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Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks

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Marine and terrestrial environments differ fundamentally in space-time scales of both physical and ecological processes. These differences will have an impact on the animals inhabiting each domain, particularly with respect to their spatial ecology. The behavioural strategies that underpin observed distributions of marine species are therefore important to consider. Comparatively little is known, however, about how wild fishes actually respond to gradients in food supply and temperature, and to potential mates. This paper describes how behavioural theory is being used to elucidate the strategies and tactics of free-ranging sharks in three specific areas of study, namely, foraging on zooplankton, behavioural energetics and sexual segregation. The studies discussed are novel because shark movements were tracked in the wild using electronic tags in relation to simultaneous measurements of prey densities and thermal resources. The results show that filter-feeding (basking shark, *Cetorhinus maximus*) and predatory (dogfish, *Scyliorhinus canicula*) sharks have relatively complex behaviour patterns integrally linked to maximizing surplus power, often through making short and longer term 'trade-off' decisions between optimal foraging and thermal habitats. Interestingly, female *S. canicula* exhibit alternative behavioural strategies compared to males, a difference resulting in spatial segregation by habitat. Sexual segregation in this species occurs primarily as a consequence of male avoidance by females. Studies on free-ranging sharks provide a useful model system for examining how a predator's strategy is shaped by its environment. More theory-based studies of the behavioural processes of sharks are required however, before critical comparisons with other vertebrate predators are possible. Suggestions for further research to address this knowledge gap are given.

Key words: behavioural ecology; elasmobranchs; movements; predator; telemetry.

INTRODUCTION

Changes in the spatial distribution of wild animals are determined to a large degree by shifts in habitat use of individuals. An animal's habitat is the place or environment in which it lives and is determined by a complex of physical and biotic factors (Freon & Misund, 1999). Appropriate habitat may be selected by responses to abiotic factors such as temperature and light, but also to ecological factors such as prey availability, predation risk and the presence of competitors. One, or a combination of factors may be important in determining spatial distribution and this will vary between species (Heithaus *et al.*, 2002). Selection of habitat may also partly depend on internal physiological factors (*e.g.* gastric volume and egg production) that establish particular preferences *via* changes in

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motivational or reproductive state (Colgan, 1993). Therefore, habitat selection can be defined as the non-random use of space resulting from voluntary movements in response to many co-varying factors (Crawshaw & O'Connor, 1997; Kramer *et al.*, 1997). A knowledge of the decision processes, or strategies, involved in selecting habitat is valuable because behaviourally driven changes in spatial distribution are arguably as important as demographic changes for understanding population dynamics more clearly (Elliott, 2002).

Using behavioural theory to examine free-ranging animal strategies is an obvious challenge, but one that has been eagerly embraced using terrestrial species as models (Packer & Pusey, 1982). Investigations of this type on marine animals such as fishes are less common, even though these 'lower' vertebrates may increase the overall understanding of the diversity and evolution of vertebrate strategies. Why fishes select certain natural habitats over others is the subject of this paper. Some recent research applying behavioural theory to the study of sharks is reviewed. This overview is not exhaustive and is not meant to be a broad review of all available literature on each of the chosen themes. Rather, it focuses on recent work by the author where advances have been made in studying behaviour of wild sharks, and which may be of general interest to behaviourists and fish biologists.

The paper is divided into three main sections. The value of studying free-ranging fishes, and sharks in particular, is described in relation to the need to elaborate natural strategies such as foraging. The second, and main part, comprises discussions of three areas of free-ranging shark behaviour, namely: (1) foraging on zooplankton, (2) trade-offs and behavioural energetics; (3) alternative strategies and sexual segregation. Each theme is introduced in relation to animal behaviour in general and the results discussed with respect to what new information they provide. The third section provides suggestions for further work and a brief conclusion.

WHY STUDY FREE-RANGING FISHES?

Marine and terrestrial ecosystems have different space-time scales and different general directions of trophic processes (Steele & Henderson, 1994; Steele, 1995). Atmospheric variability is high relative to the ocean where changes occur much more slowly. It is likely that these large differences in physical variability exert a strong influence on the evolving responses of organisms in the two domains (Steele, 1995). The space-time scales of the physics and biology of marine environments are coincident, indicating interactions are tightly coupled. Terrestrial ecosystems, in contrast, have space-time scales that are very much longer than highly variable atmospheric processes (Steele, 1995). Hence, primary producers on land (trees) have much longer life cycles than the primary producers (phytoplankton) in the ocean (Steele, 1995) resulting in opposite time-scale trajectories in trophic processes. Taken together, these differences are likely to have an impact on the organisms inhabiting each domain, not least because turnover rates of primary production, and hence food supply to upper trophic levels, are very different between land and sea. For example, the continental residence time of organic carbon is 140 times longer than the oceanic (Cohen, 1994). The effects these differences may have on the behaviour of marine animals at higher trophic levels such as fishes is therefore worthy of study. One question here, for example, is how are the foraging strategies of fishes affected by the short space-time scales characteristic of basal-level marine food supply?

The relative abundance and availability of suitable prey in the natural environment is one of the main factors determining animal distribution patterns. This is because productive habitat types are likely to be selected over poorer ones, as high consumption rates of high-quality prey increases energy intake and growth rates. The tendency for predators to aggregate in productive prey 'patches' and show adaptive food-choice behaviour can have important consequences for both predator distribution patterns and the stability of prey populations, especially in complex communities (Sutherland, 1996; Kondoh, 2003). Hence, investigating the tactics used to pursue particular strategies, such as foraging (Hart, 1997), may provide some of the clearest evidence why certain habitats are selected.

