

**Movement patterns and search behaviour of a
predatory marine fish**

Thesis submitted for the degree of

Doctor of Philosophy

at the University of Leicester

by

Joshua Louis Filer

May 2009

Abstract

Marine environments are known for their dynamic, unpredictable nature. Therefore, search behaviour is particularly important for marine animals. Despite this, movement patterns and search behaviour of marine animals, and particularly fish, are poorly known. Here I investigate some unanswered questions relating to the search behaviour of a predatory marine fish, the small-spotted catshark (*Scyliorhinus canicula*). This research uses a combination of field-based tracking and laboratory investigations to evaluate the development of search behaviour. In the wild both male and female adults exhibited movements resembling central place foraging. These movements were characterised by preferential use of core areas from which discrete excursions were made at particular times prior to return to the core area. Despite this, sex differences in movements were found. Females undertook relatively infrequent, mainly nocturnal, long range excursions whereas males made more frequent excursions of variable duration and extent throughout both the day and night. In the laboratory, movement patterns of juveniles were consistent with a simple random walk model of movement, regardless of prey distribution or density. The resulting foraging efficiencies were also similar irrespective of treatment. The movements of males in the wild also appeared to be consistent with a random walk model, although a truncated-power law was found to be a good fit to some of the step length data, with exponent (μ) values indicative of optimal Lévy-like behaviour. Behaviour switching between different movement patterns in relation to complex changes in prey availability and distribution appears likely. In contrast, the movements of adult females in the field showed some degree of determinism, resulting in poor agreement with random walk models. The results of learning experiments with juveniles in the laboratory suggest that small-spotted catsharks may be capable of developing spatial memory, and such learning may be important for the development of efficient search tactics. Given these findings, the importance of learning with regards to search behaviour in catsharks warrants further investigation.

Acknowledgements

Throughout the duration of this project there have been many people who have provided me with encouragement and advice. I would like to thank all these people, as without them the completion of this thesis would not have been possible.

Firstly, I would like to thank my supervisors and thesis committee, Professor David Sims, Professor Paul Hart and Dr Iain Barber, whose advice and guidance throughout has helped me to develop as a researcher. I am very grateful for their helpful comments and suggestions that have greatly improved the readability of this thesis.

My thanks are also extended to the Director of the Marine Biological Association of the UK for allowing me to conduct my studies at the laboratory. Whilst working at the laboratory numerous members of staff and students have provided assistance and insightful discussion. I am particularly grateful to Dr Viki Wearmouth and Nuno Queiroz for the numerous discussions and support whilst preparing figures and graphics for the thesis. I am also particularly appreciative of the help provided by John Rundle, Peter Rendle and Kevin Atkins. My thanks are also extended to the common room staff for all of the wonderful cakes!

The fieldwork that was undertaken as part of this research involved the assistance of a number of people including David Sims, Patricia Masterson, Matthew McHugh and Viki Wearmouth. Thank you all for making my experiences of fieldwork at Lough Hyne so memorable. This fieldwork would also not have been possible without the assistance of Dr Rob McAllen and University College Cork along with D. O'Donnell and P. Graham from Irish National Parks and Wildlife, who granted permits to conduct research in the Lough Hyne marine nature reserve. All research involving animals adhered to institutional and UK Home Office regulations and were carried out by licensed personnel.

I am grateful to my family for their continued support, and especially to my wife Samantha, who has been an incredible pillar of emotional support, who constantly provided me with encouragement.

Finally, this research was funded by a PhD studentship from the Fisheries Society of the British Isles, and by UK Natural Environment Research Council grant-in-aid funding to Professor D. Sims.

Table of contents

Movement patterns and search behaviour of a predatory marine fish.....	1
Abstract	i
Acknowledgements.....	ii
Table of contents	iii
List of figures.....	vii
List of tables.....	xviii
1 Introduction	1
1.1 Introduction.....	1
1.2 The predatory cycle	2
1.3 The continuum of search behaviour.....	2
1.4 Locating resources	4
1.5 Intensive and extensive search.....	5
1.6 Locating patches: modelling animal movements	7
1.7 Locating patches: spatial memory and learning.....	10
1.8 Exploiting patches	12
1.9 Aims and objectives.....	15
2 General Methodology.....	19
2.1 Experimental animal.....	19
2.2 Field-based methods.....	19
2.2.1 Study site.....	19
2.2.2 Fish capture and individual identification.....	21
2.2.3 Anaesthetic and surgical procedures.....	22
2.2.4 Fine-scale acoustic tracking.....	24

CONTENTS

2.2.5	Prey sampling.....	28
2.2.6	Data analyses.....	28
2.3	Lab-based methods.....	34
2.3.1	Experimental animal.....	34
2.3.2	Fish holding facilities.....	34
2.3.3	Experimental arena and design.....	34
2.3.4	Computer-aided video monitoring.....	36
2.3.5	Data analyses.....	36
3	Central place foraging-like behaviour of wild adult small-spotted catsharks.....	38
3.1	Introduction.....	38
3.2	Methods.....	41
3.2.1	Acoustic telemetry.....	42
3.2.2	Space use.....	42
3.2.3	Movements.....	43
3.2.4	Prey sampling.....	43
3.3	Results.....	44
3.3.1	Space use.....	46
3.3.2	Movements.....	50
3.3.3	Prey field sampling.....	61
3.4	Discussion.....	63
4	Effects of spatial distribution and density of prey on search behaviour and movement patterns of juvenile small-spotted catsharks.....	68
4.1	Introduction.....	68
4.2	Methods.....	70
4.2.1	Prey distribution experiments.....	70

CONTENTS

4.2.2	Prey density experiments.....	73
4.2.3	Data acquisition and analyses	74
4.3	Results.....	75
4.3.1	Prey distribution.....	75
4.3.2	Prey density.....	81
4.4	Discussion.....	87
5	Sex differences in the movements of wild adult small-spotted catsharks.....	91
5.1	Introduction.....	91
5.2	Methods.....	94
5.3	Results.....	94
5.3.1	First passage time.....	96
5.3.2	Movement parameters	97
5.4	Discussion.....	102
6	Ontogenetic development and learning of search behaviour	108
6.1	Introduction.....	108
6.2	Methods.....	110
6.2.1	Prey distribution experiment.....	110
6.2.2	Learning experiment	111
6.2.3	Data acquisition and analyses	113
6.3	Results.....	114
6.3.1	Prey distribution experiment.....	114
6.3.2	Learning experiment	123
6.4	Discussion.....	131
6.4.1	Prey distribution experiments.....	131
6.4.2	Learning experiment	133

CONTENTS

6.4.3	Conclusions	135
7	General discussion.....	136
7.1	Central place foraging.....	137
7.2	Foraging in different resource scenarios	137
7.3	Sex differences in movements of adults	138
7.4	Temporal changes in search behaviour and foraging efficiency	139
7.5	Conclusions.....	139
7.6	Future directions	142
	Appendices	144
	References.....	151

List of figures

Figure 1-1. The marginal value theorem showing the optimal patch residence time (t_{opt}), derived from Charnov (1976).14

Figure 2-1. Map of Lough Hyne, Ireland showing the bathymetry (top) and sediment type (Parnum, 2003) with classification of ‘habitat’ complexes by colour and code based on the JNCC biotope classification system (Connor *et al.*, 2003)(bottom). The wider location of the study site is shown as an arrow on the smaller map of Ireland (top left). Locations referred to in the text are shown for reference.....21

Figure 2-2. Attachment of acoustic pingers (V13, VEMCO) to adult small-spotted catsharks in Lough Hyne, Ireland. Plan view (A), lateral view (B) and close-up (C) prior to crimping and cutting of trailing ends of anchor tags. The tags were set in moulded epoxy harnesses and were secured to the catsharks using t-bar anchor tags (Floy) inserted sub-cutaneously and held in place with alloy crimps.23

Figure 2-3. Radio-acoustic positioning (RAP) system (VRAP, VEMCO) used to automatically track acoustically tagged small-spotted catshark movements in Lough Hyne, Ireland. The system consists of three buoys equipped with hydrophones and radio antennae (• and inset A) that detect sound pulses produced by tags and transmit information to a computer controlled base station (Inset B) where positions are recorded and displayed on screen in real time. Stippled area denotes range of detection of the array.....25

Figure 2-4. Simulation plot of the accuracy of positions determined within the detection range of the VRAP system with a hydrophone-equipped buoy receiver timing error of 0.5 ms and a transmitter depth of 10 m.....26

FIGURES

- Figure 2-5. Aggregation of n variable step lengths of an individual's movement path into moves if all intermediate positions are within x of the line connecting the first point with point n . In this case $x = 1$ m (Adapted from Turchin, 1998).31
- Figure 2-6. Schematic representation of two theoretical example tracks and their corresponding first passage time analysis results. A relatively straight path results in low variance (a), whereas a tortuous path will give peaks in variance associated with the scale of path re-crossing caused by area restricted search behaviour (b).32
- Figure 2-7. Tank setup showing experimental arena (right) and the EthoVision, computer-aided video monitoring system (far right).35
- Figure 3-1 - Hourly catch per unit effort (CPUE, fish caught per hour) of male (blue) and female (red) small-spotted catsharks during trips to Lough Hyne, Republic of Ireland, during spring (data for 2003 and 2004 from Prof David Sims, unpublished data). Darker shaded sections represent the proportion of CPUE that were recaptures.46
- Figure 3-2. Space-use patterns of female (F1-3) and male (M1-3) small-spotted catsharks in Lough Hyne, Ireland during April 2003 and May 2007, respectively. Colours represent differing densities of the utilisation distribution with red areas having the highest density and blue areas the lowest.47
- Figure 3-3. Night time and day time space use of small-spotted catsharks in Lough Hyne, Republic of Ireland. Red bars represent mean female ($n = 3$) space use as measured by the total area of the 95% contour of the utilisation distribution (UD) for both day and night positions throughout the tracking period. Blue bars indicate mean male ($n = 3$) space use using the same measure. Error bars represent standard error (S.E.). .49
- Figure 3-4. Timing of discrete excursions by female small-spotted catsharks from refuges (central places) in Lough Hyne, Republic of Ireland. Each excursion is a line whose length represents the duration of the excursion. The height of the line on the y -axis

FIGURES

- represents the total distance travelled during the excursion in meters. Shaded grey bars indicate the time between sunset and sunrise each day. Green circles and red squares indicate the start and end of the tracking period respectively.....51
- Figure 3-5. Timing of discrete excursions by male small-spotted catsharks from central places in Lough Hyne, Republic of Ireland. Each excursion is a line whose length represents the duration of the excursion. The height of the line on the *y*-axis represents the total distance travelled during the excursion in meters. Shaded grey bars indicate the time between sunset and sunrise each day. Green circles and red squares indicate the start and end of the tracking period respectively.....52
- Figure 3-6. Distances travelled during foraging excursions by female (red) and male (blue) small-spotted catsharks in Lough Hyne, Republic of Ireland. Median distances are indicated by horizontal black lines within boxes representing inter-quartile ranges. Outliers are shown as an unfilled circle (female) and an asterisk (male)..53
- Figure 3-7. A looping excursion (trip 1) made by a female small-spotted catshark (F1) in Lough Hyne, Republic of Ireland in 2003. Filled green and red circles indicate the start and end of the excursion respectively.54
- Figure 3-8. Variability of speeds (m s^{-1}) of a female small-spotted catshark (F1) during a nocturnal excursion (trip 4) from a core area (refuge) in Lough Hyne, Republic of Ireland. Dashed lines on the speed plot (bottom) delineate sections of the track shown by the red dots on the corresponding maps (top).....55
- Figure 3-9. A looping excursion made by a female small-spotted catshark (F2, trip 2) in Lough Hyne, Republic of Ireland in 2003. Filled green and red circles indicate the start and end of the excursion respectively.56
- Figure 3-10. A looping excursion made by a female small-spotted catshark (F3, trip 1) in Lough Hyne, Republic of Ireland in 2003. Filled green and red circles indicate the

FIGURES

- start and end of the excursion respectively, unfilled red circles indicate positions during fragmented section of the track where the individual moved in and out of detection range.....57
- Figure 3-11. A discrete looping excursion made by a male small-spotted catshark (M1, trip 3) in Lough Hyne, Republic of Ireland. Filled green and red circles indicate the start and end of the excursion respectively.....59
- Figure 3-12. Swimming speeds (m s^{-1}) of a male small-spotted catshark (M1) during an excursion from a core area (trip 3) in Lough Hyne, Republic of Ireland.....59
- Figure 3-13. A discrete looping excursion made by a male small-spotted catshark (M3, trip 11) in Lough Hyne, Republic of Ireland. Filled green and red circles indicate the start and end of the excursion respectively.....60
- Figure 3-14. Results of prey sampling conducted at Lough Hyne during April 2003 (top) and May 2007 (bottom). Pie charts show the mean proportional abundances of different types of prey as indicated in the key (top right), and their sizes represent the relative total abundances of prey caught at those particular locations during consecutive nights and days.62
- Figure 4-1. Spatial patterns of the distributions of prey (cut squid) for each of the three experimental treatments: (a) regular or uniform array; (b) random array; (c) aggregated array.....72
- Figure 4-2. Spatial patterns of the distributions of prey (cut squid) for the two experimental treatments: (a) low density prey, (b) high density prey.....73
- Figure 4-3. Examples of movement tracks of a juvenile male and female small-spotted catshark whilst foraging in an arena containing food distributed uniformly, aggregated and randomly. Movements are also shown for controls when no food was present but either no scent (Control I) or scent was added to the arena at the start of

FIGURES

the trial (Control II). The location of the centre of gravity of the individual when prey was captured is shown as red circles.76

Figure 4-4. The variance in first passage time, $S(r)$, as a function of radius (r) for the movement tracks of small-spotted catsharks whilst foraging. Peaks represent scales of area restricted searching (ARS).76

Figure 4-5. Mean (\pm S.E.) scales of area restricted searching (ARS) for juvenile small-spotted catsharks foraging in different distributions of prey as identified by first passage time analysis.77

Figure 4-6. Frequency distributions of turn angles exhibited by two juvenile small-spotted catsharks whilst moving in trials with three different distributions of prey and two controls (no prey). Female (F1) – red bars and blue arrows; male (M1) – blue bars and red arrows.78

Figure 4-7. Mean turn angles of male and female juvenile small-spotted catsharks whilst foraging in different distributions of prey and controls with no prey. Confidence limits are indicated by the size of the brackets around the plot perimeter. Red brackets indicate large confidence limits and therefore low reliability of the mean vector.78

Figure 4-8. A comparison of the fits of the step length distribution of a juvenile small-spotted catshark to different theoretical distributions. The data appears to fit an exponential distribution better than either a power law or truncated Pareto (power law) distribution.79

Figure 4-9. Results of MLE based analyses showing frequency distributions of move step lengths as best fits to exponential distributions for female (red, F1 and F5) and male (blue, M1-3 and 5) small-spotted catsharks movements whilst foraging in three different prey distributions. Circles indicate empirical data and lines represent best fit

FIGURES

lines to an exponential distribution above x_{\min} . For more details see general methodology.....80

Figure 4-10. (a) Mean (\pm S.E.) foraging efficiency and (b) mean (\pm S.E.) giving up times of juvenile small-spotted catsharks whilst foraging in different prey distributions. Red bars indicate females and blue bars indicate males.81

Figure 4-11. Movement tracks of juvenile small-spotted catsharks whilst foraging in low prey densities and high prey densities. The location of the centre of gravity of the individual when prey was captured is shown as red circles.82

Figure 4-12. Variance in first passage time, $S(r)$, as a function of radius (r) for five female (F1-5) and five male (M1-5) small-spotted catsharks whilst foraging. Red solid lines represent $S(r)$ for trials with high densities of prey; blue dashed lines represent $S(r)$ for trials with low prey densities. Peaks in variance are marked with filled circles and labelled with the associated spatial scale.....83

Figure 4-13. Circular frequency distributions of turn angles for a female (F1) and a male (M1) small-spotted catshark whilst foraging in low and high prey densities. Numbers on the outer circle represent degrees, the direction of the arrowheads represents the mean turn angles and their lengths represent the strength of directionality. Dashed lines indicate frequency increments of 120 to a maximum of 600.84

Figure 4-14 - Results of MLE based analyses showing frequency distributions of move step lengths as best fits to exponential distributions for female (red, F1-5) and male (blue, M1-5) small-spotted catsharks movements whilst foraging in different prey densities. Circles indicate empirical data and lines represent best fit lines to an exponential distribution above x_{\min} . For more details see general methodology.....85

FIGURES

- Figure 4-15. (a) Mean (\pm S.E.) foraging efficiency and (b) mean (\pm S.E.) giving up times of juvenile small-spotted catsharks whilst foraging in different prey distributions. Red bars indicate females and blue bars indicate males.86
- Figure 5-1. Filtered tracks of female (red lines, F1-3) and male (blue lines, M1-3) small-spotted catshark movements in Lough Hyne, Ireland during April 2003 and May 2007 respectively. Tracking periods (days) given in bottom left of each pane.96
- Figure 5-2. Variance in first passage time, $S(r)$, as a function of radius (r) for three female (Red, F1-3) and three male (blue, M1-3) small-spotted catshark movement tracks in Lough Hyne. Peaks in variance are marked with filled circles and labelled with the associated spatial scale.97
- Figure 5-3. Circular frequency distributions of turn angles for female (red, F1-3) and male (blue, M1-3) small-spotted catshark movements in Lough Hyne, Ireland. Numbers on the outer circle represent degrees, the direction of the arrowheads represents the mean turn angles and their lengths represent the strength of directionality. Brackets on the outside of the circle represent confidence intervals (95%) for the mean turn angle (Red brackets indicate low reliability of mean vector). Dashed lines indicate frequency increments of 10 to a maximum of 50 for female plots (top) and 100 to a maximum of 500 for male plots (bottom).98
- Figure 5-4. Results of MLE based analyses showing frequency distributions of move lengths as best fits to exponential (random) distributions for female (red, F1-3) and male (blue, M1-3) small-spotted catsharks movements in Lough Hyne, Ireland. Circles indicate empirical data and lines represent best fit lines to an exponential distribution above x_{\min} . For more details see general methodology.99
- Figure 5-5. Results of MLE based analyses showing frequency distributions of move lengths as best fits to power law distributions for female (red, F1-3) and male (blue,

FIGURES

M1-3) small-spotted catsharks movements in Lough Hyne, Ireland. Circles indicate empirical data and lines represent best fit lines to a power law distribution above x_{min} .

For more details see general methodology.....100

Figure 5-6. Results of MLE based analyses showing frequency distributions of move lengths as best fits to truncated power law distributions for female (red, F1-3) and male (blue, M1-3) small-spotted catsharks movements in Lough Hyne, Ireland. Circles indicate empirical data and lines represent best fit lines to a truncated power law distribution between x_{min} and x_{max} . The scaling parameter (μ) for each model fit is given in the top right of each plot. For more details see general methodology.101

Figure 6-1. The spatial arrangements of prey used throughout a learning experiment concerning the movements and foraging behaviour of juvenile male small-spotted catsharks. Individuals were either allowed to forage each week within a constant spatial arrangement of prey (the same at the start of each trial; left, filled circles), or a variable arrangement of prey (right, unfilled circles). In the final week (6) all individuals were allowed to forage within the constant spatial arrangement of prey (filled circles).....112

Figure 6-2. Morphometric changes for juvenile male (blue) and female (red) small-spotted catsharks between the start of the first foraging experiment (1) and the repeated experiment (2) three months later. (a) Length differences in mm; (b) Mass differences in g. Error bars indicate standard error of the mean values (S.E.).115

Figure 6-3. Movements exhibited by a male small-spotted catshark (M3) whilst foraging within three different prey distributions in an experiment (T1) that was repeated after a period of 3 months (T2). Movements are also shown for control trials where no prey was available and an olfactory stimulus (squid juice) was not introduced (control I) or was introduced at the start of the experiment (control II).115

FIGURES

- Figure 6-4. Mean (\pm S.E.) proportion of time (arcsine transformed) male (blue) and female (red) small-spotted catsharks spent in the central area of the tank during foraging trials with different prey distributions (uniform, aggregated and random) as part of an experiment (1) that was repeated after a period of three months (2).....116
- Figure 6-5. The variance in first passage time, $S(r)$, as a function of radius (r) for the movement tracks of selected small-spotted catsharks (F5, M1-3, 5) whilst foraging. Solid lines and filled circles indicate the initial experimental results at time 1; dashed lines and open circles indicate results for the repeat experiment at time 2, three months later. Peaks identified by circles represent scales of area restricted searching (ARS).117
- Figure 6-6. Grouped mean turn angles exhibited by female (red, $n = 5$) and male (blue, $n = 5$) juvenile small-spotted catsharks during foraging trials with different prey distributions (uniform, aggregated and random) and two controls with no prey (control I: no olfactory stimulus introduced; and control II: olfactory stimulus introduced at the start). Solid lines indicate results of the first set of trials at time 1 and dashed lines indicate results for the repeated trials at time 2, three months later. Confidence limits (95 %) are indicated by the size of the brackets around the plot perimeter.119
- Figure 6-7. Mean (\pm S.E.) distances travelled by selected juvenile small-spotted catsharks during foraging trials with three different prey distributions. Solid bars indicate results for the first experiment and unfilled bars indicate the results for the repeated experiment after a period of three months. (Selected individuals were those that foraged in each treatment and in both experiments).....121
- Figure 6-8. Foraging efficiency of juvenile small-spotted catsharks during foraging trials with different prey distributions (uniform, aggregated and random) as part of an

FIGURES

experiment (1) that was repeated after a period of three months (2). (A) Individual foraging efficiencies (see key for individual identification); (B) Mean (\pm S.E.) foraging efficiencies of male (blue) and female (red) individuals.122

Figure 6-9. Movement tracks of two groups of juvenile male small-spotted catsharks before and after a period of differential training. Solid circles indicate prey captured and unfilled circles indicate prey that was not captured.123

Figure 6-10. Mean (\pm S.E.) proportion of time spent in the central area of the test arena by two groups of juvenile male small-spotted catsharks during foraging trials before and after a period of differential foraging training. Black filled bars indicate results for the group that was trained and tested with the same spatial arrangement of prey; unfilled bars indicate results for the group that was trained and tested on different spatial arrangements of prey each trial.124

Figure 6-11. The variance of first passage time, $S(r)$, as a function of radius (r) for the movement tracks of small-spotted catsharks (C1-5 and V1-5) during foraging trials before and after a period of differential foraging training. Black filled circles indicate peaks of variance for the group that was trained and tested with the same prey distribution (C1-5); unfilled circles indicate peaks of variance for the group that was trained and tested on different prey distributions each trial (V1-5).125

Figure 6-12. Grouped mean turn angles exhibited two groups of male juvenile small-spotted catsharks during foraging trials before and after a period of differential foraging training. Solid lines indicate results for the group that was trained and tested with the same prey distribution; dashed lines indicate results for the group that was trained and tested on different prey distributions each trial. Confidence limits (95%) are indicated by the size of the brackets around the plot perimeter.126

FIGURES

- Figure 6-13. Examples of fits of step-length distributions to hypothesised truncated power law (a) and exponential (b) distributions for C3 (black filled circles and red lines; top) and V4 (unfilled grey circles and black lines; bottom) in both before and after a period of different training.....128
- Figure 6-14. Mean (\pm S.E.) foraging efficiency of two groups of juvenile male small-spotted catsharks during foraging trials before and after a period of differential foraging training. Black filled bars indicate results for the experienced group that was trained and tested with the same prey distribution; unfilled bars indicate results for the inexperienced group that was trained and tested on different prey distributions each trial.128
- Figure 6-15. Individual distances travelled (a), prey captured (b) and resulting foraging efficiency (c) for two groups of juvenile small-spotted catsharks in each week of a learning experiment where each group was allowed to forage in either a constant or variable spatial arrangement of prey.....130
- Figure 6-16. Mean (\pm S.E.) foraging efficiency of two groups of juvenile male small-spotted catsharks during foraging trials before, during and after a period of differential foraging training. Black filled circles indicate results for the group that was trained and tested with the same spatial arrangement of prey; unfilled circles indicate results for group that was trained and tested on different spatial arrangements of prey each week. (a) All individuals; (b) without individual V4.....131

List of tables

Table 3-1. Summary data of the six small-spotted catsharks tagged with acoustic transmitters in Lough Hyne, Republic of Ireland, that are analysed in this study. F denotes female, M denotes male.....	46
Table 3-2. Mean home range and core areas used by female (F1-3) and male (M1-3) small-spotted catsharks in Lough Hyne, Ireland during two separate visits in 2003 (F1-3) and 2007 (M1-3).....	48
Table 3-3. Area of 95% contours of the utilisation distributions of 3 female and 3 male small-spotted catsharks for day and night positions over the whole track.....	50
Table 5-1. Summary data of small-spotted catshark tracks	95
Table 5-2. Summary of the data used and MLE results of step-length distribution analyses for female (F1-3) and male (M1-3) small-spotted catshark movements in Lough Hyne, Ireland.....	102
Table 6-1. Summary of the data used and MLE results of step length distribution analyses for selected juvenile small-spotted catshark movements during foraging trials (1) with three different prey distributions that were repeated after a time interval of three months (2).....	120
Table 6-2. Summary of the data used and MLE results of step length distribution analyses for juvenile male small-spotted catshark movements during foraging trials before and after a period of differential foraging training.....	127

1 Introduction

1.1 Introduction

It has been hypothesised that most ecological systems can be viewed as hierarchical patch systems in which high-density patches at small scales are nested within low-density patches at larger scales (Kotliar and Wiens, 1990; Fauchald, 1999). The marine environment can be considered an example of this as it is generally not spatially uniform; in fact, it is highly variable with heterogeneous, patchy, hierarchical distributions of resources (Ashmole, 1971; Pinaud and Weimerskirch, 2005). Also, the distribution of animals within the environment is generally aggregated and not random (Weimerskirch *et al.*, 2005), and is dependent to some degree on physical processes that vary in space and time (Hunt *et al.*, 1999). Given then, that resources are distributed somewhat unpredictably, a key problem facing an organism is where and how to find resources. Resources in this sense can be food, mates or shelters, i.e. anything an organism needs for growth, development, maintenance and reproduction. Clearly then, searching behaviour is extremely important for survival, and efficient searching behaviour should lead to greater evolutionary fitness. Although searching is important for many aspects of an animal's life this review is concerned only with predators searching for prey.

An animal's search behaviour is determined by the following three types of factors: Firstly, its biological characteristics such as sensory modalities and locomotion methods; second, abiotic and biotic clues and clues from the external environment; and finally, internal factors such as hunger and motivation (Bell, 1990).

Understanding the movement patterns and search tactics of free-ranging predatory fish will facilitate greater understanding of habitat selection and population dynamics (Elliott, 2002; Sims, 2003). This in turn will enable better predictions of the spatial and

temporal distributions of both predators and their prey, which has important implications for sustainable fisheries management and conservation efforts. This review is not intended to be a comprehensive review of all the literature pertaining to the subjects covered. Instead, it is a selective overview of literature relating to each of the topics, with the aim to provide a background for new research by identifying gaps in current knowledge or approach.

1.2 The predatory cycle

In an attempt to provide information concerning the mechanisms of foraging behaviour researchers have categorized the act of predation (Holling, 1959; O'Brien, 1979; 1987). The predation cycle has been described as consisting of three components: (i) search for and locate prey; (ii) pursue and attack prey; (iii) handle and ingest prey (O'Brien *et al.*, 1990). Furthermore, depending on the predator and prey characteristics, different stages of the cycle will be most important. For example, for predators searching for prey that are larger than themselves the pursuit, attack and handling will be most important; however, if prey are smaller than the predator the search component will be most important (O'Brien *et al.*, 1990).

1.3 The continuum of search behaviour

Generally, predators have been largely divided into two broad categories based on their apparent search behaviour. Animals were classed as either “widely ranging” or “sit and wait” predators (Huey and Pianka, 1981). Animals classed in the sit and wait category would, as the term suggests, sit and wait for prey to pass by. When a prey item is encountered the predator would ambush the prey and then return to the waiting position. Perhaps the best example of the use of this strategy by a fish is that of the pike, *Esox lucius*, which has been shown to wait around near vegetated areas to ambush prey emerging from

refuges (Hart, 1997). In contrast, widely ranging animals would actively cruise around searching for prey rather than waiting for opportunistic encounters. However, O'Brien *et al.* (1990) contended that although the behaviours in these classifications were profoundly different, they represented two extremes of a continuum of search behaviour. This contention was based on previous studies of fish foraging behaviour, which showed that some predators moved in a 'stop and go' pattern whereby they would swim for periods of time between which they would pause for extended periods. This intermediate behaviour was termed saltatory search (Evans and O'Brien, 1988).

According to O'Brien's definition of saltatory search, individuals only search for prey during the pauses between movements. When stationary, they scan the search space before moving a short distance, stopping and scanning again. Since higher prey capture rates have been observed for individuals who adjust their saltatory search to incorporate longer pauses between movements when searching for cryptic prey in heterogeneous environments, it is thought that for visual predators this search tactic may help them to identify cryptic prey more easily than those individuals who do not (Ehlinger, 1989). This is thought to be a result of reducing the complexity of the search image by having a non-moving background against which to identify prey movement (Janssen, 1982; Kramer and McLaughlin, 2001).

Many species of fish have been shown to exhibit saltatory search behaviour, including bluegill sunfish, *Lepomis macrochirus* (Ehlinger, 1989; 1990); blueback herring, *Alosa aestivalis* (Janssen, 1982); white crappie, *Pomoxis annularis* (Browman and O'Brien, 1992); fat snook, *Centropomus parallelus* (Temple *et al.*, 2004); and cod, *Gadus morhua* (Ruzicka and Gallager, 2006). However, more recently saltatory search has been documented in a non-visual predator, the dwarf scorpionfish, *Scorpaena papillosa* which predominantly uses its lateral line to detect prey (Bassett *et al.*, 2007). Therefore, the potential benefits of saltatory search do not appear to be confined solely to visual predators. For predators with

mechanoreception as a major sensory mode for feeding, saltatory search may be appropriate due to a similar search image complexity reduction mechanism as that suggested for visual predators. Here, self-generated ‘noise’ such as mechanical perturbations in the water caused by swimming is eliminated by pausing, thus facilitating the detection of prey movements (Bassett *et al.*, 2007). Despite the findings of these, and similar studies, the generality of the observed patterns remains unknown as these studies have predominantly concentrated on larval or juvenile stages and as such their results may represent age-specific behaviours.

1.4 Locating resources

Animals have evolved a suite of abilities that enhance their ability to locate resources. Many animals have well developed sensory systems in which visual, mechanical, chemical and in some cases electrical information can be used with varying efficiency to locate prey. For example, studies of cod have found that olfaction is very important for locating prey as cod can be attracted to food by chemically mediated rheotaxis (Løkkeborg, 1998; Løkkeborg and Fernö, 1999; Meager *et al.*, 2005). Vision is also an important sense for many species, including cod. For example in the study by Løkkeborg and Fernö (1999), it was found that activity in response to strings of bait deployed in a Norwegian fjord was higher during the day than at night, suggesting that light was affecting the visual detection distance and ability to capture prey. Meager *et al.* (2005) found similar results with juvenile cod. In their experimental study they observed lower predation rates when the juvenile cod were foraging in complete darkness. However, this study also showed visual clues can often only be detected at much smaller distances than olfactory clues (Meager *et al.*, 2005). Other sensory modalities, used by some predators, such as electroreception and mechanoreception can also play an important role in locating resources. For example, elasmobranchs have been shown to detect small bioelectric fields that enable them to

accurately locate cryptic prey even in the absence of other sensory clues (Kalmijn, 1966; 1972; 1978; 1982; Filer *et al.*, 2008). Also fish have been shown to use a mechanosensory lateral line to detect hydrodynamic signals given off by prey (Bleckmann, 1993; Bleckmann and Zelick, 1993; Montgomery *et al.*, 1995). Furthermore, studies have shown that this system can also be used to approach prey in a saltatory type fashion (Hoekstra and Janssen, 1985; Coombs and Conley, 1997).

Despite the use of sophisticated sensory modes to detect prey, all sensory abilities have both biotic (morphological and physiological) and abiotic limitations related to spatial and temporal ranges or scales, over which information can be detected or perceived. Perceptual ranges are not only likely to differ between animals, but also between the senses used by any particular animal. Perceptual ranges of animals are generally poorly known, but are likely to be limited to small to medium spatio-temporal scales (Lima and Zollner, 1996). As the spatio-temporal scales increase the sensory information may become less reliable, and at large enough scales beyond perceptual ranges the sensory clues may be no use at all.

1.5 Intensive and extensive search

Effectively the predatory cycle outlined in section 1.2 can be separated further to include two stages to predation: (i) pre-encounter, and (ii) post-encounter. This distinction leads to the next level of the study of search behaviour. This area of investigation considers extensive and intensive search patterns and their relation to different spatio-temporal scales.

Extensive search behaviour is a description of the movement patterns of a predator before encountering prey (pre-encounter). When predators search extensively at large scales, they tend to move rapidly with little turning, covering large distances. Upon encountering (but not necessarily capturing) prey, predators tend to switch from extensive searching to a more intensive or area-restricted search pattern. This is characterised by an

increase in turning rate (klinotaxis), an increase in scanning movements and a decrease in speed (orthokinesis) (Benhamou and Bovet, 1989).

These patterns of movement have been widely documented for a diverse range of animals. For example, various researchers have observed coccinellid beetles adopt an area-restricted search pattern in the vicinity of the first prey capture site (Carter and Dixon, 1984; Nakamuta, 1985; Ferran and Dixon, 1993; Ferran *et al.*, 1994). Ants have also been shown to exhibit area-restricted search behaviour upon encountering prey (Dejean and Benhamou, 1993; Dejean *et al.*, 1993). Besides insects, this behaviour has also been observed in mammals (Bailey and Thompson, 2006), birds (Dall and Cuthill, 1997; Weimerskirch *et al.*, 1997; Pinaud and Weimerskirch, 2007) and fish (Thomas, 1974; Løkkeborg and Fernö, 1999; Hill *et al.*, 2000; Hill *et al.*, 2002; Hill *et al.*, 2003; Newlands *et al.*, 2004) including sharks (Sims and Quayle, 1998). Given the numerous and diverse examples it is clear that these movement patterns are an important aspect of search behaviour of predators, suggesting that predators are able to adapt their behaviour to short-term changes occurring in the environment.

Intensive search behaviours such as those documented in the examples given above are more amenable to scientific study than extensive search behaviours due to the scales at which each of the behaviours occur. Studying extensive search behaviours i.e. searching for targets at larger scales beyond sensorial detection is perhaps more difficult. Consequently, there has been less attention devoted to the study of these behaviours (Turchin, 1996; Zollner and Lima, 1999). However, technological advancements in the field of telemetry are providing more detailed information on large-scale movements of predators (Block, 2005). Coupled with the use of mathematical modelling, this has enabled more attention to be devoted to the study of extensive search patterns.

1.6 Locating patches: modelling animal movements

Optimal foraging theory is based on the assumption that predators should forage so as to maximise their net energy gain (MacArthur and Pianka, 1966; Stephens and Krebs, 1986), and therefore they should adjust their search patterns accordingly to maximise foraging efficiency when searching for prey (Fauchald, 1999). Their movement patterns whilst searching for prey, under this prediction, should maximise the probability of encountering prey (Pyke *et al.*, 1977; Sutherland, 1996). To achieve this without complete knowledge of the location of temporally and spatially variable prey patches (i.e. patches that are beyond the sensory detection limits of the predator) requires the predator to make adaptive decisions about which search tactics or movement patterns to employ (Sims *et al.*, 2006b).

The discovery of area-restricted searching and the suggestion that this was an adaptation for predators feeding on prey with a clumped distribution has led to many questions. Two of these questions concern the extent to which an animal should and does increase its turning rate after encountering a prey item and the length of time over which the animal should maintain such a change (Pyke *et al.*, 1977). Questions such as these led to the construction of early simulation models. Two such models concerned the tortuosity of a path and were based on the assertion that animals would undertake movements that maximise net intake of food by minimizing the frequency of path re-crossing (Cody, 1971; 1974; Pyke *et al.*, 1977; Pyke, 1978). These models are built upon the probabilities of moving in four directions: forwards, backwards, left, and right. As such these models provide early examples of the use of simple random walk models. There were mixed successes and failures when the predictions of these models were compared to empirical data (Pyke *et al.*, 1977), highlighting the need for further study to improve the assumptions underlying the model predictions.

In order to account for the discrepancies found, researchers began to embrace more complicated and hence more realistic scenarios and predictions. This led to the use of more complex random walk models from the fields of mathematics and physics to investigate the foraging movements of animals under different resource scenarios (Kareiva and Shigesada, 1983; Bovet and Benhamou, 1988). These models generally assume that the movement path of an individual is a series of discrete steps punctuated by changes in direction allowing the statistical investigation of either or both of these path parameters (Turchin, 1998). However, due to the limitation of some sampling techniques, it is not always possible to distinguish such steps in empirical datasets. Thus a step can also be represented as the distance covered in a set interval of time, and consequently changes in direction will be recorded at the same time intervals. Because of this, the sampling frequency becomes very important to consider as it can lead to problems associated with both under- and over-sampling. For more information on this topic see Turchin (1998) chapter 5.

The use of correlated random walks (CRWs) in spatial ecology represented an attempt to better consider animal behaviours when investigating animal movements. This is because CRWs could better account for the directional persistence that was evident in animal movements through the use of a non-uniform distribution of turn angles (Kareiva and Shigesada, 1983; Bartumeus *et al.*, 2005). This approach allowed researchers to provide a link between behaviour at an individual level to the spatial processes of diffusion at a population level. The use of CRW models has been confined mostly to terrestrial ecology and mainly the study of insects and mammals (Kareiva and Shigesada, 1983; Benhamou, 1990; Bergman *et al.*, 2000), although a few studies of marine vertebrates such as seals have made use of this modelling approach (Austin *et al.*, 2004; Bailey and Thompson, 2006). Although the use of CRWs has provided valuable information regarding animal

movements, the majority of studies examined movement data on small to medium spatial and temporal scales (Bartumeus *et al.*, 2005). Attempts to use CRW models to describe movements at larger scales have, in some cases been unsuccessful (Morales and Ellner, 2002).

More recently there has been a growing body of researchers who have explored the value of Lévy statistics when considering animals' large-scale search movements (Viswanathan *et al.*, 1996; Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2003; Sims *et al.*, 2008). This has come about after the finding that many physical phenomena appear well approximated by a Lévy flight. For example, the Lévy flight pattern has been found to occur in fluid dynamics, dynamical systems and micelle formation (Shlesinger *et al.*, 1993; Shlesinger *et al.*, 1995; Viswanathan *et al.*, 1996). This led to the realization that it could be possible that Lévy flights also exist in biological systems (Viswanathan *et al.*, 1996).

Lévy flight models are a special class of random walks with a uniform distribution of turn angles and whose step lengths are drawn randomly from a probability distribution with a power law tail such that short walk clusters are separated by infrequent long steps, and represented by the general power law equation (Viswanathan *et al.*, 1996),

$$P(l) = l^{-\mu} \tag{1}$$

Where $P(l)$ is a probability distribution, l is the step length, and μ is the power law exponent. This pattern is scale invariant with fractal properties and is only considered a Lévy flight when the exponent (scaling parameter, μ) ranges between 1 and 3 (Shlesinger *et al.*, 1993; Viswanathan *et al.*, 1996; Viswanathan *et al.*, 1999; Viswanathan *et al.*, 2002; Klafter and Sokolov, 2005; Bartumeus, 2007). These properties have led to the hypothesis that Lévy flights should be optimal for a predator searching for randomly or sparsely located prey. This is because new patches are more likely to be located with the presence of occasional long steps associated with Lévy flight. Additionally, re-visitation of sites

depleted of prey is less likely for Lévy flight (Viswanathan *et al.*, 1999; Viswanathan *et al.*, 2000; Bartumeus *et al.*, 2002).

Since most natural systems have heterogeneous, complex and patchily distributed resources, it is interesting that Lévy-like search behaviour has apparently been identified in many organisms including insects, birds and mammals and even zooplankton (Viswanathan *et al.*, 1996; Viswanathan *et al.*, 1999; Atkinson *et al.*, 2002; Bartumeus *et al.*, 2003; Austin *et al.*, 2004; Ramos-Fernández *et al.*, 2004; Reynolds, 2006). However, the validity of these studies has recently been called into question. Inadequate statistical methodologies and poor data quality control have likely contributed to the misidentification of Lévy-like search behaviour (Edwards *et al.*, 2007; Sims *et al.*, 2007). Using more robust and reliable analytical techniques a team of researchers recently found no evidence for Lévy-like behaviour when re-analysing data from bumblebees, deer and albatross (Edwards *et al.*, 2007). Despite this, a study utilising similarly robust statistical analyses has found evidence for Lévy-like search behaviour in a number of marine vertebrate predators (Sims *et al.*, 2008). Presently the debate for the presence of biological Lévy flights is ongoing.

1.7 Locating patches: spatial memory and learning

Once a prey patch has been found for the first time the possibility exists that its location may be remembered (Benhamou *et al.*, 1990). Therefore, learning and spatial memory may play an important role in animal search behaviour. A location can be memorized in two ways: firstly, a location may be memorized by using local landmark clues independent of the individual's own position in what is known as an exocentric coding process; secondly, a location may be memorized using an egocentric process whereby the animal remembers the route taken to get to that location in relation to its position. Both such methods have been shown to exist in mammals, birds and insects (Benhamou *et al.*, 1990). The ability to

learn to accurately locate food sources with the presence of local clues has also been demonstrated in fish (Warburton, 1990).

Despite its potential, spatial memory and learning using local clues or landmarks would only be useful if there were some consistency in the location of patches. It would be pointless to learn the location of patches that disappeared shortly after visiting them (such as for destructive sampling without subsequent patch replenishment). It may also be of little use to remember the location of patches that shift positions regularly. These scenarios are likely to occur widely in nature and especially in the marine environment. There are further complications to the use of spatial memory. These include that, in terms of exocentric spatial memory, landmarks would only be useful if they were visible from the animal's current location. In relation to this, learning of landmarks requires there to be useable landmarks present, although it is possible that animals search for known landmarks. The lack of local clues has been shown to impair learning of food location leading to more random exploratory movements in fish (Warburton, 1990). Additionally, the cognitive requirements for appropriate use of spatial memory may still be beyond the limited capacities of many animals generally. This is especially significant for egocentric coding of spatial memory since continual calculations of position, direction and distances moved are required (Benhamou *et al.*, 1990).

Asides from its obvious use in spatial memory, learning may also have further beneficial roles in search behaviour. For example, learning appropriate search tactics to employ and in what situation to employ them would be beneficial for animals whilst searching for prey. This would enable the searching individual to be flexible and adapt its behaviour in relation to its current situation more efficiently (Odling-Smee and Braithwaite, 2003). It has been found that ferrets, *Mustela putorius furo*, can learn to fine tune their use of

area-restricted search in order to efficiently exploit different spatial distributions of prey in a laboratory setting (Haskell, 1997).

Further examples of the ability to adapt to temporal differences in food availability have been shown in fish species in what is known as time-place learning (Reebs, 1999; Delicio and Barreto, 2008). In one such example, Nile tilapias, *Oreochromis niloticus*, were able to learn to move into areas during periods of high food availability in laboratory experiments (Delicio and Barreto, 2008). Despite this, time-place learning has mostly been shown in laboratory experiments with few examples in the wild (Reebs, 1999). A further problem arises when one examines the conditions when it occurs. It appears that with temporal variability of food availability, the variability has a somewhat predictable rhythm over a daily cycle. However, there are examples in nature where this is the case, but in more common, complex scenarios where the variability has a more complex rhythm or is more stochastic, time-place-learning is unlikely to be beneficial.

Recent advancements in the knowledge of learning in fishes have shown that like terrestrial vertebrates a number of fish species show impressive cognitive abilities (Brown *et al.*, 2006). In terms of foraging behaviour and movements considerable attention has been devoted to the study of spatial memory and learning. Despite the intuitive restrictions outlined above there is evidence from the laboratory that fish can and do use spatial memory and that learning is important for improving the efficiency of foraging movements (Odling-Smee and Braithwaite, 2003).

1.8 Exploiting patches

A further complication for animals foraging in heterogeneous patchy environments comes once a patch has been located. Not only can prey be cryptic, but whilst foraging in a patch the resources can also become depleted. Therefore, the availability of resources diminishes with time and consequently intake rates will decrease (Holling, 1959). The animal has to

decide how long to remain in a patch before leaving to find a new, more profitable patch. This represents a behavioural trade-off whereby the costs of ceasing foraging and searching for a new patch are balanced against the costs of lost opportunities for foraging in a potentially more profitable patch. This is further complicated by the fact that patches can vary in quality with rich patches providing a higher initial prey capture rate than poor quality patches (Stephens and Krebs, 1986).

This problem has been addressed by classical optimal foraging theory through Charnov's seminal work, the marginal value theorem (MVT) (Charnov, 1976). The theorem states that for each animal the optimal strategy is to leave a patch when the instantaneous capture rate in the patch drops to or below the average capture rate for the habitat. This can be shown graphically by a curve of diminishing returns since the initial rate of capture in a patch will be high, but will decrease as resources become depressed (either through patch depletion or evasive movements of prey) and it takes longer to find a food item. The rate of energy extraction that needs to be maximized is energy gained divided by time spent in a patch. Therefore, the tangential line from the origin to the curve of energy gained gives the optimal time spent within the patch (Figure 1-1). Both shorter stays and longer stays lead to shallower slopes and hence result in lower amounts of energy gained as a function of time (decreased efficiency). In shorter than optimal stays, the amount of energy gained is low compared to the costs of finding the patch. In longer than optimal stays the rate of energy gained decreases as the patch is depressed and the costs of foraging may outweigh the costs of moving to a new more profitable patch. This gives rise to various predictions based on the quality of the patch relative to the habitat. For example, low productivity patches should be abandoned after shorter stays than high productivity patches, patches should be abandoned more quickly when travelling times are short, and patches should be abandoned more quickly when average overall productivity is high than when it is low.

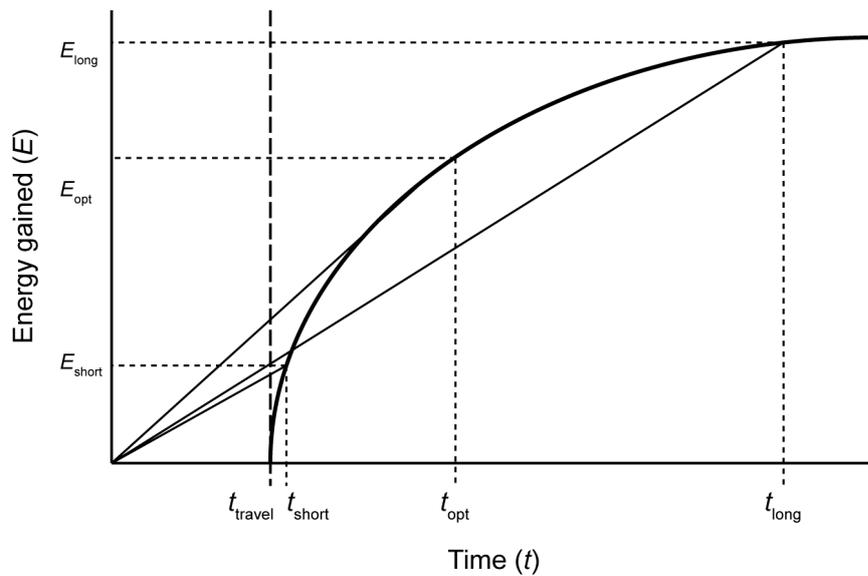


Figure 1-1. The marginal value theorem showing the optimal patch residence time (t_{opt}), derived from Charnov (1976).

Despite numerous qualitative experimental studies supporting the predictions made by the MVT (Stephens and Krebs, 1986; Nonacs, 2001), not all are convinced about the appropriateness of its assumptions (McNamara, 1982; McNamara and Houston, 1985; Nonacs, 2001). For example, this model assumes that the forager has complete information of the model parameters, recognises patch types and does not acquire or use further information whilst foraging within a patch (Stephens and Krebs, 1986). This assumption is clearly unrealistic as environments often vary in spatial and temporal availability of prey, and therefore predictability. Also, animals have been shown to exhibit learning, implying that they can and do use information gained whilst foraging to guide future decisions (Krebs *et al.*, 1978; Werner and Mittelbach, 1981; Werner *et al.*, 1981; McNamara and Houston, 1985). Furthermore, the effects of non-foraging related behaviours such as mating opportunities, competitive interactions and predator avoidance are also not accounted for (Nonacs, 2001). These non-foraging related behaviours may lead to different patch (or habitat) residency times than predicted for a forager in isolation. For example,

bluegill sunfish, *Lepomis macrochirus*, have been shown to shift habitats and select less preferred prey when in the presence of congeners as a result of competition (Werner and Hall, 1977; 1979), suggesting that leaving patches can also be a consequence of competitive interference.

As with the movement models, the patch exploitation models have been continually tested and developed. Thus, they have provided a valuable framework for the study of foraging behaviour that has not only given a number of insights, but also provides a source for framing future research questions.

1.9 Aims and objectives

This short review has highlighted that foraging behaviour is an intensively studied subject. There have been, and continue to be, many researchers adopting a variety of different approaches to answer different questions relating to many aspects of foraging behaviour. This review has identified two different approaches to the study of search behaviour. Firstly, the descriptive approach concerns aspects of foraging and predatory behaviour such as the predatory cycle and intensive and extensive searching, including the phenomenon of area restricted searching. Secondly, the modelling approach concerns the elucidation of behavioural rules that govern searching for and exploitation of patches.

The descriptive approach has yielded a wealth of information on the activities of diverse animals in different situations. In contrast, the modelling approach represents an attempt to understand why an animal performs such activities and what an animal should do in a variety of different situations, thus providing the potential for prediction of future behaviour in novel situations.

The use of random walk models has proven to be a fruitful approach to the study of animal search behaviour, stimulating much debate and providing further understanding of observed behaviours. However, there are many problems associated with the use of

random search models. Movements may not always conform to a random model for a number of reasons. Firstly, animals do not act in isolation; interactions between not only conspecifics but also predators and prey will influence an individual's behaviour whilst searching. For example, competition between individuals can lead to interactions such as avoidance (repulsion) or aggression, which may influence the observed movement patterns resulting in a composite movement path consisting of foraging and non-foraging behaviours. Another potential problem is that of orientation and navigation. If an animal can learn to identify landmarks and use spatial memory to orientate using such pilotage, or possess true goal-orientated movement regardless of any spatial displacements that may occur (navigation), then the movement patterns may be highly deterministic at least at some point along a movement path.

