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## Movements and activity of male and female dogfish in a tidal sea lough: alternative behavioural strategies and apparent sexual segregation

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**Abstract** Movements and habitat selection of male and female dogfish, *Scyliorhinus canicula*, in a tidal sea lough in south-west Ireland were determined over two temporal scales. Continuous acoustic tracking of four individuals (two males, two females) for 6 days was used to monitor fine-scale changes in behaviour patterns and extent of home ranges. Mark-recapture by number-tagging dogfish captured at sampling stations during August–September in consecutive years was used to reveal long-term philopatric behaviour. Transmitter-tagged male dogfish showed very similar behavioural patterns of low activity during the day in deep water (12–24 m depth) followed by more rapid movements into shallow areas (<4 m) at dusk to feed, before returning to the core space in deep water at dawn. Home ranges occupied by males overlapped almost entirely and were centred in an area where tidal currents form gyres and large crab prey are found. Female *S. canicula* exhibited a different behavioural strategy. They refuged in caves in shallow water (0.5–1.5 m) during the day and during the 6-day tracking period were nocturnally active two or three times, primarily in deep water. Activity areas of females did not overlap with those of males.

Acoustic telemetry, netting, underwater surveys and tag returns revealed males and females were apparently segregated by sex in the lough. Mark-recapture data showed males and females were recaptured from the locations where they were originally caught between 359 and 371 days earlier suggesting at least seasonal segregation in consecutive years. Because female dogfish store sperm enabling temporal separation of the energetically demanding act of copulation with the process of egg-laying, we suggest that this apparent spatial segregation by sex could be driven by the need for females to conserve energy by limiting multiple matings during a time when mating coincides with a peak in egg production and laying.

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### Introduction

Understanding habitat selection of marine fishes over a range of spatio-temporal scales is extremely important because habitat choice is one of the processes influencing population distribution, abundance and hence potential availability to fisheries exploitation (Freon and Misund 1999). The movements and activity of sharks in relation to the selection of particular habitats at certain times in the diel cycle have been studied in recent acoustic tracking studies (Holland et al. 1993; Morrissey and Gruber 1993a; Holland et al. 1999), and over broader spatio-temporal scales by conventional mark-recapture tagging studies (e.g. McLaughlin and O’Gower 1971). However, although home ranges of individuals have been determined through tracking (e.g. Morrissey and Gruber 1993b), there is a lack of fine-scale movement data for males and females of the same species. Determining sex-based differences in the behavioural strategies of wild fishes is of importance in marine fisheries management, as any differences will provide information on the spatio-temporal dynamics of male-female distribution and abundance, and thus their availability and catch rates.

Sexual segregation by geographic location is a general characteristic of shark populations (Springer 1967;

Klimley 1987), distributions which imply sex differences in behavioural strategy and habitat selection. Although it is thought that segregation by sex occurs predominantly for reasons associated with reproduction, the behavioural strategies underpinning sexual segregation have to date only been implied from fishery data of line-caught individuals (Klimley 1987). There is a clear need to investigate sex differences in behavioural strategies in more detail because such movement patterns may result in spatial as well as temporal segregation. Presumably one reason for the lack of information linking the physiological, behavioural and ecological determinants of segregation by sex is that a model species suitable for both laboratory and field tracking studies is lacking.

The lesser spotted dogfish, *Scyliorhinus canicula*, is an abundant, temperate, bottom-dwelling catshark of the European continental shelves and uppermost slopes (Compagno 1984). It occurs in the eastern North Atlantic from Norway and the British Isles in the north, to the Mediterranean, and extending south to Senegal and the Ivory Coast. Despite the importance of *S. canicula* as an experimental model species for physiological studies, relatively little is known of its behaviour in the wild, especially in relation to movements of males and females (Compagno 1984). Early studies suggested there may be relatively extensive migrations at certain times of the year (e.g. see references on *S. canicula* in Compagno 1984), but more recent investigations indicate philopatric behaviour (Rodriguez-Cabello et al. 1998). Behavioural strategies and habitat selection of males and females have yet to be studied in this species. Therefore, the aim of the present study was to determine the movements of male and female *S. canicula* over both narrow and broad spatio-temporal scales in an enclosed marine environment with a view to establishing whether or not there were sex differences in behavioural strategies.

## Materials and methods

### Study site

Lough Hyne (Ine) is a tidal sea lough in the far south-west of Ireland (see Fig. 1). The lough covers an area of about 0.6 km<sup>2</sup> with a maximum depth of 47 m, and is connected to the Atlantic Ocean via narrow and shallow rapids (width < 20 m, depth 1–3 m) with a distinct raised sill, which acts to limit fish movements into and out of the lough. A detailed account of Lough Hyne and its surroundings is given in Kitching and Ebling (1967).

### Collection and number tagging

Between 26 August and 1 September 1995, dogfish were captured alive using hand-nets, monofilament tangle-nets (0.5- to 1.0-h soak time) and by SCUBA diving at 12 survey locations in Lough Hyne (7 locations in the south basin, 5 in the north; see Fig. 1). Following capture, dogfish were measured (total body length), sexed by the presence or absence of paired male intromittent organs (claspers), and individually tagged with a numbered T-bar anchor tag (FD-94, Floy Tag, Seattle, USA) in the dorsal musculature before being released within 10 m of the site of capture. From 24 August to 1