To examine how the marine environment influences behaviour at upper trophic levels, studies of foraging strategies and tactics in free-ranging fishes will be particularly useful. Studies of predator responses to prey gradients will provide an experimental 'window' through which natural strategies can be viewed. Despite this, and a vast literature covering broad aspects of fish behaviour (Godin, 1997), those investigations addressing natural habitat selection by marine species have been concerned chiefly with documenting associations between abundance and various abiotic and biotic variables (Kramer *et al.*, 1997). To understand how fishes distribute themselves in nature it is important to understand not only what habitats fishes choose, but the reasons why fish select particular habitats, and not others, at certain times. Rigorous field studies that identify the behavioural decisions underlying habitat selection of free-ranging fishes in the open sea, and which test theoretical models directly, however, are lacking (Hart, 1997; Kramer *et al.*, 1997; Freon & Misund, 1999). This is in no small part due to the complex mechanisms determining habitat selection itself, but in addition, it is because of the logistical problems associated with tracking fishes at sea and monitoring simultaneously environmental variables such as prey densities.

The role that gradients in prey abundance may have in structuring the natural foraging behaviour of fishes, and hence their short-term distribution, remains largely unknown (Hart, 1997). The fine-scale foraging excursions of fish predators have rarely been examined in relation to prey abundance and availability. A major problem associated with tracking fishes in the wild is that specific foraging phases are often not possible to determine with any certainty (Carey & Scharold, 1990). Moreover, the number and type of prey actually consumed by the predator is most often not determined in relation to both fine-scale foraging and habitat quality (Holland *et al.*, 1993). For example, although individual free-ranging fish behaviour in relation to sea temperature has been investigated in detail over the last decade or so (Block *et al.*, 1992; Schaefer & Fuller, 2002), only a few studies have related movements of individuals to prey densities or availability (Carey, 1992; Josse *et al.*, 1998; Sims & Quayle, 1998; Heithaus *et al.*, 2002), even though prey abundance is likely to be a central factor influencing habitat use, especially for predators. Because of this, there has been only limited use of behavioural theory to probe free-ranging fish strategies, even though this may prove fruitful for identifying common features between their behaviour and that of other vertebrates.

SHARKS AS MODELS OF BEHAVIOUR

The shark as a model animal cannot be considered to be a 'typical' fish. The cartilaginous fishes (Chondrichthyes) and the bony fishes (Osteichthyes) were both well represented in the Devonian period and so have evolved independently for at least 350–400 million years (Young, 1981; Pough *et al.*, 1999). There are *c.* 24 000 species of extant bony fishes compared to only 900 species of living cartilaginous fishes, of which *c.* 400 species are sharks (Compagno, 1984). Increased specialization in the feeding mechanisms of bony fishes is a key feature of this major vertebrate group. In contrast, sharks are mostly predators and scavengers on fishes and invertebrates, although the group includes species that feed exclusively on zooplankton and macropredators that sometimes feed on whales (Long & Jones, 1996). Sharks, however, possess several biological characteristics that present them as interesting subjects for behavioural studies.

Sharks, skates and rays generally have larger brains than other ectothermic vertebrates. Furthermore, based on both relative size and structural complexity, many species have brain mass: body mass ratios that overlap the range for mammals and birds (Northcutt, 1977; Demski & Northcutt, 1996). This suggests that sharks may be capable of complex behaviours, for example, social systems with dominance heirarchies and segregation by sex and age (Klimley, 1987). Sex-specific differences in habitat use have been reported for several species of sharks (McLaughlin & O'Gower, 1971; Economakis & Lobel, 1998; Sims *et al.*, 2001), including sex-biased dispersal (Pardini *et al.*, 2001), which is a common feature of cetacean behaviour (Würsig, 1989; Clapham, 1996). General theories of sex-biased dispersal in mammals and birds (Greenwood, 1980) could also apply to sharks given these similarities between them (Pardini *et al.*, 2001).

Foraging strategies help to determine the social life of animals (Würsig, 1989), however, sex differences in habitat use and dispersal may also reflect specific mating systems. Sharks differ from most bony fishes in having specialized copulatory organs (claspers) and internal fertilization (Feldheim *et al.*, 2002). Behavioural studies show males compete for access to females and multiple matings of males with single females can occur (Carrier *et al.*, 1994). As for birds and some mammals (Birkhead & Parker, 1997), it is likely that sperm competition is widespread in sharks and sperm storage by females is known in a number of species (Metten, 1939; Pratt, 1979). Furthermore, sharks have diverse reproductive modes including viviparity, where a relatively small number of young are nourished by a yolk-sac placenta. It has been proposed that viviparity may have played an important role in the evolution of polyandry and speciation (Feldheim *et al.*, 2002).

Overall, sharks may be useful models of behaviour for investigating the strategies of a fish that shares certain characteristics that are arguably more similar to mammals and birds than other fishes. Studying foraging strategies, habitat use and dispersal in sharks may therefore help to increase the general understanding of how and why particular behavioural strategies have arisen and what similarities or differences these may have with those of other vertebrate groups. Most notably, investigating sharks may contribute useful information leading to a critical appraisal of how a predator's environment shapes its behaviour.

SHARKS AS MODELS: PRACTICAL CONSIDERATIONS

Sharks are tractable marine species in behavioural studies for practical as well as for purely scientific reasons. Firstly, most sharks are comparatively large bodied compared to bony fishes. This feature is of practical use because studies of wild behaviour require individuals to be tracked remotely and adult sharks, and even juveniles of some species, are large enough to carry electronic tracking devices without impeding normal behaviours (Holland *et al.*, 1999; Sims *et al.*, 2001). Most acoustic transmitters used in modern studies are small, have low drag and a negligible mass in water (Voegeli *et al.*, 2001). Similarly, archival tags are of low volume relative to body size (West & Stevens, 2001) and pop-up types are palm-sized and positively buoyant (Block *et al.*, 1998). Clearly, the larger body size of many species negates the possibility for laboratory study and this is the major drawback. Some species of sharks, such as catsharks (Scyliorhinidae), however, can be tracked in the wild but also lend themselves to experimental manipulation in the laboratory because of their intermediate size (*c.* 0·7 m total length, L_T).

