Scale-dependent to scale-free: Daily behavioural switching and optimised searching in a marine predator

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ABSTRACT

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 an 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 optimised 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 efficient 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.

KEY-WORDS

Lévy flights, search pattern, optimal foraging, rhythmic behaviour, anomalous diffusion, telemetry.

1. INTRODUCTION

Rhythmic patterns of activity occur in many taxa, frequently as an adaptive response to cyclical changes in environmental conditions (Yerushalmi and 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 and 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 the 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 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, e.g. blue sharks, *Prionace glauca* (Queiroz et al. 2010), ocean sunfish, *Mola mola* (Sims et al. 2009) and basking sharks, *Ceteorhinus 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 et al. 2004), with reverse DVM also being observed in basking (Sims et al. 2005) and blue sharks (Queiroz et al. 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, *Xiphius gladius*

(Evans et al. 2014), blue marlin, *Makaira nigricans* (Goodyear et al. 2008), bluefin, *Thunnus thynnus* (Walli et al. 2009) and bigeye tuna *T. obesus* (Schaefer and 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 datasets of movements recorded with animal-attached electronic tags (Heithaus et al. 2006, Sims et al. 2006, Jonsen et al. 2007, Sims et al. 2008, Humphries et al. 2010, Humphries et al. 2012, Sims et al. 2012, Papastamatiou et al. 2013). 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 et al. 2011). Lévy walks are specialised 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, hence is termed super-diffusive. Theory and comprehensive searching model simulations (Viswanathan et al. 1999, Viswanathan et al. 2011, Humphries and Sims 2014) show that Lévy walks optimise 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 optimisation of search strategies and predicts that searching is optimised when the move step-lengths of a random walk follows the inverse power-law distribution with exponent $\mu = 2$ (Viswanathan et al. 1999, Humphries and Sims 2014). 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 et al. 2000, Schaefer and Fuller 2002, Musyl et al. 2003, Schaefer and Fuller 2010, Matsumoto et al. 2013), with a clear crepuscular vertical migration between deep (>250 m) waters during the day and sub-surface (~50 m) waters during the night being the predominant pattern of vertical space use (Figure 1a). The more restricted movements commonly observed during the night are also, on occasion, observed during day-light hours, when the animals are associated with floating objects, including fish aggregating devices (FADs, Schaefer and 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 and 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 Figure 1. In this figure the first plot (Figure 1a) shows the most common form of movement pattern, described as 'characteristic' by Schaefer and Fuller (2010), whereby the tuna descends to between 200-300 m at dawn (~06:00) and is resident at that depth until dusk (~18:00) except for several (probably thermoregulatory) ascents to near surface waters (50 m). In Figure 1b, where the individual bigeye remained near the surface, the changing light levels are very clear. It is interesting to compare this plot with Figure 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 and 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*.

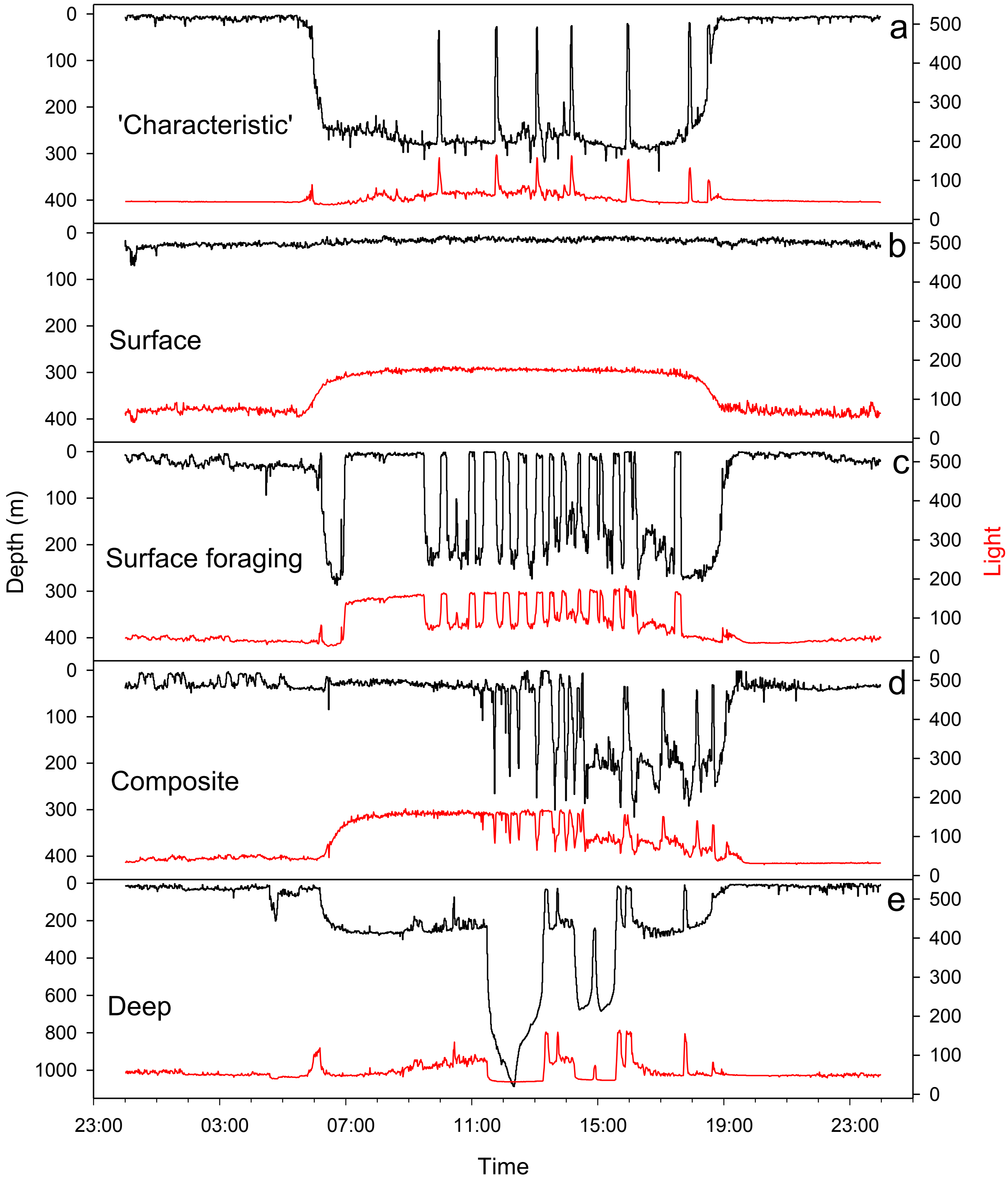

Figure 1: An illustration of the complex movements exhibited by a single individual

