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Swimming Behaviour and Energetics of Free-ranging Sharks: New Directions in Movement Analysis

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INTRODUCTION

There is now a general agreement that sharks, and pelagic sharks in particular, are facing widespread declines in population level due to fishing activity (Pauly *et al.*, 2003). Recent studies suggest dramatic reductions in relative abundance of up to 80% have occurred in as little as 15 years for some species (Baum *et al.*, 2003; Myers *et al.*, 2006), trends most likely linked to greater target catch and bycatch rates fuelled by increased demand for shark fins and meat for human consumption. Although some fisheries assessments indicate less pronounced declines for large pelagic (Sibert *et al.*, 2006) and coastal sharks (Burgess *et al.*, 2006), undoubtedly they are particularly susceptible to over-harvesting on account of slow growth rates, late age at maturity and relatively low fecundity. Many pelagic sharks are now red-listed by the World

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Conservation Union, with some now at a fraction of their historical biomass (Jackson *et al.*, 2001).

Ideally the sustainable management of shark populations requires detailed knowledge of how individuals within a species distribute themselves in relation to their environment, that is with respect to physical and biological resources. The spatial distribution of a shark species will be influenced by how swimming behaviour (linked to motivational and energy requirements) affects rates of key movements, such as search strategies and encounter rates with prey, the location of mates and timing of courtship, and occupation times in preferred habitats. Therefore, day-to-day changes in swimming movement and behaviour will influence broader scale patterns in distribution and population structure, but also signal a shark's response to environmental fluctuations. An ability firstly to understand and then to predict shark space-use patterns and responses to important variables should help identify the extent and dynamics of population distributions and essential habitats, ultimately providing spatial and temporal foci for management in relation to fishing activity and distribution.

A key problem in determining the appropriateness of management or conservation measures for highly mobile and wide-ranging species such as sharks however, is that their horizontal and vertical swimming movements, behaviour and distribution patterns remain largely unknown for the majority of species. Even the behavioural ecology of shark species' that are encountered relatively frequently (e.g., grey reef sharks) are still only partially described. Thus, without knowing where and what habitats sharks occupy, over what time scales, and what behaviour patterns drive the resulting observable changes, it is extremely difficult to determine a population's spatial dynamics and 'stock' boundaries, or to predict how they will respond to future environmental changes. For example, how sharks (and their prey) will respond to climate change that is predicted to increase sea surface temperatures by about 4°C over the next century is not clear, principally because swimming movements and behaviour leading to thermal habitat selection is insufficiently well documented over the appropriate spatio-temporal scales. Equally, how sharks are distributed in relation to fishing locations and effort is important to determine, not least because if remaining aggregations occur in areas where fishing activity is most intense, this will further exacerbate declines. Understanding these processes, therefore, relies on accurate studies of how swimming movements and behaviour in relation to environment influence population structuring and abundance changes of sharks.

Central to this problem of not knowing where sharks are is that they spend most, if not all, their time below the sea surface where they cannot be observed directly or followed to elucidate movements. Until recently

only very coarse and simplistic data on fish movements and activities were available for identifying putative fish 'stocks' and possible migrations (Harden Jones, 1968; Guenette *et al.*, 2000). What we are learning from the application of new technologies is that fish such as sharks have complicated spatial and temporal behavioural dynamics, characterised by daily and seasonal migrations, regional differences in behaviour, distinct habitat preferences, and age and sexual segregation. The picture is much more behaviourally complex than previously thought (Harden Jones, 1968). Linked to the deficiency in knowing little about shark movements and behaviour in relation to environment is the difficulty in identifying why such behaviours occur when and where they do.

In behavioural ecology much has been learnt from optimality models seeking to reveal the decision-making processes of animals (Krebs and Davies, 1997), that is, why animals behave a certain way when faced with a set of (necessarily) changing conditions. In formulating these models it is usual to define the likely decision being made by the animal (e.g., time spent in a prey patch), then to define particular currencies (e.g., maximise net rate of gain) and constraints (e.g., travel or handling time, environmental factors) for testing hypotheses about how these different constraints influence the costs and benefits of decision-making. The problem with applying this framework to the behavioural study of sharks is that such decisions, currencies, and constraints may be relatively straightforward to formalise theoretically, but in practice they are very difficult to measure accurately (if at all) for long enough time periods over which natural changes in behaviour and energetics can be recorded. Therefore, empirical tests of optimality models for shark behaviour are not in widespread use (Sims, 2003). So how can we begin to understand what behavioural mechanisms underlie shark movements given these logistical difficulties?

The purpose of this chapter is to introduce a new approach for analysing, interpreting and thinking about the movement and behaviour patterns of free-ranging sharks. In so doing, this paper will (i) briefly describe what typical generalised movement patterns of free-ranging sharks have been recorded using electronic tags, and how this new technology has revolutionised shark behavioural ecology. The chapter will (ii) progress to identify how movement types may be closely linked to habitat types and why, and how foraging and behavioural trade-off models have been used recently to test habitat selection processes in sharks. (iii) A new approach of analysing shark movement data will be described that uses methods from statistical physics to evaluate behavioural response in relation to environment. The chapter closes by providing some future perspectives for better understanding the behaviour patterns of wild sharks.

Shark Swimming Behaviour

Recording Movements

Before the advent of acoustic, datalogging and satellite-linked transmitter tags the study of wild shark behaviour was limited to brief descriptions from divers or from observers aboard vessels. It was in the 1960s when electronic devices capable of emitting or transponding sound energy first came to be used to track individual sharks (Carey, 1992). Sound is the only practical means of transmitting a signal through seawater over distances greater than a few metres as radio waves do not propagate sufficiently in such a conducting medium, at least at the frequencies used in biotelemetry (Nelson, 1990; Priede, 1992). Radio transmitters can be used to track fish in shallow fresh water but through-the-water telemetry of marine fish must be made by acoustic transmission (Nelson, 1990). Ultrasonic frequencies are used (40–78 kHz) because since frequency is proportional to transducer diameter, this is an important factor in reducing the size of the transmitter (thus the 'package' to be carried by a fish). Lower frequency transmitters of greater size due to a larger transducer have been used to track large fish (e.g., Carey and Scharold, 1990), whereas higher frequency tags are reserved for the tracking of smaller species (Sims *et al.*, 2001). A wide array of sensors were made available for acoustic tags to transmit data on water temperature, muscle temperature, depth, cranial temperature, speed, tail beat, heart rate, and multiplexed tags were capable of transmitting sensor data for up to three channels (Carey and Scharold, 1990).

In practical terms, sound pulses emitted from a transmitter attached to a fish are received using a directional hydrophone and portable receiver such that a vessel can follow the moves made by the transmitter, and hence the fish, and receive any encoded signals from sensors. The main problem with this technique for tracking large, highly migratory species that traverse 10s of km per day is that tracking individual sharks continuously in the open sea far from land becomes prohibitively expensive, especially since only one at a time can be tracked by a ship. Because of this, even by the 1990s there were relatively few horizontal and vertical tracks of sharks available for analysis, and these were understandably of short duration (hours to a few days) (e.g., Carey *et al.*, 1982; Klimley, 1993).

