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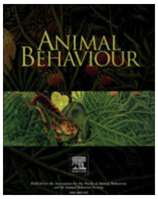

Diel activity patterns of sixgill sharks, *Hexanchus griseus*: the ups and downs of an apex predator

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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

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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).

Study Species

Sixgill sharks are large, predatory fish found in temperate and tropical seas worldwide. They are the largest resident fish in Puget Sound. Sixgill sharks are typically demersal and found in deep water along the continental shelf and upper slope; however, they may occasionally move to shallower waters, and juveniles may frequent nearshore waters (Ebert 1986, 2003; Andrews et al. 2007). In British Columbia, Canada, the abundance of immature sixgill sharks is greater during the day in summer months relative to other months of the year (Dunbrack & Zielinski 2003).

Sixgill sharks are ovoviviparous with litters ranging between 22 and 108 pups (Ebert 1986). Males appear to mature at a total body length of approximately 3.1 m while females mature at nearly 4.2 m (Ebert 2002, 2003); however, little is known about age at maturity or size at age of individuals. Growth rates of sixgill sharks are relatively unknown, although Ebert (2003) reports that young-of-year double in size during their first year. We recaptured one sixgill shark that grew from 57 kg (218 cm total length) on 22 January 2005 to 83 kg (248 cm total length) on 12 June 2007 (growth of ~1 kg or 1 cm per month). Sixgill sharks feed on a wide variety of food including other sharks, rays, pelagic and demersal teleosts, marine mammals and whale carrion (Ebert 1994, 2003).

Collecting and Tagging Sharks

Between November 2005 and August 2007, we collected and tagged 32 sixgill sharks with pressure sensor acoustic transmitters. Twenty sharks were captured in Elliott Bay, 10 near Three Tree Point, and two at the south end of Bainbridge Island (Table 1, Fig. 1). We collected sharks using standard longline operations with heads of spiny dogfish, *Squalus acanthias*, as bait. Upon capture, sharks were brought on board and their gills were irrigated with sea water. We measured (both precaudal length and total length), weighed and sexed each shark, and placed an external Floy© tag through the dorsal fin. We implanted one Vemco© V16P coded acoustic transmitter with pressure sensor into the midline of the peritoneal cavity via a 3 cm incision at the anterior end of the pelvic fins. In 23 of the 32 sharks, we also inserted a Vemco© V16 continuous transmitter into the same cavity. After the incisions were sutured, sharks were returned to the water (time out of water for each shark ranged between 5 and 10 min).

Table 1
Biological data of sharks collected and tagged with pressure sensor acoustic transmitters during November 2005–August 2007

Shark ID	Tagging date	Tagging location	Total length (cm)	Weight (kg)	Sex
25	16 Nov 2005	Three Tree Pt.	182	38	M
26	16 Nov 2005	Three Tree Pt.	204	60	F
27	16 Nov 2005	Three Tree Pt.	181	35	M
28	16 Nov 2005	Three Tree Pt.	176	33	M
29	16 Nov 2005	Three Tree Pt.	205	39	M
30	16 Nov 2005	Three Tree Pt.	140	13	F
31	16 Nov 2005	Three Tree Pt.	109	6	F
32	16 Nov 2005	Three Tree Pt.	225	72	F
33	16 Nov 2005	Three Tree Pt.	193	21	F
199	16 Nov 2005	Three Tree Pt.	203	53	F
190	4 May 2006	Elliot Bay	240	105	F
198	4 May 2006	Elliot Bay	203	53	F
200	4 May 2006	Elliot Bay	237	92	M
201	4 May 2006	Elliot Bay	285	173	M
202	4 May 2006	Elliot Bay	269	144	M
203	4 May 2006	Elliot Bay	203	50	F
204	4 May 2006	Elliot Bay	270	137	M
207	4 May 2006	Elliot Bay	293	115	F
78	21 Jan 2007	Elliot Bay	220	75	F
79	20 Mar 2007	Elliot Bay	276	126	F
81	20 Mar 2007	Elliot Bay	248	90	M
82	20 Mar 2007	Elliot Bay	245	94	M
83	20 Mar 2007	Elliot Bay	233	101	F
80	16 Apr 2007	Elliot Bay	183	33	M
84	16 Apr 2007	Elliot Bay	150	20	M
85	16 Apr 2007	Elliot Bay	202	66	M
86	16 Apr 2007	Elliot Bay	218	65	F
87	14 May 2007	Bainbridge	175	25	F
88	16 May 2007	Elliot Bay	154	17	F
89	12 Jun 2007	Bainbridge	248	83	F
90	28 Aug 2007	Elliot Bay	280	151	F
195	28 Aug 2007	Elliot Bay	250	91	F

The coded transmitters emit a train of 'pings' at 69 kHz randomly every 40–114 s that contains a specific ID code allowing users to identify individuals. Most of the coded transmitters had a life span of 1429 days. The continuous transmitters emit a signal every 2 s at a specific frequency ranging between 51 and 84 kHz and had a life span of 401 days. The continuous transmitters were used to facilitate active tracking, while the coded transmitters provided depth information and were detected by passive acoustic receivers (listening at 69 kHz) deployed throughout Puget Sound.

Active Tracking

During the summer and autumn of 2006 and 2007, and a few other opportunistic times, we used Vemco© VR100 and VR28 acoustic receivers to collect data on the depth of a shark and its GPS-based position while tracking individual sharks for 24 h periods. The VR100 hydrophone was deployed 1 m below the water's surface, while the VR28 hydrophone was towed behind a slow-moving 21' boat using a haired-fairing cable at a depth of ~5 m. The detection ability of each receiver varied with weather and site conditions, but average maximum range of detection was 300–500 m (K. Andrews, unpublished data). Most tracking events occurred in Elliott Bay or on the south end of Bainbridge Island (Table 2, Fig. 1). We used data from individual paths of sharks in analyses if we had a minimum of 5 h of tracking in both day and night hours. The depth of sharks observed during active tracking correlated well with bottom depth ($r = 0.85$; using data when signal strength (>50 decibels) and gain (<24 decibels) values suggested we were closest to the shark; Fig. 2); therefore, vertical movement of sharks occurred as sharks moved up and down the slope of the bottom, not while moving up and down through the water column.

Passive Monitoring

We deployed 10 fixed automated acoustic receivers (Vemco© VR2) in December 2005 on navigational buoys or markers in the main basin of Puget Sound (Fig. 1). These receivers continuously 'listened' for Vemco acoustic transmitters throughout the duration of this study. The average radius of detection among six of these 10 sites was 479 m (Andrews et al. 2007). These 10 sites formed the backbone of our passive acoustic monitoring array; however, there are several other research groups in Puget Sound using the same equipment, and we have received data from over 100 receivers that detected sixgill sharks from November 2005 to December 2007. We divided data collected from receivers into day or night based on the time of sunrise and sunset. We used depth data from receivers for individual sharks if the shark was detected at a site at least 10 times during the day or at least 10 times during the night on any date.

Analysis

Diel patterns of depth and levels of activity

We analysed the depth data for each actively tracked shark path with linear mixed models (PROC MIXED, SAS 2004) to determine

