

# Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark

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## Summary

1. Diel vertical migration (DVM) is a widespread phenomenon among marine and freshwater organisms and many studies with various taxa have sought to understand its adaptive significance. Among crustacean zooplankton and juveniles of some fish species DVM is accepted widely as an antipredator behaviour, but little is known about its adaptive value for relatively large-bodied, adult predatory fish such as sharks. Moreover, the majority of studies have focused on pelagic forms, which raises the question of whether DVM occurs in bottom-living predators.

2. To investigate DVM in benthic predatory fish in the marine environment and to determine why it might occur we tracked movements of adult male dogfish (*Scyliorhinus canicula*) by short- and long-term acoustic and archival telemetry. Movement studies were complemented with measurements of prey abundance and availability and thermal habitat within home ranges. A thermal choice experiment and energy budget modelling was used to investigate trade-offs between foraging and thermal habitat selection.

3. Male dogfish undertook normal DVM (nocturnal ascent) within relatively small home ranges (~100 × 100 m) comprising along-bottom movements up submarine slopes from deeper, colder waters occupied during the day into warmer, shallow prey-rich areas above the thermocline at night. Few daytime vertical movements occurred. Levels of activity were higher during the night above the thermocline compared to below it during the day indicating they foraged in warm water and rested in colder depths.

4. A thermal choice experiment using environmentally realistic temperatures supported the field observation that dogfish positively avoided warmer water even when it was associated with greater food availability. Males in laboratory aquaria moved into warm water from a cooler refuge only to obtain food, and after food consumption they preferred to rest and digest in cooler water.

5. Modelling of energy budgets under different realistic thermal-choice scenarios indicated dogfish adopting a 'hunt warm – rest cool' strategy could lower daily energy costs by just over 4%. Our results provide the first clear evidence that are consistent with the hypothesis that a benthic marine-fish predator utilizes DVM as an energy conservation strategy that increases bioenergetic efficiency.

**Key-words:** behavioural ecology, electronic tags, energetics, fish, thermocline.

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## Introduction

Diel vertical migration (DVM) is a widespread behavioural phenomenon among aquatic organisms. It is often characterized by large-amplitude movements comprising an ascent into shallow water around dusk, nighttime feeding in productive surface layers, followed by descent at dawn to deeper depths for occupation during daylight hours. Numerous hypotheses have been forwarded to explain the adaptive significance of normal DVM (nocturnal ascent) among both marine and freshwater taxa (Clark & Levy 1988; Neill 1990; Hays 2003). It was suggested over 40 years ago that there might be a metabolic advantage to DVM in zooplankton (McLaren 1963), although subsequent work has shown that predator evasion is a more likely explanation for its widespread planktonic occurrence. Studies with crustacean zooplankton show DVM represents an anti-predator behaviour shaped by the trade-off between higher predation risk in warm, food-rich surface waters and reduced growth in colder, deep water (Ohman 1990; Loose & Dawidowicz 1994; Hays 2003). Nevertheless, DVM may serve different functions in different situations and certainly the principal function may vary between invertebrates and vertebrates.

Studies of DVM in fish have also investigated potential factors contributing to the evolution of this behaviour. In juveniles of some pelagic species from freshwater lakes predation risk was found to be a main factor driving DVM (Clark & Levy 1988; Scheuerell & Schindler 2003), whereas in other species vertical movements were undertaken principally to select temperatures that maximize growth rate (Wurtsbaugh & Neverman 1988). Studies on juveniles of marine pelagic species indicate that under certain conditions DVM occurs as a response to spatio-temporal changes in prey abundance presumably to maximize foraging and growth by tracking the DVM of prey (Schabetsberger *et al.* 2000). DVM behaviour also occurs widely among mesopelagic fishes throughout the oceans (Watanabe *et al.* 1999; Watanabe, Kawaguchi & Hayashi 2002).

There is empirical support for DVM occurring in fish due to heightened predation risk, tracking of prey abundances and as an energy conservation strategy. However, the field and experimental studies undertaken to date have mainly investigated factors influencing DVM of larval and juvenile fish feeding on zooplankton in freshwater lakes (e.g. Scheuerell & Schindler 2003). By comparison, there have been few attempts to understand vertical movements in large predatory fish in the sea, such as sharks for example (West & Stevens 2001), even though the factors influencing diel movements in species with lower predation risk conferred by relatively large body size may yield interesting insights into the adaptive value of DVM. It is arguable that DVM in benthic, predatory fish would be most likely to occur in habitats with steep seabed topography and strong thermal stratification where metabolic energy savings could be made by ectothermic fish adopting an appropriate

strategy. Steep seabed habitat, often with complex vertical thermal structure in the surrounding water column is characteristic of many important marine habitats, such as temperate and tropical reefs and seamounts (Wolanski & Hamner 1988; Rogers 1994), that support diverse fish species. Therefore, it is possible that bottom-living predatory fish may also readily exploit prey and thermal gradients to increase net energy gain in a manner similar to pelagic species (Watanabe *et al.* 1999; Schabetsberger *et al.* 2000).

The ability of ectothermic marine fish to utilize environmental gradients to conserve energy is often assumed, but empirical studies demonstrating the basis for such responses are lacking. In this study we combined field studies that track the movements of adult male dogfish (*Scyliorhinus canicula*) and simultaneous sampling of prey abundances, thermal resources and predator occurrence, with laboratory studies aimed at identifying the trade-off between water temperature and food availability. Our objectives were, first, to identify whether dogfish undertake DVM, and secondly to investigate what factors might contribute to DVM in this benthic marine predator. We show for the first time, to our knowledge, that a benthic shark undertakes DVM behaviour consistent with an energy conservation strategy.

## Materials and methods

The movements and behaviour of wild male dogfish were monitored in a sheltered tidal sea lough (Lough Hyne, Republic of Ireland). Lough Hyne is an important field site for studying free-living marine fish behaviour because of its relatively small area (0.6 × 0.4 km), sheltered location allowing continuous monitoring of fish movements, diverse marine habitats (e.g. tidal flats, steep underwater cliffs) and minimal emigration of fish due to the narrow and shallow rapids (width < 20 m, depth 1–3 m) at its opening to the Atlantic Ocean (Sims, Nash & Morritt 2001). In this study male dogfish were monitored using four different techniques. Over the short term (1–2 weeks), horizontal movements were determined using acoustic telemetry (September 2001, August–September 2002) and swimming depth and thermal habitat of dogfish were recorded using electronic data-storage tags (July–August 2003). Moored acoustic receivers enabled longer term (3 months) monitoring of dogfish home ranges (May–July 2004) while conventional mark–recapture was used to provide information on philopatry over annual cycles (tagging periods: July 1995, July–August 1996, September 2001, August–September 2002, April 2003, July 2003, October 2003, January 2004).

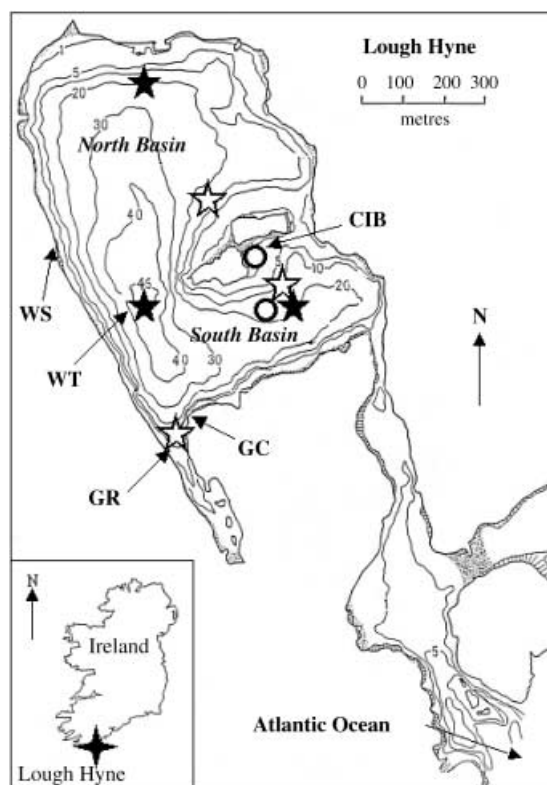
### ACOUSTIC TELEMETRY

Four male dogfish captured by nocturnal gill-netting in the shallow waters of Castle Island bay (Fig. 1; Table 1) were each fitted externally with a continuous acoustic transmitter (16 mm diameter, 65 mm long, weight in

**Table 1.** Summary data of male dogfish tracked with electronic tags

Fish no.	Mass (g)	Tag type*	Capture location†	Track start	Track period (days)	Recapture location
1	1250	AP	CIB	07 September 2001	12	—
2	1375	AP	CIB	24 August 2002	9	—
3	1350	AP	GR	24 August 2002	10	—
4	950	DST	CIB	10 August 2003	10	WS
5	1230	DST	CIB	04 July 2003	10	CIB
6	950	DST	WS	01 August 2003	10	CIB
7	890	AC	CIB	20 May 2004	81	—
8	1100	AC	CIB	20 May 2004	81	—
9	1075	AC	GC	20 May 2004	81	—
10	1000	AC	GC	20 May 2004	81	—

\*Tag type abbreviations: AP, acoustic pinger; DST, data storage tag; AC, coded acoustic transmitter. †Capture–recapture location abbreviations: CIB, Castle Island Bay; GC, Goleen Corner; GR, Goleen Refuge; WS, Western Shore.