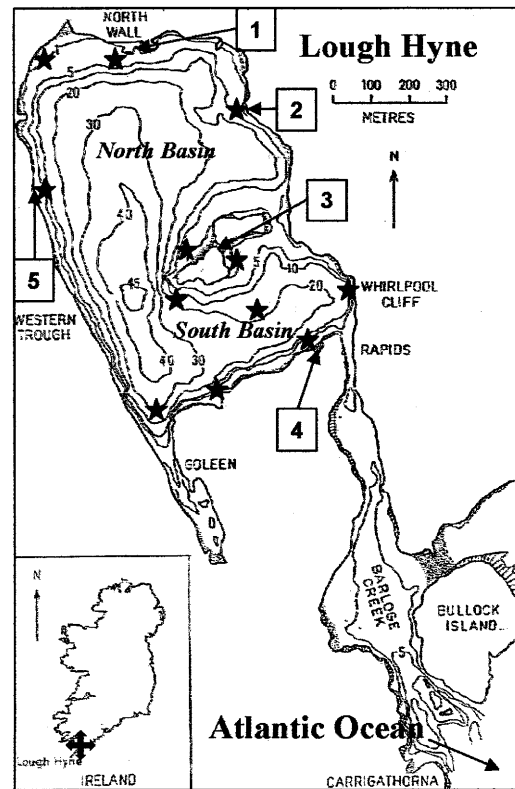


Fig. 1 Map of Lough Hyne showing bathymetry and the twelve dogfish survey locations (filled stars) together with specific positions of locations named in the text (numbered boxes): 1 North Quay Island (cave refuge); 2 Rookery Nook (cave refuge); 3 Castle Island; 4 Renouf or Scyllium Bay; 5 West Rock (refuge)

September 1996, similar surveys in the same locations were conducted. All dogfish captured were weighed and measured. The recapture location and tag number of previously tagged dogfish was recorded and any untagged fish were marked with a numbered tag in the same way as before.

### Acoustic tracking

Two adult male dogfish captured in shallow water on the south shore of Castle Island (25 August 1996) and two adult females captured from a cave at North Quay Island (26 August) were anaesthetised (MS222, Sigma) and each fitted with an acoustic transmitter (16 mm diam, 65 mm long, weight in water 10 g; VEMCO, Nova Scotia, Canada). For one male and one female, the transmitter was attached externally to the dorsal surface at a position immediately caudal to the posterior emargination of the pectoral fins. Three plastic eye-holes were glued around the forward pointing end of a transmitter and T-bar anchor tags with a spherical stopper glued to each trailing end were pushed through the eye-holes and into the dorsal musculature (depth = 0.7 cm) to hold the transmitter firmly in position. The remaining male and female dogfish each had a transmitter surgically implanted. Transmitters were placed intraperitoneally through a 3-cm incision in the abdominal wall. Incisions were sutured with three dissolvable stitches and one permanent stitch. Procedures for inserting or attaching transmitters to dogfish were completed within 10 min of initial anaesthetic administration and during which time a flow of clean seawater irrigated the gills. Following these procedures, dogfish recovered normal swimming movements within 5–10 min of being held in a stream of clean, aerated seawater. After further 15 min observation periods, during which time no adverse effects to

the anaesthetic or surgical procedures were seen, the dogfish were released. Males were released on the south shore of the South Basin, while females were released on the north shore of Castle Island (North Basin).

Movements of all four dogfish were tracked for the next 5.6–6.0 days by determining transmitter locations every 1.1–1.4 h. Transmitters were located by triangulation using an underwater, pole-mounted directional hydrophone and an acoustic receiver (Mariner Radar, Lowestoft, UK). Each transmitter produced acoustic energy on widely separated frequencies (60, 65.5, 69, 76.8 kHz) with 57 or 58 pulses/min at a power output of 147 dB re 1  $\mu$ Pa @1 m. Numbered position markers spaced every 10–100 m around the shoreline of Lough Hyne and its islands, and visible from the water's edge (Kitching and Ebling 1967), were used to fix the precise location of the boat during tracking. The small vessel (4 m long) was stationed by a shoreline marker and the direction to the strongest signal of each transmitter was determined by slowly turning the hydrophone to cover a broad horizontal arc at a depth of 1 m below the surface. Signal strength during hydrophone turning was monitored by a team member using a visual indicator display on the receiver and by listening to the audio output of the signal through headphones. When the hydrophone was pointed in the direction of strongest signal, a bearing to the signal was taken using a digital compass (Autohelm, UK) mounted to the top of the hydrophone pole. This procedure was repeated for other transmitters in the area before second and third bearings to the same transmitters were taken from markers further along the same stretch of shore, or from adjacent shore positions approximately at right angles to the first bearing. Distances of between 100 and 200 m were used between locations where bearings were taken and the time taken from determination of the first bearing to the third was 10–15 min. The accuracy of the location method was evaluated using a transmitter fixed to a surface marker at a distance of approximately 100 m. Errors associated with compass bearings to the direction of loudest signal were low and estimated to be  $\pm 5^\circ$  at the range tested. The range used for testing was typical of hydrophone-dogfish distances used during tracking.

A pair of team members tracked all four dogfish continuously for 6 h, with four pairs completing consecutive 6-h shifts in a 24-h period (0000–0600, 0600–1200, 1200–1800, 1800–0000 hours). Pairs were rotated through at least four different shift periods throughout the 6-day study. Shore-based team members measured light intensity (Lutron LX-101 lux meter, UK) during light:dark transitions at a fixed station in Renouf Bay located on the south side of the South Basin (see Fig. 1). On the basis of these measurements

the diel cycle was divided into 4 unequal time periods (day, dusk, dark, dawn). Day was from 0730 to 2000 hours, dusk was between 2000 and 2230 hours, whereas night and dawn were 2230–0500 hours and 0500–0730 hours, respectively.

Transmitter locations were mapped onto a fine-scale bathymetric chart of Lough Hyne (Hydrodata Ltd., Gallygarvan, Ireland) to reconstruct the paths taken by the four dogfish during the tracking period. Each transmitter location was mapped by drawing on the chart bearing lines from the three shoreline markers corresponding to the bearings taken to the strongest signal of each transmitter. A location was fixed spatially at the point where the three bearing lines crossed. If an error triangle ("cocked hat") was produced between bearing lines that did not cross at the same point, then a location was assumed to be in close proximity and fixed in the centre of the error triangle. The area of error triangles was never greater than 80 m<sup>2</sup>.