A second reason for using sharks to study natural behaviour is concerned with feeding modes. Some species filter-feed at the surface where individuals can be tracked visually and where prey densities can be sampled directly using plankton nets (Sims *et al.*, 1997). Furthermore, sharks have a large cardiac stomach, which coupled with their slow rates of digestion (Sims *et al.*, 1996) and propensity to vomit readily (Andrews *et al.*, 1998), means that routine recovery of stomach contents is feasible. A slow digestion rate is particularly useful for examining recent feeding history because predatory species that consume large prey whole may contain items at various stages of digestion, the chronology of which may then be matched to tracked movements.

Another consideration is that some species of shark exhibit return movements to preferred 'home' areas (McLaughlin & O'Gower, 1971; Feldheim *et al.*, 2002). This home-loving behaviour, termed philopatry, is a useful behavioural feature because it identifies a preferred activity space that can be mapped in detail by researchers to help reveal possible reasons why these particular microhabitats are selected. Philopatric behaviour also provides researchers with an increased likelihood of recapturing individuals for recovery of archival tags and stomach contents.

One major drawback in conducting behavioural studies with sharks is that they have 'slow' life-history traits. Sharks are slow growing, long lived, take a long time to reach sexual maturity and have relatively few offspring. This means they are unsuitable for studies where the behavioural responses of successive generations are the focus.

FORAGING ON ZOOPLANKTON

SHORT-TERM PATCH FORAGING

Foraging animals must make decisions about the relative value of encountered prey types so as to maximize as far as possible their chances of survival and reproductive success (McFarland, 1977). In a stochastic environment, however, foraging decisions have to be made without a complete knowledge of overall resource availability (Lessells, 1995). Consequently, a central problem facing foragers is how best to track a changing environment. The abundance of zooplankton is highly heterogeneous in space and time and is determined by various stochastic processes (Davis *et al*., 1992; Steele & Henderson, 1992). Fish foraging strategies may entail use of external directional clues for orientation to high-density patches of prey, thus minimizing the need for numerous patch visits by predators to conduct prey sampling, which may be energetically costly (Stephens & Krebs, 1986). Once a suitable prey patch is located however, further foraging decisions about whether to stay or leave the patch must be made, presumably by physiological integration of status indicators that monitor current feeding success, compared with that expected in alternative patches of food (Milinski & Regelmann, 1984). In addition, increased interference competition between predators in a prey patch may serve as an indirect indicator of patch quality, and may result in some individuals leaving to find new patches (Sutherland, 1996). Filter-feeding sharks such as the basking shark *Cetorhinus maximus* (Gunnerus) have evolved morphological, physiological and behavioural characteristics that presumably enable them to find and exploit stochastic prey successfully. Hence this species is an appropriate model for investigating the tactics of planktivory in the open sea.

Early studies suggested that basking sharks were indiscriminate planktivores that were unlikely to orientate to specific plankton-rich waters (Matthews & Parker, 1950). Recent work has demonstrated that this view is no longer tenable. To test whether basking sharks selected habitat according to specific prey assemblages with certain characteristics, fine-scale visual tracking of surface-feeding individuals was conducted together with sampling of zooplankton from their feeding paths (Sims & Quayle, 1998). Using this combination of methods the movements of individuals in relation to changes in encountered prey could be quantified directly. The results demonstrated that *C. maximus* in the English Channel showed selective foraging behaviour for zooplankton assemblages characterised by high densities of large *Calanus helgolandicus* and lower numbers of smaller calanoid copepod species (Sims & Merrett, 1997; Sims & Quayle, 1998). Sharks centred their foraging along plankton-rich thermal fronts and increased area-restricted searching (ARS) by two to three times when zooplankton density was $>1\,\mathrm{g\,m^{-3}}$ compared to when it was below this level. It was also found that sharks tracked zooplankton patches over many kilometres as patches were transported by tidal streams. Basking sharks, however, were observed to stop feeding and swim out of these areas on straight courses when zooplankton fell below *c*. $1\,\mathrm{g\,m^{-3}}$. This observation suggested that the lower threshold level of feeding for this species could be determined accurately by detailed study. Knowing when basking sharks should theoretically leave patches compared to when they are observed to do so would provide a interesting insight into their foraging tactics.

LIFE ON AN ENERGETIC KNIFE-EDGE?

In theory, any forager feeding in a patch should leave before that patch becomes unprofitable because there may be significant travel time (energy expenditure) until the next profitable patch is encountered (Valone, 1992). This may depend on an individual's behaviour or that of competitors arriving in the patch to feed. Either way, it is expected that below a lower threshold level the costs of collecting zooplankton by obligate filter feeding will exceed the net energy gain that can be derived from it (Ware, 1978; Priede, 1985). A view that has perpetuated in the literature for nearly 50 years (Parker & Boeseman, 1954) has been that basking sharks cannot use low prey densities for net energy gain and so live on an energetic 'knife-edge'. An early theoretical estimate of the minimum threshold foraging response of basking sharks suggested they would expend more energy collecting zooplankton at concentrations $<1{\cdot}36\,\mathrm{g\,m^{-3}}$ than could be obtained from it (Parker & Boeseman, 1954). A more recent study, however, investigated when basking sharks should leave patches by determining four empirical estimates and a theoretical estimate of the minimum threshold foraging response (Sims, 1999). These estimates were all aimed towards quantifying the zooplankton densities at which sharks switched from non-feeding, cruise swimming to filter-feeding. The theoretical calculations and behavioural studies of individual and group-feeding basking sharks showed they have a theoretical threshold prey density of between 0·55 and $0{\cdot}74\,\mathrm{g\,m^{-3}}$, and an observed foraging threshold of between 0·48 and $0{\cdot}70\,\mathrm{g\,m^{-3}}$ (Sims, 1999). The close agreement between theoretical and empirical threshold values indicates that the threshold for leaving patches lies close to $0{\cdot}6\,\mathrm{g\,m^{-3}}$ for this species.