**Fig. 1.** Map of the study site, Lough Hyne, showing bathymetry, temperature-depth profiling stations (filled stars), acoustic receiver moorings (open stars), baited trap locations (open circles), together with specific positions of locations named in the text (abbreviations with arrows): CIB, Castle Island bay; GC, Goleen corner; GR, Goleen refuge; WS, Western shore; WT, Western Trough. Numbers on contour lines are water depths in m.

water 10 g; Vemco Ltd, Nova Scotia, Canada) using the same method as described in Sims *et al.* (2001). The power output of the transmitters was 147 dB re 1  $\mu$ Pa at 1 m with a pulse period of 1 s, range of ~500 m, and battery life in excess of 300 days. Each dogfish was anaesthetized (ethyl p-aminobenzoate, Sigma St. Louis, Missouri, USA) before a transmitter was attached to the dorsal surface at a position level with the midpoint of the pectoral fins using three T-bar anchor tags secured

subcutaneously. The trailing end of each anchor tag was passed through one of three plastic eyeholes in the transmitter's epoxy-moulded harness. A 1-mm internal diameter alloy crimp was attached to the trailing end of each anchor tag and was used to secure the transmitter as closely as possible to the fish's dorsal surface to avoid transmitter movement. Transmitter attachment was completed within 5–10 min, following which all fish were recovered in clean, aerated seawater and held into a current such that clean seawater entered the mouth and pharynx, irrigating the gills. Each fish was supported at the surface until it recovered strong swimming movements, at which time it was released back to a holding tank. The fish were then observed for a further 15–60 min to ensure there were no adverse effects from the anaesthesia or tagging procedure before being released at the original point of capture.

The horizontal movements of these fish were monitored for the next 9–12 days by determining transmitter locations every 1–2 h. Transmitters produced sound energy on widely separated frequencies at 1 Hz repetition rate and were located by triangulation using an underwater, pole-mounted directional hydrophone and an acoustic receiver (VR11 hydrophone, VR60 receiver; Vemco Ltd). Geographical positions were determined using the method of Sims *et al.* (2001).

Four different male dogfish (Table 1) captured in Castle Island Bay and Goleen Corner were fitted with internal, coded acoustic transmitters to monitor longer term movements. Coded transmitters were of similar dimensions and mass to continuous 'pingers' and were placed intraperitoneally in an anaesthetized dogfish through a 2.5-cm long incision in the abdominal wall. Incisions were closed with four dissolvable sutures (Vicryl 4–0, Ethicon, Belgium) and one permanent suture (Mersilk 2–0, Ethicon). Procedures were completed within 5–10 min of initial anaesthetic administration and fish were recovered and released as described above. Each coded transmitter produced a sound pulse randomly between each successive 60–180-s period on the same frequency as other coded tags (Vemco Ltd) rather than on separate frequencies at 1-s intervals. The

quasi-random pulse rates of each coded transmitter were monitored by three moored acoustic receivers (VR2 receiver, Vemco Ltd). The detection radius of these receivers was found to be 250 m and they were positioned at three discrete, non-overlapping positions to record the residence times of males within these areas (Fig. 1). The receivers were recovered after a period of 3 months and data were downloaded.

#### DATA STORAGE TAGS

The data storage tags used were LTD\_2400 (designed by CEFAS, Lowestoft and manufactured by Lotek Wireless, Newmarket, Canada). The tag is cylindrical, 32 mm long  $\times$  11 mm (diameter) with the electronic components encapsulated in clear polyester resin. The device weighs 8 g in air ( $\sim$ 4 g in seawater). Data logging is controlled by a temperature compensated (0–34 °C) real-time clock having an accuracy of 1 part per million (p.p.m.) (i.e.  $\sim$ 30 s per year). The tag monitors pressure to a depth of 100 m with an accuracy of 1% full scale (i.e. 1 m) and a resolution of 0.05% full scale (i.e. 50 mm). The tag monitors temperature from 0° to 30 °C with an accuracy of 0.1° and a resolution of 0.05 °C. The internal temperature sensor takes 10 s to reach 66% of a step change from 0 to 30 °C (when in direct contact with the medium that is changing temperature). Recorded data are stored to non-volatile flash memory with a data retention time in excess of 10 years and a capacity to store 64 000 pressure and 64 000 temperature measurements.

Three male dogfish were captured in Castle Island bay or on the Western shore (Table 1) and a DST was inserted through a 1.5-cm incision in the abdominal wall of each anaesthetized fish using the same surgical and recovery procedures as for coded transmitter-tagged fish. These individuals were recaptured and full data sets of pressure (swimming depth) and ambient temperature were downloaded from tags.

#### MARK–RECAPTURE

Male dogfish were captured with gill nets (dimensions: 20  $\times$  2 m, stretched mesh size, 50 mm) deployed principally in slope habitats (spanning  $\sim$ 4–12 m depth) in the South Basin and Western Shore during the hours of darkness. Soak times were short, ranging from 40 to 120 min. Captured individuals were removed from the net and measured (length, mass) before being marked subcutaneously with colour-coded, numbered T-bar anchor tags (FD-94, Floy Tag Inc., Seattle, WA) and released at the respective capture location.

#### ENVIRONMENTAL SAMPLING

Diel changes in water temperature in two key habitats used by male dogfish (Castle Island bay, 1.7 m depth; South Basin, 18.7 m depth) were recorded by dataloggers (Minilog, Vemco Ltd) sampling temperature and

depth every 2.5 min for 4 days during the period when fish were tracked in 2002. Vertical profiles of temperature were taken at three fixed sampling stations each month at 5-m depth intervals from the surface to the seabed (WTW Oxi330i, Woburn, USA) to locate the position of the thermocline. Profiles were taken while fish were being tracked in the Western Trough (August, September 2001–02) and in the North and South Basins during September 2001 and 2002 (Fig. 1).

Cylindrical traps (0.4 long  $\times$  0.2 m diameter) constructed from plastic mesh (max. diameter 4 mm) were used to determine the relative abundance of prey in shallow and deep habitats of the South Basin. The conical entrance of each trap was 40 mm in diameter to match the maximum mouth gape of adult male dogfish. Three weighted traps baited with fresh fish fillets were deployed 2 m apart in Castle Island bay (2 m depth) both day and night for 4 days at the same time that temperature loggers were deployed. The same traps were set in the South Basin (18 m depth) both day and night for 4 further days to investigate the relative abundance of prey in the deeper water compared to the shallow area (Fig. 1). Pots were checked after each 12-h period, when any contents were removed and measured before each trap was re-baited and deployed.

Times of dawn and dusk during tag deployments at Lough Hyne were recorded using a standard light meter (Lutron LX101).

#### SEAL OCCURRENCE

To examine whether predator presence may have influenced behaviour patterns of dogfish we monitored the occurrence of grey seals (*Halichoerus grypus*). The number of grey seals observed at the water's surface was counted within the confines of the lough from a 4-m boat and from the marine-station jetty during three 13-day periods: 17–30 July 2003, 22 January–3 February 2004 and 18–31 July 2004. Within each 13-day period, surface sightings were recorded both day and night during the normal course of our research. Night-time records were restricted to times when there was sufficient moonlight, or when seal vocalizations were heard. Vocalizations were counted as a single seal. In terms of sightings effort, boat movements (rowing or powered) during which sightings could be made occurred regularly both day and night within the lough, resulting in about 12 h activity per day during each 13-day period. Although the precise number of hours spent on the water was not determined, each 13-day period comprised identical research activities so were very similar in terms of the times, and overall time, spent on the water and, thus, the amount of time during which seals could be observed or heard.

#### THERMAL CHOICE EXPERIMENT

A simple thermal choice experiment was used to determine whether male dogfish shifted distribution



dependent on water temperature. We hypothesized that if food was made available in one compartment of a two-chamber choice tank then, on average, individuals would spend more time in this side compared with the other compartment. By increasing water temperature in the feeding compartment we could then test whether male dogfish shifted to the cooler compartment or remained in the area where food was available.