The widespread availability of miniaturised data-logging computers in the 1980s revolutionised the study of wild fish behaviour. During the early 1990s dataloggers were developed that were small enough not to impede the natural swimming behaviour of the fish but with powerful batteries and memory sizes capable of recording and storing large amounts of high-quality data (termed archival data). They were also relatively cheap so large numbers could be deployed, and for commercially important species at least, tags

could be returned to scientists through the fishery. Early tags were programmed to record pressure (depth) and later models also incorporated temperature and ambient light level sensors (Arnold and Dewar, 2001). Large-scale deployments on North Sea plaice (*Pleuronectes platessa*) (Metcalfe and Arnold, 1997) and on Atlantic bluefin tuna (*Thunnus thynnus*) (Block *et al.,* 2001) were among the first studies to successfully use this technology for tracking movements and behaviour of hundreds of individual fish. Studies followed that fitted depth/temperature/light-logging tags, also known as data storage tags (DSTs), to sharks and other large pelagic fish (e.g., Schaefer and Fuller, 2002) revealing new patterns of behaviour. However, one drawback was that data retrieval was unpredictable since it relied on tags being returned through developed fisheries where return rates can vary widely depending on fishing activity in a given region, and may even be quite low (~5–10%) (Metcalfe and Arnold, 1997).

New tracking methods using satellites were developed to provide a means of collecting data at precise times and independent of fisheries returns. A study in the early 1980s showed that direct satellite tracking of a shark was feasible (Priede, 1984). In a pioneering study in the Clyde Sea off Scotland, a Platform Transmitter Terminal (PTT) moulded into a large buoyant float was attached to a large, 7-m long basking shark (*Cetorhinus maximus*) via a 10-m long tether. Whenever the shark swam near the surface the tag was able to break the surface and transmit to Argos receivers borne on polar-orbiting satellites that estimated the tag's geographical location from these transmissions with reasonable accuracy (Taillade, 1992). The shark was tracked moving in an approximately circular course for 17 days near a biologically productive thermal front (Priede, 1984). Despite this early success, there were no further studies to satellite track sharks for about another 10 years. Tags were large therefore only the largest species such as whale shark, *Rhincodon typus* (Eckert and Stewart, 2001) and basking shark were capable of towing these tags through water. Despite a successful attempt to satellite track smaller-bodied predatory sharks (a blue shark, *Prionace glauca*) using a satellite transmitter mounted on a dorsal fin 'saddle' (Kingman 1996), by the late 1990s the problem still largely remained: how could open ocean fish species' movements and behaviour be tracked at reasonable spatial resolution over longer time periods?

A solution to this problem was developed in the form of a 'hydrid' electronic tag that combined sensor datalogging with satellite transmission (Block *et al.,* 1998; for review see Arnold and Dewar, 2001). This tag, termed a pop-off satellite archival transmitter (PSAT) was attached to a fish 'host' like an external parasite, during which time it recorded 61 hourly or daily water temperature measurements (Arnold and Dewar, 2001). After a pre-programmed time the tag would release from the fish, that is 'pop-off', float to the surface and begin transmitting to Argos receivers that geolocated

the tag's position and received temperature data. Later generations of these tags were increasingly capable of recording and storing larger amounts of data and from more sensors; pressure (depth) and light level sensors were added in subsequent models. The narrow Argos receiver bandwidth however means transmitted message lengths from PSAT tags are necessarily short (360 ms) with relatively small amounts of data capable of being transmitted (32 bytes) per message. The transmission times of these tags after pop-off is limited due to rapid battery exhaustion, usually ranging from 0.5–1 month, so different methods have been employed by the manufacturers to increase rates of data recovery. Hence, for one tag type (see www.wildlifecomputers.com) comprehensive summary data in the form of histogram messages (swimming depth, water temperature, profiles of water temperature with depth, times of sunrise/sunset for use in geolocation, see below) derived from archival sensor records are transmitted remotely via satellites, whereas if a tag is physically recovered the entire archived dataset can be downloaded. For another tag type (see www.microwavetelemetry.com), times of sunrise and sunset together with hourly temperature and pressure readings can be recorded for over a year then transmitted after pop-off. In this tag, a special duty cycle timer extends transmission to one month for uploading of this archival dataset by activating the PTT only when Argos satellites are mostly likely to be in view of the tag. The development of PSAT tags, with the ability to geolocate a single position of a fish remotely and track its behaviour and habitat changes (depth and temperature) between tagging and 'pop-off, was nothing short of a revolution in large fish ecology (see below).

Although the early findings from PSATs were impressive, in terms of the details they gave about horizontal movement trajectories between tagging and pop-off, they were still quite rudimentary. PSATs at this stage were capable of providing essentially the same locational information as that obtained from conventional number tagging studies: that is, where the fish was located when tagged, and where it was after a known time period (although conventional tag return rates were low by comparison). Around the end of the 90s, PSATs and DSTs became available that could record not only pressure and temperature, but also ambient light level. This was important because longitude can be estimated by comparing the time of local midnight or midday with that at Greenwich, and latitude from estimates of day length (Wilson *et al.,* 1992). Therefore, electronic tags capable of recording light level could provide data amenable to calculations of geolocation anywhere on the Earth's surface, thereby allowing reconstruction of a fish's movement track from data retrieved from remote locations by Argos satellite (Block *et al.,* 2001).

Much recent research effort has been aimed at improving accuracy of the estimates of light-level-derived locations of sharks and other large fish

during their free-ranging movements (e.g., Teo *et al.,* 2004; Nielsen *et al.*, 2006). However, it appears that there are distinct limits to the spatial accuracy of these estimates (60 to 180 km), such that a spatial error of only 10% of a shark's daily movement distance renders detection of specific behaviours within the track prone to error (Bradshaw *et al.,* 2007). Hence, light-level geolocation appears appropriate for tracking large scale movements, but is less able to resolve the specific pattern of smaller scale movements typical of most sharks during much of their annual cycle. In view of this, researchers have re-discovered Priede's idea of direct satellite tracking of sharks, and like F.G. Carey pioneered in the 1990s, have begun attaching satellite transmitting tags directly to the first dorsal fin of large sharks (Weng *et al.*, 2005). Because many large species of shark often come to the surface (see below), as do many large bony fishes such as swordfish (*Xiphias gladius*) and ocean sunfish (*Mola mola*), this presents a new opportunity for resolving more accurately the horizontal movements of sharks across a broader range of space-time scales.

Horizontal Movements

Acoustic tracking provided the first data on the movements and behaviour of free-ranging sharks in relation to environment. For example, the movements of transmitter-tagged scalloped hammerhead sharks (*Sphyrna lewini*) were monitored using datalogging acoustic receivers moored along the plateau of a seamount (Klimley *et al.*, 1988). The departures, arrivals and occupancy times of individual sharks were recorded and showed that individuals grouped at the seamount during the day, but departed before dusk moving separately into the pelagic environment at night and returning near dawn the next day. Acoustic tracking of individual *S. lewini* using a vessel resolved those nocturnal trajectories (Klimley, 1993). Individuals generally moved away from the seamount on a straight line or meandering course into deep water before heading back in the general direction of the seamount. Trackings however, were limited to 1–2 days so the persistence of this central place behaviour within an individual and among individuals across the annual cycle was not known. Studies using the same type of technology but on smaller shark species have shown interesting parallels with these general behaviours of larger species. Small spotted catsharks (*Scyliorhinus canicula*) fitted with acoustic transmitters and tracked continuously for up to 2 weeks show similar patterns of central place refuging (Sims *et al.*, 2001, 2006). Here, males and females remain generally inactive during the day, leaving to forage before dusk and returning to the preferred daytime locations near dawn. The pattern of daytime inactivity in a small activity space centred on rock refuges and nocturnal foraging behaviour in the wider environment was a pattern sustained over many months (Sims, 2003; Sims *et al.,* 2006).