This lower threshold level is supported by independent observations of movements of sharks between patches over periods of 1–2 days. Along the Plymouth front in the English Channel, two sharks that originally fed in the same patch moved in similar directions along a zooplankton gradient from low to higher density (range: 0·47–1·11 to $1{\cdot}06$–$1{\cdot}43\,\mathrm{g\,m^{-3}}$), covering minimum distances of 9·5 and 10·6 km in 27·6 and 23 h respectively (Sims & Quayle, 1998). It was hypothesized that when they encounter threshold densities of zooplankton, basking sharks minimize travelling time between patches by using frontal boundaries to find successive patches in close proximity (Sims & Quayle, 1998). The findings of Sims (1999) also show that basking sharks are capable of feeding on prey densities down to 54% lower than previously thought. Zooplankton at these lower levels are present in shelf waters during winter (Digby, 1950). From this, a prediction was made for further testing. The results implied that *C. maximus* may not be reliant upon the 'migration-hibernation' energy-conservation strategy it is purported to exhibit when seasonal zooplankton abundance declines to $<1{\cdot}36\,\mathrm{g\,m^{-3}}$. Clearly the latter possibility can be tested directly by determining the movements and behaviour of basking sharks over seasonal scales using electronic tags (Weihs, 1999).

LONG-TERM FORAGING AND SEASONAL MOVEMENTS

It has long been thought that basking sharks migrate from summer feeding grounds to deep water for winter hibernation because they are apparently absent from surface waters at this time, and appear to shed their gill-raker filtering apparatus (Parker & Boeseman, 1954). It was proposed that during winter they exhibit an energy-conservation strategy by hibernating on the seabed until spring when zooplankton densities increase (the 'hibernation hypothesis'; Parker & Boeseman, 1954; Matthews, 1962). This indicates that the proposed change in habitat selected (from epipelagic to benthic habit) is dependent on the seasonal decline in zooplankton falling below threshold levels.

A recent study tested this hypothesis directly by attaching pop-up satellite archival transmitters to individuals as they foraged during summer in the north-east Atlantic (Sims *et al.*, 2003). Individual sharks were tracked for between 1·7 and 6·5 months. The results showed that they do not hibernate during winter but instead undertake extensive horizontal (up to 3400 km) and vertical movements (>750 m) to utilize productive continental-shelf and shelf-edge habitats during summer, autumn and winter. Although sharks were capable of locating plankton 'hotspots' over long distances (390–460 km) they did not undertake prolonged movements into open-ocean regions away from the continental shelf (Sims *et al.*, 2003). Taken together with the fact that *c.* 50% of winter-caught basking sharks do not shed the filtering gill-rakers, and have food in the stomach (Van Deinse & Adriani, 1953; Parker & Boeseman, 1954; Sims, 1999), this indicates that they are active year-round in the same productive shelf areas. Therefore, this species does not respond to the seasonal decline in food availability, or apparently water temperature, by changing habitat and markedly reducing activity.

Basking sharks tracked by Sims *et al.* (2003) encountered temperature changes of up to 6° C in <5 mins during dives through the thermocline (D.W. Sims, E.J. Southall & J.D. Metcalfe, unpubl. data). Whilst basking sharks may have sufficient thermal inertia due to their large size to move rapidly between different temperature water without significant energetic implications, smaller species may be less tolerant. An interesting question is whether smaller bodied species trade-off prey availability with water temperature to make energy savings.

BEHAVIOURAL ENERGETICS

HABITAT TRADE-OFFS

Water temperature is a central factor controlling the rate of animal physiological processes and in determining patterns of growth especially in ectothermic fishes, whose body temperature is dependant on the external environment. The concept of fishes having a thermal niche arose from laboratory studies that indicated fishes spend two-thirds of their time at a particular temperature with a range of ±2° C, and all of their time within 5° C of the preferred temperature (Magnuson & Destasio, 1997). Behavioural thermoregulation for a preferred temperature has been related to both ecological and physiological optima (Holland *et al.*, 1992), with the suggestion that fishes compete for an optimal thermal niche and, when successful, are able to maximize growth and other aspects of fitness (Crawshaw & O'Connor, 1997). Fishes may exploit available thermal gradients to maximize energetic intake by maximizing rates of feeding and digestion over both diel and seasonal cycles. Hence, thermal preferences of fishes have an important role to play in determining species habitat selection, distribution and trends in population growth rates.

As mentioned previously, prey abundance is a central factor regulating energy intake and growth rates, and hence through habitat selection, the distribution of fishes. Although food and temperature both play major roles in bioenergetics and growth of fishes, little is known about the interaction of their effects on habitat preferences, especially in free-ranging fishes. Prey abundance and occupied temperatures are linked closely to net rates of energy gain and growth, but the optimal combination of temperature and food availability may not always be associated with one another (Krause *et al*., 1998). This raises the question of how fishes should trade-off these factors against each other to enhance individual fitness (Krause *et al*., 1998).