Generally, the influence of learning on search behaviour is under represented within the literature. Most of the literature concerning learning focuses on spatial memory and time-place learning. Although these phenomena can play an important role it is possible that learning in other contexts may be more beneficial when searching, especially for targets of unknown location. For example, experience of the successful use of a random search pattern ('behavioural algorithm') in a certain situation may lead to the adoption of a similar set of movement 'rules' when foraging in a similar yet novel situation in the future. Another related aspect that has been largely overlooked is that of ontogenetic development of search behaviour and its relationship with learning (Hughes *et al.*, 1992). Mostly, the literature comprises examples of the study of age-specific behaviour. Few examples examine the search behaviour of predators of different ages despite there being numerous examples of different diet compositions and microhabitat use as a function of ontogeny.

Despite the advances that have been made, clearly there is still a need for further studies that address these knowledge gaps. This is especially true for marine predators since

most of the advances made in animal behaviour research are based on the study of terrestrial animals such as insects and mammals. The movement patterns of free-living marine predators are still poorly known, but marine vertebrates in particular present themselves as useful models for exploring many questions regarding animal search behaviour in complex, highly changeable environments (Sims, 2003; Weimerskirch *et al.*, 2005).

Addressing knowledge gaps such as these will further our understanding of the movement patterns of predatory animals and shed light on decisions underlying habitat selection. Consequently, this will enable better prediction of spatial distribution patterns of not only predatory fish but also that of their prey, which has important implications for sustainable fisheries management and conservation. Therefore, the overall aim of this research was to determine whether the search tactics (as determined by analysis of movement patterns) employed by a predatory marine fish alter with respect to prey distribution, age and sex. In order to achieve this aim the following hypotheses were developed and tested:

- (1) The search patterns adopted by predatory fish may reflect variation in prey distribution and density as predicted by theoretical models of search behaviour. For, example, simple random walk-like movements should be adopted when prey are dense and uniformly spaced, whereas more complex random walks resembling Lévy flights should be adopted when prey are sparsely aggregated (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2005).
- (2) The different sexes may exhibit different search tactics and foraging behaviour as a consequence of sexual segregation by habitat.
- (3) Search patterns or tactics used during foraging can be learned and therefore may change with age and/or previous experience.

The specific objectives of this study were therefore, to:

- (1) Determine the search patterns employed by a predatory marine fish whilst foraging in areas of different habitat quality with respect to prey availability, density and distribution (Chapters 3 and 4).
- (2) Compare observed search patterns with those predicted by theoretical random walk models (Chapter 4).
- (3) Identify the search patterns used by male and female fish during foraging and compare these using random walk-based null models (Chapters 4 and 5).
- (4) Examine the search patterns used by individuals of different age classes whilst foraging in different scenarios with respect to prey availability and distribution and over time (Chapter 6).

2 General Methodology

2.1 Experimental animal

The model species used in this study was the small-spotted catshark, *Scyliorhinus canicula* (L.). It was chosen for several reasons; firstly, small-spotted catsharks are widely considered to be free-ranging generalist marine predators of a wide range of invertebrate and fish prey (Ellis *et al.*, 1996a; Sims *et al.*, 2001; Sims, 2003). Furthermore, sharks in general are known to have relatively large and structurally complex brains with brain mass: body mass ratios that overlap the range for mammals and birds, thus they may have the capacity for complex behaviours (Northcutt, 1977). Small-spotted catsharks are also suitable for practical reasons. They are abundant in UK waters, allowing collection of wild specimens and eggs, and can be reared in captivity owing to their relatively small size, wide diet breadth and physical robustness. This allows not only laboratory investigation of naïve behaviours but also enables investigation of a wide age range of individuals. Besides from laboratory investigation, adults are also large and robust enough to be tagged with electronic devices to investigate their behaviour in the wild with little effect on normal behaviours (Sims, 2003).

2.2 Field-based methods

2.2.1 Study site

Lough Hyne is a semi-enclosed marine lough near Skibbereen, Co. Cork, in south-west Ireland (51°30'N, 9°18'W). The lough has a surface area of ~0.5 sq. km and volume of $9.64 \times 10^6 \text{ m}^3$ (Johnson *et al.*, 1995; Johnson and Costello, 2002). It reaches depths of ~50 m in a trough that runs north to south and ~ 1 km in length close to the west shore (Figure 2-1). A ridge that extends from the east shore to less than 250 m from the west shore at a depth

less than 10m serves as a division of the lough into unequally sized north and south basins. This ridge raises above sea level to form an Island called Castle Island (Kitching and Ebling, 1967). Freshwater enters the lough by direct run off and via several small streams, however, the catchment is relatively small and the freshwater supply averages <0.1 % of the Lough volume per day (Johnson *et al.*, 1995). The tide enters and leaves the lough through a narrow (12 m wide) channel known as the Rapids located in the south-east corner of the lough. This channel has a sill depth of ~1 m at low tide and leads into Barloge Creek, which then leads to the open Atlantic Ocean. This narrow channel and creek restricts tidal exchange between the lough and the Atlantic such that the estimated flushing time for the lough is 41 days (Johnson *et al.*, 1995). There is a seasonal thermocline which forms between 20 and 30 m, lasting from March until November, below which the isolated waters become anoxic as the summer progresses (Kitching *et al.*, 1976). These features result in an ecosystem that is rich in habitat types and biodiversity which are responsible for its designation as Europe's first Marine Nature Reserve in 1981. Lough Hyne therefore represents an ideal system for studying many aspects of marine biology. Indeed, it has been extensively used by scientists since 1886 for many types of hydrographic and ecological studies (Kitching and Ebling, 1967; Kitching, 1987), including those in behaviour and genetics (Minchin, 1987b; Sims *et al.*, 2001; Bell and Okamura, 2005).

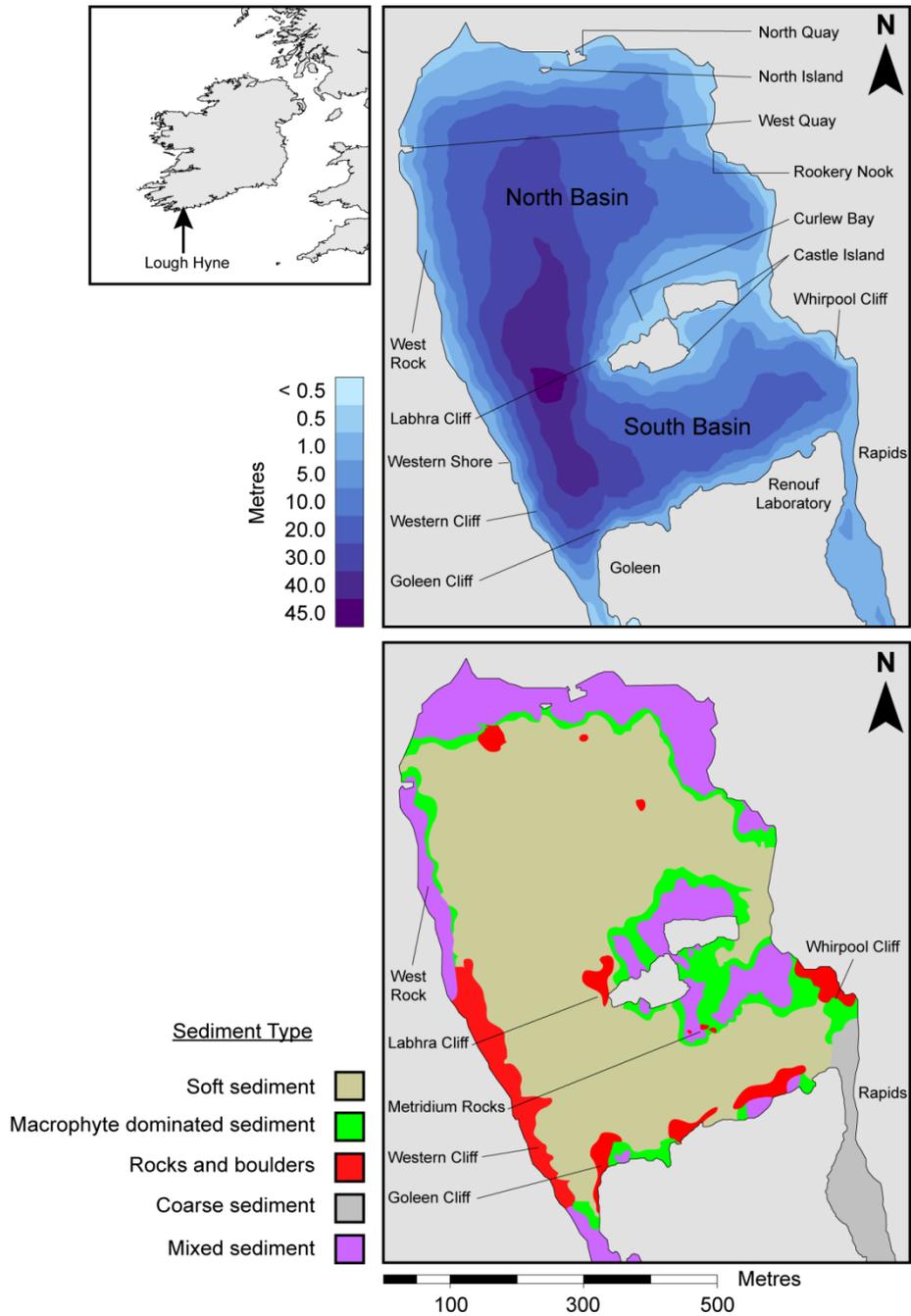


Figure 2-1. Map of Lough Hyne, Ireland showing the bathymetry (top) and sediment type (Parnum, 2003) with classification of ‘habitat’ complexes by colour and code based on the JNCC biotope classification system (Connor *et al.*, 2003)(bottom). The wider location of the study site is shown as an arrow on the smaller map of Ireland (top left). Locations referred to in the text are shown for reference.

2.2.2 Fish capture and individual identification

Adult small-spotted catsharks were captured using monofilament gill nets (20 m long x 2 m deep, 8 cm mesh size) deployed perpendicularly to the shore, at depths spanning from ~ 2

– 15 m for between 35 and 195 minutes. The sex of each individual was determined by the presence or absence of the male reproductive organs (claspers) before length (TL ; mm), girth (mm) and mass (g) measurements were recorded. Additionally, each individual was tagged using numbered and colour-coded t-bar anchor tags (FD-94, Floy Tag Inc., Seattle, Washington, USA) for identification purposes. The tags were inserted subcutaneously in the dorsal musculature above the pelvic fins using an Avery-Dennison Mk3 tag gun. Each tag was checked to ensure that it was securely attached prior to release.

2.2.3 Anaesthetic and surgical procedures

Larger individuals selected for study were checked for any external signs of injury or ill-health to minimise the risk of studying abnormal behaviours. The selected individuals were placed in aerated sea water and transported to the laboratory to be fitted with acoustic transmitters. In the laboratory, each individual was fitted with a continuous acoustic transmitter (16 mm diameter, 65 mm long, weight in water 10 g; VEMCO Division, AMIRIX Systems, Nova Scotia, Canada) using similar methods as described in Sims *et al.* (2001) and Sims *et al.* (2006a). The power output of the transmitters was 147 dB re 1 μ Pa at 1 m with a pulse period of 1 s, a range of \sim 500 m, and a battery life in excess of 300 days. Each transmitter emitted sound pulses (‘pinged’) at particular, unique frequencies to facilitate identification of individuals whilst tracking multiple individuals simultaneously. Each individual was placed in a 14 l sea water tank and 70 ml of anaesthetic solution was added (ethyl p-aminobenzoate, Sigma, St. Louis, Missouri, USA). Once the individuals were sufficiently anaesthetized, a transmitter was attached externally 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 individual's dorsal surface to avoid transmitter movement (Figure 2-2).

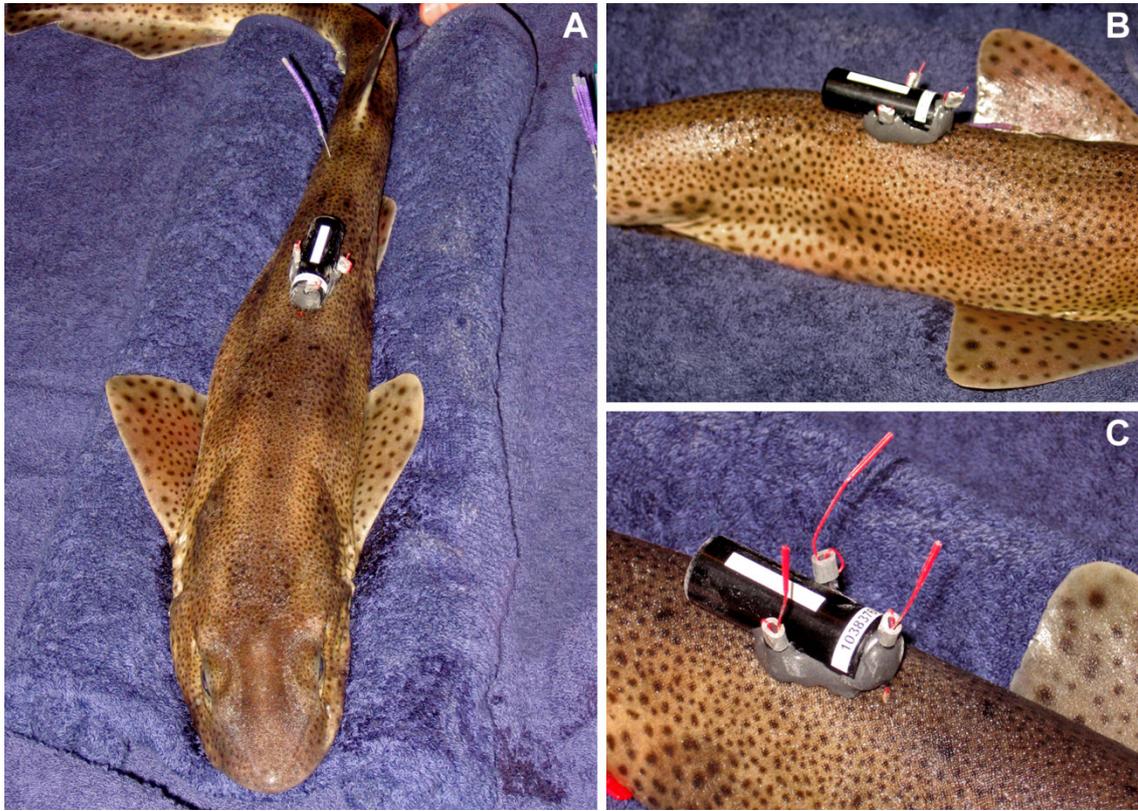


Figure 2-2. Attachment of acoustic pingers (V13, VEMCO) to adult small-spotted catsharks in Lough Hyne, Ireland. Plan view (A), lateral view (B) and close-up (C) prior to crimping and cutting of trailing ends of anchor tags. The tags were set in moulded epoxy harnesses and were secured to the catsharks using t-bar anchor tags (Floy) inserted sub-cutaneously and held in place with alloy crimps.

This procedure was completed within 5 minutes, following which all fish were left to recover in clean, aerated seawater and held into a current such that clean seawater entered the mouth and pharynx, irrigating the gills. Each individual 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 (Sims *et al.*, 2006a). All procedures were carried out in accordance

with appropriate authority from the National Parks and Wildlife Service, Republic of Ireland and after institutional (MBA) ethical review.

2.2.4 Fine-scale acoustic tracking

The movements of acoustically tagged individuals were monitored in real time and recorded using a radio-acoustic positioning (RAP) system (VRAP, VEMCO Division, AMIRIX Systems, Nova Scotia, Canada). This system consists of a triangular array of three buoys equipped with hydrophones that detect sound pulses from the transmitting tags (Figure 2-3). The buoys are also equipped with acoustic transmitters and VHF radio modems allowing them to communicate with each other and a computer-controlled base station. The base station communicates with each buoy individually, tuning automatically to listen to a prescribed frequency at pre-defined time intervals. Briefly, to geo-locate a tagged fish's position the system measures the time delay for the acoustic signals received by each buoy. This information is relayed to the base station via radio and is then used by the software to calculate the x and y coordinates of the tagged individuals allowing their locations to be plotted in real time on a PC and saved to an electronic file. The accuracy of the positioning system is not uniform within the range of detection. The positional accuracy is greatest within the buoy triangle and decreases outside of the array triangle. Additionally there are shadow zones around the buoys where there are two possible solutions to position calculations. The software chooses the best position based on previous positions but this can lead to errors thus reducing the accuracy of the calculation.

The positional accuracy of the VRAP array was estimated using a simulation program (PosSim, VEMCO). This program calculated arrival times at each of the three buoys for a signal from a particular position within an area measuring $\sim 950 \times 750$ m, surrounding the array. A temporal error in the detection (arrival) times was then introduced by increasing or decreasing times by ≤ 0.5 ms for each buoy. The positions of the signals were calculated

using a standard trigonometry distance equation. This process was repeated many times and the distances between each new position were calculated, allowing determination of a standard deviation. This whole process was repeated for each position within detection distance of the array producing a map of standard deviation values indicating theoretical positional accuracy (Figure 2-4). For more details concerning calculation of positional accuracy see Klimley *et al.* (2001a).

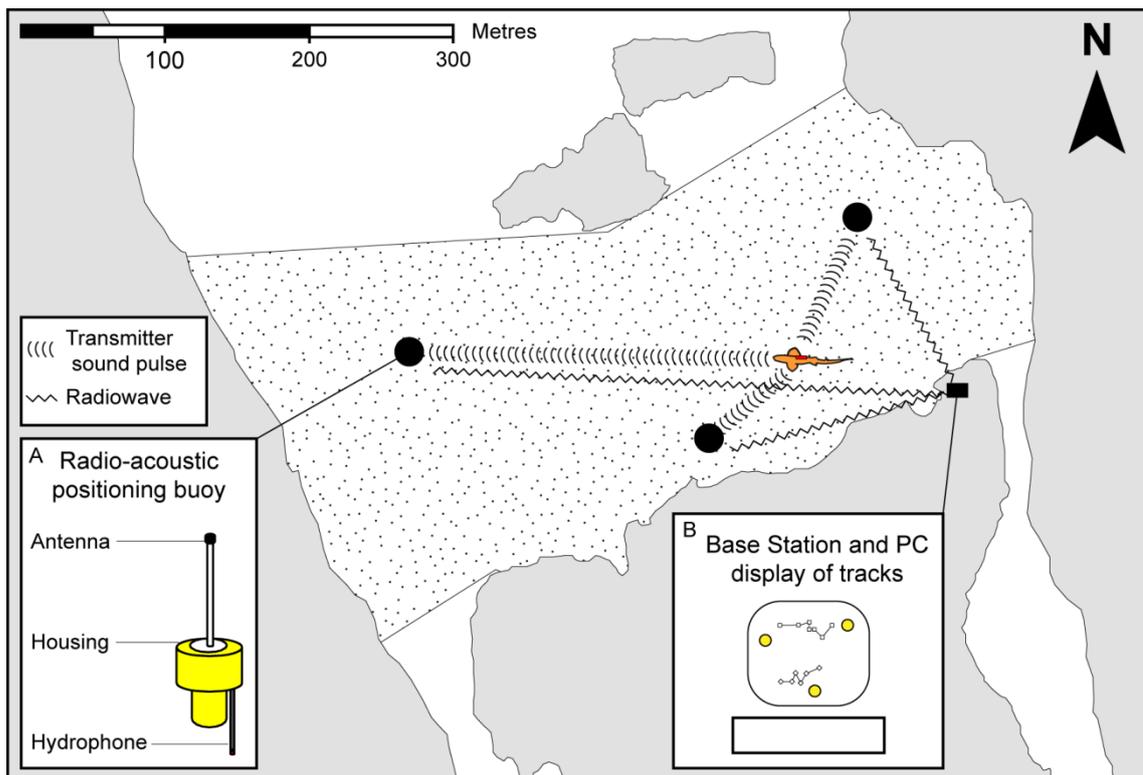


Figure 2-3. Radio-acoustic positioning (RAP) system (VRAP, VEMCO) used to automatically track acoustically tagged small-spotted catshark movements in Lough Hyne, Ireland. The system consists of three buoys equipped with hydrophones and radio antennae (● and inset A) that detect sound pulses produced by tags and transmit information to a computer controlled base station (Inset B) where positions are recorded and displayed on screen in real time. Stippled area denotes range of detection of the array.

The theoretical accuracy of positions in this study was generally high ($< 1\text{m}$) within an area containing the buoy array (Figure 2-4). Positional accuracy was still high ($< 2\text{m}$) within a ‘bell’ shaped area surrounding the buoy array up to 200m distance. Accuracy was

lower (from < 10 to < 20 m) in small triangular areas behind each of the buoys, with their being either no solution or two solutions for the areas bordering these triangles. These regions of low or no accuracy extended outwards from these positions as expanding bands to the edge of the simulated area (Figure 2-4 red).

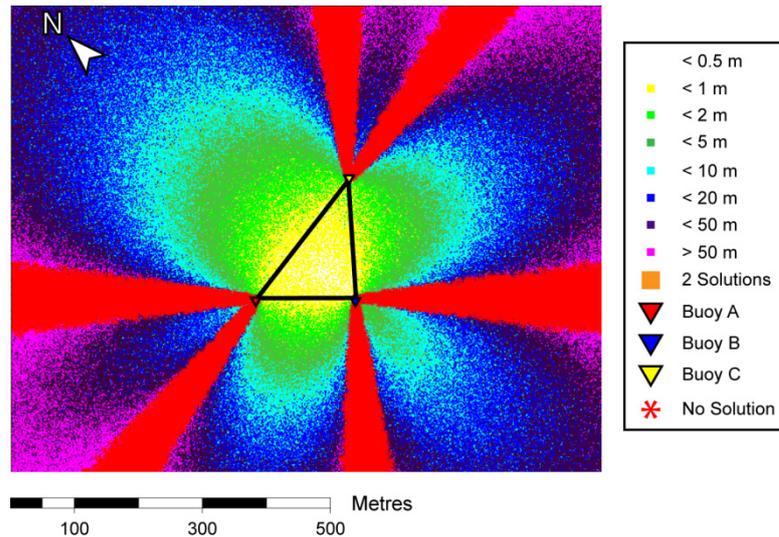


Figure 2-4. Simulation plot of the accuracy of positions determined within the detection range of the VRAP system with a hydrophone-equipped buoy receiver timing error of 0.5 ms and a transmitter depth of 10 m.

The theoretical positional accuracy was verified in the field by placing transmitters at known locations. This was achieved by placing a transmitter in a bag and submerging it in the water from the side of the vessel as it drifted across the buoy array. GPS positions were recorded at set time intervals and these were compared to the VRAP recorded positions at the closest time available. Due to the difficulty of recording accurate positions whilst drifting on board a vessel only three positional comparisons were made (whilst drifting slowly over the centre of the array). These showed that positional accuracy was 1.840, 1.001 and 7.01 m respectively. These verifications showed that the positional accuracy was somewhat comparable to the simulated theoretical accuracy and that of other studies

(O'Dor *et al.*, 1998; Klimley *et al.*, 2001a; Klimley *et al.*, 2001b; Zamora and Moreno-Amich, 2002).

Despite the level of accuracy determined, there were anomalous positions within the data as some points were calculated to be either on land or were in parts of the lough where the buoy array could not have detected them (i.e. opposite side of Castle Island or in Barloge Creek), or were separated from one another by greater distances than an individual would plausibly travel given the time interval. These anomalies could have arisen for a number of reasons including the fact that acoustic signals reflect/reverberate off various topographical features of the lough, thus affecting the sound pulse arrival time at one or more buoys.

In addition to the automated tracking, individuals were also located once daily, where possible, by means of manual positioning to fix a known location of the fish (“ground zero”) and thus to validate the VRAP-derived position. This manual positioning involved the use of a directional hydrophone and acoustic receiver (VR60, VEMCO) to range in on a tag’s sound pulse train. This hydrophone was submerged underwater at a depth of approximately 1 m and rotated in the horizontal plane to determine the direction of the strongest acoustic signal for a transmitter. The vessel was then moved to travel in the direction of the signal and was positioned such that the sound signal strength was the same in all directions. At this point a ground zero position was taken using a handheld global positioning system (GPS) unit (GPSMAP® 76, Garmin (Europe) Ltd., Southampton, UK). The procedure was repeated to locate subsequent transmitters. These ground-zero positions were used to verify the positions recorded by the RAP system. However, some inconsistencies between manually recorded ground zero positions and automatically recorded positions from the VRAP system were encountered due to a number of sources of possible error. These included the accuracy of the handheld GPS, the amount of boat

drift whilst recording positions, the accuracy of the location of the position using the hand held hydrophone (especially important if the animal is actively moving) and the positional accuracy of the VRAP system (see above).

2.2.5 Prey sampling

During field visits, surveys of potential prey species were conducted to quantify abundances in different areas of the lough. Custom-built traps (similar to commercial pots) consisting of a metal frame measuring 550 x 400 x 300 mm covered with 5 mm plastic mesh were baited with suspended chunks of mackerel (*Scomber scombrus*) before being deployed at several different locations throughout the lough. These traps had two funnelled holes that facilitated entry and prevented exit by prey species. The diameter of the holes were 50 mm, roughly equal to the gape size of an adult male small-spotted catshark, ensuring that only prey that could plausibly be ingested were captured. The traps were left to soak for approximately 12 hours either overnight or throughout the day. Upon retrieval the trap contents were emptied into marked plastic containers filled with seawater. Traps were then re-baited with fresh mackerel and re-deployed. The contents of the pots were identified to species level, where possible, and mass and length measurements in addition to abundances were recorded. Although it is possible that less mobile prey can be consumed by small-spotted catsharks, this sampling method captures the predominant prey species ingested by catsharks, namely decapod crustaceans such as crabs and prawns.

2.2.6 Data analyses

Since positional accuracy attenuates from the centre of the buoy array and positional determination relies on the detection of sound pulses, erroneous positions can occur (see above: 2.2.4). Therefore a crucial first step before analysing the data was to remove any clearly erroneous positions. Firstly, the data were extracted and all positions were plotted

onto a geo-referenced map of the lough created in ArcGIS version 9.3 (Environmental Systems Research Institute (ESRI), Redlands, California, USA). All positions recorded within 24 hours of release were then deleted to remove the influence of possible tagging effects on movements. Following this, any positions that were placed on land were removed. Positions that could not have been possible, such as those that were beyond the line of sight of all three buoys, were also removed. Finally, step lengths were calculated between successive positions and all spurious positions were removed, where spurious positions were defined as those showing abnormally large steps, identified by using a maximum swim speed filter set to 0.35 m s^{-1} . In addition, some further erroneous positions found in female tracks (collected during previous research conducted at the lough in 2003 and unpublished) were corrected. Using the playback function of the VRAP software (VRAP version 5.1.4, VEMCO) it was possible to identify discrete foraging trips made by females. Between these trips there was considerable error in the positions determined as well as gaps in the track when no positions were recorded. It is likely that the positions recorded during these periods were a result of reflections of the acoustic signal from various physical features of the lough whilst females were residing in rocky refuges in shallow water (Sims, 2003). Therefore, these errors were identified and collapsed onto the locations of these refuges preventing the loss of considerable numbers of data points from the track. It was important to retain these positions for the accurate calculation of space use (see below).

2.2.6.1 Kernel density estimation

Space use of male and female small-spotted catsharks was investigated by calculating the utilization distribution through kernel smoothing. The utilization distribution (UD) is an estimate of the probability of an animal occurring in an area during a specified time (Worton, 1995). Kernel density estimation works by placing a kernel (probability density)

with a given width, determined by a smoothing parameter (h), over each observation. The value of the probability density at any given point is then calculated by summing the value of the overlapping kernels at that point thus the density estimate will be high in areas with many observations. Contours were determined containing certain percentages of the UD thus representing differences in space use. Commonly home ranges have been defined as containing 95% of the UD and core areas as containing 50% (Seaman and Powell, 1996; Roth *et al.*, 2004). Therefore, 95% and 50% contours were calculated for this study using the fixed kernel method in Hawth's Analysis Tools extension for ArcGIS (Beyer, 2004). To determine the appropriate smoothing factor a number of different methods for its calculation were attempted. Least Squares Cross Validation (LSCV) and the reference bandwidth (h_{ref}) were calculated for a representative data set using Animal Space Use 1.2 (Horne and Garton, 2006). Least Squares Cross Validation (LSCV) and the reference bandwidth (h_{ref}) were both found to provide too little or too much smoothing during preliminary analyses; therefore a user defined value of 10 was selected.

2.2.6.2 Path aggregation

To investigate the movement path characteristics in more detail the cleaned raw tracks were further processed. This processing was necessary in order to avoid oversampling and determine biologically meaningful movement parameters. This was achieved by implementing Turchin's method for aggregating steps into moves (Turchin, 1991). This method involved aggregating n steps into one flight/move if $n-1$ intermediate spatial positions were no more than 1 m away from the line connecting the beginning of the first step to the end of the last one (Turchin, 1991; 1998) (Figure 2-5). The value of 1 m used to aggregated steps into moves was decided upon following investigation of a number of possible values. Taken the size of the animal and the sinuous swimming movements values investigated followed from the length of the small-spotted catsharks and the value that

gave the best representation of the raw track was chosen. The process of path aggregation described here was conducted in a computer program using custom written algorithms (Track Analysis, MBA 2009).

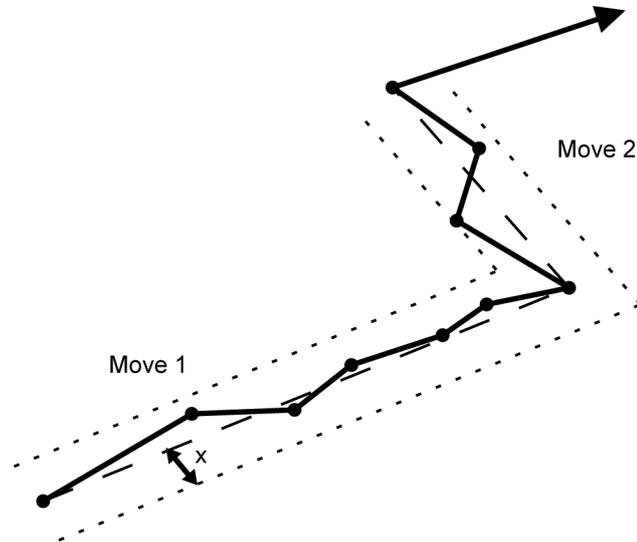


Figure 2-5. Aggregation of n variable step lengths of an individual's movement path into moves if all intermediate positions are within x of the line connecting the first point with point n . In this case $x = 1$ m (Adapted from Turchin, 1998).

2.2.6.3 First passage time

For movement paths in the form of discrete steps the scales of area-restricted searching were identified using variance of the first passage times. First passage time is defined as the time it takes for an animal to cross a circle of a given radius, and can therefore be used to examine tortuosity of movements (Fauchald and Tveraa, 2003; Pinaud and Weimerskirch, 2007). If the movement path is straight then the time to cross the circle will be short and conversely if the path is highly tortuous the time will be longer. Also, larger circles will encompass more of the path tortuosity than smaller circles especially if the path is highly tortuous. Therefore, if circles of increasing radius are placed along a path peaks in variance of first passage time will correspond to the scales of tortuosity within the path, providing information on the scales over which an animal is concentrating its search effort (Fauchald and Tveraa, 2003) (Figure 2-6).

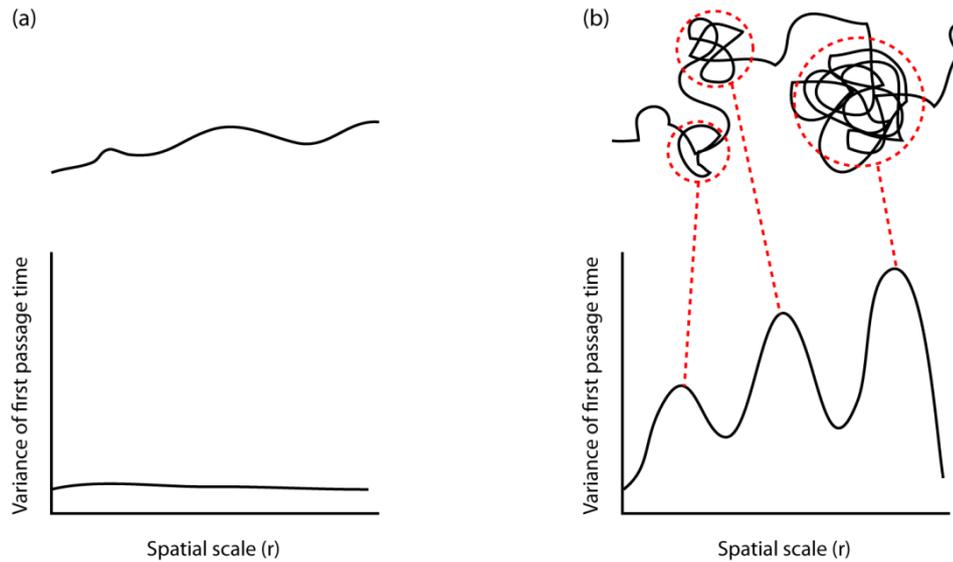


Figure 2-6. Schematic representation of two theoretical example tracks and their corresponding first passage time analysis results. A relatively straight path results in low variance (a), whereas a tortuous path will give peaks in variance associated with the scale of path re-crossing caused by area restricted search behaviour (b).

2.2.6.4 Statistical properties of movement parameters

The statistical properties of the movement track, i.e. move step length and turn angle distributions, were also investigated. Turn angle distributions were investigated using Oriana version 3.0 (Kovach Computing Services, Anglesey, Wales) to calculate mean angular direction (orientation) and the strength of directionality (length of mean resultant vector). Rayleigh's uniformity tests were conducted to determine departures from uniform circular distributions and χ^2 tests were performed to investigate differences between turn angle distributions.

The move step length distributions were investigated using a Maximum Likelihood Estimation (MLE) approach (Clauset *et al.*, 2007) to test whether the data fits various theoretically derived frequency distributions of move step lengths. This study considered exponential, power law and truncated power law distributions. These distributions have been hypothesised to represent different animal movement behaviours, for example movement data that follow a power law distribution with an exponent or scaling parameter

$(\mu) \approx 2$ (known as Lévy flight) has been hypothesised to be the optimal solution for locating sparse, unpredictably located targets (Viswanathan *et al.*, 1996; Bartumeus *et al.*, 2002; Bartumeus *et al.*, 2005; Bartumeus, 2007).

Maximum Likelihood Estimation determines the parameter values of a model that maximises the likelihood given the data (White *et al.*, 2008). In this study, MLE was used to determine the scaling parameter (μ) of best fit models for each of three theoretical distributions to the empirical data. Each theoretical distribution has its own MLE equation that estimates μ . To do this the MLE equation requires a lower bound to the fit of the distribution (x_{\min}). In the case of the truncated power law a further parameter, the upper bound of the fit of the distribution (x_{\max}) is also required to be estimated. Because estimation of x_{\min} and x_{\max} has no analytical solution the lowest value and highest value in the data are selected as the starting condition for the calculation of μ . The next stage involves randomly generating a best fit dataset using these parameters and comparing this with the real data using a Kolmogorov-Smirnov (K-S) test to calculate the goodness of fit, D . However, the true x_{\min} may not just be the smallest value in the dataset, so it was necessary to find a more realistic estimate of x_{\min} . This is achieved by the use of a numerical search algorithm, which involves generating synthetic best fit datasets using increasing values of x_{\min} . These datasets were compared to the real data using the K-S procedure to calculate D values. The x_{\min} with the lowest D value was a more reliable estimate of the true x_{\min} and was used to determine the appropriate scaling parameter (μ) for the best fit model. In the case of the truncated power law x_{\max} was also determined using a similar procedure. For a more detailed description of the principles of this approach see Clauset *et al.* (2007). Both first passage time and MLE analyses were conducted in custom written software (Track Analysis, MBA 2009).

2.3 Lab-based methods

2.3.1 Experimental animal

Laboratory experiments used juvenile small-spotted catsharks, hatched in captivity from eggs produced by wild-caught adult females from the western English Channel off Plymouth (50-51° N, 04-05° W). The juvenile fish were aged between 18-24 months post hatching and ranged from 194 – 334 mm in total length, *TL* at the start of experiments.

2.3.2 Fish holding facilities

Fish were maintained (post-hatching) in tanks with running filtered seawater in a 12L:12D cycle. The system was supplied by Tropical Marine Centre custom installation and combined UV treatment, biological filtration and protein skimming (TMC Ltd., Chorleywood, UK). The temperature of this water varied according to seasonal fluctuations in the range between 12 – 19.6°C. Fish were fed, twice weekly, a diet of cut squid, *Loligo forbesi*, and whiting, *Merlangius merlangus*, supplemented with liposome enrichment spray and dry food pellets (Marine Liposome Spray and Marine pellets, New Era Aquaculture Ltd., Thorne, UK). Rations varied according to the size and age of the fish but individuals were fed an equivalent of 3% wet body mass per feed (Sims and Davies, 1994).

2.3.3 Experimental arena and design

The experimental arena comprised one half of a large seawater tank measuring 260 cm length and 170 cm width. The water depth during experimental trials was ~40 cm. The floor and sides of this tank were painted white with waterproof, non-toxic A1 pond paint (Antel Eclipse Ltd., Hampshire, UK) to enhance the contrast between the fish and the background for video monitoring purposes (see 2.3.4).

The experimental arena was illuminated with diffuse light, which was achieved by positioning a standard fluorescent strip light facing the white ceiling and walls. This minimised reflections on the water surface and facilitated video monitoring. A Panasonic WV-BP122E CCTV camera with a Computar H2Z4515CS wide-angle lens was fixed directly above the array in the test arena and video recordings of all trials were made. White, waterproof fabric screens were placed along the side of the arena to eliminate visual stimuli or disturbance from observers during experimental treatments (Figure 2-7).

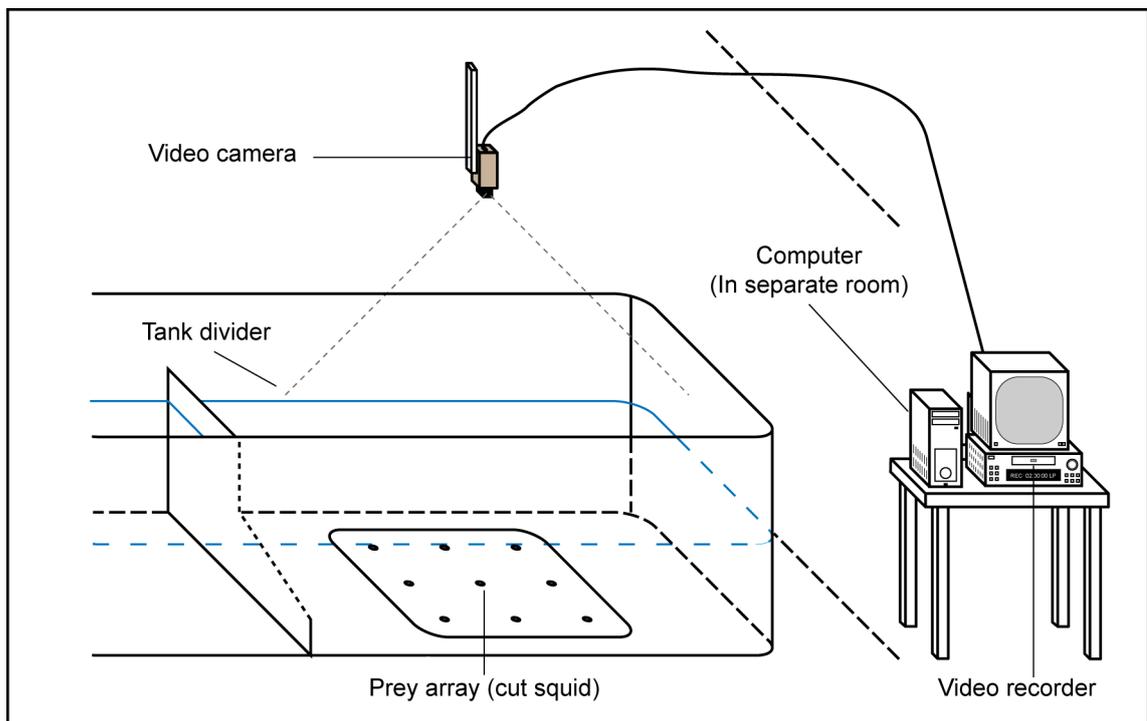


Figure 2-7. Tank setup showing experimental arena (right) and the EthoVision, computer-aided video monitoring system (far right).

Before each trial the appropriate prey pattern was set up in the experimental arena. Once the water surface was still, an acclimation chamber (300 x 250 x 610 mm), made from transparent acrylic and open at the top and bottom, was placed in the experimental arena. A single juvenile was placed in the acclimation chamber and allowed to recover from any handling stress and settle in its new surroundings for at least an hour. After this time the chamber was removed and the juvenile was released with very little, if any, disturbance. In

most cases the juveniles were motionless, resting on the tank floor when the acclimation chamber was removed. Each trial was recorded continuously for two hours, after which the juvenile was removed and transferred to its holding pen and the prey array was re-established ready for the next trial.

2.3.4 Computer-aided video monitoring

Movement of the juvenile fish whilst foraging was videotaped from above and the x and y coordinates were acquired using EthoVision[®] video tracking software (Noldus Information Technology Inc., Wageningen, The Netherlands). This tracking software automatically detects movements by a number of image processing methods. For this study a process of subtraction was used, whereby images were compared to a reference image at a sampling rate of 1Hz. The coordinates of the centre of gravity of areas that were darker than the reference image above a certain threshold pixel size were recorded. These areas represent the locations of objects not visible on the reference image; therefore for this process to work there has to be sufficient contrast between the object and the background. Data acquisition using this method was very accurate with very few missed samples or erroneous positions.

2.3.5 Data analyses

The data required minimal post-hoc editing to remove spurious positions or interpolate missing positions. However, occasionally very small movements (< 1 cm) were recorded when no movement had been made, which was most likely a consequence of small water surface movements. These errors were easily removed through the use of a minimum distance filter (Track Analysis, MBA 2009).

At the sampling rates used for this study 7200 positions were recorded per trial. Although this provides very detailed and accurate tracks it can also cause problems for data

analyses as a result of high variability and autocorrelation. More importantly, using set time intervals results in arbitrarily defined turns that may not represent biologically meaningful behavioural events (Turchin, 1991; 1998). To avoid oversampling and its associated problems, the same approach to path aggregation as used for the field data was followed for processing the laboratory data (see section 2.2.6.2). However, the positions were aggregated into moves if $n-1$ intermediate positions were no more than 1 cm from the line connecting the first and last positions (Figure 2-5).

The movement tracks were analysed in much the same way as the field data, with analyses of variance in first passage time, circular statistics of turn angle distributions and analyses of move step length distributions through Maximum Likelihood Estimation (MLE) techniques (see field based methods 2.2.6.4). In addition to these movement analyses further analyses relating to prey capture events were possible. Firstly, foraging efficiency was calculated for each individual by dividing the number (distribution treatments) or percentage (density treatments) of prey by the total length of the movement track. Secondly, giving up times (GUTs) were determined by recording the time interval between prey capture and the next pause in the track. Both foraging efficiency and giving up times were then analysed using appropriate statistical procedures to investigate differences between treatments and sexes and time related trends. Further details relating to specific experiments are provided in each of the chapters (2 and 4).

3 Central place foraging-like behaviour of wild adult small-spotted catsharks

3.1 Introduction

Since it is widely accepted that movement patterns and space use of individuals play a critical role in determining local population density and community composition, knowledge of individual behaviour is clearly important (Turchin, 1991; Freon and Misund, 1999; Sims *et al.*, 2001). As a result of their ecological importance space use patterns of animals have been widely investigated. Many patterns of movement have been described for a wide range of taxa, from insects to humans (Kramer and Nowell, 1980; Kacelnik, 1984; Kacelnik *et al.*, 1986; Benhamou and Bovet, 1989; Ehlinger, 1990; O'Brien *et al.*, 1990; Weimerskirch *et al.*, 1997; Hill *et al.*, 2000; Brockmann *et al.*, 2006). One of the predominant patterns of animal movement is that of central place foraging.

To describe central place foraging one must first define the term 'home range'. Home range was initially defined as the area traversed during an animal's normal activities between dispersal movements (Burt, 1943). However, with the increasing knowledge of animal movements, this early definition has been modified to account for the non-static nature of observed home ranges that was made possible by better tracking technologies (Kenward *et al.*, 2001; Block, 2005; Sims *et al.*, 2006b). Therefore a more accurate definition is that a home range is an area that is repeatedly traversed within a given time period for the purpose of finding resources and thus fulfilling survival and reproductive needs (Dingle, 1996; Kenward *et al.*, 2001). Central place foraging consists of the biased use of a core or central area within the animal's home range, such as a nest or burrow, from which occasional long-range excursions or trips are made from and to. The most common examples of this type of movement come from avian taxa. Here, birds travel to and from a

particular nest to forage and also bring food back to the nest for their young. An extreme example of this type of behaviour is the wandering albatross, *Diomedea exulans*, which has been recorded taking single foraging trips covering between 3600 and 15,000 km (Jouventin and Weimerskirch, 1990).

Given the widespread use of this pattern of movement in avian taxa, birds have been widely used in modelling studies to predict optimal foraging which is constrained by having to return to a central place. These central place models make predictions of when prey should be attacked at different distances from the central place; this problem has been called the Encounter at Distance model (Schoener, 1979). The Single Prey Loader model predicts the choices of particular prey which should be taken back to the central place (Orians and Pearson, 1979) whilst the Multiple Prey Loader model of Orians and Pearson (1979) predicts the number of prey items to be collected. These classical models have provided a useful theoretical framework for the study of central place foraging and have been developed and tested on a range of different taxa including fish.

Examples of central place foraging-like behaviour by fish include examples from the juvenile stream-dwelling salmonids. These have been found to territorially defend a central place from which they attacked prey at different distances (Grant *et al.*, 1989; Biro *et al.*, 1997). Furthermore, young-of-the-year (YOY) Atlantic Salmon, *Salmo salar*, were found to make frequent use of more than one feeding station and thus can be considered multiple central place foragers (Steingrímsson and Grant, 2008). Primarily, the examples of central place foraging amongst fish have been mainly concerned with territorial defence of one or more foraging stations within the home range and thus differ slightly from the bird examples where provisioning for young has received greater attention.

Further examples of temporal variation in movements and space use of fish also resemble central place foraging. In particular, tropical reef fish species have well

documented diel patterns in use of refuge and feeding locations (see Ogden and Quinn (1984) and Quinn and Brodeur (1991)). For example, grunts (Haemulidae) are known to move from diurnal reef territories to nocturnal feeding grounds in the surrounding sand flats and grass beds (Ogden and Quinn, 1984; Quinn and Brodeur, 1991; Burke, 1995). Furthermore, many other fish species have been shown to use certain areas within their home range differentially by spending a greater proportion of time in core areas within the extent of their home range (tiger sharks, *Galeocerdo cuvier*, (Tricas *et al.*, 1981); juvenile hammerhead sharks, *Sphyrna lewini*, (Holland *et al.*, 1993); stingrays, *Dasyatis lata*, (Cartamil *et al.*, 2003); juvenile blacktip sharks, *Carcharhinus limbatus*, (Heupel and Simpfendorfer, 2005)). Various explanations for these patterns of space use have been postulated, including predator avoidance (Holland *et al.*, 1993), refuging, sexual segregation (Sims *et al.*, 2001; Sims *et al.*, 2005), territoriality (Hojesjo *et al.*, 2007; Kane *et al.*, 2009), and the influence of environmental factors such as temperature, water currents (Jorgensen *et al.*, 2006; Pittman *et al.*, 2007; Hindell *et al.*, 2008). It is possible that these movements are a result of a central place foraging strategy.

Despite the insights that have been gleaned from the study of fish space use, there does appear to be a bias in the available literature towards tropical and subtropical species. Consequently, fine-scale space use and movement patterns of temperate marine predatory fish are still poorly known. Given that water temperatures are much higher in the tropics, metabolic demands of tropical fish will be different than for temperate fish, which is likely to have consequences for feeding and therefore foraging behaviour. This study therefore investigated the movement patterns of male and female small-spotted catsharks, *Scyliorhinus canicula*, in a temperate marine ecosystem (Lough Hyne, Ireland). Previous work on this species has shown that in the study location, core areas within home ranges of males and females appear to be spatially segregated as 70% of females observed were caught in the

North Basin of Lough Hyne (see General Methodology 2.2.1 and Figure 2-1) and all males were caught in the South Basin (Sims *et al.*, 2001). This latter study also found behavioural differences in terms of the movements and space use of males and females. Males occupied core areas in deep water during the day from where they would venture out into shallower areas crepuscularly and nocturnally. In contrast, females occupied rock crevices in shallow water during the day and venture out nocturnally into deeper water once every two or three days (Sims *et al.*, 2001).

Therefore, it seems plausible to suggest that small-spotted catsharks are central place foragers. However, detailed information regarding fine-scale horizontal movements (at fine temporal resolution) is lacking in this species, preventing investigation of the central place foraging hypothesis. This chapter describes the fine-scale movements of small-spotted catsharks and provides information on the temporal variation of movement patterns of this species. Differences in the spatial and temporal patterns of movements between the sexes are investigated and the possible explanations for the observed results are discussed.

3.2 Methods

This research combines data collected during separate visits to Lough Hyne in 2003 and 2007. The data collected in 2003 were part of a previous NERC-funded research project (NER/A/S/2001/01053) led by Professor David Sims to investigate female movements and activity. These data have not been analysed in the ways described here so this study represents a novel analysis. Combining the selected data, a total of 8 adult small-spotted catsharks (4 male and 4 female) ranging from 638-688 mm in total length were tagged with both Floy tags and continuously pinging, ultrasonic acoustic transmitters (V9 and V16, VEMCO). Small-spotted catsharks were caught via gill netting (General Methodology 2.2.2) before being transported to the laboratory for anaesthetisation and surgical attachment of transmitters (General Methodology 2.2.3). Once recovered from the effects

of surgery, individuals were released at the location of initial capture. The whole process of capture, tag attachment, recovery (including observation) and release was completed within 2 hours. All procedures were carried out under permits provided by the National Parks and Wildlife Service, Republic of Ireland, after institutional (MBA) ethical review.

3.2.1 Acoustic telemetry

Movements of small-spotted catsharks were recorded using a radio-acoustic positioning system (General Methodology 2.2.4) that was deployed in two different areas of the lough in separate visits. The reason for the differences in location of the VRAP system was due to the previous observations of differential space use of male and female dogfish in the lough (Sims *et al.*, 2001). By locating the buoy array in the South Basin in 2007, the chances of detecting male movements were maximised.

In addition to the automated tracking, positions of each individual were recorded occasionally in 2003 by Prof D. Sims and his research team and daily during 2007 by myself and Prof Sims, using a hand held hydrophone (General Methodology 2.2.4). These positions allowed for validation of the automated tracking as well as determination of location if beyond the detection boundaries of the VRAP system.