The short duration of acoustic tracking of large pelagic sharks is perhaps even more of a problem when tracking individuals that were captured on lines prior to tagging. Klimley (1993) attached tags underwater to free-swimming sharks without the need for capture, but other studies requiring fish to be hooked on lines are naturally dealing with more distressed fish. Horizontal acoustic trackings of blue shark off the U.S. northwest coast showed that in late summer and autumn they generally moved south and southeast offshore following tagging and release (Carey and Scharold, 1990). It was suggested this consistent pattern of movement may have been related to seasonal migration, but it was also recognised that in part these movements may be a general reaction of pelagic fish to move into deep water offshore after being captured for tagging (Carey and Scharold, 1990). For longer trackings where the shark was tagged without the need for capture, horizontal movements are more likely to provide insights into natural foraging or ranging movements. For example, a white shark (*Carcharodon carcharias*) that was tagged feeding in the vicinity of a whale carcass off Long Island, U.S.A., continued feeding and swimming within a 3 km radius of the whale for 1.5 days (Carey *et al.,* 1982). The shark then moved southwest following quite closely the 25 m isobath for a further 2 days.

Before light level sensors were available on electronic tags, tagging and 'pop-off' locations provided information on dispersal distances over timescales much greater than was possible with acoustic telemetry. For example, bluefin tuna (*Thunnus thynnus*) fitted with PSATs off the eastern U.S. coast were found to travel over 3,000 km east across the North Atlantic Ocean in 2–3 months (Block *et al.*, 1998; Lutcavage *et al.,* 1999). In addition, the longer range movements of the white shark (*Carcharodon carcharias*) were generally unknown, but those aggregating around small islands in the coastal waters of California were generally thought to remain in shelf waters, moving up and down the coast according to season. However, PSAT tagging revealed some incredible movements of these apex predators; tagged white sharks moved into the open ocean away from the coast and one shark made the journey from California to Hawaii (some 3,800 km across the North Pacific Ocean) in less than 6 months, making dives down to 700 m and experiencing temperatures as low as 5°C (Boustany *et al.*, 2002).

Among the first studies to use light-level intensity changes to calculate large-scale horizontal movements of pelagic fish were those with bluefin tuna (Block *et al.*, 2001) and basking shark (*Cetorhinus maximus*) (Sims *et al.*, 2003). Reconstructed tracks of bluefin tuna tagged off North Carolina, U.S.A., showed movements between foraging grounds in the western Atlantic prior to transatlantic migrations into the Mediterranean Sea for spawning. Bluefins were also shown to dive to over 1,000 m depth during these excursions (Block *et al.*, 2001). The question of diving activity and what
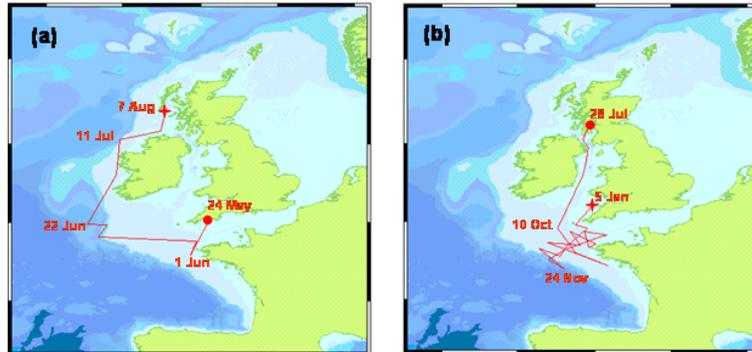
Fig. 13.1 Seasonal movements of basking sharks (*Cetorhinus maximus*) from archival tagging. (a) Reconstructed track of a 4.5-m long shark moving from the tagging location in the Western English Channel, around the west of Ireland and into Scottish waters over 77 days and covering an estimated minimum distance of 1,878 km. (b) Movement of a 7.0-m long shark from the Clyde Sea in Scotland, through the Irish Sea and into waters off southwest Britain, a journey tracked over 162 days and an estimated minimum distance of 3,421 km. Adapted from Sims *et al.* (2003).

large fish in temperate waters might do when, with changing season, food levels decline, is particularly relevant to the plankton-feeding basking shark. This species, the world's second largest fish, is most frequently seen in coastal waters feeding at the waters' surface during summer months (Sims and Quayle, 1998). In the northwest and northeast Atlantic, surface foraging occurs from around April to October usually with a peak in sightings from May until August. The seasonal increase in the surface sightings of *C. maximus* coincides with increased zooplankton abundance at this time (Sims *et al.*, 1997; Cotton *et al.*, 2005). Basking sharks tagged with PSATs were tracked moving between waters off south-west England to Scotland, and *vice versa*, sometimes over periods of only a few weeks (Sims *et al.*, 2003) (Fig. 13.1). Sharks travelled long distances (390 to 460 km) to locate temporally discrete productivity 'hotspots' along tidal fronts and on shelf-break fronts. It was also shown from basking shark trackings over seasonal scales (up to 7.5 months) that they were active during winter and do not hibernate, as was once supposed (Matthews 1962). Instead, they conduct extensive horizontal (up to 3,400 km) and vertical (> 200 m depth) movements to utilise productive continental-shelf and shelf-edge habitats during summer, autumn and winter (Sims *et al.*, 2003).

The long-range movements of the salmon shark (*Lamna ditropis*) also appear linked to seasonal changes in conditions. Using fin-mounted Argos satellite transmitters, salmon sharks were tracked from summer feeding locations in Alaskan coastal waters southward to overwintering areas encompassing a wide range of habitats from Hawaii to the North American

Pacific coast (Weng *et al.*, 2005). Some individuals, however, overwintered in Alaskan waters and in so doing experienced water temperatures between 2 and 8°C and dived no deeper than 400 m. Those sharks migrating south by contrast, occupied depths where sea water temperatures were up to 24°C and regularly dived into cooler waters to depths over 500 m (Weng *et al.*, 2005). This illustrates that in our attempts to understand the movements and behaviour of free-ranging sharks it is as important to consider swimming movements in the vertical as well as horizontal plane.

Vertical Movements

Pelagic sharks, like many other marine vertebrates, spend relatively little time at the sea's surface but instead may remain for long periods in the near-surface layers or at depth, and almost always make frequent dives through the water column, sometimes to very deep depths. What we are learning from the deployments of electronic tags on different species of shark is that although the different patterns of vertical movement can be as varied as they are complex, some general patterns appear similar among different species (Shepard *et al.*, 2006) (Fig. 13.2).