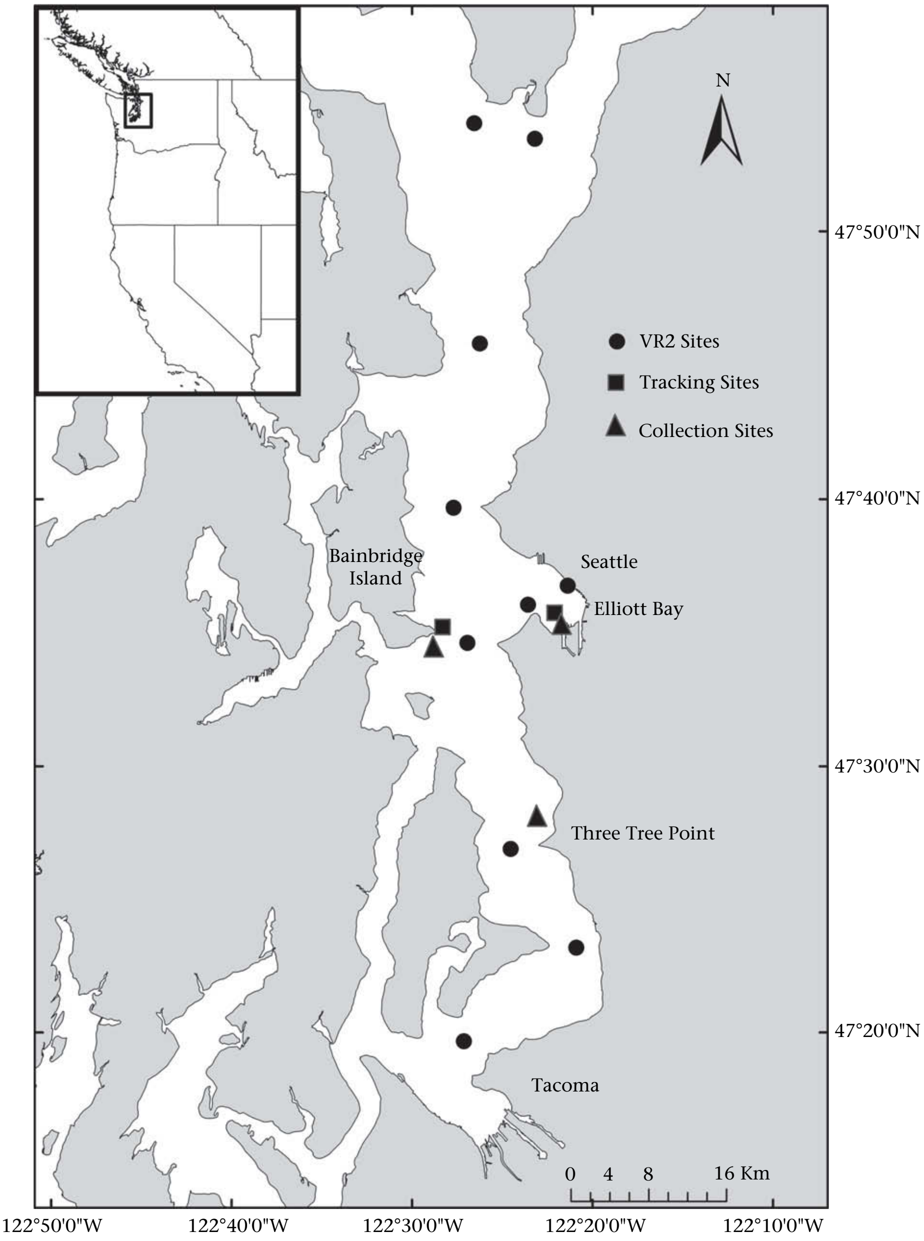

Figure 1. Locations in Puget Sound, WA of 10 primary VR2 acoustic receivers (●), active tracking locations in Elliott Bay and near Bainbridge Island (■), and sites of sixgill shark collections (▲).

whether sharks inhabited different depths during day and night, and to test for differences in the variance of depth (level of activity) between day and night. Shark and path number (nested within shark) were random variables with time of day (day or night) as a fixed variable. We analysed the two tracking sites (Elliott Bay and Bainbridge Island) separately because they varied greatly in maximum depth (100 m and 250 m, respectively). We used a Tukey–Kramer adjustment to test for differences between the least squares means for each categorical main effect throughout all analyses.

We used passive monitoring data from across Puget Sound for a subset of frequently detected sharks (sharks that were detected in at least 7 months of the year in the main channel of the central basin of Puget Sound) to investigate whether behavioural patterns of vertical movement occur at scales larger than 24 h tracking and whether patterns of vertical movement vary temporally. This criterion provided data across all hours of the day and most months of the year for eight sharks tagged at Three Tree Point and six sharks tagged in Elliott Bay. For each month, we calculated the mean depth and mean rate of vertical movement (m/h) during the day and night for each shark across all sites. We used a linear mixed model with mean depth as the dependent variable, shark as a random effect, and time, month, bottom depth of site and month*time as fixed effects to determine whether the depth of sharks varied between day and night at this larger spatial scale and whether the pattern varied temporally.

We calculated the mean rate of vertical movement by summing the absolute values of all vertical movements made during each day/night period for every date for each shark and dividing by the total time of detection for each time period. We used a linear mixed model with the mean rate of vertical movement as the dependent variable, shark as a random effect, and time, month, bottom depth

Table 2
Tracking information of sharks actively tracked during December 2005–September 2007

Shark ID	Tracking location	Tracking date	Hours tracked
25	Bainbridge	20 Dec 2005, 29 Jun 2006, 10 Aug 2006, **24 Aug 2006**, 26 Jul 2007, **23 Aug 2007**	4, 4, 3, **12**, 1, **24**
26	Bainbridge	21 Dec 2005	1
27	Bainbridge	**13 July 2006**, 24 Aug 2006, **21 Sep 2006**, 26 Jul 2007, **9 Aug 2007**, 23 Aug 2007	**19**, 4, **24**, 1, **24**, 1
29	Tacoma	19 Apr 2006	1
30	Bainbridge	13 Feb 2006, 13 Jul 2006, **10 Aug 2006**	2, 4, **25**
31	Robinson Pt.	2 May 2006, 10 Aug 2006	2, 1
32	Three Tree Pt.	20 Dec 2005	2
33	Bainbridge	**29 Jun 2006**	**24**
78	Elliot Bay	**26 Feb 2007**, 13 Jun 2007, 5 Jul 2007, **12 Jul 2007**, 9 Aug 2007, **13 Sep 2007**, 27 Sep 2007	**24**, 1, 6, **24**, 1, **24**, 3
82	Bainbridge	**23 Aug 2007**	**24**
86	Bainbridge	6 Jul 2007, **26 Jul 2007**, **9 Aug 2007**, 23 Aug 2007	2, **24**, **24**, 4
190	Elliot Bay	17 May 2006, **23 May 2006**	4, **24**
195	Elliot Bay	**13 Sep 2007**, 27 Sep 2007	**24**, 5
200	Elliot Bay	17 May 2006, **23 May 2007**, **27 Jul 2006**, **25 Jan 2007**, 26 Feb 2007, 13 Jun 2007	1, **10**, **24**, **24**, 11, 1

Tracking sessions shown in bold were used in analyses.

of site, and month*time as fixed effects to determine whether the level of activity of these sharks differed during day and night and whether the pattern varied on a monthly or seasonal basis.

Association of size and sex on patterns of vertical movement

We used the passive monitoring data from all 27 sharks detected to investigate whether diel patterns of vertical movement were related to size or sex of sharks. We calculated the mean depth during the day and night for each shark across all sites and used these values as the dependent variable in a linear mixed model with shark as a random effect, and time, total length of shark, bottom depth and sex as the main fixed effects.

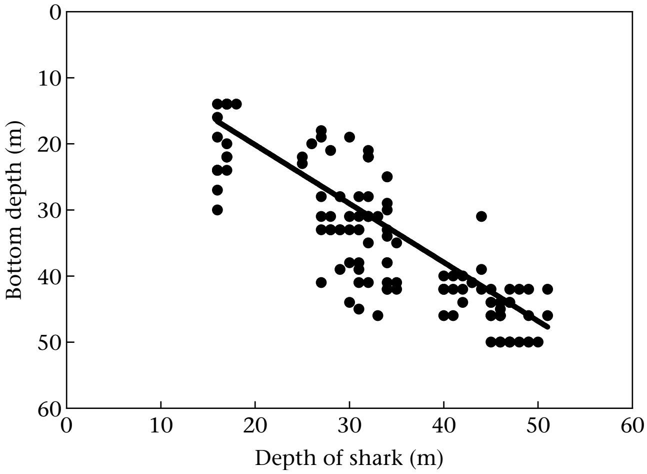

Figure 2. Bottom depth versus shark depth using active tracking detections with signal strength > 50 dB and gain < 24 dB in Elliott Bay.

Vertical movement patterns of sharks detected simultaneously

On three occasions, we were able to actively track pairs of sharks simultaneously for an entire 24 h period. We tracked another pair via passive monitoring in Elliott Bay continuously over a 24 h period. To determine the degree to which pairs of sharks showed synchronized vertical movement, we examined the cross correlation of pairs of depth profiles (SYSTAT 2004). For this analysis, we were interested primarily in relative changes in depth rather than absolute depth. Thus, prior to analysis, we standardized the depth profiles to a mean of zero.

Predicting fast rates of vertical movement

Using the active tracking data, we calculated the rate of vertical movement (ascent and descent rates) between successive detections for each of the shark paths. Each rate was categorized by the time of day (day or night) and status of the tide (ebb or flood). We then determined if rare, relatively fast movements (>2 SD greater than mean vertical movement) were linked to individual sharks, time of day and/or tidal status. We modelled the probability of a rare event (in an events/trials framework where trials were the total relocations for a single path) using a logistic regression model (PROC GLIMMIX, SAS 2004), with time, tide and time*tide as fixed effects, and shark and path (nested within shark) as random effects.