3.2.2 Space use

A key first step in characterising an individual's space use is defining and measuring its home range. Therefore, following the removal of erroneous positions (General Methodology 2.2.6), space use was investigated by calculation of home range areas through kernel density estimation, using the utilization distribution (UD; see General Methodology section 2.2.6.1). The area of contours containing 95 and 50% of the UD calculated as part of the kernel density estimation approach were calculated and a Mann-Whitney *U* test and a *t*-test were employed to examine sex differences between home ranges and core areas

respectively. Temporal patterns in space use were also investigated using kernel density estimation (General Methodology 2.2.6.1) to calculate the areas of 95 % contours of the utilisation distribution for all day time vs. night time positions. In addition to kernel density estimation, a mixed ANOVA with one between subjects (sex) factor and one within subjects (time of day) factor was used to determine whether space use differed temporally and between the sexes.

3.2.3 Movements

Discrete excursions to and from a number of core areas were easily identified during playback of the tracks using VRAP software. The sections of tracks corresponding with these excursions were extracted and cleaned to remove spurious positions (General Methodology 2.2.6). Due to the small numbers of positions available for each discrete excursion a robust analysis of these individual trips using maximum likelihood estimation methods was not appropriate. Therefore, this chapter provides a detailed description of a selection of representative trips for each of the individuals. This involved the calculation of a number of descriptive parameters such as the duration of each trip and the total distance travelled during the trip, as calculated by summing the distances between positions (steps) of the track. The swimming speeds between each step of the track were also calculated as the distance travelled divided by the time between the start and end of each step. Due to the small sample sizes, trips were pooled by sex irrespective of individual for comparison of distances travelled. These data were analysed using a Mann Whitney *U* test.

3.2.4 Prey sampling

During both visits in 2003 and 2007 prey were sampled using custom built traps baited with pieces of chopped mackerel (*Scomber scombrus*) suspended in a net in the centre of the trap (General Methodology 2.2.5). The traps were deployed at several locations throughout

the lough in order to provide an idea of the prey landscape that the tracked individuals may have experienced during the study. The traps were deployed both overnight and during the day for periods of roughly 12 hours. Upon retrieval the contents were transferred to plastic pots and the traps were re-baited and re-deployed. In 2003, half the locations (1-7) were sampled over three days and nights, whilst the other half (1A and B, 5A and B, 7A, B and C) were sampled over two days and nights. In 2007, all locations were sampled over three days and nights. The contents of the pots were identified and length and mass measurements were taken.

Due to the inconsistent prey sampling methods between the two years only descriptive statistics were calculated for prey data. Data were not only pooled by species groups within locations but also by time of deployment (day or night). The proportional abundances of these groups were calculated and these data are displayed graphically to provide a visual representation of the temporal and spatial availability of prey, and to aid interpretation of the movement data.

3.3 Results

Despite increased effort, catching small-spotted catsharks to tag proved difficult in 2007-08 with fewer individuals being caught per unit effort than during previous research at the Lough (Figure 3-1). Overall during trips in 2007 and 2008 only 18 male small-spotted catsharks were caught as compared to previous research trips where 29 were caught in spring 2003 and 41 in spring 2004 (Sims *et al.*, unpublished data).

In total, 8 males were tagged with acoustic transmitters during May of 2007 and 2008 (four in each year). Of these sufficient data was only available from 3 males, all of which were tracked during 2007 thus preventing a robust inter-annual analysis of male movements. During both 2007 and 2008, tagged individuals moved out of the detection areas of the VRAP array. In 2007 two individuals left the detection area after 1 and 3 days

respectively; both were subsequently located in the North Basin, where they remained for the remainder of the research period. Of these individuals one provided 2 days of movement data within the detection range of the VRAP array; the other did not. In 2008, 3 individuals left the detection area after 1, 4 and 5 days respectively, and were located by manual positioning (see General Methodology) in the North Basin after daily focussed searches. However, one of these individuals could not be located manually anywhere in the lough after initially moving to the North Basin despite considerable search efforts throughout the entire Lough. It is possible that this individual left the Lough via the rapids. Other possibilities include tag failure and that the individual may have been located in areas of the Lough, such as rocky caves or crevices, which prevented acoustic signals from being detected. The remaining individual remained stationary for the duration of the trip directly under one of the VRAP buoys, thus it is possible that the tag had become detached from the individual and was lying on the bottom of the Lough. After processing the data from individuals tagged in 2008 it was clear that none of these individuals had data of sufficient quantity or quality to investigate further.

Of the small-spotted catsharks tagged during 2003, a further 3 individuals (all female) provided sufficient data to provide a robust analysis of fine-scale movements. Therefore, in total 6 individuals (3 male and 3 female) were used for this investigation. These individuals were tracked between 2 and 12 days during which time 47 discrete excursions from a central place were identified (Table 3-1). The males were tracked for shorter periods than the females as a result of the difficulty of capturing suitable male subjects in 2007, which delayed deployments of tags as suitable subjects were not collected at the start of the field trip in 2007 as they were in 2003 (Table 3-1 and Figure 3-1).

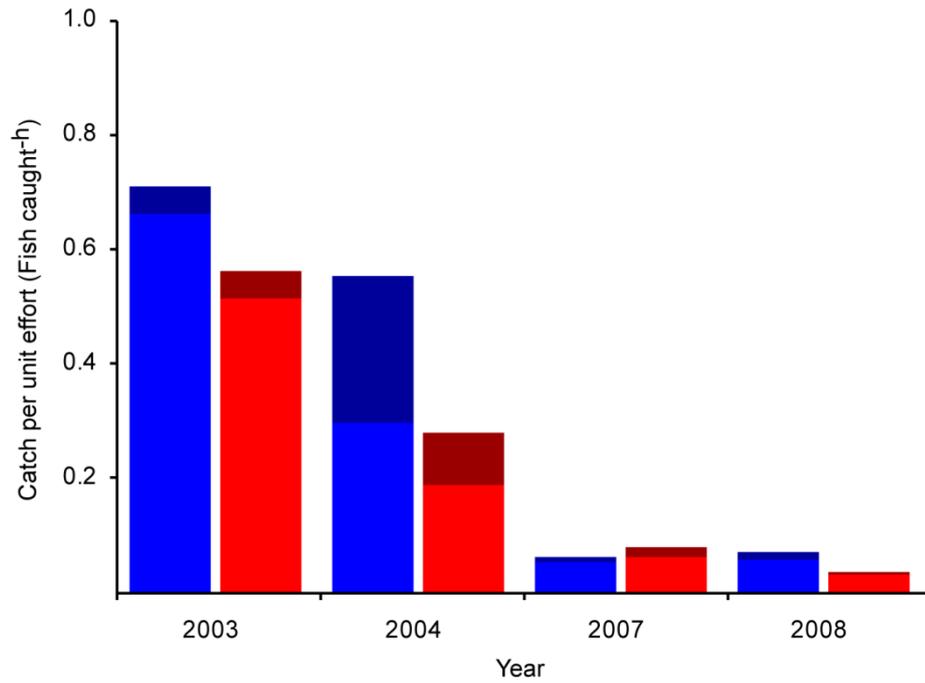


Figure 3-1 - Hourly catch per unit effort (CPUE, fish caught per hour) of male (blue) and female (red) small-spotted catsharks during trips to Lough Hyne, Republic of Ireland, during spring (data for 2003 and 2004 from Prof David Sims, unpublished data). Darker shaded sections represent the proportion of CPUE that were recaptures.

Table 3-1. Summary data of the six small-spotted catsharks tagged with acoustic transmitters in Lough Hyne, Republic of Ireland, that are analysed in this study. F denotes female, M denotes male.

<i>Individual</i>	<i>Date tagged</i>	<i>Tracking duration (days)*</i>	<i>Number of trips</i>	<i>Mean distance travelled per trip (m)</i>	<i>Mean trip duration (hr)</i>	<i>Mean displacement between trips (m)</i>
F1	15/04/2003	11.4	5	2092.0	5.50	121.7
F2	15/04/2003	12.2	3	2892.8	5.06	159.4
F3	16/04/2003	11.2	2	2824.2	9.85	38.6
M1	06/05/2007	8.5	22	1983.1	4.55	12.0
M2	09/05/2007	2.0	4	1192.6	3.15	78.0
M3	10/05/2007	4.6	11	695.8	2.57	43.9

* Excluding the 1st 24 hours

3.3.1 Space use

Females tended to occupy shallow, rocky areas along the coast in the southwest corner of the lough. In contrast, males rested on the bottom in more centrally located open habitats,

or were distributed around the edges of topographical features in the south basin. These differences were reflected in the home range areas calculated using kernel density estimation (Table 3-2 and Figure 3-2) where the area of the contours containing 95% of the utilisation distribution (UD) were significantly different between the sexes with females in 2003 having larger home ranges than males in 2007 (Mann-Whitney; $U = 0.0$, $Z = -1.964$, $n_1 = 3$, $n_2 = 3$, $p < 0.05$).

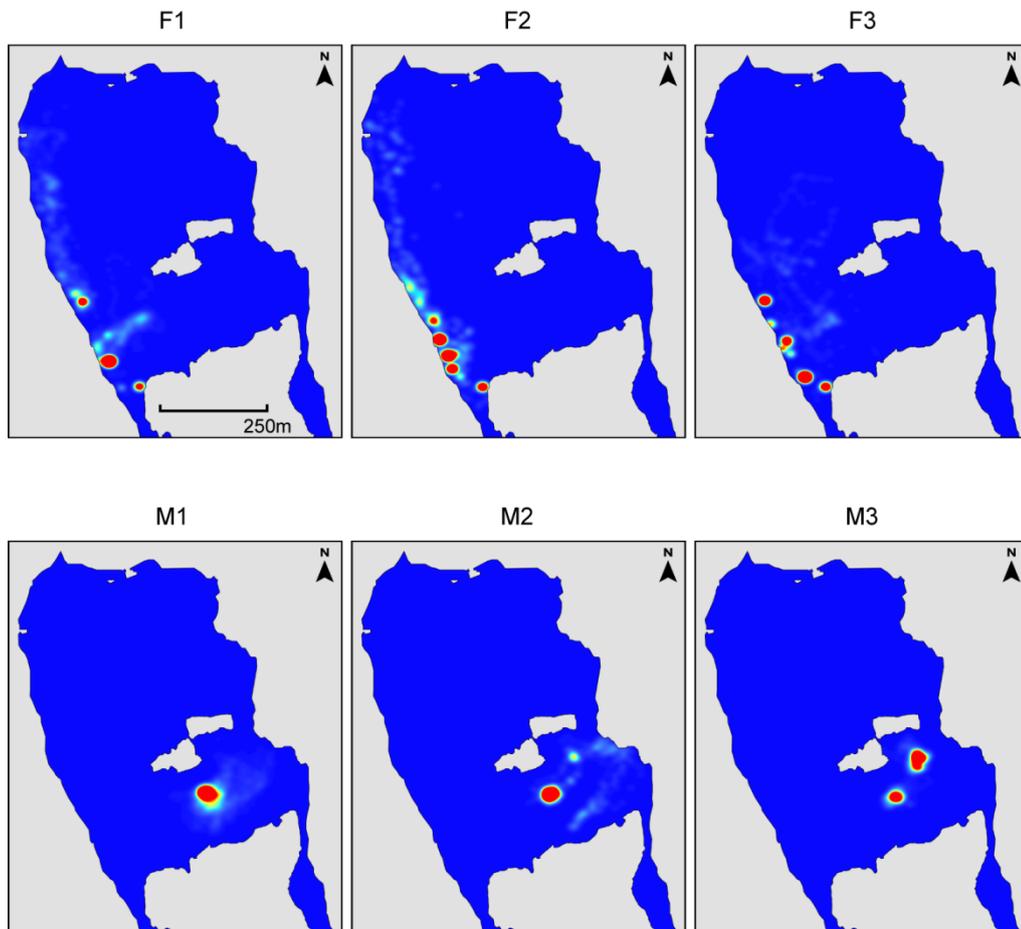


Figure 3-2. Space-use patterns of female (F1-3) and male (M1-3) small-spotted catsharks in Lough Hyne, Ireland during April 2003 and May 2007, respectively. Colours represent differing densities of the utilisation distribution with red areas having the highest density and blue areas the lowest.

Table 3-2. Mean home range and core areas used by female (F1-3) and male (M1-3) small-spotted catsharks in Lough Hyne, Ireland during two separate visits in 2003 (F1-3) and 2007 (M1-3).

<i>Individual</i>	<i>Mean home range area (m²)</i>	<i>Mean Core area (m²)</i>
F1	31651	541
F2	27059	1195
F3	18346	797
M1	15711	803
M2	16034	665
M3	6402	1113

Additionally, two of the females' core areas were fragmented into four smaller areas (ranging in size from 15 m² to 560 m²) as a result of residing in refuges, between which they often switched. Males' core areas consisted of one or two smaller areas that varied in size between 343 m² and 802 m². The total sizes of male and female core areas (50% contours of the UD) were not different with core areas of roughly 1000 m² for both males and females. There was clear overlap in the positions of the fragmented core areas between individuals of the same sex. For females these positions likely represent the locations of refuges. Male core areas may also be linked to topographical features of the lough as one of the core areas that was used by all males coincides with the location of a prominent topographical reef feature known as Metridium Rocks.

One of the males (M2) moved out of the detection range of the VRAP system after two days of continuous tracking. This individual was subsequently located manually during focussed searches in the North Basin between North Quay Island and Rookery Nook on a daily basis (for locations refer to Figure 2-1). The locations were mostly clustered closely together (all except one position were within 30 m of one another) on each day indicating that the male had switched its core area and was not simply on a long-range foraging excursion similar to that exhibited by the females.

Furthermore, space use of the small-spotted catsharks was also variable temporally. For example, during the night F1 used an area almost four times the size of the area used

during the day (38887 and 10899 m² respectively, Table 3-3). In contrast, M2 used an area of similar size during both the day and night (Table 3-3). Generally, females used larger areas than males during the night and, with the exception of F2, space use during the day was similar for both males and females (Figure 3-3). There were no significant differences in home range areas between sexes (Mixed ANOVA; $F_{1,4} = 6.522, p > 0.05$) or time of day (Mixed ANOVA; $F_{1,4} = 1.027, p > 0.05$) despite the apparent difference between females during the day and night evident in Figure 3-3.

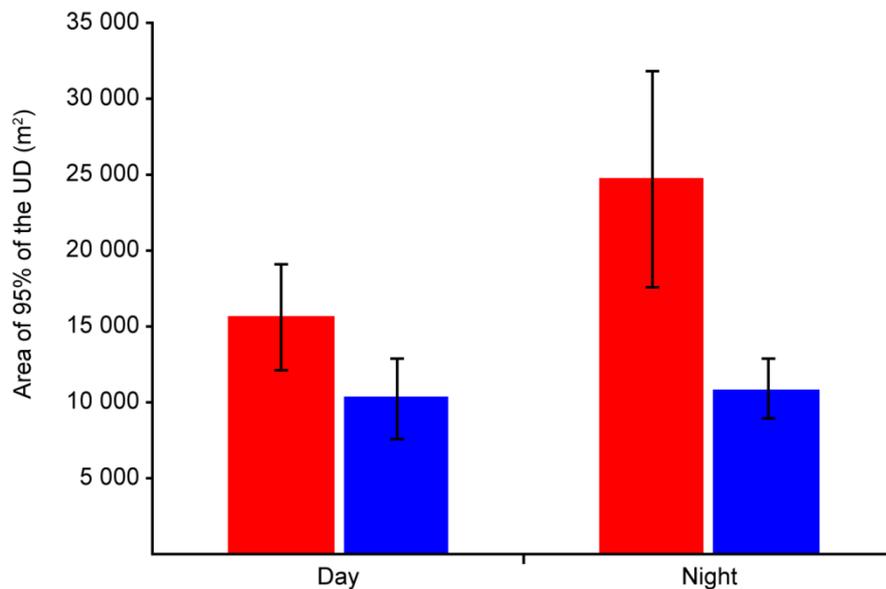


Figure 3-3. Night time and day time space use of small-spotted catsharks in Lough Hyne, Republic of Ireland. Red bars represent mean female ($n = 3$) space use as measured by the total area of the 95% contour of the utilisation distribution (UD) for both day and night positions throughout the tracking period. Blue bars indicate mean male ($n = 3$) space use using the same measure. Error bars represent standard error (S.E.).

Table 3-3. Area of 95% contours of the utilisation distributions of 3 female and 3 male small-spotted catsharks for day and night positions over the whole track.

<i>Individual</i>	<i>Space use (m²)</i>	
	<i>Day</i>	<i>Night</i>
F1	10899	38827
F2	22336	20053
F3	13957	15513
M1	14267	13557
M2	11592	12256
M3	5338	7140

3.3.2 Movements

During playback of the recorded tracks it was possible to identify discrete excursions from and between these core areas for each of the 6 small-spotted catsharks. Each individual undertook a different number of trips with F3 exhibiting the fewest number of trips (2) and M1 the most (22). In general, males undertook more trips than females. Timing and durations of trips also varied within and between individuals with trips ranging in duration from approximately 15 minutes (M1 trip 19) to almost 18 hours (F3 trip 1) and occurring throughout both the day and night (Figure 3-4 and Figure 3-5).

Of the 10 trips made by females, six occurred only during the night; of the remaining four, only one took place wholly during the day, the rest spanned night as well as day. In contrast, roughly equal numbers of trips were made by males both during the day and night. Another difference between males and females was the regularity of trips and distances travelled on trips; males made at least one trip every day they were tracked, whereas females did not. One female (F3) did not undertake a trip for over 6 days after the first (Figure 3-4). Generally, females travelled greater distances on trips than males with a median distance travelled per trip of 2.10 km compared to 0.95 km for males (Mann Whitney, $U = 95$, $n_1 = 10$, $n_2 = 37$, $Z = -2.339$, $p < 0.05$; Figure 3-6).

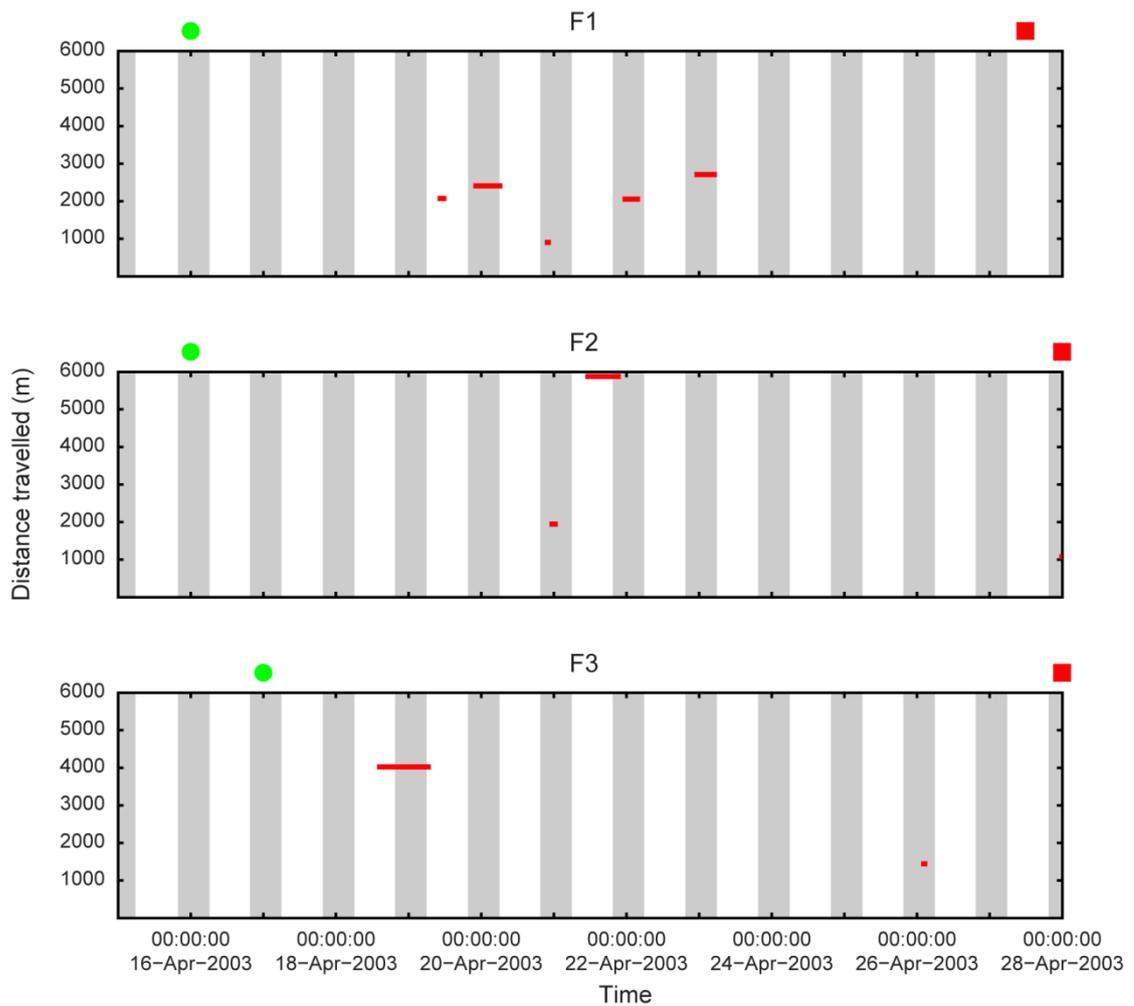


Figure 3-4. Timing of discrete excursions by female small-spotted catsharks from refuges (central places) in Lough Hyne, Republic of Ireland. Each excursion is a line whose length represents the duration of the excursion. The height of the line on the *y*-axis represents the total distance travelled during the excursion in meters. Shaded grey bars indicate the time between sunset and sunrise each day. Green circles and red squares indicate the start and end of the tracking period respectively.

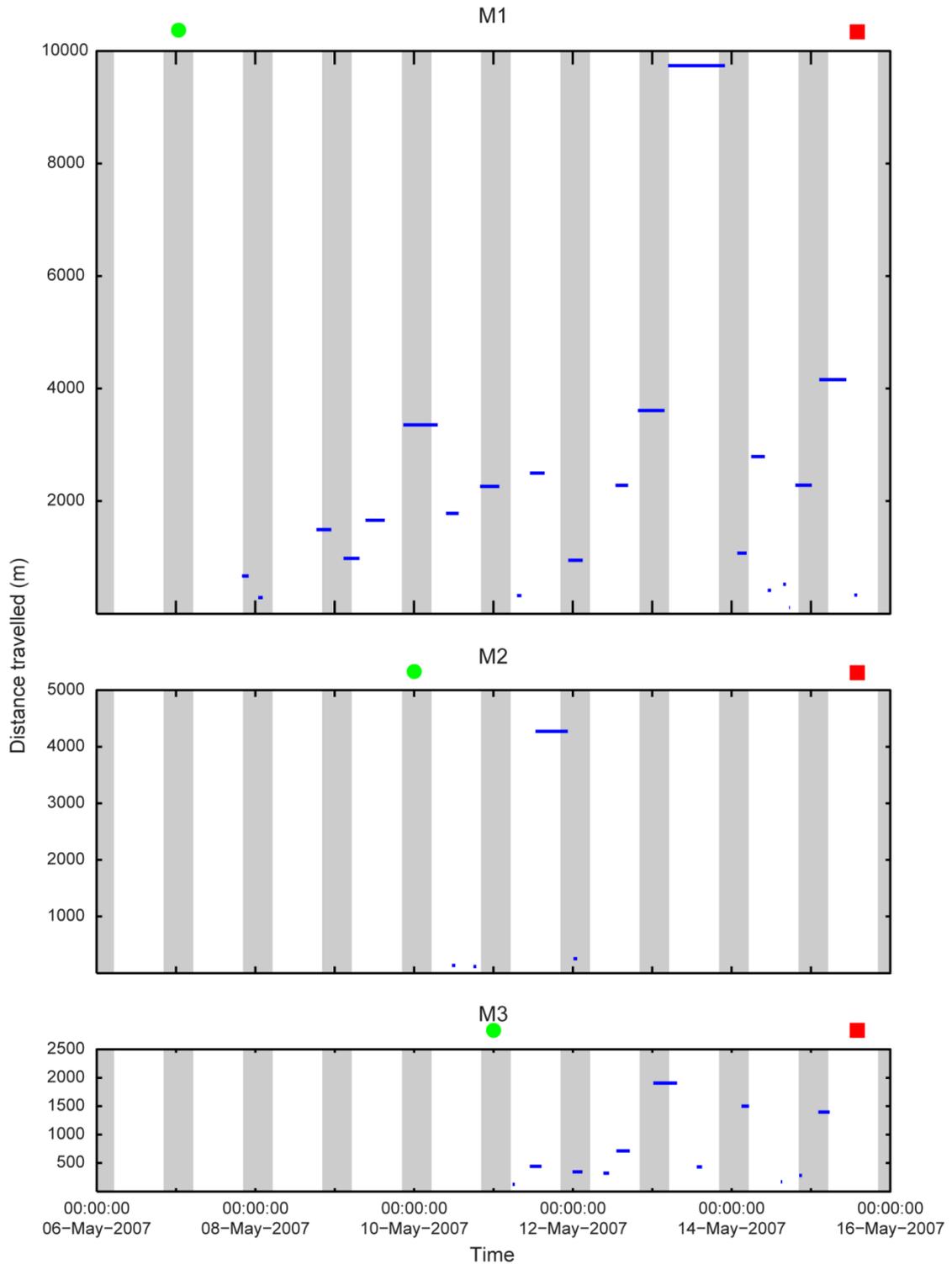


Figure 3-5. Timing of discrete excursions by male small-spotted catsharks from central places in Lough Hyne, Republic of Ireland. Each excursion is a line whose length represents the duration of the excursion. The height of the line on the y-axis represents the total distance travelled during the excursion in meters. Shaded grey bars indicate the time between sunset and sunrise each day. Green circles and red squares indicate the start and end of the tracking period respectively.

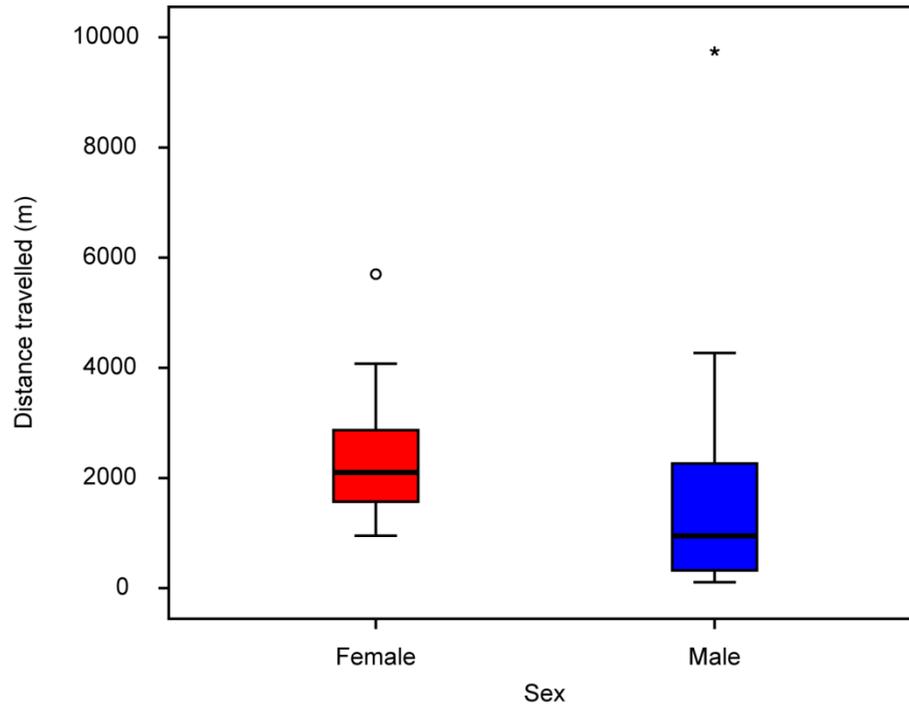


Figure 3-6. Distances travelled during foraging excursions by female (red) and male (blue) small-spotted catsharks in Lough Hyne, Republic of Ireland. Median distances are indicated by horizontal black lines within boxes representing inter-quartile ranges. Outliers are shown as an unfilled circle (female) and an asterisk (male).

F1 undertook five long-range excursions, presumably from rocky refuges located in the south-west corner of the Lough. The first trip commenced on the 19th April 2003 at 09:33 from west cliff in the south and lasted for almost 3 hours, during which time F1 travelled 2.1 km. At first, F1 swam in a directed fashion northwards along the shoreline to the North Basin. In the North Basin the movements became less directed with more frequent turns and shorter steps before F1 began to travel southwards along the same line as the outward trip before stopping short of the start location opposite Labhra Cliff (Figure 3-7).

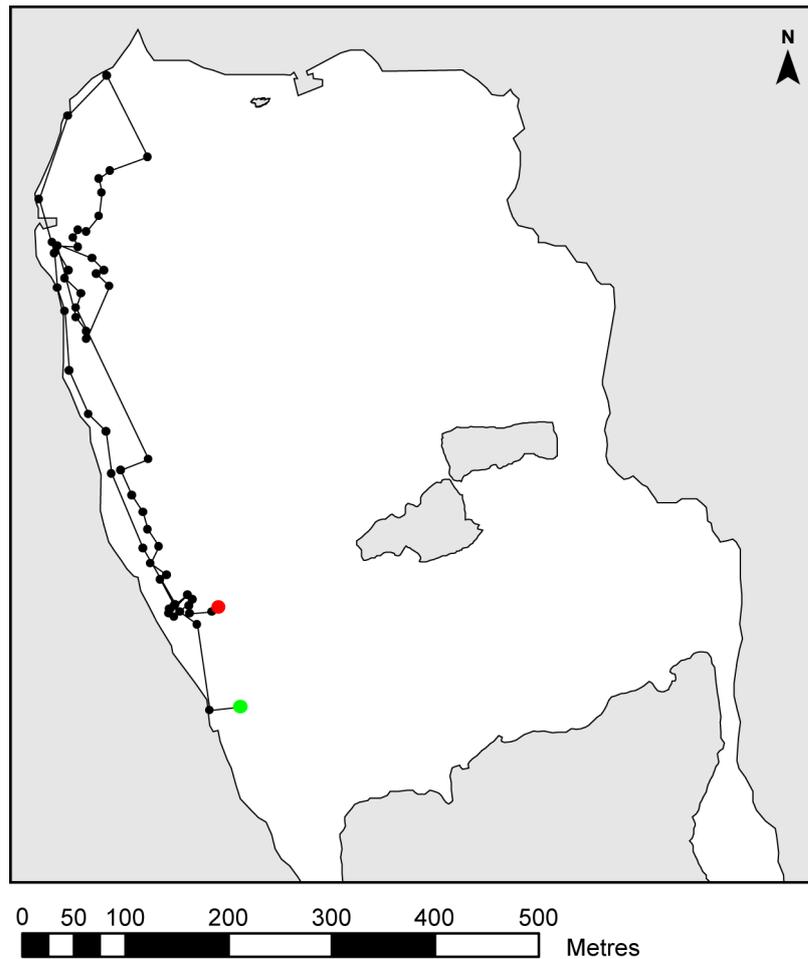


Figure 3-7. A looping excursion (trip 1) made by a female small-spotted catshark (F1) in Lough Hyne, Republic of Ireland in 2003. Filled green and red circles indicate the start and end of the excursion respectively.

The remaining trips made by F1 commenced during the night and followed a similar looping pattern. Trip 4 commenced at 22:46, again originating from a core area in the southwest corner of the Lough. This trip lasted almost 5.75 hours during which time roughly 2.1 km were traversed before F1 returned to an area just 30m from where the trip started. The movements of this trip were very similar to that of trip 1 in that F1 travelled northwards along the western shore to an area near Kelly's Quay in the North Basin (northwest corner) before looping around and returning along a similar path southwards along the western shore to roughly the same area. During this trip the speed varied but was faster at the start ($\sim 0.4 \text{ m s}^{-1}$) decreasing as F1 moved north until reaching the North Basin.

Here speeds increased again but also showed greater variability, fluctuating between higher (0.3 m s^{-1}) and lower (0.01 m s^{-1}) speeds before reaching an area opposite Labhra Cliff (Castle Island) on the return leg where speeds became slower and less variable. Speeds increased again before returning to the original core area at the end of the trip (Figure 3-8).

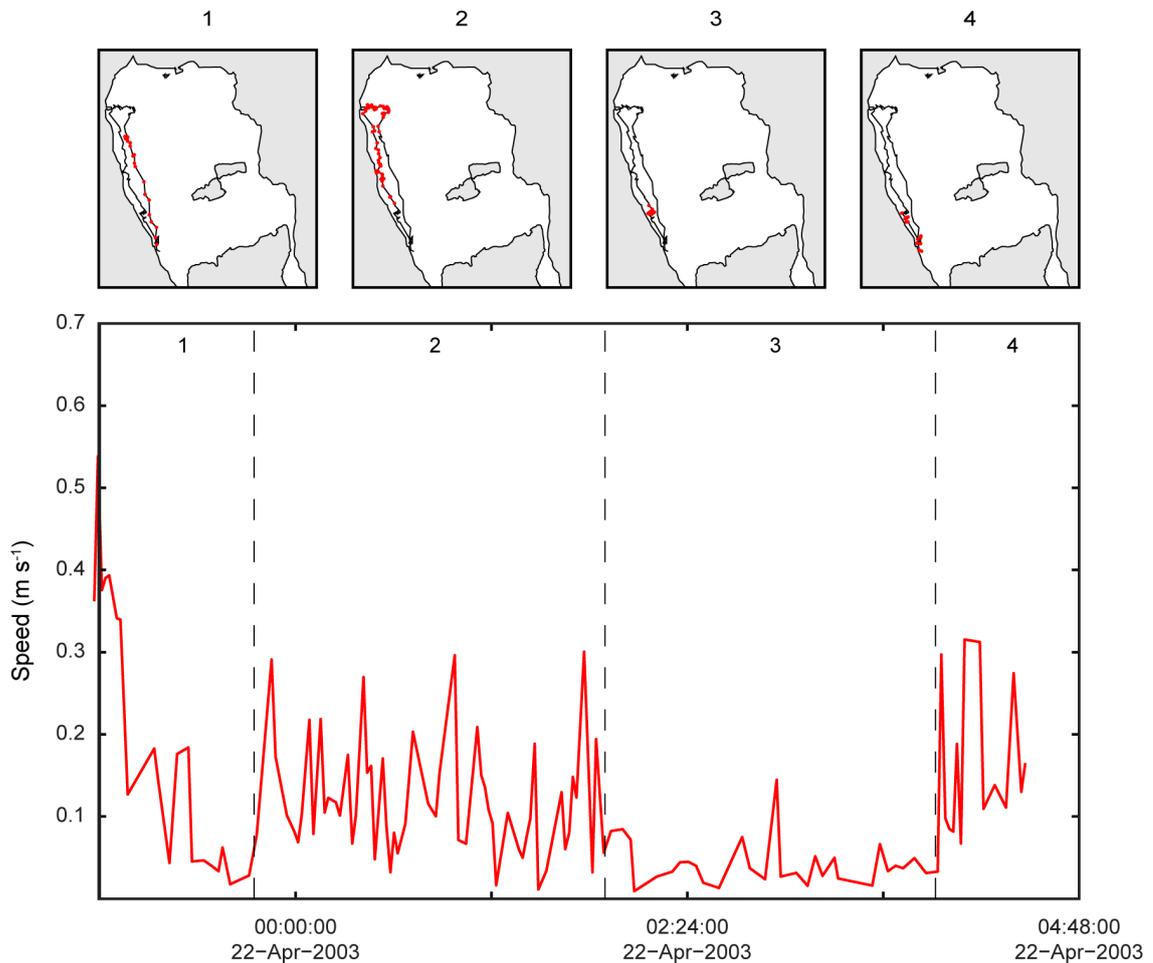


Figure 3-8. Variability of speeds (m s^{-1}) of a female small-spotted catshark (F1) during a nocturnal excursion (trip 4) from a core area (refuge) in Lough Hyne, Republic of Ireland. Dashed lines on the speed plot (bottom) delineate sections of the track shown by the red dots on the corresponding maps (top).

The same general pattern of movements from core areas in the southwest along the western shore to the north basin before returning to the southwest corner was observed in all trips by F2. Each of the trips undertaken by F2 were different in duration and the distances travelled; trips 1 and 3 commenced at night between 22:30 and 23:00 and lasted

for 2 hours 40 minutes and 53 minutes respectively. However, trip 2 commenced during the day at around 10:27 and lasted for 11 hours 37 minutes. During this trip there were multiple loops and path re-crossing was more common resulting in an overall more tortuous path (Figure 3-9).

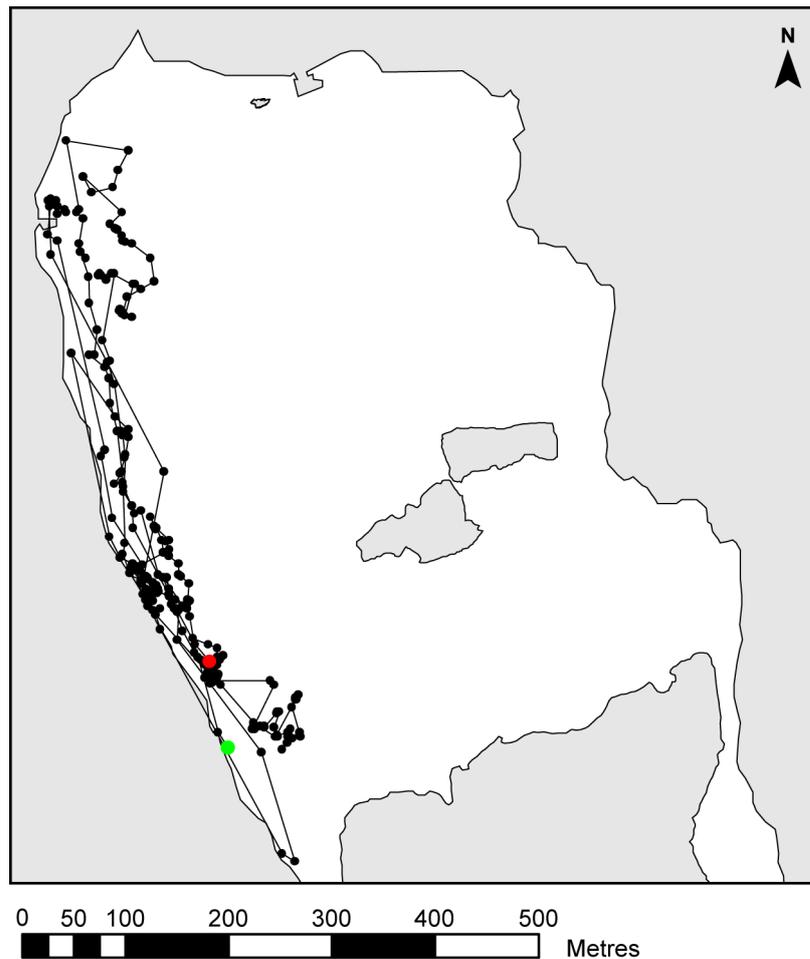


Figure 3-9. A looping excursion made by a female small-spotted catshark (F2, trip 2) in Lough Hyne, Republic of Ireland in 2003. Filled green and red circles indicate the start and end of the excursion respectively.

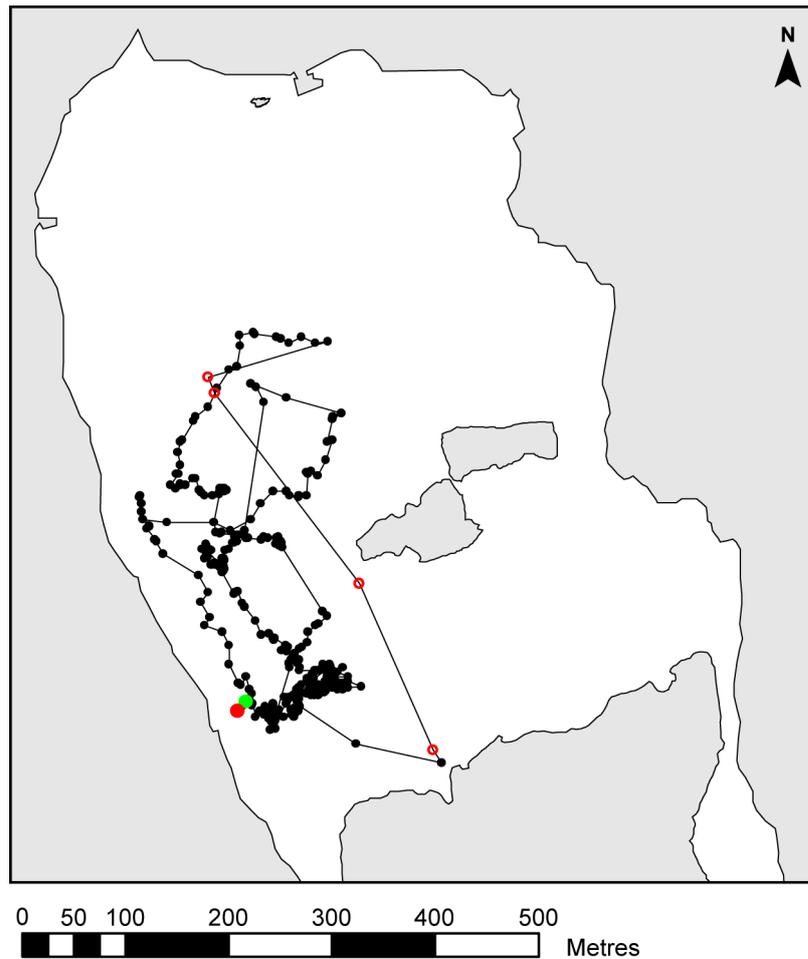


Figure 3-10. A looping excursion made by a female small-spotted catshark (F3, trip 1) in Lough Hyne, Republic of Ireland in 2003. Filled green and red circles indicate the start and end of the excursion respectively, unfilled red circles indicate positions during fragmented section of the track where the individual moved in and out of detection range.

F3 exhibited different movements than the other two females. Although both trips initially followed a similar route northwards along the western shore to the North Basin, on both occasions F3 moved east towards the centre of the Lough just north of Castle Island, further south than the northernmost extent of trips by F1 and F2. During trip 1, which began at 13:36, F3 travelled initially north before moving east into the north basin just north of castle island before looping back around and returning to the south to an area known as the western trough, where small-scale movements were carried out before

another loop slightly further north into the north basin. Here, at around 22:30, the individual moved out of detection range of the VRAP array before eventually returning to within 14 m of where the trip commenced near the west shore from the south basin at around 06:30 (Figure 3-10).

M1 undertook 22 excursions within the south basin that varied in timing, duration, and distance travelled (Figure 3-5 and Table 3-1). For example, trip 14 commenced at 04:51 on the 13th May and lasted for just over 17 hours during which time M1 travelled 9.7 km, whereas trip 19 commenced at 17:25 on the 14 May and lasted for just under 15 minutes with M1 travelling just 107 m. The movements of M1 during some trips resembled the looping pattern of trips made by females. Trip 3 consisted of M1 moving out of a core area in the centre of the south basin at 18:30 and travelling in a looping fashion radiating from the core area (Figure 3-11). One such loop extended from the core area north east into the shallower water of Castle Island bay. Path re-crossing was common and the track was highly tortuous. At the end of the trip nearly 4 hours 30 minutes later M1 had returned to an area within 12 m of the starting location after traversing just under 1.5 km. The swimming speed of M1 varied considerably throughout the trip with no clear patterns associated with different sections of the track (Figure 3-12). Generally, male tracks appeared less directed and more tortuous than females and the trips were smaller in scale.

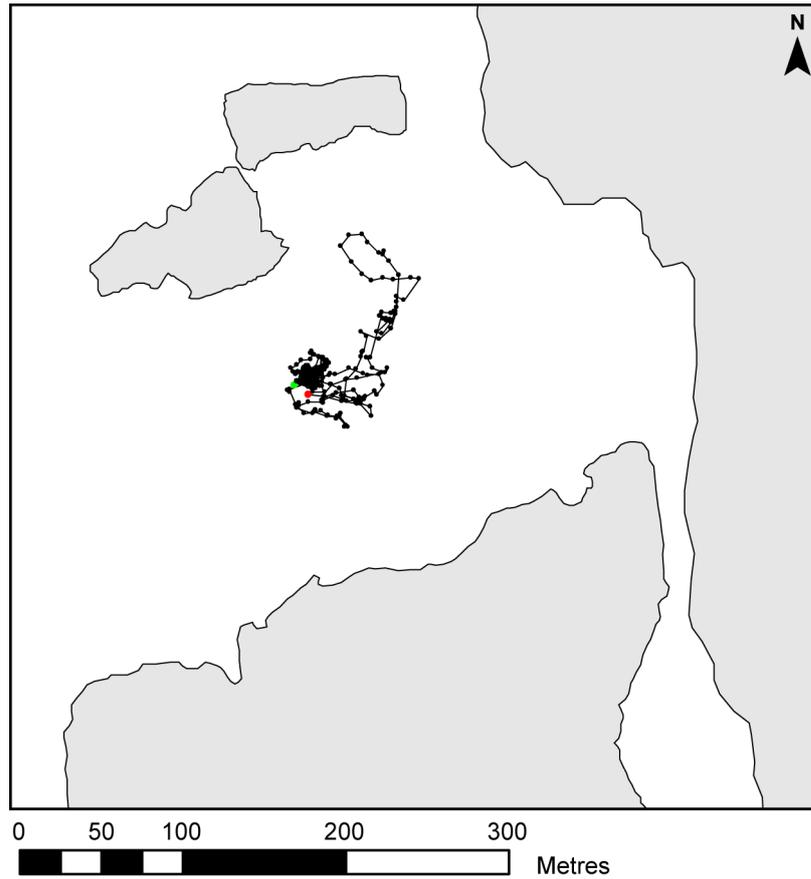


Figure 3-11. A discrete looping excursion made by a male small-spotted catshark (M1, trip 3) in Lough Hyne, Republic of Ireland. Filled green and red circles indicate the start and end of the excursion respectively.

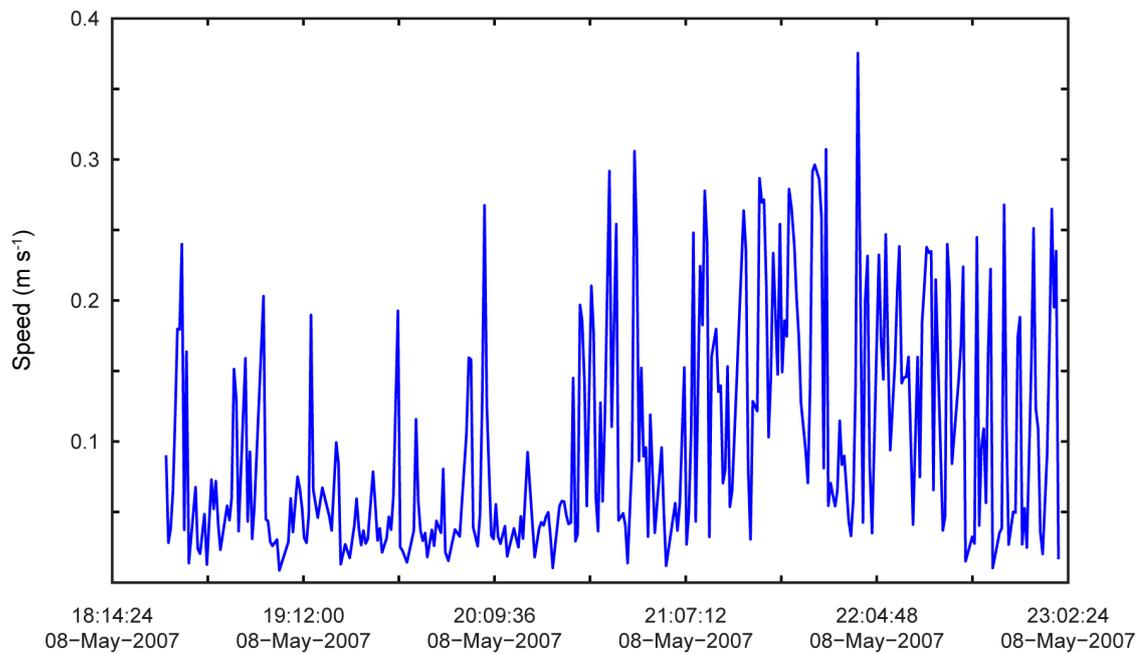


Figure 3-12. Swimming speeds (m s⁻¹) of a male small-spotted catshark (M1) during an excursion from a core area (trip 3) in Lough Hyne, Republic of Ireland.

The same general looping, highly tortuous excursions were observed for all males. In some cases the males would return to the same core area following an excursion (M1: all trips; M2: trips 1 and 2; M3: trips 1-3 and 5-9), whereas in others the males would return to a different core area. For example, on 15 May at 02:20 M3 left a core area near the centre of the south basin corresponding to an area with a known topographical reef feature known as Metridium Rocks. After 3 hours and 23 minutes the trip concluded at another core area to the north east, near castle island bay, roughly 110 m away from the original core area (Figure 3-13). Asides from this, the movement pattern was similarly tortuous and looping as other male tracks, such as the one described previously for M1.

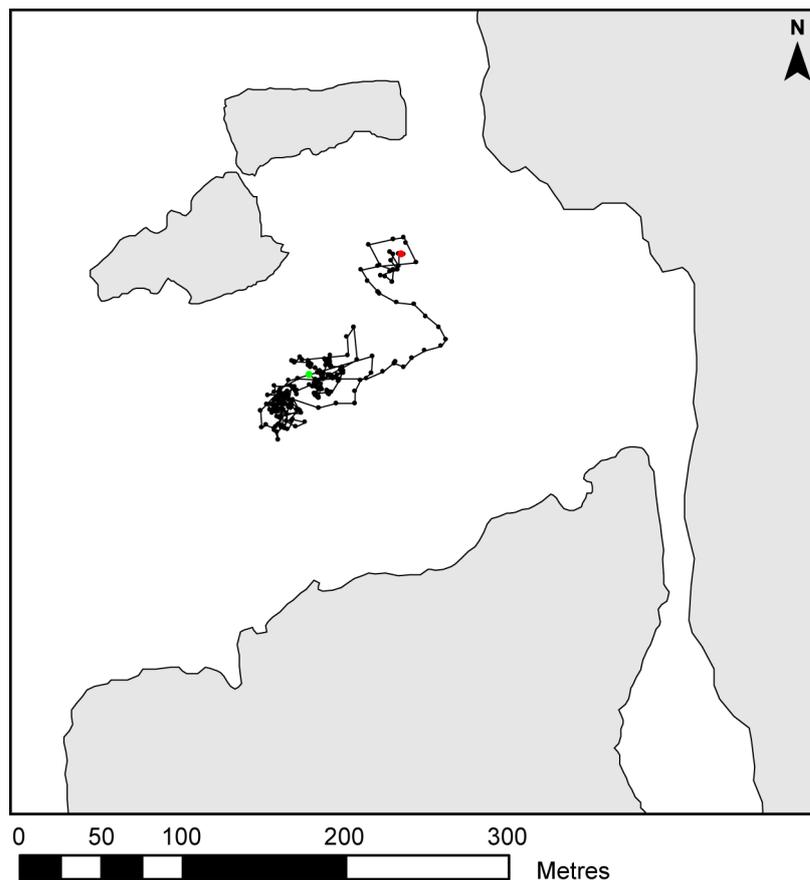


Figure 3-13. A discrete looping excursion made by a male small-spotted catshark (M3, trip 11) in Lough Hyne, Republic of Ireland. Filled green and red circles indicate the start and end of the excursion respectively.