The blue shark was one of the first pelagic shark species to be tracked regularly in the open sea by acoustic telemetry yielding insights into the pattern and range of its vertical movements (for overview see Carey and Scharold, 1990). In general it was found that blue sharks tracked on the Northeast U.S. continental shelf and shelf edge exhibited depth oscillations and that this diving pattern was seasonal. During late summer, autumn and winter, sharks showed remarkably regular vertical oscillations, particularly during daylight hours, from the surface or near surface to about 400 m depth and back, whereas at night oscillations were usually confined to the top 100 m. Interestingly, sharks tracked in summer further inshore (water depth < 80 m) did not show these large, regular changes in swimming depth. In early and mid summer blue sharks remained in the upper 10 m, seldom diving deeper into colder water below the thermocline at 15 m (Carey and Scharold, 1990). In contrast, acoustic transmitter-tagged tiger sharks (*Galeocerdo cuvier*) tracked off the south coast of Oahu, Hawaii, across deep water to the Penguin Banks did not show night-day differences in depth oscillations or overall swimming depth (Holland *et al.*, 1999). In water >100 m depth they swam predominantly close to the seabed, whereas in deeper water (>300 m) they remained within the top 100 m in the warm, mixed layer above the thermocline (at 60–80 m depth) irrespective of time of day. Nevertheless, tiger sharks did undertake oscillations in swimming depth during their horizontal movements, albeit of relatively small amplitude (~50 m) compared with blue sharks swimming over deep water.
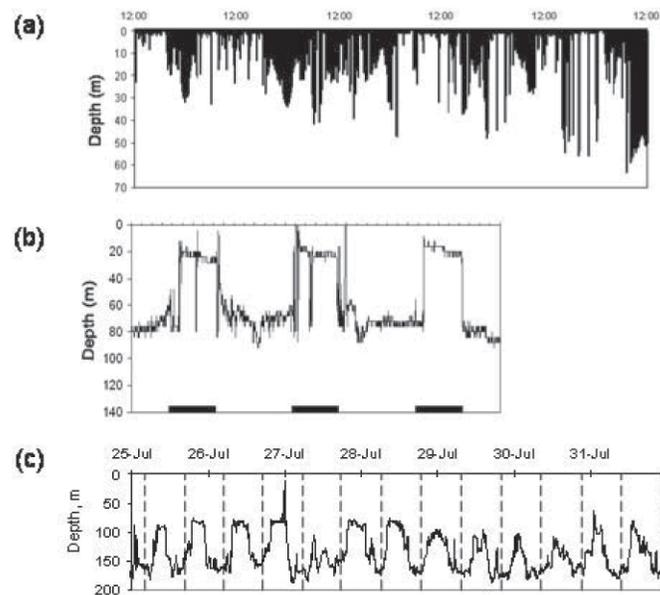
Fig. 13.2 Diving behaviours of basking shark (*Cetorhinus maximus*). (a) Vertical movements appear complex, such as this archival dive time-series over 5 days in shelf waters of the Western English Channel. (b) Some behaviours are readily recognisable and are linked to habitat type, such as this normal diel vertical migration (DVM) of a 6.5-m shark in strongly stratified waters of the Clyde Sea, Scotland. Reverse DVM exhibited by basking sharks is associated with tidal fronts, the biologically productive boundaries between stratified and mixed shelf waters. Dark bars denote nighttime. (c) Circa-tidal vertical movement of a basking shark in a deep gully in the English Channel. The date is shown on the x-axis. Times of low water are indicated by dashed vertical lines to demonstrate the consistency of the shark's movements with the tidal phase. Adapted from Sims *et al.* (2005) and Shepard *et al.* (2006).

These studies raise two principal questions: first, why do sharks show regular diving oscillations through the water column, or at least through a portion of it? And second, when they do, why are there diel and seasonal changes in these patterns? It was suggested for blue shark that regular dives through the water column were related to searching for prey. Vertical excursions are probably the most efficient way of sampling olfactory sources that spread largely horizontally in the ocean due to current shear between layers of differing density (Carey and Scharold, 1990). Frequent oscillations in swimming depth have also been recorded for other acoustically tracked species including the whale shark (*Rhincodon typus*) during foraging movements off Ningaloo Reef, Australia (Gunn *et al.*, 1999). Tracked sharks

made regular dives through the water column from the surface to near the bottom at 60–80 m. It was suggested the sharks were searching the water column for food since the dives were not related closely to changes in hydrographic features.

The use of data storage tags (DSTs) and satellite-linked archival transmitters on sharks has provided more detailed temporal information on their depth utilisations over longer time periods. Viewed at this high resolution over days to months, longer term and sometimes quite different patterns in shark swimming behaviour are evident. For example, DST tracking of school shark (*Galeorhinus galeus*) showed vertical rhythms in swimming depth over the diel cycle. In continental shelf waters off southern Australia *G. galeus* spent the day at depth before ascending at night into shallower water often for several hours (West and Stevens, 2001). When *G. galeus* was in deeper water off the continental shelf this pattern was maintained, with descent at dawn to depths of up to 600 m before ascent to shallower waters at dusk. In maintaining this pattern it appears the school shark exhibits what is termed a 'normal' diel vertical migration (DVM) (dusk ascent, dawn descent) for much of the time when ranging and foraging off southern Australia. This pattern may represent prey tracking of vertically migrating populations of squid for example, that also undertake similar daily vertical movements as those observed in school sharks (West and Stevens, 2001).

By contrast, white sharks tagged and tracked off southern Australia appear to exhibit at least three different vertical movement patterns. A pattern of regular vertical oscillations from about 50 m depth to the surface irrespective of day or night was apparent during directed westerly movements of white sharks (Bruce *et al.,* 2006). These swimming movements were reminiscent of blue shark oscillations during straight-line movements. However, this pattern was not maintained when ranging within the Spencer Gulf inlet where bottom-oriented behaviour with few ascents to the surface was the dominant pattern. Furthermore, a third pattern comprised diel vertical movements with shallow depths between the surface and 25 m depth occupied principally during the day, and depths around 50 m selected at night (Bruce *et al.,* 2006). This diel vertical movement pattern occurred when the white shark was present at offshore islands. Therefore, it appears that large sharks display different vertical movements as a function of habitat and also in response to differing prey distribution, abundance and availability.

Habitat Selection

Central to an understanding of shark movements is identification of the role of environment and habitat characteristics in shaping movement and behaviour patterns. For such an understanding, it becomes necessary to investigate closely the links between different behaviour types and concomitant changes in the environment, and to try to separate habitat *selection* or preferences from habitat *correlations*. Detecting selection of sharks and other animals for particular habitats is difficult since movements generally convey little about why those habitats have been selected (Kramer *et al.*, 1997). Simple mapping of shark movements on to environmental fields, for example a horizontal trajectory overlaid on a satellite remote-sensing map of sea surface temperature, provides a view of where and in what type of habitat the individual was located, but actually tells us nothing in itself about the habitat selection processes underlying the movement; that is, why the habitat was selected from those habitats available. To understand why sharks go where they do, it becomes important to be able to move beyond simple shark-habitat correlations, and to monitor where the sharks are in comparison with where they are not. By comparing the habitat types where sharks are located to the types of other (presumably) equally available habitats where they are not located at a given time, it allows us to delve into the dynamics of habitat *selection*. As mentioned previously (see Introduction), an understanding of habitat choices moves us closer to being able to predict the movements and behaviour of sharks when faced with a particular set of environmental conditions.