Each plot shows depth and light readings for example 24 hour sections from the dive time series of a single individual (BET 27 – see Supplementary Table 1), illustrating the complex range of behaviours one animal can exhibit. a) Shows a typical day's activity with the animal descending at dawn to forage at the DSL and ascending at dusk, described as 'Characteristic' by Schaefer and Fuller (2010). Six thermoregulatory ascents are performed during the foraging period in this example; in b) there is no discernible difference between daytime and night-time activity; this behaviour is commonly observed when the tuna are associated with a fish aggregating device (FAD); in c) the tuna is essentially resident in surface waters but is diving repeatedly to the deep scattering layer (~250 m) to forage; d) illustrates a complex mixture of behaviours and e) shows the occasional deep dives performed by these animals (note the different depth scale).

T. obesus, when exhibiting characteristic behaviour, therefore show a directed scale dependent transition between occupying near surface waters during the night and deeper waters during the day. This scale dependent diel rhythm should produce a clear 1 cycle day^{-1} 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 Figure 2, where the 1 cycle day^{-1} 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 hypothesised, therefore, that these fine scale movements (illustrated in Figure 3) represent scale-free, optimised searching and foraging activities, best described as Lévy walks (Viswanathan et al. 1999, Viswanathan et al. 2011).

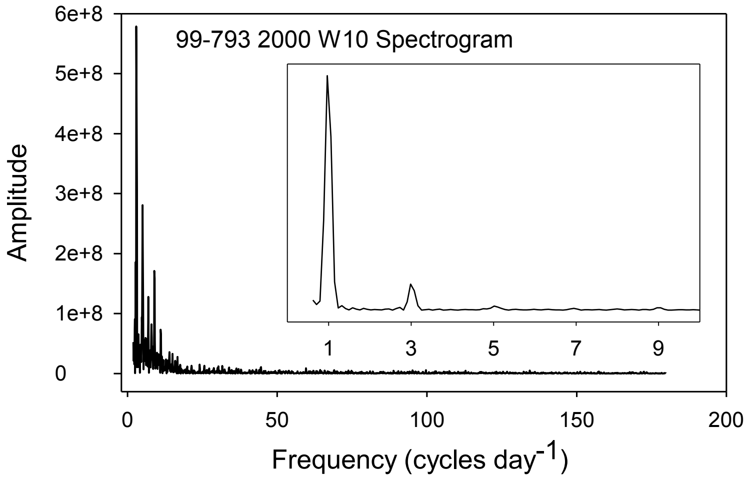

Figure 2: Fast Fourier Transform analysis of depth time series

In a FFT spectrogram of an example track section, while the dominant signal has a frequency of 1 cycle day^{-1}, resulting from the diel vertical migration of the animal (see inset), it is also clear that there is a contribution from much higher frequencies, up to the cut-off at a frequency of 180 cycles day^{-1}, corresponding to the sampling frequency of 4 minutes.

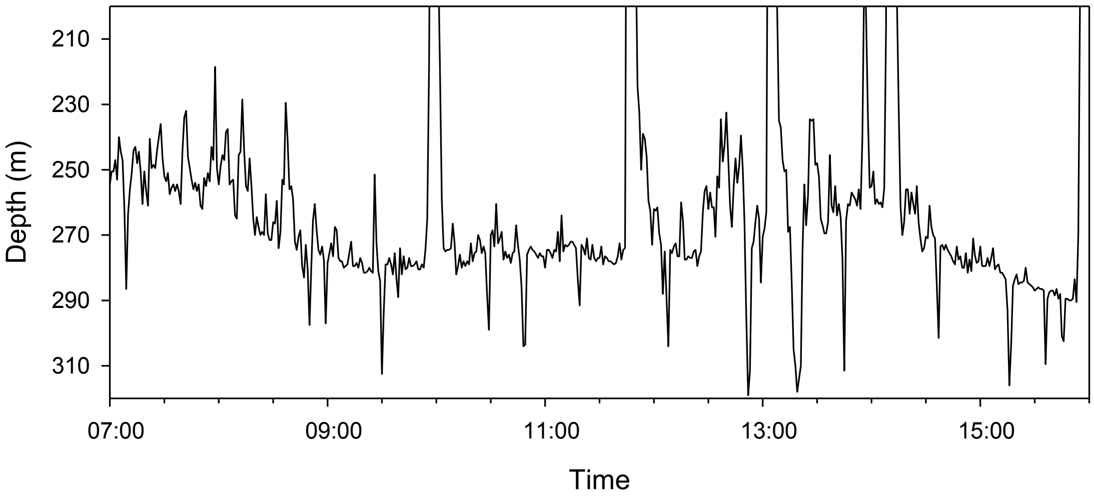

Figure 3: Daytime foraging detail

The plot shows daytime details from the plot in Figure 1e. Although the animal spends most of the time in the relatively narrow depth range of ~240 to ~290m there is considerable activity, suggestive of searching and active foraging within this layer.

The fine scale vertical movement patterns of *T. obesus* have been analysed previously in the context of the Lévy Foraging (LF) hypothesis (Sims et al. 2008, Humphries et al. 2010). 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 Chl ‘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 light and dark phases of the daily cycle of DVM have not been tested quantitatively in this species.