## Results

### Number tagging

A total of 62 dogfish were number-tagged in Lough Hyne over both years of study, including four that were also fitted with acoustic transmitters. Males ( $n=26$ ) were caught only in the South Basin, whereas 70% of females were captured in the North Basin. Movements of dogfish between 1995 and 1996 were limited (Table 1). Of three males tagged on the south shore of Castle Island in 1995, two were recaptured in the same place between 360 and 364 days later, and another male was caught only 170 m from the location of first capture some 371 days previously. Similarly, five females first captured from caves at North Quay Island in 1995 were captured there again between 359 and 364 days later. They were found in these refuges with between 3 and 13 other female dogfish. The number-tagging study also revealed some short-term movements. A female found with other females in a rock crevice at Rookery Nook in 1995 was

**Table 1** Tag recapture data for male ( $n=3$ ) and female ( $n=8$ ) dogfish, *Scyliorhinus canicula*, in Lough Hyne, Ireland, between 26 August and 1 September 1995 and 24 August and 1 September 1996. (F female; M male)

Capture/tagging date	Sex (tag no.)	Location	Recapture date	Location	Days at liberty since last capture	Minimum distance between capture sites (m)
26.8.95	F (994)	South, Castle Island	1.9.95	North Quay Island	6	700
29.8.95	F (704)	Rookery Nook	30.8.95	Rookery Nook	<1	0
			1.9.95	North Quay Island	<2	350
30.8.95	F (729)	Rookery Nook	1.9.95	Rookery Nook	<2	0
			1.9.95	Rookery Nook	<1	0
31.8.95	F (943)	North Quay Island	1.9.95	North Quay Island	<1	0
			26.8.96	North Quay Island	359	0
26.8.95	M (1000)	South, Castle Island	25.8.96	South, Castle Island	364	0
26.8.95	M (989)	South, Castle Island	31.8.96	South, Castle Island	371	170
30.8.95	M (908)	South, Castle Island	25.8.96	South, Castle Island	360	0
1.9.95	F (934)	North Quay Island	26.8.96	North Quay Island	360	0
1.9.95	F (939)	North Quay Island	26.8.96	North Quay Island	360	0
			31.8.96	North Quay Island	4	0
1.9.95	F (930)	North Quay Island	31.8.96	North Quay Island	364	0
1.9.95	F (928)	North Quay Island	31.8.96	North Quay Island	364	0

recaptured from the cave system at North Quay Island 2 days later. However, one of the 11 females caught and tagged on the south shore of Castle Island in 1995 was found in the caves at North Quay Island 6 days later, a minimum distance of 700 m away (Table 1).

### Acoustic tracking

Four adult dogfish were tracked by acoustic telemetry between 25 August and 1 September 1996 during which time between 111 and 120 individual position fixes per fish were determined (Table 2).

### Males

Horizontal movements of adult males were generally characterised by short-range movements away from and back to a central activity area in the South Basin (Fig. 2a). Contour plots of the percentage of position fixes in grid cells (12×15 m) dividing up the entire activity area showed that 52% of fixes for male 96-1 were within an area 72×60 m (4,320 m<sup>2</sup>). Similarly, 55% of locations for male 96-2 were within an area 72×75 m (5,400 m<sup>2</sup>) and centred on grid cell (M8), which was immediately adjacent to the centre of activity for male 96-1 (grid cell L8) (Fig. 3 a,b). Movements away from the central activity area were infrequent and males did not range out of the South Basin before returning to this central area. Within these areas, males showed very similar behavioural characteristics. They covered similar minimum horizontal distances between position fixes (step lengths) and overall moved minimum distances of 5.18 and 5.24 km over the tracking period of 143.2 h (Table 2). Although the step lengths were of similar magnitude at similar times between males, they showed

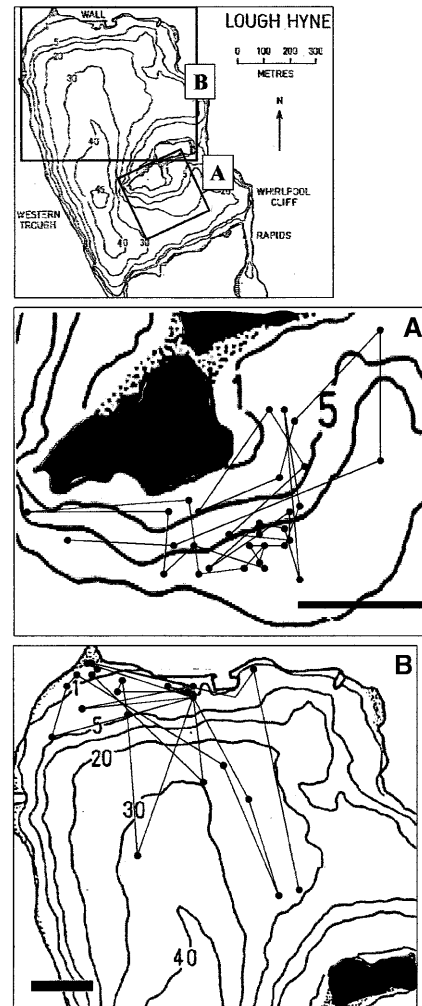
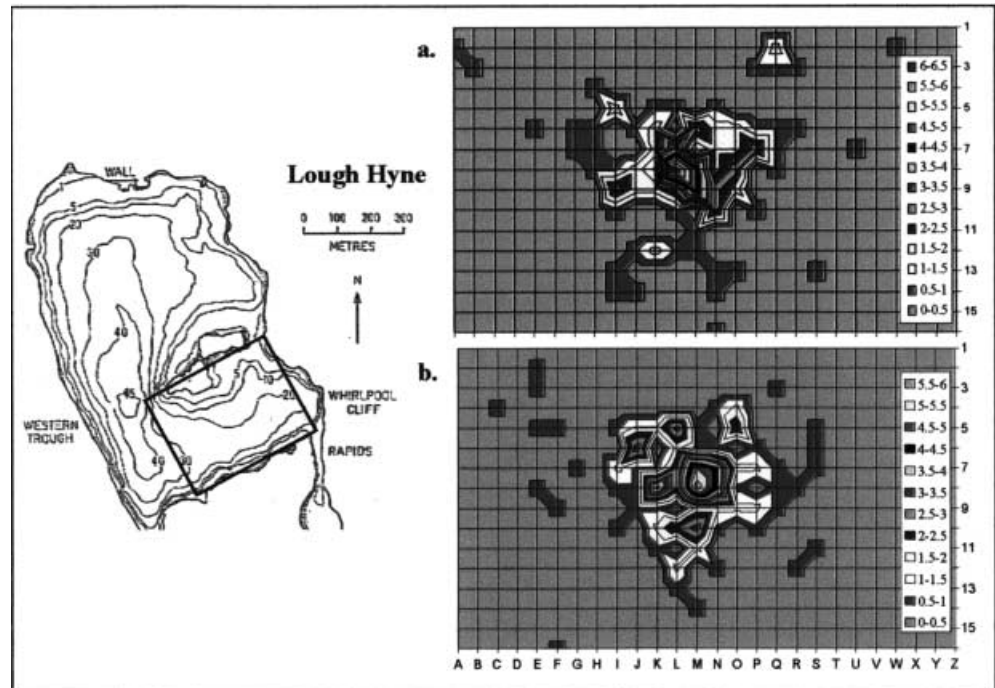