There is a growing literature documenting the locations of sharks through time in relation to different habitat types encountered. Generally, the aim has been to describe the habitat correlations of the various species studied to try to gain a mechanistic insight into what may control movement patterns. Less attention however has been paid to comparing occupied habitat types with other habitats available to detect potential differences regarding biotic and abiotic factors, such as prey presence or water temperature. In addressing the former, horizontal trajectories have been plotted on maps of sea surface temperature (e.g., Priede, 1984; Skomal *et al.,* 2004; Weng *et al.,* 2005; Bonfil *et al.,* 2005), bathymetry (e.g., Holland *et al.,* 1999; Sims *et al.,* 2003), geomagnetic anomalies (Carey and Scharold, 1990) and primary (Sims *et al.,* 2003) and secondary productivity (Sims and Quayle, 1998; Sims *et al.,* 2006). Vertical movements of sharks have been mapped on to variations in vertical thermal structure (e.g., Carey and Scharold, 1990), in relation to seabed depth (e.g., Gunn *et al.,* 1999) and with respect to concentrations of prey species (Sims *et al.,* 2005) (Fig. 13.2b). Assessing movements in relation to prey is perhaps one of the most useful environmental fields to use, at least over the short-term, because the distribution of prey is a key factor influencing

predator movements. It is expected that clear and persistent changes in swimming movements should be related to specific changes in prey abundance and availability.

Acoustic tracking studies of large pelagic fish have shown vertical movements linked closely to changes in prey distribution over the diel cycle. Depth movements of a large swordfish (*Xiphias gladius*) were related to an echogram made with a 50-kHz echosounder (Carey, 1992). A dense assemblage of prey organisms, probably squid and fish, produced a heavy band of echos (termed a sound-scattering layer, SSL) near the surface at night, where the swordfish also occurred. About an hour before sunrise at around 04: 30h, the SSL gradually descended from surface waters to about 300 m. The swordfish appeared to track this change in SSL depth closely during the short tracking, probably preying on squid and fish both near the surface at night and at depth during the day (Carey, 1992). Similarly, a bigeye tuna (*Thunnus obsesus*) was tracked gradually moving with the downward migrating SSL from 100 to 350 m, and remaining within it until early morning after which the tuna moved upward into warm, shallow waters, perhaps for reasons related to behavioural thermoregulation rather than feeding opportunities (Holland *et al.,* 1990; **see Bernal *et al.*, chapter XX**).

Movements of sharks have been linked with long-term diel vertical migration of prey. The vertical movements of basking sharks recorded with archival tags in the Northeast Atlantic were found to be consistent with those associated with foraging on diel vertically migrating zooplankton prey (Sims *et al.*, 2005). In deep, thermally stratified waters sharks exhibited normal diel vertical migration (nDVM), comprising a dusk ascent into surface waters followed by a dawn descent to deeper depths. This corresponded closely with migrating sound-scattering layers made up of *Calanus* and euphausiids that moved into surface waters at dusk, returning to depths of 50–80 m at dawn where they remained during the day until dusk. Basking sharks occupying thermally stratified waters were recorded undertaking a nDVM pattern tracking zooplankton movements for up to a month before moving to new areas or changing their vertical movement pattern. Interestingly, the vertical pattern of movement was found to vary between different oceanographic habitat types. In contrast to basking sharks in stratified waters, individuals occupying shallow, inner-shelf areas near thermal fronts conducted reverse DVM, comprising a dusk descent to depths between 20–80 m before ascending at dawn into surface waters where they remained during the day (Sims *et al.,* 2005). This difference in shark swimming movements in fronts compared with thermally stratified waters was due to induction of reverse DVM in *Calanus* by the presence of high concentrations of chaetognaths (important predators of calanoid copepods) at the surface during the night, followed by downward migrations of chaetgnaths during the day (i.e., the normal DVM of the predators produced

a behavioural switch to reverse DVM in the copepod prey). Other changes in vertical movements of basking sharks are known from the Northeast Atlantic. Dive patterns of one cycle per day (e.g., DVM) give way to depth oscillations of two cycles per day, in response to tidally-mediated migrations of zooplankton, when basking sharks moved into strongly tidal waters of the English Channel (Shepard *et al.,* 2006) (Fig. 13.2c).

Relating shark movements to environmental fields such as those in the aforementioned studies has revealed much about the diversity of behaviours present in the wild. It has provided insights into what environmental factors may influence observed patterns. However, the findings of such studies often represent simple habitat correlations that may or may not be the product of habitat selection. In such studies, random correlation may be an equally likely explanation of the observed patterns because other areas not occupied by the shark are not included in the analysis, only where the shark occurs. The question is, what is it about the location where the shark occurs that renders it different from the surrounding habitats that are not apparently selected? Explicit tests of habitat preferences of sharks are much less common in the literature, although some useful recent examples suggest what is possible to gain from such an approach.

The general approach used in preference-testing studies is to compare the amount of time spent or prey encountered in each habitat as a function of the movement track observed, compared with predicted values for that individual based on random walks through the same environment. The habitat preferences of tiger sharks in a shallow, seagrass ecosystem in Australia were examined by acoustic tracking and animal-borne cameras (Crittercams) as they moved through different habitats (Heithaus *et al.,* 2002). Tracks of actual sharks were used to estimate the proportion of time spent in two different habitats, shallow and deep. These were then compared with habitats visited during random walks. To produce a random walk, the distances moved between 5-minute position fixes in an actual tiger shark track, termed the move step lengths, were randomised to form a new track of the same length, but with a new direction of travel angle assigned to each move step taken from the distribution of commonly observed travel angles of tiger shark tracks. A particular strength of this approach is that actual shark tracks were each compared with 500 random tracks so significance levels of actual versus random could be calculated. The analysis showed that although there was individual variation in habitat use, tiger sharks preferred shallow habitat where prey was more abundant (Heithaus *et al.,* 2002).

Assessing the habitat selection of sharks in relation to dynamic prey 'landscapes' has been a more difficult goal to achieve. The principal reason for this is that temporally changing prey-density fields are not available for the vast majority of marine predators. One of the few cases where this is

possible however, is for filter-feeding sharks. As mentioned previously, basking sharks feed selectively on large calanoid copepods in specific assemblages of zooplankton (Sims and Quayle, 1998). In the north Atlantic the Continuous Plankton Recorder (CPR) survey has for over 50 years undertaken broad-scale measurements of zooplankton abundance to species level (Richardson *et al.,* 2005). The large-scale spatial coverage of individual plankton samples (minimum spatial and temporal resolutions of 56 x 36 km and 14 days, respectively) means it was possible to relate the broad-scale foraging movements of satellite-tracked basking sharks to the spatio-temporal abundance of their copepod prey. Basking shark tracks were mapped onto time-referenced copepod abundance fields in a recent study, with the amount of zooplankton 'encountered' estimated for each movement track (Sims *et al.,* 2006). The total prey encountered along each track was compared with that encountered by 1000 random walks of model sharks, where the move steps taken by each random walker were drawn from the distribution of move steps observed for real sharks. The study showed that movements of adult and sub-adult basking sharks yielded consistently higher prey encounter rates than 90% of random-walk simulations. This suggests that the structure of movements undertaken by basking sharks were aimed at exploiting preferred habitats with the richest zooplankton densities available across their range.

