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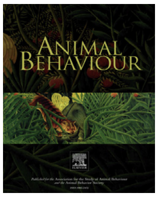

Scale-dependent to scale-free: daily behavioural switching and optimized searching in a marine predator

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Rhythmic activity patterns are ubiquitous in animals and in the marine environment a dominant rhythmic activity is the diel vertical migration (DVM) of pelagic organisms, moving or 'migrating' from deep waters during the day to shallower waters at night. While this overall pattern of movement is well understood, the cryptic nature of the marine environment has limited the study of fine-scale movements within each phase. Active pelagic predators, such as tuna, perform consistent, predictable large-scale vertical movements; however, the fine-scale movements nested within these larger movements have not previously been investigated in detail. Further, the prey field densities are known to differ significantly between day and night, presenting an opportunity to study differences in foraging patterns between these two phases. Here, using long-term depth time series recorded from 93 bigeye tuna, *Thunnus obesus*, with electronic tags (18 003 days of data), fine-scale changes in vertical movement patterns between day and night time phases were investigated in the context of the Lévy foraging hypothesis, which predicts a Lévy distribution of move steps during foraging when prey is scarce, but an exponential distribution when prey is abundant and searching is not required. During the day, *T. obesus* were found to exhibit scale-free movements well fitted by a Lévy distribution indicating optimized searching for sparsely distributed prey. During night-time hours, however, exponentially distributed scale-dependent move step lengths were found to be dominant, supporting a simple, Brownian, movement pattern sufficient where prey is abundant. This study not only confirms the predictions of the Lévy foraging hypothesis but suggests that the identification of Lévy patterns in movement data can be a useful indicator of foraging activity in animals that are difficult to observe directly.

Rhythmic patterns of activity occur in many taxa, frequently as an adaptive response to cyclical changes in environmental conditions (Yerushalmi & Green, 2009). In many cases these patterns represent switching between active and resting phases, for example, littoral or terrestrial gastropod molluscs responding to tidal or diurnal cycles, respectively. In other cases the responses are migratory, and often associated with central-place foraging, such as starlings travelling between roost sites and foraging grounds (Davis & Lussenhop, 1970). Thus many of the rhythmic patterns of behaviour can be considered to be deterministic, where the animal undertakes predictable patterns of movement or behaviour in response to predictable environmental changes (Nelson et al., 1997). Such directed, scale-dependent, movements form only part of the rich behavioural repertoire exhibited by most animals. Nested within these movements are other behaviours and movement patterns, such as searching or foraging. Although directed patterns have been well documented among animals, where and when other movements, such as searching, occur within the directed behaviour patterns has received much less attention by comparison.

One of the most ubiquitous directed movements in the marine environment is the diel (daily) vertical migration (DVM) of plankton. This migration of planktonic organisms from deeper water during the day to shallow waters at night is the largest known daily migration of metazoan organisms (Hays, 2003). It is thought that this behaviour pattern results from the avoidance of

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visual predators (Lampert, 1989) because in lakes without fish or where the principal predators are tactile (e.g. scyphozoans) the DVM is reduced or absent (Hays, 2003). Many large, active predators from a broad range of taxa have also been observed to perform DVM, presumably in pursuit of their vertically migrating prey, for example blue sharks, *Prionace glauca* (Queiroz, Humphries, Noble, Santos, & Sims, 2010), ocean sunfish, *Mola mola* (Sims, Queiroz, Doyle, Houghton, & Hays, 2009) and basking sharks, *Cetorhinus maximus* (Shepard et al., 2006). However, the pattern of behaviour is complex, with some pelagic organisms either not performing DVM or performing reverse DVM (Irigoien, Conway, & Harris, 2004), with reverse DVM also being observed in basking (Sims, Southall, Tarling, & Metcalfe, 2005) and blue sharks (Queiroz, Humphries, Noble, Santos, & Sims, 2012). While the overall pattern of migration has been well studied, activity patterns during the different phases and the motivations underlying the behaviour are poorly known and, consequently, less well understood. Some pelagic predators exhibit strong and consistent DVM behaviour, among them swordfish, *Xiphias gladius* (Evans et al., 2014), blue marlin, *Makaira nigricans* (Goodyear et al., 2008), bluefin, *Thunnus thynnus* (Walli et al., 2009) and bigeye tuna, *Thunnus obesus* (Schaefer & Fuller, 2002), but the DVM patterns have not been investigated quantitatively to analyse fine-scale movements or to explore when and where other patterns, such as searches, intersperse DVM.