Correlation between vertical movements and temperature profile

We used temperature profile data from the Washington Department of Ecology (DOE 2008) to determine the depth of the thermocline (if present) at locations near our active tracking sites throughout the year. We then used our active tracking data to examine whether patterns of vertical movement correlated with the depth of the thermocline. Specifically, we calculated the proportion of detections during the day and night in depth bins for each shark path (2 m bins for Elliott Bay paths and 5 m bins for Bainbridge Island paths) to compare with temperature profile data.

RESULTS

Sixgill sharks collected in Elliott Bay were larger than sharks collected near Three Tree Point, both in total length (mean ± SE: 233 ± 9 cm versus 178 ± 13 cm, respectively; t test: $t_{28} = 3.61$, $P = 0.001$) and weight (mean ± SE: 90 ± 9 kg versus 34 ± 13 kg; $t_{28} = 3.84$, $P < 0.001$). Of the 32 sharks collected and tagged, 19 were female and 13 were male (Table 1). We were able to relocate 14 of 32 sharks via active tracking in Elliott Bay or at Bainbridge Island (Table 2), while we detected 27 of 32 sharks at 48 different sites with the array of acoustic receivers in Puget Sound from December 2005 to December 2007.

Hypothesis 1: Foraging Behaviour

Diel patterns of depth and activity

We show examples of individual patterns of vertical movement for sixgill sharks actively tracked over 24 h periods from Elliott Bay and Bainbridge Island sites in Fig. 3. Sharks showed a broad range of individual variation in behaviour, although sharks in Elliott Bay had a narrower range than sharks at Bainbridge Island. At each of these sites, actively tracked sharks showed differences in the depths they inhabited during the day and night (Table 3, Fig. 4). Sharks in Elliott Bay ($N = 8$ paths from four sharks) had a mean (±SE) depth of

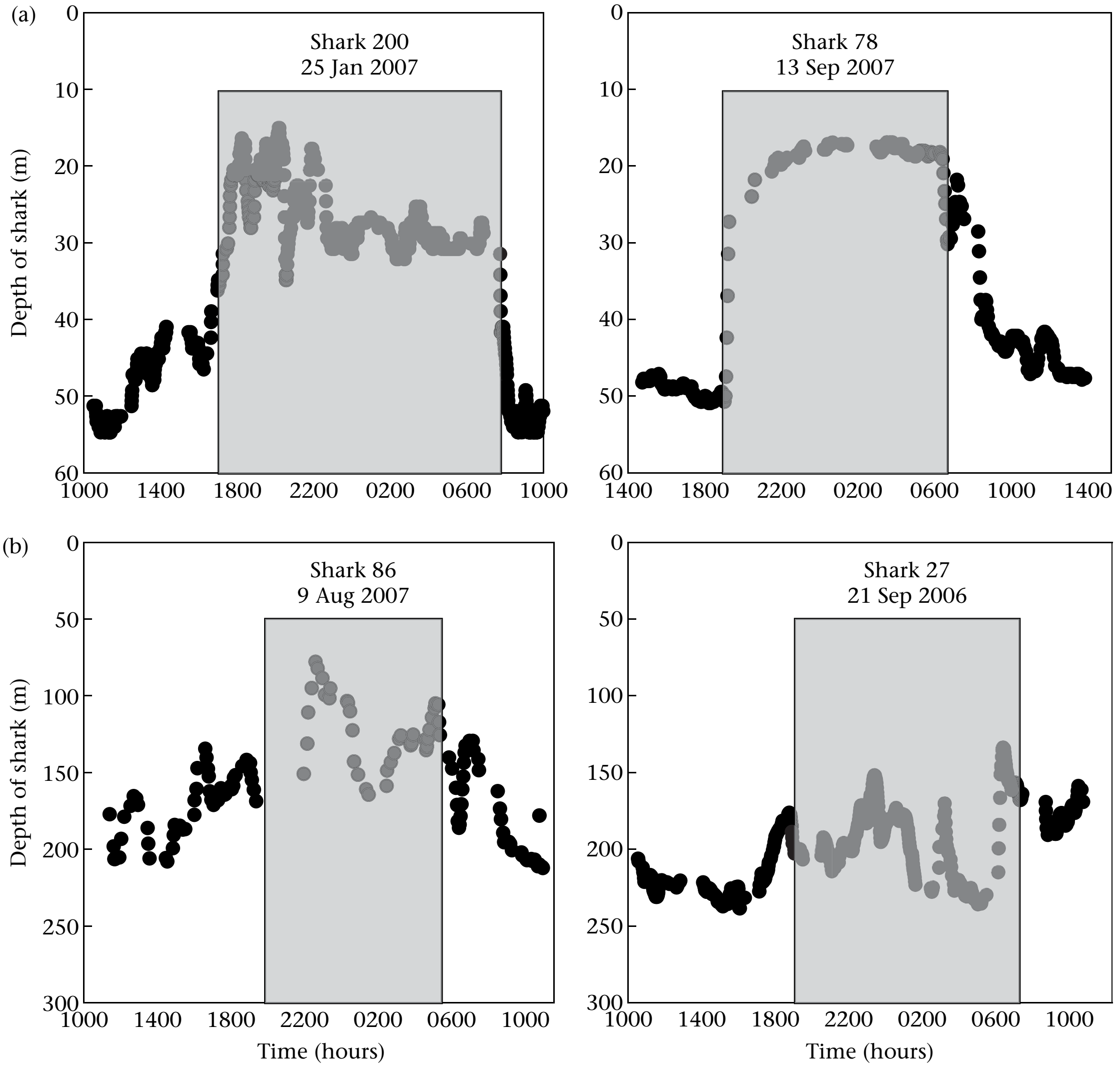

Figure 3. Examples of 24 h depth profiles of individual sixgill sharks from (a) Elliott Bay and (b) Bainbridge Island active tracking locations. Grey blocks of time are hours of darkness.

42 ± 2 m during the day and 25 ± 2 m during the night, while sharks tracked at Bainbridge Island ($N = 10$ paths from six sharks) had a mean depth of 170 ± 10 m during the day and 141 ± 10 m at night. The activity level of sharks also differed between day and night (estimates of residual day and residual night in Table 3). Elliott Bay sharks had 1.7 times more variance in their depths at night compared to the day, while sharks tracked at Bainbridge Island had 1.5 times more variance in their depths at night.

Table 3
Linear mixed models of depth of sixgill sharks during active tracking at Elliott Bay and Bainbridge Island

Covariance parameter	Estimate	SE	Z	P
Elliott Bay				
Shark	0			
Path (shark)	41.8687	22.4743	1.86	0.0312
Residual day	42.9812	1.5130	28.41	<0.0001
Residual night	73.0073	3.4530	21.14	<0.0001
Fixed effect day/night: $F_{1,3295}$=3463				<0.0001
Bainbridge Island				
Shark	38.6731	599.60	0.06	0.4743
Path (shark)	875.61	658.43	1.33	0.0918
Residual day	772.29	31.1132	24.82	<0.0001
Residual night	1173.87	49.7630	23.59	<0.0001
Fixed effect day/night: $F_{1,3038}$=635.29				<0.0001

According to passive monitoring data, the 14 frequently detected sixgill sharks showed differences in the depths they occupied between day and night across the entire year throughout Puget Sound (Fig. 5a). Sharks had an overall mean ± SE depth of 152 ± 6 m during the day and 136 ± 6 m during the night (linear mixed model: $F_{1,1123} = 53.26$, $P < 0.0001$). Monthly estimates for mean depth also differed significantly ($F_{11,1123} = 14.85$, $P < 0.0001$), with the primary differences being that sharks were significantly deeper in the autumn and winter months (September–January) than in the spring (March–May). The interaction between month and time of day was nonsignificant ($F_{11,1123} = 1.75$, $P = 0.0585$), indicating that these sharks were, on average, deeper during day than night in all months of the year.