Fig. 2 Representative examples of movements of a male dogfish, *Scyliorhinus canicula*, in Lough Hyne (inset map) over a 2-day period (a), and the movements shown by a female over a 6-day period (b). Scale bar 100 m in both panels

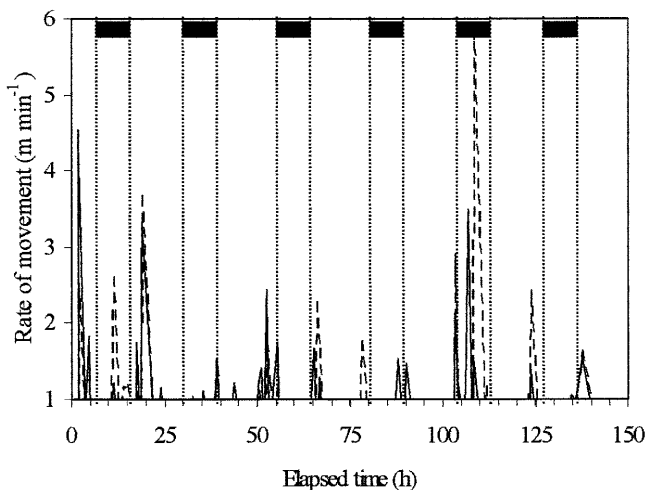
**Table 2** Summary characteristics of tracks obtained from acoustic transmitter-tagged dogfish, *S. canicula*, in Lough Hyne, Ireland. (M male; F female; Int internal; Ext external)

Dogfish ID code		96-1	96-2	96-3	96-4
Sex		M	M	F	F
Body mass (g)		1,100	1,250	1,000	1,000
Tag type		Int	Ext	Int	Ext
Total time tracked (h)		143.2	143.2	135.7	138.5
No. of location fixes		111	120	113	112
Mean location fix interval (h)		1.4	1.4	1.2	1.1
Step length (m interval <sup>-1</sup> )	Mean	46.3	43.7	134.6	123.4
	SD	30.0	32.3	93.4	126.4
	Median	41.0	35.0	149.0	68.0
Seabed depth at fix location (m)	Mean	11.8	11.4	5.9	12.1
	SD	6.0	6.1	10.1	11.6
	Median	12.2	11.5	1.5	12.0
Minimum rate of movement (m min <sup>-1</sup> )	Mean	0.80	0.76	2.59	3.46
	SD	0.81	0.74	2.77	4.92
	Median	0.61	0.54	1.65	1.32
Cumulative minimum distance moved (km)		5.18	5.24	3.90	5.06

**Fig. 3** Contour plots of percentage fixes per grid square showing the home ranges of male dogfish, *S. canicula*, 96-1 (a) and 96-2 (b) in the South Basin of Lough Hyne



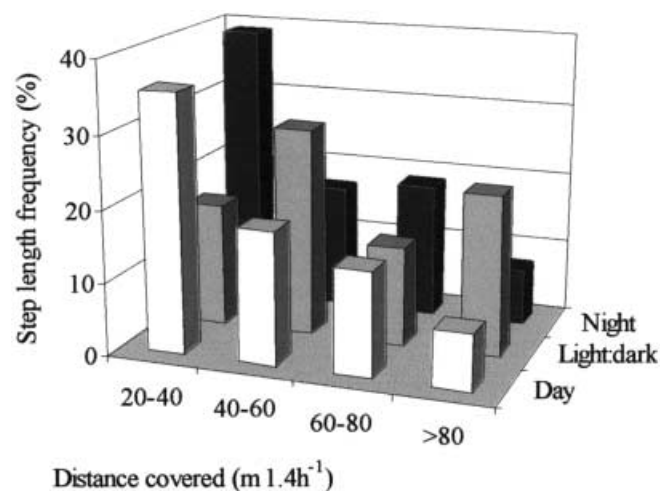
distinct variations for both males over the light:dark cycle. During periods when natural illumination was increasing and decreasing maximally (dawn and dusk), rates of movement increased from  $<1 \text{ m min}^{-1}$  to between 1.1 and  $5.8 \text{ m min}^{-1}$  (Fig. 4). As a consequence of increased rates of crepuscular movement, there was a 14% increase in the frequency of step lengths  $>80 \text{ m}$  between successive fixes (per  $1.4 \text{ h}$  time increment) during light:dark transitions of dawn and dusk compared to during daylight or night time (contingency table chi-squared analysis of frequency distributions of pooled step lengths in light vs light: dark;  $\chi^2 = 12.08$ ,  $\chi^2_{0.05,3} = 7.82$ ,  $P < 0.01$ ) (Fig. 5). This increase in



**Fig. 4** The rates of movement of both male dogfish, *S. canicula*, showing peaks at dawn and dusk. (Male 96-1 dashed line; male 96-2 solid line)

dawn:dusk step length was balanced by a 19% decrease in the frequency of step lengths between 20 and  $40 \text{ m}$   $1.4 \text{ h}^{-1}$  at dawn and dusk compared to that during day and night-time (Fig. 5). In contrast, the frequency distribution of step lengths were very similar between day and night.