3.3.3 Prey field sampling

The composition of prey caught in baited traps as measured by the proportional abundance of different prey types, is clearly different both temporally and spatially throughout the lough as shown by the divisions of the pie charts in Figure 3-14. In addition, total abundances of all prey were different temporally and spatially in the same way shown by the visibly different diameters of the pie charts in Figure 3-14. In 2003, there appeared to be a gradient of prey abundances increasing northwards along the western shore into the North Basin, which was especially pronounced at night. The composition of prey also followed this trend with increasing proportions of prawns and crabs and decreasing proportions of fish. Additionally, the prey compositions differed between day and night samples with greater proportions of prawns in night samples. This pattern does not hold for samples collected in the South Basin in either 2003 or 2007. In these samples there were comparable abundances and compositions of prey in day and night samples as well as in all locations. These abundances were similar to those found in the North Basin during the night in 2003 and thus were generally higher and contained greater proportions of prawns than those found along the western shore and in the North Basin during the day in 2003.

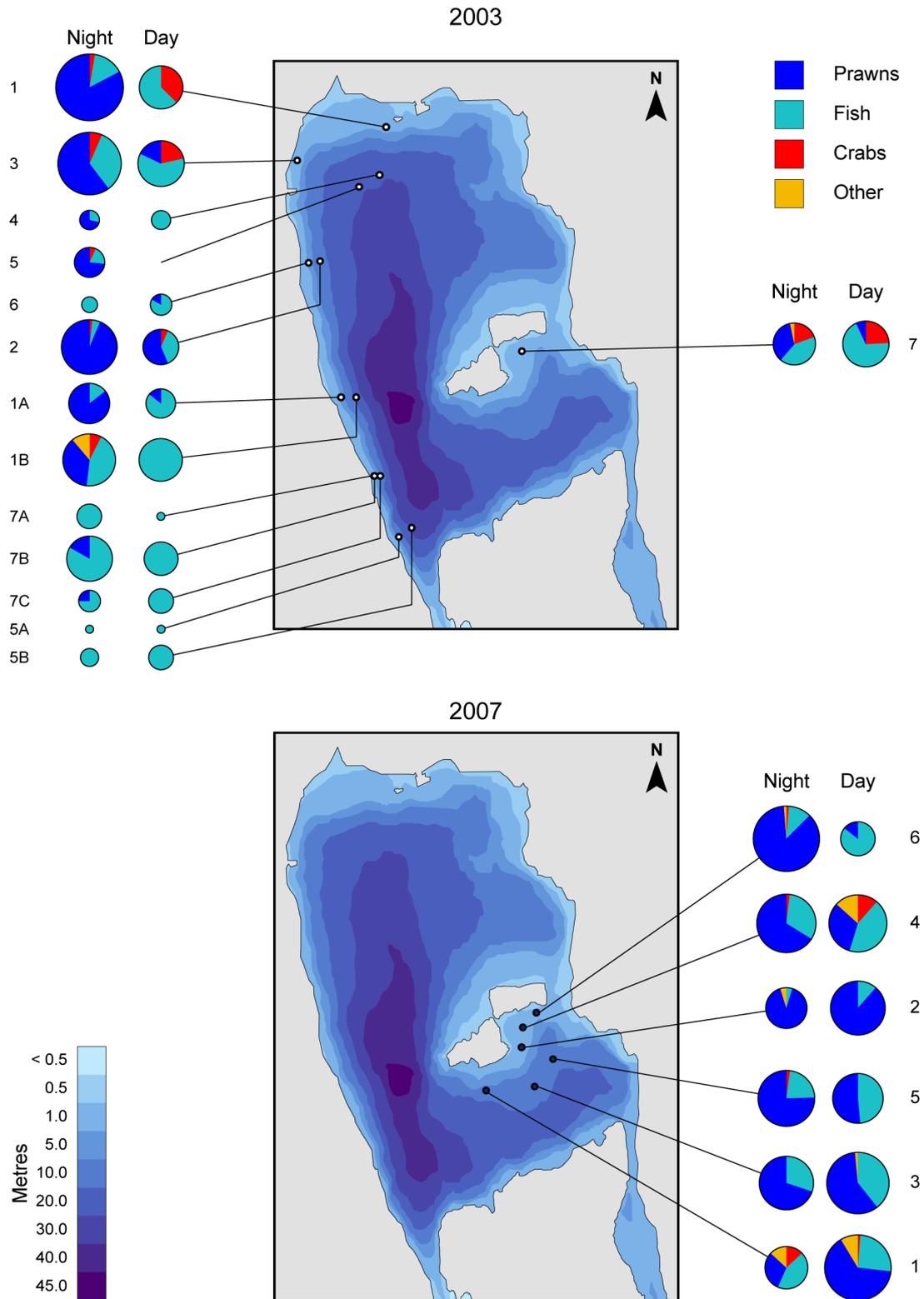


Figure 3-14. Results of prey sampling conducted at Lough Hyne during April 2003 (top) and May 2007 (bottom). Pie charts show the mean proportional abundances of different types of prey as indicated in the key (top right), and their sizes represent the relative total abundances of prey caught at those particular locations during consecutive nights and days.

3.4 Discussion

The general space-use patterns of small-spotted catsharks in this study are similar to those demonstrated by previous research and confirm those findings (Sims *et al.*, 2001; Sims *et al.*, 2006a). The present study extends previous work by resolving the fine-scale movements of small-spotted catsharks in the field and investigates the apparent central place foraging undertaken by both sexes of this species in a temperate marine lough, Lough Hyne, Republic of Ireland. The results of this chapter show temporal (diel) variation in female space use with greater areas of the lough used during the night than the day. In contrast, male space use was the same regardless of time of day. On closer inspection of the tracks it was clear that both males and females exhibited temporal differences in movement behaviour. For both males and females discrete excursions from and to one or more core areas (central places) were identified. For females these excursions occurred mostly during the night whilst during the day they remained inactive, most likely occupying refuges in labyrinthine rock systems in the southwest corner of the lough. Night time excursions did not occur every night and also varied in duration and the distances travelled both within and between individuals. In contrast, males undertook more trips which were not restricted by time of day, taking place both during the day and the night on a daily basis. Male trips also varied in duration and distances travelled as female trips did, but they were generally shorter in terms of both of these parameters.

Despite the apparent general similarities in the patterns of these trips between the sexes with both males and females exhibiting looping paths out and back to central places, the timing and path structure of the trips were often different. The female excursions generally occurred at night, were over a larger scale than male trips, and incorporated a commuting phase along the western shore. This was characterised by directed movements and gradually decreasing speeds as the individuals approached the North Basin, where the

step lengths became shorter and the speeds varied with frequent fluctuations between rapid and slow movements. In contrast, male excursions were generally over a smaller scale and step lengths were short and speeds variable throughout the trip. Given the structure of these excursions, and the knowledge of spatial distributions of prey (Figure 3-14) and refuge locations within the lough, the most likely function of these trips is foraging. It would appear that males can and do forage throughout the diel cycle in the same general vicinity as their core areas, whereas females commute to forage nocturnally in prey patches further from their refuges or core areas. The differences in timing and scales of these foraging excursions may therefore be explained by the prey landscapes. The preferred prey of small-spotted catsharks has been reported to consist of predominantly decapod crustaceans such as prawns and crabs (Ellis *et al.*, 1996b; Sims *et al.*, 2001). In the North Basin and along the western shore there is a trend for lower prey abundances and lower proportions of the preferred decapods in the day compared to the night. In contrast, abundances of preferred prey were generally higher in the South Basin than along the western shore and comparable to that of the North Basin. There were also no clear differences in prey availability over the diel cycle in the South Basin, with similar compositions and abundances of prey available both during the day and night. This would allow males in the south basin to forage just as successfully both during the day and night and therefore may be a contributing factor to the unrestricted timing of their foraging excursions.

Differential space use over the diel cycle with core areas being inhabited during the day and nocturnal excursions away from the core area has been observed in other species of fish (Tricas *et al.*, 1981; Ogden and Quinn, 1984; Holland *et al.*, 1993; Burke, 1995; Jadot *et al.*, 2006), and this has often been attributed to foraging during the night with spending the days in a refuge (Holland *et al.*, 1993). Similarly, asynchronous non-periodic feeding

patterns, like those found for males in this study, have previously been reported also for lemon, sandbar and juvenile hammerhead sharks, and this has often been attributed to differences in feeding success and digestion rates (Medved and Marshall, 1983; Wetherbee *et al.*, 1990; Holland *et al.*, 1993). However, differences in movement patterns between the two sexes, such as those found in this study, has received little attention.

Asides from the differences in movements between the sexes discussed above, the most striking feature of this study is the identification of central place foraging-like behaviour not only for female, but also for male small-spotted catsharks. Both females and males undertook excursions from a central place or multiple central places throughout the study. Patterns of movement consistent with central place foraging have been widely documented for a number of species (Kacelnik, 1984; Kacelnik *et al.*, 1986; Bowers and Ellis, 1993; Steingrímsson and Grant, 2008). However, much of the literature concerns birds and insects and focuses on provisioning for young in the nest or the colony respectively (Kacelnik, 1984; Kacelnik *et al.*, 1986). Since small-spotted catsharks are oviparous and parental care is absent in this species (Ellis and Shackley, 1997), provisioning for young as a cause of central place foraging can be ruled out.

In examples of central place foraging by fish, the main focus has been on territorial defence of foraging stations from which prey and intruders are attacked at varying distances from single or multiple central places (Grant *et al.*, 1989; Biro *et al.*, 1997; Steingrímsson and Grant, 2008). Territoriality in small-spotted catsharks is not documented and is unlikely given the large aggregations that are often found in nature (Rodríguez-Cabello *et al.*, 2007). A further explanation for central place foraging is that of predator avoidance through the use of refuges (central places), from which foraging excursions are made (Kramer and Nowell, 1980; Bowers and Ellis, 1993). However, predators of sharks are few and are usually other, larger elasmobranchs and marine mammals. Although

sightings of larger elasmobranchs species in Lough Hyne are rare, a few larger species including the nursehound, *Scyliorhinus stellaris*, the angelshark, *Squatina squatina* and the thornback ray, *Raja clavata* have been encountered (Minchin, 1987a). Grey seals, *Halichoerus grypus*, have also been sighted in the Lough and could pose a threat to small-spotted catsharks. Despite this there is little evidence that small-spotted catsharks in Lough Hyne have been targeted by these potential predators and given the availability of other more preferred prey of these species it is unlikely that predation is a significant risk factor for small-spotted catsharks in Lough Hyne (Sims *et al.*, 2006a). Furthermore in this study, only the use of a core area by females was related to refuging behaviour as males were not observed refuging. Given that small-spotted catsharks are sexually monomorphic with respect to body size, one would expect both sexes to use refuges if predator avoidance was important.

Since refuging behaviour in female small-spotted catsharks is not likely to be a result of predator avoidance; other factors must play a role. It has been hypothesised that refuging by female small-spotted catsharks is a result of sexual segregation driven by mate avoidance (Sims *et al.*, 2001; Sims *et al.*, 2005; Wearmouth and Sims, 2008). Copulatory behaviour can be aggressive between small-spotted catsharks, with multiple males pursuing and violently tugging at a single female (Dodd, 1983; Sims *et al.*, 2001). Thus, the spatial separation and different movement behaviours presented in this chapter are most likely due to the females balancing the need to forage efficiently against the need to avoid potentially costly, unsolicited mating attempts by males. Therefore, it follows that sexual segregation and mate avoidance may explain central place foraging in female small-spotted catsharks. Since predation risk and territoriality are unlikely, why males should undertake central place foraging is more difficult to explain and thus requires further investigation.

It is likely that the movements of small-spotted catsharks are tightly linked with tracking of prey (or other resources such as mates), and as such they are likely to vary in relation to changing prey landscapes. This assumption is supported by the prey sampling data presented in this chapter. The apparent stability in prey availability both in the day and night could be at least one reason why males choose to remain in localised areas within the South Basin for much of the time. In contrast, females make directed movements to areas of the North Basin where prey is more abundant during the night compared to during daytime. That females rarely moved away from refuges during the day could arise due to the need to avoid males, but also due to lower prey abundance (or its decreased availability) during the day in areas away from the concentration of males in the South Basin. The relative scarcity of prey may make daytime foraging less successful for females displaced to areas further away from aggressive males. However, more detailed information concerning prey availability and prey capture events is required to test this idea fully. Therefore, further investigation of central place foraging in this species would require knowledge of prey encounter and capture events during foraging excursions. The ever advancing field of biotelemetry and specific feeding ‘sensors’ will allow prey capture events of free ranging marine predators to be resolved, and thus facilitate empirical testing of the theoretical predictions of optimality models. This would in turn provide further insight into the behavioural decisions made by free-ranging marine fish predators.

To explore the possibilities raised here the following chapter examines the possible influences of environmental variability (prey distribution and density) on the movements and search behaviour of small-spotted catsharks, in relation to optimal movement models.

4 Effects of spatial distribution and density of prey on search behaviour and movement patterns of juvenile small-spotted catsharks

4.1 Introduction

The distribution of resources in natural systems is variable both spatially and temporally as a result of many interacting physical and biological processes (Ashmole, 1971; Pinaud and Weimerskirch, 2005). This heterogeneity poses a significant obstacle to the successful foraging behaviour of animals lacking complete information regarding the spatial and temporal availability of prey (Stephens and Krebs, 1986). Therefore, the search tactics employed by animals, and the resulting movements, have a crucial role in determining the successful exploitation of resources and hence their survival (Bell, 1990; 1991; Viswanathan *et al.*, 1999; Zollner and Lima, 1999).

Optimal foraging theory assumes that foragers maximise net energy gain (Stephens and Krebs, 1986), and therefore predicts that search tactics employed by predators should lead to movements that maximise the probability of encountering prey, thus increasing foraging efficiency (Sutherland, 1996). This reasoning also leads to the prediction that the search tactics employed by predators should be flexible within changing environments so as to adjust the search strategy towards optimisation under varying conditions (Fauchald, 1999).

As a result of the importance of animal movements, study of the search behaviour of animals has been a central focus in ecology (Pyke *et al.*, 1977; Kareiva and Shigesada, 1983; Bell, 1990; 1991; Turchin, 1998; Bartumeus *et al.*, 2005; Benhamou, 2006; Reynolds, 2008; Sims *et al.*, 2008). Many studies have attempted to quantify the movements of animals and predict optimal search rules; however, the majority of this work has concentrated on

terrestrial systems using insect, bird or mammalian models with relatively few aquatic examples. For example, starlings were found to search differently depending upon the order of experience of different prey distributions (Dall and Cuthill, 1997). Similarly, the movements of goats were found to be slower and more tortuous in a high prey density environment than in a low density environment (de Knegt *et al.*, 2007). Of the aquatic examples, plaice have also been shown to use different behaviour when searching for prey items that are distributed differently. When foraging on aggregated prey, plaice exhibited both extensive and intensive search behaviour, whereas only extensive search was used when prey were dispersed (Hill *et al.*, 2002).

There are a number of ways an animal can search for food including deterministic, systematic and random approaches. These approaches may not be mutually exclusive with elements of each being utilised simultaneously to differing degrees. Different tactics have been hypothesised to be more efficient in certain scenarios than others. For example, variations of random walks are considered to be most efficient for foraging on randomly distributed resources (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2002; Sims *et al.*, 2008), whereas systematic searches are thought to be most efficient for uniformly distributed resources (Dusenbery, 1989; Zollner and Lima, 1999; Higgins and Strauss, 2004). Even amongst random walk models, some have been proposed to be more efficient than others in different contexts, for example Lévy flights are considered optimal for sparse, randomly distributed prey whereas Brownian motion can be the optimal movement pattern when prey are densely clumped (Bartumeus *et al.*, 2002).

Random walk models have been increasingly used to study animal behaviour. This is possibly a result of the fact that these models imply little in the way of cognitive skills to perform the searching behaviour (Higgins and Strauss, 2004). This little requirement on cognitive processing power results in the possibility that random walk models may

represent general search rules that can be adopted by a wide range of animals (Sims *et al.*, 2008). Despite these theoretical predictions, empirical evidence is still lacking, especially for marine vertebrate predators. One such study has found that the dive behaviour of a number of marine vertebrates including fish, turtles and birds exhibit Lévy walk-like properties close to the theoretical optimum (Sims *et al.*, 2008).

This study aims to determine the search tactics used by a benthic marine predator, the small-spotted catshark, *Scyliorhinus canicula* (L.), when foraging on different distributions and densities of prey and relate these to foraging efficiency. Furthermore these search patterns will be compared to theoretically derived, optimal movement models. Understanding the movement patterns of predatory animals will shed light on decisions underlying habitat selection and enable us to better predict spatial distribution patterns of predatory fish and possibly also those of their prey.

4.2 Methods

4.2.1 Prey distribution experiments

Experimental trials were conducted between June and July 2007 using juvenile fish aged between 20-24 months post hatching. These fish ranged from 270 – 305 mm in total length at the start of the experiment.

Prior to the period of experimental trials, ten individuals (five female and five male) were transferred to holding pens within a large experimental tank (length = 480 cm; width = 170 cm; depth = 50 cm) with re-circulating seawater to acclimatize to the experimental tank conditions. The holding pens consisted of a plastic tubular frame structure (170 cm x 130 cm x 60 cm) separated into six equally sized pens (65 cm x 55 cm x 60 cm) by extruded plastic mesh (mesh size = 1 cm, Collins Nets Ltd., Dorset, UK). Two individuals (one male and one female) were placed in five of the pens, leaving one free to facilitate the

transfer of fish to and from the experimental arena. These pens were housed at one end of the experimental tank separated from the experimental arena by an acrylic divider. Further details concerning the experimental arena can be found in the general methodology chapter (section 2.3.3).

A 12:12 hourly cycle of light and dark was used and the water temperature was maintained between 13-14°C throughout the investigation. Whilst in the holding pens the juveniles were maintained on the same diet as they were whilst in the holding tanks (General Methodology 2.3.2). However, two weeks prior to each of the experimental trials they were fed five times per week in the first week and not at all for the second week (to increase feeding motivation). These timings were determined based on calculations of energy requirements of juvenile small-spotted catsharks (Sims, 1996).

In the centre of this arena five small anchors made from PVC sheeting with nylon bolts and wing nuts, secured the prey array to the tank floor. The prey array consisted of a white PVC sheet (122 cm x 122 cm) with pairs of holes drilled into it at distances separated by 5 cm, giving 24 x 24 pairs of holes. These holes allowed prey (cut squid pieces $\approx 0.5 \text{ cm}^3$) to be loosely tethered to the sheet using monofilament line to maintain their position underwater. The prey items were tethered loosely enough so that the juvenile small-spotted catsharks could remove them with little effort (determined during pilot trials).

Three treatments, with nine pieces of cut squid (prey) arranged in either a uniform, random or aggregated pattern were established by attaching prey to the array at pre-defined coordinates (Figure 4-1). The coordinates of uniformly distributed prey were evenly spaced in a 3 x 3 grid on the array. In contrast, coordinates of randomly distributed prey were generated by a random number generator (Research Randomizer; Social Psychology Network, www.randomizer.org/form.htm). Similarly, the coordinates of aggregated prey were generated using a stratified random number generation approach. The array was

separated into 12 equal squares, and three randomly generated numbers were used to determine the grid squares that contained the patches. Three sets of three randomly generated coordinates were then used as the positions of the individual prey items within the patches.

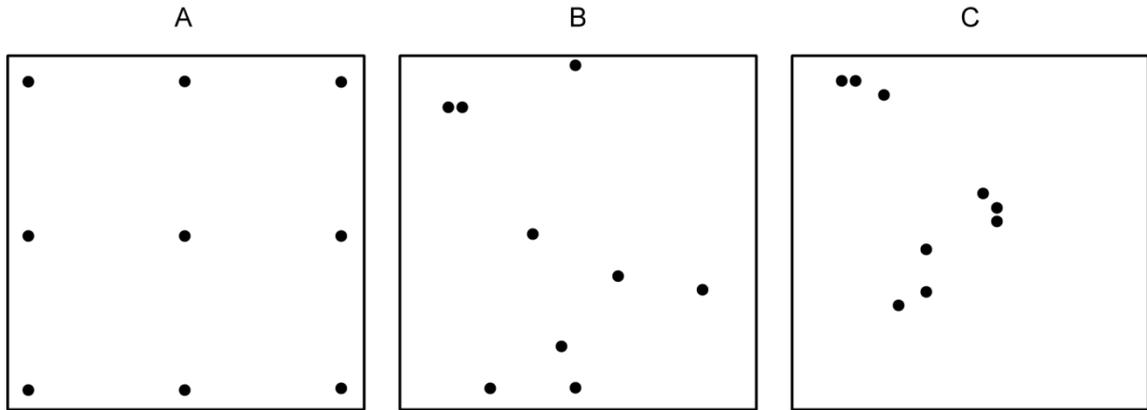


Figure 4-1. Spatial patterns of the distributions of prey (cut squid) for each of the three experimental treatments: (a) regular or uniform array; (b) random array; (c) aggregated array.

Before each trial the appropriate prey pattern was set up on the prey array and this was then secured to the tank floor. Once the water surface was still, an acclimation chamber (30 cm x 25 cm x 61 cm), made from transparent acrylic and open at the top and bottom, was placed in the experimental arena. A single juvenile was placed in the acclimation chamber and allowed to recover from any handling stress and settle in its new surroundings for at least an hour. After this time the chamber was removed and the juvenile was released with very little, if any, disturbance. In most cases the juveniles were motionless, resting on the tank floor when the acclimation chamber was removed. Each trial was recorded continuously for two hours, after which the juvenile was removed and transferred to its holding pen and the prey array was re-established ready for the next trial.

Each of the ten individuals was exposed to all three treatments in random sequence order. If no prey were found, individuals were fed after the trial in the spare holding pen, before being placed back in their original holding pen. There were at least four days

between trials for the same individual. Two different control trials were also run for each individual. The procedure remained the same as for the treatments except no prey were provided in either control. However, in one of the controls (Control II) an olfactory clue was presented at the start of the trial in the centre of the array. This was achieved by injecting squid and fish juice mixed with seawater through an odour delivery tube into the arena.

4.2.2 Prey density experiments

The density experiment was conducted during March 2008 and followed the same methods as the distribution experiment except that ten different individuals were used and different treatments were investigated. In this experiment there were only two experimental treatments: high and low density. In the high density treatment, twenty pieces of cut squid were attached to the array, whereas in the low density treatment only five pieces of squid were attached (Figure 4-2). In both cases the prey were distributed randomly, using coordinates generated by a random number generator.

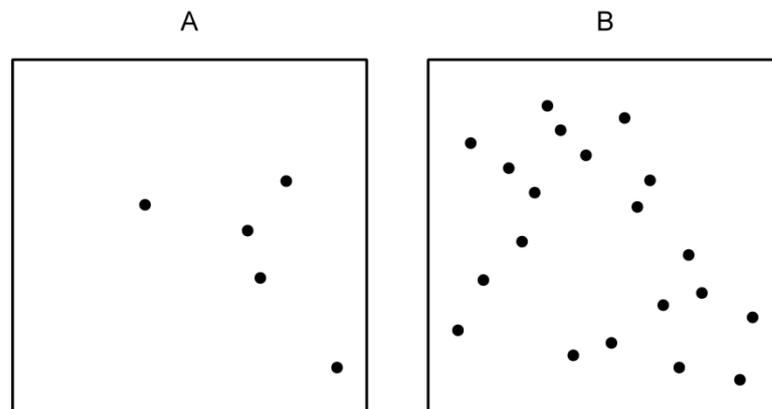


Figure 4-2. Spatial patterns of the distributions of prey (cut squid) for the two experimental treatments: (a) low density prey, (b) high density prey.

Each individual was exposed to each treatment, with five individuals (three females and two males) experiencing low density treatments first, and five individuals (three males

and two females) experiencing high density treatments first. Trials on the same individual were therefore separated by one week. If no prey were found, individuals were fed after the trial in the spare holding pen as in the previous experiment.

4.2.3 Data acquisition and analyses

Prior to the start of each trial a single individual was transferred to an acclimation chamber within the experimental arena, where the appropriate prey arrangement was already established. After approximately 60 minutes the acclimation chamber was removed and the trial began. Movement data were recorded by a computer aided video monitoring system (General Methodology 2.3).

Post acquisition, data were first edited to remove a small number of clearly erroneous positions that were likely caused by light reflections on the surface of the water, or more rarely, when an object other than the fish was detected by the software. These tracks were then further processed with a minimum distance moved filter to remove very small movements that were recorded when it was clear from the video that the animal was stationary.

After the tracks were cleaned various analyses were conducted including the investigation of path tortuosity and area restricted search behaviour through first passage time analysis (General Methodology 2.2.6.3) and the investigation of turn angle distributions using circular statistics (General Methodology 2.2.6.4). Move step length distributions were also investigated using Maximum Likelihood Estimation techniques (General Methodology 2.2.6.4). Furthermore, analyses of foraging efficiency and the timing of prey capture events were also investigated using standard statistical tests such as repeated measures ANOVA models and equivalent non-parametric tests as appropriate.

4.3 Results

4.3.1 Prey distribution

4.3.1.1 *Movements*

Throughout the experiment individuals were generally settled and not moving at the start of a trial (after the acclimation period). After a varying length of time spent motionless in the start position almost all individuals began to move. In the majority of cases this movement signalled the onset of foraging behaviour, and was characterised by sudden and frequent changes in direction and speed. However, in some cases movement was not related to foraging. Instead, short, slow and occasional movements resulting in changes of resting positions were carried out. These movements often resulted in movement along a boundary with frequent reversals in direction. These types of non-foraging movements were seen in nearly all trials at some point, interspersed with either foraging behaviour or pauses, or a combination of the two. These types of movements resulted in tracks of varying length and tortuosity (Figure 4-3).

The tortuosity of the movement paths and their complexity was reflected in results of first passage time analyses. There was considerable variation in the observed scales of area restricted search behaviour and this was supported by the different locations of peaks in variance of first passage time for movements during trials with different distributions of prey (Figure 4-4). No differences in scales of area restricted search (ARS) behaviour were found between treatments (Mixed ANOVA; $F_{2, 16} = 1.831, p > 0.05$) or sexes (Mixed ANOVA; $F_{1, 8} = 0.308, p > 0.05$) and it was clear that there was considerable variation between individuals (Figure 4-5). The main scales of area restricted search often reflected the dimensions of the experimental arena.

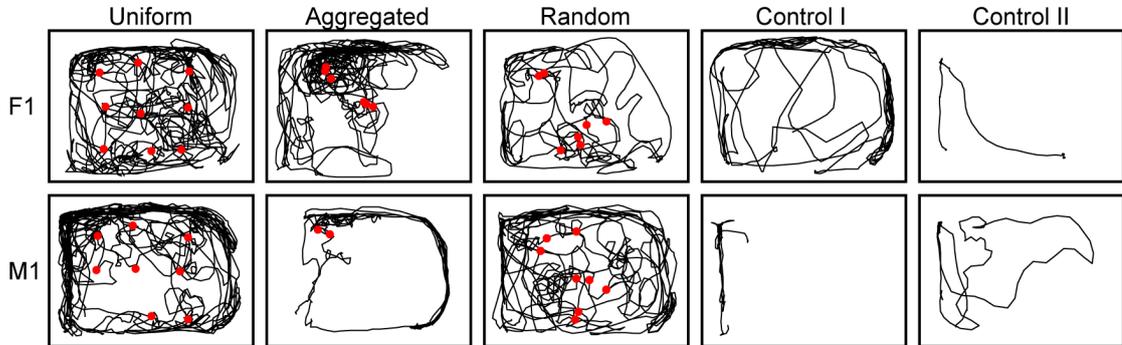


Figure 4-3. Examples of movement tracks of a juvenile male and female small-spotted catshark whilst foraging in an arena containing food distributed uniformly, aggregated and randomly. Movements are also shown for controls when no food was present but either no scent (Control I) or scent was added to the arena at the start of the trial (Control II). The location of the centre of gravity of the individual when prey was captured is shown as red circles.

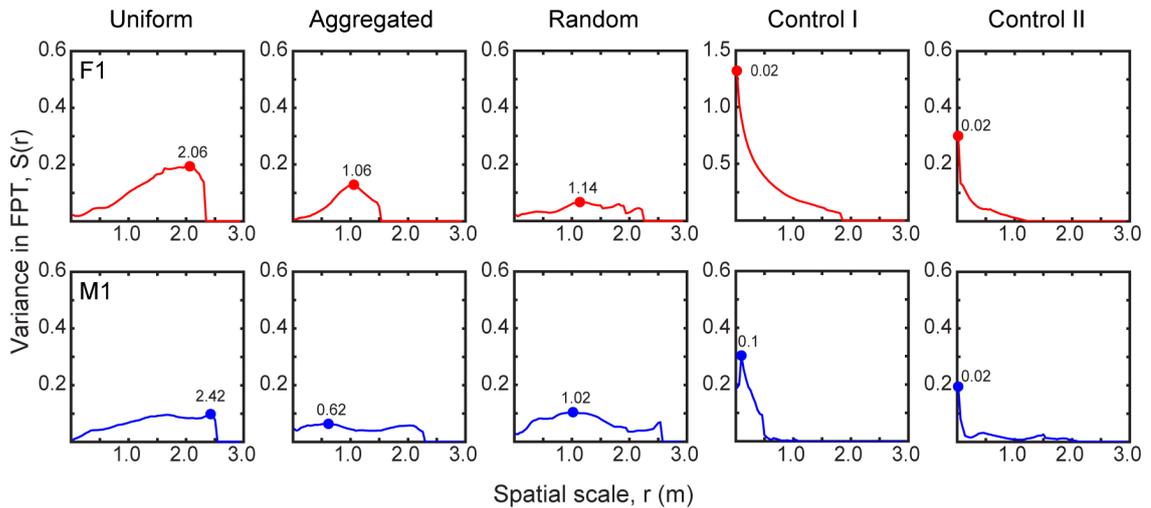


Figure 4-4. The variance in first passage time, $S(r)$, as a function of radius (r) for the movement tracks of small-spotted catsharks whilst foraging. Peaks represent scales of area restricted searching (ARS).

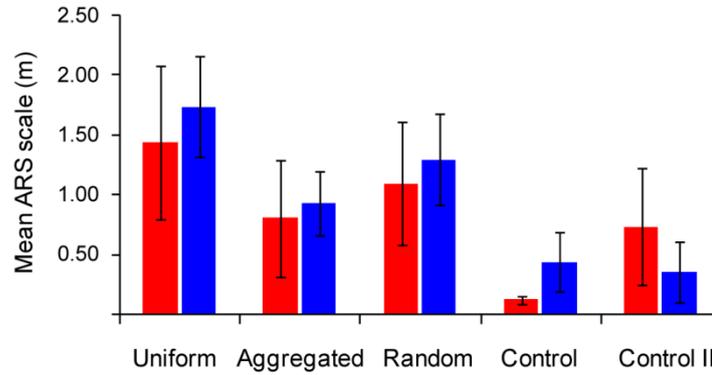


Figure 4-5. Mean (\pm S.E.) scales of area restricted searching (ARS) for juvenile small-spotted catsharks foraging in different distributions of prey as identified by first passage time analysis.

With the exception of 8 trials out of 50, the distributions of turn angles were significantly different from a circular normal distribution (Rayleigh's uniformity tests, $p < 0.05$). Inspection of the circular histograms of turn angles (Figure 4-6) suggests directed behaviour, as the greatest frequencies tended to be grouped closely together in a particular direction, mostly straight ahead with mean vectors (μ) close to 0° . This was further supported by the strength of directionality, which was generally high (~ 0.6). Despite this, there were differences in the strength of directionality between treatments with lower values for control tracks and higher values for foraging tracks in the three prey distributions (ANOVA on ranks; $F_{4, 32} = 2.80$, $p < 0.05$). These differences are evident in Figure 4-7 as large confidence limits indicated by red segments of the circle's circumference.

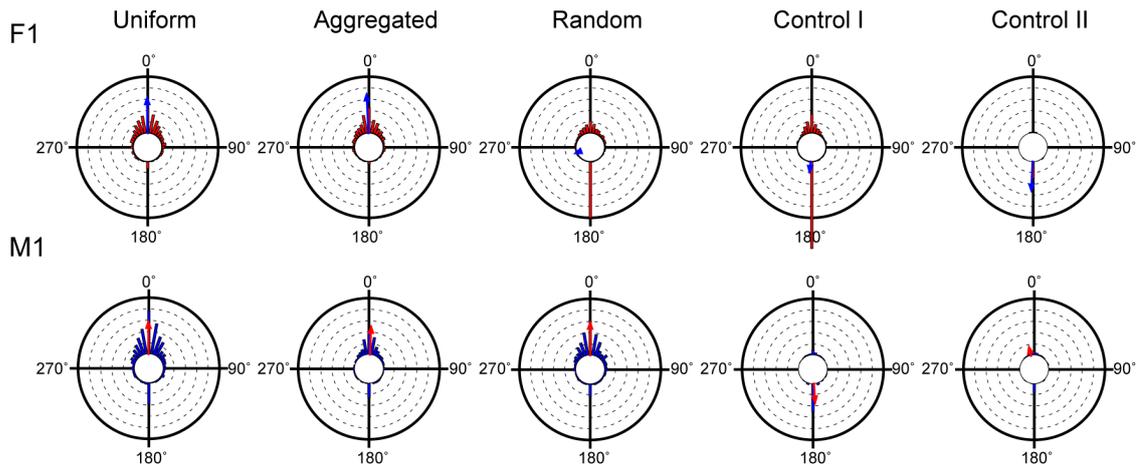


Figure 4-6. Frequency distributions of turn angles exhibited by two juvenile small-spotted catsharks whilst moving in trials with three different distributions of prey and two controls (no prey). Female (F1) – red bars and blue arrows; male (M1) – blue bars and red arrows.

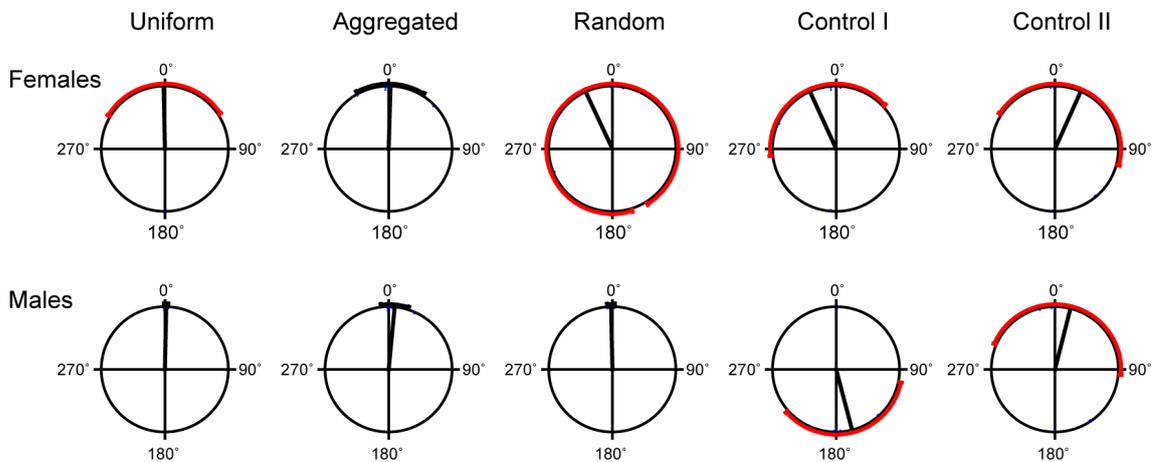


Figure 4-7. Mean turn angles of male and female juvenile small-spotted catsharks whilst foraging in different distributions of prey and controls with no prey. Confidence limits are indicated by the size of the brackets around the plot perimeter. Red brackets indicate large confidence limits and therefore low reliability of the mean vector.

Some individuals remained motionless or exhibited very little movement during trials (Figure 4-3). As a result there were only a small number of steps available for analyses and it was decided to exclude any individual that did not show evidence of search behaviour in all three treatments. For similar reasons it was not possible to analyse control tracks and therefore only tracks recorded for the three treatments were subjected to maximum likelihood estimation (MLE) based analyses. Results of the MLE-based methods for analysing move-length distributions showed that of the three distributions tested, the best fit distribution to the empirical data was the exponential in all cases (Figure 4-8 and Figure 4-9). There was little variation between exponential exponent values and there were no significant differences between sexes or treatments (Figure 4-9).

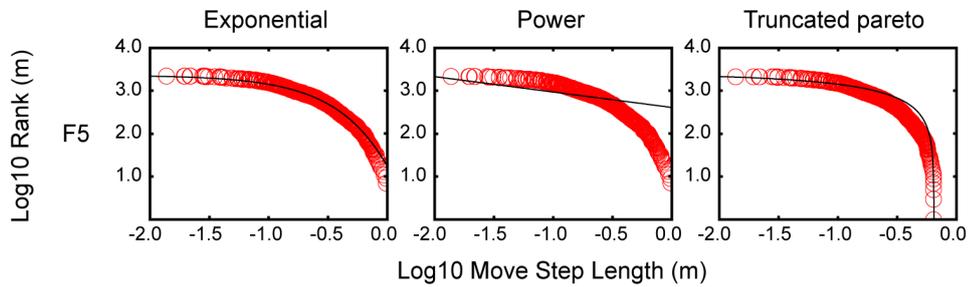


Figure 4-8. A comparison of the fits of the step length distribution of a juvenile small-spotted catshark to different theoretical distributions. The data appears to fit an exponential distribution better than either a power law or truncated Pareto (power law) distribution.

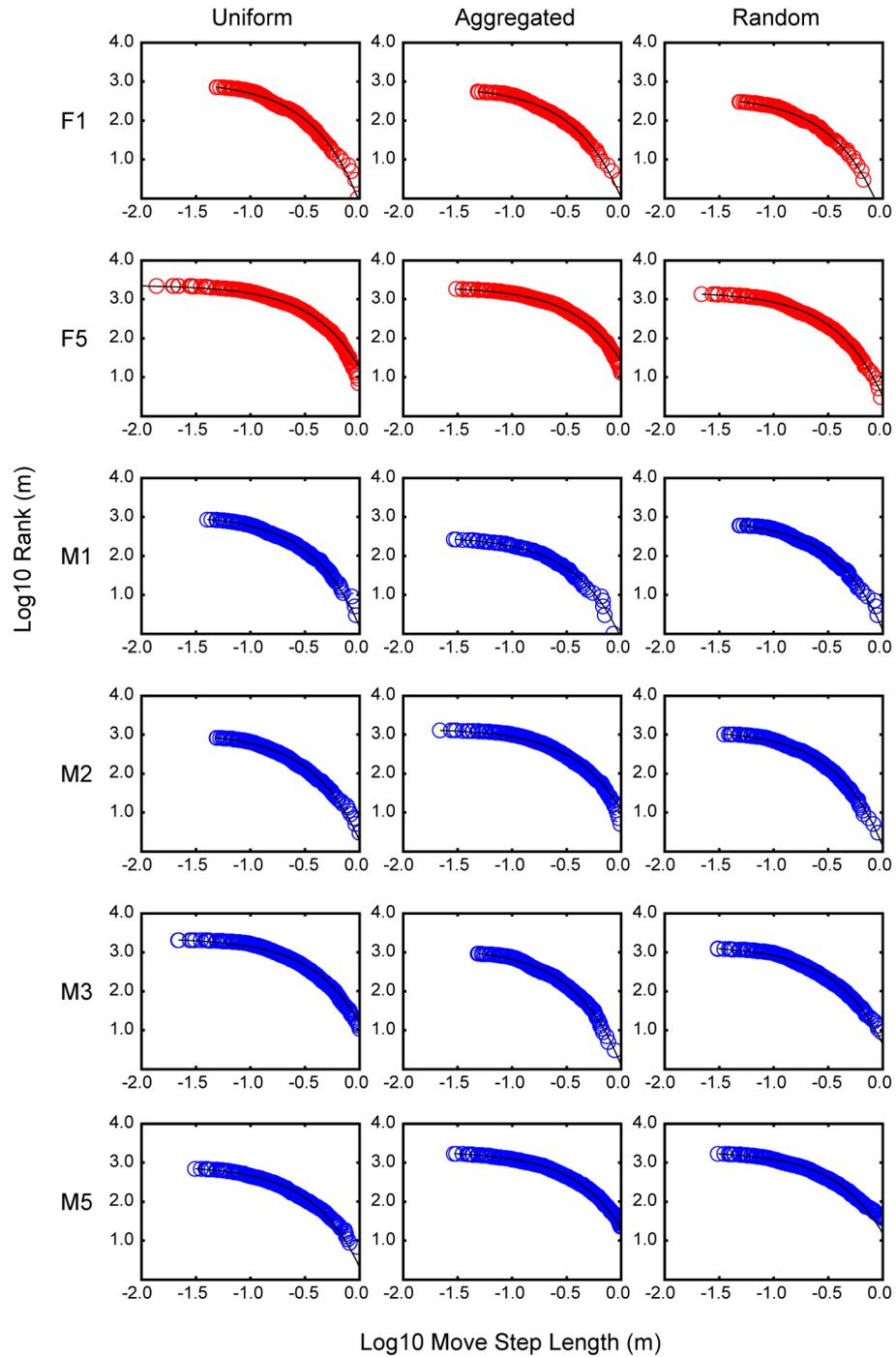


Figure 4-9. Results of MLE based analyses showing frequency distributions of move step lengths as best fits to exponential distributions for female (red, F1 and F5) and male (blue, M1-3 and 5) small-spotted catsharks movements whilst foraging in three different prey distributions. Circles indicate empirical data and lines represent best fit lines to an exponential distribution above x_{\min} . For more details see general methodology.

4.3.1.2 Foraging success

The variation between individuals and treatments seen in the results of the movement analyses is translated to the foraging efficiencies. There was large variation between individuals as indicated by the large error bars in Figure 4-10. Two-way mixed ANOVA results show that there were also no significant differences in foraging efficiencies between different treatments ($F_{2,16} = 0.532, p > 0.05$) or between sexes ($F_{1,8} = 0.004, p > 0.05$; Figure 4-10a). Additionally, there was considerable variation in the length of time an individual would continue to search after finding a prey item (giving up time, GUT). No differences were found between sexes (ANOVA on square root transformed data, $F_{1,10} = 1.37, p > 0.05$) or treatments for mean giving up times ($F_{2,10} = 2.67, p > 0.05$; Figure 4-10b).

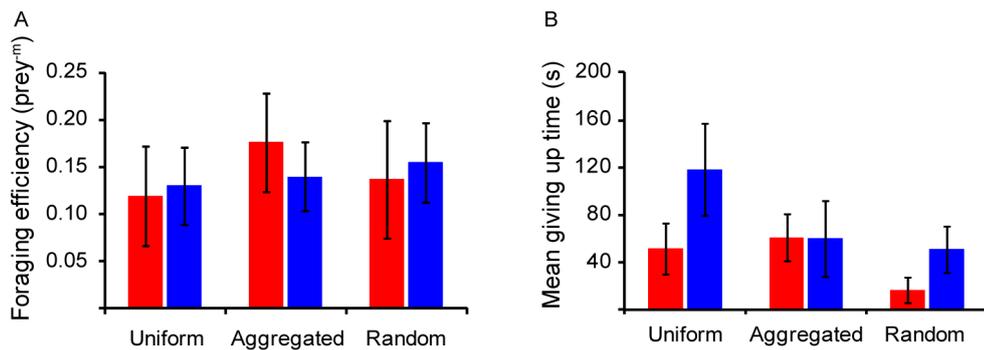


Figure 4-10. (a) Mean (\pm S.E.) foraging efficiency and (b) mean (\pm S.E.) giving up times of juvenile small-spotted catsharks whilst foraging in different prey distributions. Red bars indicate females and blue bars indicate males.

4.3.2 Prey density

4.3.2.1 Movements

The same pattern of movements was evident during trials with different prey densities as with different distributions. Thus the tracks were also variable in terms of their length and tortuosity (Figure 4-11).

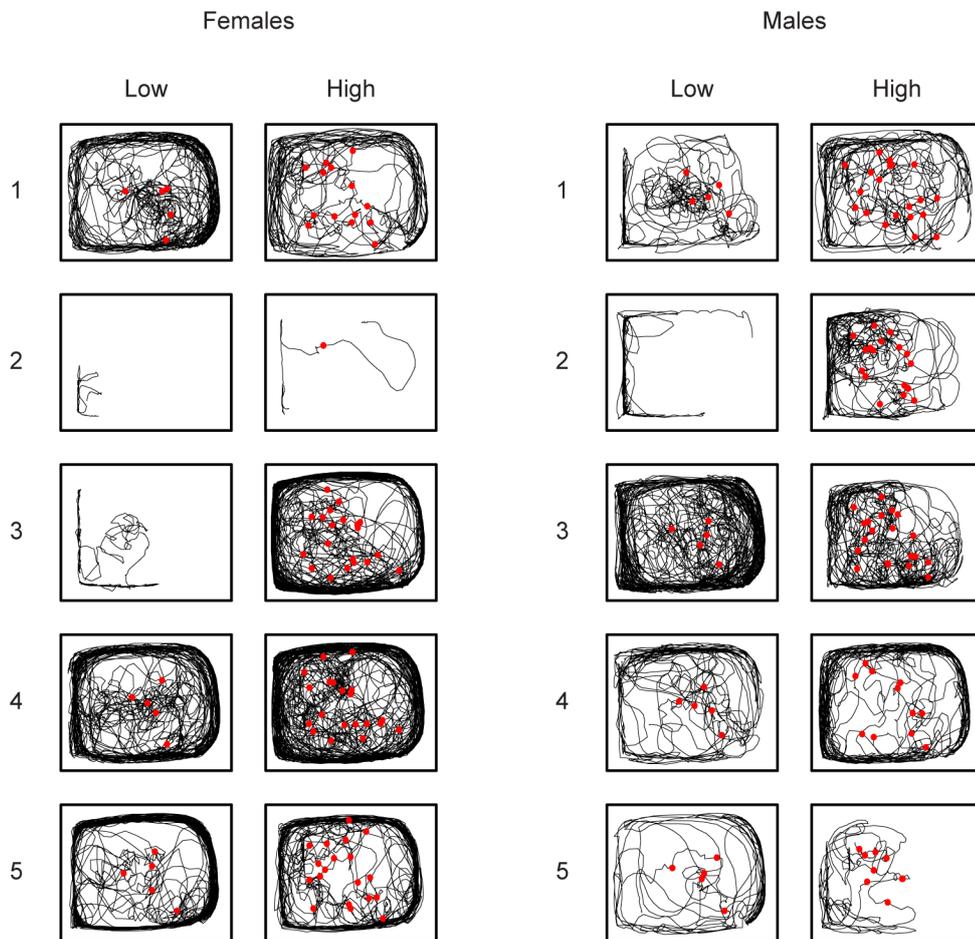


Figure 4-11. Movement tracks of juvenile small-spotted catsharks whilst foraging in low prey densities and high prey densities. The location of the centre of gravity of the individual when prey was captured is shown as red circles.

The variance in first passage time was variable and showed no clear pattern. The peaks in variance associated with area restricted searching of males and females were not different to one another and there was no evidence for differences between treatments. Mostly the scales identified corresponded with the dimensions of the experimental arena (Figure 4-12).

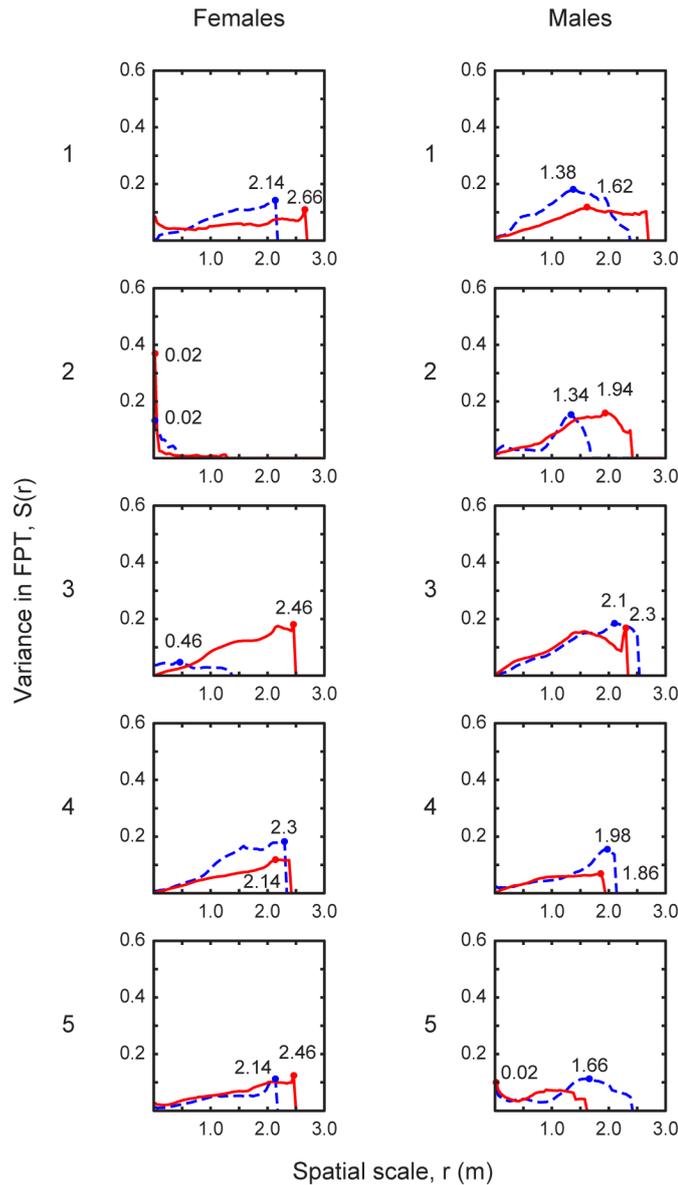


Figure 4-12. Variance in first passage time, $S(r)$, as a function of radius (r) for five female (F1-5) and five male (M1-5) small-spotted catsharks whilst foraging. Red solid lines represent $S(r)$ for trials with high densities of prey; blue dashed lines represent $S(r)$ for trials with low prey densities. Peaks in variance are marked with filled circles and labelled with the associated spatial scale.

The circular distributions of turn angles for all tracks were found to differ from a uniform distribution (Rayleigh's uniformity tests, $p < 0.05$). The mean vectors were also similar to those found for individuals foraging in different prey distributions as they were grouped closely around 0° (Figure 4-13) and were not significantly different between sexes or treatments. The strength of directionality was high (~ 0.6) but not significantly different

between sexes (ANOVA on arcsine transformed data, $F_{1,8} = 0.28, p > 0.05$) or treatments (ANOVA on arcsine transformed data, $F_{1,8} = 0.05, p > 0.05$).