Four adult males (each ~0.9 kg mass) were captured during routine Marine Biological Association (MBA) trawls approximately 6 miles south of Plymouth in July 2001. Environmental temperatures at the site of capture (mean temperature data: surface, 14.7 °C; 19.7 m depth, 13.4 °C) were similar to those used in the experiment. Dogfish were placed into a re-circulating seawater aquarium (1.8 × 0.8 × 0.8 m) at the MBA laboratory with a Perspex sheet dividing the tank into two equal compartments. A rectangular hole (0.2 × 0.1 m) in one bottom corner of the Perspex allowed dogfish to move freely between the two compartments. The distribution of fish between the compartments was recorded every 0.5 h between 09:00 and 17:00 h for 5 days (Monday–Friday) each week for 6 weeks. Dogfish were fed on chopped fish and squid (100 g) given twice per week (Monday and Thursday). This food was made available in compartment C2 over the 6-week period. Light–dark (L:D) phases were timer-controlled with each phase lasting 12 h (light 08:00–20:00 h). To approximate wild conditions ‘daytime’ illumination was kept at a relatively low level between 148 and 170 lux, while the dark phase was < 10 lux (Lutron LX101). All conditions were held constant during the experiment except in weeks 3 and 4, when the water temperature of C2 was increased by 0.9 °C compared to C1 (mean temperature: C1, 14.4 °C ± 0.3 SE,  $n = 9$ ; C2, 15.3 °C ± 0.2 SE,  $n = 9$ ). The experiment was conducted during July and August at the same time of year when field trackings were also undertaken.

#### ENERGETICS MODEL

To examine potential energetic mechanisms underlying observed behaviour of male dogfish we calculated the energy costs associated with occupying different-temperature habitat at varying levels of activity and feeding metabolism (specific dynamic action: SDA). Depth and temperature records from each of the three data-storage-tagged dogfish comprised the empirical data used to build a model of energy expenditure (model 1) which was then subjected to manipulations of thermal regime according to fixed and biased-random functions (models 2–5). For each 10-day period over which each male was tracked there were 1440 records of temperature and depth available to examine temporal and spatial changes in energy expenditure. The internal temperatures recorded by tags served as a good proxy of external water temperature because dogfish are ectothermic. From these temperature data the energy expenditure attributable to standard metabolism ( $R_S$ )

(metabolic rate at zero swimming speed) was determined using the oxygen consumption–body mass relationship at 15 °C given in Sims (1996):

$$\dot{V}O_2 = 0.104M^{0.855}$$

where  $\dot{V}O_2$  is oxygen consumption in mg O<sub>2</sub> h<sup>-1</sup> and  $M$  is mass in grams. This relationship was applied to the temperature values of each male to produce mass-corrected standard metabolic rates at 15 °C. These same values were temperature-corrected using the  $Q_{10}$  value for *S. canicula* of 2.16 determined between 7 and 17 °C (Butler & Taylor 1975), and the  $Q_{10}$ -metabolic rate conversion equation given in Davenport & Sayer (1993).

Change in levels of metabolism associated with activity (active metabolism,  $R_A$ ) was incorporated into model 1 by first calculating the change in depth selected by a dogfish between each successive 10-min interval. We assumed that increases in the rate of change of depth with time were correlated with increased locomotor intensity that would, in turn, result in higher metabolic rates. Secondly, the energetic costs of activity of tagged dogfish were estimated using data for oxygen consumption measurements of adult dogfish in laboratory aquaria at three levels of activity, measured as the minutes per hour spent actively swimming (low swimming activity, 5 min h<sup>-1</sup>; medium, 10 min h<sup>-1</sup>; high, 30 min h<sup>-1</sup>) (Sims 1994). Activity values (depth change with time) for tagged fish were separated into three levels corresponding broadly to the expenditure levels identified in the laboratory study: ‘low’ (0.1–1.9 m 10 min<sup>-1</sup>), ‘medium’ (2.0–4.9 m 10 min<sup>-1</sup>) and ‘high’ (5.0–12.0 m 10 min<sup>-1</sup>), where activity was measured as the vertical depth in metres moved within each 10-min time period. The oxygen consumption rate at each level of activity was then applied to the empirical data and, using each temperature value corresponding to each activity value, The empirical estimates of active metabolic rate were temperature-corrected as described previously. Standard metabolic rate was subtracted from active metabolic rate for each 10-min time period.

We also incorporated feeding metabolism ( $R_F$ ) into model 1. Based on data of feeding frequency in wild sharks (Wetherbee, Gruber & Cortes 1990), we assumed a dogfish captured prey items of mass equivalent to 6.5% of the dogfish’s mass at a rate of 0.3 prey masses per day during the 10-day tracking period. For the purposes of the model we used this prey amount because feeding metabolic costs at the 6.5% level have been determined (Sims & Davies 1994), so costs associated with different thermal regimes can be accurately estimated. The feeding frequency of wild dogfish is not known, but the low percentage of stomach emptiness observed in trawl-caught specimens (Wetherbee *et al.* 1990) indicates frequent feeding probably close to the level we assumed. The energetic costs were calculated using the relationship between SDA and time for adult dogfish (mass ~800 g) at 15 °C given in Sims & Davies (1994). This relationship is described adequately by the linear regression:

$$VO_2 = -0.0128t + 135.61 \quad r^2 = 0.80$$

where  $VO_2$  is oxygen consumption in  $\text{mg O}_2 \text{ h}^{-1}$  and  $t$  is time in hours. Using this relationship the activity-free energy expenditure attributable to food consumption and digestion was determined for each 10-min interval over a total period of 90 h (the SDA duration for a 6.5% body-weight meal; Sims & Davies 1994). As for activity,  $R_F$  values were temperature-corrected according to the water temperature selected by the fish at each time interval and standard metabolic rate was subtracted from feeding metabolic rate at each 10-min time period.

The model 1 data set summarized realistic changes in metabolism ( $R_S$ ,  $R_F$  and  $R_A$ ) for the actual thermal habitat occupied by each tagged dogfish over the 10-day tracking periods. To investigate how temperature selection influenced energy costs and, hence, why particular thermal habitats may have been selected over others, the model 1 data set was manipulated in four separate models, repeated for each fish. In model 2, 1440 random temperatures were generated for substitution with the actual water temperature experienced by each dogfish. Here, the random numbers were generated using a normal distribution with the mean and standard deviation (SD) derived from 'warm' temperatures above the thermocline that were occupied by each tracked fish. The energy expenditure within each successive 10-min interval was re-calculated with model 1 as a template, but this time using random 'warm' temperatures for temperature correction. Model 3 consisted of randomly generated 'cold' temperatures below the thermocline for re-calculation of energy expenditure. Random temperatures were generated using a normal distribution with the mean and SD taken from the temperatures selected by tagged fish when below the thermocline. Models 4 and 5 were isothermal models where the temperatures for substitution into the model 1 template were fixed at 10 °C (model 4) and 17 °C (model 5). Energy expenditure for each model was summed separately for each 10-day period.

#### STATISTICAL METHODS

The depth of the thermocline was estimated empirically by field measurement; however, we also identified the thermocline statistically using data from fish tags (DSTs). For each fish all water temperature values were plotted against corresponding depth for the entire 10-day tracking period. Because the thermocline represents the minimum depth range over which there is maximal temperature change it was detected as the inflection point in the scatterplot of temperature and depth using a piecewise linear regression with breakpoint (STATISTICA v, Statsoft, Tulsa, USA).

To test whether dogfish selected shallow habitat for foraging, the frequency of potential feeding activity was determined for each fish by identifying the number of time intervals satisfying the criterion of medium activity ( $> 2 \text{ m} \times 10 \text{ min}^{-1}$ ) occurring in warm, above-

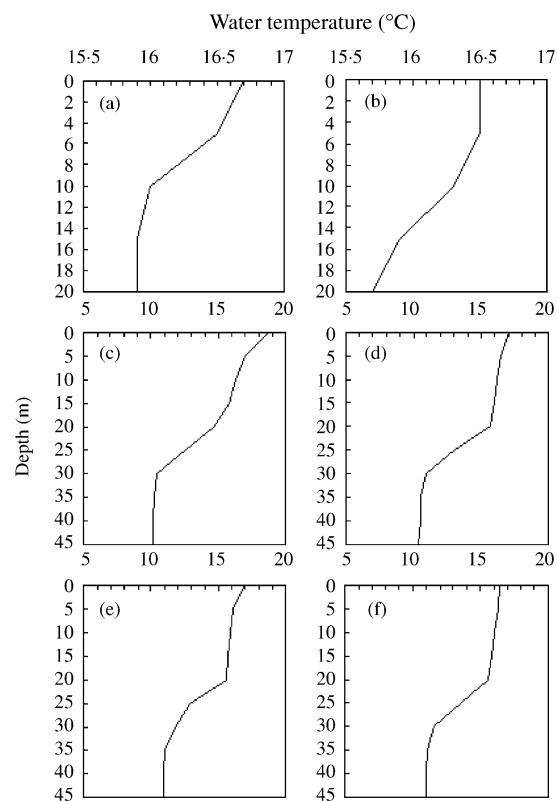
thermocline water temperature. This frequency was then compared statistically using  $\chi^2$  tests (Minitab 13.31, Minitab Inc., State College, USA) with the frequency of potential feeding events derived from the same activity data but with randomly generated temperature data (normal distribution, using the mean and SD of real temperature data).