Vertical movements of male dogfish ranged from locations with seabed depths between 1.5 and  $22.5 \text{ m}$ . The mean sea bottom depth at positions fixed for dogfish was very similar between males (Table 2) and



**Fig. 5** Changes in the distribution of step-length frequencies between four step-length distance classes for male dogfish, *S. canicula*, during the diurnal (light), nocturnal (night) and crepuscular (light:dark) phases. Significantly greater distance between fixes was covered during the crepuscular phase. Note that statistical analysis was carried out on actual frequencies not percentage data

temporal variations in depth followed very similar trends for both males over the entire tracking period (Fig. 6). In general these variations showed that shallower habitat was selected during crepuscular and nocturnal activity. Frequency distribution of habitat depth selected by dogfish demonstrated that males spent 57% of the daylight phase in locations with depths between 12 and 20 m (Fig. 7). By contrast, during crepuscular phases, when males were more active (see above), there was a shift to shallow areas with 52% of time spent in habitat with depths from 0 to 8 m when compared to during daytime (contingency table chi-squared analysis of frequency distributions of pooled location depths in light vs light: dark;  $\chi^2 = 23.97$ ,  $\chi^2_{0.05,5} = 11.07$ ,  $P < 0.001$ ) (Fig. 7). Nocturnal habitat depth selected by male dogfish was approximately intermediate between crepuscu-

lar and diurnal depths, with 48% of fixes occurring between 4 and 12 m depth.

### Females

Horizontal movements of females were characterised by long periods spent resting in caves or under rocks (behaviour verified by surface and SCUBA-diving observations), interspersed periodically with longer-range movements of short temporal duration over much of the North Basin (Fig. 2b). Female 96-3 utilised one cave refuge located on the south side of North Quay Island (NQI) for resting, whereas female 96-4 rested in two refuges, a cave in the North Wall and an algae-covered rock on the west shore of the North Basin (see Fig. 1). Females 96-3 and 96-4 spent 73 and 62% of the total track time, respectively, resting in refuges which indicated the importance of this habitat to female dogfish (Tables 2; Fig. 8). Following release after transmitter attachment both females located these refuges within 2-4 h even though they were released some 300-400 m away. Over the tracking period female 96-3 made nocturnal movements away from the refuge with a rhythmicity of approximately 48 h, and these were broadly similar to the nocturnal and crepuscular (with some daytime) activity of female 96-4 (Fig. 8b,d). When active, the females ranged up to 450 m away from refuges (Fig. 9 a,b). Female 96-3 refuged in NQI and spent most time during activity (68%) close to the north shoreline only moving south and south-east across the North Basin three times (Fig. 9a). In contrast, female 96-4 refuged predominantly under West Rock, but spent roughly equal time during bouts of activity close to the north, east and west shorelines, with only a relatively small amount of overlap in activity area with the other female (Fig. 9b). Spatial analysis of movements using Poisson probabilities of location frequency per grid cell compared with observed location frequency per grid cell showed that locations visited by both females during active periods were not randomly distributed (goodness-of-fit tests: female 96-3,  $\chi^2 = 8.27$ ,  $\chi^2_{0.05,2} = 5.99$ ,  $P < 0.025$ ; female 96-4,  $\chi^2 = 14.62$ ,  $\chi^2_{0.05,1} = 3.84$ ,  $P < 0.001$ ). Furthermore, the variance in location frequency per grid cell ( $\sigma^2$ ) divided by the mean frequency per grid cell ( $\mu$ ) was greater than 1 for both females which indicated that the distribution of locations visited were clustered (underdispersed) rather than uniform ( $\sigma^2/\mu$ : female 96-3, 1.7; female 96-4, 1.2).

The mean step length of females when active was very similar (Table 2) and almost three times greater than the mean distance moved per step by males. Consequently, the median rates of movement of females during activity were higher than median movement rates employed by both males. As a result of faster rates and broader range of movements, the minimum total distances moved by females over the 6-day tracking period were strikingly similar to distances covered by males even though females spent far less time being active (Table 2).

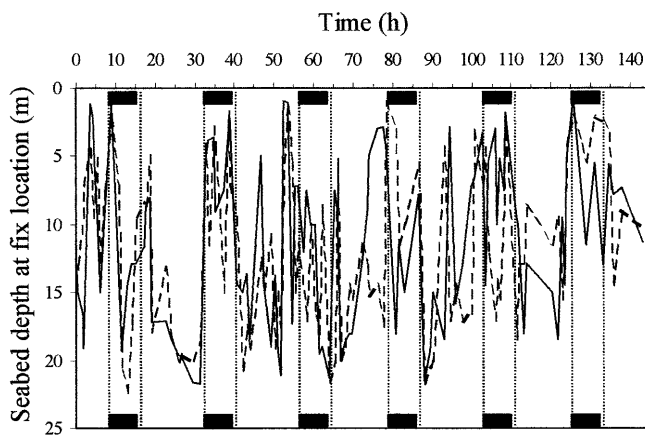


Fig. 6 Changes in seabed depth at successive fix locations for both male dogfish, *S. canicula*, showing similar vertical habitat selection in each diel cycle over the 6-day tracking period. Shallower depths were selected during nocturnal phases. (Male 96-1, solid line; male 96-2, dashed line)