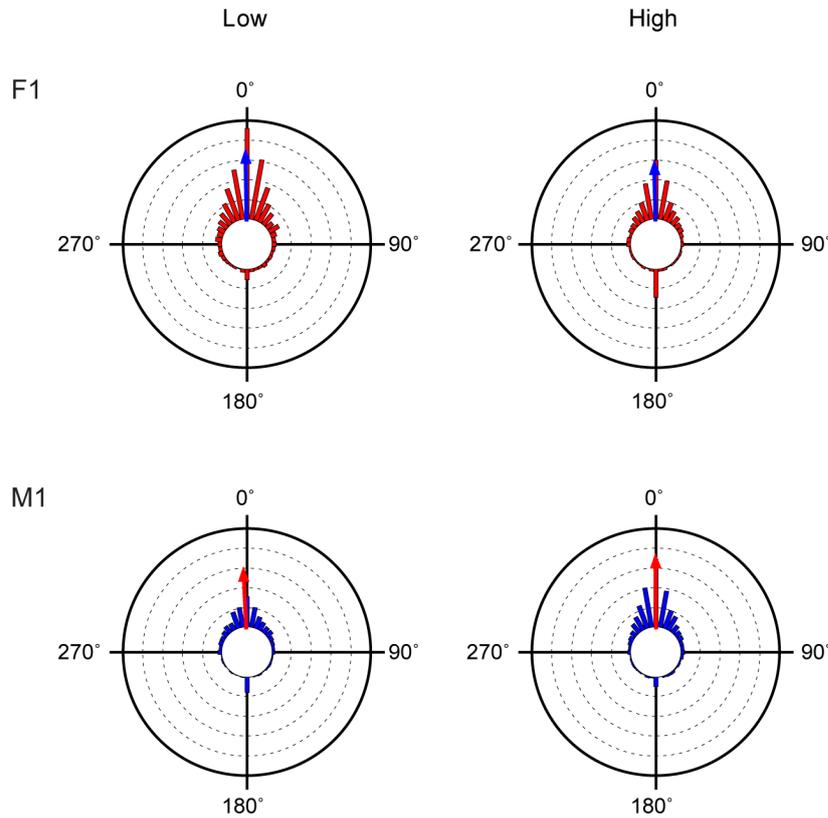


Figure 4-13. Circular frequency distributions of turn angles for a female (F1) and a male (M1) small-spotted catshark whilst foraging in low and high prey densities. Numbers on the outer circle represent degrees, the direction of the arrowheads represents the mean turn angles and their lengths represent the strength of directionality. Dashed lines indicate frequency increments of 120 to a maximum of 600.

Results of the MLE-based methods for analysing move-length distributions again showed that of the three distributions tested, the best fit distribution to the empirical data was the exponential in all cases. There was little variation between exponential exponent values and there were no significant differences between sexes (ANOVA; $F_{1,8} = 0.56, p > 0.05$) or treatments (ANOVA; $F_{1,8} = 0.30, p > 0.05$, Figure 4-14).

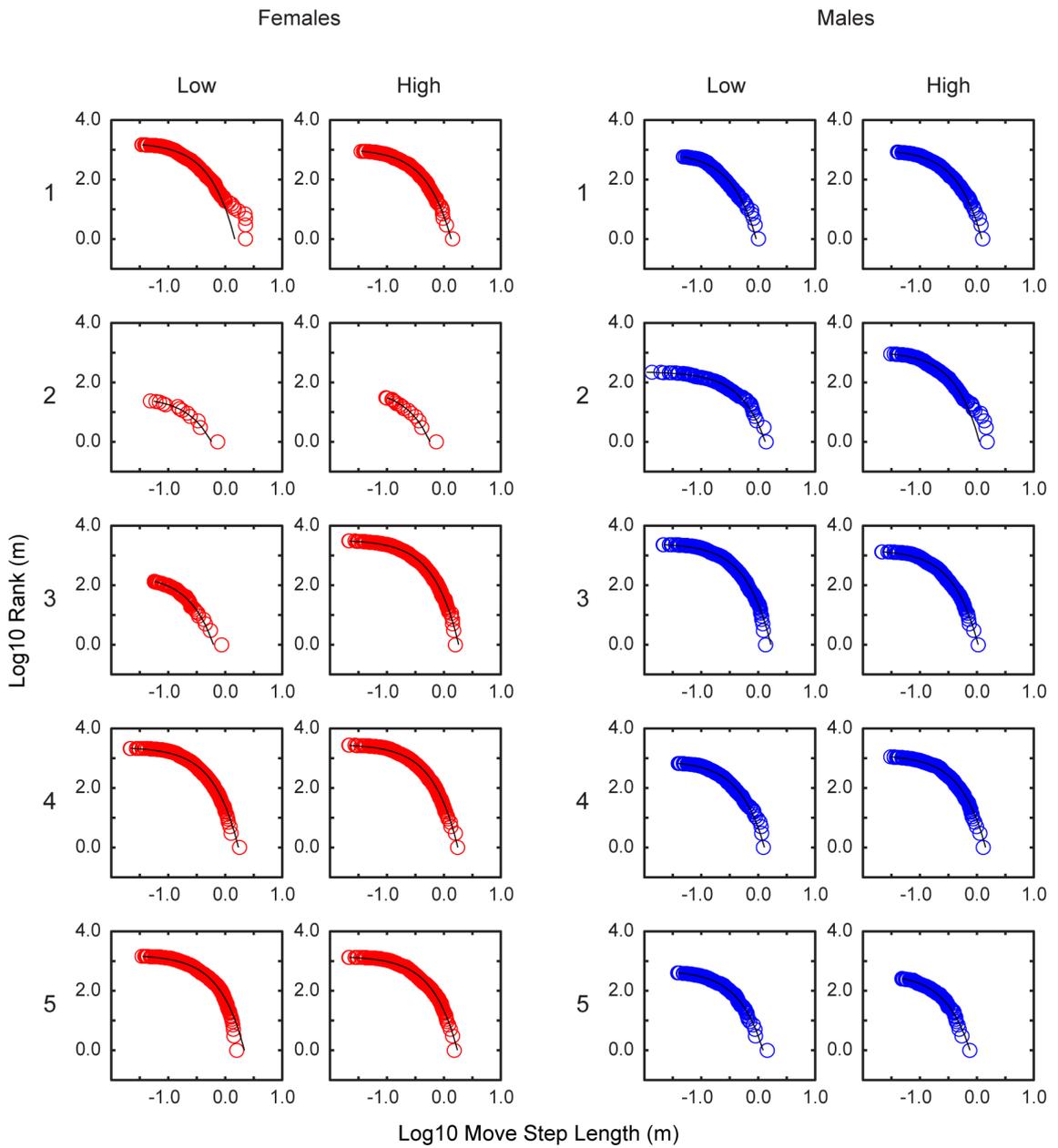


Figure 4-14 - Results of MLE based analyses showing frequency distributions of move step lengths as best fits to exponential distributions for female (red, F1-5) and male (blue, M1-5) small-spotted catsharks movements whilst foraging in different prey densities. Circles indicate empirical data and lines represent best fit lines to an exponential distribution above x_{\min} . For more details see general methodology.

4.3.2.2 Foraging success

The variation between individuals and treatments seen in the results of the movement analyses is again translated to the foraging efficiencies. There was large variation between individuals as indicated by the large error bars in Figure 4-15. Despite appearing to be higher in high density trials there were no significant differences in foraging efficiencies between different treatments (ANOVA; $F_{1,8} = 0.373, p > 0.05$) or between sexes ($F_{1,8} = 5.102, p > 0.05$; Figure 4-15a).

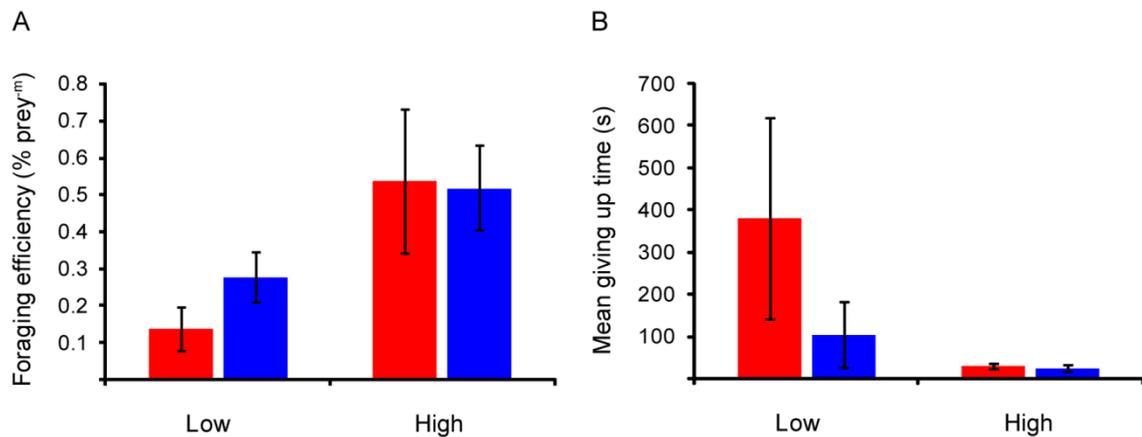


Figure 4-15. (a) Mean (\pm S.E.) foraging efficiency and (b) mean (\pm S.E.) giving up times of juvenile small-spotted catsharks whilst foraging in different prey distributions. Red bars indicate females and blue bars indicate males.

This was also true for giving up times as there appeared to be longer giving up times in low density treatments, but this pattern was shown not to be significantly different (ANOVA on ranks, $F_{1,5} = 1.06, p > 0.05$; Figure 4-15b).

4.4 Discussion

Various hypotheses concerning animal search behaviour have been proposed, each built upon the premise of maximising net energy gain and thus increasing Darwinian fitness (Pyke *et al.*, 1977; Stephens and Krebs, 1986; Bartumeus *et al.*, 2002). This research aimed to test some of these predictions using juvenile small-spotted catsharks. Specifically, the effect of spatial distribution and density of prey on the search behaviour and resulting movement patterns were investigated. In the literature, different movement models have been proposed to be optimal given different situations. For example, a Lévy walk consisting of small step clusters separated by infrequent long displacements has been proposed to be the optimal random walk solution when foraging for sparse, randomly distributed prey. In contrast a Brownian walk consisting of random step lengths has been proposed to be optimal when searching for densely clumped prey (Bartumeus *et al.*, 2002).

The results of this research do not show any differences in search behaviour between animals foraging for differently distributed prey or different densities of prey. In both cases the animals appear to adopt a random search tactic similar to a Brownian walk regardless of prey distribution or density. This apparent contradiction with theoretical predictions may be explained by a number of factors. It is possible that the spatial and temporal scales used in this research were less suitable for the detection of pre-encounter search behaviour. Perceptual range is an important aspect of search behaviour and if the perceptual abilities of the searcher are sufficiently great, these can negate the importance of prey spatial distribution on population dynamics (Fahrig and Paloheimo, 1988; Zollner and Lima, 1999). Given the well documented sensory ability of sharks, it is possible that the lack of consistent differences between treatments found here is related to the perceptual abilities of the small-spotted catsharks. It is possible that olfactory information was detected by the individuals, regardless of their position in the tank, as a result of the relatively small

dimensions of the tank. Study areas have been shown to impact upon the results of movement studies. For example, a linear relationship between the size of study areas and the distances moved by butterflies, implying study area limitation, has been found (Schneider, 2003). Therefore, the behaviours observed here may represent post-encounter, within-patch foraging behaviour. It is widely documented that within patches animals often adopt area-restricted searching behaviour consisting of shorter steps and more turns, in contrast to between patch movements that are often more directed, with fewer turns and longer steps (Baars, 1979; Carter and Dixon, 1984; Ims, 1995; Løkkeborg and Fernö, 1999; Hill *et al.*, 2002; Johnson *et al.*, 2002; Pinaud and Weimerskirch, 2007; Schtickzelle *et al.*, 2007). The movement tracks found here appear to fit this description of area-restricted search behaviour. If this is the case then the distribution and density of prey may have been too similar between treatments to be detected as different by juvenile small-spotted catsharks.

The observed random search behaviour may have been a response that enabled the individuals to harvest a patch adequately by remaining in close proximity to that patch once it was detected (Fauchald, 1999). This may also explain the small amount of movement exhibited by some individuals. Stopping and waiting may represent the best option to avoid moving out of a favourable patch when it is encountered. Similarly, juveniles may not exhibit the long ranging inter-patch search behaviours seen in adults as a result of their need to remain in close proximity to shelter or refuge, given that they are often more vulnerable to predation due to differences in body size and learned anti-predator responses (Holland *et al.*, 1993; Sogard, 1997; Krause *et al.*, 1998; Krause *et al.*, 2000a; Krause *et al.*, 2000b; Armstrong and Griffiths, 2001; Brown and Braithwaite, 2004).

Given the age of the individuals, the simple (correlated) random walk tactic may also represent an innate mechanism for searching for prey in unknown environments rather

than an emergent tactic chosen due to perceptions of local prey distribution and density. A heritable basis for movement has been documented in the literature, although most examples have been found for insects (Kent and Rankin, 2001) and birds (Hansson *et al.*, 2003). However, differences in foraging behaviour of fish have also been shown to have a genetic basis (Skúlason *et al.*, 1993).

The foraging efficiencies echo the movements, in that there were no observable differences between distributions or densities. Therefore, the use of random walk search behaviour resulted in similar success rates irrespective of the foraging situations that they were presented with. This suggests that the spatial distribution and density of prey was unimportant to the success of the individual in terms of food capture. Presumably, the level of foraging efficiency regardless of movement pattern was adequate as all of the individuals used in these studies showed body mass increases throughout the period of investigation.

The behaviour of juveniles in the experiments of this chapter contrast with that of the adult behaviour found in the studies described in the previous chapter. There are a number of possible reasons for this. Firstly, the context of the foraging situations was undoubtedly different. The adult behaviour was recorded in natural conditions as compared to the laboratory conditions used for juveniles, and thus differences are to be expected. However, it is also likely that age-related differences do exist. In addition to morphological and physiological differences there will potentially be cognitive differences as a result of different amounts of experience and associated learning. Previous research has found marked differences in movements between juvenile and adult individuals, for example (Shepard *et al.*, 2006) found that a juvenile basking shark exhibited a different periodicity of vertical (dive) movements than adults. Therefore, it is possible that the simple random search tactics employed by juvenile small-spotted catsharks in this study represent naïve behaviours. Since this tactic requires little cognitive processing (Higgins and Strauss, 2004)

it may provide a suitable base upon which search behaviour can be improved or modified through experience and ontogenetic development. The potential influence of learning and experience will be explored in a later chapter (Chapter 6). However, as well as individual differences in behaviour contributing to complex re-distribution patterns of fish, within species sex differences in behaviour also play a role. Nevertheless, the extent to which the underlying movements, and in particular the search tactics, for example, differ between the sexes has been little studied in the context of the emerging 'movement ecology' paradigm.

5 Sex differences in the movements of wild adult small-spotted catsharks

5.1 Introduction

Sexual segregation has been defined as the separation of the sexes of a particular species such that they live apart either in groups or singly (Ruckstuhl, 2007; Wearmouth and Sims, 2008). It is a phenomenon that is widespread among animals and examples have been found in many mammal, bird, reptile and fish species (Sims *et al.*, 2001; Bowyer *et al.*, 2002; Lewis *et al.*, 2002; Shine *et al.*, 2003; Croft *et al.*, 2006). There are believed to be two main types of sexual segregation: habitat and social. Habitat segregation occurs when members of different sexes differ in the use of their physical environment, whilst social segregation occurs when animals form single sex groups. These two categories are not mutually exclusive and both can co-occur. Furthermore, both can result in spatial segregation of the sexes, although this is not always the case (Ruckstuhl, 2007; Wearmouth and Sims, 2008).

Although more widely studied in terrestrial mammals (Bowyer *et al.*, 2002; Shine *et al.*, 2003), many examples of sexual segregation of fish species have also been documented. Mostly these examples of sexual segregation have been determined from sex biased catches of fish. For example, smoothhound, *Mustelus vulgaris*, landings in the western English Channel off Plymouth, UK were dominated by males and autumn landings of spurdog, *Squalus acanthias*, were female dominated (Ford, 1921). These differences in sex ratios were attributed to the presence of unisexual aggregations caused by sexual segregation (Ford, 1921). However, other studies have used differential stomach contents as an indication of different dietary preferences and hence sexual segregation (blue shark, *Prionace glauca* (McCord and Campana, 2003)).

Although identification of sexual segregation is clearly possible, determining the causes of this segregation can be more difficult. Several hypotheses have been proposed to explain sexual segregation, including the forage selection hypothesis, concerning sex differences in dietary preferences or requirements; the activity budget hypothesis, involving differences in body size and activity levels; the thermal niche-fecundity hypothesis, concerning differences in the optimal temperatures for egg and sperm development; the predation risk hypothesis, concerning differences in susceptibility to predation (in terms of both sexual body size dimorphism and care of offspring); and the social factors hypothesis, concerning social interactions between the sexes (aversion or affinity). For an in-depth review of these hypotheses and sexual segregation in marine vertebrates generally see Wearmouth and Sims (2008). Each of the hypotheses mentioned has received varying levels of support or criticism and therefore the underlying causes of sexual segregation are not fully understood (Ruckstuhl, 2007; Wearmouth and Sims, 2008). Whether there is a unifying hypothesis for the explanation of sexual segregation is heavily debated. Regardless of that contention, it is generally agreed that sexual segregation is an important factor contributing to the spatial dynamics of animal populations (Bowyer *et al.*, 2002; Shine *et al.*, 2003; Ruckstuhl, 2007; Wearmouth and Sims, 2008).

Elucidating the movement decisions made by animals is a key topic in behavioural ecology and will aid our understanding of spatial distributions of populations, including factors underlying sexual segregation (Turchin, 1991; Elliott, 2002; Sims, 2003; Sims *et al.*, 2008). Various theoretically optimal movement models have been proposed for different searching scenarios. For example, Lévy flights where move lengths are drawn from a power law distribution have been found to be theoretically optimal when prey is sparse and unpredictably distributed (Viswanathan *et al.*, 1996; Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2002; Viswanathan *et al.*, 2002; Bartumeus *et al.*, 2005). Testing theoretically optimal

movement models such as Lévy flights represents a potentially fruitful approach to gain insights into animal movements (Sims *et al.*, 2008).

Despite the advances made in the field of modelling animal movements, a key factor has not been considered. The models presented above merely describe an optimal searcher, making no distinction of the sex of the searcher, and thus making no allowances for sex differences in behaviour. Given the numerous and diverse examples of sexual segregation in nature, and the potentially differential selection pressures (and motivations) of each of the sexes, sex differences in behaviour such as the adoption of different search rules are likely. Such differences could result in unrealistic predictions if they are not accounted for by movement or search models.

In the previous chapter environmental variability did not seem to affect the search behaviour of juvenile small-spotted catsharks as predicted by theoretical models and there were also no sex-related differences in behaviour in fish of this size and at the spatio-temporal scales tested. Both juvenile males and females appeared to adopt a simple random walk search tactic irrespective of prey distribution or density. The lack of sex differences in these aspects of behaviour could potentially be due to the immaturity of the individuals. One would expect that differential selection pressures would appear as the individuals become sexually mature. Therefore, sex differences in behaviour should be more prominent in adults. Despite the broad descriptions of sex differences in space use and movements of marine fish (see Chapter 3) there is still a need to investigate the pattern and structure of their fine-scale movements that contribute to the differences in their observed space use. Thus, this chapter aims to explore the statistical properties of the movements of adult male and female small-spotted catsharks to better understand potential underlying mechanism, but in doing so also to investigate the theoretical predictions relating to optimal random search behaviour.

5.2 Methods

The movement data collected during visits to Lough Hyne that was described in a previous chapter are used again here to investigate the statistical structure of small-spotted catshark movements. For further information regarding these data see Chapter 3 (section 3.2).

Following error removal and data processing (General Methodology 2.2.6), first-passage time analyses were conducted on the movement tracks of both male and female adults to investigate tortuosity and identify scales of area restricted searching. The main scale of area restricted searching (as identified by the largest peak of variance in first-passage time) was examined for differences using a Mann-Whitney test.

Tortuosity and directionality of the movements of male and female small-spotted catsharks were also investigated through the analyses of turn angle distributions (General Methodology 2.2.6.4). In addition to calculation of circular statistics, circular histograms are presented to provide a visual representation of the directionality of movements.

Finally, step length parameters such as maximum step length and step-length distributions were investigated. Maximum step lengths were examined for sex differences using a Mann-Whitney test and step length distributions were analysed using maximum likelihood estimation (MLE) based methods to assess fits to three theoretical distributions, (exponential, power law and truncated power law – see General Methodology 2.2.6.4).

5.3 Results

For varying lengths of time up to 24 hours following release after being tagged, individuals exhibited untypical (erratic) behaviour uncharacteristic of the rest of the track, before eventually settling, either in a refuge or simply remaining relatively stationary in a particular area of the lough. To exclude any of these post-tagging effects, the first 24 hours of each track were excluded from the analyses. Of the four males tracked in 2007 and the four

females tracked in 2003, as before, only three in each year provided sufficient data for robust analysis. This is because the resolution of one of the female tracks was low since it regularly undertook movements in areas of the lough that were not detectable by the VRAP tracking system. Similarly, one of the males moved out of the detection range of the VRAP system within 24 hours of release and did not return again during the study. Therefore, no data was available for that individual. The six individuals that provided sufficient data were tracked for different lengths of time ranging from 2 to 11 days, yielding between 48 and 273 hours of track data, during which time individuals traversed between 7.5 and 56.7 km (Table 5-1 and Figure 5-1).

Table 5-1. Summary data of small-spotted catshark tracks

<i>Individual</i>	<i>Date tagged</i>	<i>Track length (km)</i>	<i>Track duration (h)</i>
F1	15/04/2003	22.9	273
F2	15/04/2003	12.5	206
F3	16/04/2003	7.9	268
M1	06/05/2007	56.7	204
M2	09/05/2007	7.5	48
M3	10/05/2007	19.8	110

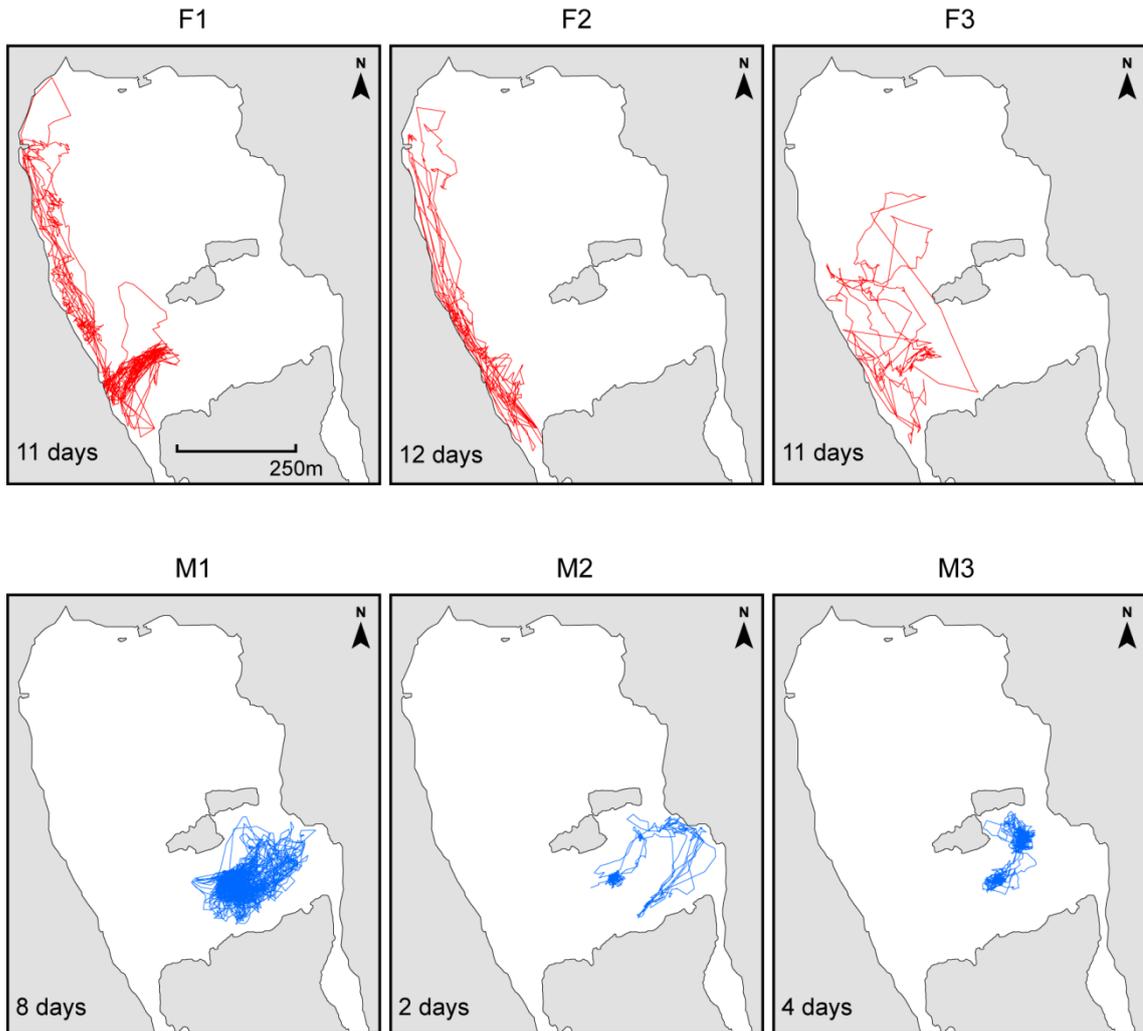


Figure 5-1. Filtered tracks of female (red lines, F1-3) and male (blue lines, M1-3) small-spotted catshark movements in Lough Hyne, Ireland during April 2003 and May 2007 respectively. Tracking periods (days) given in bottom left of each pane.

5.3.1 First passage time

The variance in first passage time (General Methodology 2.2.6.3) for males (M1-3) was relatively large and showed clear peaks at radii of 34, 24 and 20 m respectively (Figure 5-2). Further peaks in variance were also evident at radii between 40 and 230 m. In contrast, variance in first passage time for females (F1-3) was relatively low but with identifiable peaks at radii of 126, 362 and 90 m respectively. Also, there were only multiple identifiable peaks for one female (F3). Although there were no significant differences between the radii

associated with the largest peak in variance of first passage time (Mann-Whitney; $U = 2$, $Z = -1.091$, $n_1 = 3$, $n_2 = 3$, $p > 0.05$) for each of the sexes, females appeared to operate on larger scales.

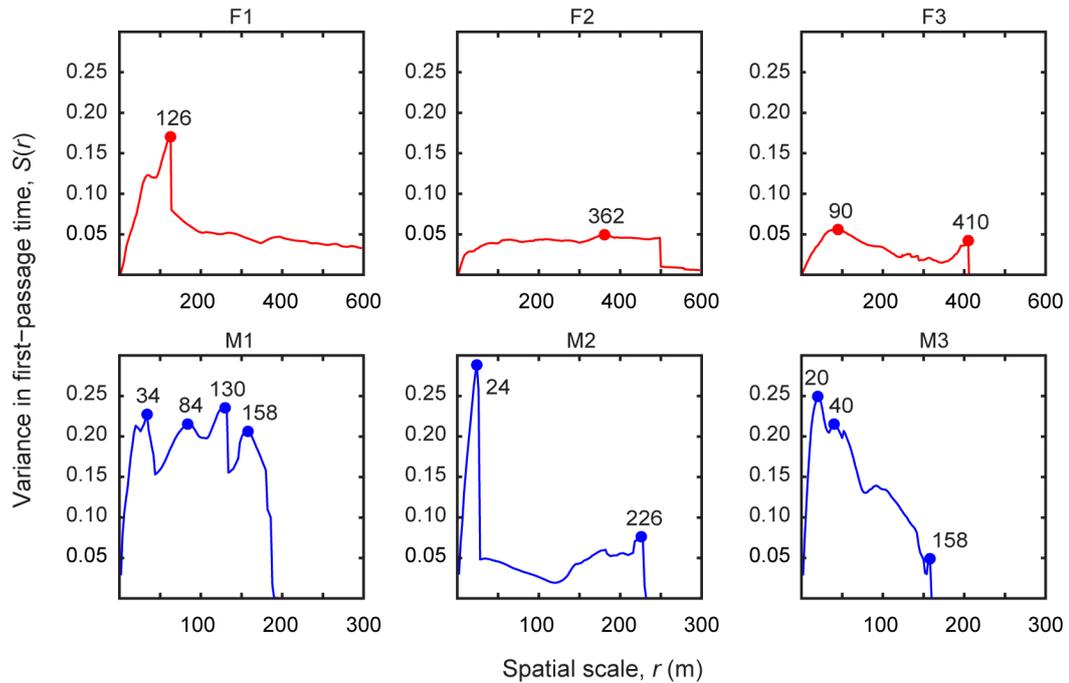


Figure 5-2. Variance in first passage time, $S(r)$, as a function of radius (r) for three female (Red, F1-3) and three male (blue, M1-3) small-spotted catshark movement tracks in Lough Hyne. Peaks in variance are marked with filled circles and labelled with the associated spatial scale.

5.3.2 Movement parameters

The distributions of turn angles in all cases were significantly different from a uniform circular distribution (Rayleigh's uniformity tests; $p < 0.05$). The turn angle distributions were also different from one another (χ^2 test $p < 0.05$). The angular means of the turn angle distributions were 170° , 332° and 1° for females F1, F2 and F3 respectively, suggesting that these individuals tended to travel straight ahead in the same direction at subsequent intervals. In contrast angular means were 176° , 176° and 182° for males M1, M2 and M3 suggesting that males frequently reversed and travelled in the opposite direction at

subsequent intervals. However, the strength of directionality was low (~ 0.1) for both males and females and was not significantly different between the sexes. This low strength of directionality indicates that the turns were not concentrated in the same direction but were more dispersed with turns of a wide range of angles being exhibited. This is further supported for females with the large confidence intervals in Figure 5-3. Although the confidence intervals for males are not as large the data are still dispersed.

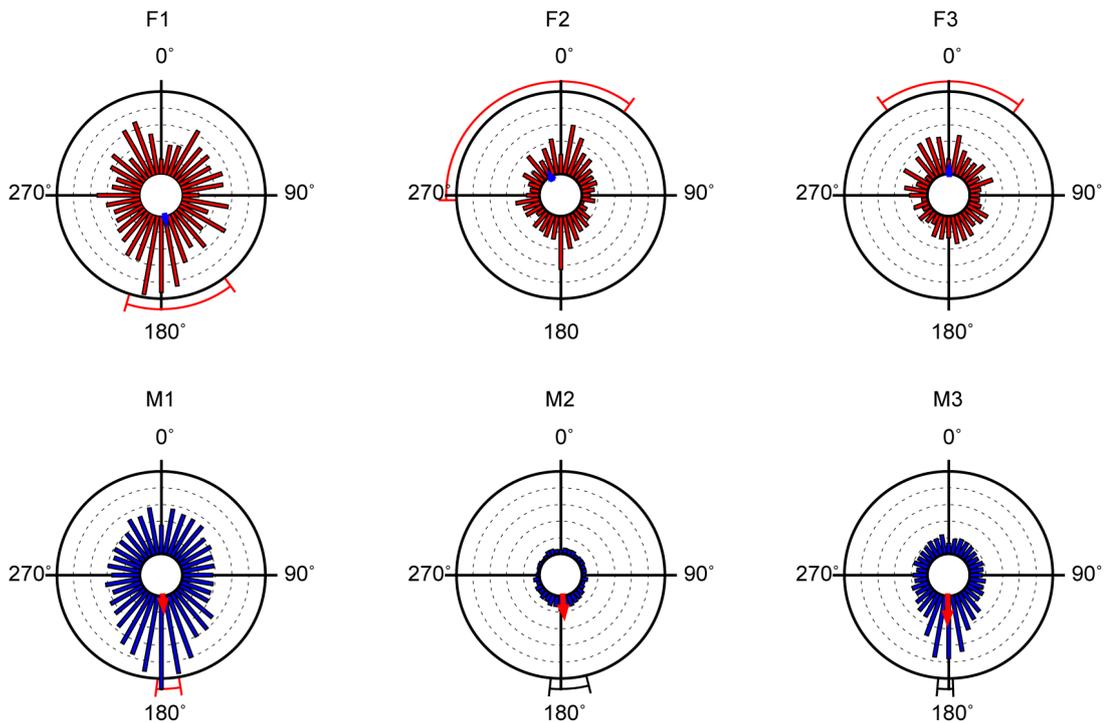


Figure 5-3. Circular frequency distributions of turn angles for female (red, F1-3) and male (blue, M1-3) small-spotted catshark movements in Lough Hyne, Ireland. Numbers on the outer circle represent degrees, the direction of the arrowheads represents the mean turn angles and their lengths represent the strength of directionality. Brackets on the outside of the circle represent confidence intervals (95%) for the mean turn angle (Red brackets indicate low reliability of mean vector). Dashed lines indicate frequency increments of 10 to a maximum of 50 for female plots (top) and 100 to a maximum of 500 for male plots (bottom).

Maximum likelihood estimation based analyses for fitting the step length distributions to various hypothetical distributions show that the step length distributions of

all individuals in this study were poorly described by an exponential distribution (Figure 5-4). The lack of fit to an exponential distribution suggests that small-spotted catsharks did not adopt purely a simple (Brownian) random walk tactic throughout the period of tracking.

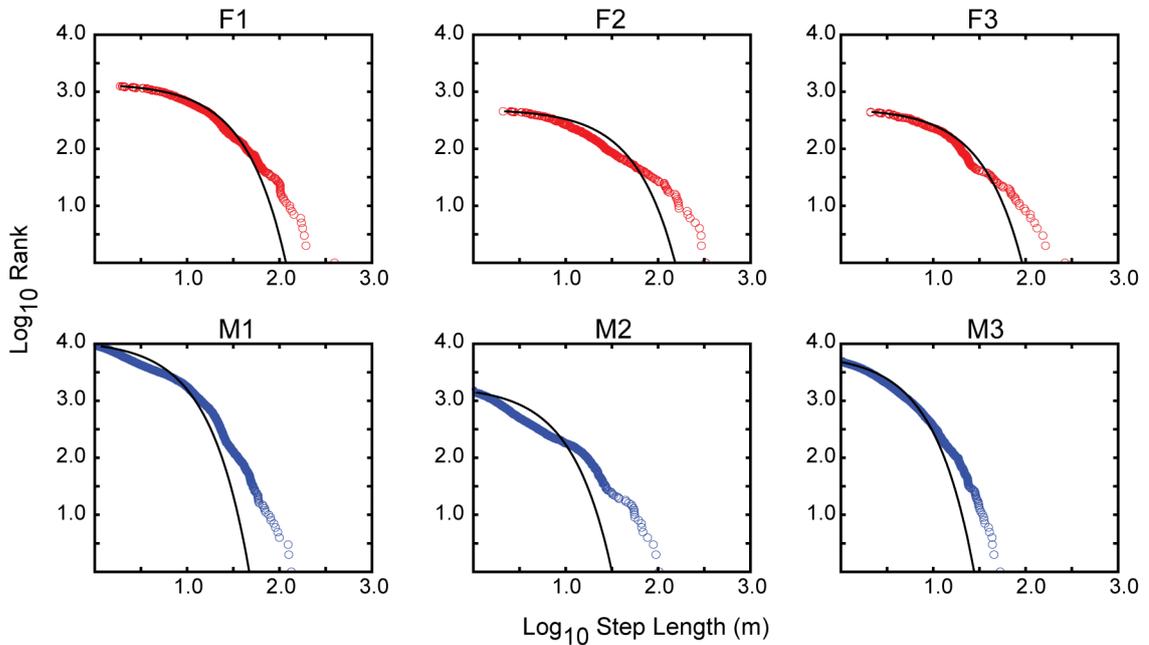


Figure 5-4. Results of MLE based analyses showing frequency distributions of move lengths as best fits to exponential (random) distributions for female (red, F1-3) and male (blue, M1-3) small-spotted catsharks movements in Lough Hyne, Ireland. Circles indicate empirical data and lines represent best fit lines to an exponential distribution above x_{\min} . For more details see general methodology.

Similarly poor fits were found between the empirical step length data and hypothetical power law distributions (Figure 5-5). Hence, it does not appear that free-ranging small-spotted catshark movements are consistent with a pure power law model of movement either. In fact, the fits to a power law were far worse than those observed for an exponential distribution, with only smaller move steps within the empirical move step distribution conforming to a power law-like pattern.

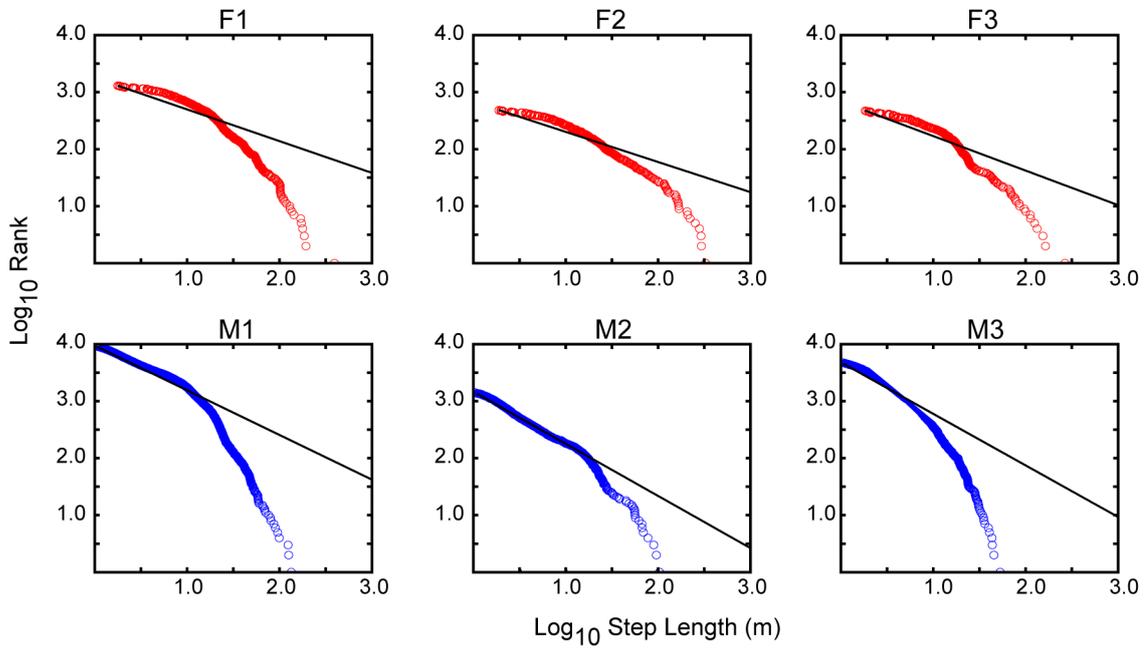


Figure 5-5. Results of MLE based analyses showing frequency distributions of move lengths as best fits to power law distributions for female (red, F1-3) and male (blue, M1-3) small-spotted catsharks movements in Lough Hyne, Ireland. Circles indicate empirical data and lines represent best fit lines to a power law distribution above x_{\min} . For more details see general methodology.

Fitting of a truncated power law distribution (Pareto distribution) gave exponents within the Lévy range of between 1 and 3 for all but one of the individuals (F3) (Figure 5-6). Females had lower exponent values closer to 1, whereas males had higher values closer to the hypothesised optimal Lévy exponent of 2. Despite this result, two of the female tracks and one of the male tracks showed some departures from the hypothesised model fit for a truncated power law distribution (indicated by arrows). These departures were likely to be a consequence of there being more complex distributions or composites of two or more distributions within the datasets (Humphries *et al.*, Submitted).

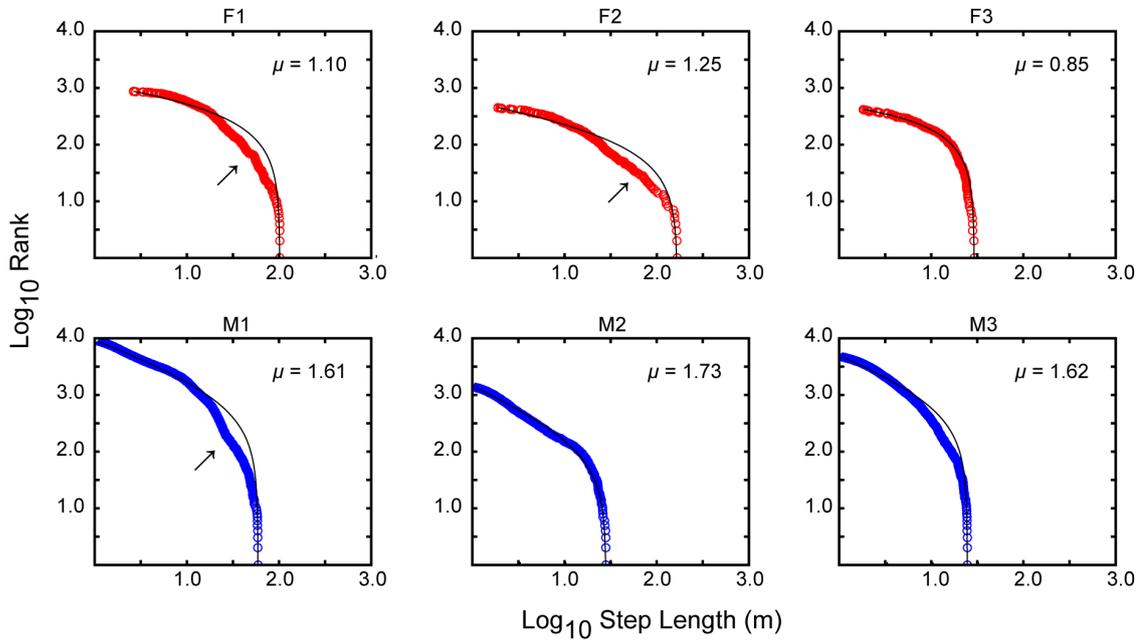


Figure 5-6. Results of MLE based analyses showing frequency distributions of move lengths as best fits to truncated power law distributions for female (red, F1-3) and male (blue, M1-3) small-spotted catsharks movements in Lough Hyne, Ireland. Circles indicate empirical data and lines represent best fit lines to a truncated power law distribution between x_{\min} and x_{\max} . The scaling parameter (μ) for each model fit is given in the top right of each plot. For more details see general methodology.

The maximum step lengths performed by each of the individuals showed considerable variation between individuals with a range from just under 55 m for M3 to nearly 617 m for F1 (Table 5-2). However, despite this variation a clear pattern of differences between the sexes emerged. All females performed longer maximum step lengths than males, in fact the shortest maximum step length performed by a female was still 133 m longer than the longest maximum step performed by a male (F3 compared to M1; Table 5-2).

Table 5-2. Summary of the data used and MLE results of step-length distribution analyses for female (F1-3) and male (M1-3) small-spotted catshark movements in Lough Hyne, Ireland.

<i>Parameter</i>	<i>Females</i>			<i>Males</i>		
	<i>F1</i>	<i>F2</i>	<i>F3</i>	<i>M1</i>	<i>M2</i>	<i>M3</i>
Distance (km)	21.0	12.5	7.9	56.7	7.5	19.8
No. Steps	5046	2076	5356	9899	1501	4962
Maximum step length (m)	616.96	327.73	266.73	134.24	106.48	54.71
Minimum step length (m)	1.78	1.78	1.84	1.00	1.00	1.00
Best fit distribution	TP	TP	TP	TP	TP	TP
Best fit exponent (μ)	1.100	1.248	0.852	1.607	1.733	1.619
x_{\min}	2.637	1.892	1.837	1.004	1.004	1.004
Goodness of Fit (D)	0.134	0.129	0.048	0.042	0.065	0.087
p -value	0.000	0.000	0.000	0.000	0.000	0.000
x_{\max}	102.27	167.60	29.37	59.24	27.45	23.79
No steps larger than x_{\max}	14	8	37	18	30	35
% steps larger than x_{\max}	0.28	0.39	0.69	0.18	2.00	0.71

5.4 Discussion

One of the principal aims of this chapter was to investigate possible sex differences in the statistical structure of movements of a free-ranging marine predator, the small-spotted catshark. Fine-scale, high resolution movement data for free ranging marine predators is difficult to obtain as a result of the relative inaccessibility of their environment. However, telemetry technology such as the automated acoustic tracking used in this study facilitates data collection for marine animal movements. In this study the temporal and spatial resolution of the data collected was high, with positions being recorded roughly every 2 minutes, down to 0.5 m accuracy, for periods of up to 12 days. Using this data and a variety

of processing and analytical techniques the movement tracks of six adult small-spotted catsharks, three of each sex, were reconstructed and investigated. The results show clear differences between the sexes with respect to their movements. Distributions of turn angles for female movements showed that, in general they tended to travel in the same direction with each successive step, although this pattern was at times weak during a track. Furthermore, females frequently performed long steps/moves that were interspersed with much smaller steps. In contrast, males tended to reverse direction with each successive step (again this tendency was sometimes weak), and made fewer long steps.

A pattern of movement that is consistent with a power law such as the Lévy distribution has been hypothesised to be the optimal solution for an animal searching for sparse, patchily distributed resources (Bartumeus *et al.*, 2002). Broadly, the movement statistics of both male and female tracks resembled the hypothetical Lévy like pattern. Both males and females performed varying frequencies of long steps interspersed with more frequent smaller steps, with this occurring at different scales. However, these movements did not conform to a pure power law, perhaps understandably (see Sims *et al.*, 2008), as there was considerable truncation in the distribution of step lengths of both sexes. Given the nature of the Lévy distribution used in the Lévy flight hypothesis (and that of power law distributions generally), this was expected. A true Lévy flight consists of instantaneous jumps that can be infinitely long (Shlesinger *et al.*, 1993; Viswanathan *et al.*, 1996; Viswanathan *et al.*, 1999; Viswanathan *et al.*, 2002; Klafter and Sokolov, 2005; Bartumeus, 2007). In natural systems, such as the movement of animals this is clearly impossible since it takes time for an animal to cover distances and animals live within bounded environments (even if those boundaries are quite large e.g. ocean basins).

A key feature of the power law distribution is the heavy tail caused by infrequent long steps; therefore, animal movements that are characterised by infrequent long steps

may resemble a power law distribution within bounds (Humphries *et al.*, Submitted). The truncated power law distribution (or truncated Lévy flight) eliminates the arbitrarily large steps of the Lévy distribution (Mantegna and Stanley, 1994; Bruno *et al.*, 2004). Therefore, this distribution is more suitable than a pure power law for identifying possible Lévy-like search behaviour when analysing animal movements. In this chapter, results of the maximum likelihood estimation (MLE) based methods for analysing move-length distributions show that the best fit distribution to the empirical data was the truncated power law in all cases, suggesting Lévy-like behaviour. Further support for this suggestion is provided by the fact that exponent values were generally within the Lévy range of 1 to 3. However, this is where a key difference between female and male movements arises. Exponent values for males were generally close to the theoretical optimum value of 2 and the fits to a truncated power law were visually very good. However, exponent values for females were closer to 1 indicating more directed, ballistic movement, and the fits were visually poorer with some departures from the hypothetical distribution evident in the plots. Analyses of the turn angle distributions were also in accordance with this and reflected the differences in step length distributions. Mean turn angles of female tracks (170° , 332° and 1°) suggested that females tended to travel in the same direction over successive steps. In contrast mean turn angles for male tracks (176° , 176° and 182°) suggested that males frequently reversed direction between successive steps. Despite this, the strength of directionality was low indicating that turns in many different directions were common. Interestingly, a uniform distribution of turn angles is another feature of a pure Lévy flight.

The departures of step length distributions of female tracks from the hypothesised Lévy-like search pattern (represented by a truncated power law) indicate that the distributions of female step lengths may be quite complex and are likely to represent a

composite of more than one distribution. This assertion is further supported by results of recent simulations conducted by Humphries *et al.* (submitted) that showed that composite tracks consisting of two different model distributions, representing two different movement patterns, gave poor fits to the best fit truncated power law (Pareto) model. Furthermore, they found that the fits to some empirical datasets from differing fish species resembled the poor fits of the simulated data. These poor fits also resemble those found here for female small-spotted catsharks. Given that whole tracks including the movements over several days were analysed it is reasonable to suggest that behaviours other than stochastic searches would have taken place within these time periods. Since the Lévy flight hypothesis concerns optimal random search behaviour, it does not strictly account for these other behaviours that, in some cases, may be deterministic in nature. The long directed steps performed by females may have been a commuting phase of a pre-planned round trip to a particular location that was known to be profitable in terms of prey availability as a result of previous successful experiences associated with that location. Once at the location the females may have adopted a random search pattern, but given the potential amalgamation of two or more distributions within the whole track it is difficult to confirm or reject this idea. One way would be to separate the tracks manually into sections representing different behaviours and to analyse them individually.

In order to analyse sections of the track independently, sound judgement of how to break up the tracks based on pre-existing knowledge of the animal and the environmental context is required. However, the resulting sections may still not be suitable for analysis. The MLE based methods used here to identify Lévy like behaviour require a minimum of 500 steps to provide a suitably robust analysis. This is because, when there are fewer than 500 steps, large statistical fluctuations are likely to occur. These fluctuations can lead not only to poor fits to hypothesised distributions, but more importantly to inaccuracies in the

estimation of exponents for those fits (Bradshaw *et al.*, 2007; Sims *et al.*, 2007; White *et al.*, 2008). In this study the separation of the tracks into discrete foraging trips did not yield data suitable for application of these techniques, since the number of steps for each of the resulting sections was well below 500 in most cases (Chapter 3).

It has been documented previously that male and female small-spotted catsharks segregate spatially at the study location in Lough Hyne (Sims *et al.*, 2001). Furthermore, spatial segregation by sex has been found for this species in other areas such as the Cantabrian Sea (Rodriguez-Cabello *et al.*, 2007). This spatial separation of sexes could be a consequence of different movement patterns. For example, the sexes may move in such a way as to reduce contact with each other for much of the time or, conversely to solicit contact, resulting in either aggregation or segregation of the sexes. Equally, the use of different habitats may result in the requirement of different movement patterns by the sexes for their adequate exploitation.

In conclusion, this chapter has analysed the high resolution movement data of both male and female small-spotted catsharks in the natural environment. The main focus of this chapter has been the sex related differences in the structure of movements. The distributions of turning angles for all individuals were all significantly different from a circular normal distribution but mean vectors for females were generally straight ahead, whereas the opposite was true for males with frequent reversals being a key feature. Despite this, directionality was low for both males and females. In terms of step lengths, females exhibited larger maximum step lengths than males, although males tended to travel greater distances (daily) as a result of a greater number of smaller steps. The step length distributions were also generally different between sexes. All distributions were best-fit by a hypothesised truncated power law distribution, however these fits were generally poorer for females and exponents were lower than those found for males. These results indicate

that the sexes performed different movement patterns and therefore suggest that they employed different search tactics. Furthermore, the departures from theoretically optimal random search models are in accordance with the findings of the previous chapter: that is, it is likely these patterns were a consequence of a degree of determinism in the movements and search behaviour of small-spotted catsharks. These results therefore lend support to the idea that small-spotted catsharks may be capable of spatial memory and learning, a topic which is explored in controlled learning experiments for juvenile small-spotted catsharks in the following chapter.