Previous studies testing the LF hypothesis (e.g. Humphries et al. 2010, Humphries et al. 2012, Sims et al. 2012) have been generally hampered by limited observational data on the actual activities the animals are engaged in, or in the actual distribution of prey experienced by the animals. Direct observation of environmental conditions along each animal’s track are not currently possible and remote sensing of proxies, such as Chl ‘A’, are at too low a spatial resolution to be useful for very fine scale studies such as the one presented here. Therefore, while there has been strong empirical evidence for the presence of either Lévy or exponentially distributed movements, it has been difficult to correlate these reliably with environmental conditions, especially prey distributions, or with known actual behaviour (for an exception see Sims et al. 2012). With the activity patterns of the T. obesus, however, there is strong evidence to support a shift in prey field density between sparse during the day and more aggregated during the night (Ménard and Marchal 2003). Mesopelagic fish, cephalopods, and crustaceans are the major components in the diet in the equatorial central Pacific Ocean (CPO) and east Pacific Ocean (EPO) (King and Ikehara 1956, Blunt 1960) and are the primary components of the vertically migrating deep-scattering layer, observed throughout the equatorial Pacific (Longhurst 1976, Tont 1976). Further, studies into the vertical distribution of a typical mesopelagic animal, oceanic lightfish (*Vinciguerria nimbaria*), suggests that these important prey form loose schools during the day but larger aggregations at night, likely making daytime foraging less productive and more dependent on searching (Ménard and Marchal 2003). Night time feeding on gonostomatids, myctophids, and cephalopods has been observed, from stomach contents analysis, for *T. obesus* associated with FADs (Schaefer and Fuller 2005). However there is little evidence for night time feeding for tuna exhibiting 'characteristic' behaviour, principally because studies on feeding patterns (e.g. Boggs 1992) have been based on day-time long-line captures.

The extensive datasets of high resolution vertical movement data available to this study (18,003 days in total, mean 193, range 37 to 2761 days) therefore afford an opportunity to perform a fine-scale test of the LF hypothesis. Based on the application of the LF hypothesis to existing interpretations of *T. obesus* behaviour we hypothesise that daytime movement patterns will be approximated by inverse power-law distributions of move step-lengths consistent with optimised searching (foraging) activity for patchy prey at depth. In contrast, during night-time when prey is more aggregated and the tuna are not searching, we hypothesise that simple exponentially distributed move step-lengths, representing Brownian movement, will be prevalent. Therefore, it is predicted that finer, scale-free, foraging and search movements are nested within the obvious scale-dependent diel vertical migrations. In this context, scale-free does not imply un-bounded, clearly all vertical movements performed by the tuna are bounded by environmental and physiological constraints. Rather, it is suggested that the finer-scale movements have a fractal self-similar structure, with the same pattern repeated at all scales, up to the natural limit of the step-lengths.

To summarise, the Lévy foraging hypothesis is concerned specifically with two distributions, the power (or truncated power) law and the exponential. These two distributions represent quite different behaviours. Power laws (and truncated power-laws) produce movements characterised by many small steps connected by rarer long relocations with this pattern being repeated at all scales, resulting in super-diffusive fractal patterns. Exponential distributions give rise to simple Brownian motion with scale dependant patterns and classical diffusivity. Importantly, not only have power-law distributed move-steps been identified in many empirical studies (e.g. Humphries et al. 2010) covering a wide range of taxa, but they have been conclusively shown to optimise searches performed during foraging (Viswanathan et al. 1999, Viswanathan et al. 2000, Viswanathan et al. 2001, Bartumeus et al. 2002, Raposo et al. 2003, Viswanathan et al. 2011, Humphries and Sims 2014, Wosniack et al. 2015). They are therefore with reason considered to be a signature of foraging for sparse resources, a hypothesis that is explored further in this paper. Therefore, for specific testing of the LF hypothesis, this study specifically compares these two models because they give rise to the two predictions, that Levy walks optimise searching where prey is sparse, while Brownian walks are sufficient where prey is abundant (Viswanathan et al. 2011).

In regards to the other models that might describe the behaviour, correlated random walks would not be appropriate as we are dealing here with long time series and it has been shown that over long time scales correlated random walks converge on an exponential distribution (Brownian motion at the long-term limit; see Viswanathan et al. 2011). The issue of composite random walks (i.e. composite, multi-scale or hyper-exponentials) has been discussed previously (de Jager et al. 2012, Jansen et al. 2012, Reynolds 2013, Reynolds 2014, Sims et al. 2014) with the conclusion that these distributions simply represent an alternative underlying mechanism for the generation of movement patterns that tend to converge on Lévy distributions. The approximate equivalence, in terms of foraging efficiency, of these composite distributions, when modelled on truncated power-law distributions, has also been demonstrated (Humphries and Sims 2014).

Therefore, as the hypothesis being tested in this study is specifically whether switching between Lévy and exponential movement patterns can be observed in the fine-scale movements of bigeye tuna, it is appropriate that the distributions being tested are a truncated power-law and an exponential. To remove possible bias caused by comparing a truncated power law to an exponential with no upper truncation we have, in this study, opted to use a truncated exponential distribution.