Behavioural Trade-offs and Energetics

So far in this discussion we have generally considered only single factors at a time, such as prey or water temperature, to be influencing the behaviour pattern of sharks. Necessarily when these simple relationships break down, we suggest other factors to test. Assessing changes in shark swimming movements due to a single factor in piecemeal fashion is likely to be a simplification in our approach, one that makes it easier for us to identify apparent relationships more readily than if many factors are appraised. However, as we can all appreciate, sharks move through complex environments and their behaviours are in response to a myriad of changing influences. So, how can we investigate the effects of co-varying factors on shark behaviour? And if we can reliably, what do such studies show?

Although studies of the effects of multiple factors on habitat selection behaviour of birds and teleost fish under captive or semi-natural conditions have been investigated in carefully designed experiments, similar work on sharks is generally lacking. In part this is due to the logistical problems associated with keeping large sharks in sufficiently large aquaria such that experiments can be reliably undertaken. But in addition, it is due to the comprehensive knowledge needed of the natural habitats where sharks occur to begin such studies, how different factors may co-vary to influence shark movement patterns, and also the energetic costs of movement and
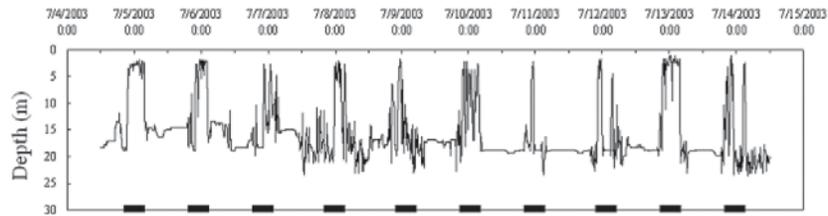
Fig. 13.3   The normal diel vertical migration (DVM) pattern of a male small spotted catshark (Scyliorhinus canicula) in a tidal sea lough in southwest Ireland. Movements into shallow water are usually made by ascending submarine slopes from deeper water. Dark bars denote nighttime. Adapted from Sims *et al.* (2006).

other functions, and of undertaking certain behaviours. Some progress has been made recently by linking tracking studies of wild sharks with environmental surveys and long-term monitoring, with laboratory experiments designed to test the field observations of behaviour, and combined with energetic modelling to help identify the costs of particular behaviour patterns. Nevertheless, this has so far only been attempted with small-bodied catsharks; we will come back to the problem of understanding the movements and behaviour of pelagic sharks in section 5.

The movements of the small-spotted catshark (*Scyliorhinus canicula*) have been closely studied in a tidal sea lough in the Republic of Ireland (for overview see Sims 2003). The lough is characterised by steep submarine slopes and it was found that male *S. canicula* spend the daytime resting in cool, deep water before moving up-slope at dusk into warm, shallow habitats for nocturnal foraging (Sims *et al.,* 2001, 2006). This approximates a normal diel vertical migration (nDVM) (Fig. 13.3); however, what factors determine this particular pattern of movement since similar nDVM of benthic prey is not evident in this environment? Long-term field deployments of water temperature-depth dataloggers showed that temperatures in the shallow habitat varied from 15.5 (at night) to 17.5°C (during daytime), whereas in their deep habitat the temperature remained between about 15–16°C (Sims *et al.*, 2006). Furthermore, deployments of baited traps showed high abundance of prey in warm, shallow areas (~2 m depth) during both day and night, but in deep water abundances were an order of magnitude less irrespective of light phase. This raised the possibility that this ectothermic catshark was exhibiting a trade-off between optimal foraging and thermal habitats. It appeared shallow, prey rich areas were entered only during periods when water temperatures were lowered during nighttime (when energy costs would be concomitantly lower), with sharks moving to deeper, cold water after foraging.

A laboratory manipulation of behaviour was designed to investigate the effects of water temperature and food availability on catshark habitat selection. Four male catsharks were trained to receive food in one compartment of a two-compartment choice chamber (water temperature, 14.4°C), the compartments being linked by a small tunnel through which the fish were free to move. After the training period, and for the next two weeks, the frequency of habitat (compartment) use strongly favoured that where food was made available (3 or more individuals were present there ~90% of the time). Throughout the following two weeks, the water temperature of the food-delivery compartment was maintained 0.9°C above the other compartment (i.e., elevated to 15.3°C), and habitat choice was recorded. By the end of the second week, the four catsharks were spending 90% of their time in the cooler side, only moving into the warmer habitat to obtain food, and which was consistent with wild behaviour of males. When the temperature gradient was removed for the next two weeks, habitat occupation switched back to the food-delivery compartment (Sims *et al.*, 2006). Thus, the thermal choice experiment using environmentally realistic temperatures supported the field observation that catsharks positively avoided warmer water even when it was associated with greater food availability.

To estimate the energetic costs of this behaviour extensive measurements of catshark metabolic rate (indirectly from oxygen consumption) were undertaken to determine the three principal components of a fish's energy budget: standard metabolism (metabolic rate at zero swimming speed), and feeding and active metabolic rates (Sims and Davies, 1994; Sims, 1996). From this data, potential energetic mechanisms underlying observed behaviour were approached by calculating the energy costs associated with occupying different-temperature habitat at varying levels of activity and feeding metabolism (termed specific dynamic action, SDA). Depth and temperature records from data-storage tagged catsharks comprised the empirical data used to build a model of energy expenditure which was then subjected to manipulations of thermal regime, that is, replacement of actual water temperature values with fixed (isothermal cold or warm temperatures) or biased-random values (within a range generated from warm or cold average 'seed' values) (Sims *et al.,* 2006). Modelling of energy budgets under these different realistic thermal choice scenarios determined by temperature and activity records from electronic tags attached to catsharks revealed that adopting a "hunt warm, rest cool" strategy could lower daily energy costs by just over 4%. Although in the short-term this saving appears small, this species is known to live for at least 15 years, during which time time these daily energy savings may contribute significantly to increasing lifetime reproductive success. Overall the findings were consistent with male *S. canicula* undertaking nDVM movements to increase energetic benefits through trade-offs between foraging opportunity and the effect of

thermal resources on energy expenditure (Sims *et al.*, 2006). The results provide the first clear evidence that benthic sharks, at least, are capable of utilizing DVM as an energy conservation strategy that increases bioenergetic efficiency.

Macroscopic Patterns of Behaviour

It is relatively straightfoward to see how measurements of energy expenditure, manipulative laboratory experiments and field tracking of smaller-bodied sharks can be combined to test explicit hypotheses in behavioural ecology. Doing the same for large pelagic sharks however is logistically prohibitive. As we have seen (Horizontal Movements 2.2 and Vertical Movements 2.3), large sharks often undertake complicated horizontal and vertical movements but as has been mentioned already what is less well known is what they are doing during such movements and why. Generally speaking it has proved very difficult to identify what behaviours sharks are exhibiting, whether they are searching, feeding, commuting, resting, or migrating, and so on. Until electronic devices capable of providing a "daily diary" of shark activities and energy expenditure becomes a practical reality (for concept see Wilson *et al.*, 2008), we are reliant upon using inferential approaches to help tease out particular behaviours and, in some cases, the strategies potentially used by sharks to find resources (food, mates, refuge, etc). Here, I will describe some analysis techniques taken from the field of statistical physics and indicate where these have recently proved useful in helping to understand shark swimming movements and behaviour in the wild, in particular those associated with searching.