6 Ontogenetic development and learning of search behaviour

6.1 Introduction

Learning can play an important role in the foraging behaviour of animals for a number of reasons. Firstly, learning how to forage through alterations of the foraging skills associated with prey encounter and capture can improve foraging efficiency. For example, increased experience of certain prey types can lead to decreased pursuit and handling times, resulting in increased foraging efficiency (Beukema, 1968; Ware, 1971; Croy and Hughes, 1991). Similarly, learning about foraging through the gathering and processing of information concerning the quality of foraging habitats or patches can also lead to increased foraging efficiency, since low quality or depleted patches can be avoided and the location of high quality patches can be remembered. For example, nectar feeding bats can learn to avoid depleted locations after unsuccessful visits (Winter and Stich, 2005). Furthermore, learning to recognise conspecifics can also lead to greater foraging efficiency for a number of reasons including cooperation (predator vigilance), information transfer (Swaney *et al.*, 2001), and reduced competition for resources as a result of familiarity, either through reduced aggressive interactions or avoidance of particular competitors (Utne-Palm and Hart, 2000; Griffiths, 2003).

The former example is achieved through spatial memory, as the bat learned the locations of profitable and unprofitable locations and used this cognitive map to guide its future behaviour. There are numerous examples of the use of spatial memory during foraging for a wide range of taxa (Benhamou *et al.*, 1990), including insects such as bumblebees, *Bombus impatiens* (Burns and Thomson, 2006), mammals such as bats (Winter and Stich, 2005), birds such as the common murre, *Uria aalge* (Davoren *et al.*, 2003), and fish such as goldfish, *Carassius auratus* (Pitcher and Magurran, 1983; Warburton, 1990) and

the goby, *Bathygobius soporator* (Aronson, 1951; 1971). Spatial memory of prey patches can be formed in different ways: firstly, a location may be memorized using an egocentric process whereby the animal remembers the route taken to get to that location in relation to its position; secondly, a location may be memorized by using local landmark clues independent of the individual's own position in what is known as an exocentric coding process (Benhamou *et al.*, 1990). The clues used in an exocentric process can come in a variety of forms including both visual and olfactory clues (Warburton, 2006).

Despite the advantages that learning can provide to foraging animals, certain conditions can reduce the importance of learning for foraging success. For example, spatial memory with knowledge of the locations of profitable patches and of landmarks can only be beneficial if those patches or clues remain in the same place for certain lengths of time. This has led to the idea that the influence of learning on habitat selection should be enhanced when the profitability of habitats does not vary much within the lifetime of the animal but varies markedly between generations (Stephens, 1993; Segura *et al.*, 2007). Conversely, spatial memory and learning is not expected to be as beneficial in highly dynamic and unpredictable environments.

Another drawback of learning concerns the cognitive processing capabilities required for effective learning. Although, there are numerous examples of impressive cognitive capacities of a wide range of taxa, the benefits of dealing with large quantities of complex information may be nullified in certain scenarios. For example, when the environment is highly heterogeneous both spatially and temporally, simple search rules may facilitate comparable or enhanced success when compared to learned behaviours. Increased experience can lead to increased foraging efficiency (Werner *et al.*, 1981; Gibbons *et al.*, 2005; Hewitson *et al.*, 2005; Winter and Stich, 2005; Burns and Thomson, 2006), but if that

experience is variable and unpredictable then its value may be expected to be lower (especially for spatial memory formation).

Despite the attention learning in fish has received in the literature (reviews by (Hughes *et al.*, 1992; Kieffer and Colgan, 1992), there is little information concerning learning in relation to movement parameters whilst foraging in elasmobranchs. This chapter investigates the possibility that learning leads to greater foraging success of small-spotted catsharks, and also the potential effect of differences in previous experiences of foraging behaviour. It was expected that foraging efficiencies would increase over time, and that previous experiences of temporally stable prey distributions would lead to greater improvements in foraging efficiency than temporally variable prey distributions. It was also expected that changes in foraging efficiencies would be related to differences in search tactics used whilst foraging.

6.2 Methods

6.2.1 Prey distribution experiment

The first experiment of this chapter consists of a repeat of an experiment performed as part of a previous chapter (Chapter 4, section 4.2.1). This repeat used the same ten individuals and the same procedure as the first, but was undertaken roughly three months after the conclusion of the first experiment in October and November 2007. The purpose of this experiment was to determine whether age and experience can influence future foraging behaviour and thus formed the pilot experiment for the main focus of this chapter.

6.2.2 Learning experiment

This experiment was designed to examine further, the possibility that previous experience influences foraging behaviour in juvenile small-spotted catsharks. Learning experimental trials were conducted over a six week period commencing in October 2008. For these trials, a new group of ten size-matched, male small-spotted catsharks were used (*TL* range: 194-231 mm). Prior to the period of experimental trials these ten males were transferred to individual holding pens within a large experimental tank (length, 480 cm; width, 170 cm; depth, 50 cm) with re-circulating seawater to acclimatize to the experimental tank conditions.

In contrast to previous experiments that used the prey array and pieces of cut-up squid as prey items, this experiment did not use the prey array or squid prey items. Instead, small marine pellets (6 mm³) were placed on the bottom of the test arena in a number of different spatial arrangements. Since these pellets were used as part of their maintenance diet (General Methodology section 2.3.2), the juvenile small-spotted catsharks were well acclimated to this source of food. In total, seven different spatial arrangements consisting of ten prey items were used, each determined using a random number generator to create ten sets of coordinates for each pattern (Foraging Lab program, MBA 2009). These coordinates were based on a grid pattern that divided the test arena into grid squares measuring 4.13 cm x 4.13 cm.

This experiment consisted of three phases: the initial testing phase, the training phase and the final testing phase. The ten males were divided into two groups of randomly selected individuals. In the initial testing phase, individuals from one of these groups were allowed to forage (solitarily) in the test arena amongst a randomly distributed prey field containing 10 prey items (pellets) for a period of two hours. Individuals from the other group were also allowed to forage solitarily in the test arena for a period of two hours.

However, the spatial arrangement of prey was different to that of the previous group. In the training phase, the individuals from one of the groups were allowed to forage solitary with the same spatial arrangement of prey as before, once a week for four weeks. However, individuals from the other group were exposed to a different spatial arrangement of prey each week, which was never the same as that of the group experiencing a constant spatial arrangement of prey. In the final testing phase, both groups were allowed to forage with the same spatial arrangement of prey. This final arrangement was the same as the one that was constant for one of the groups throughout the entire experiment (Figure 6-1).

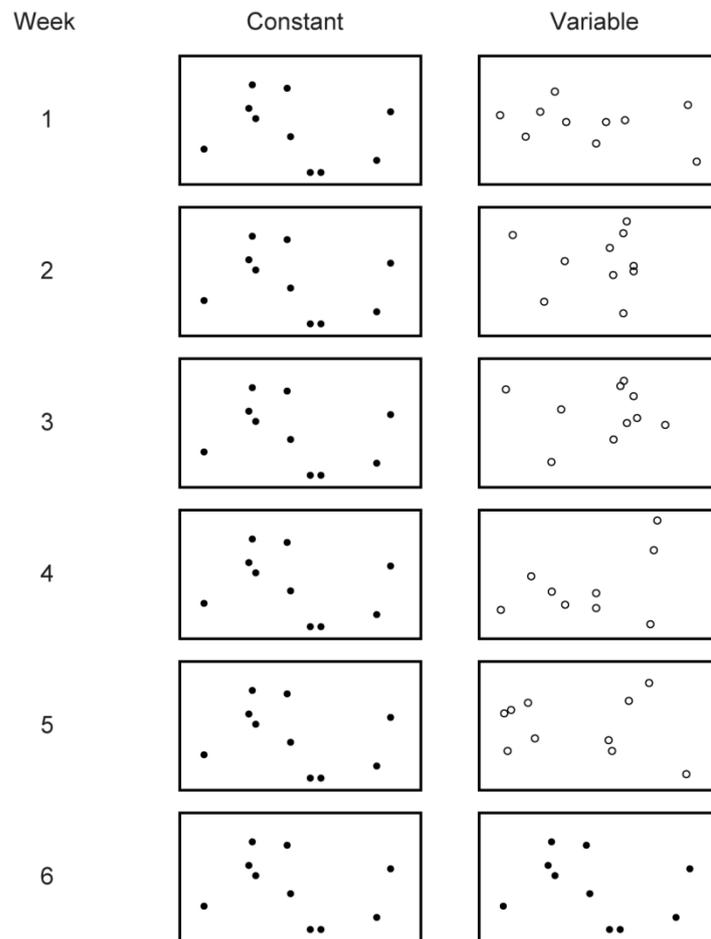


Figure 6-1. The spatial arrangements of prey used throughout a learning experiment concerning the movements and foraging behaviour of juvenile male small-spotted catsharks. Individuals were either allowed to forage each week within a constant spatial arrangement of prey (the same at the start of each trial; left, filled circles), or a variable arrangement of prey (right, unfilled circles). In the final week (6) all individuals were allowed to forage within the constant spatial arrangement of prey (filled circles).

Prior to each individual trial the appropriate prey arrangement was established on the tank bottom. This was achieved by using a scaled grid, equivalent to that used to determine each prey pattern, drawn onto an OHP slide. This grid was placed on the video monitor showing a live image of the tank allowing prey pellets to be placed in the correct position using the grid on the monitor as a reference.

Once the prey arrangement was established and the water surface was flat calm, one individual was transferred to an acclimation chamber within the test arena. After approximately 60 minutes the acclimation chamber was removed and the trial began. After two hours the individual was removed from the arena and placed back in the holding pen. The appropriate spatial arrangement of prey was subsequently re-established ready for the next trial. Each individual was only used in one trial per week and there were exactly seven days between trials on the same individual. Individuals that did not consume all of the prey during the trial were given the remaining prey in the holding pen. The ten prey items weighed roughly 2-3 g in total, representing around 15 % of their body weight, so individuals were not fed between trials.

6.2.3 Data acquisition and analyses

Prior to the start of each trial a single individual was transferred to an acclimation chamber within the experimental arena, where the appropriate prey arrangement was already established. After approximately 60 minutes the acclimation chamber was removed and the trial began. Movement data were recorded by a computer aided video monitoring system (General Methodology 2.3). Post acquisition, data were first edited to remove a small number of clearly erroneous positions that were likely caused by light reflections on the surface of the water, or more rarely, when an object other than the fish was detected by the software. These tracks were then further processed with a minimum distance moved filter

to remove very small movements that were recorded when it was clear from the video that the animal was stationary.

Following data processing a number of parameters for each of the trials were calculated. These included basic path statistics such as distances travelled, the variance of first passage time throughout the track, circular statistics of turn angles (including mean vectors and length of mean vectors), exponents of step length distributions (determined using maximum likelihood estimation techniques) and prey capture events (see General Methodology).

Space use was investigated as the proportion of time spent within a central area (190 x 140 cm) within the test arena. This central area was chosen to encompass the areas where food was available and to exclude any time spent searching the boundary of the arena not directly related to foraging.

Finally, foraging efficiency was also determined for each trial using the total number of prey captured divided by the total distance traversed by that individual during the trial. Mixed repeated measures ANOVAs were used as appropriate following testing of assumptions of normality and equal variances to investigate differences between treatments, time and sexes (prey distribution experiment) or experience (learning experiment).

6.3 Results

6.3.1 Prey distribution experiment

The individuals were all significantly larger in terms of both body mass and length in the repeated experiment (ANOVA, $F_{1,8} = 1083.19$, $p < 0.01$ and $F_{1,8} = 473.33$, $p < 0.01$). There were no differences between sexes in either length or mass measurements ($F_{1,8} = 0.023$ and $F_{1,8} = 0.248$, both $p > 0.05$; Figure 6-2).

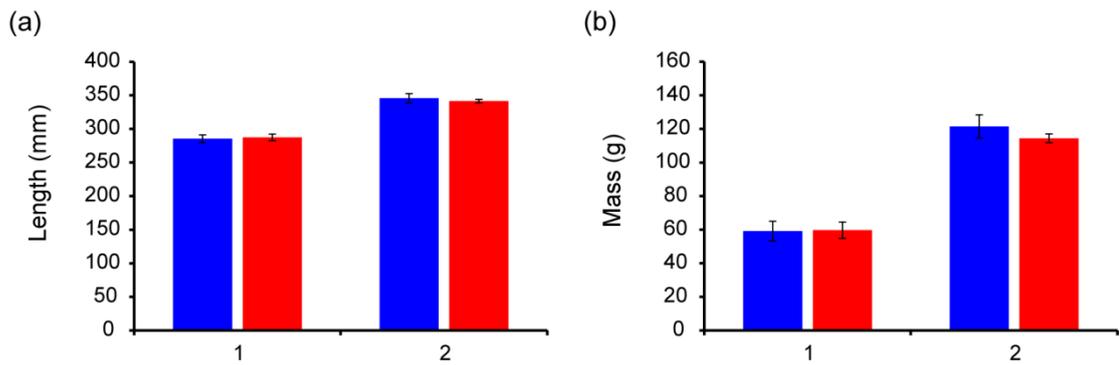


Figure 6-2. Morphometric changes for juvenile male (blue) and female (red) small-spotted catsharks between the start of the first foraging experiment (1) and the repeated experiment (2) three months later. (a) Length differences in mm; (b) Mass differences in g. Error bars indicate standard error of the mean values (S.E.).

Over the course of the experiment foraging behaviour varied widely with some individuals exhibiting lots of movement throughout trials in all treatments whereas others moved less in particular trials (Appendix 1 and 2). The general movement patterns of the repeated set of trials at time 2 were similar to that of the initial set of trials (Chapter 4, Figure 4-3). Generally, less movement was observed in control trials as opposed to treatments with prey (Figure 6-3).

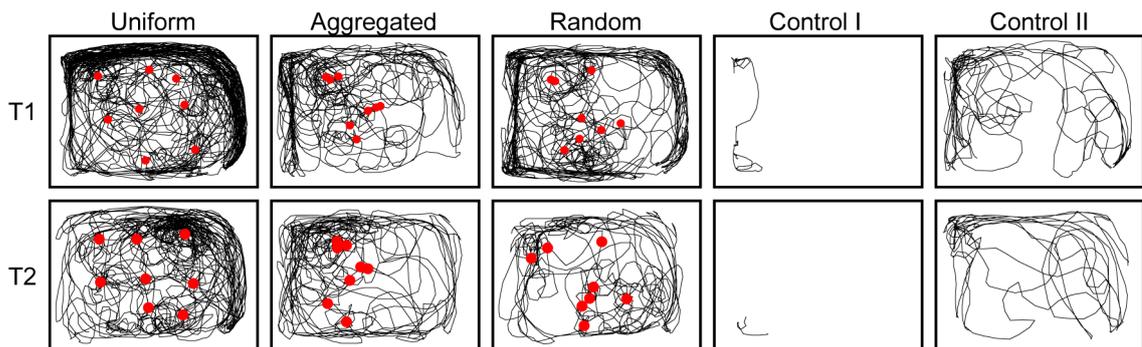


Figure 6-3. Movements exhibited by a male small-spotted catshark (M3) whilst foraging within three different prey distributions in an experiment (T1) that was repeated after a period of 3 months (T2). Movements are also shown for control trials where no prey was available and an olfactory stimulus (squid juice) was not introduced (control I) or was introduced at the start of the experiment (control II).

During trials with different prey distributions, individuals spent variable amounts of time within a central area of the test arena. Proportions of time spent within this central area were generally low (overall mean = 0.16 ± 0.17) and there were no significant differences between prey treatments (ANOVA; $F_{2,16} = 0.352, p > 0.05$), sexes ($F_{1,8} = 0.448, p > 0.05$) or times ($F_{1,8} = 1.738, p > 0.05$, Figure 6-4).

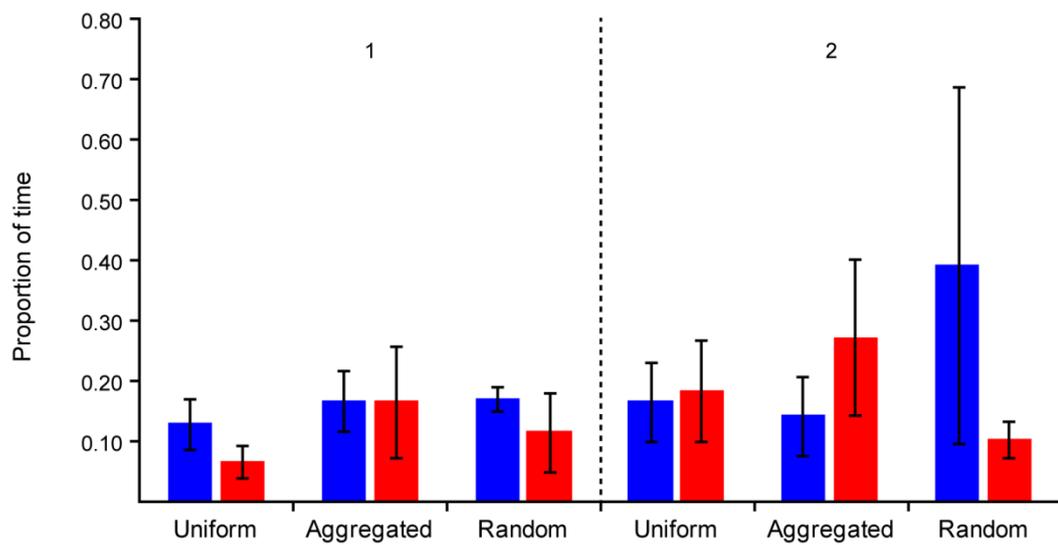


Figure 6-4. Mean (\pm S.E.) proportion of time (arcsine transformed) male (blue) and female (red) small-spotted catsharks spent in the central area of the tank during foraging trials with different prey distributions (uniform, aggregated and random) as part of an experiment (1) that was repeated after a period of three months (2).

Scales of area restricted search (ARS) identified by first passage time analysis were also highly variable across all trials with values ranging between 2 cm and 266 cm. Despite this variability, significant differences were found between treatments with larger ARS scales being found in control trials for both the initial and repeated trials (ANOVA on ranks; $F_{4,28} = 3.755, p < 0.05$). There were no significant differences between ARS scales for each of the sexes ($F_{1,7} = 0.280; p > 0.05$) and there were also no differences between ARS scales in repeated trials at time 1 and 2 ($F_{1,7} = 1.589; p > 0.05$, Figure 6-5).

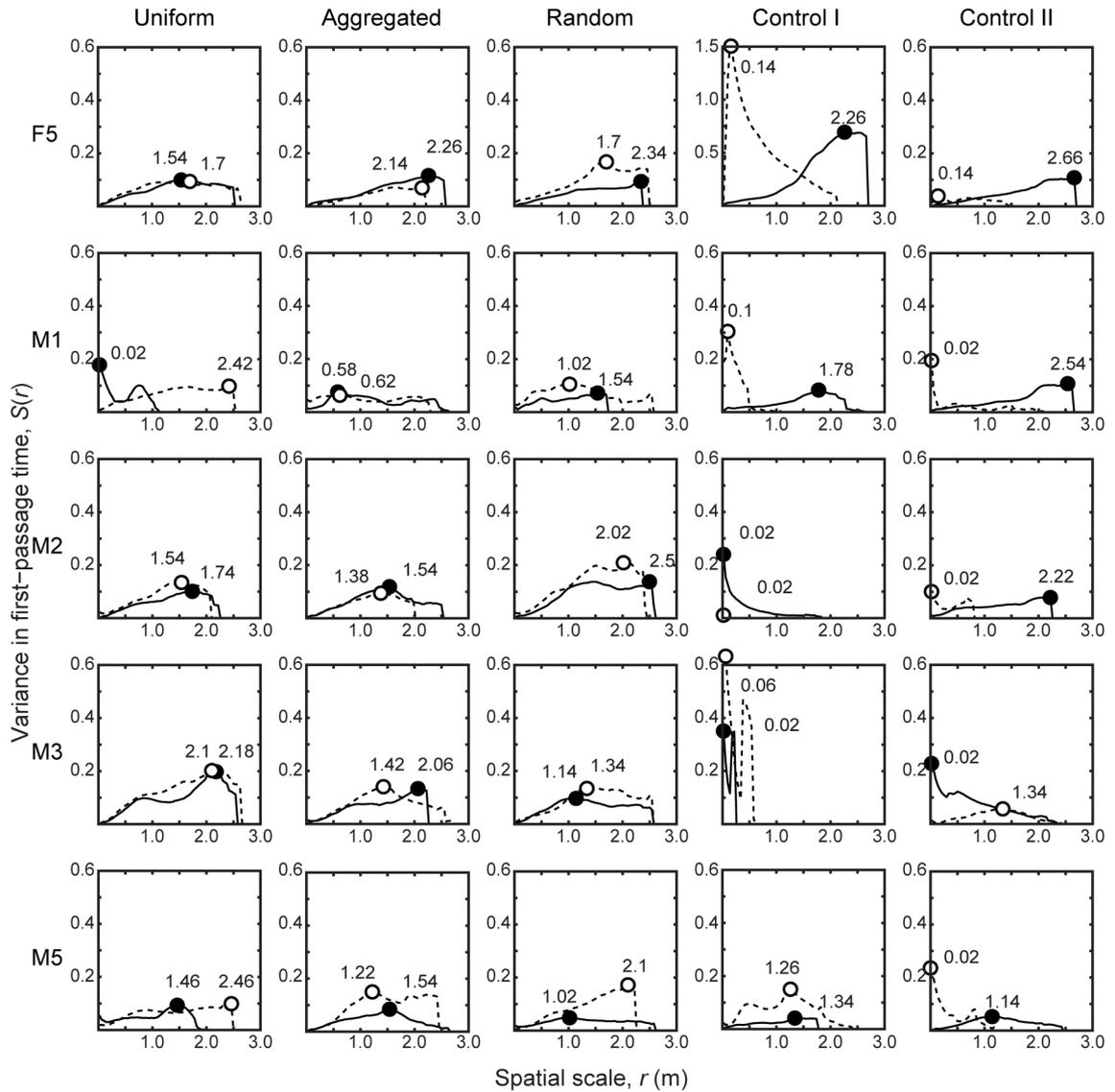


Figure 6-5. The variance in first passage time, $S(r)$, as a function of radius (r) for the movement tracks of selected small-spotted catsharks (F5, M1-3, 5) whilst foraging. Solid lines and filled circles indicate the initial experimental results at time 1; dashed lines and open circles indicate results for the repeat experiment at time 2, three months later. Peaks identified by circles represent scales of area restricted searching (ARS).

Turn angle distributions of movements continued the trend of high variability with 86 % of all trials differing significantly from a normal circular distribution (Rayleigh's uniformity tests, $p < 0.05$). Of the remaining 14% that were not significantly different from a normal circular distribution, roughly 57 % (8 % of trials) were for movements conducted during control trials. All of the trials in which turn angle distributions were not found to differ from normal, had similarly limited movements resulting in a small number of samples to perform the analyses (mean of 228.8 compared to the mean of 1562.9 for the trials that were significantly different from normal).

The grouped mean turn angles were generally centred ~~o~~indicating that the individuals tended to travel straight ahead (Figure 6-6). However, there was considerable variability (as indicated by the confidence limits in Figure 6-6) with the strength of directionality varying between 0.01 and 0.98. Overall, there was a significant interaction between time and treatment for the strength of directionality (ANOVA on arcsine transformed data; $F_{4, 28} = 3.642, p < 0.05$) that was attributed to the movements during controls having weaker directionality in the initial set of trials and greater directionality in the repeated set of trials.

Due to the limited movements of a number of individuals throughout the entire experiment MLE analyses of step length distributions could only be performed on data from 5 individuals. These were active in all trials with each of the prey distributions for both the first and the repeated experiments. Summary results of these analyses, given in Table 6-1, show that the step length distributions were generally best fit by an exponential (E) distribution, indicating random foraging movements. However, the step length distributions of three individuals (M1, M2 and M3) best fit a truncated power law (TP) distribution in some of the trials. Despite this exponent values of fits to the truncated power law indicate ballistic movements (~ 1) in all three cases.

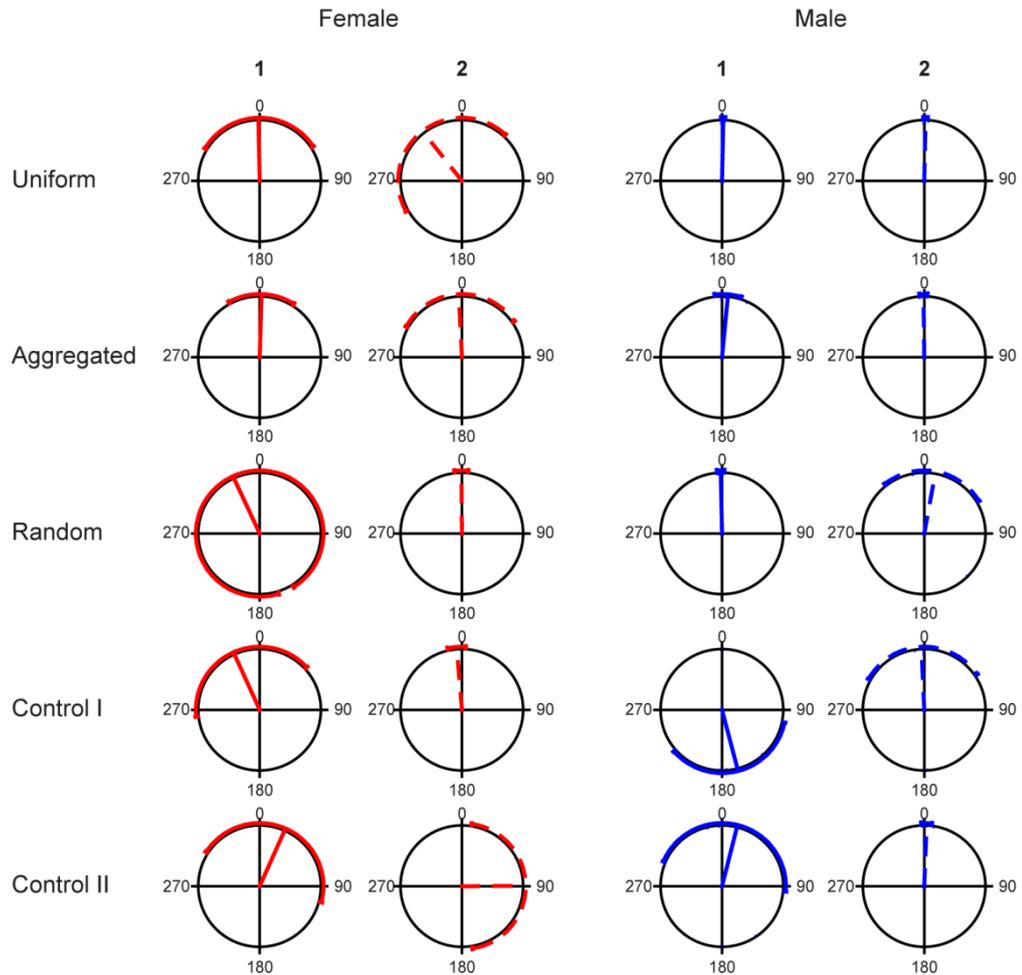


Figure 6-6. Grouped mean turn angles exhibited by female (red, $n = 5$) and male (blue, $n = 5$) juvenile small-spotted catsharks during foraging trials with different prey distributions (uniform, aggregated and random) and two controls with no prey (control I: no olfactory stimulus introduced; and control II: olfactory stimulus introduced at the start). Solid lines indicate results of the first set of trials at time 1 and dashed lines indicate results for the repeated trials at time 2, three months later. Confidence limits (95 %) are indicated by the size of the brackets around the plot perimeter.

Table 6-1. Summary of the data used and MLE results of step length distribution analyses for selected juvenile small-spotted catshark movements during foraging trials (1) with three different prey distributions that were repeated after a time interval of three months (2).

<i>Time</i> (Exp)	<i>Treatment</i>	<i>Individual</i>	<i>Distance</i> <i>travelled (m)</i>	<i>Max. step</i> <i>length (m)</i>	<i>Best fit</i> <i>distribution</i>	<i>Best fit</i> <i>exponent</i>	<i>Xmin</i>	<i>GOF</i>	<i>P-value</i>	<i>Xmax</i>
1	Uniform	F5	512.60	0.261	E	4.870	0.010	0.089	0	N/A
		M1	173.00	0.250	E	6.573	0.040	0.065	0	N/A
		M2	174.14	0.521	E	6.352	0.049	0.083	0	N/A
		M3	468.44	0.376	TP	0.770	0.031	0.128	0	0.617
		M5	142.34	0.186	E	5.911	0.031	0.055	0	N/A
	Aggregated	F5	482.26	0.353	E	4.389	0.031	0.053	0	N/A
		M1	59.30	0.431	E	5.959	0.029	0.060	0	N/A
		M2	302.95	0.345	E	4.820	0.022	0.112	0	N/A
		M3	183.23	0.306	E	6.907	0.049	0.107	0	N/A
		M5	430.10	0.434	E	4.468	0.029	0.022	0.108	N/A
	Random	F5	259.85	0.227	E	6.165	0.022	0.093	0	N/A
		M1	130.44	0.256	E	6.466	0.049	0.113	0	N/A
		M2	192.76	0.220	E	6.832	0.035	0.100	0	N/A
		M3	256.88	0.388	E	5.801	0.031	0.108	0	N/A
		M5	404.84	0.372	E	4.784	0.031	0.049	0	N/A
2	Uniform	F5	415.61	0.256	E	4.699	0.022	0.063	0	N/A
		M1	18.79	0.201	E	6.170	0.029	0.070	0	N/A
		M2	171.04	0.381	E	6.131	0.039	0.095	0	N/A
		M3	271.23	0.480	TP	0.860	0.040	0.137	0	0.441
		M5	59.20	0.183	E	6.392	0.049	0.057	0	N/A
	Aggregated	F5	459.27	0.572	E	4.787	0.022	0.070	0	N/A
		M1	45.03	0.367	E	6.305	0.039	0.076	0	N/A
		M2	122.12	0.313	E	5.806	0.040	0.090	0	N/A
		M3	157.12	0.354	E	6.175	0.049	0.150	0	N/A
		M5	149.50	0.246	E	6.007	0.040	0.065	0	N/A
	Random	F5	437.40	0.293	E	4.874	0.022	0.068	0	N/A
		M1	19.98	0.214	E	8.097	0.044	0.035	0	N/A
		M2	263.27	0.827	TP	0.736	0.040	0.103	0	0.500
		M3	114.77	0.257	E	7.634	0.062	0.075	0	N/A
		M5	136.69	0.395	E	5.519	0.049	0.028	0.015	N/A

Furthermore, there were no differences between the maximum step lengths of either males or females or between the two repeated experiments (ANOVA; $F_{1,4} = 0.477, p < 0.05$). Despite a clear trend for lower mean distances moved in the second trials compared with the first, these were not statistically different (ANOVA; $F_{1,4} = 5.221, p > 0.05$, Figure 6-7).

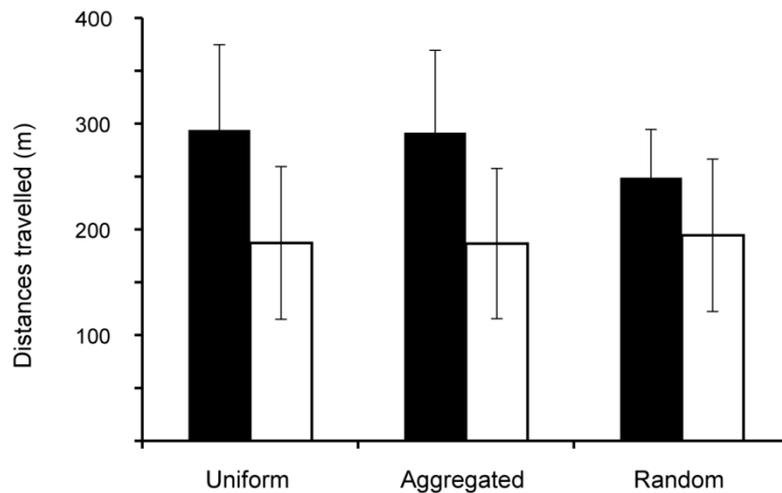


Figure 6-7. Mean (\pm S.E.) distances travelled by selected juvenile small-spotted catsharks during foraging trials with three different prey distributions. Solid bars indicate results for the first experiment and unfilled bars indicate the results for the repeated experiment after a period of three months. (Selected individuals were those that foraged in each treatment and in both experiments).

Foraging efficiencies were significantly different between sets of experiments with generally greater foraging efficiencies on the repeated experiment than the first (ANOVA; $F_{1,8} = 6.568, p < 0.05$). However, there were no differences between sexes or prey distributions (Figure 6-8). In trials with a uniform prey distribution, 6 individuals foraged more efficiently (between 10 and 100 % increase) and 1 individual was less efficient in the second set of trials (100% decrease), the remaining 3 foraged with similar efficiency in both

sets of trials. This pattern was also repeated in trials with aggregated and randomly distributed prey where 7 and 5 individuals improved their foraging efficiency (between 2 and 100 %, and between 33 and 100 % increases, respectively) and 2 and 4 individuals foraged less efficiently (between 16 and 25 %, and between 8 and 30 % decreases, respectively), in the second set of trials (Figure 6-8).

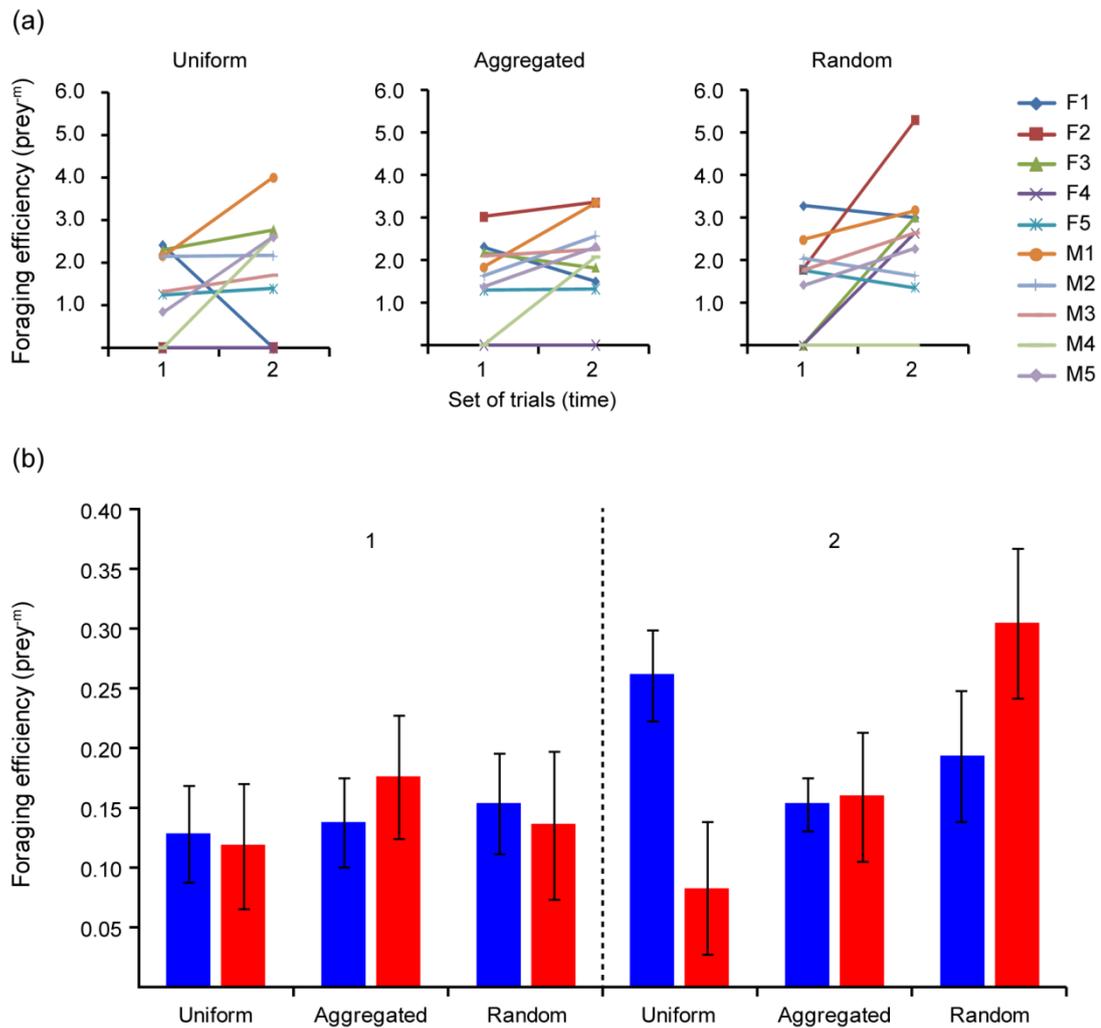


Figure 6-8. Foraging efficiency of juvenile small-spotted catsharks during foraging trials with different prey distributions (uniform, aggregated and random) as part of an experiment (1) that was repeated after a period of three months (2). (A) Individual foraging efficiencies (see key for individual identification); (B) Mean (\pm S.E.) foraging efficiencies of male (blue) and female (red) individuals.

6.3.2 Learning experiment

Variable movement behaviour was exhibited by all individuals throughout the learning experiment, resulting in tracks with vastly different appearances (Figure 6-9). Despite the differences in overall patterns of movement as evident in Figure 6-9, it is also clear that individuals spent a significantly greater proportion of their time in the central area of the test arena after a period of training (ANOVA; $F_{1,8} = 33.985, p < 0.01$, Figure 6-10).

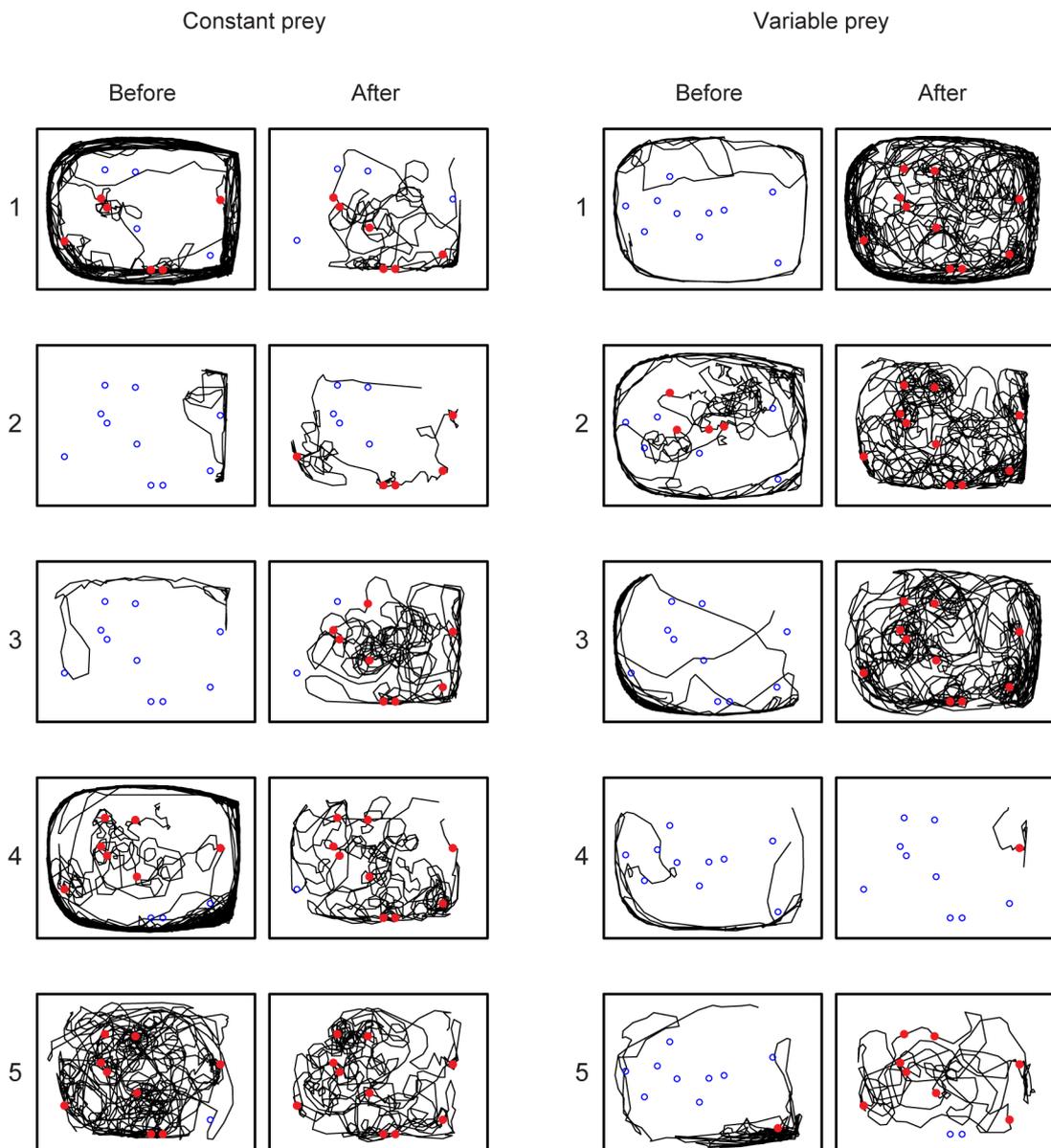


Figure 6-9. Movement tracks of two groups of juvenile male small-spotted catsharks before and after a period of differential training. Solid circles indicate prey captured and unfilled circles indicate prey that was not captured.

There also appeared to be differences between the groups, with individuals that had foraged within a constant spatial arrangement of prey (C1-5) spending a greater proportion of their time in the central area than individuals that foraged within a variable spatial arrangement of prey (V1-5) (Figure 6-10). However, these differences were not found to be statistically significant (ANOVA; $F_{1,8} = 1.549, p > 0.05$).

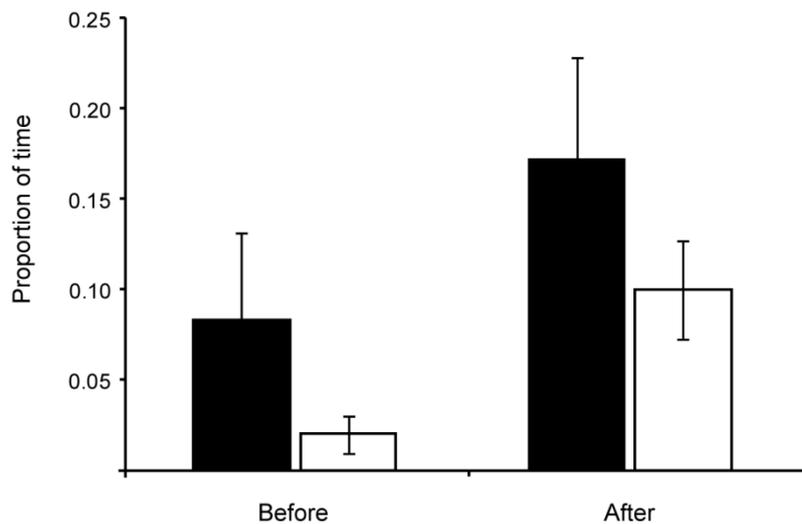


Figure 6-10. Mean (\pm S.E.) proportion of time spent in the central area of the test arena by two groups of juvenile male small-spotted catsharks during foraging trials before and after a period of differential foraging training. Black filled bars indicate results for the group that was trained and tested with the same spatial arrangement of prey; unfilled bars indicate results for the group that was trained and tested on different spatial arrangements of prey each trial.

The tortuosity of movement paths was highly variable and the resulting ARS scales identified by first passage time reflected this (Figure 6-11). There was no clear pattern of differences between individuals in different groups that foraged upon different stabilities of spatial prey arrangements or within individuals before and after the training period. The range of different scales of ARS for all individuals fell between 16 cm and 246 cm, with some individuals concentrating their search efforts at multiple spatial scales. For example, C1 had two clear peaks of variance at scales of 52 and 206 cm (Figure 6-11).

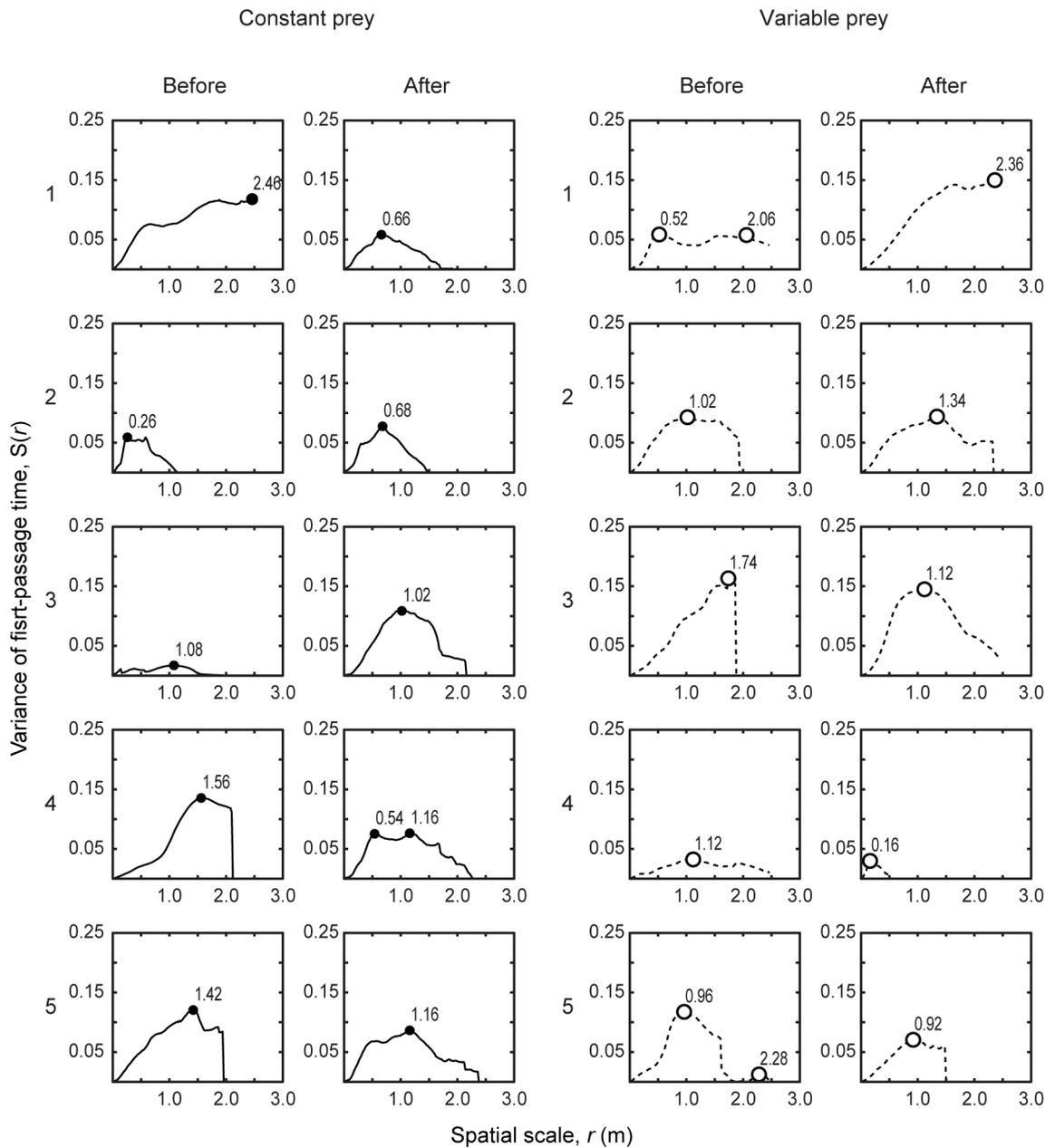


Figure 6-11. The variance of first passage time, $S(r)$, as a function of radius (r) for the movement tracks of small-spotted catsharks (C1-5 and V1-5) during foraging trials before and after a period of differential foraging training. Black filled circles indicate peaks of variance for the group that was trained and tested with the same prey distribution (C1-5); unfilled circles indicate peaks of variance for the group that was trained and tested on different prey distributions each trial (V1-5).

This pattern of variability in tortuosity was also reflected by the turn angle distributions. All but one of the distributions (V2, after training), for the trials before and after training, were significantly different from a circular normal distribution (Rayleigh's uniformity tests, $p < 0.05$). The exception can be explained by a small number of samples as a result of limited movements (Figure 6-9). Generally, mean turn angles were centred on 0° and the strength of directionality was high (between 0.9 and 0.99) and this is reflected in the grouped mean turn angles with narrow confidence limits in Figure 6-12.

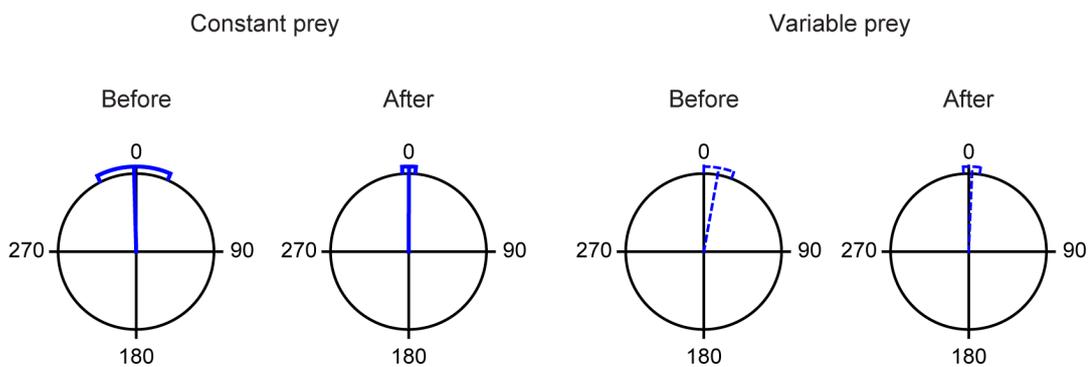


Figure 6-12. Grouped mean turn angles exhibited two groups of male juvenile small-spotted catsharks ($n1 = 5$, $n2 = 5$) during foraging trials before and after a period of differential foraging training. Solid lines indicate results for the group that was trained and tested with the same prey distribution; dashed lines indicate results for the group that was trained and tested on different prey distributions each trial. Confidence limits (95%) are indicated by the size of the brackets around the plot perimeter.