2. MATERIALS AND METHODS

2.1 TAGGING PROCEDURES

Tagging was conducted on the chartered FV Her Grace, a 17.7-m live-bait pole-and-line fishing vessel. Bigeye associated with Tropical Atmosphere–Ocean (TAO) moorings, the tagging vessel, and drifting fish-aggregating devices (FADs), were captured, tagged, and released between 2°N and 2°S, and 95° and 97°W, during March to May of 2000 and 2002 through 2005. In total 323 tuna were tagged and released. Archival data storage tags (Wildlife Computer MK7 or MK9 or Lotek Wireless LTD_2310) were surgically implanted in the peritoneal cavity with the fish being returned within about 2 minutes without any apparent adverse effects. Implantation is essential for these tags to remain attached to the tunas for prolonged periods. Fish were also tagged with two serially numbered 12.5-cm green plastic dart tags (Hallprint, Pty., Holden Hill, Australia) by using tubular stainless steel applicators. Details of the fish tagged are given in supplementary information table S1. Full details regarding the materials and methods utilised in the capture, tagging, and release of the fish are given by Schaefer and Fuller (2002, 2009, 2010). Briefly, the tagging in 2000, from which the current paper draws data, proceeded as follows. Bigeye tuna specimens were captured by using handline gear during the day and night. Each fish was brailed with a heavy-gauge aluminum rigid-framed net of knotless webbing and landed on a wet foam pad covered with smooth vinyl. The eyes of the fish were immediately covered with a wet synthetic chamois, the hook was removed, and the condition of the fish was determined. If the fish was in excellent condition (i.e. no damage to the eyes or gills and no significant bleeding), the surgery required for implanting the archival tag was initiated. An incision about 2 cm long was made in the abdominal wall about 10 cm anterior of the anus and about 2 cm to the left of the centre line of the fish. Special care was taken to cut through the dermis only and partially through the muscle, but not into the peritoneal cavity. A gloved finger was inserted into the incision and forced through the muscle into the peritoneal cavity. The tag, sterilized by soaking it in Betadine solution, was inserted, pointed end first, through the incision into the peritoneal cavity. The tag was then manipulated to the caudal end of the incision, and two sutures were placed rostral of where the stalk protruded to close the incision by using a sterile needle and suture material (Ethicon (PDS II) size 0, cutting cp-1, 70 cm). Given the brevity of the procedure and the difficulties in anesthetising the animals at sea, no anaesthetic was used. The 96 bigeye tuna captured during the period of 15–22 April 2000 and released with archival tags were measured to the nearest centimetre with a calliper then picked up by hand and released back into the sea by one or more individuals standing in a rack at the stern of the vessel. The total time most of the fish were out of the water was recorded to the nearest second (mean=2 min 17 sec, 95% CI=0:06, range=1:27–4:19, n=86). All fish released with archival tags were observed to swim rapidly down and away from the vessel after release, and all appeared to be in excellent condition. Of the 323 tuna tagged, 163 tags were returned of which 98 were at liberty for more than 30 days. Of these, 93 tag datasets were available for this study. Given the animals were tagged and released in the Equatorial Pacific and were recaptured principally by commercial purse seiners working the area, it is not possible to use the release-recapture statistics to estimate tagging mortality.

2.2 ETHICS NOTE

There were no permits or licences required for this investigation. The tagging was done outside the 200 nm EEZ of Ecuador. The IATTC is an international fisheries management organization and is not required to comply with any laws of the US government pertaining to ethical treatment of animals used for research.

2.3 TAG DATA ANALYSIS

The data from individual *T. obesus* tagged in the equatorial Pacific comprised 93 time-series of depth, light and temperature measurements, recorded either at intervals of 4 minutes with a vertical resolution of 0.5 m (28 tracks) or at 1 minute and 1 m (65 tracks); see Supplementary information, Table S1.

Many of the time-series were very long, comprising on average 193 days of data, and would therefore encompass a broad range of behaviours in terms of vertical habitat use and the distributions of step-lengths, as illustrated in Figure 1. To reduce the behavioural variability introduced by these long datasets, and the naturally complex behaviour of the tunas, all datasets were divided into weekly sections. Data prior to the first midnight were discarded, as were any sections that did not represent complete weeks, such as the final section and any section containing gaps. These weekly sections, being shorter, were predicted to exhibit greater behavioural consistency, thus improving the reliability of the analysis. Previous studies have used analytical methods, such as a split moving window analysis, to determine objectively behavioural discontinuities in the depth time series and then divided the time series into sections at these points (e.g. Humphries et al. 2010). However, in this study, because the comparison was within section (i.e. night *vs* day), rather than between sections, this simpler method, which produces sections of identical length, was considered more appropriate. Division of the 93 datasets resulted in a total of 2222 weekly sections. From each weekly section the night-time and daytime ‘sub-sections’ were then selected using the hours of 07:00 to 16:00 to define daytime and 19:00 to 04:00 for the night. These times were chosen to avoid the hours during which the vertical migrations typically occur to avoid bias from inclusion of very long transiting steps in the move step-length analysis. To confirm differences in vertical habitat use between night and day each section was analysed to produce a time-depth profile (TDP) and a time-activity profile (TAP). For the TDP analysis the depths from each sub-section were binned by hour of the day and a mean depth was calculated for each; an overall mean depth was also calculated for the daytime and night-time hours. For the TAP the speed of each step was calculated and analysed in the same way to give a mean speed for each hour.

Vertical displacements were calculated from the difference between consecutive depth measurements after correcting sampling artefacts by coalescing steps that formed part of a continuous movement, as described in Humphries *et al.* (2010). The vertical step-lengths for each sub-section were then analysed using Maximum Likelihood Estimation (MLE) to determine whether the data were best fit by a truncated Pareto distribution (TP, truncated power-law) characteristic of a truncated Lévy walk, or, a truncated exponential (TE) distribution describing Brownian movement, or neither, i.e. a ‘mixed’ model. Following this analysis therefore each sub-section was then classified as TP, TE or mixed model.

Full details of the MLE analysis and model selection methods are given in Supplementary Information, section 1. To summarise, however, MLE is used to attempt to fit in turn a truncated Pareto (TP) and a truncated exponential (TE) distribution to the dataset and derive an estimate of the exponent and best fit values for x_{min} and x_{max}. The PDFs for the two distributions are as follows:

$$TPpdf = (\lambda + 1)(x_{max}^{\lambda+1} - x_{min}^{\lambda+1})^{-1}x^{\lambda}$$ (White et al. 2008)

$$TEpdf = \frac{\lambda e^{-\lambda x}}{e^{-x_{min}\lambda} - e^{-x_{max}\lambda}}$$ (Lominashvili and Patsatsia 2013),

where $0 < x_{min} < x_{max}$.

In each case a sub-set of the dataset, covering the range of step-lengths defined by the fitted x_{min} and x_{max} parameters is then tested by the alternate distribution (i.e. TE for TP and *vice* *versa*). This fitting exercise produces two sets of Akaike weights, and two sets of Goodness of Fit Values which are then used in the model selection process; one set derived from the fitting of the TP, the other from the fitting of the TE. This method ensures that Akaike weights are only used to compare equivalent datasets. The final outcome is the categorisation of each weekly dataset as TP, TE or, where neither distribution is an unequivocal fit, mixed. The model selection processed used is conservative, only classifying datasets as TP or TE where the Akaike weights (or GOF values) provide not only support in favour of the distribution, but against the alternative.

The tuna in this study occasionally performed dives to depths of over 1000 m (maximum recorded depth was 1902 m). These dives produce rare, long step-lengths and therefore it is possible that their inclusion could skew the MLE results in favour of a Lévy distribution where the ‘tail’ of the distribution comprises very long, rare steps. Because these relatively rare dives were not considered to form part of the normal repertoire of behaviour being investigated here, step-lengths > 500 m were omitted from the MLE analysis.