The catch per unit effort (CPUE, number of prey items  $\text{h}^{-1}$ ) of baited traps during night and day in both shallow and deep habitats was analysed by ANOVA (Minitab 13.31) on  $\log(x + 1)$ -transformed data to normalize variances, with significant differences being identified using a Tukey multiple comparisons test.

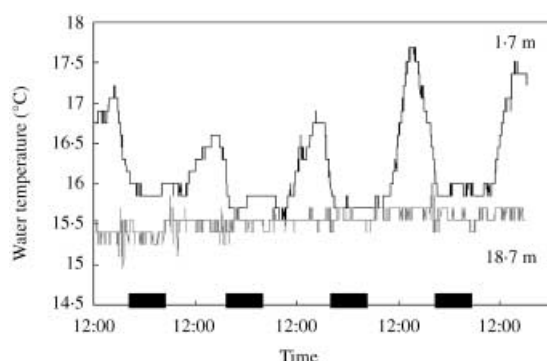
## Results

### THERMAL GRADIENTS

Vertical temperature profiles in the lough showed that surface waters in September were 0.8 °C warmer than water at 20 m depth in both the North and South Basins (Fig. 2a,b). In the deeper Western area there was a 5.4–8.6 °C difference between surface and 45-m temperatures in August and September in both 2001 and 2002 (Fig. 2c–f) indicating strong vertical thermal stratification occurs annually in this location. The depth of the thermocline varied between each of the three sampling stations, reflecting differences in tidal flow



**Fig. 2.** Temperature–depth profiles in the (a) North and (b) South Basins in September 2002, in the Western Trough in (c) August and (d) September 2001, and during (e) August and (f) September 2002.



**Fig. 3.** Diel variations of water temperature in shallow (1.7 m) and deeper (18.7 m) habitats occupied by dogfish in the South Basin. Black bars represent periods from dusk to dawn obtained from direct light measurements.

speed and seabed depth between sites. The September thermocline was found at 6–15 m and 5–10 m in the South and North Basins, respectively, and between 15 and 30 m in the deeper Western Trough in August and September (Fig. 2). Continuous records of water temperature from Castle Island bay and the South Basin showed large fluctuations due to insolation in the shallow habitat (range, 15.6–17.7 °C; mean, 16.2 °C  $\pm$  0.5 SD;  $n$  = 3067) compared to deep water (range, 14.9–16.0 °C; mean, 15.5 °C  $\pm$  0.1 SD;  $n$  = 3047) (Fig. 3).

#### PREY ABUNDANCE

The most common dogfish prey species captured in the baited traps were prawn (*Palaemon serratus*), gobies (Gobiidae) and swimming crab (*Liocarcinus depurator*). The shallow habitat yielded 17.8 and 78.0 times the mean number of animals per unit time than the deep area for night and day deployments, respectively (Table 2). Both night and day CPUE in shallow water were significantly higher than either of those from deep water (ANOVA:  $F_{3,44} = 49.42$ ,  $P < 0.001$ ; Tukey's multiple comparisons, shallow day vs. deep day,  $q_{4,44} = 13.68$ ,  $P < 0.001$ ; shallow day vs. deep night,  $q_{4,44} = 13.59$ ,

$P < 0.001$ ; shallow night vs. deep day,  $q_{4,44} = 10.50$ ,  $P < 0.001$ ; shallow night vs. deep night,  $q_{4,44} = 10.30$ ,  $P < 0.001$ ). The low catch rates in deep water were not different between night and day (Tukey's multiple comparison:  $q_{4,44} = 0.77$ ,  $P > 0.50$ ), but in shallow habitat the day CPUE was marginally higher than that found at night (Tukey's multiple comparison:  $q_{4,44} = 3.95$ ,  $0.05 > P > 0.025$ ). The biomass (g h<sup>-1</sup>) captured in traps in shallow water was 5.5 and 11.0 times greater than in deep water for night and day deployments, respectively (ANOVA:  $F_{3,44} = 24.16$ ,  $P < 0.001$ ) (Table 2). The differences in both CPUE and biomass were driven principally by the high abundance of *P. serratus* found in shallow habitat, which were more than 73 times more numerous than in deep water regardless of light phase (ANOVA:  $F_{3,44} = 51.07$ ,  $P < 0.001$ ) (Table 2).

#### SEAL OCCURRENCE

No grey seals (*H. grypus*) were observed within the lough in summer (July) 2003 and 2004. However, 76 sightings were recorded in winter (January–February) 2004, with a mean of 5.8 ( $\pm$  4.6 SD) sightings per day over the 13-day period. These sightings comprised single animals as well as groups of two or three individuals. This shows that the occurrence of grey seals in the lough was seasonal with an absence during summer.

#### HORIZONTAL MOVEMENTS

Male dogfish tracked continuously for 9–12 days were found to exhibit short-range movements away from and back to a central activity area located in the South Basin (fish 1–3; Table 1). They spent the major part of time within relatively small areas: fish 1 and 2 spent 72% and 64% of time in core areas measuring 72  $\times$  120 m and 120  $\times$  105 m, respectively (Fig. 4), while fish 3 spent 50% in an area of 60  $\times$  255 m situated around the western tip of Castle Island. The locations of core activity were associated with steep sloping habitat, with dogfish generally occurring in deeper water during

**Table 2.** Abundance of potential prey items of dogfish captured in baited traps in shallow (2 m depth) and deep (18 m) water during day and night. Number of deployments per treatment given in parentheses

			Shallow		Deep	
			Night ( $n$ = 12)	Day ( $n$ = 9)	Night ( $n$ = 15)	Day ( $n$ = 12)
All prey	CPUE ( $N$ h <sup>-1</sup> )	Mean	2.32 <sup>a</sup>	3.90 <sup>a</sup>	0.13 <sup>b</sup>	0.05 <sup>b</sup>
		Median	2.41	4.04	0.09	0
		SD	1.60	1.95	0.11	0.08
Biomass (g h <sup>-1</sup> )		Mean	9.24	15.74	1.67	1.43
		Median	8.10	15.43	1.14	0
		SD	6.73	6.19	0.10	0.08
<i>P. serratus</i>	CPUE ( $N$ h <sup>-1</sup> )	Mean	2.19	3.68	0.03	0
		Median	2.24	3.93	0	0
		SD	1.55	1.91	0.06	0

Means with different superscript were significantly different,  $P < 0.001$  (ANOVA on  $\log(x + 1)$ -transformed data and Tukey's multiple comparisons).

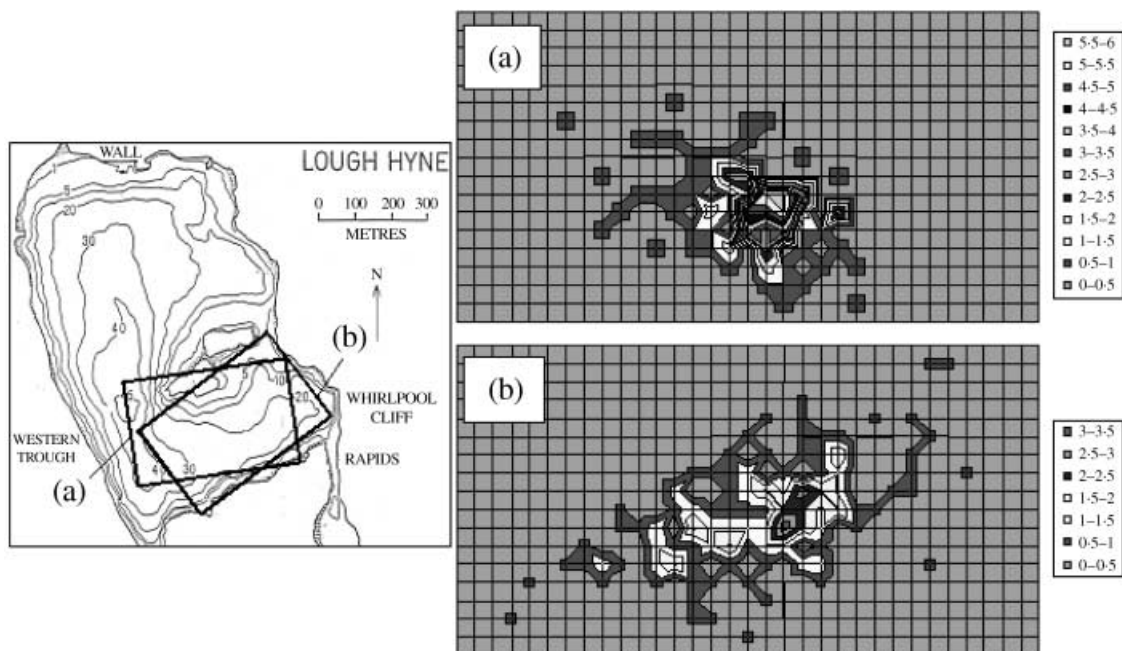


Fig. 4. Contour plots of percentage fixes per grid square showing the home ranges of male dogfish (a) 1 and (b) 2 in the South Basin.

