed in order to track migrating prey. Skates are generalist predators with a broad dietary niche comprising principally fish and crustaceans (Ellis et al. 1996, Farias et al. 2006, Šantić et al. 2012, Pinnegar 2014) with typical prey of the skates studied here being crabs (e.g. *Liocarcinus*, *Carcinus* spp.) or sand eels (e.g. *Ammodytes marinus*). Sand eels are generally nocturnal and spend the autumn and winter buried in sediments (Greenstreet et al. 2010) where they might make easy prey for skates that can use their electroreception to detect them (Wueringer 2012). Interestingly, it is the two species with a greater preference for fish in their diets (Pinnegar 2014, Wearmouth et al. 2014) that perform more nektobenthic DVM in autumn (*R. microocellata* and *R. montagui*). In the North Sea, there is evidence of sand eels performing DVM, whereby they occupy pelagic habitats during the day and return at night to shallower waters where suitable habitats exist in which to burrow (van der Kooij et al. 2008). If sand eels perform similar migrations, and are a preferred prey of skates in the area studied here then this might represent a possible driver for the observed events. However, sand eel movements have not been well documented around the south west coast of England so this potential explanation remains speculative. Similarly, crabs (e.g. *Liocarcinus depurator*) have been shown to have diel activity rhythms, burying in substrate during the day and emerging and becoming active at night (Aguzzi et al. 2009, Aguzzi et al. 2015), along with other endobenthic and nektobenthic animals (Aguzzi and Company 2010). These prey items, being in the open and mobile are probably more easily located by skates during the night and the availability of such prey might be a driver of either inshore migrations or a trigger for increased activity in the skates. However, at present there remains no clear reason why the skates would then return to deeper water after each foraging bout.

Rajidae are oviparous, laying eggs which are commonly found in high density in nursery beds often located in shallower depths than the preferred depths in these species (Ellis et al. 2005b). However,

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while in some species the peak in egg laying frequency coincides with the peak in event frequency (Holden 1975, Ellis and Shackley 1995, Koop 2005) egg-laying can be discounted as a possible driver for DVM as the events are observed more frequently in males, and while males could be following egg laying females to gain access to mating opportunities, the coincidence between nektobenthic DVM and egg laying peaks is not sufficiently consistent. Light level, possibly coupled with intrinsic behavioural rhythms, therefore remains the only clear trigger for the behaviour with the majority of events beginning just after sunset and ending shortly after dawn where the skates appear to avoid the increasing light levels by moving to deeper, darker waters. This hypothesis is also confounded, however, by skates frequently spending extended periods of time in shallow water, e.g. Figure 8. This particular skate is not unusual in performing a migration to shallower water and remaining there, despite the increased light levels during August and September and having previously performed regular nektobenthic DVM.

Conclusions

The difficulties in obtaining sustained observations or in geo-locating active highly mobile benthic animals, such as skates, present a significant obstacle in our understanding of the movement ecology of these important predators. Through a detailed analysis of high resolution depth time-series data this study has identified previously unknown diel inshore-offshore migrations that likely result in the animals having a wider dispersal and larger area of occupancy than might otherwise have been considered over short timescales. The limitations of the depth time-series data hamper attempts to determine the factors that motivate the animals to perform these migrations; although some potential drivers, such as behavioural thermoregulation, are not supported in this study and can be discounted. From the patterns of activity observed here, and the comparisons with nektobenthic DVM in other marine predators, it seems most likely that the movements represent foraging excursions. A principal finding in this paper was that the nektobenthic DVM observed provides evidence for possible central place foraging by the skate species we studied, a behaviour that has not, to our knowledge, been identified by previous investigations. This study cannot provide any clear motivation for central place foraging in skates, however, and therefore in future studies efforts should be made to determine in more detail what activities the animals are performing in each phase. To this end, tagging studies using accelerometers (Brownscombe et al. 2014) might provide important new evidence. Additionally, in the coastal regions inhabited by these skates, video tags or transects could provide more detailed habitat maps (Kendall et al. 2005) which might provide further evidence as to why skates perform these inshore-offshore migrations.