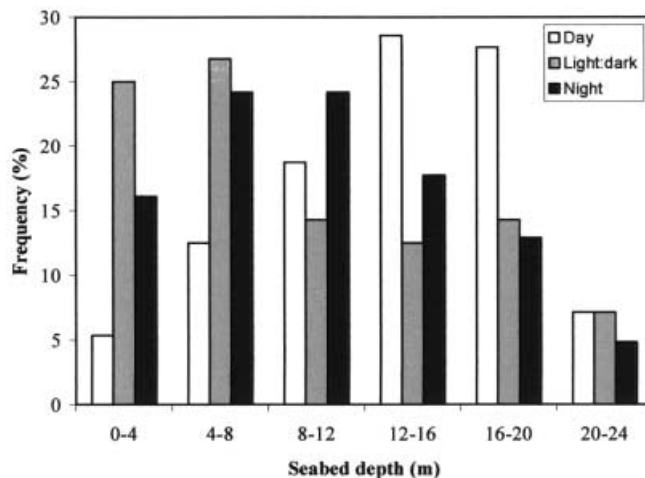
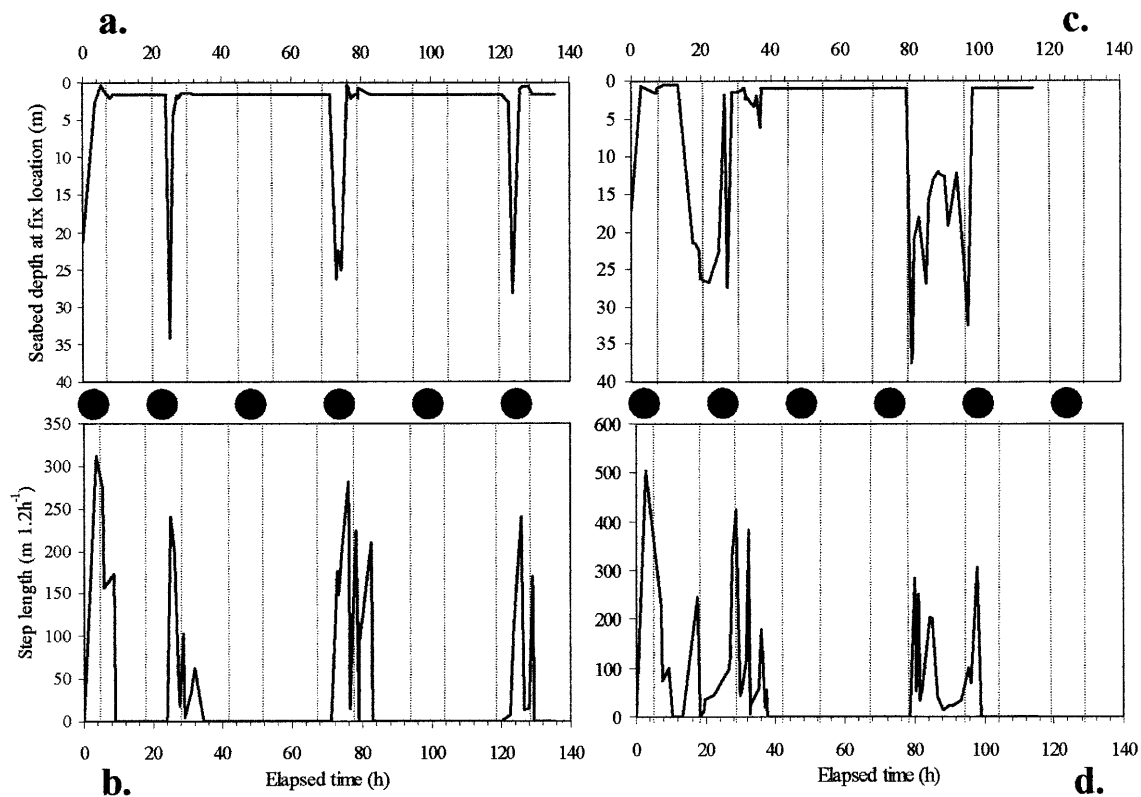


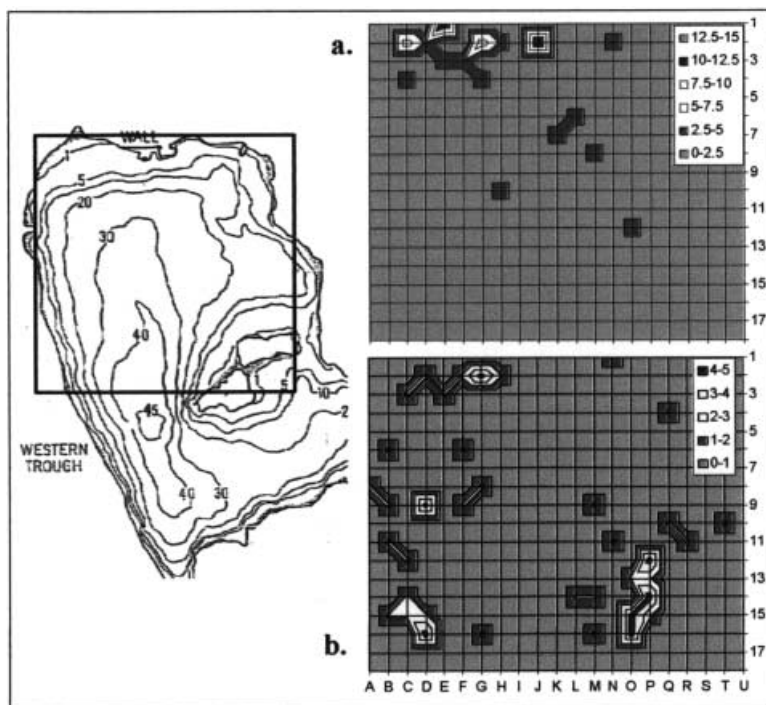
Fig. 7 Significant shift in habitat selection, from deep (daytime) to shallow (crepuscular) seabed depths, by male dogfish, *S. canicula*, within each diel cycle over the tracking period



**Fig. 8** Activity patterns of female dogfish, *S. canicula*, 96-3 (a,b) and 96-4 (c,d) over the 6-day tracking period showing surface refuges were occupied during both day and night with occasional but temporally rhythmic, rapid movements into deeper water. (Filled circles denote dark phases)

Vertical movements of females ranged from habitat with seabed depths between 0.5 and 38.0 m (Fig. 8a,b). The female refuges were located in shallow water between 0.5 and 1.5 m. The nocturnal movements of

**Fig. 9** Contour plots of percentage fixes per grid square (minus refuge locations) showing the home ranges of female dogfish, *S. canicula*, 96-3 (a) and 96-4 (b) in the North Basin of Lough Hyne. The distribution of locations selected by both females during activity bouts were not randomly distributed, but were clustered



female 96-3 occurred around the midpoint of darkness and consisted of excursions into deeper water (20–35 m) at first followed by returns to shallow water between 0.5 and 5.0 m depth (Fig. 1; Fig. 8a). Almost identical habitat depths were selected by female 96-3 during consecutive activity bouts that showed a marked rhythmicity of 48 h. Similarly, the vertical movements of female 96-4 were characterised by excursions into deep water (20–38 m) at the start of an activity bout followed by return movements to shallow water (Fig. 8c; Fig. 9a). However, female 96-4 often returned to deeper water from shallow depths during an activity bout before returning to a refuge. Broadly similar 2-day rhythmicity in activity was observed for female 96-4 although the timing was less predictable compared to the other female.