Frequently detected sixgill sharks also showed differences in rate of vertical activity between day and night for most of the year (Fig. 5b). Overall, the mean activity rate was greater at night (mean ± SE = 76 ± 7 m/h) than during the day (58 ± 7 m) ($F_{1,4377} = 115.78$, $P < 0.0001$). Monthly estimates for mean activity

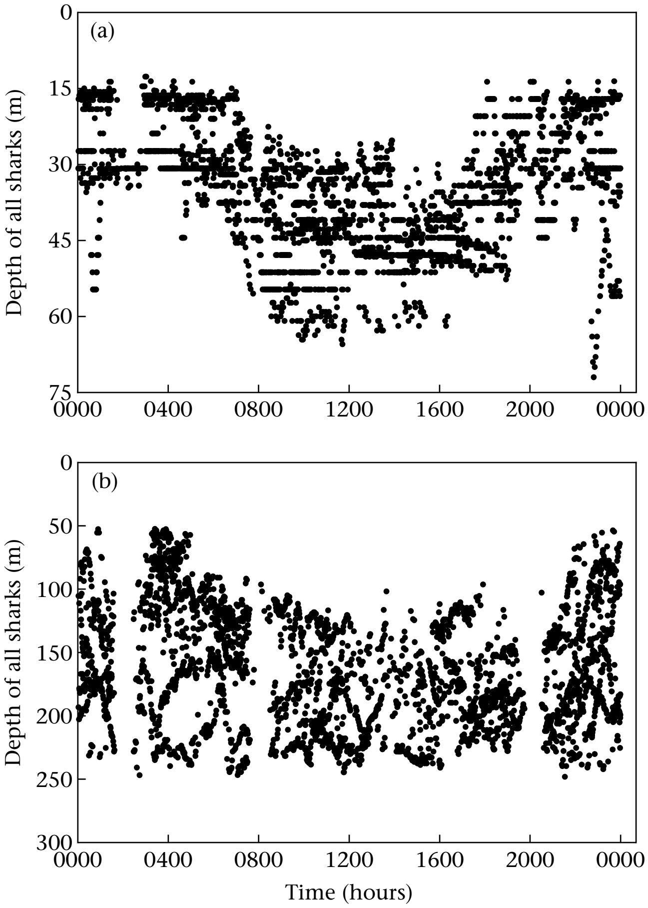

Figure 4. Depths of all sixgill shark active tracking paths during 2006 and 2007 at (a) Elliott Bay and (b) Bainbridge Island active tracking locations.

rates were also significantly different ($F_{11,4377} = 6.87$, $P < 0.0001$), with sharks having greater activity rates during the autumn months (October, November, December) than during the rest of the year except for March and May. Bottom depth of site was also a significant predictor of mean activity rate ($F_{1,4377} = 24.47$, $P < 0.001$). There was a significant interaction between month and time of day ($F_{11,4377} = 7.10$, $P < 0.0001$); however, this interaction was driven by just one month (December) when sharks had greater activity rates during the day than during the night. Sharks had significantly greater activity rates during the night in all other months (Tukey's HSD: $P < 0.01$) except January ($P = 0.98$) and February ($P = 0.3884$), when no differences were observed.

Association of size and sex with diel patterns of depth

The mean depth of all 27 passively monitored sharks differed between day and night, which is consistent with the actively tracked sharks and the passively monitored, frequently detected sharks. The mean ± SE depth of all passively monitored sharks during the day was 121 ± 5 m and the mean depth at night was 106 ± 5 m (linear mixed model: $F_{1,446} = 21.19$, $P < 0.0001$). The mean depth of sharks varied with bottom depth of site ($F_{1,446} = 500.86$, $P < 0.0001$) and the length of shark ($F_{1,446} = 13.56$, $P = 0.0003$). There was no significant difference between the mean depths of females (118 ± 6 m) and males (108 ± 6 m) ($F_{1,446} = 0.10$, $P = 0.75$), and there were no significant interaction effects (time*sex: $F_{1,446} = 0.50$, $P = 0.48$; length*sex: $F_{1,446} = 0.29$, $P = 0.59$). Larger sharks occupied shallower depths than smaller sharks during the day ($F_{1,25} = 6.87$, $r^2 = 0.22$, $P = 0.0147$) and during the night ($F_{1,25} = 9.31$, $r^2 = 0.27$, $P = 0.0053$; Fig. 6).

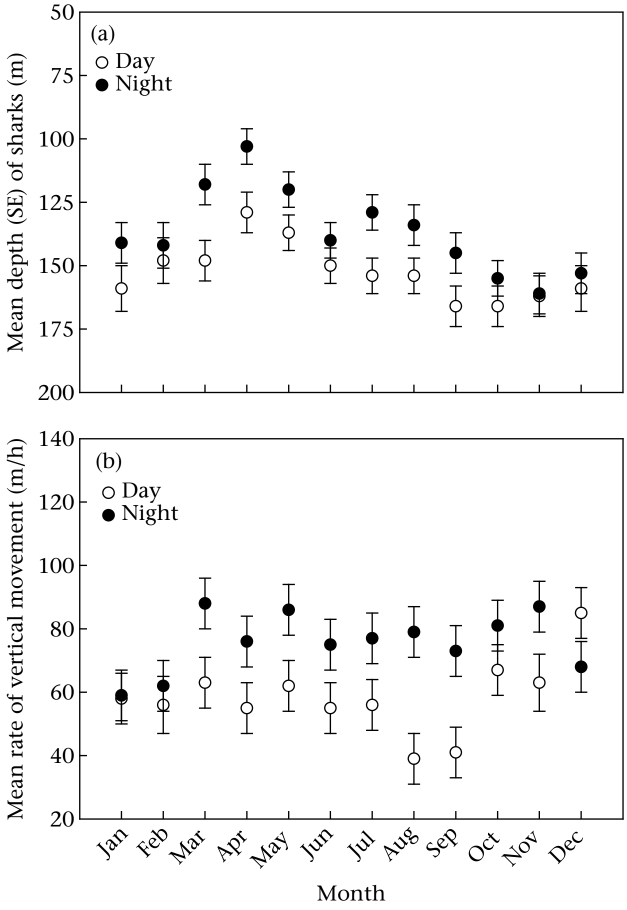

Figure 5. Mean (a) depth and (b) rate of vertical movement each month during December 2005–December 2007 for sixgill sharks detected at least 7 months out of the year by VR2s in Puget Sound ($N = 14$ sharks).

Pairs of sharks moving together

The depth profiles of pairs of sharks tracked and monitored simultaneously over 24 h periods in Elliott Bay showed obvious patterns of synchrony (Fig. 7a, b). Cross-correlation analysis showed that both time series were highly correlated (Pearson correlation: $r_{277} = 0.89$ and $r_{290} = 0.85$, respectively). At Bainbridge

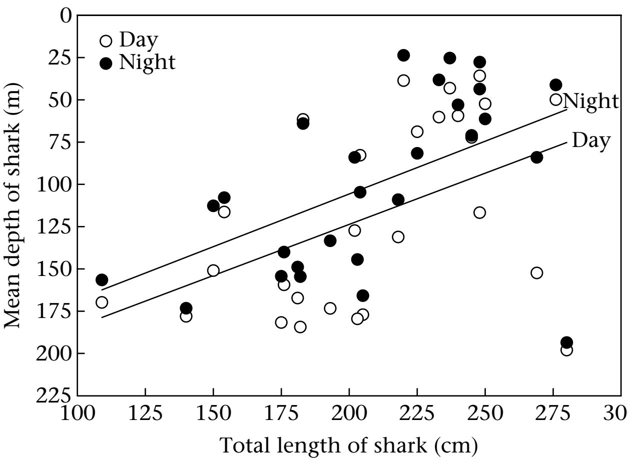

Figure 6. Mean depth of all 27 sharks during day and night as detected by passive monitoring VR2 receivers between December 2005 and December 2007 across all sites within Puget Sound.