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The observations presented here suggest that skates are highly mobile at finer scales than were previously expected, making the effectiveness of spatial protected areas or fishing controls more difficult to accurately define. The diel mobility patterns of skates suggest that protected areas should be large enough to encompass these movements and that fishing controls should consider the nature of the nocturnal activity which likely makes the skates more susceptible to capture during the night in either trawls or set nets. Finally, the common occurrence of nektobenthic DVM in the skates studied here suggests that nektobenthic DVM might be a common behaviour in many other benthic organisms, unobserved and unreported as yet because of the difficulties in determining the fine scale movements of temperate benthic animals.

Acknowledgements

We thank V. Wearmouth, M. McHugh and S. Cotterell for tagging, B. Seeley for help assembling the habitat data, and the captains and crew of RV *MBA Sepia* and RV *Plymouth Quest* for provision of animals. We thank three anonymous reviewers for comments that helped to improve the paper. Tagging was supported by the UK Natural Environment Research Council (NERC) *Oceans 2025* Strategic Research Programme through an award to D.W.S., and a Marine Biological Association Senior Research Fellowship to D.W.S. S.J.S was supported by a University of Southampton SPITFIRE Doctoral Training Partnership Ph.D. studentship, funded jointly by the Natural Environmental Research Council [Grant number NE/L002531/1] and the Marine Biological Association of the UK (MBA). We also thank all the fishers who returned tags.

References

- Adachi, T., D. P. Costa, P. W. Robinson, S. H. Peterson, M. Yamamichi, Y. Naito, and A. Takahashi. 2016. Searching for prey in a three-dimensional environment: hierarchical movements enhance foraging success in northern elephant seals. *Functional Ecology*:361–369.
- Aguzzi, J. and J. B. Company. 2010. Chronobiology of deep-water decapod crustaceans on continental margins. Pages 155-225 in M. Lesser, editor. *Advances in Marine Biology*, Vol 58. Elsevier Academic Press Inc, San Diego.
- Aguzzi, J., J. B. Company, and J. A. García. 2009. Ontogenetic and gender-modulated behavioural rhythms in the deep-water decapods *Liocarcinus depurator* (Brachyura: Portunidae), *Munida tenuimana* and *Munida intermedia* (Anomura: Galatheididae). *Marine Ecology* **30**:93-105.

DVM In benthic predators

- Aguzzi, J., V. Sbragaglia, S. Tecchio, J. Navarro, and J. B. Company. 2015. Rhythmic behaviour of marine benthopelagic species and the synchronous dynamics of benthic communities. *Deep-Sea Research Part I-Oceanographic Research Papers* **95**:1-11.
- Ajayi, T. O. 1982. FOOD AND FEEDING-HABITS OF RAJA SPECIES (BATOIDEI) IN CARMARTHEN BAY, BRISTOL CHANNEL. *Journal of the Marine Biological Association of the United Kingdom* **62**:215-223.
- Andrews, K. S., G. D. Williams, D. Farrer, N. Tolimieri, C. J. Harvey, G. Bargmann, and P. S. Levin. 2009. Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator. *Animal Behaviour* **78**:525-536.
- Appa Rao, T. and B. Krishnamoorthi. 1982. Diurnal variation in the catches of demersal fishes in the northwest region of bay of bengal india during 1959-1960. *Indian Journal of Fisheries* **29**:134-143.
- Auster, P. J., R. J. Malatesta, and S. C. Larosa. 1995. Patterns of microhabitat utilization by mobile megafauna on the southern New-England (USA) continental-shelf and slope. *Marine Ecology Progress Series* **127**:77-85.
- Brownscombe, J. W., L. F. G. Gutowsky, A. J. Danylchuk, and S. J. Cooke. 2014. Foraging behaviour and activity of a marine benthivorous fish estimated using tri-axial accelerometer biologgers. *Marine Ecology Progress Series* **505**:241-251.
- Burns, J. M., M. A. Hindell, C. J. A. Bradshaw, and D. P. Costa. 2008. Fine-scale habitat selection of crabeater seals as determined by diving behavior. *Deep Sea Research Part II: Topical Studies in Oceanography* **55**:500-514.
- Casey, J. M. and R. A. Myers. 1998. Diel variation in trawl catchability: is it as clear as day and night? *Canadian Journal of Fisheries and Aquatic Sciences* **55**:2329-2340.
- Collin, S. P. 2012. The Neuroecology of Cartilaginous Fishes: Sensory Strategies for Survival. *Brain Behavior and Evolution* **80**:80-96.
- Cott, P. A., M. M. Guzzo, A. J. Chapelsky, S. W. Milne, and P. J. Blanchfield. 2015. Diel bank migration of Burbot (*Lota lota*). *Hydrobiologia* **757**:3-20.
- De Vos, A., M. J. O'Riain, M. A. Meyer, P. G. H. Kotze, and A. A. Kock. 2015. Behavior of Cape fur seals (*Arctocephalus pusillus pusillus*) in response to spatial variation in white shark (*Carcharodon carcharias*) predation risk. *Marine Mammal Science* **31**:1234-1251.
- Di Santo, V., E. L. Blevins, and G. V. Lauder. 2017. Batoid locomotion: effects of speed on pectoral fin deformation in the little skate, *Leucoraja erinacea*. *Journal of Experimental Biology* **220**:705-712.