The role of temperature and food availability on animal distribution and growth can be examined using three simple models: optimal foraging theory, behavioural thermoregulation and behavioural energetics. The influence of food density and type on habitat choice has been explored using optimal foraging theory (Stephens & Krebs, 1986), where it is assumed that animals choose habitats based on the rate of net energy gain, largely independent of habitat temperature regime, even when these might confer higher rates of digestion and growth. In contrast, the behavioural thermoregulation model assumes fishes occupy a more or less optimal temperature for much of the time independent of food availability, even though in these areas the net rate of energy gain may be sub-optimal. The behavioural energetics hypothesis seeks to unify optimal foraging and behavioural thermoregulation hypotheses of behaviour by stating that fishes should selectively choose the habitat with the highest net energy value (*i.e.* the highest surplus power) relative to other habitats, and exhibit energy conservation measures such as moving to cooler temperatures during non-feeding periods (Wildhaber & Crowder, 1990). Generally, however, laboratory studies combining the effects of food and temperature on habitat choices of freshwater fishes show higher water temperature to be selected over higher rates of feeding (Wildhaber & Crowder, 1990; Krause *et al*., 1998). This behaviour indicates a hierarchical decision-making response; fishes choose habitat by temperature then by food, even at the cost of slower growth in the short-term.

Experimental studies on the effects of food and temperature interaction on habitat choice (in the absence of predation risk) generally emphasize the dominance of a behavioural thermoregulatory strategy (Matern *et al*., 2000), rather than the behavioural energetics model for predicting fish distribution. The spatial behaviour and realised distribution of wild fishes, however, may not be adequately explained by the behavioural thermoregulation model. An important field investigation demonstrated that the post-feeding thermotaxic behaviour of fish (*Cottus extensus* Bailey & Bond) in a lake was consistent with the behavioural energetics model (Wurtsbaugh & Neverman, 1988). The latter study serves to illustrate the importance of determining fish distribution in relation to naturally-occurring food and temperature gradients for more realistic assessments of behavioural strategies.

BEHAVIOUR OF MALE DOGFISH

The behavioural energetics hypothesis states that fishes should selectively choose the habitat with the highest net energy value (highest surplus power).

Central to this is the concept of optimal habitat selection, that is, an environment chosen for the most favourable combination of factors that may result in an animal maximizing its lifetime reproductive success (Freon & Misund, 1999). Therefore, if the optimal foraging habitat is spatially separated from the optimal thermal habitat, then under the behavioural energetics hypothesis it is predicted that individuals should move between these two habitats to maximize surplus power.

Male dogfish *Scyliorhinus canicula* (L.) tracked continuously using acoustic transmitters in a tidal sea lough showed similar patterns of low activity during the day in deep water (12–24 m) followed by more rapid movements into shallow areas (<4 m) at dusk (Sims *et al.*, 2001). Males returned to the core space in deep water at dawn. In contrast to the crepuscular activity peaks, nocturnal distances moved and rates of movement were similar to those during daytime. Male dogfish generally remained in shallow-water areas nocturnally, but saltatory activity was reduced to daytime levels before the return to deep water at dawn. A conventional mark-recapture study and underwater observations confirmed the telemetry results, that fish tagged at night in shallow areas returned to deep water during the day (Sims *et al.*, 2001).

The dogfish is considered a generalist feeder and opportunist benthic macropredator on a wide range of invertebrate and fish prey (Lyle, 1983; Ellis *et al.*, 1996). The dietary preferences of *S. canicula* reflect the general abundance and availability of prey in the habitat it occupies (Wetherbee *et al.*, 1990). The dogfish studied by Sims *et al.* (2001) consumed primarily decapod crustaceans (swimming crabs, *Liocarcinus* spp., the prawn, *Palaemon serratus*) and small teleost fishes. Deployments of baited traps in the deep (18 m depth) and shallow (1·3 m depth) areas during both day and night indicated that the abundance of crabs, prawns and small fishes was 17 and 72 times higher in shallow-water compared to deep habitat irrespective of light phase (Fig. 1). This indicates that the movements of dogfish into shallow areas were most probably related to foraging. Why do male dogfish not occupy shallow habitat during the daytime to remain close to their prey?

Recently, data loggers recording temperature every 2 min were moored in the shallow (1·5 m depth) and deep (18 m depth) habitats occupied by male dogfish in the sea lough at the same time of year (August to September) when tracking studies have been undertaken (D.W. Sims, unpubl. data). These data show that daytime temperatures in the shallow, prey-rich areas ranged from 16·0 to 17·7° C, whereas at dusk temperature decreased rapidly so that during night-time the shallows were <15·7° C. Temperatures recorded in the deep habitat ranged from 14·9 to 15·7° C indicating that dogfish moved into, and remained in, shallow habitat when the temperature of water there converged with that found in the deep habitat. Indeed, preliminary laboratory studies show male dogfish presented with a choice between two chambers differing by only 1° C, actively select the colder side (D.W. Sims, unpubl. data).