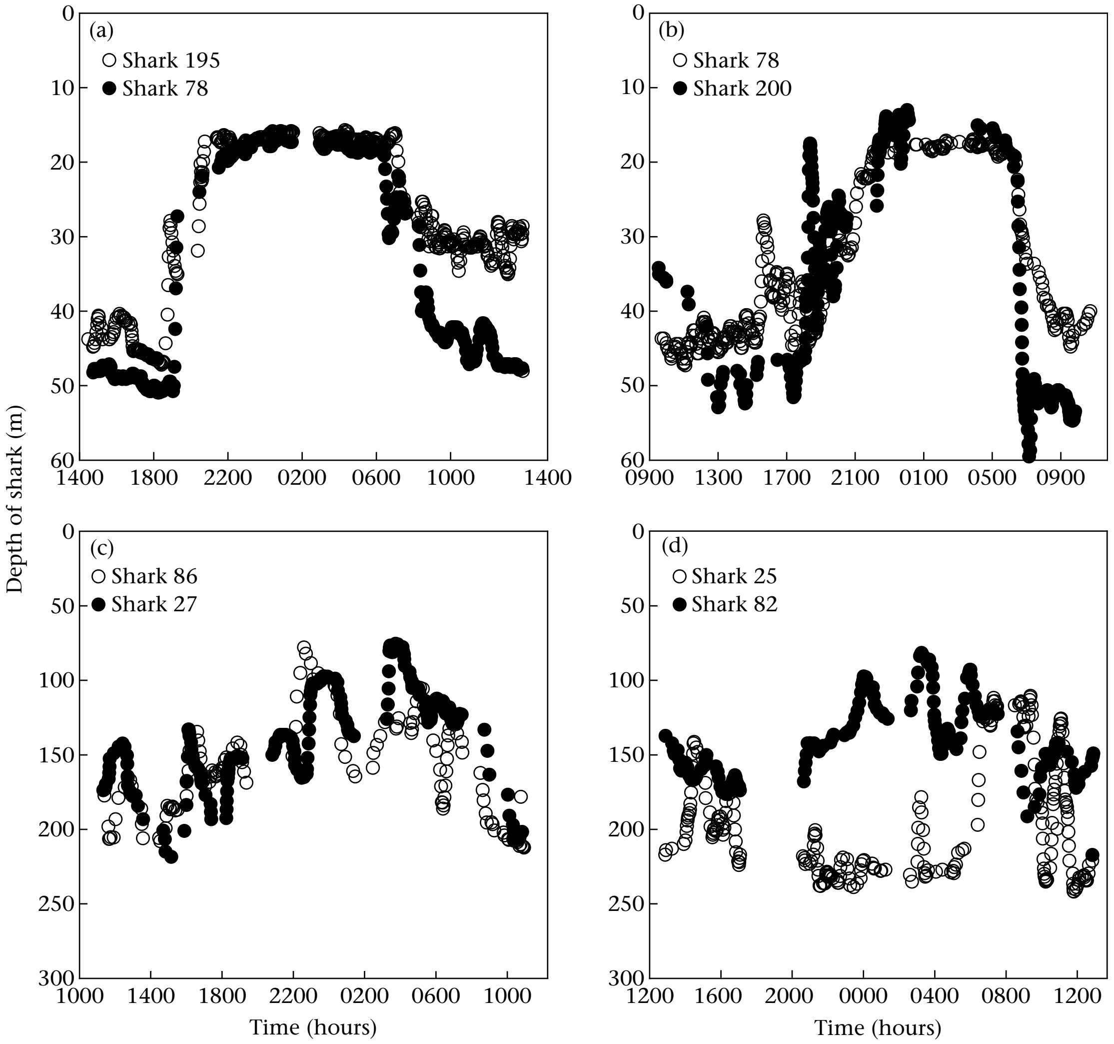

Figure 7. Depth profiles of pairs of sixgill sharks actively tracked simultaneously over an entire 24 h session: (a) Elliott Bay, 13 September 2007; (b) Elliott Bay, 7 May 2007; (c) Bainbridge, 9 August 2007; (d) Bainbridge, 23 August 2007.

Island, sharks tracked together did not show the clear crepuscular movement seen in Elliott Bay, but one shark pair (Fig. 7c) did show highly correlated changes in behaviour over the entire 24 h ($r_{264} = 0.72$). However, the second pair of sharks at Bainbridge Island (Fig. 7d) showed much more independence in their depth profiles ($r_{264} = -0.09$).

Hypothesis 2: Avoiding Predators or Competitors

Predicting fast rates of vertical movement

The absolute rates of vertical movement by sixgill sharks measured during active tracking were greater at Bainbridge Island than at Elliott Bay (linear mixed model: $F_{1,6316} = 18.69$, $P < 0.0001$) and greater during the night than during the day ($F_{1,6316} = 41.46$, $P < 0.0001$) at both tracking sites (Bainbridge: day = 1.25 m/min, night = 1.51 m/min; Elliott Bay: day = 0.30 m/min, night = 0.47 m/min). The maximum ascent rate observed was 14 m/min and the maximum descent rate observed was 13 m/min (Fig. 8). There were significantly higher probabilities of rare events of vertical movement (>2 SD from each shark path's mean) occurring at night than day (logistic regression: $F_{1,46} = 45.78$, $P < 0.0001$) and during an ebb tide than during a flood tide ($F_{1,46} = 14.42$, $P = 0.0004$). Comparing each day/tide combination, rare vertical movements were most likely to occur during night-time ebb tides and least likely to occur during daytime flood tides (Fig. 9). There were no differences

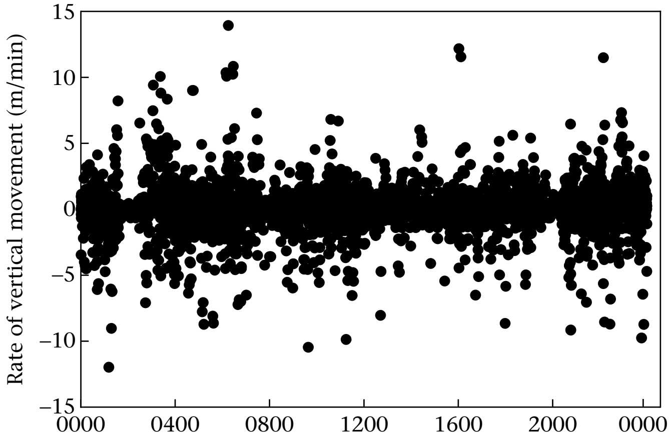

Figure 8. Rates of vertical movement (ascents and descents) across 18 24-h tracking sessions of 10 sixgill sharks.

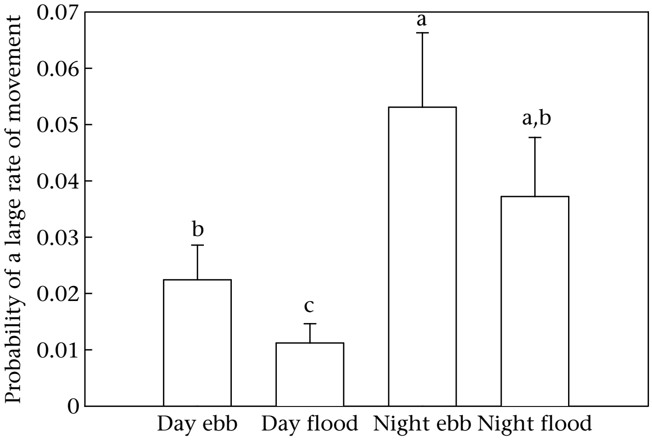

Figure 9. Probability of a rare rate (>2 SD from mean rate) of vertical movement among day/night ebb/flood categories. Different letters above bars denote significant differences between groups ($P < 0.05$).

between shark, site and path (shark) ($P > 0.05$) and there was no significant interaction between time and tide ($P = 0.2765$).

Hypothesis 3: Bioenergetics Advantages

We found no evidence that actively tracked sixgill sharks used temperature to behaviourally thermoregulate on a diel basis (Fig. 10). Water temperature in the winter of 2006 and 2007 varied less than 1 °C from the surface to >200 m depth in the main channel of Puget Sound, so there is limited scope for thermoregulation in winter. Actively tracked sharks in Elliott Bay experienced less than 1 °C change across all vertical movements in both summer and winter (Fig. 10a, b). During the summer, when the main channel is stratified, sixgill sharks tracked at Bainbridge Island did not rise above the thermocline (40–60 m depth) during any of our active tracking paths (Fig. 10c, d).

DISCUSSION

In this study, we examined patterns of vertical movement of 27 sixgill sharks for up to 2 years. Having behavioural data on 27 individual sharks is unique, as most studies looking at the movement patterns of sharks have relied on data from a much smaller number of animals, generally six or fewer individuals (one notable exception is the 22 blue sharks, *Prionace glauca*, tracked by Carey & Scharold (1990)). Moreover, the array of acoustic receivers deployed in Puget Sound by various city, county, state, federal and tribal agencies (up to 250 sites in Puget Sound) provided a unique opportunity to gather high-resolution information across a very large spatial scale.