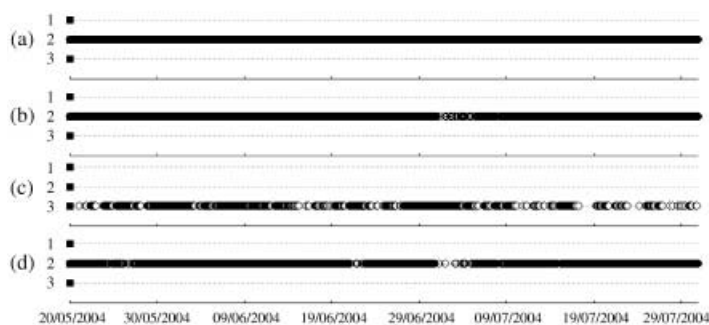


Fig. 5. Occupancy of transmitter-tagged male dogfish 7–10 (a–d) within home ranges in the South Basin (line 2, South Basin opposite Castle Island; line 3, Goleen corner) from May to August 2004 as recorded by moored acoustic receivers. None of these fish entered the North Basin (line 1).

the day and shallow areas at night. This station-keeping behaviour was also evident over broader temporal scales. Four male dogfish (nos 7–10; Table 1) tracked using moored receivers remained within 250-m radii of the South Basin (SB) and Goleen Refuge (GR) receivers for periods of up to 81 days (until the receiver was removed for data retrieval) (Fig. 5a–d). Fish 7 remained within range of the SB receiver continually for 81 days, whereas dogfish 8 and 10 spent two short periods of about 5 days moving out of and back into range (Fig. 5b,d). Fish 9 was the only individual to occupy a home range close to the GR underwater cliff and spent short periods moving between this and other habitats close by for about 50% of the 81-day track time. Taken together, the short and longer-term tracking episodes indicate male dogfish in the lough occupy relatively small home ranges close to steep underwater slopes for several months.

Dogfish were always caught in the first two meshes directly above the leaded footline of the gill-nets, indicating that they travel very close to the sea-bottom during

night-time foraging. Between 1995 and 2003, 174 male dogfish were marked with numbered tags in the lough. During this period 17.8% were recaptured, with 18 individuals recaptured in the same location where they were caught originally, having been at liberty for between 76 and 2185 days (mean, 325.2 days; median, 165.5 days). These results and those from acoustic telemetry show male dogfish exhibit distinct philopatry to particular slope habitat over temporal scales ranging from a few days to several years.

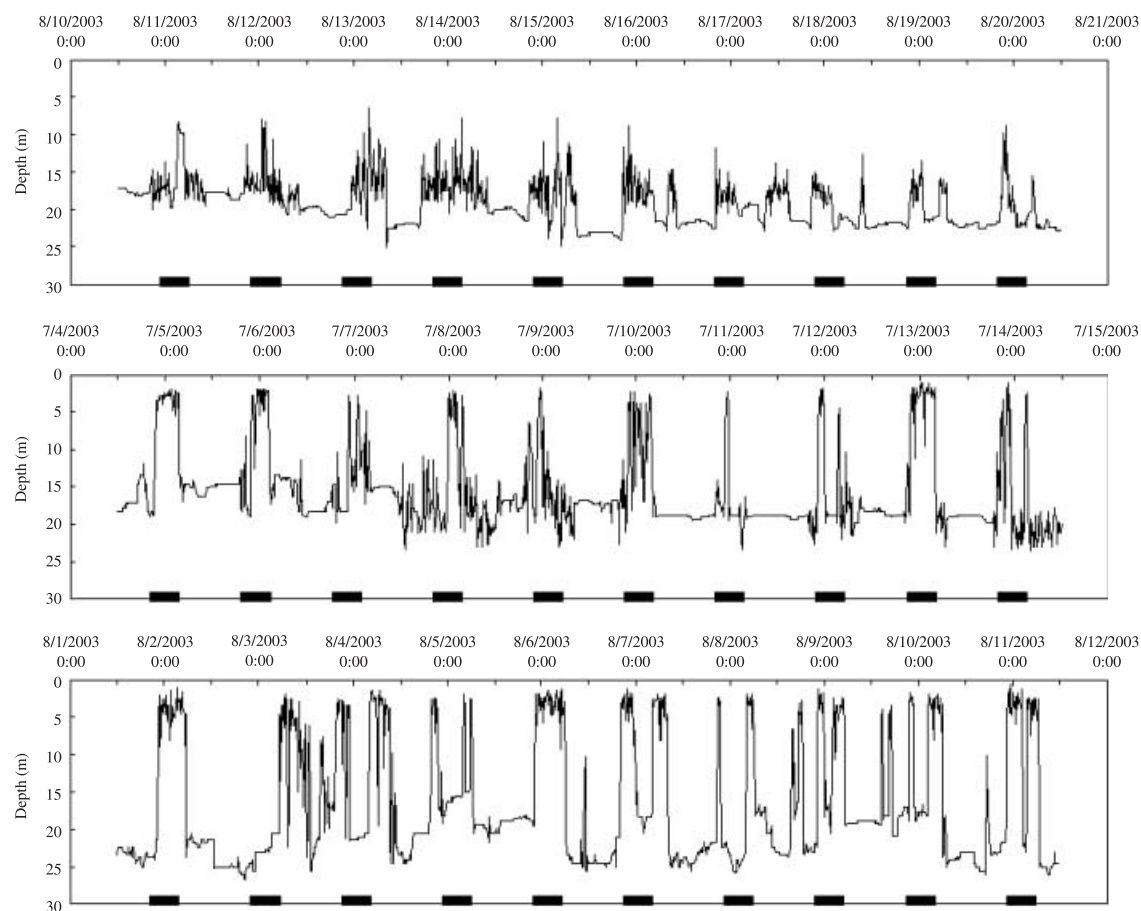
#### DIEL VERTICAL MIGRATION

Dogfish 4, 5 and 6 showed similar general patterns of behaviour over the 10-day tracking periods. During daylight hours males tended to stay in deeper water (17.8–20.2 m) (Table 3) but at dawn, dusk and during darkness they showed clear upward vertical migrations and generally ranged into shallow water (0.5–10 m) around Castle Island and the Western shore (Fig. 6a–c).



**Table 3.** Day and night depth and water temperature preferences of male dogfish (nos 4–6) recorded with data storage tags in relation to the thermocline depth and temperature

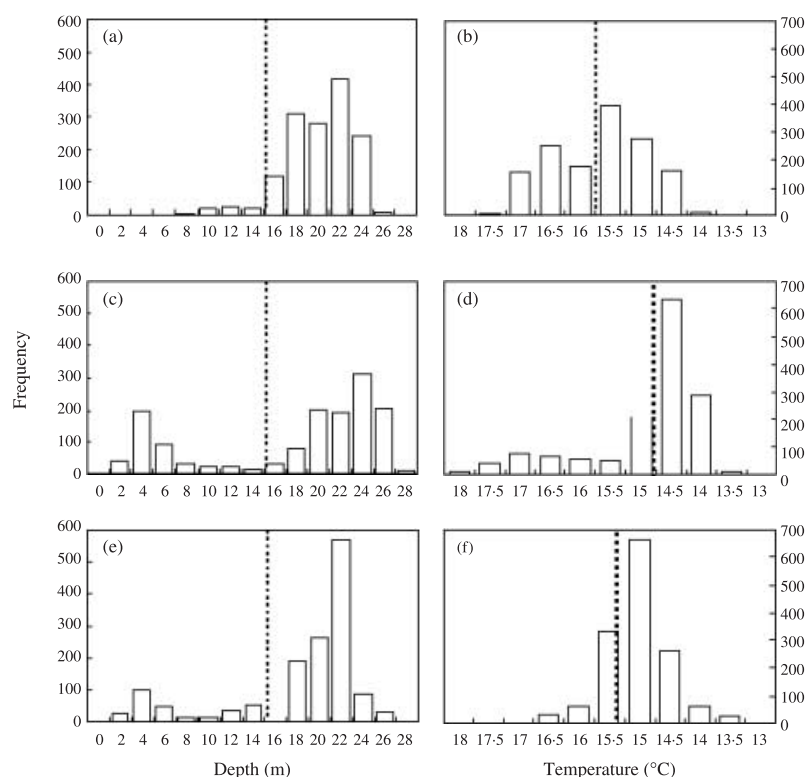
			Male dogfish		
			4	5	6
Depth (m)					
Day (05 : 00–18 : 50 h)	Mean		20.21	18.87	17.83
	Median		21.20	21.40	18.30
	SD		2.57	7.02	2.07
Night (19 : 00–04 : 50 h)	Mean		18.36	13.82	12.72
	Median		18.5	17.40	15.65
	SD		3.08	8.73	6.93
Temperature (°C)					
Day (05 : 00–18 : 50 h)	Mean		15.11	14.44	14.60
	Median		15.02	14.29	14.59
	SD		0.67	0.74	0.35
Night (19 : 00–04 : 50 h)	Mean		15.82	14.98	15.01
	Median		15.96	14.46	15.02
	SD		0.75	1.07	0.58
Thermocline depth (m)			15.45	14.66	14.77
Temperature at thermocline (°C)	Mean		16.18	14.54	14.91
	SD		0.54	0.15	0.19