Maximum step lengths were not significantly different after a period of training in either of the groups and the distributions of step lengths were also variable between trials with no clear pattern between groups before and after training. The distributions of step lengths of some individuals' movements were best fit by an exponential distribution before training and a truncated power law after training (e.g. C1 and V5, Table 6-2), whereas for

others the converse was true (e.g. C4 and V2, Table 6-2). Also, the step length distributions of some individuals were a best fit to a particular distribution before and after training (e.g. C2 and V4). Of the distributions that best fit a truncated power law only those found after training had exponents close to the theoretically optimal Lévy exponent of 2 (C1, C3 and V4, Table 6-2). Examples of plots used to assess fits to a particular distribution are shown in Figure 6-13. It is clear from this figure that fits to a truncated power law were visually better than fits to an exponential distribution for individuals C3 and V4 before and after training.

Table 6-2. Summary of the data used and MLE results of step length distribution analyses for juvenile male small-spotted catshark movements during foraging trials before and after a period of differential foraging training.

<i>Time</i>	<i>Prey arrangement</i>	<i>Individual</i>	<i>Distances travelled (m)</i>	<i>Max step length (m)</i>	<i>Best fit distribution</i>	<i>Best fit exponent</i>	<i>Xmin</i>	<i>GOF</i>	<i>P</i>	<i>Xmax</i>
Before	Constant	C1	397.65	1.326	E	4.30	0.021	0.027	0.031	N/A
		C2	14.58	1.198	E	7.42	0.041	0.073	0	N/A
		C3	11.32	0.455	TP	1.11	0.065	0.051	0	0.395
		C4	618.37	1.080	TP	0.55	0.023	0.059	0	0.919
		C5	166.23	1.262	E	8.10	0.038	0.103	0	N/A
	Variable	V1	38.38	0.859	TP	0.76	0.076	0.087	0	0.570
		V2	111.85	0.906	E	5.98	0.030	0.067	0	N/A
		V3	121.45	1.037	TP	0.52	0.059	0.097	0	0.611
		V4	28.33	0.949	TP	0.48	0.053	0.051	0	0.494
		V5	48.88	1.125	E	5.76	0.038	0.043	0	N/A
After	Constant	C1	45.70	0.753	TP	2.03	0.088	0.059	0	0.336
		C2	18.74	0.839	E	10.48	0.043	0.052	0	N/A
		C3	77.04	1.047	TP	1.90	0.095	0.074	0	0.374
		C4	72.52	0.670	E	10.62	0.061	0.119	0	N/A
		C5	90.28	0.704	E	10.62	0.074	0.088	0	N/A
	Variable	V1	339.18	1.283	E	5.60	0.034	0.092	0	N/A
		V2	160.35	0.822	TP	1.00	0.053	0.125	0	0.340
		V3	202.52	1.255	E	7.79	0.075	0.093	0	N/A
		V4	2.64	0.574	TP	2.03	0.057	0.176	0	0.574
		V5	44.45	0.730	TP	1.37	0.071	0.064	0	0.476

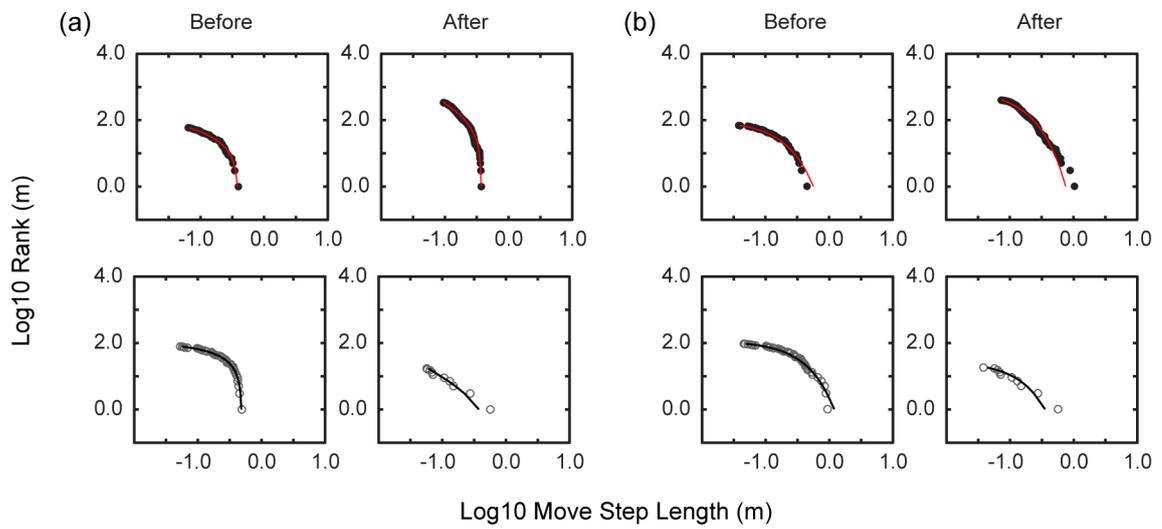


Figure 6-13. Examples of fits of step-length distributions to hypothesised truncated power law (a) and exponential (b) distributions for C3 (black filled circles and red lines; top) and V4 (unfilled grey circles and black lines; bottom) in both before and after a period of differential training.

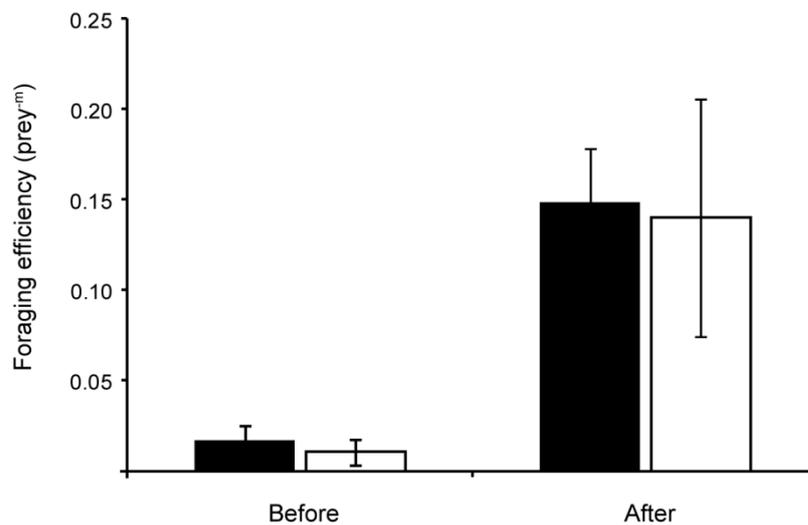


Figure 6-14. Mean (\pm S.E.) foraging efficiency of two groups of juvenile male small-spotted catsharks during foraging trials before and after a period of differential foraging training. Black filled bars indicate results for the experienced group that was trained and tested with the same prey distribution; unfilled bars indicate results for the inexperienced group that was trained and tested on different prey distributions each trial.

The foraging efficiencies of individuals from both groups were significantly improved after a period of training (ANOVA, $F_{1,8} = 11.74, p < 0.01$). The improvement in foraging efficiency averaged 86 % for both groups of individuals. There were no differences in foraging efficiencies between groups both before and after training (ANOVA, $F_{1,8} = 0.031, p > 0.05$, Figure 6-14). All individuals showed increased foraging efficiencies after the period of training, with the least improvement of 42 % shown by V2. However, throughout the course of the experiment there was considerable variability in both of the parameters used to calculate foraging efficiency, namely distances travelled and prey captured during a trial (Figure 6-15 a and b). However, generally the distances travelled by individuals from the group that were allowed to forage on the same constant spatial arrangement of prey decreased from the start of the experiment to the end and also became less variable between individuals (Figure 6-15 a) This was not true for the group that foraged on a variable spatial arrangement of prey each week. For these individuals, distances travelled were generally low and showed no trend for increasing or decreasing from beginning to end (Figure 6-15 a). Prey capture was variable for both groups throughout the experiment (Figure 6-15 b). Taken together, the resulting foraging efficiencies show similar variability but a general upward trend for both groups, although this is most pronounced for the group that foraged within a constant spatial arrangement of prey (Figure 6-15 c).

The mean foraging efficiency reflects these trends and further highlights the intra- and inter-individual variability (Figure 6-16). Taken together with the individual foraging efficiency trajectories it is clear that the upward trend for the group that foraged within variable spatial arrangements of prey was caused by the increases for just one individual in the final testing week (V4, Figure 6-15 c). On inspection of the track for this individual it is clear that the high foraging efficiency is related to the chance encounter with one prey item

after moving a short distance in a relatively inactive trial (total distance covered = 2.64 m; Table 6-2 and Figure 6-9). Interestingly, if the results for that individual are removed from the analyses, the upward trend is significantly less pronounced (Figure 6-16).

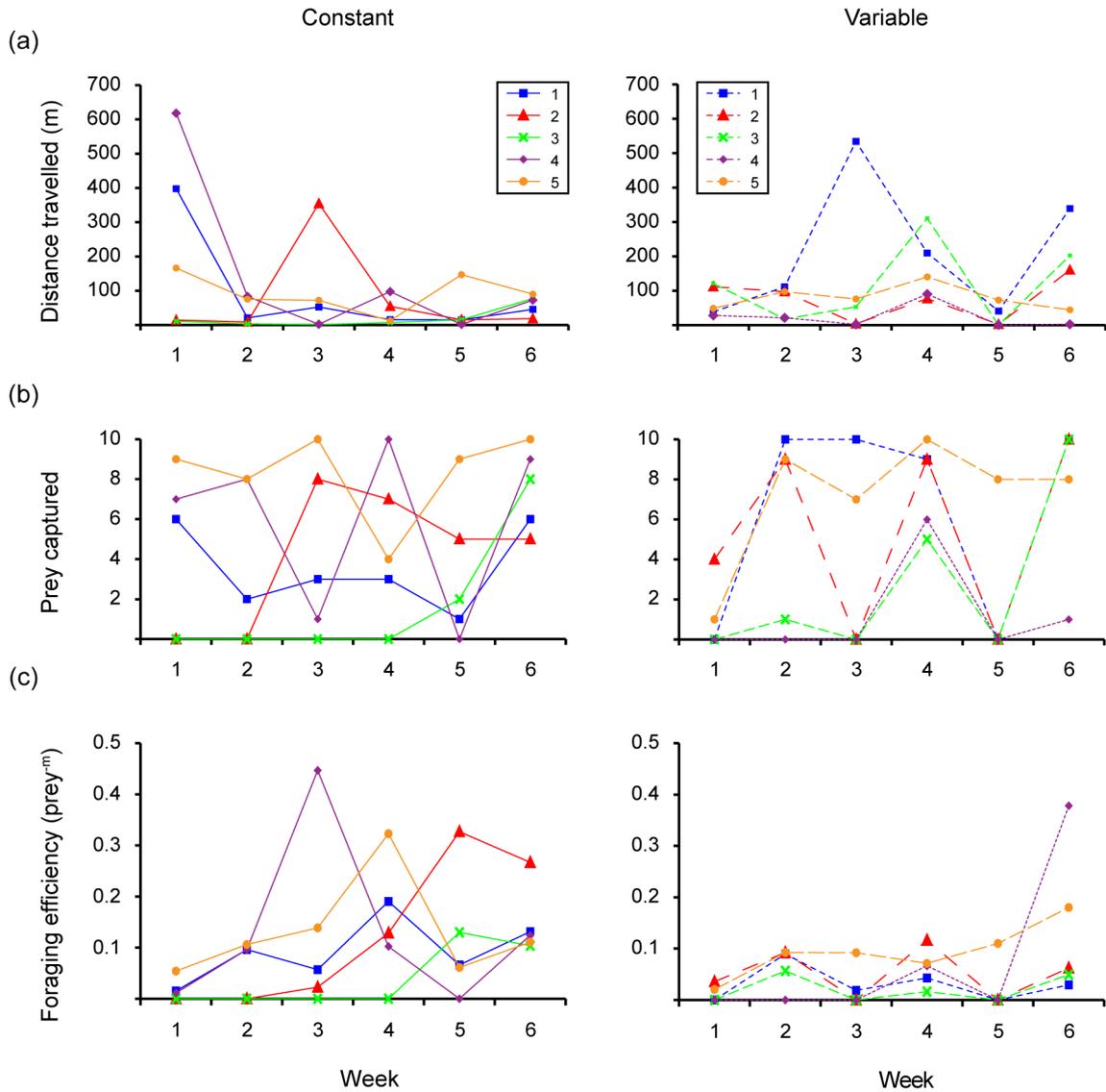


Figure 6-15. Individual distances travelled (a), prey captured (b) and resulting foraging efficiency (c) for two groups of juvenile small-spotted catsharks in each week of a learning experiment where each group was allowed to forage in either a constant or variable spatial arrangement of prey.

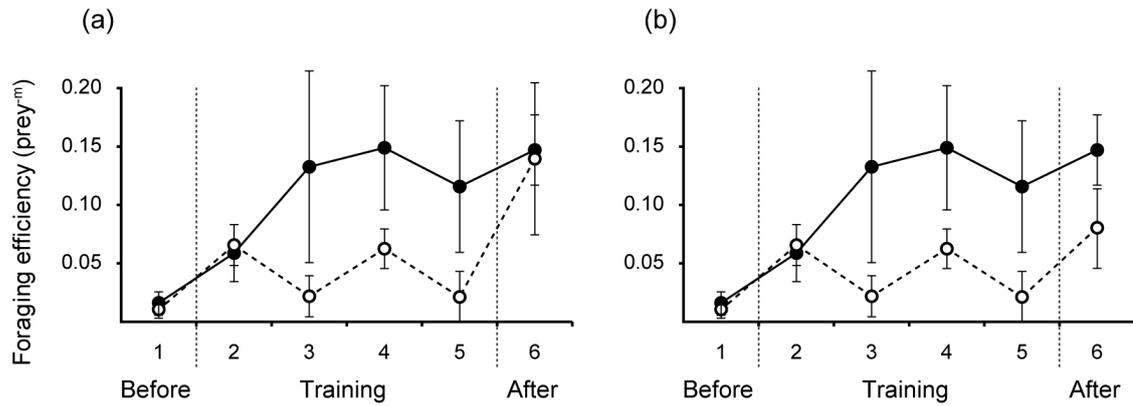


Figure 6-16. Mean (\pm S.E.) foraging efficiency of two groups of juvenile male small-spotted catsharks during foraging trials before, during and after a period of differential foraging training. Black filled circles indicate results for the group that was trained and tested with the same spatial arrangement of prey; unfilled circles indicate results for group that was trained and tested on different spatial arrangements of prey each week. (a) All individuals; (b) without individual V4.

6.4 Discussion

6.4.1 Prey distribution experiments

Results of the repeated prey distribution experiment showed that there were no differences between treatments in terms of the foraging efficiencies of either male or female small-spotted catsharks. However, foraging efficiency had improved markedly after a period of roughly three months between trials with the same prey distributions for the majority of individuals. The movement parameters were highly variable both within and between individuals throughout the experiment, with no clear patterns that matched the foraging efficiency results. Although scales of area restricted search and strength of directionality were different between treatments, these differences were related to the differences between controls and prey distributions that were either the same differences for both sets of trials (ARS scales identified for controls were greater than for the prey distributions in both sets of trials) or different between sets of trials (the strength of directionality of turn angle distributions for controls was weaker than that for prey distribution treatments in the

first set of trials and stronger than those for the treatments in the second). No clear differences were found between factors for maximum step lengths or proportions of time spent within a central area of the test arena, and of those individuals that foraged in each treatment in both sets of trials (50%), roughly 86 % of the step length distributions were best fit by an exponential distribution indicating random search behaviour.

The results of the repeated prey distribution experiment showed clear improvements in foraging efficiency for the majority of individuals. This pattern of increased foraging efficiency may be linked to age related differences in the foraging skills used either as a result of learning or ontogenetic development. It is well documented that performance traits such as pursuit and handling of prey can improve with age as a result of physiological changes, leading to improved locomotor performance (Herrel and Gibb, 2006) or sensory detection (Sisneros *et al.*, 1998). However, the beneficial effects of previous experiences and learning on foraging behaviour have also been well documented (Werner *et al.*, 1981; Gibbons *et al.*, 2005; Hewitson *et al.*, 2005; Winter and Stich, 2005; Burns and Thomson, 2006).

Given the relatively short memory windows of marine fish (Mackney and Hughes, 1995; Warburton, 2006), and the fact that in the prey distribution experiment presented in this chapter, each individual only experienced the same prey treatment twice (separated by at least three months), it may be unlikely that the increased foraging efficiencies found were related to learning. However, since learning experiments are scant for this species their memory window size is unknown and therefore learning cannot be ruled out. Furthermore, the movement parameters for this experiment do not provide further explanation of the observed differences in foraging efficiencies. The reason for this is the lack of a clear correlating pattern, as a result of high inter- and intra-individual variation of movements and space use. The high inter- and intra-individual variation in movements exhibited by

small-spotted catsharks in this experiment is a common feature of animal movements. Within the fish taxa intra-specific variation in movements and space use has been found for recently emerged brook charr, *Salvelinus fontinalis* (McLaughlin *et al.*, 1992); Atlantic salmon, *Salmo salar* (Armstrong *et al.*, 1999; Hiscock *et al.*, 2002); salemma, *Sarpa sarpa* (Jadot *et al.*, 2006); and juvenile lemon sharks, *Negaprion brevirostris* (Sundström *et al.*, 2001).

6.4.2 Learning experiment

The results of the learning experiment presented in this chapter were intended to provide further explanation of the results found in the repeated prey distribution experiment. In this experiment juvenile male small-spotted catsharks exhibited similar improvements in foraging efficiency after a 4 week training period. However, although different training experiences (constant versus variable prey arrangements) did not result in differences in foraging efficiency after training, this was most likely due to the chance encounter of a single prey item by one individual (V4) in the test week. With that individual removed the improvements made by the two groups were different, with the stable-prey group showing far greater improvement, which was sustained. As in the previous experiment, many movement parameters were also not found to differ. There were no differences between groups that were given different training experiences either before or after training in terms of the scales of area-restricted searching (ARS), mean turn angles and strength of directionality, or maximum step lengths. However, both groups spent a significantly greater proportion of time within a central area of the test arena after the training period.

Over a relatively short period of just 6 weeks the improvement in foraging efficiencies of male small-spotted catsharks from both experimental treatment groups was high (between 40 and 100%). Despite this, there were no overall differences between experimental treatment groups. Although no differences would be expected at the start of

the experiment, it was expected that those receiving training with a stable or constant prey arrangement would perform better than those receiving training with variable prey arrangements at the conclusion of the experiment. The lack of differences between the experimental groups was most likely a consequence of the improvements of one individual. This individual was trained on a variable prey arrangement and showed no trend for improvement throughout the experiment, except at the end when its foraging efficiency improved markedly. Without this huge improvement, in just one week by one individual as a result of a chance encounter, the experimental groups showed clear differences in their improvement of foraging efficiency. Generally, the improvements in foraging efficiency of individuals exposed to constant prey arrangements were greater and more rapid than those exposed to variable prey arrangements.

The improvements in foraging efficiency seen in this experiment were most likely due to changes in the use of space, since the juvenile small-spotted catsharks spent a greater proportion of time within the central area of the tank after a period of training. Given the spatial arrangements of prey, the probability of locating a prey item was much higher in this part of the arena. Given the relatively short period of time (6 weeks), the differences in foraging efficiency and space use are unlikely to be a consequence of ontogenetic development. Instead, the results of this second experiment suggest that the individuals had learned to use a more profitable area of the test arena (the central area), where more prey was available (compared to outer regions).

The results of this experiment are similar to examples found in the literature. For example, bluegill sunfish (*Lepomis macrochirus*) were found to increase their foraging efficiency by up to fourfold after a course of only 6-8 foraging bouts (Werner *et al.*, 1981). Similarly, nectar feeding bats were able to learn the location of pre-visited sites within 3 trials and learned to avoid these depleted sites within 10 trials (Winter and Stich, 2005).

Further examples of spatial learning studies have shown that differences in experiences can lead to differences in learning and therefore foraging efficiency. For example, sheep would visit more depleted sites and would re-visit high quality sites less when their previous experiences were less predictable (Hewitson *et al.*, 2005).

Interestingly, despite the shift in space use, the movements of small-spotted catsharks showed no clear pattern of differences in terms of step length and turn angle distributions before and after training. However, the fits of an individual's step length distribution to a truncated power law showed differences in the exponents before and after training. Before training, empirical data fits to a truncated power law gave exponents of approximately 1 or below (i.e. not within the Lévy range). However, after training fits to a truncated power law had exponents close to the theoretical optimal Lévy μ of 2 (Bartumeus *et al.*, 2002). The quality of the fits was variable, but this suggests that small-spotted catsharks may be able to learn when to adopt a particular random search tactic to forage closer to optimality.

6.4.3 Conclusions

Learning through experience has been widely documented for a number of species and it is widely acknowledged that it can play an important role in the foraging behaviour of animals. The results of this chapter suggest that learning about the variability of the environment may play an important role in guiding future foraging decisions of small-spotted catsharks. However, further research is needed to investigate the role of learning over greater temporal and spatial scales both in the laboratory and more importantly in the field, and for a wider range of age classes.

7 General discussion

All animals must find, gather and consume sufficient food to fulfil energy requirements that are vital for survival and reproductive success (Pyke *et al.*, 1977). Given this importance, foraging behaviour is clearly a central topic in behavioural ecology. Many different approaches to the study of foraging behaviour have been adopted, but a main focus has been the use of optimality models (Charnov, 1976; Pyke *et al.*, 1977; Schoener, 1979; Pyke, 1984; Stephens and Krebs, 1986). Traditionally these models have concerned prey choice and patch residency (Charnov, 1976), but more recently attention has been directed towards the study of optimal movements and search behaviour (Viswanathan *et al.*, 1999; Bartumeus *et al.*, 2002; Edwards *et al.*, 2007; Sims *et al.*, 2008). Various theoretical models of animal movements under different conditions with respect to the temporal and spatial availability of prey and the amount of information that a forager has, have been developed (Zollner and Lima, 1999; Bartumeus *et al.*, 2002; Sims, 2003; Higgins and Strauss, 2004). However, empirical tests of such models are few and incomplete, especially for free-ranging marine predators. Generally, it is poorly understood what search patterns predatory animals exhibit and whether these alter with changes in perceived distributions of prey as predicted by theoretical models (Sims, 2003). Despite recent advancements many questions regarding animal search behaviour still remain. Some of these questions concern the development of search behaviour, for example are there sex differences in search behaviour and are search tactics learned or innate? This study aimed to describe and investigate the movements and search behaviour of the small-spotted catshark under a variety of different prey (availability and distribution) scenarios both in the field and the laboratory. Here, the findings of this research are summarised, highlighting the key insights and suggested areas for future work.

7.1 Central place foraging

The overall space use patterns of adult small-spotted catsharks showed clear differences between the sexes, with females using multiple small core areas within relatively large home range areas. In contrast, males made use of fewer core areas within a much smaller home range. These patterns reflect and confirm previous research. Despite the overall differences in space use, both male and female adult small-spotted catsharks in the wild were found to exhibit horizontal movements that resemble central place foraging (Chapter 3). However, the timing and extent of these movements was markedly different between the sexes. Males frequently undertook discrete excursions from and back to a central place throughout the day and night. These excursions were generally highly tortuous and remained within a relatively small distance surrounding the core area (central place). In contrast, discrete excursions by females were infrequent, mainly restricted to night time, and were generally less tortuous with long range commutes to distances much farther from the core area or refuge (central place). Although prey encounter or capture information was unavailable, these different patterns may have been related to differences in prey encounter as the prey field sampling results (Figure 3.14) suggested that each of the sexes may have experienced different prey landscapes.

7.2 Foraging in different resource scenarios

Foraging behaviour of juvenile small-spotted catsharks in the laboratory was highly variable both between and within individuals, and showed no clear differences in terms of movements or resulting foraging efficiencies between different resource scenarios (prey distribution or density). Whether the prey was uniformly, aggregated or randomly distributed, movements appeared to conform to a simple random walk model of movement (Brownian motion), as there were generally good fits of the step length

distributions to hypothetical exponential models and a wide range of turn angles. The same pattern was also true for individuals when the prey varied in density. These results can be explained by a number of factors, including the possibility that the scales of the movements may represent within patch foraging where the distribution and density of prey may be relatively unimportant when compared to the between patch variation in distribution and density. It could also be that the behaviours exhibited were naïve innate behaviours that were relatively under-developed.

7.3 Sex differences in movements of adults

The statistical properties of adult movements in the field reflected their overall space use patterns. Generally, females concentrated their search efforts at larger scales than males as a consequence of their long range excursions throughout the Lough. Furthermore, females tended to be more directed than males whose movements often resulted in frequent reversal in direction. Finally, step length distributions of all individual's best fit a truncated power law distribution, suggesting Lévy-like behaviour during foraging. Interestingly, these fits were much better for males than females and it appeared as if male step length distributions conformed to a pattern of movement consistent with optimal Lévy-like characteristics (i.e. $\mu \approx 2$). However, due to the lack of information concerning prey capture success the idea that males adopt an optimal search tactic cannot be fully investigated. In contrast to the relatively good fits for male movements, fits were generally poorer for female movements as there were clear departures from the hypothetical truncated power law movement models. These departures suggest that female movements are complex and are more likely to consist of two or more different step length distributions, possibly relating to different degrees of determinism of their behaviour. Despite the relatively poor fits, the exponent values for female step length distributions were also lower than those for the males, a likely consequence of the more directed

movements during long range excursions, reminiscent of ballistic-type movements. Male movements did not consist of commuting phases and this is therefore reflected by the less directed values for the exponents. Given the results of Chapter 3, it is highly likely that differences in the statistical properties of movements between the two sexes are a reflection of the differences in use of different habitats possibly as a consequence of sexual segregation.

7.4 Temporal changes in search behaviour and foraging efficiency

Laboratory experiments showed that foraging efficiency of juvenile small-spotted catsharks increased with age; however, this increase could not be attributed to any clear pattern of differences in movement parameters. In a separate learning experiment juvenile male small-spotted catsharks improved their foraging efficiency over a six week period of training. The level of improvement appeared to be different depending on the previous foraging experiences of an individual. Those who had foraged on a constant spatial arrangement of prey throughout the experiment improved faster and to a greater extent than those who had foraged on a variable spatial arrangement of prey. These improvements could be attributed to the differences in space use of the two groups of individuals as both groups of individuals spent a greater proportion of their time within a central area in the test arena. Presumably they had learned to expect food in this area since there was generally a greater probability of encounter with prey in this area as a result of the spatial arrangements of prey.

7.5 Conclusions

In accordance with the hypothesis that predators should vary their search behaviour to reflect variations in spatial and temporal distributions of prey, adult small-spotted catsharks did exhibit differential movements in areas with seemingly different prey landscapes.

However, these differences did not reflect the predictions of optimal models of search behaviour since fits of step length distributions to hypothesised distributions for females, whose prey landscape appeared to be sparse and patchy, did not conform to a Lévy flight with a μ of 2.

Movements of adult dogfish were complex and were most likely comprised of several different behaviours with different levels of determinism. For example, the movements of both male and female small-spotted catsharks resembled the central place foraging behaviour exhibited by many bird species (Jouventin and Weimerskirch, 1990), thus implying that small-spotted catsharks have some spatial memory capacity. For females this behaviour was more pronounced with long commuting phases on outward and return sections of the excursions. These movements were likely to have been deterministic and related to the prey landscape available for females as a result of their requirement to refuge in relatively prey poor areas of the lough. These commuting movements may have been responsible for the relatively poor fits to a truncated power law distribution of female's step lengths, since these movements were absent in males, whose movements were relatively well described by a theoretically optimal distribution of step lengths.

The movements of juveniles whilst in areas varying in prey density and distribution were in contrast to that of the adults. There were no clear differences reflected by the variation in resource availability and there were also no differences between sexes. Generally the movements were well described by a random (exponential) distribution of step lengths. This may be related to the restricted spatial scale of the laboratory experiments such that the movements are restricted to within patch scales, which may not require differential tactics as has been predicted for between patch foraging. The perceptual ranges of the small-spotted catsharks may have meant that pre-encounter behaviour could not be investigated, given the constraints of laboratory experiments such as limited tank

sizes. On the other hand the movements could be the result of naive behaviours, thus suggesting that learning of appropriate search tactics and movement patterns may be important. This is further supported by the absence of sex differences in juveniles that contrasts with the clear presence of sex differences for movements of adults as one would expect there to be no differences between sexes at any age if movement tactics were innate.

The results of Chapter 6 lend further support to the possibility that search tactics and movement patterns are honed through experience, since the movements of juveniles changed over a period of six weeks such that individuals spent a greater proportion of time in areas where the probability of finding food was greater. These changes also led to improvements in foraging efficiencies. Furthermore, when the spatial arrangement of prey was constant week after week, the improvements in foraging efficiencies were more rapid and greater than when the spatial arrangement varied week to week. The results of this chapter suggest that there may have been a learned expectation of prey availability in certain areas possibly as a result of previous experience. These results lend further support to the growing body of literature concerning the cognitive abilities of fish species and the importance of learning for efficient foraging behaviour.

It is important to note here that despite the findings of this study there were limitations that must be considered. In particular, the numbers of animals used in both the laboratory experiments and field tracking were low. This was partly a product of the inherent difficulty of tracking the movements of marine predators in the field. For example, technical and financial issues relating to the deployment of multiple tags simultaneously limited the number of animals that could be tracked at high resolution. This was further compounded by potential tag failures and subjects leaving the study area. As a result subjects were tracked in separate years, introducing potentially confounding factors related to environmental differences between years. In regards to low numbers of

laboratory subjects, the limited availability of experimental tanks large enough to conduct the experiments prevented simultaneous trials, and therefore limited the number of trials that could be carried out. In relation to this, a further limitation was tank size. The tank used may not have provided a suitable environment for examining search behaviour at several scales. Since it was logistically and financially unrealistic to use a larger tank it may be that another model species may have been more suitable. Although the usual model species for this type of work are mainly insect species, it was anticipated that the small-spotted catshark would bridge the gap and provide a link between small scale laboratory investigation and the study of larger marine vertebrate species in the field. However, there may be another more suitable species that could provide this link.

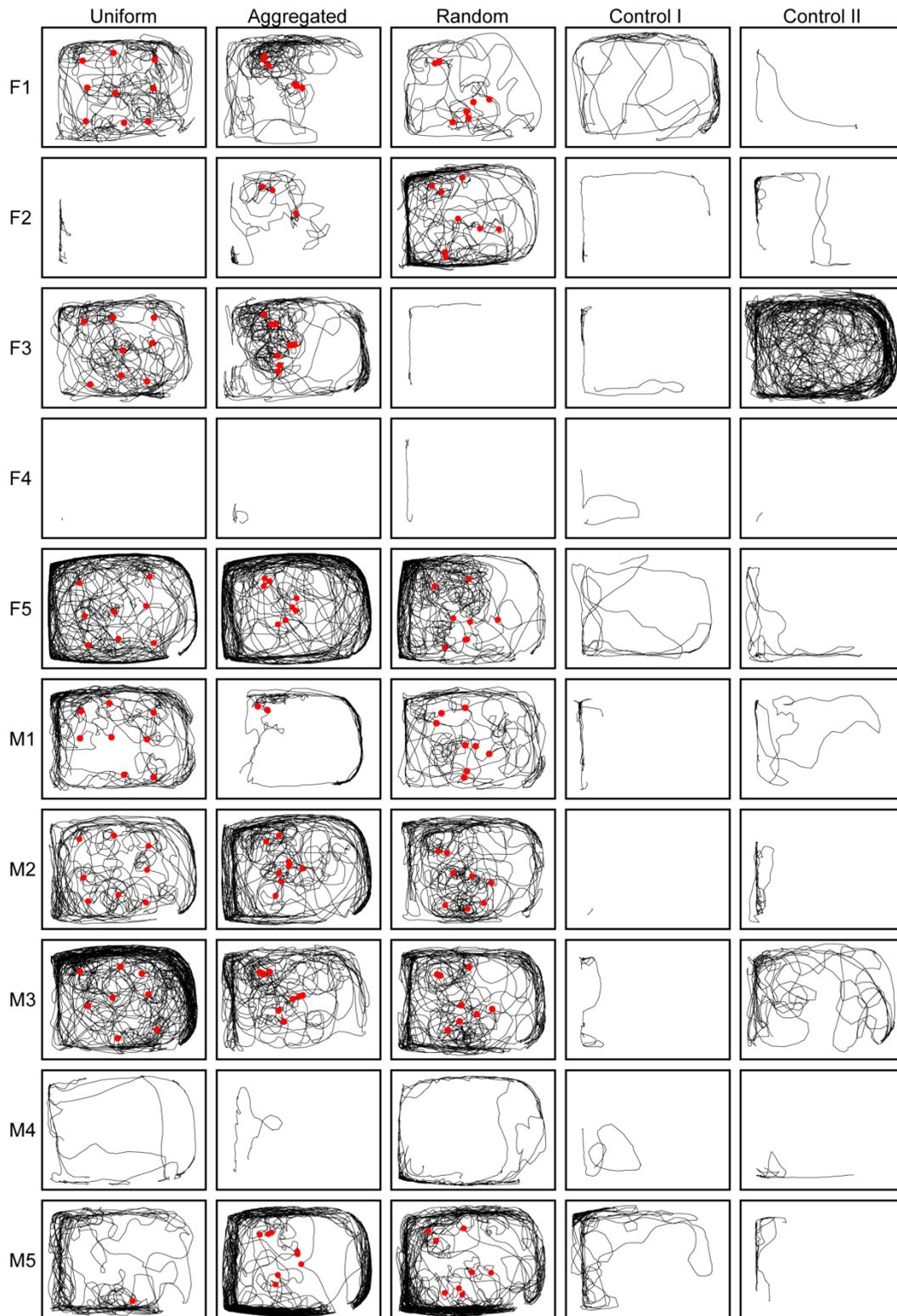
7.6 Future directions

This research has highlighted a number of possible directions for future research. Firstly, the specific role of movement patterns in the wild could only be interpreted loosely given the sampled prey availability. Furthermore, the foraging success of field movements of adults was not measured due to the difficulties of recording prey capture events of wild fish. Recent improvements in tagging technology could help to solve this problem since there are currently a number of devices available or being developed to record prey capture events. For example, one such device known as an inter-mandibular angle sensor (IMASEN) can record the opening and closing of the jaws of an animal from voltage differences as a function of changing distance recorded by a jaw-mounted Hall-effect sensor opposing a rare earth magnet on the opposing mandible. These sensors have previously been shown to provide data concerning the ingestion of prey, including prey size (Wilson *et al.*, 2002; Hochscheid *et al.*, 2005). Only with this information can movements be interpreted in greater detail and optimality models begun to be tested.

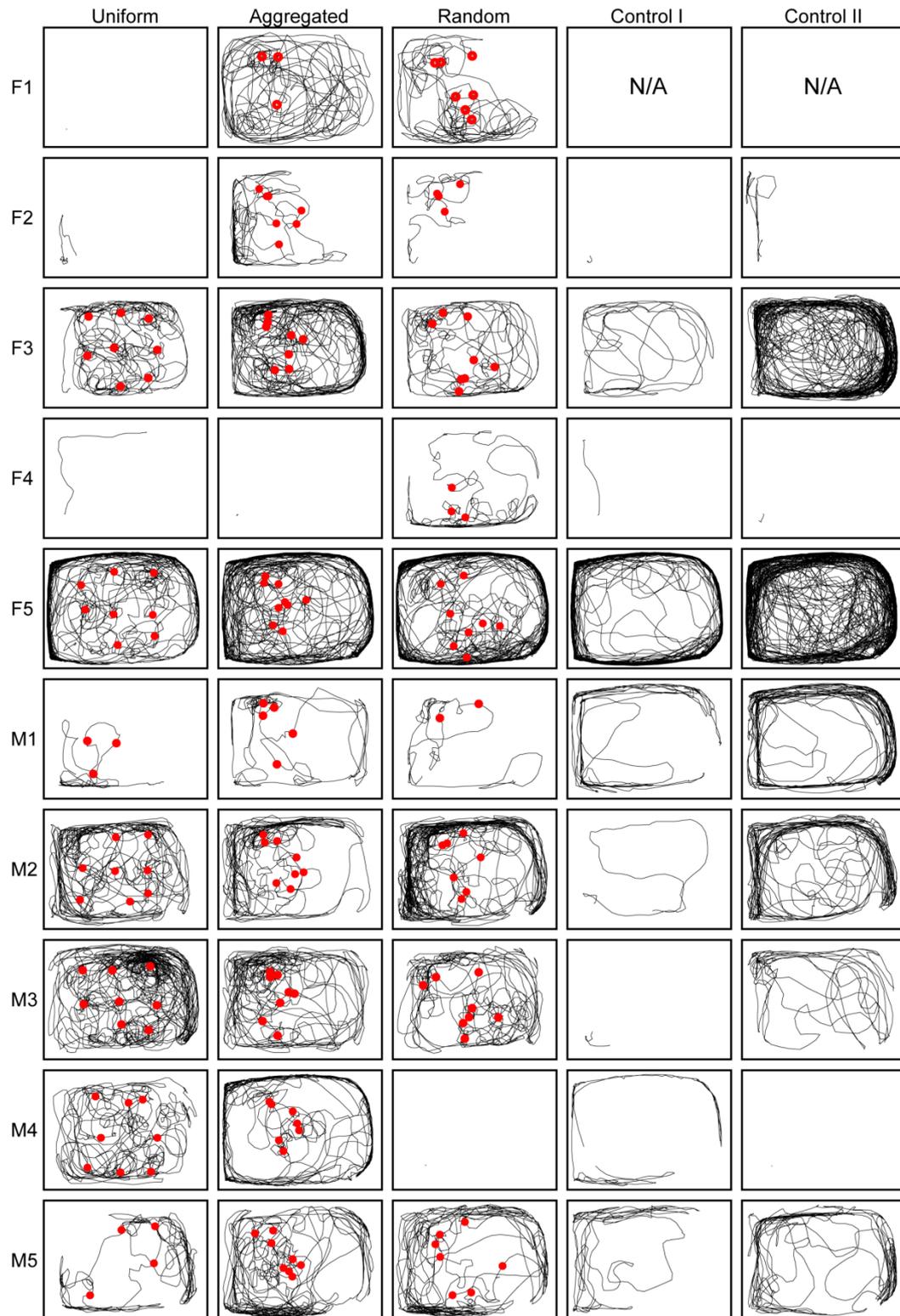
Further information regarding the temporal variation of horizontal movements of small-spotted catsharks in the wild as well as the laboratory is also required so that the possibility of seasonal or annual variation in search behaviour can be investigated. Such work could include further learning experiments or field manipulations that can provide more information on the learning capacity of free-ranging marine predators. Such information has steadily been gathered, but elasmobranchs such as the small-spotted catshark have been relatively overlooked. Another interesting and related opportunity arises to study social learning in small spotted catsharks. Since individuals of this species are known to aggregate in groups, the potential for social learning exists. For example, social transmission of information regarding the location of prey patches through a local enhancement process has been demonstrated in other species of fish (Brown and Laland, 2006), and may confer benefits to small-spotted catsharks also.

Finally, the movements of adults were observed in a semi-enclosed marine lough and therefore these results may not reflect the movements of small-spotted catsharks or predators in other environments such as the open sea. However, there is tracking information and photographic evidence that similar behaviours (e.g. female refuging) take place on the open coastline (Wearmouth, 2001), suggesting that the results here may have wider significance in sexually segregated shark populations generally. Further investigation of movements of small-spotted catsharks in such habitats would clearly identify the broader applicability of some of the results presented in this study.

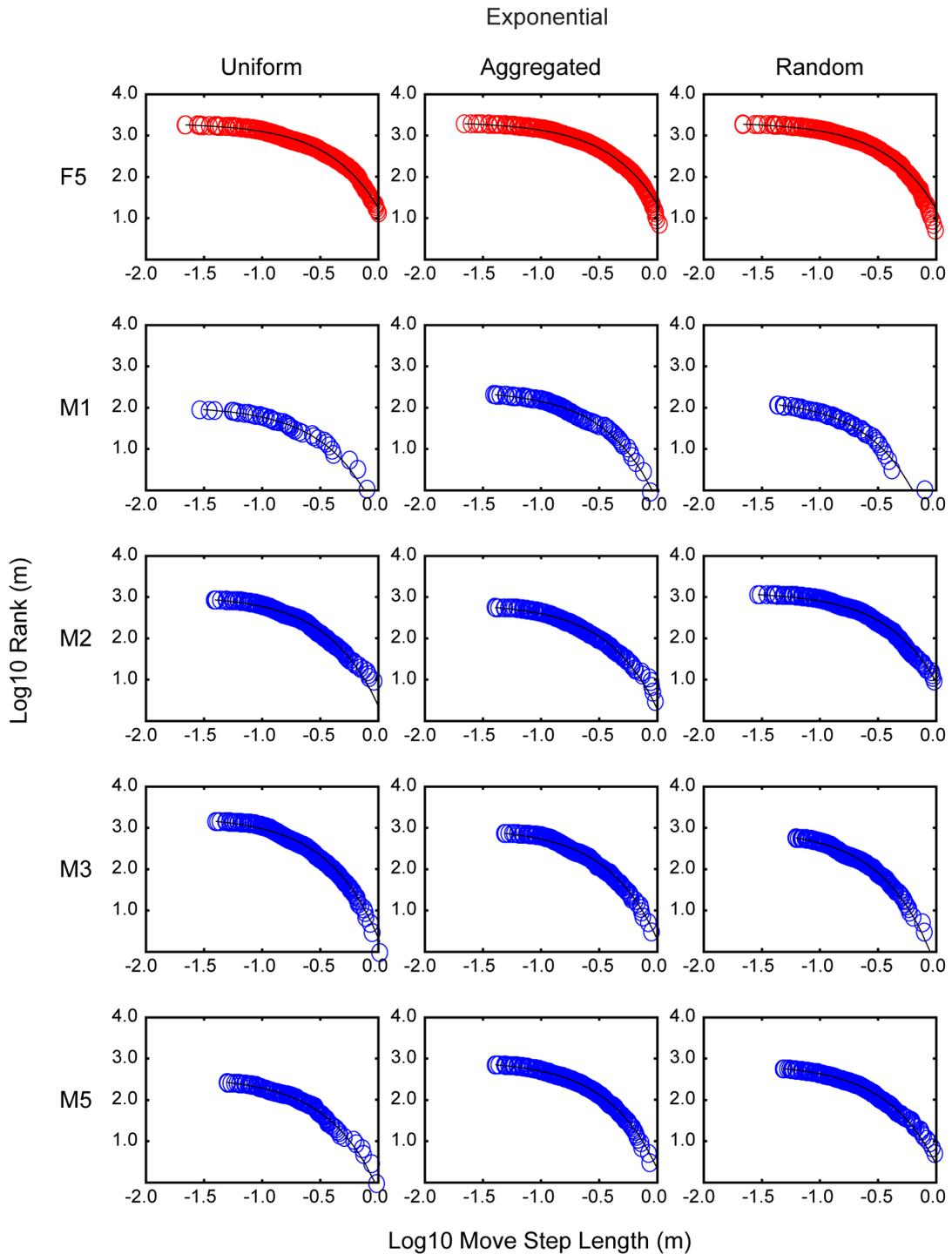
Appendices



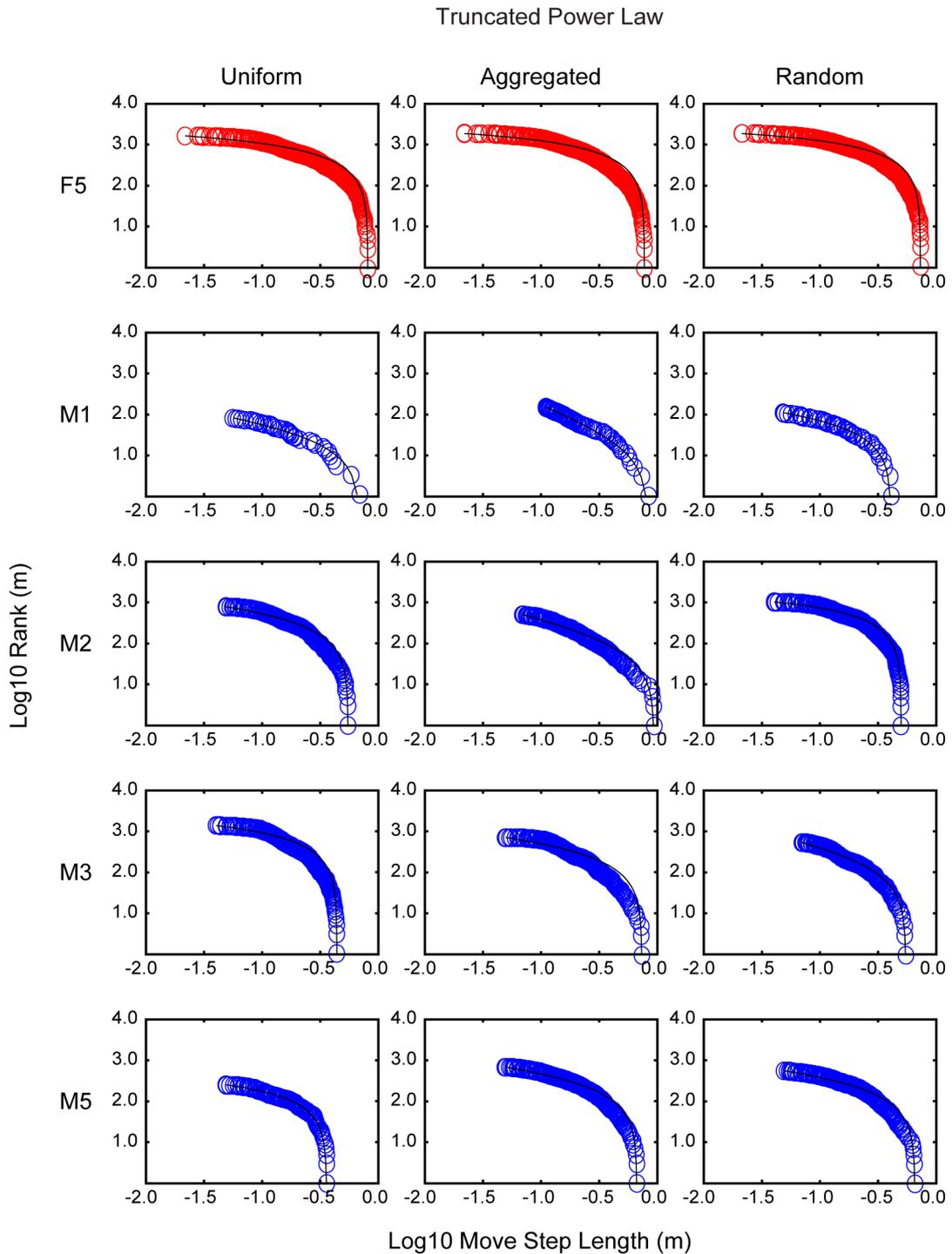
Appendix 1. Movement tracks of juvenile small-spotted catsharks whilst foraging in an arena containing food distributed uniformly, aggregated and randomly. Movements are also shown for controls when no food was present but either (I) no scent or (II) scent was added to the arena at the start of the trial. The location of the centre of gravity of the individual when prey was captured is shown as red circles.



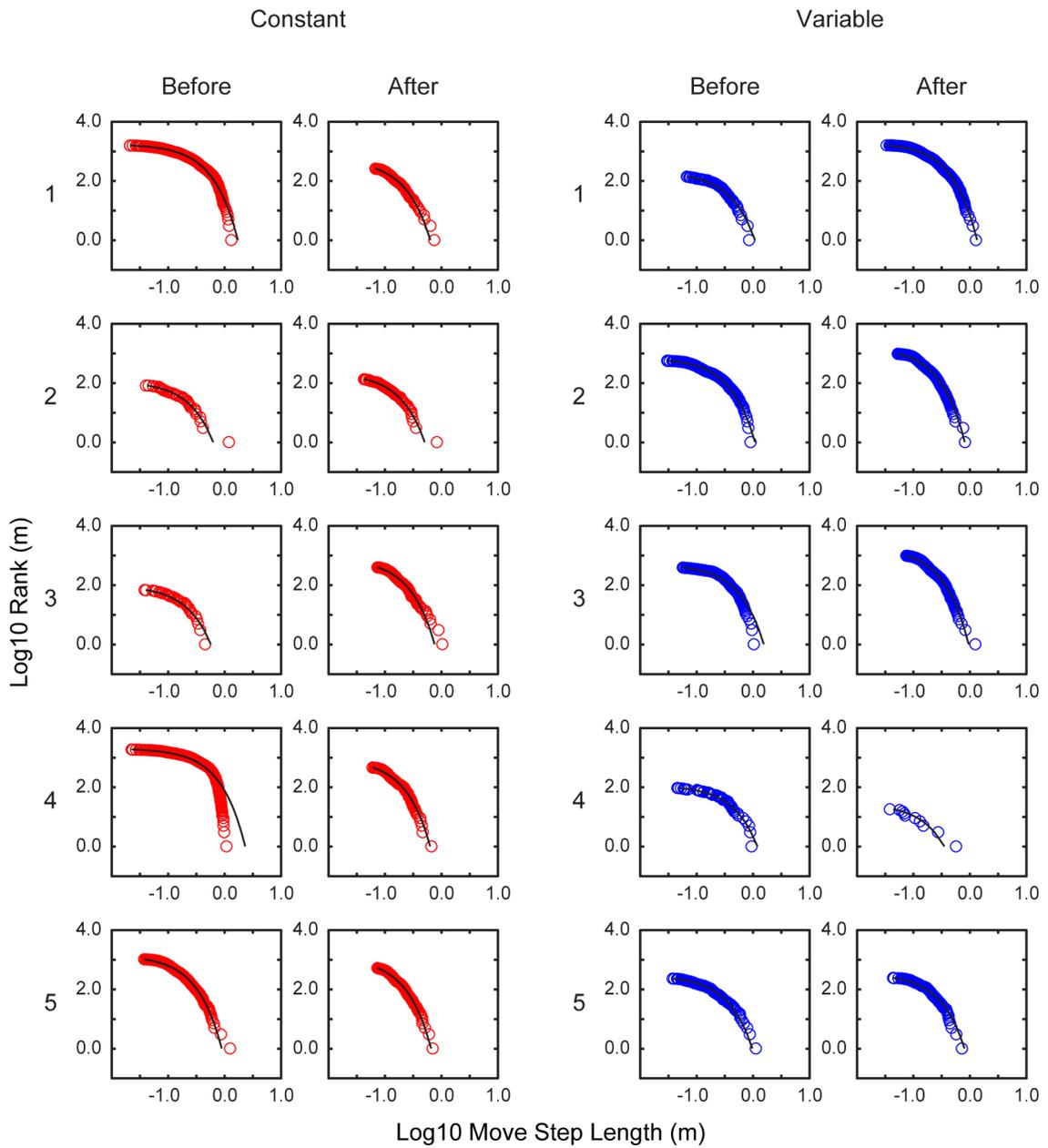
Appendix 2. Movement tracks of juvenile small-spotted catsharks whilst foraging in an arena containing food distributed uniformly, aggregated and randomly for a repeated experiment (3 months after the first, fig A1). Movements are also shown for controls when no food was present but either (I) no scent or (II) scent was added to the arena at the start of the trial. The location of the centre of gravity of the individual when prey was captured is shown as red circles.