3. RESULTS

The time-depth and time-activity profiles are in agreement with the differences previously observed in the behaviour of *T. obesus* between daytime and night-time and confirm that the day and night sections analysed here represent different foraging activities. During the day the mean depth was significantly greater being 155.2 m (S.D. 73.7; $n = 2222$), while at night it was 21.4 m (S.D. 27.2; $n = 2222$; Mann-Whitney Rank Sum Test, $p < 0.001$).

The mean daytime depth is, however, somewhat misleading as the depth occupancy analysis shown in Figure 4 illustrates. Here a clear bimodal pattern can be seen in daytime vertical space use with ~36% of time spent in the upper 50 m and 40% spent between 200-300 m. Time spent above 50 m is likely the result of surface-oriented associative behaviour occurring in some of the day time sections. Activity, measured as the mean speed per hour, also showed a clear diel pattern with daytime activity of 0.195 ms^{-1} (S.D. 0.09; n = 2222) being 3 times greater than night time activity of 0.0633 ms^{-1} (S.D. 0.05; n = 2222, Figure 5). While this study only has detailed information about vertical displacements, and cannot therefore determine horizontal speeds and activity, these animals are moving in a 3 dimensional environment and it is likely that changes in levels of vertical activity are likely similar to the overall level of 3D activity (Weng et al. 2013).

Figure 6 shows the day and night-time light and temperature levels from the time-series shown in Figure 1a, and clear dichotomies were evident in both light and temperature. Of the 352 daytime light levels recorded for this tuna, 255 (72%) are greater than the maximum night-time level, as indicated by the dashed red line in Figure 6a. Therefore, even though the tuna was occupying deeper, darker water during the day, greater illumination was available to the tuna while foraging at depth than was experienced during the night. Apart from a few daytime temperatures that result from the thermoregulatory ascents, all the foraging temperatures are below 15 °C, confirming that this tuna was foraging in colder water below the thermocline and probably in association with the deep scattering layer.

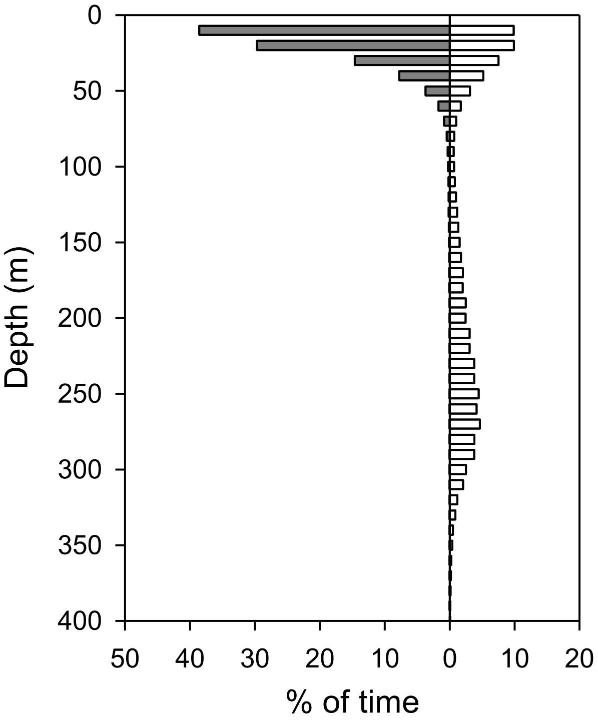

Figure 4: Diel depth occupancy

Dark grey bars (left) show night-time occupancy; white bars (right) show daytime occupancy. In this plot intermediate steps (i.e. those representing movement between depths) have been ignored. There is a clear dichotomy between daytime and night-time space use, and a bimodal pattern of daytime space use.

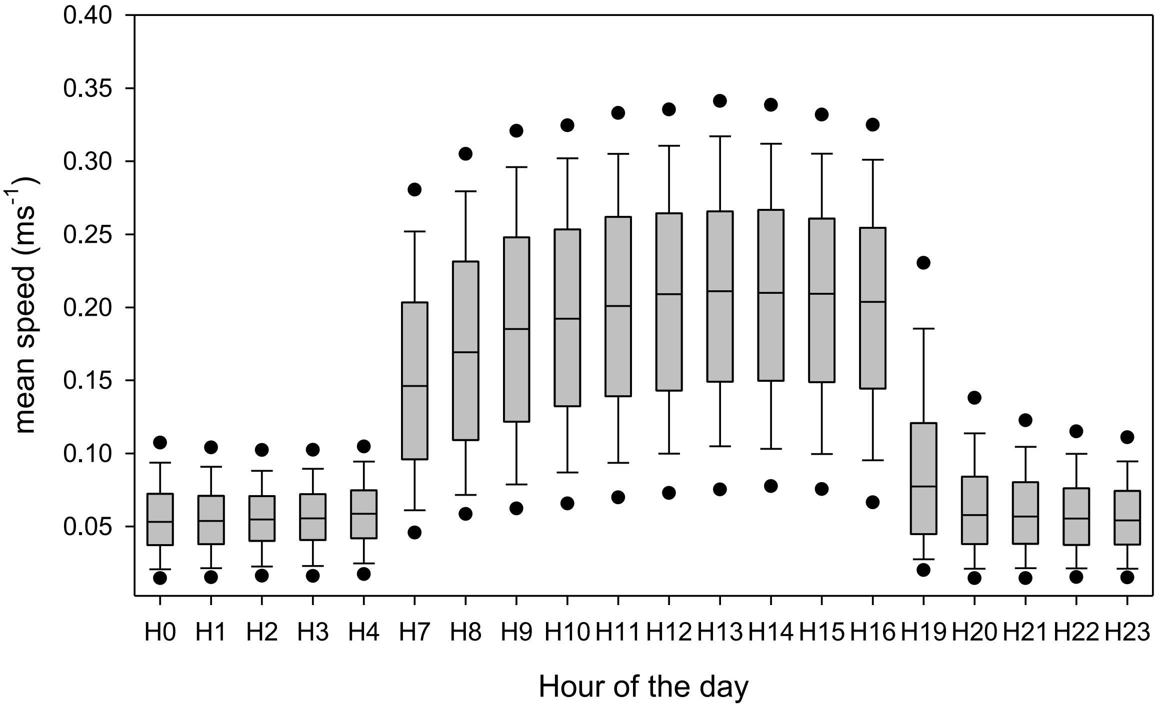

Figure 5: Diel activity profile

The box plot shows the mean activity of the 93 tunas as the mean vertical speed in each hour, for the hours 07:00 to 16:00 for daytime and 19:00 to 04:00 for night-time. Whiskers show standard deviation, dots show 5/95% outliers. The animals show significantly more vertical activity during the day, with quite abrupt changes in behaviour at dawn and dusk