Overall, we found that sixgill sharks have consistent diel behavioural patterns throughout the year in Puget Sound where sharks inhabit greater depths during the day than during the night and are more active (greater variation in depth and greater rates of vertical movement) at night than during the day. These patterns were confirmed by data from actively tracked sharks, passively monitored sharks that were frequently detected, and passively monitored sharks as a whole. Our observations may reveal more about sixgill shark behaviour in Puget Sound (or about behaviour of subadult individuals) than they do about sixgill shark behaviour in general, as Carey & Clark (1995) did not observe diel patterns of activity for two sixgill sharks tracked for 2 and 4 days in Bermuda. These two sharks were much larger (3.5 and 3.8 m total length) than those tracked in this study and inhabited much deeper waters (600–1000 m).

The clear and consistent patterns of vertical movement and levels of activity across size and sex of sharks and across multiple spatial scales most broadly support the hypothesis that foraging behaviour influences diel patterns of vertical movement in sixgill sharks. Moreover, synchronous movements of pairs of sharks provide evidence that sharks are responding to similar stimuli and not trying to evade other sharks as potential predators or competitors.

The change in vertical distribution of sharks between day and night differed between tracking sites (just a few kilometres apart). In Elliott Bay, sharks typically made one large vertical move at dawn and another at dusk. At Bainbridge Island, sharks tended to make many large vertical movements during the night at shallower depths than they occupied during the day. These different behaviours between sites could represent differences in foraging activity. It is likely that the abundance and distribution of prey differs between a shallow embayment and the deeper main channel. Potential prey species that display diel activity patterns similar to the observed patterns of sixgill sharks in Puget Sound include white-spotted ratfish (Quinn et al. 1980; K. S. Andrews, unpublished data), Pacific hake, *Merluccius productus* (Gustafson et al. 2000), English sole, *Parophrys vetulus* (M. L. Moser, unpublished data), and Dungeness crab, *Cancer magister* (Holsman et al. 2006). English sole and spotted ratfish inhabit all depths and are the most abundant species collected in central Puget Sound trawl surveys since 1991 (T. Quinn, unpublished data). Sixgill sharks are known to be generalist predators in other parts of the world (e.g. Ebert 1994, 2003), so it is likely they would take advantage of these abundant prey resources, but our attempts to sample stomach contents in Puget Sound have revealed only empty stomachs ($N = 18$).

Changes in light intensity during crepuscular periods have been hypothesized to initiate foraging behaviours in some pelagic fishes (Carey & Robison 1981; Carey & Scharold 1990; Cartamil & Lowe 2004). The abrupt changes in depth that we observed for sixgill sharks in Elliott Bay may be related to changes in light intensity at dawn and dusk; however, at both tracking sites and across all passive receiver sites, we detected higher levels of activity at night when changes in light intensity would be negligible. Therefore, changes in light intensity are not directly responsible for vertical movements but may indeed initiate a transition between behaviours as seen in the diel activity of other marine (e.g. Zaret & Suffern 1976; Neilson & Perry 1990; Watanabe et al. 1999) and terrestrial species (e.g. Erkert 1978; Wauters 2000; Erkert & Kappeler 2004; Maloney et al. 2005).

The activity level of sixgill sharks was greater at night throughout the entire year (except December), which would suggest that sixgill sharks are engaged in nocturnal behaviours that are energetically profitable. The Greenland shark, *Somniosus microcephalus* (Stokesbury et al. 2005), and small-spotted catshark (Sims et al. 2006) are other demersal shark species that are also more active at night. However, many pelagic fishes are more vertically active during the day (*Megachasma pelagios*: Nelson et al. 1997; *Mola mola*: Cartamil & Lowe 2004; juvenile *Isurus oxyrinchus*: Sepulveda et al. 2004; juvenile *Carcharodon carcharias*: Weng et al. 2007). These periods of increased vertical activity for pelagic species have been associated with foraging into the deep scattering layer (Bernal et al. 2001; Klimley et al. 2002), while the benthic small-spotted catshark forages in shallow waters during periods of increased activity (Sims et al. 2006).

The observed pattern of diel vertical migration is the defining behaviour of many aquatic prey species trying to avoid predation risk (Cushing 1951; Harris 1963; Enright & Hamner 1967; Zaret & Suffern 1976). Similarly, terrestrial insects use nocturnal or diurnal

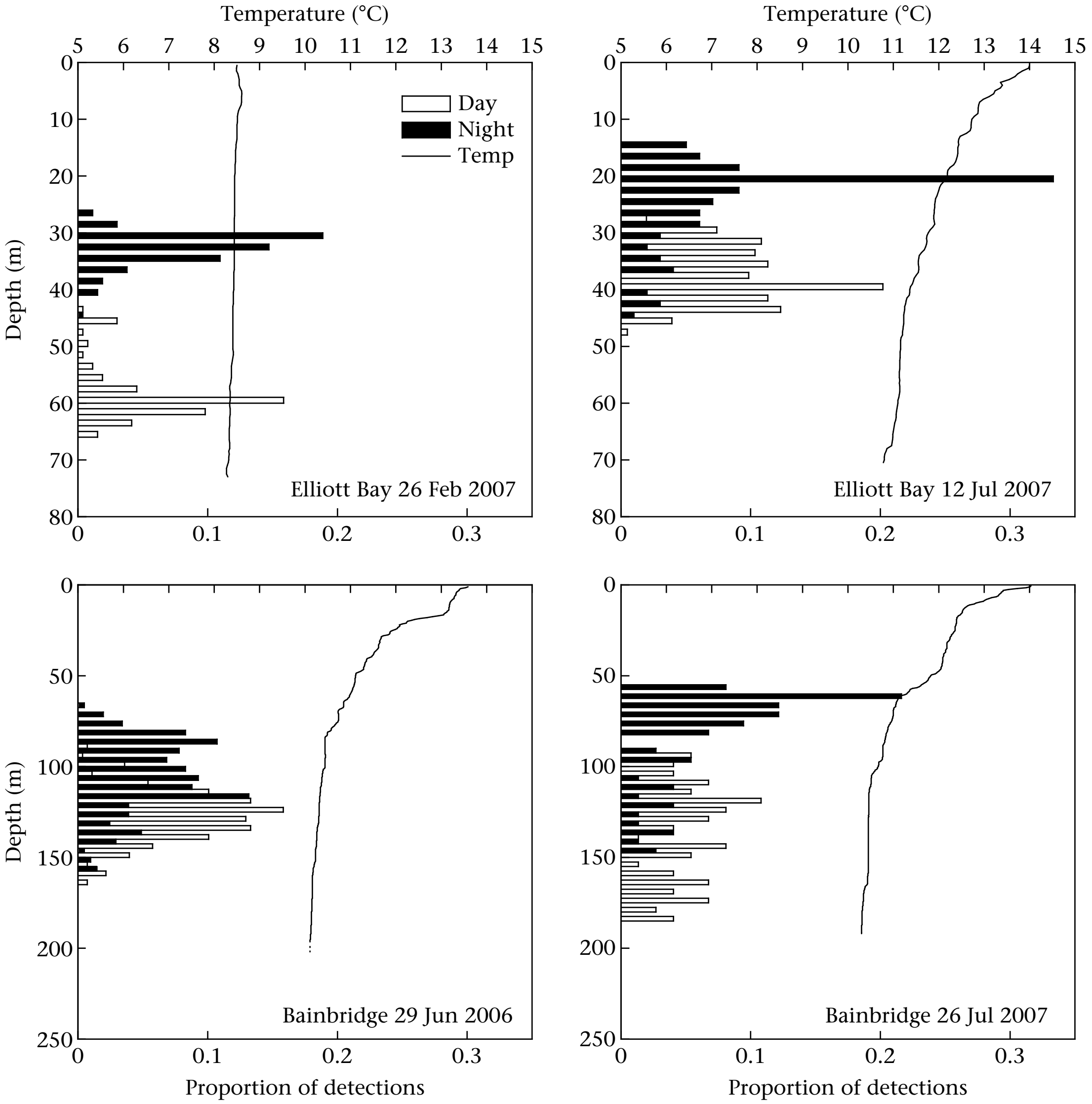

Figure 10. Proportion of active tracking detections during the day and night by depth in relation to water temperature profile at nearby water quality sampling stations (DOE 2008).

behavioural patterns to avoid visually adapted predators or predators with echolocation abilities, respectively (Fullard & Napoleone 2001). Even large predators such as the cheetah, *Acinonyx jubatus* (Durant 2000) or the black bear (MacHutchon et al. 1998) will alter their foraging behaviour or diel activity when other predators or competitors are present. However, sixgill sharks are the largest resident fish in Puget Sound and have few potential predators or competitors in the area besides other sixgill sharks. Both male and female sharks within the size range that we studied all showed the same diel pattern of vertical movement, so smaller sharks did not alter their diel patterns to avoid larger sharks. (However, there may be spatial segregation by size occurring at a different timescale, as we did observe larger sharks inhabiting shallower sites than smaller sharks.) Moreover, the fastest rates of ascent and descent occurred in a predictable manner during night ebb tides. Therefore, the distinct, consistent and predictable changes in behaviour between day and night are not likely to be the result of sixgill sharks avoiding predators or competitors.