DVM In benthic predators

- Dulvy, N. K., J. D. Metcalfe, J. Glanville, M. G. Pawson, and J. D. Reynolds. 2000. Fishery stability, local extinctions, and shifts in community structure in skates. *Conservation Biology* **14**:283-293.
- Ellis, J., N. K. Dulvy, S. Jennings, M. Parker-Humphreys, and S. I. Rogers. 2005a. Assessing the status of demersal elasmobranchs in UK waters: a review. *Journal of the Marine Biological Association of the United Kingdom* **85**:1025-1047.
- Ellis, J. and S. Shackley. 1995. Observations on egg-laying in the thornback ray. *Journal of Fish Biology* **46**:903-904.
- Ellis, J. R., A. Cruz-Martinez, B. D. Rackham, and S. I. Rogers. 2005b. The distribution of chondrichthyan fishes around the British Isles and implications for conservation. *Journal of Northwest Atlantic fishery science* **35**:195-213.
- Ellis, J. R., M. G. Pawson, and S. E. Shackley. 1996. The Comparative Feeding Ecology of Six Species of Shark and Four Species of Ray (Elasmobranchii) In The North-East Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **76**:89-106.
- Evans, K., F. Abascal, D. Kolody, T. Sippel, J. Holdsworth, and P. Maru. 2014. The horizontal and vertical dynamics of swordfish in the South Pacific Ocean. *Journal of Experimental Marine Biology and Ecology* **450**:55-67.
- Farias, I., I. Figueiredo, T. Moura, L. S. Gordo, A. Neves, and B. Serra-Pereira. 2006. Diet comparison of four ray species (*Raja clavata*, *Raja brachyura*, *Raja montagui* and *Leucoraja naevus*) caught along the Portuguese continental shelf. *Aquatic Living Resources* **19**:105-114.
- Fock, H. O. 2014. Patterns of extirpation. I. Changes in habitat use by thornback rays *Raja clavata* in the German Bight for 1902-1908, 1930-1932, and 1991-2009. *Endangered Species Research* **25**:197-207.
- Fuller, D. W., K. M. Schaefer, J. Hampton, S. Caillot, B. M. Leroy, and D. G. Itano. 2015. Vertical movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial central Pacific Ocean. *Fisheries Research* **172**:57-70.
- Genner, M. J., D. W. Sims, A. J. Southward, G. C. Budd, P. Masterson, M. McHugh, P. Rendle, E. J. Southall, V. J. Wearmouth, and S. J. Hawkins. 2010. Body size-dependent responses of a marine fish assemblage to climate change and fishing over a century-long scale. *Global Change Biology* **16**:517-527.
- Goodyear, C. P., J. G. Luo, E. D. Prince, J. P. Hoolihan, D. Snodgrass, E. S. Orbesen, and J. E. Serafy. 2008. Vertical habitat use of Atlantic blue marlin *Makaira nigricans*: interaction with pelagic longline gear. *Marine Ecology-Progress Series* **365**:233-245.