The reasons why male dogfish do not choose to occupy warm, shallow habitat during the day is most probably related to the higher energy costs associated with remaining there. In the laboratory a temperature increase of 10° C (from 7 to 17° C) more than doubles oxygen uptake in *S. canicula* (Butler & Taylor, 1975), suggesting natural movements into warm water would have

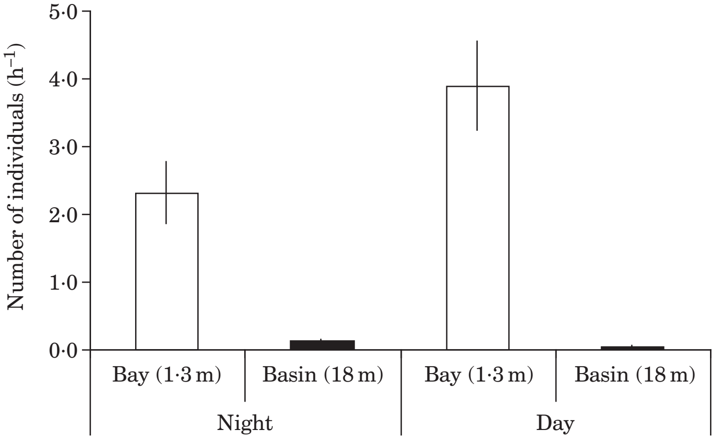

FIG. 1. Mean ± S.E. numbers of potential prey items of dogfish captured in fish-baited traps in shallow (bay; $n = 21$ deployments) and deep (basin; $n = 27$ deployments) habitats during the day and night. Species represented were swimming crab (*Liocarcinus depurator*), shore crab (*Carcinus maenas*), prawn (*Palaemon serratus*) and teleost fishes (Gobiidae).

similar effects of raising standard metabolism (defined as the metabolic rate at zero swimming speed). For dogfish, the standard metabolism-body mass relationship at 15° C (Sims, 1996) and the Q_{10} value of 2·16 (Butler & Taylor, 1975) can be used to calculate the energy costs attributable to standard metabolism for males remaining in shallow *v*. deep habitat. The results from these simple calculations indicate that remaining for 24 h in cooler water (15·3° C) compared to that available during the day in warm-shallow habitat (16·5° C) would represent a saving of 1·23 kJ, or 8·8% of standard metabolic costs. In reality, the energy savings conferred by the observed strategy are likely to be even greater because feeding (specific dynamic action, SDA) and active metabolic rates are many times higher than standard rates (Sims *et al.*, 1993; Sims & Davies, 1994), so by conducting activity and digestion in cooler water, as dogfish seem to, metabolic costs can be further reduced (Wildhaber & Crowder, 1990).

The strategy used by male dogfish, of entering shallow areas to feed only when the thermal regime converges with that found in deeper water, appears consistent with the behavioural energetics hypothesis. Moving into cooler habitat probably serves to conserve energy, however this strategy may also result from a thermal effect on the reproductive organs of male dogfish. It has been shown that temperature may have a very pronounced effect on steroid biosynthesis in the dogfish testis, with yields of testosterone showing a broad peak at 11–16° C (Kime & Hews, 1982). This temperature range corresponds to the most favourable temperature for division of spermatogonia in this species (Dobson & Dodd, 1977). The tracking study of Sims *et al.* (2001) shows that dogfish do not occupy shallow, prey-rich habitat during the day when temperatures exceed 16° C. Hence, an interacting factor behind the observed absence of males from warm, prey-rich habitat may be that sperm production decreases if habitats >16° C are selected. If cool-water habitat selection also occurs for reasons in part related to optimal sperm production, an interesting question is whether similar behaviours are observed in females.

ALTERNATIVE STRATEGIES AND SEXUAL SEGREGATION

Sexual segregation is widespread across many taxa in the animal kingdom, including fishes. It can occur on three different levels: on the social, spatial or habitat requirement scale. Species may live in sexually segregated social groups or as solitary individuals. The sexes may use different habitats entirely (habitat segregation), or use the same habitat but at different times (Main *et al.*, 1996; Conradt *et al.*, 1999). Sexual segregation could arise through predation risk, competitive exclusion, alternative seasonal resource requirements, or by reproductive choices associated with pre- or post-mating strategies. Hypotheses to explain sexual segregation have focused on sex differences in predator avoidance strategies (ultimate explanation), differences in nutrient requirements, competition, and social preferences (all proximate explanations) (Ruckstuhl & Neuhaus, 2000).

Many of the animal species exhibiting sexual segregation also show distinct body dimorphism between the sexes. This difference in body size may be related to sexual segregation in some species. It has been proposed for some sexually dimorphic mammal species that males are less vulnerable to predation than females and juveniles because of their larger size. Hence males seek habitats with high food availability and may take more risks while foraging, while females choose habitats that are primarily safe from predators (Main *et al.*, 1996). Theories of the evolution of sexual segregation, however, remain controversial (Conradt *et al.*, 1999).

Sexual segregation is a general characteristic of shark populations (Ford, 1921; Springer, 1967; Klimley, 1987). Some species apparently separate into social units of subadults of both sexes, sexually mature adult males and adult females (Springer, 1967). It has been suggested that such separation may be based on different swimming capabilities, dietary preferences, or absence of aggression between similar size sharks. Spatial separation of juveniles and adults probably functions to reduce intraspecific predation, whereas one study proposes selection for thermal habitat by females as an important factor (Economakis & Lobel, 1998). To date, the behavioural basis for sexual segregation has only been implied from fishery data of line-caught individuals (Klimley, 1987). One hypothesis contends that sexual segregation in scalloped hammerhead sharks *Sphyrna lewini* (Griffith & Smith) occurs through female-mediated choice for habitat with more abundant, energy-rich prey, leading to females attaining a larger body size at maturity than males and thus maximizing reproductive capacity (Klimley, 1987).

Sexual dimorphism with respect to body size appears more common among shark species where females have viviparous and ovoviviparous reproductive modes. These reproductive strategies are presumably more energy demanding than oviparity because relatively large, well-developed offspring are nourished inside the uterus over a long period, implying that there is a strong selection pressure for large body size in live-bearing females. In addition, sexual segregation in these species may be driven to a large extent by the need for females to grow faster to synchronize their lifetime period of reproductive activity with that of males (Klimley, 1987). Therefore, spatial segregation between the sexes may be, at least in part, accounted for by the alternative habitat requirements of females in live-bearing species. Here, however, is the weakness of studies that use fishery catches to infer something about behaviour. The fact that female hammerhead sharks apparently occupied different habitat and therefore consumed different prey compared to males does not categorically demonstrate that they selected this habitat directly for reasons related to prey and growth rates. These potential benefits may represent a component of a strategy that may have been aimed primarily at reducing predation, especially when sub-adult (Heupel & Simpfendorfer, 2002). Selection of different habitat by sexually mature females may also occur at the time of birth to reduce predation on offspring. This may be why female lemon sharks *Negaprion brevirostris* (Poey) display philopatric behaviour by returning to shallow nursery areas away from adult males to give birth (Feldheim *et al.*, 2002).