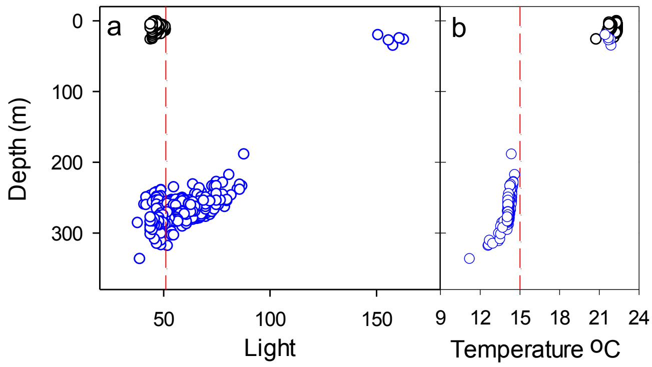

Figure 6: Daytime and night-time light and temperature from Figure 1a

a) Black circles show night-time light levels; blue circles show daytime levels. 72% of the daytime light levels are higher than the highest night-time level, indicated by the dashed red line. Differences are significant at $p < 0.001$ (Mann-Whitney Rank Sum Test); b) Black circles show night-time temperatures; blue circles show daytime temperatures. Apart from a few points, representing thermo-regulatory ascents, all the daytime temperatures are below 15 °C, indicating foraging below the thermocline. Again, differences are significant at $p < 0.001$ (Mann-Whitney Rank Sum Test).

The MLE analysis showed a clear difference between the daytime and night-time sections, with 1729 (78%) daytime sections being classified as best approximated by a truncated Pareto (TP) distribution and only 338 (15%) as a truncated exponential; 155 (7%) were identified as mixed model (Table 1, Figure 7). For the night-time sections the TP distribution of move steps was no longer the dominant pattern, with 663 (30%) sections being classified as TP and 1112 (50%) as truncated exponential; 447 (20%) were mixed model. For the sections best fit by a TP distribution there was also a significant difference in exponent (μ) between the daytime and night-time sections, with daytime sections having a mean exponent of 1.64 (S.D 0.32) and night-time sections a mean exponent of 2.53 (S.D 0.37; Mann-Whitney Rank Sum Test, $p < 0.001$). Higher exponent values result in fewer long move steps and have patterns similar to Brownian (exponential) movements. This finding therefore adds further support to the clear differences in the fine-scale behaviour patterns we have quantified for bigeye tuna between day and night. The shift to more Brownian-like movement patterns during the night is further supported by the mixed model results, of which 418 of the 447 (93%) were best fitted by a truncated Pareto distribution, but with an exponent (μ) > 3.0, which is beyond the Lévy range and consistent with Brownian-like movements.

In addition, we found within-section behavioural switching in 856 of the 2222 sections (38%) where the daytime sub-sample was best fit by a TP and the night-time sub-sample, of the same weekly section, was best fit by an exponential distribution. To further illustrate the behavioural switching, rank step-length plots from the MLE analysis for several example datasets which exhibited switching are shown in Figure 8.

To determine whether the daytime thermoregulatory ascents were having an effect on the results the MLE analysis was repeated with step-lengths > 120m ignored. The results are given in Figure 7 and Table 2, and while the difference between the number of TP and exponential fits is slightly reduced it is clear that TP is still the predominant daytime movement pattern. Using a step-length cut-off in this way will also remove step-lengths that are part of the searching movements we wish to investigate, and so is a rather simplistic approach which will inevitably reduce the number of TP fits. However, as this simple approach would tend to bias the results in favour of the simpler exponential distribution, rather than towards the hypothesised Lévy distribution, a more complex approach for the removal of these movements is not warranted.

Table 1: Summary MLE results

Number of datasets best fit by either truncated Pareto (TP), truncated exponential (TE) or mixed model (unclassified – U).

	Day	*%*	*Night*	*%*
TP	1729 (μ=1.64)	77.81	663 (μ=2.45)	29.84
TE	338	15.21	1112	50.04
U	155	6.98	447	20.12

Table 2: Summary MLE results for daytime sections with steps > 120m removed

Vertical displacements > 120m were removed to reduce the effect that the thermoregulatory ascents might have on the MLE analysis; in particular any bias that might be introduced in the classification of a section as TP.

	Day	*%*
TP	1238	55.72
TE	782	35.19
U	202	9.9.09

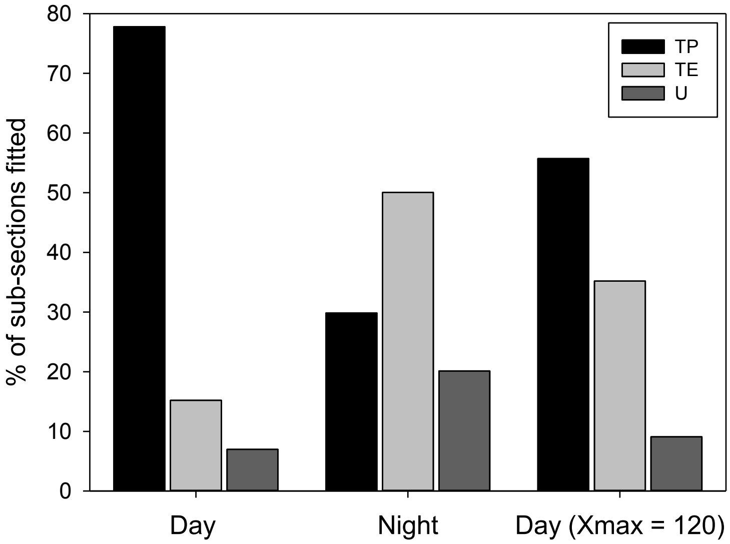

Figure 7: Day and night best fit distributions

There is a clear difference between the day and night-time sub-sections, with truncated Pareto (TP) being the dominant behaviour during the day and truncated exponential (TE) being dominant during the night. Mixed model (or unclassified) fits (U) are more common during the night. TP was still the dominant daytime behaviour when the maximum step-length (x_{max}) was limited to < 120 m in order to exclude the daytime thermoregulatory ascents.