DVM In benthic predators

- Gorman, O. T., D. L. Yule, and J. D. Stockwell. 2012. Habitat use by fishes of Lake Superior. I. Diel patterns of habitat use in nearshore and offshore waters of the Apostle Islands region. *Aquatic Ecosystem Health & Management* **15**:333-354.
- Greenstreet, S. P. R., G. J. Holland, E. J. Guirey, E. Armstrong, H. M. Fraser, and I. M. Gibb. 2010. Combining hydroacoustic seabed survey and grab sampling techniques to assess "local" sandeel population abundance. *ICES Journal of Marine Science* **67**:971-984.
- Harrison, P. M., L. F. G. Gutowsky, E. G. Martins, D. A. Patterson, A. Leake, S. J. Cooke, and M. Power. 2013. Diel vertical migration of adult burbot: a dynamic trade-off among feeding opportunity, predation avoidance, and bioenergetic gain. *Canadian Journal of Fisheries and Aquatic Sciences* **70**:1765-1774.
- Hays, G. C. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia* **503**:163-170.
- Holden, M. 1975. The fecundity of *Raja clavata* in British waters. *Journal du Conseil* **36**:110-118.
- Hove, J. R. and S. A. Moss. 1997. Effect of MS-222 on response to light and rate of metabolism of the little skate *Raja erinacea*. *Marine Biology* **128**:579-583.
- Humphries, N. E., K. M. Schaefer, D. W. Fuller, G. E. M. Phillips, C. Wilding, and D. W. Sims. 2016a. Scale-dependent to scale-free: daily behavioural switching and optimized searching in a marine predator. *Animal Behaviour* **113**:189-201.
- Humphries, N. E., S. J. Simpson, V. J. Wearmouth, and D. W. Sims. 2016b. Two's company, three's a crowd: fine-scale habitat partitioning by depth among sympatric species of marine mesopredator. *Marine Ecology Progress Series* **561**:173-187.
- Hunter, E., A. A. Blickley, C. Stewart, and J. D. Metcalfe. 2005a. Repeated seasonal migration by a thornback ray in the southern North Sea. *Journal of the Marine Biological Association of the United Kingdom* **85**:1199-1200.
- Hunter, E., A. A. Buckley, C. Stewart, and J. D. Metcalfe. 2005b. Migratory behaviour of the thornback ray *Raja clavata*, in the southern North Sea. *Journal of the Marine Biological Association of the United Kingdom* **85**:1095-1105.
- Irigoin, X., D. V. P. Conway, and R. P. Harris. 2004. Flexible diel vertical migration behaviour of zooplankton in the Irish Sea. *Marine Ecology Progress Series* **267**:85-97.
- Kadri, H., S. Marouani, M. N. Bradai, and A. Bouaïn. 2014. Diet and feeding strategy of thornback ray, *Raja clavata* (Chondrichthyes: Rajidae) from the Gulf of Gabes (Tunisia—Central Mediterranean Sea). *Journal of the Marine Biological Association of the United Kingdom* **94**:1509-1516.

DVM In benthic predators

- Kendall, M. S., O. P. Jensen, C. Alexander, D. Field, G. McFall, R. Bohne, and M. E. Monaco. 2005. Benthic mapping using sonar, video transects, and an innovative approach to accuracy assessment: A characterization of bottom features in the Georgia Bight. *Journal of Coastal Research* **21**:1154-1165.
- Kimber, J., D. Sims, P. Bellamy, and A. Gill. 2013. Elasmobranch cognitive ability: using electroreceptive foraging behaviour to demonstrate learning, habituation and memory in a benthic shark. *Animal Cognition*:1-11.
- Koester, D. M. and C. P. Spirito. 2003. Punting: An unusual mode of locomotion in the little skate, *Leucoraja erinacea* (Chondrichthyes : Rajidae). *Copeia*:553-561.
- Koop, J. H. 2005. Reproduction of captive Raja spp. in the Dolfinarium Harderwijk. *Journal of the Marine Biological Association of the United Kingdom* **85**:1201-1202.
- Kotwicki, S. and K. L. Weinberg. 2005. Estimating capture probability of a survey bottom trawl for Bering Sea skates (*Bathyraja* spp.) and other fish. *Alaska Fishery Research Bulletin* **11**:135-145.
- Krebs, J. R. and N. B. Davies. 1997. *Behavioural Ecology: An Evolutionary Approach*. 4th edition. Blackwell, Oxford.
- Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology* **3**:21-27.
- Lawton, P. 1987. Diel activity and foraging behavior of juvenile american lobsters, *Homarus americanus*. *Canadian Journal of Fisheries and Aquatic Sciences* **44**:1195-1205.
- Lucifora, L. O. and A. I. Vassallo. 2002. Walking in skates (Chondrichthyes, Rajidae): anatomy, behaviour and analogies to tetrapod locomotion. *Biological Journal of the Linnean Society* **77**:35-41.
- Macesic, L. J. and S. M. Kajiura. 2010. Comparative Punting Kinematics and Pelvic Fin Musculature of Benthic Batoids. *Journal of Morphology* **271**:1219-1228.
- Matern, S. A., J. J. Cech, and T. E. Hopkins. 2000. Diel movements of bat rays, *Myliobatis californica*, in Tomales Bay, California: Evidence for behavioral thermoregulation ? *Environmental Biology of Fishes* **58**:173-182.
- Mehner, T. 2012. Diel vertical migration of freshwater fishes - proximate triggers, ultimate causes and research perspectives. *Freshwater Biology* **57**:1342-1359.
- Mehner, T., P. Kasprzak, and F. Holker. 2007. Exploring ultimate hypotheses to predict diel vertical migrations in coregonid fish. *Canadian Journal of Fisheries and Aquatic Sciences* **64**:874-886.
- Murphy, C. J. and H. C. Howland. 1990. The functional-significance of crescent-shaped pupils and multiple pupillary apertures. *Journal of Experimental Zoology*:22-28.

