Animal Behaviour 78 (2009) 525–536

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/yanbe

Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator

Kelly S. Andrews[a,*], Greg D. Williams[a], Debbie Farrer[b], Nick Tolimieri[a], Chris J. Harvey[a], Greg Bargmann[b], Phillip S. Levin[a]

[a] *Northwest Fisheries Science Center/National Oceanic and Atmospheric Administration, Seattle, WA, U.S.A.*
[b] *Marine Fish Program, Washington Department of Fish and Wildlife, Olympia, WA, U.S.A.*

ARTICLE INFO

Article history:
Received 4 November 2008
Initial acceptance 13 February 2009
Final acceptance 18 May 2009
Published online 17 July 2009
MS. number: A08-00714R

Keywords:
acoustic telemetry
apex predator
diel pattern
foraging activity
Hexanchus griseus
sixgill shark
vertical movement

The activity patterns for most animals are determined through a trade-off among competing processes, such as foraging behaviour, predator or competitor avoidance, and maintaining bioenergetic efficiency. We used active and passive acoustic telemetry to examine what processes may contribute to diel and seasonal patterns of vertical movement in 27 sixgill sharks in Puget Sound, WA, U.S.A., from December 2005 to December 2007. We found clear and consistent patterns of diel activity; sixgill sharks were typically shallower and more active at night than during the day. In Elliott Bay, WA, sixgill sharks made direct vertical movements at sunrise and sunset, while vertical movements were more variable in deeper, main channel waters. The greatest rates of ascent and descent in sixgill sharks occurred most often during night-time ebb tides. Seasonally, sixgill sharks occupied deeper habitats during the autumn and winter than during spring and were most active in the autumn. We also found synchronous vertical movements in three of four shark pairs tracked simultaneously, evidence that these sharks were responding to similar stimuli. Clear and consistent patterns of diel activity throughout the year across size and sex of sharks and across multiple spatial scales is most consistent with the hypothesis that foraging behaviour is responsible for the patterns of diel vertical movement of sixgill sharks in Puget Sound.

Describing and understanding diel patterns of activity has been the focus of numerous research programmes across a broad range of animal taxa. Differences in behaviour between day and night are generally a trade-off among three core processes: opportunistic foraging, predator or competitor avoidance and maintaining bioenergetic efficiency (e.g. Clark & Levy 1988; Wurtsbaugh & Neverman 1988). Most taxa show patterns of diel activity that allow them to forage most effectively (e.g. visual predators forage during the day and rest at night), but individuals often vary their behaviour when predators, competitors or unfavourable abiotic conditions occur. As examples, coastal black bears, *Ursus americanus*, are active foragers during the day, but they become more active at night in areas where grizzly bears, *Ursus arctos*, are more diurnally active (MacHutchon et al. 1998); larval tiger salamanders, *Ambystoma tigrinum*, will switch to open, deeper waters at night when predatory beetles, *Dytiscus dauricus*, move into prey-rich shallow waters (Holomuzki 1986), and black wildebeest, *Connochaetes gnou*, switch their grazing activity from day to night when daytime temperatures get too hot during the warm season (Maloney et al. 2005). In addition, the activity patterns of many carnivores are influenced by their prey's own circadian rhythms (Zielinski 2000), as opposed to herbivores, whose food supply does not move.

In marine environments, daily patterns of behaviour typically occur with circadian and/or circa tidal rhythm and are often expressed by changes in the individual's vertical distribution in the water column. The behaviour of zooplankton is a classic example of circadian rhythm (e.g. Cushing 1951; Enright & Hamner 1967); they make daily vertical migrations into shallow waters at dusk and then descend to deeper waters at dawn. This diel pattern of behaviour allows zooplankton to avoid many visually based predators while foraging in food-rich areas at night (Zaret & Suffern 1976); however, avoiding predation by inhabiting deeper, colder waters during the day comes with the cost of reduced growth (Ohman 1990; Hays 2003) and fecundity (Orcutt & Porter 1983; Stich & Lampert 1984). Diel vertical migration to avoid predation is also widespread among pelagic marine fishes (Neilson & Perry 1990; Watanabe et al. 1999). Many intertidal organisms display circadian and circa tidal patterns of movement (e.g. Gray & Hodgson 1999) that are the result of opportunistic foraging during times when predators are absent and

* Correspondence: K. S. Andrews, Northwest Fisheries Science Center/NOAA Fisheries Service, 2725 Montlake Boulevard East, Seattle, WA 98112, U.S.A.
E-mail address: kelly.andrews@noaa.gov (K.S. Andrews).

0003-3472/$38.00 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd.
doi:10.1016/j.anbehav.2009.05.027

abiotic conditions are favourable (Naylor 1988; Lampert 1989; Palmer 1995).