Diel changes in behaviour or activity levels for bioenergetic reasons are well established in studies of terrestrial species. Ectothermic vertebrates (Magnuson et al. 1979; Bauwens et al. 1996) as well as large endothermic mammals (Ben Shahar & Fairall 1987; Maloney et al. 2005) regulate their temperature behaviourally by being active when and where abiotic conditions are favourable. In the marine environment, changing depth allows individuals to regulate their temperature through behaviour. Pelagic blue sharks can sustain warmer body temperatures than the surrounding water for several hours at depth after they make vertical migrations into warm surface waters (Carey & Scharold 1990). The benthic small-spotted catshark, *Scyliorhinus canicula*, shows diel changes in its vertical distribution similar to the sixgill shark, and this pattern conveys bioenergetic advantages for the catshark where it can hunt in prey-rich, warmer waters at night and rest in cooler waters during the day, which is presumably easier for digestive processes (Sims et al. 2006). However, all of our active tracking data at Bainbridge Island showed that sharks did not rise above the thermocline (~40–60 m), and sharks in Elliott Bay experienced less than 1 °C change when they moved from 50 m up to 20 m. Therefore, the scope of behavioural thermoregulation is limited because water temperatures are relatively constant for most of the sharks' vertical movements. Although sharks did not rise above the thermocline while actively tracked, passive monitoring data showed that 9% of the detections in the main channel were above 50 m (even as shallow as 3 m at two nearshore main channel sites during the summer); thus, there does not appear to be a thermal barrier for sixgill sharks in Puget Sound.

Conclusions

Hypotheses explaining diel patterns of behaviour in animals generally involve trade-offs between avoiding competitors or predators, bioenergetic efficiency via thermoregulation, and optimal foraging strategies. For carnivorous predators, this behaviour is often related to the behaviour and activity patterns of their prey (Zielinski 1988, 2000). The diel, tidal and seasonal rhythms of activity that we found in sixgill sharks are most consistent with the hypothesis that foraging activity is responsible for diel patterns of vertical movement. As an active predator and a passive scavenger, sixgill sharks are able to forage across the entire food web, making them a good candidate as an indicator species for the overall health of the Puget Sound ecosystem. With advances in acoustic, satellite and radiotracking technology, we can observe the behaviour of animals over extended periods and across large spatial scales. Changes in the behaviour or patterns of activity for a species, particularly apex predators, may provide early indications of fundamental changes occurring in the ecosystem.

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References

Andrews, K. S., Levin, P. S., Katz, S. L., Farrer, D., Gallucci, V. F. & Bargmann, G. 2007. Acoustic monitoring of sixgill shark movements in Puget Sound: evidence for localized movement. *Canadian Journal of Zoology*, **85**, 1136–1142.

Bauwens, D., Hertz, P. E. & Castilla, A. M. 1996. Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology*, **77**, 1818–1830.

Ben Shahar, R. & Fairall, N. 1987. Comparison of the diurnal activity patterns of blue wildebeest and red hartebeest. *South African Journal of Wildlife Research*, **17**, 49–54.

Bernal, D., Dickson, K., Shadwick, R. & Graham, J. 2001. Review: analysis of the evolutionary convergence for high performance swimming in lamnid sharks and tunas. *Comparative Biochemistry and Physiology A-Molecular & Integrative Physiology*, **129**, 695–726.

Carey, F. & Clark, E. 1995. Depth telemetry from the sixgill shark, *Hexanchus griseus*, at Bermuda. *Environmental Biology of Fishes*, **42**, 7–14.

Carey, F. & Robison, B. 1981. Daily patterns in the activities of swordfish *Xiphias gladius* observed by acoustic telemetry. *Fishery Bulletin*, **79**, 277–292.

Carey, F. & Scharold, J. 1990. Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, **106**, 329–342.

Carey, F., Kanwisher, J., Brazier, O., Gabrielson, G., Casey, J. & Pratt, H. 1982. Temperature and activities of a white shark, *Carcharodon carcharias*. *Copeia*, **1982**, 254–260.

Cartamil, D. & Lowe, C. 2004. Diel movement patterns of ocean sunfish *Mola mola* off southern California. *Marine Ecology Progress Series*, **266**, 245–253.

Chapman, D., Pikitch, E., Babcock, E. & Shivji, M. 2007. Deep-diving and diel changes in vertical habitat use by Caribbean reef sharks *Carcharhinus perezi*. *Marine Ecology Progress Series*, **344**, 271–275.

Clark, C. W. & Levy, D. A. 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *American Naturalist*, **131**, 271–290.

Cushing, D. H. 1951. The vertical migration of planktonic crustacea. *Biological Reviews*, **26**, 158–192.

Dewar, H., Mous, P., Domeier, M., Muljadi, A., Pet, J. & Whitty, J. 2008. Movements and site fidelity of the giant manta ray, *Manta birostris*, in the Komodo marine Park, Indonesia. *Marine Biology*, **155**, 121–133.

DOE 2008. *Washington State Department of Ecology*. Accessed January 2008. http://www.ecy.wa.gov/programs/eap/mar_wat/data.html.

Dunbrack, R. & Zielinski, R. 2003. Seasonal and diurnal activity of sixgill sharks (*Hexanchus griseus*) on a shallow water reef in the Strait of Georgia, British Columbia. *Canadian Journal of Zoology-Revue Canadienne De Zoologie*, **81**, 1107–1111.

Durant, S. 2000. Living with the enemy: avoidance of hyenas and lions by cheetahs in the Serengeti. *Behavioral Ecology*, **11**, 624–632.

Ebert, D. A. 1986. Biological aspects of the sixgill shark, *Hexanchus griseus*. *Copeia*, **1986**, 131–135.

Ebert, D. A. 1994. Diet of the sixgill shark *Hexanchus griseus* off southern Africa. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap*, **14**, 213–218.

Ebert, D. A. 2002. Some observations on the reproductive biology of the sixgill shark *Hexanchus griseus* (Bonnaterre, 1788) from Southern African waters. *South African Journal of Marine Science-Suid-Afrikaanse Tydskrif Vir Seewetenskap*, **24**, 359–363.

Ebert, D. A. 2003. *Sharks, Rays and Chimaeras of California*. Berkeley: University of California Press.

Enright, J. T. & Hamner, W. M. 1967. Vertical diurnal migration and endogenous rhythmicity. *Science*, **157**, 937–941.

Erkert, H. 1978. Sunset related timing of flight activity in neotropical bats. *Oecologia*, **37**, 59–67.

Erkert, H. & Kappeler, P. 2004. Arrived in the light: diel and seasonal activity patterns in wild Verreaux's sifakas (*Propithecus v. verreauxi*; Primates: Indriidae. *Behavioral Ecology and Sociobiology*, **57**, 174–186.

Fullard, J. & Napoleone, N. 2001. Diel flight periodicity and the evolution of auditory defences in the Macrolepidoptera. *Animal Behaviour*, **62**, 349–368.

Gray, D. & Hodgson, A. 1999. Endogenous rhythms of locomotor activity in the high-shore limpet, *Helcion pectunculus* (Patellogastropoda). *Animal Behaviour*, **57**, 387–391.

Gustafson, R. G., Lenarz, W. H., McCain, B. B., Schmitt, C. C., Grant, W. S., Builder, T. L. & Methot, R. D. 2000. *Status Review of Pacific Hake, Pacific Cod, and Walleye Pollock from Puget Sound, Washington*. Washington, D.C.: U.S. Department of Commerce NOAA Technical Memorandum NMFS-NWFSC-44.

Harris, J. E. 1963. The role of endogenous rhythms in vertical migration. *Journal of the Marine Biological Association*, **43**, 153–166.

Hays, G. 2003. A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, **503**, 163–170.

Heupel, M. & Simpfendorfer, C. 2005. Quantitative analysis of aggregation behavior in juvenile blacktip sharks. *Marine Biology*, **147**, 1239–1249.