DVM In benthic predators

- Pade, N. G., N. Queiroz, N. E. Humphries, M. J. Witt, C. S. Jones, L. R. Noble, and D. W. Sims. 2009. First results from satellite-linked archival tagging of porbeagle shark, *Lamna nasus*: Area fidelity, wider-scale movements and plasticity in diel depth changes. *Journal of Experimental Marine Biology and Ecology* **370**:64-74.
- Papastamatiou, Y. P., Y. Y. Watanabe, D. Bradley, L. E. Dee, K. Weng, C. G. Lowe, and J. E. Caselle. 2015. Drivers of Daily Routines in an Ectothermic Marine Predator: Hunt Warm, Rest Warmer? *Plos One* **10**.
- Patrick, S. C., S. Bearhop, D. Grémillet, A. Lescroël, W. J. Grecian, T. W. Bodey, K. C. Hamer, E. Wakefield, M. Le Nuz, and S. C. Votier. 2014. Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. *Oikos* **123**:33-40.
- Pedersen, M. W., D. Righton, U. H. Thygesen, K. H. Andersen, and H. Madsen. 2008. Geolocation of North Sea cod (*Gadus morhua*) using hidden Markov models and behavioural switching. *Canadian Journal of Fisheries and Aquatic Sciences* **65**:2367-2377.
- Pingree, R. D. and D. K. Griffiths. 1978. Tidal fronts on the shelf seas around the British Isles. *Journal of Geophysical Research: Oceans* **83**:4615-4622.
- Pinnegar, J. K. 2014. DAPSTOM - An Integrated Database & Portal for Fish Stomach Records. *in* F. A. S. Centre for Environment, Lowestoft, UK., editor.
- Pinto, C. and L. Spezia. 2016. Markov switching autoregressive models for interpreting vertical movement data with application to an endangered marine apex predator. *Methods in Ecology and Evolution* **7**:407-417.
- Queirolo, D., E. Gaete, I. Montenegro, M. C. Soriguer, and K. Erzini. 2012. Behaviour of fish by-catch in the mouth of a crustacean trawl. *Journal of Fish Biology* **80**:2517-2527.
- Queiroz, N., N. E. Humphries, L. R. Noble, A. M. Santos, and D. W. Sims. 2010. Short-term movements and diving behaviour of satellite-tracked blue sharks *Prionace glauca* in the northeastern Atlantic Ocean. *Marine Ecology Progress Series* **406**:265-279.
- Queiroz, N., N. E. Humphries, L. R. Noble, A. n. M. Santos, and D. W. Sims. 2012. Spatial Dynamics and Expanded Vertical Niche of Blue Sharks in Oceanographic Fronts Reveal Habitat Targets for Conservation. *Plos One* **7**:e32374.
- Ringelberg, J. and E. Van Gool. 2003. On the combined analysis of proximate and ultimate aspects in diel vertical migration (DVM) research. *Hydrobiologia* **491**:85-90.
- Šantić, M., B. Rađa, and A. Pallaoro. 2012. Diet and feeding strategy of thornback ray *Raja clavata*. *Journal of Fish Biology* **81**:1070-1084.