**Fig. 6.** Patterns of diel vertical migration in dogfish (a) 4 in August 2003, (b) 5 in July 2003 and (c) 6 in August 2003. Black bars represent periods from dusk to dawn obtained from direct light measurements.

However, this behaviour was not always uniform within or between individuals. During the night, each fish made upward vertical migrations, with movements to < 10 m depth on between 70, 90 and 100% of nights

during the period studied for fish 4, 6 and 5, respectively (Fig. 6a–c). Fish rarely stayed at the shallowest depths for the entire dark period. Statistical analysis of temperature–depth profiles stored by the tags showed that



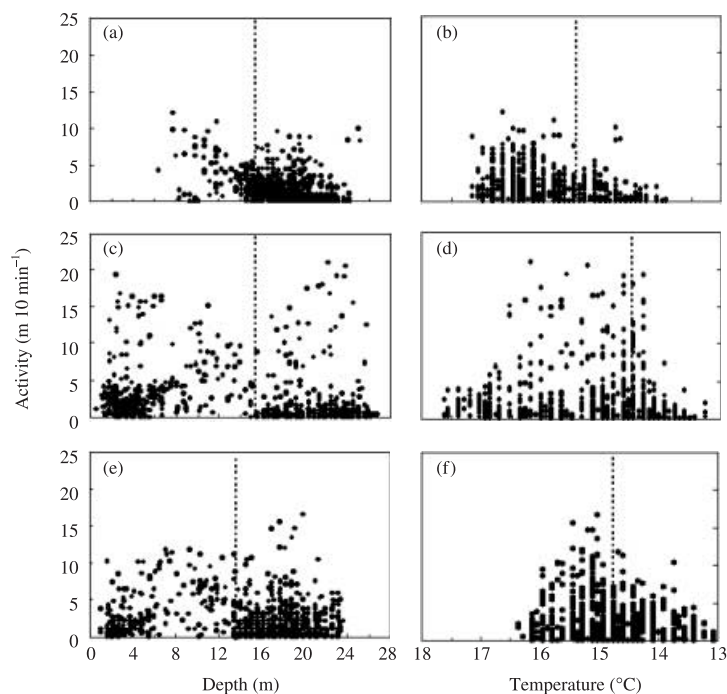
**Fig. 7.** Depth and thermal habitat selection of dogfish (a, b) 4, (c, d) 5 and (e, f) 6 in relation to depth (left panel) and mean temperature (right panel) of the thermocline (dotted lines) in July and August 2003. Note that most time was spent in deeper, colder waters below the thermocline with relatively shorter excursions into shallow, warmer habitats.

**Table 4.** Day and night activity rates of data-storage-tagged male dogfish (nos 4–6) and activity rates above and below the thermocline

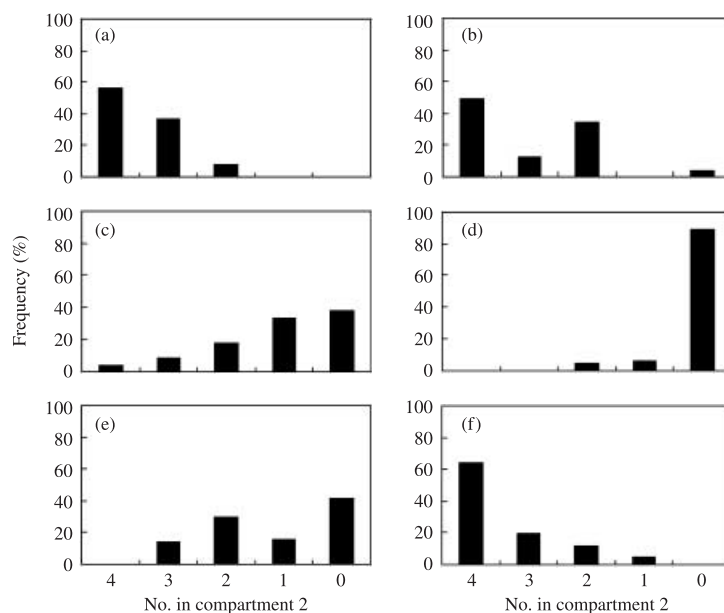
		Male dogfish		
		4	5	6
Activity (m 10 min <sup>-1</sup> ) Day (05 : 00–18 : 50 h)	Mean	0.56	1.30	0.57
	Median	0	0	0
	SD	1.23	2.96	1.25
Night (19 : 00–04 : 50 h)	Mean	1.43	1.46	2.42
	Median	0.70	0.50	1.30
	SD	1.95	3.02	2.91
Activity above thermocline	Mean	1.88	2.83	1.97
	Median	1.20	1.40	0.60
	SD	2.04	3.87	2.93
	<i>n</i>	594	406	572
Activity below thermocline	Mean	0.34	0.80	0.91
	Median	0	0	0
	SD	0.91	2.33	1.64
	<i>n</i>	847	1035	869

the thermocline depths for all fish were between 14.66 and 15.45 m. Male dogfish spent the majority of the time below the thermocline (71.4–91.9%; Fig. 7a,c,e) in water that was generally less than 15.5 °C (Fig. 7b,d,f). Nocturnal vertical movements were into areas that were between 0.41 and 0.71 °C warmer than habitat occupied during the day below the thermocline (Table 3). Analysis of changes in vertical step length per unit time

(a proxy for activity) showed that males were, in general, 2.6 times more active at night than during the day (Table 4). Levels of activity were significantly higher in shallow areas above the thermocline than below it (Mann–Whitney *U*-tests with equal sample sizes: fish 4,  $U' = 282\,514$ ,  $P < 0.0001$ ; fish 5,  $U' = 122\,607$ ,  $P < 0.0001$ ; fish 6,  $U' = 221\,272$ ,  $P < 0.0001$ ) (Table 3; Fig. 8a,e). Hence, cooler water below the thermocline



**Fig. 8.** Activity rates of dogfish (a, b) 4, (c, d) 5 and (e, f) 6 at different depths (left panel) and water temperature (right panel) in July and August 2003. Note that there were lower activity rates in colder water below the thermocline.



**Fig. 9.** Frequency of occurrence of four male dogfish in compartment C2 of a two-compartment, thermal-choice chamber over weeks 1–6 (a–f). Food was provided in C2 twice per week with isothermal conditions occurring in weeks 1 and 2 (a, b), an increase in temperature of 0.9 °C in C2 during weeks 3 and 4 (c, d), and return to isothermal conditions between C1 and C2 in weeks 5 and 6 (e, f).

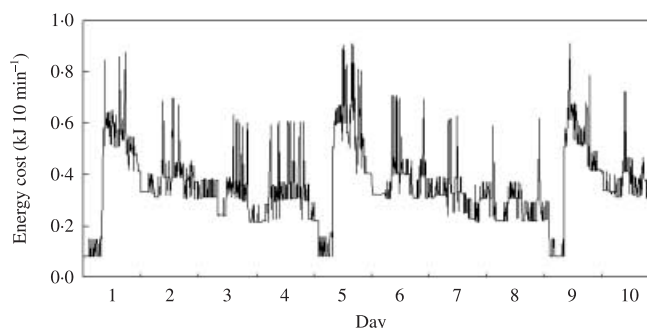
was characterized by low levels of activity (Table 4; Fig. 8b,d,f).

The high levels of activity exhibited by males in shallow, warm areas were significantly greater than expected by chance ( $\chi^2$  test, real data vs. random:  $\chi^2 = 6.91$ ,  $\chi^2_{0.05,2} = 5.99$ ,  $P = 0.03$ ). Higher activity levels occurred in warm water more often than would be expected according to the random activity–temperature model (see Statistical methods). High activity levels in warm, shallow areas above the thermocline were consistent with prey

searching behaviour, compared to areas below the thermocline where low activity rates and resting behaviour occurred.