Holland, K., Wetherbee, B., Lowe, C. & Meyer, C. 1999. Movements of tiger sharks (*Galeocerdo cuvier*) in coastal Hawaiian waters. *Marine Biology*, **134**, 665–673.

Holomuzki, J. 1986. Predator avoidance and diel patterns of microhabitat use by larval tiger salamanders. *Ecology*, **67**, 737–748.

Holsman, K., McDonald, P. & Armstrong, D. 2006. Intertidal migration and habitat use by subadult Dungeness crab *Cancer magister* in a NE Pacific estuary. *Marine Ecology Progress Series*, **308**, 183–195.

Holts, D. & Bedford, D. 1993. Horizontal and vertical movements of the shortfin mako shark, *Isurus oxyrinchus*, in the southern California bight. *Australian Journal of Marine and Freshwater Research*, **44**, 901–909.

Hulbert, L., Sigler, M. & Lunsford, C. 2006. Depth and movement behaviour of the Pacific sleeper shark in the northeast Pacific Ocean. *Journal of Fish Biology*, **69**, 406–425.

Klimley, A., Beavers, S., Curtis, T. & Jorgensen, S. 2002. Movements and swimming behavior of three species of sharks in La Jolla Canyon, California. *Environmental Biology of Fishes*, **63**, 117–135.

Lampert, W. 1989. The adaptive significance of diel vertical migration of zooplankton. *Functional Ecology*, **3**, 21–27.

MacHutchon, A. G., Himmer, S., Davis, H. & Gallagher, M. 1998. Temporal and spatial activity patterns among coastal bear populations. *Ursus*, **10**, 539–546.

Magnuson, J., Crowder, L. & Medvick, P. 1979. Temperature as an ecological resource. *American Zoologist*, **19**, 331–343.

Maloney, S. K., Moss, G., Cartmell, T. & Mitchell, D. 2005. Alteration in diel activity patterns as a thermoregulatory strategy in black wildebeest (*Connochaetes gnou*). *Journal of Comparative Physiology A*, **191**, 1055–1064.

Nakano, H., Matsunaga, H., Okamoto, K. & Okazaki, M. 2003. Acoustic tracking of bigeye thresher shark *Alopias superciliosus* in the eastern Pacific Ocean. *Marine Ecology Progress Series*, **265**, 255–261.

Naylor, E. 1988. Clock-controlled behaviour in intertidal animals. In: *Behavioral Adaptation to Intertidal Life* (Ed. by G. Chelazzi & M. Vannini), pp. 1–14. New York: Plenum.

Neilson, J. & Perry, R. 1990. Diel vertical migrations of marine fishes: an obligate or facultative process? *Advances in Marine Biology*, **26**, 115–168.

Nelson, D., McKibben, J., Strong, W., Lowe, C., Sisneros, J., Schroeder, D. & Lavenberg, R. 1997. An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular vertical migrator. *Environmental Biology of Fishes*, **49**, 389–399.

NMFS 2007. *Sound Science: Synthesizing Ecological and Socioeconomic Information about the Puget Sound Ecosystem* (M.H. Ruckelshaus & M.M. McClure, Coordinators; prepared in cooperation with the Sound Science collaborative team). Seattle, Washington: U.S. Department of Commerce, National Oceanic and Atmospheric Administration (NMFS), Northwest Fisheries Science Center.

Ohman, M. 1990. The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs*, **60**, 257–281.

Orcutt, J. & Porter, K. 1983. Diel vertical migration by zooplankton: constant and fluctuating temperature effects on life-history parameters of *Daphnia*. *Limnology and Oceanography*, **28**, 720–730.

Palmer, J. 1995. *The Biological Rhythms and Clocks of Intertidal Animals*. New York: Oxford University Press.

Quinn, T., Miller, B. & Wingert, R. 1980. Depth distribution and seasonal and diel movements of ratfish *Hydrolagus colliei* in Puget Sound, Washington. *Fishery Bulletin*, **78**, 816–821.

Quinnell, S. & Schmitt, C. 1991. *Abundance of Puget Sound Demersal Fishes: 1987 Research Trawl Survey Results*. Olympia: Washington State Department of Fisheries.

Reum, J. C. & Essington, T. E. 2008. Seasonal variation in guild structure of the Puget Sound demersal fish community. *Estuaries and Coasts*, **31**, 790–801.

SAS 2004. *SAS 9.1.3*. Cary, North Carolina: SAS Institute.

Sepulveda, C., Kohin, S., Chan, C., Vetter, R. & Graham, J. 2004. Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Marine Biology*, **145**, 191–199.

Shepard, E., Ahmed, M., Southall, E., Witt, M., Metcalfe, J. & Sims, D. 2006. Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology Progress Series*, **328**, 205–213.

Sims, D., Wearmouth, V., Southall, E., Hill, J., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G., Righton, D., Metcalfe, J., Nash, J. & Morritt, D. 2006. Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology*, **75**, 176–190.

Skomal, G. & Benz, G. 2004. Ultrasonic tracking of Greenland sharks, *Somniosus microcephalus* under Arctic ice. *Marine Biology*, **145**, 489–498.

Staubitz, W. W., Bortleson, G., Seamans, S. D., Tesoriero, A. J. & Black, R. W. 1997. Water-quality assessment of the Puget Sound Basin, Washington: environmental setting and its implications for water quality and aquatic biota. In: Water-Resources Investigations Report 97-4013. Tacoma, Washington: U.S. Geological Survey.

Stich, H. & Lampert, W. 1984. Growth and reproduction of migrating and non-migrating *Daphnia* species under simulated food and temperature conditions of diurnal vertical migration. *Oecologia*, **61**, 192–196.

Stokesbury, M., Harvey-Clark, C., Gallant, J., Block, B. & Myers, R. 2005. Movement and environmental preferences of Greenland sharks (*Somniosus microcephalus*) electronically tagged in the St Lawrence Estuary, Canada. *Marine Biology*, **148**, 159–165.

Strickland, R. M. 1983. *The Fertile Fjord*. Seattle: Washington Sea Grant.

SYSTAT 2004. *SYSTAT 11.0 for Windows*. Richmond, California: SPSS.

Watanabe, H., Moku, M., Kawaguchi, K., Ishimaru, K. & Ohno, A. 1999. Diel vertical migration of myctophid fishes (family Myctophidae) in the transitional waters of the western North Pacific. *Fisheries Oceanography*, **8**, 115–127.

Wauters, L. A. 2000. Squirrels: medium sized granivores in woodland habitats. In: *Activity Patterns in Small Mammals: an Ecological Approach* (Ed. by S. Halle & N. Stenseth), pp. 131–143. Berlin: Springer-Verlag.

Weng, K. & Block, B. 2004. Diel vertical migration of the bigeye thresher shark (*Alopias superciliosus*), a species possessing orbital retia mirabilia. *Fishery Bulletin*, **102**, 221–229.

Weng, K., O'Sullivan, J., Lowe, C., Winkler, C., Dewar, H. & Block, B. 2007. Movements, behavior and habitat preferences of juvenile white sharks *Carcharodon carcharias* in the eastern Pacific. *Marine Ecology Progress Series*, **338**, 211–224.

West, G. & Stevens, J. 2001. Archival tagging of school shark, *Galeorhinus galeus*, in Australia: initial results. *Environmental Biology of Fishes*, **60**, 283–298.

Winter, D. F., Banse, K. & Anderson, G. C. 1975. Dynamics of phytoplankton blooms in Puget Sound, a fjord in northwestern United States. *Marine Biology*, **29**, 139–176.

Witteveen, B. H., Foy, R. J., Wynne, K. M. & Tremblay, Y. 2008. Investigation of foraging habits and prey selection by humpback whales (*Megaptera novaeangliae*) using acoustic tags and concurrent fish surveys. *Marine Mammal Science*, **24**, 516–534.

Wurtsbaugh, W. A. & Neverman, D. 1988. Post-feeding thermotaxis and daily vertical migration in a larval fish. *Nature*, **333**, 846–848.

Zaret, T. & Suffern, J. 1976. Vertical migration in zooplankton as a predator avoidance mechanism. *Limnology and Oceanography*, **21**, 804–813.

Zielinski, W. 1988. The influence of daily variation in foraging cost on the activity of small carnivores. *Animal Behaviour*, **36**, 239–249.

Zielinski, W. 2000. Weasels and martens: carnivores in northern latitudes. In: *Activity Patterns in Small Mammals* (Ed. by S. Halle & N. Stenseth), pp. 95–118. Berlin: Springer-Verlag.