The lack of testability of Klimley's (1987) hypothesis for hammerhead sharks identifies the need for behavioural studies that test directly which factors are most important in shaping strategies that result in sexual segregation. In contrast to many live-bearing species, egg-layers such as *S. canicula* do not display sexual size dimorphism (Compagno, 1984). A test of the hypothesis forwarded by Klimley (1987) for live-bearers would be to determine whether sexual segregation is observed in egg-laying species. The prediction would be that in the absence of sex differences in size, females presumably do not require different habitat containing different prey so would be expected to occupy the same habitat as males. Historical observations of unequal sex ratios in trawl catches of *S. canicula* (Ford, 1921) indicate that sexual segregation is weak in this species compared to viviparous and ovoviviparous species (Klimley, 1987). The main questions here are, firstly, whether females utilize different habitat to males, and second, what factors drive any observed differences.

REFUGING BY FEMALE DOGFISH

Female dogfish studied by Sims *et al.* (2001) in a tidal sea lough exhibited a different behavioural strategy to males. Ultrasonic tracking and mark-recapture tagging showed that females refuged together in labyrinthine caves in warm, shallow water (0·5–1·5 m) during the day whereas males remained in cool, deep water. Overall, females spent between 62 and 73% of the time resting in shallow water but were active for a few hours every second or third night, primarily in deep water (Sims *et al.*, 2001). There was little or no overlap in habitat selected. These observations strongly suggest male and female dogfish exhibit alternative strategies that act to segregate them in both space and time. But what are the factors contributing to these different patterns of behaviour?

Female refuging as a predator avoidance strategy seems an unlikely explanation given that males remain in the open during the day, lying on the gravel substratum (Sims *et al.*, 2001). Moreover, predators of dogfish are few, especially in the tidal lough where they were studied. A plausible explanation of female behaviour is that they occupy shallow-water habitat to remain close to egg-laying sites, which are typically located in 1–5 m depth (Minchin, 1987). This seems an unlikely explanation though, given the low costs of transport in sharks this size (Parsons, 1990) and the abundance of suitable egg-laying habitat available in the lough that implies low competition for oviposition sites between females. Another possibility, related to the thermal effects on metabolism, could be that shallow-water refuging also facilitates increased rates of egg development. But why do female dogfish aggregate in well-hidden caves and crevices if occupying shallow, warmer water was the primary consideration? It is not unreasonable to suppose that females occupy these refuges to reduce predation from birds, but even though herons were abundant during behavioural trackings in the lough, adult dogfish probably represent too large a prey item.

In addition to the increased egg development (fecundity) hypothesis, Sims *et al.* (2001) found that the claspers of male dogfish had reddened tips indicating they had recently been involved in mating activity. Mating takes place primarily during summer for dogfish (Compagno, 1984) and appears to be energetically demanding. Courtship and copulation in *S. canicula*, much like that observed in other shark species (Tricas & Le Feuvre, 1985; Carrier *et al.*, 1994), is protracted and usually consists of many males pursuing the female, tugging violently and biting her (Dodd, 1983). It was hypothesized by Sims *et al.* (2001) that females form female-only aggregations in refuges to reduce energetically demanding mating activity. Females store sperm, permitting egg-laying throughout most of the year (Metten, 1939; Harris, 1952) so constant access to males by females is unnecessary.

The male-avoidance hypothesis suggested by Sims *et al.* (2001) should result in males actively seeking females. The prediction is that males should concentrate their activity at female-only refuges when females are most likely to be available. Because the caves are labyrinthine, with very narrow entrances and little room inside, copulation within the caves may be difficult. Direct observations of a female refuge in the lough were made over a period of 3·5 days to test this hypothesis. The number of females using the refuge was estimated to be at least 25. The observations showed that females left the refuge primarily at dusk and returned at dawn (0·5–4·0 individuals $15\,\text{min}^{-1}$), with lower numbers returning or leaving almost continually during the night (<2·0 individuals $15\,\text{min}^{-1}$) (Fig. 2). When returning or leaving, females circled the refuge entrance once or twice before swimming away. In contrast, males were seen undertaking looping swimming patterns outside the refuge only at dusk, when most of the females left, or at dawn when females returned. They were not seen at other times of the day or night (Fig. 2). Males that were individually identifiable were observed to visit the refuge on at least two occasions during the observation period. A few males were seen to enter the refuge but remained inside for only a few minutes. Taken together, these results indicate that males only appeared outside the refuge when the largest numbers of females were leaving or returning. This finding is consistent with the idea of males actively seeking females and supports refuging as a male-avoidance strategy. Laboratory studies are necessary, however, to test how much females are willing to 'pay' to avoid males by quantifying how long they spend in warm-water chambers to escape males, but that will increase their metabolic costs significantly.