#### THERMAL CHOICE EXPERIMENT

Male dogfish in the laboratory choice chamber during the first 2 weeks showed clear preferences for compartment 2 (C2), the compartment where food was provided (Fig. 9a,b). Three or four fish occupied C2 for



**Fig. 10.** Example of the variability in energy costs of male dogfish movements and behaviour over a 10-day period estimated using Model 1 (see text for explanation).

between 62.3 and 92.4% of the time over this period. In weeks 3 and 4 when a thermal gradient of 0.9 °C was maintained between C1 and C2, the fish gradually spent more time in the cooler compartment (C1) (Fig. 9c,d). In week 3 there were no fish occupying C2 for 37.6% of the time, increasing to 89.4% in week 4. The shift in fish distribution in weeks 1 and 2 compared with 3 and 4 was significant ( $\chi^2$  test on raw counts with  $2 \times 5$  contingency table:  $\chi^2 = 220.0$ ,  $\chi^2_{0.05,4} = 9.49$ ,  $P < 0.001$ ), indicating that the change was not independent of temperature. The small amounts of time spent in the warmer side were associated with obtaining food. When the thermal gradient was removed for weeks 5 and 6, the fish spent progressively more time in C2, with the distribution in week 6 being no different to that observed in week 1 ( $\chi^2 = 5.92$ ,  $\chi^2_{0.05,4} = 9.49$ ,  $P > 0.10$ ) (Fig. 9a,f).

#### ENERGY MODELS

Figure 10 shows an example of the changes in energetic expenditure estimated by energy model 1 for dogfish 4 over the 10-day period for which there was swimming depth and temperature data. The daily peaks in expenditure signify periods of activity and larger step increases were associated with the effect on metabolism of consuming food. The average daily (24 h) estimated energy costs of dogfish 4, 5 and 6 ranged from 51.30 to 52.15 kJ based on actual water temperatures and activity levels measured by tags (model 1). Substituting random 'warm' (above thermocline) temperatures (model 2) into the energy model increased daily costs by between 1.31 and 4.02% ( $t$ -test, model 1 vs. model 2:  $F_{0.05,4} = -3.63$ ,  $P = 0.022$ ). Model 3 substituted random 'cold' (below thermocline) temperatures into model 1 and energy costs were lowered by between 1.45 and 2.84% with this strategy. Substitution of constant high (17 °C, model 4) or low (10 °C, model 5) temperatures into model 1 yielded, as expected, higher (5.04–8.28%) and lower (22.52–25.72%) daily energy costs, respectively.

#### Discussion

Three general hypotheses have been proposed to account for DVM in several fish species occupying freshwater lakes, namely: bioenergetic efficiency, forag-

ing opportunity and predator avoidance hypotheses (Scheuerell & Schindler 2003). The bioenergetic efficiency hypothesis is based on the idea that individuals make vertical movements to select temperatures that maximize growth rate (Brett 1971; Wurtsbaugh & Neverman 1988). The hypothesis predicts that to maximize surplus power, fish undertake night-time movements into surface waters to feed on abundant prey before moving deeper to rest and digest in cooler waters during the day. The foraging-opportunity hypothesis predicts that fish closely follow spatio-temporal changes in prey abundance to maximize foraging and subsequent growth rates (Narver 1970; Levy 1990), whereas the predator-avoidance hypothesis states that fish move vertically in the water column primarily in response to predators (Clark & Levy 1988; Scheuerell & Schindler 2003).

For male dogfish to adopt the nocturnal ascent DVM pattern we observed as a consequence of predator activity it seems logical to assume that under this scenario dogfish actively avoid shallow areas during daytime to reduce predation risk, and instead occupy deep habitat as a daytime refuge from predators. This implies that predators of dogfish are present when putative predator-evasion behaviour (i.e. DVM) was observed. It seems unlikely, however, that the risk of predation could account for the behaviour patterns we observed in male dogfish. First, dogfish are large (~0.7 m long) macrobenthic predators with few natural predators in the sea lough where they were studied (Sims 2003). The only potential predator of adult males known to be present in the lough is the grey seal, *H. grypus*. Moreover, our observations show that grey seals were not present in the lough during the summer when the tracking and environmental sampling was conducted. If DVM behaviour of male dogfish was linked closely to the risk of predation as demonstrated for some juvenile fish species (e.g. Scheuerell & Schindler 2003), we would expect that a strong presence of seals would be necessary to shape the clear and persistent DVM we observed in dogfish. It is well known that fish respond rapidly to the risk of predation (Milinski 1993), so in the absence of seals we should have observed a concomitant absence of DVM behaviour of dogfish. Clearly, this was not the case for dogfish during summer.



However, even if grey seals were sometimes present in summer but went unrecorded in our study, they conduct benthic foraging during the day and night in both shallow and deep habitats, behaviour which would be unlikely to elicit daytime deep-water refuging by male dogfish.

It was also clear that the DVM behaviour of male dogfish was inconsistent with the foraging-opportunity hypothesis. Dogfish feed on a wide variety of invertebrate and fish prey (Ellis, Pawson & Shackley 1996), and in Lough Hyne consume predominantly prawn (*P. serratus*), swimming crabs (*Liocarcinus* spp.) and teleosts, presumably because they are the most abundant prey available (Sims *et al.* 2001; Sims 2003). The contents of the baited traps in shallow and deep habitats occupied by dogfish showed prey to be very abundant in shallow water both day and night, but it was never abundant below the thermocline (~15 m). If male dogfish undertook DVM to track high concentrations of prey we would have expected greater abundances of prey during the day in deep water, together with low densities in shallow habitats, and *vice versa* at night. However, this pattern of prey distribution was not observed by us, indicating that dogfish do not track their prey closely.

Overall, our findings are consistent with male *S. canicula* undertaking DVM to increase energetic benefits through trade-offs between foraging opportunity and the effect of thermal resources on energy expenditure. Our field and laboratory studies show that bottom-living male dogfish select habitats above and below the thermocline for different activities that, when combined, are likely to confer energetic advantages. Shallow water was characterized by high prey abundances both day and night and was used principally for night-time foraging presumably because of the higher energy costs associated with being active in warm habitat during the day. Crabs, prawns and shrimps become active at night in Lough Hyne (Kitching & Ebling 1967) which may increase their availability to dogfish foraging nocturnally, even though diurnal prey abundances were higher. However, putative diel changes in prey availability cannot explain fully why male dogfish do not remain in shallow water during daytime. The role of higher water temperature as a principal factor in eliciting movements to depth by dogfish during daytime, by contrast, can account for the observed DVM behaviour, as was shown by the thermal-choice experiment.

It was apparent that above-thermocline habitat was used for night-time foraging whereas below-thermocline habitat was used for resting (and presumably digestion) by male dogfish because energy expenditure in these cool regions was estimated to be lower than it would be above the thermocline. This type of energy conservation strategy achieved by adopting a specific pattern of DVM in a heterogeneous foraging and thermal environment has been suggested to occur in demersal marine fish species (e.g. cod, *Gadus morhua*; Clark & Green 1991). However, despite the intuitive appeal of

this proposal, studies designed to test the hypothesis have been inconclusive. This is because predator movements in relation to prey abundances, thermal habitat availability, and the energy costs and benefits of different behavioural scenarios were not estimated, nor were competing hypotheses addressed directly. Similarly, frequent vertical movements through the water column (and across the thermocline) during the daily cycle have been observed in many large ectothermic fish species such as blue (*Prionace glauca*) (Carey & Scharold 1990), megamouth (*Megachasma pelagios*) (Nelson *et al.* 1997) and school sharks (*Galeorhinus galeus*) (West & Stevens 2001). Although these movements have been suggested to be, in part, related to behavioural thermoregulation aimed at energy conservation, competing hypotheses such as foraging opportunity (prey tracking) were not investigated simultaneously. Therefore, in most cases where diel vertical movements of free-living ectotherms in the sea have been detected it has proved difficult to establish what factors actually underpin observed behaviours. To our knowledge, our study is the first to provide evidence for the bioenergetic efficiency hypothesis underlying DVM in free-ranging adults of a marine fish species through a combination of field, laboratory and modelling approaches.