## Discussion

The short-soak-time netting and SCUBA-diving methods used to capture dogfish in this investigation provided fish in good condition for behavioural studies and minimised capture stress prior to tagging and subsequent release. The procedure for attaching number tags was rapid (<2 min). The fact that males and females were recaptured after a 1-year period close to where they were originally caught, and all showed positive growth increments similar to those expected for wild dogfish (Rodríguez-Cabello et al. 1998), indicates there was little long-term deleterious effects of number tags on dogfish behaviour or growth.

The methods for attaching acoustic transmitters internally or externally were also relatively rapid (10–15 min) and transmitters weighed only 0.8–1.0% of dogfish body mass. Within 2–4 h post-release both male and female dogfish occupied areas within the home ranges from which they were originally caught. These transmitter-tagged dogfish exhibited general behaviour patterns that were consistent with those expected for wild *S. canicula* on the basis of observations of nocturnal activity in juveniles and adults in the laboratory (Metcalf and Butler 1984; Sims et al. 1993). Furthermore, there was no apparent difference in the behaviour of internally or externally tagged fish within the sexes. This indicates that any effect on behaviour of surgical implantation of the transmitter was negligible when compared with external attachment, which confirms previous studies (McKibben and Nelson 1986; Gruber et al. 1988; Holland et al. 1999).

The behavioural strategy employed by acoustically tracked male dogfish in the South Basin consisted of crepuscular short-range movements either away from a central daytime activity area into shallow water <4 m depth at dusk, primarily along the south shoreline of Castle Island, or back to the daytime space at dawn. This demonstrates that male dogfish exhibit low activity in deeper water during the day and increase activity at dusk as they move into shallow water, before returning

at dawn to deeper water. In contrast to the crepuscular activity peaks of dogfish, nocturnal distances moved and rates of movement were similar to those during the daylight phase. Habitats with intermediate water depths of ~8 m were selected however, indicating male dogfish generally remained in shallow water areas nocturnally, but reduced activity to daytime levels before returning to deeper water at dawn. Laboratory studies on juvenile dogfish also showed crepuscular activity peaks (Sims et al. 1993). However, adults in laboratory actograph experiments had activity peaks coinciding approximately with the midpoint of darkness (Metcalf and Butler 1984). Other benthic shark species such as horn (*Heterodontus francisci*) and swell sharks (*Cephaloscyllium ventriosum*) also showed general increases in activity during the nocturnal phase in the laboratory (Nelson and Johnson 1970), although other shark species tracked in the natural environment showed similar crepuscular patterns of movement to those seen for male *S. canicula* in Lough Hyne (Sciarrotta and Nelson 1977; Gruber et al. 1988; Klimley et al. 1988).

The dogfish, *S. canicula*, is considered a generalist feeder and opportunistic benthic macropredator and scavenger on a wide range of invertebrate and fish prey (Ford 1921; Steven 1930; Eales 1949; Lyle 1983; Ellis et al. 1996). These studies show that the dietary preference of *S. canicula* reflects the general abundance and availability of prey in the habitat it occupies (Wetherbee et al. 1990). The diet of dogfish in Lough Hyne has not been the subject of quantitative studies, but stomach contents from 20 dogfish (15 males, 5 females) examined from incidental captures indicate the predominate prey to be decapod crustaceans (swimming crabs, *Liocarcinus* spp., the prawn, *Palaemon serratus*) and small teleost fishes (D. Morritt, unpublished observations). This is in agreement with previous studies which reported that epibenthic crustaceans, especially decapods, were significant food items for dogfish (e.g. Lyle 1983; Ellis et al. 1996). Swimming crabs (*L. puber*, *L. arcuatus*), shore crabs (*Carcinus maenas*), prawns (e.g. *P. serratus*) and shrimps are nocturnally active in Lough Hyne both in the sublittoral and littoral zones (Kitching and Ebling 1967). This suggests that male dogfish in the present study selected shallow water habitat during the crepuscular and nocturnal phases because crustacean prey emerged from daytime refuges at these times and were active in these areas.

The spatio-temporal movements of both male dogfish in Lough Hyne were very similar and the activity areas they occupied fully overlapped which suggests male dogfish aggregate during the day and forage during the dark over the same spatially limited area. On several occasions in the present study we SCUBA-dived at the location of the core daytime area of the home range of males in the South Basin of Lough Hyne. During one particular 30-min dive just prior to dusk, about 20 dogfish were observed at 21 m depth lying very close together and making frequent movements. Four of these dogfish had coloured number tags identifying them as



having been tagged on the south shore of Castle Island. This shows that other dogfish occupied the same daytime area as transmitter-tagged males. Furthermore, males also foraged in the same shallow water areas during the night because previously tagged males were caught in the same shallow bay south of Castle Island that was visited by the acoustically tracked males. Similar observations have been made for horn sharks that show site fidelity to a particular sublittoral reef off New South Wales in Australia (McLaughlin and O'Gower 1971).

Eddy currents or gyres are set up in the eastern part of the South Basin of Lough Hyne by the incoming tide (Bassindale et al. 1948), and this area differs from the rest of the lough in the more frequent occurrence of the large swimming crab, *L. puber* (Kitching and Ebling 1967). The general position of these gyres and greater availability of large crab prey (Kitching and Ebling 1967) coincide closely with the home ranges of male dogfish tracked in the present study. Therefore, the movements and localised activity areas of males could be explained in terms of spatio-temporal movements and distribution of large crab prey in the South Basin. Furthermore, our results suggest that male dogfish in the South Basin of Lough Hyne utilise the same habitat at similar times over the diel cycle, implying they form a mobile predatory or scavenging fish assemblage.