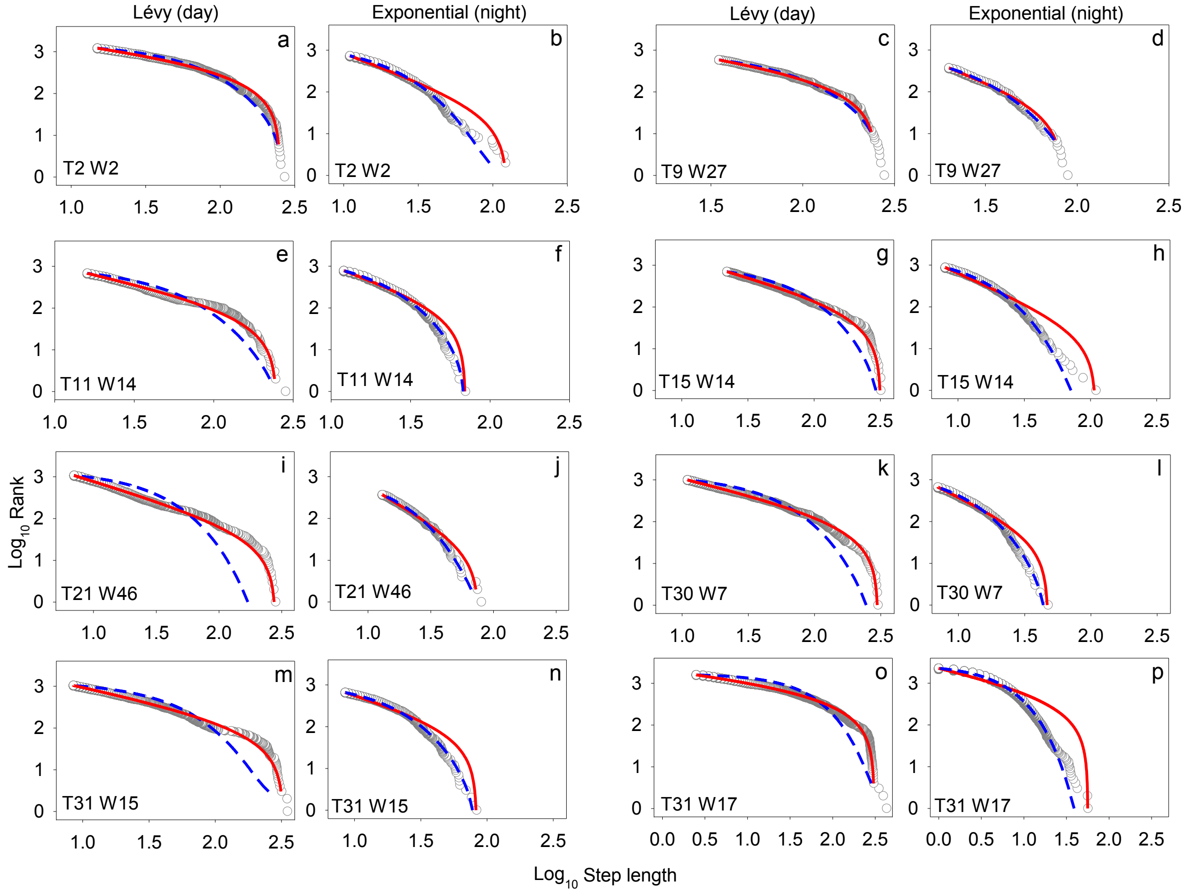

Figure 8: MLE example plots showing behavioural switching

Rank step-length plots showing TP fits to daytime sub-sections and E fits to night time sub-sections for 8 weekly sections, with TP fits shown in red and TE fits shown in dashed blue; grey circles are observations; a) T2W2 (i.e. tuna 2, week 2) day-time; b) T2W2 night-time; c.d) T9W27; e.f) T11W14; g.h) T15W14; i.j)T21W46; k.l) T30W7; m.n) T31W15; o.p) T31W17.

4. DISCUSSION

Bigeye tuna are epipelagic to mesopelagic predators targeted by purse-seine and long-line fishing fleets with catches only exceeded by skipjack (*Katsuwonus pelamis*) and yellowfin tunas (*Thunnus albacores*) (Fonteneau 1998, Miyabe and Bayliff 1998, Stobberup et al. 1998). Their commercial value, however, exceeds all other tuna species, consequently, a considerable research effort has been focused on understanding their biology and behaviour (Stobberup et al. 1998). Many of these studies have employed electronic tags, either archival data storage tags, recording depth, temperatures and light level (e.g. Musyl et al. 2003, Schaefer et al. 2009, Matsumoto et al. 2013) or pop-up satellite archival tags which transmit position estimates and summarized environmental data (Lam et al. 2014).

While the general pattern of diel vertical migration has long been known for *T. obesus* (Saito 1975, Holland et al. 1992), the fine-scale movements performed within these scale-dependent rhythms have received less attention. Recent advances in the study of optimal searching and foraging behaviour have made available analysis techniques to investigate these behaviours, and can now provide some insight into a previously unobservable aspect of the animal's activities (Clauset et al. 2009, Humphries et al. 2010, Humphries et al. 2012). Analytical and simulation studies have confirmed that an inverse power-law distribution of step-lengths with an exponent in the Lévy range ($1 < \mu \leq 3$) optimises random searches, especially when prey patches are sparsely and randomly distributed and where the next prey patch is most likely beyond sensory range (Viswanathan et al. 2011, Humphries and Sims 2014). *T. obesus* foraging at depth are doing so under reduced light conditions in a complex and dynamic environment which reduces the benefits of environmental cues or memory that are useful to terrestrial animals in more predictable environments. While association with the deep scattering layer (Josse et al. 1998, Matsumoto et al. 2013) will help the animals locate an appropriate depth at which to search, prey will still have a patchy and more dispersed distribution (Ménard and Marchal 2003), and therefore an optimised random search in the form of a Lévy movement pattern is very likely to confer an advantage. The Lévy foraging (LF) hypothesis therefore predicts power-law distributed move step-lengths during daytime hours. The present study has tested this prediction and our results confirm its applicability to *T. obesus*; daytime fine-scale movement patterns were well approximated by optimal Lévy search patterns with a median exponent (μ) of 1.63 ($n = 1729$).