A recent advance in furthering our understanding of free-ranging animal behaviour, particularly that of marine predators, has been the use of random-walk modelling in the analysis of large data sets of movements recorded with animal-attached electronic tags (Heithaus, Hamilton, Wirsing, & Dill, 2006; Humphries et al., 2010; Humphries, Weimerskirch, Queiroz, Southall, & Sims, 2012; Jonsen, Myers, & James, 2007; Papastamatiou et al., 2013; Sims, Humphries, Bradford, & Bruce, 2012; Sims et al., 2008; Sims, Witt, Richardson, Southall, & Metcalfe, 2006). Such studies can provide some insight into the motivations underlying observed movement patterns, including microhabitat use (Heithaus et al., 2006), optimal foraging (Sims et al., 2008) and philopatric behaviours (Papastamatiou et al., 2013). A random-walk model that has received much attention recently in relation to animal movement is the Lévy walk (Viswanathan, da Luz, Raposo, & Stanley, 2011). Lévy walks are specialized movement paths that comprise clusters of small steps connected by rarer, long relocations, with this pattern repeated at all scales. In a Lévy walk the step lengths are chosen from a probability distribution with a power law tail, resulting in step lengths with no characteristic scale (i.e. exhibiting fractal scale invariance), where $P(l) \sim l^{-\mu}$, with $1 < \mu \leq 3$ where l is the step length and μ the power law exponent. Over many iterations a Lévy walk will be distributed much further from its starting position than a Brownian walk of the same length, and hence is termed superdiffusive. Theory and comprehensive searching model simulations (Humphries & Sims, 2014; Viswanathan et al., 1999, 2011) show that Lévy walks optimize search efficiencies compared with other strategies by increasing the probability of encountering new, more distant patches. The Lévy foraging (LF) hypothesis is concerned with the optimization of search strategies and predicts that searching is optimized when the move step lengths of a random walk follow the inverse power law distribution with exponent $\mu = 2$ (Humphries & Sims, 2014; Viswanathan et al., 1999). An important prediction of the LF hypothesis is that Lévy patterns should be prevalent when an animal is searching for sparse or patchily distributed prey, but simple, exponential patterns (representing Brownian movements) are more likely when the animal is not searching, i.e. when prey is abundant or when the animals are engaged in other activities.

The general vertical movement patterns of bigeye tuna in particular have been studied extensively (Dagorn, Bach, & Josse, 2000; Matsumoto, Kitagawa, & Kimura, 2013; Musyl et al., 2003; Schaefer & Fuller, 2002, 2010), with a clear crepuscular vertical migration between deep (>250 m) waters during the day and subsurface (ca. 50 m) waters at night being the predominant pattern of vertical space use (Fig. 1a). The more restricted movements commonly observed at night are also, on occasion, observed during daylight hours, when the animals are associated with floating objects, including fish aggregating devices (FADs, Schaefer & Fuller, 2005). Occasional very deep dives (>1000 m) have also been observed, usually during the day, and are thought to represent forays into deep water searching for squid (Schaefer & Fuller, 2010). Typically the movement patterns are complex and variable, with a single individual often exhibiting different patterns on different days with no clear sequence or trend; i.e. the animals are responding in an ad hoc fashion to varying environmental conditions related to oceanography, prey distributions and the movements of conspecifics. As an illustration of this complexity, five sections of daily activity from a single individual are shown in Fig. 1. Figure 1a shows the most common form of movement pattern, described as ‘characteristic’ by Schaefer and Fuller (2010), whereby the tuna descends to between 200 and 300 m at dawn (ca. 0600 hours) and is resident at that depth until dusk (ca. 1800 hours) except for several (probably thermoregulatory) ascents to near-surface waters (50 m). In Fig. 1b, where the individual bigeye remained near the surface, the changing light levels are very clear. It is interesting to compare this plot with Fig. 1a, where, as soon as it is light, the animal descends to the foraging depth, ascending again as soon as the light level falls and, consequently, there is little change in the subjective light level, indicating this individual may be following an isolume. These patterns of vertical space use have been well described and discussed previously (Schaefer & Fuller, 2010) and are reported again here principally to highlight the pattern of characteristic behaviour and the overall complexity of movements exhibited by *T. obesus*.

Thunnus obesus, when exhibiting characteristic behaviour, therefore show a directed scale-dependent transition between occupying near-surface waters at night and deeper waters during the day. This scale-dependent diel rhythm should produce a clear 1 cycle/day signal in a spectral analysis of the dive time series movement, and indeed this is the dominant frequency observed in the fast Fourier transform spectrogram shown in Fig. 2, where the 1 cycle/day signal clearly has the largest amplitude. However, it is also clear that much higher frequencies make a contribution to the spectrum, indicating, as one would expect, a wide range of faster, smaller movements at many different scales, essentially ‘nested’ within the pattern of diel vertical migration. It is hypothesized, therefore, that these fine-scale movements (illustrated in Fig. 3) represent scale-free, optimized searching and foraging activities, best described as Lévy walks (Viswanathan et al., 1999, 2011).

The fine-scale vertical movement patterns of *T. obesus* have been analysed previously in the context of the LF hypothesis (Humphries et al., 2010; Sims et al., 2008). In these studies *T. obesus* were found, in some cases, to exhibit a large-scale (spatial) behavioural switch whereby in prey-rich waters (identified through the proxy of remotely sensed chlorophyll ‘a’) an exponential pattern was predominant in the distribution of vertical displacements (step lengths), while in prey-sparse waters a truncated power law (truncated Pareto) distribution of vertical step lengths was prevalent, in broad agreement with the LF hypothesis. However, the behaviours responsible for the fine-scale movement patterns in the