It has historically been difficult to study long-term behaviour patterns of large marine predators such as sharks. However, acoustic, satellite and radiotracking technology now allow scientists to describe the spatial and temporal patterns of behaviour of these species. Many shark species display diel patterns of activity in which individuals occupy deeper water during the day and move closer to shore or to the surface at night (*Megachasma pelagios*: Nelson et al. 1997; *Galeorhinus galeus*: West & Stevens 2001; *Alopias superciliosus*: Nakano et al. 2003; Weng & Block 2004; *Somniosus microcephalus*: Stokesbury et al. 2005; *Carcharhinus perezi*: Chapman et al. 2007; juvenile *Carcharodon carcharias*: Weng et al. 2007). Basking sharks *Cetorhinus maximus* change the depths they inhabit on diel and tidal cycles to follow aggregations of prey (Shepard et al. 2006), while diel patterns of vertical movement in the small-spotted catshark, *Scyliorhinus canicula*, confer a bioenergetics advantage; individuals hunt in warmer surface waters at night and use deeper waters during the day where cooler temperatures increase the efficiency of digestive processes (Sims et al. 2006). However, in other studies, sharks have not shown diel patterns in their overall activity (*Carcharodon carcharias*: Carey et al. 1982; *Isurus oxyrinchus*: Holts & Bedford 1993; *Hexanchus griseus*: Carey & Clark 1995; *Galeocerdo cuvier*: Holland et al. 1999; *Somniosus pacificus*: Hulbert et al. 2006). Moreover, some studies describe conflicting diel behavioural characteristics in the same species of shark (e.g. *Somniosus microcephalus*: Skomal & Benz 2004; Stokesbury et al. 2005). When patterns of activity are not clear and consistent, it is difficult to hypothesize what processes are responsible for movement. A major caveat for most behavioural studies on sharks, however, is that they are based on a very limited number of individuals (mean of 4.4 individuals per study from all studies cited in this paragraph).

Understanding the behaviour of large apex predators, such as sharks, and determining whether changes in their behaviour are the result of foraging opportunities, predator/competitor avoidance, or bioenergetic advantages is important for determining what effect these individuals have on ecological communities and how susceptible they may be to environmental perturbations (e.g. habitat loss or climate change). In the past, tests of these hypotheses have been problematic for large marine animals, since laboratory studies can be impractical, it is virtually impossible to control for the abundance of prey and predators in the field, and tagging experiments in the field have frequently necessitated small sample sizes. However, new acoustic tracking technology has recently greatly increased our insights into the behaviour of large marine species (e.g. Heupel & Simpfendorfer 2005; Dewar et al. 2008; Witteveen et al. 2008). In this study, we integrate data from both active acoustic tracking and an extensive array of passive acoustic receivers to identify diel patterns of activity in sixgill sharks, *Hexanchus griseus*, in Puget Sound, WA. Specifically, we test the three primary processes responsible for diel changes in behaviour in animals (foraging, predator/competitor avoidance and maintaining bioenergetic efficiency) against each other to determine which is/are most likely responsible for the observed patterns of movement.

HYPOTHESES AND EXPECTATIONS

Hypothesis 1: Foraging Behaviour Influences Diel Patterns of Movement

If foraging behaviour is responsible for diel patterns of vertical movement, we predicted that our observations would show several defining characteristics. First, sharks should show consistent diel patterns of vertical movement at multiple temporal scales and these patterns would be coherent at different spatial scales. Second, sharks should be more active at specific times of day on a consistent basis. Third, diel patterns of movement should be consistent across individuals of different sizes and sex. Fourth, sharks detected in the same location should make synchronous movements as they respond to similar distributions of prey.

Hypothesis 2: Predator or Competitor Avoidance Influences Diel Patterns of Movement

If sixgill sharks change their diel patterns of vertical movement in response to predators or competitors, we expected different characteristics from those proposed in Hypothesis 1. First, diel patterns of vertical movement should vary among individual sharks, particularly by size, as sharks try to avoid other sixgill sharks. Second, sharks should make fast vertical movements in an unpredictable manner as competitors or predators are encountered. Third, synchronous vertical movements over long periods should not be observed between sharks detected in the same location.

Hypothesis 3: Bioenergetic Advantages Influence Diel Patterns of Movement

If sixgill sharks use their vertical movement patterns for bioenergetic advantages, we expected that sharks would show similarly consistent and predictable patterns of vertical movement as proposed in Hypothesis 1; however, vertical movements should be closely related to the depth of the thermocline, such that we would observe sharks moving above or below the thermocline at specific times of day. Moreover, these patterns of vertical movement should change throughout the year as the thermocline disappears in the winter in Puget Sound.

METHODS

Study Location

We collected and acoustically monitored sixgill sharks in the main basin of Puget Sound, WA, U.S.A. Puget Sound is the second-largest estuary on the west coast of the United States covering an area of 2330 km^2 with nearly 4000 km of coastline. Relatively shallow sills isolate the main basin from other sub-basins within Puget Sound, restricting ocean circulation and the movement of many organisms, sediments and contaminants. Tides, gravitational forces and seasonal freshwater inflows drive circulation patterns in Puget Sound. The main basin of Puget Sound is generally stratified in the summer, due to river discharge and solar heating, and is often well mixed in the winter (Staubitz et al. 1997). The average depth of greater Puget Sound is 62.5 m at mean low tide, while the main shipping channel exceeds depths of 250 m. Puget Sound is also home to nearly 4 million residents and ~52% of the coastline in the main basin has been modified by human activities (NMFS 2007).

The food web of Puget Sound is determined, in general, by the seasonal production of phytoplankton and macroalgae (e.g. Winter et al. 1975), which influences the abundance of consumers and predators in the pelagic and benthic communities (Strickland 1983). The demersal fish community of Puget Sound consists largely (~67% of total biomass) of flatfishes and white-spotted ratfish, *Hydrolagus colliei* (Quinnell & Schmitt 1991). The diets of the demersal fish community converge on abundant prey resources during the summer and diverge in the less productive winter (Reum & Essington 2008).