Exponential movement patterns in daytime sub-sections were rare (n=338, 15%) but it is interesting to note that of those, 47 (14%) were in the first weekly section of the time-series.

The tuna used in this study were captured when in association with fish aggregating devices (FADs) used by fisheries, or the research vessel, and many maintained the association for some time post-release, as previously noted (Holland et al. 1990, Schaefer and Fuller 2005, 2010). During this association the fish were observed to spend time within the mixed layer above the thermocline during both the day and night, with restricted vertical movements that closely match the characteristic night-time behaviour. Therefore, in the present study the rare exponential patterns observed during daytime were probably movements associated with aggregation at a FAD and/or the research vessel.

Foraging activity appears to be strongly limited by light levels with the tuna in this study only diving to the foraging depths when light at depth exceeds the night-time surface light levels. Only during the occasional very deep dives (>1000 m) did light levels fall below night-time surface levels. During the night *T. obesus* occupied the surface layers and exhibited a much reduced use of the water column with dives rarely being made below 100 m (only 211 out of the 2222 weekly sections, 9.4%, had night-time maximum depths > 100 m). At the onset of dusk the tuna quickly return to surface waters. This behaviour also appears similar to penguins where deeper feeding dives at night are curtailed to surface waters by low light levels (Wilson et al. 1993).

The predominance of exponentially distributed move steps during the night when prey is expected to be found in larger aggregations (Ménard and Marchal 2003), indicates movements not associated with optimal searching. This result therefore further supports the predictions of the LF hypothesis that night time activity involves significantly less searching and that Lévy movements are no longer predominant. It has been shown both experimentally and analytically that the truncation of Lévy movements as a result of encounters with sufficiently abundant targets results in exponential movement patterns (de Jager et al. 2014). Consequently, night time activity may comprise feeding on abundant prey, or on activities other than feeding where searching is not involved. Where night-time Lévy movements were detected the median exponent was 2.45 (n = 663), significantly higher than the daytime value of 1.64 (n = 1729; Mann-Whitney Rank Sum Test, $p < 0.001$). This increase in the exponent is also predicted by de Jager *et al.* (2014) in response to target encounters. In addition, it was observed that 93% of sections classed as mixed model were in fact best fitted by a TP distribution, but with an exponent > 3.0 (i.e. beyond the Lévy range), indicating movement patterns closer to Brownian, to which Lévy patterns tend to converge when the exponent approaches 3.0.

In summary we have confirmed that *T. obesus* behave as vertical central place foragers, with 'site fidelity' to the warm surface layers during night-time where the animals exhibit greatly reduced searching activity, with bouts of foraging in the deep, cold waters of the deep scattering layer during daytime when searching is often the predominant movement pattern. These activities result in a large scale-dependent pattern of movement with a dominant spectral signal of 1 cycle day^{-1}, and, nested within this was daytime foraging, a scale-free movement pattern best fitted by a Lévy distribution suggesting optimal searching for sparse prey. During the night, when light levels are too low for foraging at depth, a further set of nested activities result in movement patterns best fit by exponential, scale-dependent distributions. Therefore, our detailed analysis of a very large dataset of animal movements shows fine-scale temporal shifts between scale-free and scale-dependent movement patterns consistent with predator responses to changing prey distributions and abundances, as predicted by the Lévy foraging hypothesis.

The LF hypothesis has drawn criticism, and generated controversy, partly from the contention that Lévy movements are expected to be the dominant movement pattern at all times i.e. either the animal always moves in a Lévy pattern, or never does, and therefore that the LF hypothesis represents an incomplete model of animal movement (Benhamou 2007, Plank and

James 2008, James et al. 2011, Regular et al. 2013). This contention has led to alternative models being suggested that might encompass all the observed behaviours (e.g. Benichou et al. 2006, Gautestad 2012). However, it is clear from the movement patterns of *T. obesus* analysed here that searching, of which Lévy movements are a signature, is simply one part of a complex behavioural repertoire, as previously suggested (Humphries et al. 2010, Sims et al. 2012). All higher animals are well known to exhibit complex behaviours, and even simpler animals have been shown to switch from searching to patch exploitation (e.g. jellyfish; Ugland et al. 2014). Consequently, it is more productive to view Lévy movements as the signature of a bout of searching within a sequence of movements that also encompass many other behavioural patterns.

Overall, our results add further support to the contention that animals frequently engaged in searching activities will exhibit a Lévy movement pattern when prey is sparse but that this pattern will tend towards an exponential pattern either when prey is abundant, and encounters are frequent, or when the animal is engaged in other activities (Humphries et al. 2010, Humphries et al. 2012, de Jager et al. 2014). These findings represent the first observations of fine-scale behavioural switching in Lévy movements and the first under conditions where both the distribution of prey and the activity of the predator are well understood. Consequently, this study provides not only further evidence in support of the Lévy foraging hypothesis, but also suggests its utility for the objective identification of when foraging and searching activity occurs in free-ranging animal movement time-series. The cryptic nature of the marine environment often means that no data other than the recorded movement time-series is available for the elucidation of an animal's behaviour. The methods for the identification of move step-lengths (Humphries et al. 2013) are now reliable and robust, and therefore the statistical analysis of step-length distributions in the context of the Lévy foraging hypothesis (Viswanathan et al. 1999, Sims et al. 2008, Humphries et al. 2010, Viswanathan et al. 2011, Humphries et al. 2012) offers a new approach to the analysis of complex, high resolution 1D and 2D movement data. Given this it seems probable that the Lévy foraging framework will not only provide deeper insights into the behavioural phases of animals in relation to environmental heterogeneities, but will support common comparisons across widely separated taxa, given that the dimensionless parameter μ summarises movement complexity spanning the continuum from deterministic to probabilistic patterns.

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