SUGGESTIONS FOR FURTHER WORK

Sharks offer themselves as tractable model animals in studies of free-ranging animal behaviour because they have not only a diverse set of biological

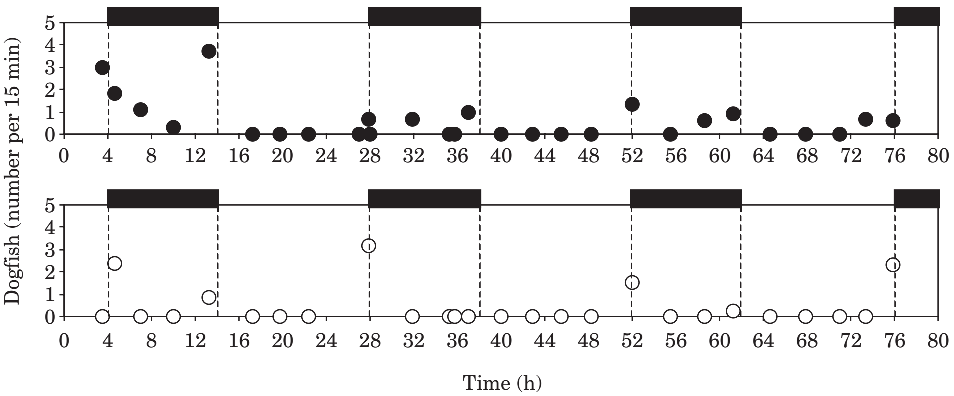

FIG. 2. Mean numbers of female (●) dogfish observed leaving from and returning to a female-only cave refuge in Lough Hyne, Ireland over a 3·5 day period, compared to the numbers of males (○) seen circling in front of the same refuge. ▬, nighttime; ¦, times of dawn and dusk.

characteristics, but possess features that identify them as useful models for tackling particular questions, *e.g.* what determines sexual segregation in a sexually monomorphic species where females store sperm? The fact that some species are also small enough to maintain in laboratory aquaria further enhances their value to field behavioural ecologists.

The most pressing question with regard to foraging on zooplankton relates to determining patch residence times of free-ranging individuals. What is the effect on an individual when competitors arrive in a patch, and how does this modify their foraging behaviour? Field tests of behavioural models of interference competition (Sutherland, 1996) are warranted. The advent of video-camera tags (Heithaus *et al.*, 2001; Hooker *et al.*, 2002) combined with conventional positional transmitters deployed on plankton-feeding sharks may provide the means to conduct a field test of competitive interference through quantification of changes in the prey fields through time and space.

Testing whether the behavioural energetics strategy is being utilized by dogfish is at present limited by a lack of information on the specific costs of different activity levels and feeding metabolism in the field. Without these, constructing accurate energy budgets incorporating field-activity and feeding costs remains problematic. Laboratory measures of oxygen consumption in fishes that provide a proxy for their metabolic rate may not represent true 'field' metabolic rates. More studies are required to relate metabolic rate of free-ranging sharks to indicators such as heart rate and tail-beat frequency. These physiological rates may vary predictably with metabolism and can be recorded with appropriate tags and transmitted to remote receivers (Priede, 1985; Scharold & Gruber, 1991; Lowe *et al.*, 1998).

Of equal importance is the need to determine not only what prey items are consumed by fishes, but what was selected with respect to available prey in the habitat. Before simple foraging models, such as the optimal diet model (ODM) (Hughes, 1997) can be tested rigorously in the field, key variables need to be measured. It should be remembered that the ODM generally fails to predict the diet-choice behaviour of predators on mobile prey, whereas it describes predator choice of immobile prey adequately (Sih & Christensen, 2001). One main reason for this is that the vulnerability (encounter rate and capture success) of mobile prey is difficult to determine and so is often ignored. Testing ODM for predators of mobile prey, such as dogfish, may be possible by combining fine-scale tracking of individuals with detailed surveys of prey species present across different microhabitats. Identifying what prey was selected on foraging trips compared to what was available will involve capturing tracked individuals and sampling their stomach contents after particular trips. This is a necessary first step to determining prey vulnerability in the wild.

Studies of oviparous shark species such as dogfish will be particularly useful for testing theories about mechanisms and evolution of sexual segregation. As dogfish do not show sexual size dimorphism, the null model that males and females do not differ in habitat selection can be stated explicitly. This is because there is no *a priori* reason for assuming that they have different habitat requirements based on predator risk or nutritional considerations. These are assumed to be equal for same-sized sexes. In this sense, it may be clearer to test the relative importance of male avoidance, fecundity and predation hypotheses in monomorphic species.

CONCLUSIONS

Sharks are predators that live at the upper trophic level of marine ecosystems, systems that have very different space-time scales of physical and ecological processes compared to terrestrial ones. Sharks also possess certain biological characteristics more similar to mammals and birds than other fishes. It is interesting to ask therefore, whether their behavioural strategies reflect these fundamental differences. Mainly through recent advances in transmitter technology for tracking individual fishes and recording environmental variables simultaneously, there now exist increased opportunities to conduct experimental biology at sea. The research described in this short review indicates that testing behavioural theory on free-ranging sharks is feasible, but depends, unsurprisingly, on selecting an appropriate species and experimental situation. Interesting aspects of the behavioural strategies of sharks are now emerging from tests of theory developed using terrestrial species. Critical comparisons of strategies such as foraging and sex differences in habitat use of sharks with other vertebrates have yet to be rigorously undertaken, despite the fact that these comparisons may help in the understanding of how environment influences behaviour. Do predatory sharks in the wild use the same decision rules as terrestrial predators, or does being in a 'watery world' confer several key differences? More theory-based behavioural studies of free-ranging sharks are required before critical comparisons can be attempted. Clearly, an understanding of how aquatic predators respond to their environment and what habitat they select is of pure interest in the context of animal behaviour studies. There is also, however, an applied perspective to such studies. Knowing what habitats fishes select and why they do so at given times over seasonal scales has obvious practical implications for determining not only catch rates of fisheries in specific regions, but also for their effective regulation.

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