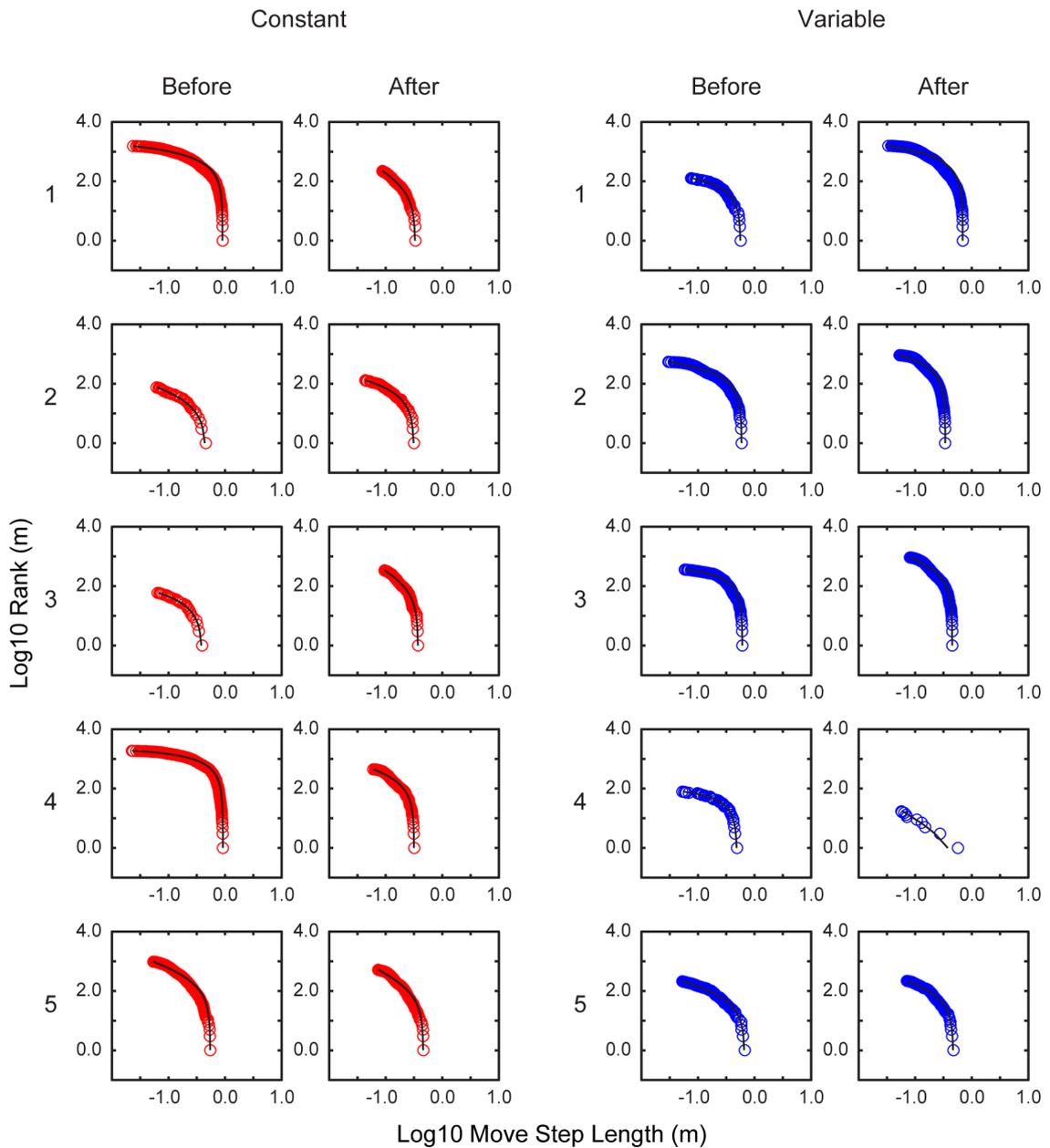
Appendix 3. Results of MLE based analyses showing frequency distributions of move step lengths as best fits to exponential distributions for female (F5) and male (blue, M1-3 and 5) juvenile small-spotted catsharks movements whilst foraging in three different prey distributions in a repeated experiment (Chapter 6) three months after the first (Chapter 4). Circles indicate empirical data and lines represent best fit lines to an exponential distribution above x_{\min} . For more details see general methodology (Chapter 2).



Appendix 4. Results of MLE based analyses showing frequency distributions of move step lengths as best fits to truncated power law distributions for female (F5) and male (blue, M1-3 and 5) juvenile small-spotted catsharks movements whilst foraging in three different prey distributions in a repeated experiment (Chapter 6) three months after the first (Chapter 4). Circles indicate empirical data and lines represent best fit lines to an exponential distribution above x_{\min} . For more details see general methodology (Chapter 2).



Appendix 5. Results of MLE based analyses showing frequency distributions of move step lengths as best fits to exponential distributions for two groups of male small-spotted catsharks movements during foraging trials before and after a period of differential foraging training. Red circles indicate results for the group that was trained and tested with the same prey distribution (C1-5); blue circles indicate results for the group that was trained and tested on different prey distributions each trial (V1-5).



Appendix 6. Results of MLE based analyses showing frequency distributions of move step lengths as best fits to truncated power law distributions for two groups of male small-spotted catsharks movements during foraging trials before and after a period of differential foraging training. Red circles indicate results for the group that was trained and tested with the same prey distribution (C1-5); blue circles indicate results for the group that was trained and tested on different prey distributions each trial (V1-5).

References

- Armstrong, J.D. & Griffiths, S.W. (2001). Density-dependent refuge use among overwintering wild Atlantic salmon juveniles. *Journal of Fish Biology* **58**, 1524-1530.
- Armstrong, J.D., Huntingford, F.A. & Herbert, N.A. (1999). Individual space use strategies of wild juvenile Atlantic salmon. *Journal of Fish Biology* **55**, 1201-1212.
- Aronson, L.R. (1951). Orientation and jumping behavior in the Gobiid fish, *Bathygobius soporator*. *American Museum of Novitates* **1486**, 1-22.
- Aronson, L.R. (1971). Further studies on orientation and jumping behavior in the Gobiid fish, *Bathygobius soporator*. *Annals of the New York Academy of Sciences* **188**, 378-392.
- Ashmole, N.P. (1971). Sea bird ecology and the marine environment. In *Avian Biology* (Farner, D. S. & King, J. R., eds.), pp. 223-286 Academic Press.
- Atkinson, R.P.D., Rhodes, C.J., Macdonald, D.W. & Anderson, R.M. (2002). Scale-free dynamics in the movement patterns of jackals. *Oikos* **98**, 134-140.
- Austin, D., Bowen, W.D. & McMillan, J.I. (2004). Intraspecific variation in movement patterns: Modeling individual behaviour in a large marine predator. *Oikos* **105**, 15-30.
- Baars, M.A. (1979). Patterns of movements of radioactive carabid beetles. *Oecologia* **44**, 125-140.
- Bailey, H. & Thompson, P. (2006). Quantitative analysis of bottlenose dolphin movement patterns and their relationship with foraging. *Journal of Animal Ecology* **75**, 456-465.
- Bartumeus, F. (2007). Levy processes in animal movement: An evolutionary hypothesis. *Fractals-Complex Geometry Patterns and Scaling in Nature and Society* **15**, 151-162.
- Bartumeus, F., Catalan, J., Fulco, U.L., Lyra, M.L. & Viswanathan, G.M. (2002). Optimizing the encounter rate in biological interactions: Lévy versus Brownian strategies. *Physical Review Letters* **88**, 901-904.
- Bartumeus, F., Da Luz, M.G.E., Viswanathan, G.M. & Catalan, J. (2005). Animal search strategies: A quantitative random-walk analysis. *Ecology* **86**, 3078-3087.
- Bartumeus, F., Peters, F., Pueyo, S., Marrasé, C. & Catalan, J. (2003). Helical Lévy walks: Adjusting searching statistics to resource availability in microzooplankton. *Proceedings of the National Academy of Sciences of the United States of America* **100**, 12771-12775.
- Bassett, D.K., Carton, A.G. & Montgomery, J.C. (2007). Saltatory search in a lateral line predator. *Journal of Fish Biology* **70**, 1148-1160.

- Bell, J.J. & Okamura, B. (2005). Low genetic diversity in a marine nature reserve: re-evaluating diversity criteria in reserve design. *Proceedings of the Royal Society B: Biological sciences* **272**, 1067-1074.
- Bell, W.J. (1990). Searching behaviour patterns in insects. *Annual Review of Entomology* **35**, 447-467
- Bell, W.J. (1991). *Searching behaviour. The behavioural ecology of finding resources*. London: Chapman and Hall.
- Benhamou, S. (1990). An analysis of movements of the wood mouse *Apodemus sylvaticus* in its home range. *Behavioural Processes* **22**, 235-250.
- Benhamou, S. (2006). Detecting an orientation component in animal paths when the preferred direction is individual-dependent. *Ecology* **87**, 518-528.
- Benhamou, S. & Bovet, P. (1989). How animals use their environment: a new look at kinesis. *Animal Behaviour* **38**, 375-383.
- Benhamou, S., Sauve, J.P. & Bovet, P. (1990). Spatial memory in large scale movements: Efficiency and limitation of the egocentric coding process. *Journal of Theoretical Biology* **145**, 1-12.
- Bergman, C.M., Schaefer, J.A. & Luttich, S.N. (2000). Caribou movement as a correlated random walk. *Oecologia* **123**, 364-374.
- Beukema, J.J. (1968). Predation by the three-spined stickleback (*Gasterosteus aculeatus*): the influence of hunger and experience. *Behaviour* **31**, 1-126.
- Beyer, H.L. (2004). Hawth's Analysis Tools for ArcGIS. Available at <http://www.spatial ecology.com/htools>.
- Biro, P.A., Ridgeway, M.S. & Noakes, D.L.G. (1997). The central-place territorial model does not apply to space-use by juvenile brook charr *Salvelinus fontinalis* in lakes. *Journal of Animal Ecology* **66**, 837-845.
- Bleckmann, H. (1993). Role of the lateral line in fish behaviour In *The behaviour of teleost fishes* (Pitcher, T. J., ed.), pp. 201-246. London: Chapman and Hall.
- Bleckmann, H. & Zelick, R. (1993). The responses of peripheral and central mechanosensory lateral line units of weakly electric fish to moving objects. *Journal of Comparative Physiology A-Neuroethology, Sensory, Neural and Behavioral Physiology* **172**, 115-128.
- Block, B.A. (2005). Physiological ecology in the 21st Century: Advancements in biologging Science. *Integrative and Comparative Biology* **45**, 305-320.

- Bovet, P. & Benhamou, S. (1988). Spatial-analysis of animals' movements using a correlated random-walk model. *Journal of Theoretical Biology* **131**, 419-433.
- Bowers, M.A. & Ellis, A. (1993). Load size variation in eastern chipmunk, *Tamias striatus*: The importance of distance from burrow and canopy cover *Ethology* **94**, 72-82.
- Bowyer, R.T., Stewart, K.M., Wolfe, S.A., Blundell, G.M., Lehmkuhl, K.L., Joy, P.J., McDonough, T.J. & Kie, J.G. (2002). Assessing sexual segregation in deer. *Journal of Wildlife Management* **66**, 536-544.
- Bradshaw, C.J.A., Sims, D.W. & Hays, G.C. (2007). Measurement error causes scale-dependent threshold erosion of biological signals in animal movement data. *Ecological Applications* **17**, 628-638.
- Brockmann, D., Hufnagel, L. & Geisel, T. (2006). The scaling laws of human travel. *Nature* **439**, 462-465.
- Browman, H.I. & O'Brien, W.J. (1992). The ontogeny of search behavior in the white crappie, *Pomoxis annularis*. *Environmental Biology of Fishes* **34**, 181-195.
- Brown, C. & Braithwaite, V.A. (2004). Size matters: a test of boldness in eight populations of the poeciliid *Brachyrhaphis episcopi*. *Animal Behaviour* **68**, 1325-1329.
- Brown, C. & Laland, K. (2006). Social Learning in Fishes. In *Fish Cognition and Behavior* (Brown, C., Laland, K. & Krause, J., eds.): Blackwell Publishing.
- Brown, C., Laland, K. & Krause, J., eds. (2006). *Fish Cognition and Behavior*. Blackwell Publishing.
- Bruno, R., Sorriso-Valvo, L., Carbone, V. & Bavassano, B. (2004). A possible truncated-Lévy-flight statistics recovered from interplanetary solar-wind velocity and magnetic-field fluctuations. *Europhysics Letters* **66**, 146-152.
- Burke, N.C. (1995). Nocturnal foraging habitats of French and bluestriped grunts, *Haemulon flavolineatum* and *H. sciurus*, at Tobacco Caye, Belize. *Environmental Biology of Fishes* **42**, 365-374.
- Burns, J.G. & Thomson, J.D. (2006). A test of spatial memory and movement patterns of bumblebees at multiple spatial and temporal scales. *Behavioral Ecology* **17**, 48-55.
- Burt, W.H. (1943). Territoriality and home range concepts as applied to mammals. *Journal of Mammalogy* **24**, 346-352.
- Cartamil, D.P., Vaudo, J.J., Lowe, C.G., Wetherbee, B.M. & Holland, K.N. (2003). Diel movement patterns of the Hawaiian stingray, *Dasyatis lata*: implications for ecological interactions between sympatric elasmobranch species. *Marine Biology* **142**, 841-847.

- Carter, M.C. & Dixon, A.F.G. (1984). Foraging behaviour of Coccinellid larvae: duration of intensive search. *Entomologia Experimentalis et Applicata* **36**, 133-136.
- Charnov, E.L. (1976). Optimal foraging, the marginal value theorem. *Theoretical Population Biology* **9**, 129-136.
- Clauset, A., Shalizi, C.R. & Newman, M.E.J. (2007). Power-law distributions in empirical data. arXiv:0706.1062v0702 [physics.data-an].
- Cody, M.L. (1971). Finch flocks in the Mohave Desert. *Theoretical Population Biology* **2**, 142-158.
- Cody, M.L. (1974). Optimization in ecology. *Science* **183**, 1156-1164.
- Connor, D.W., Allen, J.H., Golding, N., Lieberknecht, L.M., Northern, K. & Reker, J.B. (2003). Marine nature conservation review: marine biotope classification for Britain and Ireland. Volume 2. Sublittoral biotopes. Version 03.02. Peterborough: Joint Nature Conservation Committee.
- Coombs, S. & Conley, R.A. (1997). Dipole source localization by mottled sculpin. I. Approach strategies. *Journal of Comparative Physiology A-Neuroethology, Sensory, Neural and Behavioral Physiology* **180**, 387-399.
- Croft, D.P., Morrell, L.J., Wade, A.S., Piyapong, C., Ioannou, C.C., Dyer, J.R.G., Chapman, B.B., Yan, W. & Krause, J. (2006). Predation risk as a driving force for sexual segregation: A cross-population comparison. *American Naturalist* **167**, 867-878.
- Croy, M.I. & Hughes, R.N. (1991). The role of learning and memory in the feeding behaviour of the fifteen-spined stickleback, *Spinachia spinachia* L. *Animal Behaviour* **41**, 149-159.
- Dall, S.R.X. & Cuthill, I.C. (1997). Searching in patches by European starlings, *Sturnus vulgaris*. *Behavioural Processes* **39**, 149-159.
- Davoren, G.K., Montevecchi, W.A. & Anderson, J.T. (2003). Search strategies of a pursuit-diving marine bird and the persistence of prey patches. *Ecological Monographs* **73**, 463-481.
- de Knegt, H.J., Hengeveld, G.M., van Langevelde, F., de Boer, W.F. & Kirkman, K.P. (2007). Patch density determines movement patterns and foraging efficiency of large herbivores. *Behavioral Ecology* **18**, 1065-1072.
- Dejean, A. & Benhamou, S. (1993). Orientation and foraging movements in a patchy environment by the ant *Serrastruma lujae* (formicidae-myrmicinae). *Behavioural Processes* **30**, 233-243.

- Dejean, A., Lachaud, J.P. & Beugnon, G. (1993). Efficiency in the exploitation of patchy environments by the ponerine ant *Paltothyreus tarsatus*: an ecological consequence of the flexibility of prey capture behavior. *Journal of Ethology* **11**, 43-53.
- Delicio, H.C. & Barreto, R.E. (2008). Time-place learning in food-restricted Nile tilapia. *Behavioural Processes* **77**, 126-130.
- Dingle, H. (1996). *Migration. The Biology of Life on the Move*. Oxford: Oxford University Press.
- Dodd, J.M. (1983). Reproduction in cartilaginous fishes (Chondrichthyes). In *Fish Physiology, vol 9: Reproduction: endocrine tissues and hormones* (Hoar, W. S., Randall, D. J. & Donaldson, D. M., eds.), pp. 31-87. New York: Academic Press.
- Dusenbery, D.B. (1989). Ranging strategies. *Journal of Theoretical Biology* **136**, 309-316.
- Edwards, A.M., Phillips, R.A., Watkins, N.W., Freeman, M.P., Murphy, E.J., Afanasyev, V., Buldyrev, S.V., da Luz, M.G.E., Raposo, E.P., Stanley, H.E. & Viswanathan, G.M. (2007). Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. *Nature* **449**, 1044-1048.
- Ehlinger, T.J. (1989). Learning and individual variation in bluegill foraging: habitat specific techniques. *Animal Behaviour* **38**, 643-658.
- Ehlinger, T.J. (1990). Habitat choice and phenotype-limited feeding efficiency in bluegill: individual differences and trophic polymorphism. *Ecology* **71**, 886-896.
- Elliott, J.M. (2002). A quantitative study of day-night changes in the spatial distribution of insects in a stony stream. *Journal of Animal Ecology* **71**, 112-122.
- Ellis, J.R., Pawson, M.G. & Shackley, S.E. (1996a). The comparative feeding ecology of six species of shark and four species of ray (elasmobranchii) in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **76**, 89-106.
- Ellis, J.R., Pawson, M.G. & Shackley, S.E. (1996b). The comparative feeding ecology of six species of shark and four species of ray (elasmobranchii) in the north-east Atlantic. *Journal of the Marine Biological Association of the United Kingdom* **76**, 89-106.
- Ellis, J.R. & Shackley, S.E. (1997). The reproductive biology of *Scyliorhinus canicula* in the Bristol Channel, U.K. *Journal of Fish Biology* **51**, 361-372.
- Evans, B.I. & O'Brien, W.J. (1988). A re-analysis of the search cycle of a planktivorous salmonid. *Canadian Journal of Fisheries and Aquatic Sciences* **45**, 187-192.
- Fahrig, L. & Paloheimo, J. (1988). Effects of spatial arrangement of habitat patches on local population size. *Ecology* **69**, 468-475.

- Fauchald, P. (1999). Foraging in a hierarchical patch system. *American Naturalist* **153**, 603-613.
- Fauchald, P. & Tveraa, T. (2003). Using first-passage time in the analysis of area-restricted search and habitat selection. *Ecology* **84**, 282-288.
- Ferran, A. & Dixon, A.F.G. (1993). Foraging behaviour of ladybird larvae (Coleoptera: Coccinellidae). *European Journal of Entomology* **90**, 383-402.
- Ferran, A., Ettifouri, M., Clement, P. & Bell, W.J. (1994). Sources of variability in the transition from extensive to intensive search in coccinellid predators (Homoptera: Coccinellidae). *Journal of Insect Behavior* **7**, 633-647.
- Filer, J.L., Booker, C.G. & Sims, D.W. (2008). Effects of environment on electric field detection by small spotted catshark *Scyliorhinus canicula* (L.). *Journal of Fish Biology* **72**, 1450-1462.
- Ford, E. (1921). A contribution to our knowledge of the life-history of the dogfishes landed at Plymouth. *Journal of the Marine Biological Association of the UK* **12**, 468-505.
- Freon, P. & Misund, O.A. (1999). Dynamics of Pelagic Fish Distribution and Behaviour: Effects on Fisheries and Stock Assessment. Oxford: Blackwell Science.
- Gibbons, M.E., Ferguson, A.M. & Lee, D.R. (2005). Both learning and heritability affect foraging behaviour of red-backed salamanders, *Plethodon cinereus*. *Animal Behaviour* **69**, 721-732.
- Grant, J.W.A., Noakes, D.L.G. & Jonas, K.M. (1989). Spatial distribution of defence and foraging in young-of-the year brook charr, *Salvelinus fontinalis*. *Journal of Animal Ecology* **58**, 773-784.
- Griffiths, S.W. (2003). Learned recognition of conspecifics by fishes. *Fish and Fisheries* **4**, 256-268.
- Hansson, B., Bensch, S. & Hasselquist, D. (2003). Heritability of dispersal in the great reed warbler. *Ecology Letters* **4**, 290-294.
- Hart, P.J.B. (1997). Foraging tactics. In *Behavioural Ecology of Teleost Fishes* (Godin, J.-G. J., ed.), pp. 104-133. Oxford: Oxford University Press.
- Haskell, D.G. (1997). Experiments and a model examining learning in the area-restricted search behavior of ferrets (*Mustela putorius furo*). *Behavioral Ecology* **8**, 448-449.
- Herrel, A. & Gibb, A.C. (2006). Ontogeny of performance in vertebrates. *Physiological and Biochemical Zoology* **79**, 1-6.

- Heupel, M.R. & Simpfendorfer, C.A. (2005). Quantitative analysis of aggregation behaviour in juvenile blacktip sharks. *Marine Biology* **147**, 1239-1249.
- Hewitson, L., Dumont, B. & Gordon, I.J. (2005). Response of foraging sheep to variability in the spatial distribution of resources. *Animal Behaviour* **69**, 1069-1076.
- Higgins, C.L. & Strauss, R.E. (2004). Discrimination and classification of foraging paths produced by search-tactic models. *Behavioral Ecology* **15**, 248-254.
- Hill, S., Burrows, M.T. & Hughes, R.N. (2000). Increased turning per unit distance as an area-restricted search mechanism in a pause-travel predator, juvenile plaice, foraging for buried bivalves. *Journal of Fish Biology* **56**, 1497-1508.
- Hill, S., Burrows, M.T. & Hughes, R.N. (2002). Adaptive search in juvenile plaice foraging for aggregated and dispersed prey. *Journal of Fish Biology* **61**, 1255-1267.
- Hill, S.L., Burrows, M.T. & Hughes, R.N. (2003). The efficiency of adaptive search tactics for different prey distribution patterns: a simulation model based on the behaviour of juvenile plaice. *Journal of Fish Biology* **63**, 117-130.
- Hindell, J.S., Jenkins, G.P. & Womersley, B. (2008). Habitat utilisation and movement of black bream *Acanthopagrus butcheri* (Sparidae) in an Australian estuary. *Marine Ecology-Progress Series* **366**, 219-229.
- Hiscock, M.J., Scruton, D.A., Brown, J.A. & Pennel, C.J. (2002). Diel activity pattern of juvenile Atlantic salmon (*Salmo salar*) in early and late winter. *Hydrobiologia* **483**, 161-165.
- Hochscheid, S., Maffucci, F., Bentivegna, F. & Wilson, R.P. (2005). Gulps, wheezes, and sniffs: how measurement of beak movement in sea turtles can elucidate their behaviour and ecology. *Journal of Experimental Marine Biology and Ecology* **316**, 45-53.
- Hoekstra, D. & Janssen, J. (1985). Non-visual feeding behavior of the mottled sculpin, *Cottus bairdi*, in Lake Michigan. *Environmental Biology of Fishes* **12**, 111-117.
- Hojesjo, J., Okland, F., Sundström, L.F., Pettersson, J. & Johnsson, J.I. (2007). Movement and home range in relation to dominance; a telemetry study on brown trout *Salmo trutta*. *Journal of Fish Biology* **70**, 257-268.
- Holland, K.N., Wetherbee, B.M., Peterson, J.D. & Lowe, C.G. (1993). Movements and distribution of hammerhead shark pups on their natal grounds. *Copeia*, 495-502.
- Holling, C.S. (1959). The components of predation as revealed by a study of small-mammal predation of the European pine sawfly. *Canadian Entomologist* **91**, 293-320.

REFERENCES

- Horne, J.S. & Garton, E.O. (2006). Animal Space Use 1.2. Available at http://www.cnr.uidaho.edu/population_ecology/animal_space_use.htm.
- Huey, R.B. & Pianka, E.R. (1981). Ecological consequences of foraging mode. *Ecology* **62**, 991-999.
- Hughes, R.N., Kaiser, M.J., Mackney, P.A. & Warburton, K. (1992). Optimizing foraging behaviour through learning. *Journal of Fish Biology* **41**, (Supplement B) 77-91.
- Humphries, N.E., Dyer, J.R.M., Queiroz, N., Pade, N.G., Musyl, M.K., Schaefer, K., Brunnschweiler, J.M., Doyle, T.K., Houghton, J.D.R., Hays, G.C., Jones, C.S., Noble, L.R., Wearmouth, V.J., Southall, E.J. & Sims, D.W. (Submitted). Prevalence and diversity of Lévy flight search patterns in open ocean predators.
- Ims, R.A. (1995). Movement patterns related to spatial structures. In *Mosaic landscapes and ecological processes* (Hansson, L., Fahrig, L. & Merriam, G., eds.), pp. 85-109. London: Chapman & Hall.
- Jadot, C., Donnay, A., Acolas, M.L., Cornet, Y. & Bégout Anras, M.L. (2006). Activity patterns, home-range size, and habitat utilization of *Sarpa salpa* (Teleostei: Sparidae) in the Mediterranean Sea. *ICES Journal of Marine Science* **63**, 128-139.
- Janssen, J. (1982). Comparison of searching behaviour for zooplankton in an obligate planktivore, Blueback herring (*Alosa aestivalis*) and a facultative planktivore, Bluegill (*Lepomis macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences* **39**, 1649-1654.
- Johnson, C.J., Parker, K.L., Heard, D.C. & Gillingham, M.P. (2002). Movement parameters of ungulates and scale-specific responses to the environment. *Journal of Animal Ecology* **71**, 225-235.
- Johnson, M.P. & Costello, M.J. (2002). Local and external components of the summertime plankton community in Lough Hyne, Ireland a stratified marine inlet. *Journal of Plankton Research* **24**, 1305-1315.
- Johnson, M.P., Costello, M.J. & O'Donnell, D. (1995). The nutrient economy of a marine inlet: Lough Hyne, south west Ireland. *Ophelia* **41**, 137-151.
- Jorgensen, S.J., Kaplan, D.M., Klimley, A.P., Morgan, S.G., O'Farrell, M.R. & Botsford, L.W. (2006). Limited movement in blue rockfish *Sebastes mystinus*: internal structure of home range. *Marine Ecology Progress Series* **327**, 157-170.
- Jouventin, P. & Weimerskirch, H. (1990). Satellite tracking of Wandering albatrosses. *Nature* **343**, 746-748.

- Kacelnik, A. (1984). Central place foraging in starlings (*Sturnus-vulgaris*).1. Patch residence time. *Journal of Animal Ecology* **53**, 283-299.
- Kacelnik, A., Houston, A.I. & Schmid-Hempel, P. (1986). Central-place foraging in honey bees *Apis mellifera* the effect of travel time and nectar flow on crop filling. *Behavioral Ecology and Sociobiology* **19**, 19-24.
- Kalmijn, A.J. (1966). Electro-perception in sharks and rays. *Nature* **212**, 1232-1233.
- Kalmijn, A.J. (1972). Bioelectric fields in sea water and the function of the ampullae of Lorenzini in elasmobranch fishes. *Scripps Institution of Oceanography Reference Series* **72-83**, 1-21.
- Kalmijn, A.J. (1978). Electric and magnetic sensory world of sharks. In *Sensory Biology of Sharks, Skates and Rays* (Hodgson, E. S. & Mathewson, R. F., eds.), pp. 507-528. Washington DC, USA: Government Printing Office.
- Kalmijn, A.J. (1982). Electric and magnetic field detection in elasmobranch fishes. *Science* **218**, 916-918.
- Kane, C., Brooks, A., Holbrook, S. & Schmitt, R. (2009). The role of microhabitat preference and social organization in determining the spatial distribution of a coral reef fish. *Environmental Biology of Fishes* **84**, 1-10.
- Kareiva, P.M. & Shigesada, N. (1983). Analyzing insect movement as a correlated random walk. *Oecologia* **56**, 234-238.
- Kent, J.W. & Rankin, M.A. (2001). Heritability and physiological correlates of migratory tendency in the grasshopper *Melanoplus sanguinipes*. *Physiological Entomology* **26**, 371-380.
- Kenward, R.E., Walls, S.S. & Hodder, K.H. (2001). Life path analysis: scaling indicates priming effects of social and habitat factors on dispersal distances. *Journal of Animal Ecology* **70**, 1-13.
- Kieffer, J.D. & Colgan, P.W. (1992). The role of learning in fish behaviour. *Reviews in Fish Biology and Fisheries* **2**, 125-143.
- Kitching, J.A. (1987). Ecological studies at Lough Hyne. *Advances in Ecological Research* **17**, 115-186.
- Kitching, J.A. & Ebling, F.J. (1967). Ecological studies at Lough Ine. *Advances in Ecological Research* **4**, 197-291.
- Kitching, J.A., Ebling, F.J., Gamble, J.C., Hoare, R., McLeod, A.A.Q.R. & Norton, T.A. (1976). The ecology of Lough Hyne XIX. Seasonal changes in the western trough. *Journal of Animal Ecology* **45**, 731-758.

- Klafter, J. & Sokolov, I.M. (2005). Anomalous diffusion spreads its wings. *Physics World* **18**, 29-32.
- Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F. & Van Sommeran, S. (2001a). Radio-acoustic positioning as a tool for studying site-specific behavior of the white shark and other large marine species. *Marine Biology* **138**, 429-446.
- Klimley, A.P., Le Boeuf, B.J., Cantara, K.M., Richert, J.E., Davis, S.F., Van Sommeran, S. & Kelly, J.T. (2001b). The hunting strategy of white sharks (*Carcharodon carcharias*) near a seal colony. *Marine Biology* **138**, 617-636.
- Kramer, D.L. & McLaughlin, R.L. (2001). The behavioral ecology of intermittent locomotion. *American Zoologist* **41**, 137-153.
- Kramer, D.L. & Nowell, W. (1980). Central place foraging in the eastern chipmunk *Tamias striatus*. *Animal Behaviour* **28**, 772-778.
- Krause, J., Cheng, D.J.-S., Kirkman, E. & Ruxton, G.D. (2000a). Species-specific patterns of refuge use in fish: the role of metabolic expenditure and body length. *Behaviour* **137**, 1113-1127.
- Krause, J., Loader, S.P., McDermot, J. & Ruxton, G.D. (1998). Refuge use by fish as a function of body length-related metabolic expenditure and predation risks. *Proceedings of the Royal Society B: Biological sciences* **265**, 2373-2379.
- Krause, J., Longworth, P. & Ruxton, G.D. (2000b). Refuge use in sticklebacks as a function of body length and group size. *Journal of Fish Biology* **56**, 1023-1027.
- Krebs, J.R., Kacelnik, A. & Taylor, P. (1978). Test of optimal sampling by foraging great tits. *Nature* **275**, 27-31.
- Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T.N., Wanless, S. & Hamer, K.C. (2002). Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London Series B-Biological Sciences* **269**, 1687-1693.
- Lima, S.L. & Zollner, P.A. (1996). Towards a behavioral ecology of ecological landscapes. *Trends in Ecology & Evolution* **11**, 131-135.
- Løkkeborg, S. (1998). Feeding behaviour of cod, *Gadus morhua*: activity rhythm and chemically mediated food search. *Animal Behaviour* **56**, 371-378.
- Løkkeborg, S. & Fernö, A. (1999). Diel activity pattern and food search behaviour in cod, *Gadus morhua*. *Environmental Biology of Fishes* **54**, 345-353.
- MacArthur, R.H. & Pianka, E.R. (1966). On the optimal use of a patchy environment. *American Naturalist* **100**, 603-609.

- Mackney, P.A. & Hughes, R.N. (1995). Foraging behaviour and memory window in sticklebacks. *Behaviour* **132**, 1241-1253.
- Mantegna, R.N. & Stanley, H.E. (1994). Stochastic process with ultraslow convergence to a Gaussian: the truncated Lévy flight. *Physical Review Letters* **73**, 2946-2949.
- McCord, M.E. & Campana, S.E. (2003). A quantitative assessment of the diet of the blue shark (*Prionace glauca*) off Nova Scotia, Canada. *Journal of Northwest Atlantic Fishery Science* **32**, 57-63.
- McLaughlin, R.L., Grant, J.W.A. & Kramer, D.L. (1992). Individual variation and alternative patterns of foraging movements in recently-emerged brook charr (*Salvelinus fontinalis*). *Behaviour* **120**, 286-301.
- McNamara, J.M. (1982). Optimal patch use in a stochastic environment. *Theoretical Population Biology* **21**, 269-288.
- McNamara, J.M. & Houston, A.I. (1985). Optimal foraging and learning. *Journal of Theoretical Biology* **117**, 231-249.
- Meager, J.J., Solbakken, T., Utne-Palm, A.C. & Oen, T. (2005). Effects of turbidity on the reactive distance, search time, and foraging success of juvenile Atlantic cod (*Gadus morhua*). *Canadian Journal of Fisheries and Aquatic Sciences* **62**, 1978-1984.
- Medved, R.J. & Marshall, J.A. (1983). Short-term movements of young sandbar sharks, *Carcharhinus plumbeus*. *Ibid* **33**, 87-93.
- Minchin, D. (1987a). Fishes of the Lough Hyne marine reserve. *Journal of Fish Biology* **31**, 343-352.
- Minchin, D. (1987b). Sea-water temperature and spawning behaviour in the seastar *Marthasterias glacialis*. *Marine Biology* **95**, 139-143.
- Montgomery, J., Coombs, S. & Halstead, M. (1995). Biology of the mechanosensory lateral line in fishes. *Reviews in Fish Biology and Fisheries* **5**, 399-416.
- Morales, J.M. & Ellner, S.P. (2002). Scaling up animal movements in heterogeneous landscapes: the importance of behaviour. *Ecology* **83**, 2240-2247.
- Nakamuta, K. (1985). Mechanism of the switch over from extensive to area-concentrated search behavior of the ladybeetle, *Coccinella septempunctata bruckii*. *Journal of Insect Physiology* **31**, 849-856.
- Newlands, N.K., Lutcavage, M.E. & Pitcher, T.J. (2004). Analysis of foraging movements of Atlantic bluefin tuna (*Thunnus thynnus*): individuals switch between two modes of search behaviour. *Population Ecology* **46**, 39-53.

- Nonacs, P. (2001). State dependent behavior and the Marginal Value Theorem *Behavioral Ecology and Sociobiology* **12**, 71-83.
- Northcutt, R.G. (1977). Elasmobranch central nervous system organization and its possible evolutionary significance. *American Zoologist* **17**, 411-429.
- O'Brien, W.J. (1979). The predator-prey interaction of planktivorous fish and zooplankton. *American Scientist* **67**, 572-581.
- O'Brien, W.J. (1987). Planktivory by freshwater fish: Thrust and parry in the pelagia. In *Predation: Direct and Indirect Impacts on Aquatic Communities* (Kerfoot, W. C. & Sih, A., eds.), pp. 3-16: University Press of New England.
- O'Brien, W.J., Browman, H.I. & Evans, B.I. (1990). Search strategies of foraging animals. *American Scientist* **78**, 152-160.
- O'Dor, R.K., Andrade, Y., Webber, D.M., Sauer, W.H.H., Roberts, M.J., Smale, M.J. & Voegeli, F.M. (1998). Applications and performance of Radio-Acoustic Positioning and Telemetry (RAPT) systems. *Hydrobiologia* **371/372**, 1-8.
- Odling-Smee, L. & Braithwaite, V.A. (2003). The role of learning in fish orientation. *Fish and Fisheries* **4**, 235-246.
- Ogden, J.C. & Quinn, T.P. (1984). Migration in coral reef fishes: ecological significance and orientation mechanisms. In *Mechanisms of Migration in Fishes* (McCleave, J. D., Arnold, G. P., Dodson, J. J. & Neil, W. H., eds.), pp. 293-308. New York: Plenum Press.
- Orians, G.H. & Pearson, N.E. (1979). On the theory of central place foraging. In *Analysis of Ecological Systems* (Horn, D. J., Mitchell, R. D. & Stairs, G. R., eds.), pp. 154-177. Columbus: Ohio State University Press.
- Parnum, I. (2003). Mapping sublittoral habitats using acoustic techniques and Geographic Information Systems in Lough Hyne, Ireland. MSc Thesis. University of Wales, Bangor.
- Pinaud, D. & Weimerskirch, H. (2005). Scale-dependant habitat use in a long-ranging central place predator. *Journal of Animal Ecology* **74**, 852-863.
- Pinaud, D. & Weimerskirch, H. (2007). At-sea distribution and scale-dependent foraging behaviour of petrels and albatrosses: a comparative study. *Journal of Animal Ecology* **76**, 9-19.
- Pitcher, T.J. & Magurran, A.E. (1983). Shoal size, patch profitability and information exchange in foraging goldfish. *Animal Behaviour* **31**, 546-555.

- Pittman, S.J., Caldwell, C., Hile, S.D. & Monaco, M.E. (2007). Using seascape types to explain the spatial patterns of fish in the mangroves of SW Puerto Rico. *Marine Ecology-Progress Series* **348**, 273-284.
- Pyke, G.H. (1978). Are animals efficient harvesters? *Animal Behaviour* **26**, 241-250.
- Pyke, G.H. (1984). Optimal foraging theory: a critical review. *Annual Review of Ecology and Systematics* **15**, 523-575.
- Pyke, G.H., Pulliam, H.R. & Charnov, E.L. (1977). Optimal foraging: a selective review of theory and tests. *Quarterly Review of Biology* **52**, 137-154.
- Quinn, T.P. & Brodeur, R.D. (1991). Intra-specific variations in the movement patterns of marine animals. *American Zoologist* **31**, 231-241.
- Ramos-Fernández, G., Mateos, J.L., Miramontes, O., Cocho, G., Larralde, H. & Ayala-Orozco, B. (2004). Lévy walk patterns in the foraging movements of spider monkeys (*Ateles geoffroyi*). *Behavioral Ecology and Sociobiology* **55**, 223-230.
- Reebs, S.G. (1999). Time-place learning based on food but not on predation risk in a fish, the inanga (*Galaxias maculatus*). *Ethology* **105**, 361-371.
- Reynolds, A.M. (2006). Cooperative random Lévy flight searches and the flight patterns of honeybees. *Physics Letters, Section A: General, Atomic and Solid State Physics* **354**, 384-388.
- Reynolds, A.M. (2008). Optimal random Levy-loop searching: New insights into the searching behaviours of central-place foragers. *Europhysics Letters* **82**.
- Rodríguez-Cabello, C., Sanchez, F. & Olaso, I. (2007). Distribution patterns and sexual segregations of *Scyliorhinus canicula* (L.) in the Cantabrian Sea. *Journal of Fish Biology* **70**, 1568-1586.
- Roth, J.E., Kelly, J.P., Sydeman, W.J. & Colwell, M.A. (2004). Sex differences in space use of breeding common ravens in western Marin County, California. *The Condor* **106**, 529-539.
- Ruckstuhl, K.E. (2007). Sexual segregation in vertebrates: proximate and ultimate causes. *Integrative and Comparative Biology* **47**, 245-257.
- Ruzicka, J.J. & Gallager, S.M. (2006). The saltatory search behavior of larval cod (*Gadus morhua*). *Deep-Sea Research Part II: Topical Studies in Oceanography* **53**, 2735-2757.
- Schneider, C. (2003). The influence of spatial scale on quantifying insect dispersal: An analysis of butterfly data. *Ecological Entomology* **28**, 252-256.
- Schoener, T.W. (1979). Generality of the size-distance relation in models of optimal feeding. *American Naturalist* **114**, 902-914.

- Schtickzelle, N., Joiris, A., Van Dyck, H. & Baguette, M. (2007). Quantitative analysis of changes in movement behaviour within and outside habitat in a specialist butterfly. *BMC Evolutionary Biology* **7**, 4.
- Seaman, D.E. & Powell, R.A. (1996). An evaluation of the accuracy of kernel density estimators for home range analysis. *Ecology* **77**, 2075-2085.
- Segura, D.F., Viscarret, M.M., Carabajal Paladino, L.Z., Ovruski, S.M. & Cladera, J.L. (2007). Role of visual information and learning in habitat selection by a generalist parasitoid foraging for concealed hosts. *Animal Behaviour* **74**, 131-142.
- Shepard, E.L.C., Ahmed, M.Z., Southall, E.J., Witt, M.J., Metcalfe, J.D. & Sims, D.W. (2006). Diel and tidal rhythms in diving behaviour of pelagic sharks identified by signal processing of archival tagging data. *Marine Ecology Progress Series* **328**, 205-213.
- Shine, R., Shine, T. & Shine, B. (2003). Intraspecific habitat partitioning by the sea snake *Emydocephalus annulatus* (Serpentes, Hydrophiidae): the effects of sex, body size, and colour pattern. *Biological Journal of the Linnean Society* **80**, 1-10.
- Shlesinger, M.F., Zaslavsky, G. & Frisch, U., eds. (1995). *Lévy Flights and Related Topics in Physics*. Berlin: Springer.
- Shlesinger, M.G., Zaslavsky, G.M. & Klafter, J. (1993). Strange kinetics. *Nature* **363**, 31-37.
- Sims, D.W. (1996). The effect of body size on the standard metabolic rate of the lesser spotted dogfish. *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.
- Sims, D.W. & Quayle, V.A. (1998). Selective foraging behaviour of basking sharks on zooplankton in a small-scale front. *Nature* **393**, 460-464.
- Sims, D.W., Righton, D. & Pitchford, J.W. (2007). Minimizing errors in identifying Lévy flight behaviour of organisms. *Journal of Animal Ecology* **76**, 222-229.
- Sims, D.W., Southall, E.J., Humphries, N.E., Hays, G.C., Bradshaw, C.J.A., Pitchford, J.W., James, A., Ahmed, M.Z., Brierley, A.S., Hindell, M.A., Morritt, D., Musyl, M.K.,

- Righton, D., Shepard, E.L.C., Wearmouth, V.J., Wilson, R.P., Witt, M.J. & Metcalfe, J.D. (2008). Scaling laws of marine predator search behaviour. *Nature* **451**, 1098-1102.
- Sims, D.W., Southall, E.J., Wearmouth, V.J., Hutchinson, N., Budd, G.C. & Morritt, D. (2005). Refuging behaviour in the nursehound *Scyliorhinus stellaris* (Chondrichthyes : Elasmobranchii): preliminary evidence from acoustic telemetry. *Journal of the Marine Biological Association of the United Kingdom* **85**, 1137-1140.
- Sims, D.W., Wearmouth, V.J., Southall, E.J., Hill, J.M., Moore, P., Rawlinson, K., Hutchinson, N., Budd, G.C., Righton, D., Metcalfe, J., Nash, J.P. & Morritt, D. (2006a). Hunt warm, rest cool: bioenergetic strategy underlying diel vertical migration of a benthic shark. *Journal of Animal Ecology* **75**, 176-190.
- Sims, D.W., Witt, M.J., Richardson, A.J., Southall, E.J. & Metcalfe, J.D. (2006b). Encounter success of free-ranging marine predator movements across a dynamic prey landscape. *Proceedings of the Royal Society B: Biological sciences* **273**, 1195-1201.
- Sisneros, J.A., Tricas, T.C. & Luer, C.A. (1998). Response properties and biological function of the skate electrosensory system during ontogeny. *Journal of Comparative Physiology A-Neuroethology, Sensory, Neural and Behavioral Physiology* **183**, 87-99.
- Skúlason, S., Snorrason, S.S., Ota, D. & Noakes, D.L.G. (1993). Genetically based differences in foraging behaviour among sympatric morphs of arctic charr (Pisces: Salmonidae). *Animal Behaviour* **45**, 1179-1192.
- Sogard, S.M. (1997). Size selective mortality in the juvenile stage of teleost fishes: a review. *Bulletin of Marine Science* **60**, 1129-1157.
- Steingrímsson, S.O. & Grant, J.W.A. (2008). Multiple central-place territories in wild young-of-the-year Atlantic salmon *Salmo salar*. *Journal of Animal Ecology* **77**, 448-457.
- Stephens, D.W. (1993). Learning and behavioral ecology: incomplete information and environmental predictability. In *Insect Learning: Ecological and Evolutionary Perspectives* (Papaj, D. R. & Lewis, A. C., eds.), pp. 195-218. New York: Chapman & Hall.
- Stephens, D.W. & Krebs, J.R. (1986). *Foraging Theory*. New Jersey: Princeton University Press.
- Sundström, L.F., Gruber, S.H., Clermont, S.M., Correia, J.P., de Marniac, J.R.C., Morrissey, J.F., Lowrance, C.R., Thomassen, L. & Oliveira, M.T. (2001). Review of elasmobranch behavioural studies using ultrasonic telemetry with special reference to the lemon shark, *Negaprion brevirostris*, around Bimini Islands, Bahamas. *Environmental Biology of Fishes* **60**, 225-250.

- Sutherland, W.J. (1996). *From Individual Behaviour to Population Ecology*. Oxford: Oxford University Press.
- Swaney, W., Kendal, J., Capon, H., Brown, C. & Laland, K. (2001). Familiarity facilitates learning of foraging behaviour in the guppy. *Animal Behaviour* **62**, 591-598.
- Temple, S., Cerqueira, V.R. & Brown, J.A. (2004). The effects of lowering prey density on the growth, survival and foraging behaviour of larval fat snook (*Centropomus parallelus* Poey 1860). *Aquaculture* **233**, 205-217.
- Thomas, G. (1974). The influences of encountering a food object on subsequent searching behaviour in *Gasterosteus aculeatus* L. *Animal Behaviour* **22**, 941-952.
- Tricas, T.C., Taylor, L.R. & Naftel, G. (1981). Diel behavior of the tiger shark, *Galeocerdo cuvier*, at French Frigate Shoals, Hawaiian-Islands. *Copeia*, 904-908.
- Turchin, P. (1991). Translating foraging movements in heterogeneous environments into the spatial distribution of foragers. *Ecology* **72**, 1253-1266.
- Turchin, P. (1996). Fractal analyses of animal movement: a critique. *Ecology* **77**, 2086-2090.
- Turchin, P. (1998). *Quantitative Analysis of Movement*. Massachusetts: Sinauer Associates, Inc.
- Utne-Palm, A.C. & Hart, P.J.B. (2000). The effects of familiarity on competitive interactions between threespined sticklebacks. *Oikos* **91**, 225-232.
- Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (2000). Lévy flights in random searches. *Physica A: Statistical Mechanics and its Applications* **282**, 1-12.
- Viswanathan, G.M., Afanasyev, V., Buldyrev, S.V., Murphy, E.J., Prince, P.A. & Stanley, H.E. (1996). Lévy flight search patterns of wandering albatrosses. *Nature* **381**, 413-415.
- Viswanathan, G.M., Bartumeus, F., Buldyrev, S.V., Catalan, J., Fulco, U.L., Havlin, S., da Luz, M.G.E., Lyra, M.L., Raposo, E.P. & Stanley, H.E. (2002). Lévy flight random searches in biological phenomena. *Physica A: Statistical Mechanics and its Applications* **314**, 208-213.
- Viswanathan, G.M., Buldyrev, S.V., Havlin, S., da Luz, M.G.E., Raposo, E.P. & Stanley, H.E. (1999). Optimizing the success of random searches. *Nature* **401**, 911-914.
- Warburton, K. (1990). The use of local landmarks by foraging goldfish. *Animal Behaviour* **40**, 500-505.

- Warburton, K. (2006). Learning of Foraging Skills by Fishes. In *Fish Cognition and Behavior* (Brown, C., Laland, K. & Krause, J., eds.), pp. 9-27. Oxford: Blackwell Publishing Ltd.
- Ware, D.M. (1971). Predation by rainbow trout (*Salmo gairdneri*): the effect of experience. *Journal of the Fisheries Research Board of Canada* **28**, 1847-1852.
- Wearmouth, V.J. (2001). Movements of male and female lesser spotted dogfish, *Scyliorhinus canicula* (Linnaeus, 1758), off the coast of Plymouth, over three temporal scales. MSc Thesis. University of Aberdeen.
- Wearmouth, V.J. & Sims, D.W. (2008). Sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Advances in Marine Biology* **54**, 107-170.
- Weimerskirch, H., Gault, A. & Cherel, Y. (2005). Prey distribution and patchiness: factors in foraging success and efficiency of wandering albatrosses. *Ecology* **86**, 2611-2622.
- Weimerskirch, H., Wilson, R.P. & Lys, P. (1997). Activity pattern of foraging in the wandering albatross: A marine predator with two modes of prey searching. *Marine Ecology Progress Series* **151**, 245-254.
- Werner, E.E. & Hall, D.J. (1977). Competition and habitat shift in two sunfishes (Centrarchidae). *Ecology* **58**, 869-876.
- Werner, E.E. & Hall, D.J. (1979). Foraging efficiency and habitat switching in competing sunfishes. *Ecology* **60**, 256-264.
- Werner, E.E. & Mittelbach, G.G. (1981). Optimal foraging: field tests of diet choice and habitat switching. *American Zoologist* **21**, 813-829.
- Werner, E.E., Mittelbach, G.G. & Hall, D.J. (1981). The role of foraging profitability and experience in habitat use by the bluegill sunfish. *Ecology* **62**, 116-125.
- Wetherbee, B.M., Gruber, S.H. & Cortés, E. (1990). Diet, feeding habits, digestion and consumption in sharks, with special reference to the lemon shark *Negaprion brevirostris*. In *Elasmobranchs as living resources: advances in the biology, ecology, systematics, and status of the fisheries* (Pratt Jr., H. L., Gruber, S. H. & Taniuchi, T., eds.): NOAA Tech. Rep. 90.
- White, E.P., Enquist, B.J. & Green, J.L. (2008). On estimating the exponent of power-law frequency distributions. *Ecology* **89**, 905-991.
- Wilson, R.P., Steinfurth, A., Ropert-Coudert, Y., Kato, A. & Kurita, M. (2002). Lip-reading in remote subjects: an attempt to quantify and separate ingestion, breathing and

REFERENCES

- vocalisation in free-living animals using penguins as a model. *Marine Biology* **140**, 17-27.
- Winter, Y. & Stich, K.P. (2005). Foraging in a complex naturalistic environment: capacity of spatial working memory in flower bats. *Journal of Experimental Biology* **208**, 539-548.
- Worton, B.J. (1995). Using Monte-Carlo simulation to evaluate kernel-based home-range estimators. *Journal of Wildlife Management* **59**, 794-800.
- Zamora, L. & Moreno-Amich, R. (2002). Quantifying the activity and movement of perch in a temperate lake by integrating acoustic telemetry and a geographic information system. *Hydrobiologia* **483**, 209-218.
- Zollner, P.A. & Lima, S.L. (1999). Search strategies for landscape-level interpatch movements. *Ecology* **80**, 1019-1030.