The female dogfish behavioural strategy was characterised by crepuscular or nocturnal excursions into deep water from their daytime, shallow-water cave refuges followed by returns to shallow areas close to refuges for the remainder of the dark period. Overall, when females were active they showed peaks in activity at similar times in the diel cycle to males. However, what was markedly different in behaviour between sexes was the depth of habitat selected at specific times in the diel cycle. Females selected to rest during the day, and on occasions during the night, in water between 0.5 and 1.5 m deep, whereas males occupied deeper water between 12 and 20 m. Males undertook movements into shallow water (foraging) areas each diel cycle for the entire 6-day tracking period, whereas females exhibited only 2 or 3 main activity bouts which included movements into deep water between 20 and 38 m. Although the reasons for sex differences in behavioural strategy observed in this study remain unclear at present, behaviour of female dogfish may be the result of reproductive factors in addition to nutritional ones.

The main difference between the behaviour of male and female dogfish was that females spent between 62 and 73% of the time (measured in terms of position fixes per location) resting in shallow water under rocks or in caves. One obvious explanation of this behaviour is that caves and rocks act as central refuges against predation whilst the fish rest during the day. However, adult dogfish have few predators, particularly so in Lough Hyne, and furthermore this would not explain why this behaviour was absent in male dogfish tracked in the South Basin. SCUBA-diving observations verified that

large numbers of males in the South Basin did not refuge in caves during the day, but remained lying on the gravel substratum. Moreover, the dogfish occupying shallow refuges in the North Basin were exclusively females which we determined by removing individuals from the refuges for tagging purposes at the beginning and end of each study period. Between 3 and 13 females were observed together in these refuges and no males were ever recorded. Similar aggregation behaviour of female *H. portusjacksoni* in reef caves off Australia has been observed (McLaughlin and O'Gower 1971). By analogy with observations for horn sharks, our results suggest that female *S. canicula* aggregate in refuges and the observed sex differences in diel habitat selection were most probably related to reproductive behaviour.

A recent mark-recapture study demonstrated spatially-limited movements of dogfish on an open coastline (Rodriguez-Cabello et al. 1998). Our study supports this idea that dogfish are highly philopatric, but with an important addition. Our results of acoustically tracking male and female dogfish, in addition to tagging individuals during netting and SCUBA-diving surveys, also indicates spatial segregation by sex in the lough. During the tracking period male and female dogfish showed site fidelity to highly localised areas within the South and North basins of Lough Hyne, respectively (which together only cover 0.6 km<sup>2</sup>). At no time during the tracking study did male activity areas overlap those of females. As well as short-term trackings, tag returns were consistent with apparent spatial segregation according to sex. Male dogfish caught on the south shore of Castle Island in 1995, and females tagged off North Quay Island, were recaptured from the same location one year later. No males were ever caught in the North Basin. Furthermore, a female caught and tagged on the south shore of Castle Island (South Basin) was found 6 days later in the North Quay Island cave with other females, perhaps suggesting that females found near Castle Island were probably at the southern limit of their area. In the present study, it appears that the apparent sexual segregation observed is a result of philopatric behaviour over at least two temporal scales: male and female dogfish move away from and orient back to horizontally and vertically separated core areas over the 24-h cycle, and at the end of August in consecutive years (at least) they select the same location within sexes, but different areas between sexes.

Sexual segregation by geographic location has been described for a number of shark species (Springer 1967; Klimley 1987) and could arise through intraspecific competition, alternative seasonal habitat (resource) requirements, or by reproductive choices associated with pre- or post-mating strategies. It is generally thought that sexual segregation is related to reproduction. It was hypothesized in a previous study that sex differences in habitat selection led to females growing more rapidly to reproductive size and attaining a larger body size at maturity compared to males, and thus maximised reproductive capacity (Klimley 1987). Although this

hypothesis has yet to be tested, data from previous investigations suggest *S. canicula* has a weak tendency to segregate by sex (Klimley 1987). Ford (1921) showed, from the numbers of adult male and female *S. canicula* caught off Plymouth in the English Channel, that there were seasonal biases in sex ratio consistent with distinct differences in habit between the two sexes. Adult female *S. canicula* were only present for a short period of time compared to males in an area studied off the Isle of Man, Irish Sea (Lyle 1983), which implies some degree of sexual segregation. However, the pattern of vertical distribution of dogfish in the North Aegean region of the Mediterranean Sea did not exhibit any sexual segregation (D'Onghia et al. 1995). Our observations for *S. canicula*, however, demonstrate for the first time that sexual segregation can occur over an extremely fine-scale even within the confined environment of Lough Hyne. It was clear that the entire lough was not utilised by either sex, although the relative confinement of the dogfish within the lough may exaggerate the expression of sexual segregation responses compared to open coast environments. However, this identifies the dogfish "population" in Lough Hyne as an important model system for studies on the determinants of sexual segregation in marine fishes.

In Lough Hyne, female dogfish are known to lay eggs on seaweed in shallow water (1–5 m) (Minchin 1987). Therefore, occupation of shallow water areas by females could also result from selective behaviour to remain close to egg-laying sites. Another possibility to explain the different behaviour of females could be that shallow-water refuging behaviour also facilitates increased rates of egg development as water temperature in shallow, compared to deep areas, will be some 3–4°C higher because Lough Hyne stratifies thermally during summer (Kitching and Ebling 1967). However, in the present study we found that the claspers of male dogfish had reddened tips indicating that they had recently been involved in mating activity. Mating itself is thought to take place in late summer for *S. canicula* (Compagno 1984) and appears to be an energetically costly activity. Observations made by A.C. Brooks (cited in Dodd 1983) showed that copulation lasted for up to 30 min and during courtship and copulation the pair were pursued by up to eight males that were tugging violently at the female. We suggest that females may form female-only aggregations in refuges spatially separated from males to reduce energetically demanding mating activity. Females store sperm, permitting egg-laying throughout most of the year (Ford 1921; Metten 1939a, b; Harris 1952). We suggest females avoid multiple copulations to conserve energy in the peak mating and egg-laying season (Ellis and Shackley 1997). Studies are currently underway to test these ideas.

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