DVM In benthic predators

- Schaefer, K. M. and D. W. Fuller. 2002. Movements, behavior, and habitat selection of bigeye tuna (*Thunnus obesus*) in the eastern equatorial Pacific, ascertained through archival tags. *Fishery Bulletin* **100**:765-788.
- Schaefer, K. M. and D. W. Fuller. 2010. Vertical movements, behavior, and habitat of bigeye tuna (*Thunnus obesus*) in the equatorial eastern Pacific Ocean, ascertained from archival tag data. *Marine Biology* **157**:2625-2642.
- Scharf, F. S., F. Juanes, and R. A. Rountree. 2000. Predator size - prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic-niche breadth. *Marine Ecology Progress Series* **208**:229-248.
- Shepard, E. L. C., M. Z. Ahmed, E. J. Southall, M. J. Witt, J. D. Metcalfe, and D. W. Sims. 2006. Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology-Progress Series* **328**:205-213.
- Simpson, S. D., S. Jennings, M. P. Johnson, J. L. Blanchard, P. J. Schon, D. W. Sims, and M. J. Genner. 2011. Continental Shelf-Wide Response of a Fish Assemblage to Rapid Warming of the Sea. *Current Biology* **21**:1565-1570.
- Sims, D. W., E. J. Southall, G. A. Tarling, and J. D. Metcalfe. 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., V. J. Wearmouth, E. J. Southall, J. M. Hill, P. Moore, K. Rawlinson, N. Hutchinson, G. C. Budd, D. Righton, J. Metcalfe, J. P. Nash, and D. Morritt. 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology* **75**:176-190.
- Steven, G. A. 1932. Rays and Skates of Devon and Cornwall. II. A Study of the Fishery; with Notes on the Occurrence, Migrations and Habits of the Species. *Journal of the Marine Biological Association of the United Kingdom* **18**:1-33.
- Sutton, T. T. 2013. Vertical ecology of the pelagic ocean: classical patterns and new perspectives. *Journal of Fish Biology* **83**:1508-1527.
- Sutton, T. T. and T. L. Hopkins. 1996. Trophic ecology of the stomiid (Pisces: Stomiidae) fish assemblage of the eastern Gulf of Mexico: Strategies, selectivity and impact of a top mesopelagic predator group. *Marine Biology* **127**:179-192.
- van der Kooij, J., B. E. Scott, and S. Mackinson. 2008. The effects of environmental factors on daytime sandeel distribution and abundance on the Dogger Bank. *Journal of Sea Research* **60**:201-209.

DVM In benthic predators

- Vaske, T., P. E. Travassos, F. H. V. Hazin, M. T. Tolotti, and T. M. Barbosa. 2012. Forage fauna in the diet of bigeye tuna (*Thunnus obesus*) in the western tropical Atlantic ocean. *Brazilian Journal of Oceanography* **60**:89-97.
- Walli, A., S. L. H. Teo, A. Boustany, C. J. Farwell, T. Williams, H. Dewar, E. Prince, and B. A. Block. 2009. Seasonal Movements, Aggregations and Diving Behavior of Atlantic Bluefin Tuna (*Thunnus thynnus*) Revealed with Archival Tags. *Plos One* **4**.
- Wearmouth, V. J., M. J. McHugh, N. E. Humphries, A. Naegelen, M. Z. Ahmed, E. J. Southall, A. M. Reynolds, and D. W. Sims. 2014. Scaling laws of ambush predator 'waiting' behaviour are tuned to a common ecology. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **281**.
- Wearmouth, V. J. and D. W. Sims. 2009. Movement and behaviour patterns of the critically endangered common skate *Dipturus batis* revealed by electronic tagging. *Journal of Experimental Marine Biology and Ecology* **380**:77-87.
- Weimerskirch, H., T. Mougey, and X. Hindermeier. 1997. Foraging and provisioning strategies of black-browed albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* **8**:635-643.
- Wheeler, A. 1969. *The Fishes of the British Isles and North-West Europe*. Macmillan, London.
- Wilson, R. P., K. Puetz, C. A. Bost, B. M. Culik, R. Bannasch, T. Reins, and D. Adelung. 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.
- Wueringer, B. E. 2012. Electroreception in Elasmobranchs: Sawfish as a Case Study. *Brain Behavior and Evolution* **80**:97-107.
- Wueringer, B. E., L. S. Jnr, S. M. Kajiura, I. R. Tibbetts, N. S. Hart, and S. P. Collin. 2012. Electric Field Detection in Sawfish and Shovelnose Rays. *Plos One* **7**.
- Zouhiri, S. and J. C. Dauvin. 1996. Diel changes of the Benthic Boundary Layer macrofauna over coarse sand sediment in the western English Channel. *Oceanologica Acta* **19**:141-153.