Searching Natural Environments

A central issue in behavioural ecology is understanding how organisms search for resources within heterogeneous natural environments (MacArthur and Pianka 1966; Stephens and Krebs 1986). Organisms are often assumed to move through an environment in a manner that optimises their chances of encountering resource targets, such as food, potential mates, or preferred refuging locations. For a forager searching for prey in a stable, unchanging environment, prior expectation of when and where to find items will inform a deterministic search pattern (Stephens and Krebs, 1986; Houston and McNamara, 1999). However, foragers in environments that couple complex prey distributions with stochastic dynamics will not be able to attain a universal knowledge of prey availability. This raises the question of how should a forager best search across complex landscapes to optimise the probability of encountering suitable prey densities? Because nearly all motile animals face this same problem it suggests the possibility that a general foraging rule for

optimising search patterns has emerged in animals by natural selection. Pelagic sharks such as the blue shark (*Prionace glauca*) appear well designed for sustained cruising at low swimming speeds, presumably in part as a consequence of their need to search large areas and depths to locate sparse resources in sufficient quantities. Hence, pelagic sharks may be ideal candidates for testing ideas about optimal searching by applying Lévy statistics to movement patterns, and in so doing this may reveal insights about what governs aspects of their behaviour.

Optimal Lèvy flights

Recent progress in optimal foraging theory has focused on probabilistic searches described by a category of random-walk models known as Lévy flights (Viswanathan *et al.,* 2000; Bartumeus *et al.*, 2005). Lévy flights are specialised random walks that comprise "walk clusters" of relatively short step lengths, or flight intervals (distances between turns), connected by longer movement 'jumps' between them, with this pattern repeated across all scales (Bartumeus *et al.*, 2005). In a Lévy flight the move step lengths are chosen from a probability distribution with a power-law tail, resulting in step lengths with no characteristic scale: $P(l_j) \sim l_j^{-\mu}$, with $1 < \mu \leq 3$ where l_j is the flight length and μ is the exponent (or Lévy exponent) of the power law. Theoretical studies indicate Lévy flights represent an optimal solution to the biological search problem in complex landscapes where prey are sparsely and randomly distributed outside an organism's sensory detection range (Viswanathan *et al.*, 1999, 2000; Bartumeus *et al.*, 2005). Simulation studies indicate an optimal search has a Lévy exponent of $\mu \cong 2$ (Viswanathan *et al.*, 1996). The advantage to predators of selecting step lengths with a Lévy distribution compared with simple Brownian motion for example, is that Lévy flight increases the probability of encountering new patches compared with other types of searches (Viswanathan *et al.*, 2000; Bartumeus *et al.*, 2002). Recent studies (Benhamou, 2007; Edwards *et al.*, 2007; Sims *et al.*, 2007) contend Lévy flights have been wrongly ascribed to some species through use of incorrect methods, while others indicate Lévy-like behaviour with optimal power-law exponents (Bartumeus *et al.*, 2005), supporting the hypothesis that $\mu \cong 2$ may represent an evolutionary optimal value of the Lévy exponent (Bartumeus, 2007).

Here then, is a theoretical prediction about searching movements that can be tested with empirical data. The approach is to ask whether individual animals exhibit movement patterns that are consistent with Lévy behaviour, that is, whether the move step length frequency distribution is well described by a power law form with a heavy tail. If there is sufficient support for observed movements to be approximated by a Lévy distribution of move step lengths, where $1 < \mu$ d" 3 , then we can infer that the animal might be adopting a probabilistic, Lévy-like searching pattern. Furthermore, if the

calculated exponent lies close to $\mu \cong 2$, it is possible the structure of movements undertaken by an animal may be optimal. Similarly, fluctuations or changes in the Lévy exponent of movements could signal ecologically important shifts in behaviour.

Testing Empirical Data

Marine vertebrates such as large sharks that feed on ephemeral resources like zooplankton and smaller pelagic fish typify the type of predator that might undertake such probabilistic searches described with Lévy distributions. This is principally because they have sensory detection ranges limited by the seawater medium and experience extreme variability in food supply over a broad range of spatio-temporal scales (Mackus and Boyd, 1979; Makris *et al.*, 2006). Although at near-distance scales sharks use sensory information of resource abundance and distribution, and at very broad scales some may have awareness of seasonal and geographical prey distributions, across the broad range of mesoscale boundaries (1 to 100s of km) pelagic sharks, in many instances such as during searching, are more like probabilistic or 'blind' hunters than deterministic foragers. Across such scales, the necessary spatial knowledge required for successful foraging will depend largely on the search strategy employed.

Lévy-like movement behaviour has apparently been detected among diverse organisms, including amoeba (Schuster and Levandowsky, 1996), zooplankton (Bartumeus *et al.*, 2003), insects (honeybees) (Reynolds *et al.*, 2007), social canids (jackals) (Atkinson *et al.*, 2002), arboreal primates (spider monkeys) (Ramos-Fernandez *et al.*, 2004) and even in human movements (Brockmann *et al.*, 2006; Gonzalez *et al.*, 2008). Recent studies indicated some methodological errors associated with early studies of organism movements (Edwards *et al.*, 2007; Sims *et al.*, 2007), perhaps resulting in false detections of Lévy behaviour; however, robust statistical methods have now been developed (Clauset *et al.*, 2007). It was during this recent period of methodological progress that marine vertebrate predator movements were tested rigorously for the first time (Sims *et al.*, 2008).

Most studies to date have analysed the horizontal trajectories of organisms to test for Lévy flights. However, when considering fully aquatic marine vertebrates such as sharks, this presents a problem since the horizontal tracks are subject to significant spatial errors. Inaccurate location determinations, either from direct Argos satellite tracking or from reconstructed tracks using light-level geolocation, are not necessarily important when considering large-scale movements such as migration. This is because the gross movement displacement is greater than the quantified error field. However, in testing for the presence of Lévy flights the move step lengths whether they be small or large are important to measure accurately as they form the frequency

distribution, and it is from this that the Lévy exponent is determined. Simulation studies show that a Lévy exponent of a move step frequency distribution cannot be recovered from the original Lévy flight movement when locations are subjected to spatial errors of about 10% of the maximum daily movement distance (Bradshaw *et al.*, 2007). This means that for a shark moving say 50 km per day, the spatial location error during tracking can be no greater, and ideally much less, than 5 km, otherwise a Lévy flight that is present is unlikely to be reliably detected. This is clearly a problem if light-level geolocations of shark trajectories are used because error fields are large for this method (e.g. ~ 50–250 km). Although Argos satellite geolocations (class 1–3) of fin-mounted transmitters are much more accurate (Weng *et al.*, 2005), the gaps in transmissions caused by a shark not necessarily surfacing regularly enough are a problem since move step lengths cannot be determined accurately if locations in the trajectory are missing.