Our results indicate that in the absence of high levels of predation risk large-bodied ectotherms adopt a strategy that increases surplus power by selecting an appropriate combination of thermal and foraging resources. Previous studies on the effects of thermal gradients on fish have found that individuals of a particular species will spend 75% of their time within  $\pm 2^\circ\text{C}$  of their preferred temperature (Magnuson & Destasio 1997). This thermal preferendum has been shown to match the optimal temperature for physiological activity, that is, the temperature at which maximum growth is achieved (Magnuson *et al.* 1979). Ectothermic sharks possess thermoreceptors capable of detecting temperature differences down to about  $0.001^\circ\text{C}$  (Brown 2003) and respond behaviourally to thermal gradients in the laboratory by selecting preferred temperatures (Crawshaw & Hammel 1973; Casterlin & Reynolds 1979). In the current study we found free-ranging dogfish occupied similarly narrow thermal limits in the natural environment (Table 3) despite the availability of a wider range of thermal resources in the sea lough in which they were studied (Figs 2 and 3). The thermal choice experiment we conducted showed that a temperature increase of  $0.9^\circ\text{C}$  within an established food patch was sufficient to elicit movements away from the warm-water patch. Thus, our study demonstrates that bottom-living male dogfish, like some demersal and pelagic fish predators (Holland *et al.* 1992), are able to exert fine control over selection of their thermal niche, presumably to approach an optimal temperature for activity and growth by undertaking trade-offs between foraging and thermal habitat selection. Because thermal gradients of the magnitude observed in Lough Hyne are common in the coastal marine environment,

it is possible that similar studies of other large-bodied marine ectotherms will reveal that energy conservation strategies occur more widely among bottom-living species than is realized currently.

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### References

- Brett, J.R. (1971) Energetic responses of salmon to temperature. A study of some thermal relations in physiology and freshwater ecology of sockeye salmon (*Oncorhynchus nerka*). *American Zoologist*, **11**, 99–113.
- Brown, B.R. (2003) Sensing temperature without ion channels. *Nature*, **421**, 495.
- Butler, P.J. & Taylor, E.W. (1975) The effect of progressive hypoxia on respiration in the dogfish (*Scyliorhinus canicula*) at different seasonal temperatures. *Journal of Experimental Biology*, **63**, 117–130.
- Carey, F.G. & Scharold, J.V. (1990) Movements of blue sharks (*Prionace glauca*) in depth and course. *Marine Biology*, **106**, 329–342.
- Casterlin, M.E. & Reynolds, W.W. (1979) Shark thermoregulation. *Comparative Biochemistry and Physiology A*, **64**, 451–453.
- Clark, D.S. & Green, J.M. (1991) Seasonal variation in temperature preference of juvenile Atlantic cod (*Gadus morhua*), with evidence supporting an energetic basis for their diel vertical migration. *Canadian Journal of Zoology*, **69**, 1302–1307.
- Clark, C.W. & Levy, D.A. (1988) Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *American Naturalist*, **131**, 271–290.
- Crawshaw, L.I. & Hammel, H.T. (1973) Behavioural temperature regulation in the California horn shark, *Heterodontus francisci*. *Brain, Behaviour and Evolution*, **7**, 447–452.
- Davenport, J. & Sayer, M.D.J. (1993) Physiological determinants of distribution in fish. *Journal of Fish Biology*, **43**, 121–145.
- Ellis, J.R., Pawson, M.G. & Shackley, S.E. (1996) The comparative feeding ecology of six species of shark and four species of ray (Elasmobranchii) in the north-east Atlantic. *Journal of the Marine Biology Association of the United Kingdom*, **76**, 89–106.
- Hays, G.C. (2003) A review of the adaptive significance and ecosystem consequences of zooplankton diel vertical migrations. *Hydrobiologia*, **503**, 163–170.
- Holland, K.N., Brill, R.W., Change, R.K.C., Sibert, J.R. & Fournier, D.A. (1992) Physiological and behavioural thermoregulation in bigeye tuna (*Thunnus obesus*). *Nature*, **358**, 410–412.
- Kitching, J.A. & Ebling, F.J. (1967) Ecological studies at Lough Ine. *Advances in Ecological Research*, **4**, 197–291.
- Levy, D.A. (1990) Reciprocal diel vertical migration behaviour in planktivores and zooplankton in British Columbia Lakes. *Canadian Journal of Fisheries and Aquatic Sciences*, **47**, 1755–1764.
- Loose, C.J. & Dawidowicz, P. (1994) Trade-offs in diel vertical migration by zooplankton: the costs of predator avoidance. *Ecology*, **75**, 2255–2263.
- Magnuson, J.J., Crowder, L.B. & Medvick, P.A. (1979) Temperature as an ecological resource. *American Zoologist*, **19**, 331–343.
- Magnuson, J.J. & Destasio, B.T. (1997) Thermal niche of fishes and global warming. *Global Warming: Implications for Freshwater and Marine Fish* (eds C.M. Wood & D.G. McDonald), pp. 377–408. Cambridge University Press, Cambridge.
- McLaren, I.A. (1963) Effect of temperature on growth of zooplankton and the adaptive value of vertical migration. *Journal of the Fisheries Research Board of Canada*, **26**, 199–220.
- Milinski, M. (1993) Predation risk and feeding behaviour. *Behaviour of Teleost Fishes* (ed. T.J. Pitcher), pp. 285–305. Chapman & Hall, London.
- Narver, D.W. (1970) Diel vertical movements and feeding of underyearling sockeye salmon and the limnetic zooplankton in Babine Lake, British Columbia. *Journal of the Fisheries Research Board of Canada*, **27**, 281–316.
- Neill, W.E. (1990) Induced vertical migration in copepods as a defence against invertebrate predation. *Nature*, **345**, 524–526.
- Nelson, D.R., McKibben, J.N., Strong, W.R., Lowe, C.G., Sisneros, J.A., Schroeder, D.M. & Lavenberg, R.J. (1997) An acoustic tracking of a megamouth shark, *Megachasma pelagios*: a crepuscular diel vertical migrator. *Environmental Biology of Fishes*, **49**, 389–399.
- Ohman, M.D. (1990) The demographic benefits of diel vertical migration by zooplankton. *Ecological Monographs*, **60**, 257–281.
- Rogers, A.D. (1994) The biology of seamounts. *Advances in Marine Biology*, **30**, 305–350.
- Schabetsberger, R., Brodeur, R.D., Ciannelli, L., Napp, J.M. & Swartzman, G.L. (2000) Diel vertical migration and interaction of zooplankton and juvenile walleye pollock (*Theragra chalcogramma*) at a frontal region near the Pribilof Islands, Bering Sea. *ICES Journal of Marine Science*, **57**, 1283–1295.
- Scheuerell, M.D. & Schindler, D.E. (2003) Diel vertical migration by juvenile sockeye salmon: empirical evidence for the antipredation window. *Ecology*, **84**, 1713–1720.
- Sims, D.W. (1994) *Physiological factors regulating appetite in dogfish*. PhD thesis, University of Plymouth, UK.
- Sims, D.W. (1996) The effect of body size on the standard metabolic rate of lesser spotted dogfish, *Scyliorhinus canicula*. *Journal of Fish Biology*, **48**, 542–544.
- Sims, D.W. (2003) Tractable models for testing theories about natural strategies: foraging behaviour and habitat selection of free-ranging sharks. *Journal of Fish Biology*, **63**, 53–73.
- Sims, D.W. & Davies, S.J. (1994) Does specific dynamic action (SDA) regulate return of appetite in the lesser spotted dogfish, *Scyliorhinus canicula*? *Journal of Fish Biology*, **45**, 341–348.
- Sims, D.W., Nash, J.P. & Morritt, D. (2001) Movements and activity of male and female dogfish in a tidal sea lough:

- alternative behavioural strategies and apparent sexual segregation. *Marine Biology*, **139**, 1165–1175.
- Watanabe, H., Kawaguchi, K. & Hayashi, A. (2002) Feeding habits of juvenile surface-migratory myctophid fishes (Family Myctophidae) in the Kuroshio region of the western North Pacific. *Marine Ecology Progress Series*, **236**, 263–272.
- 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.
- West, G.J. & Stevens, J.D. (2001) Archival tagging of school shark, *Galeorhinus galeus*, in Australia: initial results. *Environmental Biology of Fishes*, **60**, 283–298.
- Wetherbee, B.M., Gruber, S.H. & Cortes, E. (1990) *Diet, Feeding Habits, and Consumption in Sharks, with Special Reference to the Lemon Shark Negaprion brevirostris: Elasmobranchs as Living Resources: Advances in the Biology, Ecology, Systematics, and the Status of the Fisheries*. NOAA Technical Report 90 (eds H.L. Pratt, S.H. Gruber & T. Tanuchi), pp. 29–47. National Oceanic and Atmospheric Administration, Seattle.
- Wolanski, E. & Hamner, W.M. (1988) Topographically controlled fronts in the ocean and their biological significance. *Science*, **241**, 177–181.
- Wurtsbaugh, W.A. & Neverman, D. (1988) Post-feeding thermotaxis and daily vertical migration in a larval fish. *Nature*, **333**, 846–848.

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