The limitations location errors or gaps put on using horizontal movement data from pelagic sharks has precluded, so far, their use in testing for Lévy flights. Recent progress however has been made in analysing vertical movements for Lévy behaviour (Sims *et al.*, 2008). Here, the change in consecutive depth measurements recorded by shark-attached electronic tags form a time-series of move steps suitable for analysis of macroscopic patterns across the long temporal scale (Fig. 13.4). A time series of consecutive vertical steps is reminiscent of a Lévy walk rather than a Lévy flight, since vertical move steps are determined across equal time intervals rather than between turns (turning points in a Lévy walk form a Lévy flight; see Shlesinger *et al.*, 1993). Using this approach it was demonstrated that move step frequency distributions of basking shark, bigeye tuna and Atlantic cod (*Gadus morhua*) tracked on their foraging grounds were consistent with Lévy-like behaviour (Sims *et al.*, 2008) (Fig. 13.4). A modification in the time-series was needed for air breathers such as leatherback turtles (*Dermochelys coriacea*) and Magellanic penguins (*Spheniscus magellanicus*), but they too showed move step patterns consistent with Lévy motion. Interestingly, the Lévy exponents for these five species were close to the theoretically optimal $\mu \cong 2$ exponent. Analysis of prey abundance time series and a predator-prey computer simulation was also undertaken and suggested that marine vertebrates in stochastic environments necessitating probabilistic searching may derive benefits from adapting movements described by Lévy processes (Sims *et al.*, 2008).

These results indicate that archival tag-derived data from pelagic species, including sharks, may be particularly amenable to movement analysis using the techniques described in various recent studies (Bartumeus *et al.*, 2003; Shepard *et al.*, 2006; Clauset *et al.*, 2007; Sims *et al.*, 2007; Sims *et al.*, 2008). Perhaps more importantly though, the recent investigation (Sims *et al.*, 2008) showed that in the absence of more direct information (experiments,
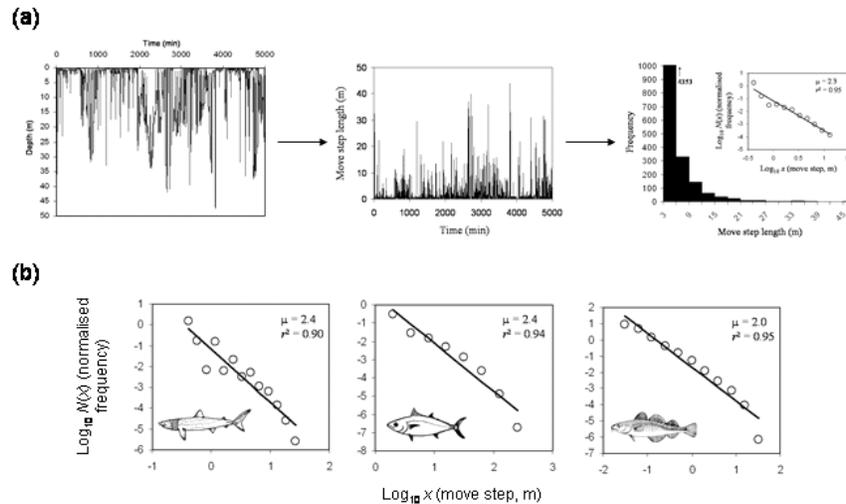
(a)

(b)

Fig. 13.4 Lévy-like scaling law among diverse marine vertebrates. (a) Movement time series recorded by electronic tags are analysed to determine the Lévy exponent to the heavy-tailed distribution. First panel: time series of swimming depths of a 4.5-m long basking shark (*Cetorhinus maximus*). Second panel: The vertical move (dive) steps (*n* = 5,000) for the same shark and time period showing an intermittent structure of longer steps. Third panel: The move step-length frequency distribution for the same data with, inset, the normalised log-log plot of move step frequency versus move step length giving an exponent (μ) within ideal Lévy limits (μ = 2.3). (b) Normalised log-log plots of the move-step frequency distributions for (first panel) sub-adult and adult basking shark (*n* = 503,447 move steps), (second panel) bigeye tuna (*Thunnus obesus*) (*n* = 222,282 steps), (third panel) Atlantic cod (*Gadus morhua*) (*n* = 94,314 steps). Analysis shows these Lévy-like movements across species are close to the theoretical optimal for searching (μ_{opt} = 2). Adapted from Sims *et al.* (2008).

observations) this approach provides a useful and insightful starting point concerning when and where sharks might be searching, the likely efficiency of such searches, and indeed, why a particular search pattern may be adopted under a particular set of environmental conditions. Determination of the potential movement 'rules' sharks (and other animals) have evolved to utilise their environment will allow a better predictive framework to develop. Hence, Lévy processes may be useful to consider for developing more realistic models of how sharks re-distribute themselves in response to environmental changes such as fishing and ocean warming (Sims *et al.*, 2008). Key to this conceptual advance will be the practical one of improvement in accuracy and regularity of locational data during tracking of shark movements so horizontal trajectories are open to rigorous spatial analyses.

Future Perspectives

The application of cutting edge tracking and datalogging technology, together with movement analysis and simulation modelling has recently pointed to potential mechanisms underlying the complex patterns of shark behaviour. There are several other examples that could have been discussed in this chapter that are equally important and interesting, and this illustrates that the field of shark movement ecology is entering a rapid phase of formal progress. So what lies ahead for us in the study of shark swimming movements in the wild? How can new technologies be applied to further enhance our understanding of free-ranging shark behaviour? Of central importance will be clear identification and testing of behavioural ecology hypotheses combining advanced movement analysis with simulations and modelling to better understand habitat preferences and hence re-distribution patterns. Patterns and dynamics of sexual segregation in sharks will be particularly important to elucidate, not least because of the potential for biased fishing effects on one sex over another and its likely deleterious population implications (Sims, 2005). Linked to this is the need for the next generation of instruments that will provide data of such good quality that much deeper insights into sharks behaving in their natural environments will be possible—we will then be capable of tackling those 'why' questions routinely. Some innovative advances will be global positioning system (GPS) tags for sharks for providing more accurate locations, the availability of datalogging sensors for signalling prey size and type ingested, and which will be needed to undertake natural experiments in shark foraging ecology. The advent of electronic "daily diaries" for sharks that reveal fine-scale data on movement, feeding events, energy expenditure and so on, over long time scales, is predicted to have a large impact in the field.

In this regard, over the last few years tests have been made of pop-up datalogging tags that instead of transmitting to satellites are capable of downloading data to mobile telephone networks. This has the advantage over satellite transmission, where message lengths are small, in that archival rather than summary data can be transmitted so long as the 'line' remains open. This year also sees the test of a new hybrid tag, this time a combination of an Argos satellite transmitter and a Fastloc GPS transmitter. This will improve the accuracy of locations of the fish by several orders of magnitude than can presently be obtained using Argos transmitters. However, fish carrying the tag must come to the surface to facilitate acquisition of the GPS satellite constellation for location fixing, which is very fast, about 50 ms (hence the 'Fastloc' name). Several recent studies show the potential of attaching a satellite transmitter to a shark's fin for example, to track it more

accurately than is possible from light-level geolocation, so it seems likely that GPS tracking of large pelagic fish is just around the corner.

Tracking sharks in the wild is a new frontier in ecological science but one that has already resulted in significant advances in understanding behaviour. Development of ever smaller and more sophisticated tags to address clear science questions will ensure that this knowledge widens yet further to include more species, and will provide key data to improve the possibility for better shark management and conservation.

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